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Research Article

Quagga mussel (*Dreissena rostriformis bugensis*) population structure during the early invasion of Lakes Mead and Mohave January-March 2007

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Abstract

Shell length-frequencies were determined for samples of *Dreissena rostriformis bugensis* collected <2 m depth from Las Vegas Boat Harbor (LVBH), Callville Bay Marina (two samples, CBM-1 and CBM-2), and Lake Mead Marina (LMM) in the Boulder Basin of Lake Mead and Katherine Landing Marina (KLM) in the lower end of Lake Mohave within two months of initial discovery of *D. rostriformis bugensis* in Lake Mead at LVBH on 06/01/2007. Two annual shell length (SL) cohorts were present at all four sites consisting of individuals presumed to have settled during spring-fall of 2005 and 2006, respectively. Members of the most recently settled 2006 cohort numerically dominated all samples; relative ratios of individuals in the LVBH, CBM-2, LMM, and KLM 2006 versus 2005 cohorts being 174:1, 95:1, 172:1 and 65:1, respectively. Mean shell lengths of the LVBH, CBM-1, CBM-2, KLM and LMM 2006 cohorts were 6.86 (s.e. = ±0.126), 9.59 (±0.080), 9.31 (±0.194), 10.49 (±0.287) and 12.15 mm (±0.105), respectively. The mean shell lengths of the 2005 cohorts in the LVBH, CBM-2, KLM and LMM samples were 17.5 mm (n = 1), 18.9 mm (n = 4), 21.2 mm (n = 1) and 20.1 mm (n = 4), respectively. The occurrence of the 2005 cohort in all four sampled sites suggested that quagga mussel introduction to the Boulder Basin occurred prior to 2005. This supposition is based on the very low probability of individuals from a localized initial introduction appearing in the samples. 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 veliger larvae to settle as relatively wide-spread members of the 2005 cohort and be transported downstream to establish a 2005 cohort at KLM in lower Lake Mohave. Essentially equivalent population structures at all three sampled sites makes speculation on the original site of quagga mussel introduction to the Boulder Basin difficult.

Key words: cohorts, invasion, juvenile settlement, shell length, size distribution

Introduction

An extensive GARP analysis (i.e., genetic algorithm for rule-set production) of the potential distribution of zebra mussels (*Dreissena polymorpha* Pallas, 1771) in the United States indicated a very low probability for the invasion of water bodies in the lower Colorado River drainage (Drake and Bossenbroek 2004). Because quagga mussels (*Dreissena rostriformis bugensis* Andrusov, 1897) appear to have physiological resistance adaptations similar to zebra mussels (McMahon, 1996), particularly in regard to incipient upper thermal limits (Domm et al. 1993; Spidle et al. 1995; Morse 2009) and minimal calcium concentration limits (Whittier et al. 2008) with the minimal calcium limits of quagga mussels being perhaps somewhat greater than those of zebra mussels (Zhudlidov et al. 2004), it was somewhat surprising that the first discovery of dreissenid mussels in the western US was that of quagga mussels on 06/01/2007 in the Boulder Basin of Lake Mead on the lower Colorado River (United States Geological Survey (USGS) 2010a). This infestation was discovered by divers inspecting submerged concrete anchor blocks, steel cables and rubber tires in the Las Vegas Boat Harbor (36.0269°N, 114.7756°W). The population was relatively sparse with density estimated to be 65 mussels·m^{-2}, ranging from 6-15 mm in shell length (SL) (USGS 2010a). Lake Mead may have been at high risk for dreissenid invasion because it is a major destination for recreational boaters in the western United States (Britton and McMahon 2005, 2006) and recreational boating is considered to be the main overland vector for dreissenid dispersal (Buchan and Padilla 1999; Wilson et al. 1999; Bossenbroek et al. 2001).

After the initial discovery of quagga mussels in Las Vegas Boat Harbor, further inspections during January 2007 revealed the presence of established quagga mussel populations in the Boulder Basin of Lake Mead at Lake Mead Marina, Callville Bay Marina, Hemenway Harbor, Kingman Wash, the Lake Mead Fish Hatchery, on an intake tower of Hoover Dam, on intakes of the Southern Nevada Water Authority, and in the Narrows between the Boulder and Virgin Basins. Mussels were also found downstream of Lake Mead on rocks in the Colorado River below the Hoover Dam spillway and in the Whitsett Intake of the Los Angeles Metropolitan Water District´s Colorado River Aqueduct pumping station and at Katherine Landing Marina in lower Lake Mohave (Nevada Department of Wildlife 2007). By the end of 2007, quagga mussel infestations had been identified at 35 other deep and shallow water sites in the Boulder Basin of Lake Mead and at 13 sites on the Colorado River below Lake Mead including Lakes Mohave and Havasu. In contrast, no mussels were found in the upstream basins of Lake Mead, suggesting that the Boulder Basin was the epicenter for the original infestation. During 2008, a quagga mussel population was discovered in the Imperial Reservoir near the California/Arizona border with Mexico and mussels had become established in portions of the upper basins of Lake Mead above the upstream end of the Boulder/Virgin Basin Narrows (USGS 2010b). Presently *D. rostriformis bugensis* populations have been confirmed throughout Lake Mead, in portions of Lakes Mohave and Havasu, the Imperial Reservoir and the Colorado River (USGS 2010c) suggesting that it has become well established throughout the lower Colorado River and its associated impoundments.

After their initial discovery in the Boulder Basin of Lake Mead and Lake Mohave in January 2007, there were questions regarding the length of time that quagga mussel populations had been established in the lower Colorado Drainage, the structure of their populations and their site of initial introduction. These questions were addressed by analyzing the size-age structure of quagga mussel samples taken from shallow water sites within two months of their initial 06/01/2007 discovery in Las Vegas Boat Harbor and Lake Mead Marina (Nevada Department of Wildlife 2007). The mussel sampling sites included the original site of discovery in the Las Vegas Boat Harbor and sites in Callville Bay and Lake Mead Marinas in the Boulder Basin of Lake Mead and Katherine Landing Marina in lower Lake Mohave. This paper describes the results of those analyses and discusses their implications regarding the time of initial establishment and spread of *Dreissena rostriformis bugensis* in the Lower Colorado River.

Methods

Five samples of *D. rostriformis bugensis* were collected by scraping mussels from hard surfaces and house boat pontoons at depths of less than 2 m in the Boulder Basin of Lake Mead and lower Lake Mohave on the Colorado River Drainage by US National Park Service Divers. Samples were fixed in 95% ethanol and shipped to my laboratory at The University of Texas at Arlington where they were refrigerated until analyzed. Four samples were taken in the Boulder Basin of Lake Mead including a sample from Las Vegas Boat Harbor (LVBH, 36.0318°N: 114.773°W) on 16/1/07 (n = 175, depth <2 m, surface sampled unknown), two samples from submerged surfaces of houseboat pontoons in Callville Bay Marina (CBM-1 and CBM-2, 36.142°N: 114.718°W) on 26/01/07 and 16/03/07 (n = 833 and 190, respectively), and a sample (n = 686) taken at Lake Mead Marina (LMM, 36.057°N: 114.805°W) on 24/02/07 from submerged cement blocks and connecting cross bars at depth of 1.2 m. A fifth sample (n = 130) was taken from the submerged portions of houseboat hulls at Katherine Landing Marina (KLM, 35.212°N: 114.568°W) near the southern end of Lake Mohave on 24/02/07 (see Figure 1 for sampling sites locations).

The shell lengths (SL, the greatest distance from the anterior tip of the umbos to the posterior edge of the shell) of individuals in each sample with SL greater than ≈ 8.5 mm were measured to the nearest 0.1 mm with electronic digital calipers. Those of individuals with SL less than ≈ 8.5 mm where measured to the nearest 0.1 mm with an eyepiece micrometer at 10X under a binocular dissecting microscope. For each sample, the number of individuals in each 0.1 mm SL size class was expressed as a percent of the total number of sampled individuals which was graphically displayed to allow visualization of the samples' SL size

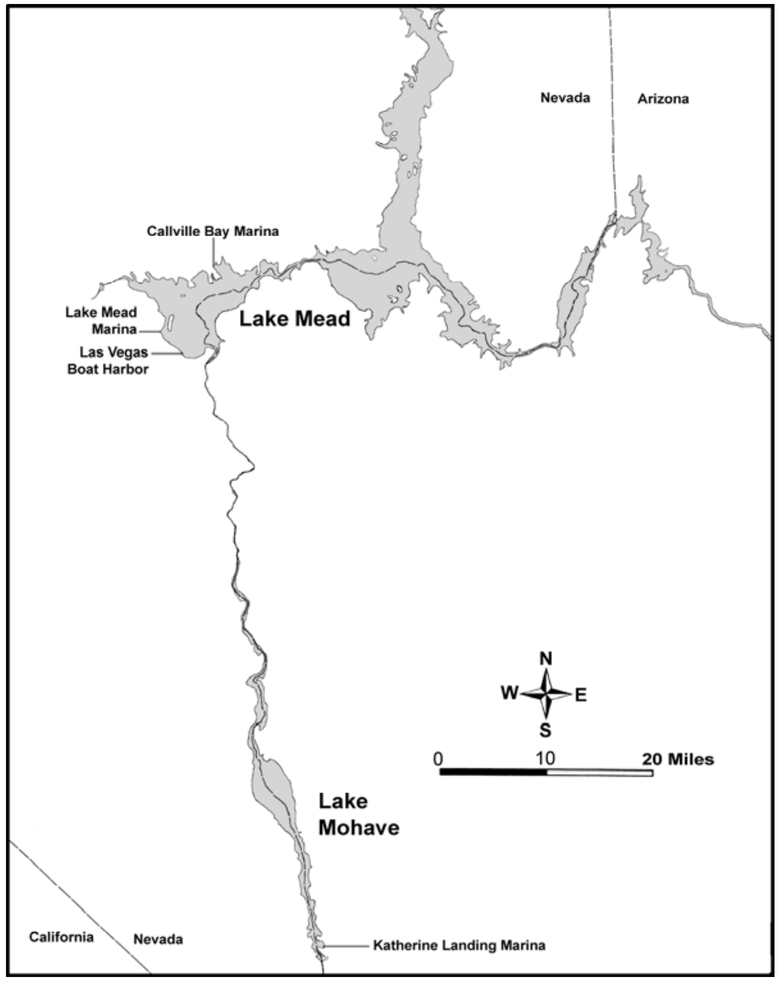

Figure 1. Map of Lakes Mead and Mohave showing the location of the four sites from which quagga mussel (*Dreissena rostriformis bugensis*) populations were sampled including Las Vegas Boat Harbor (LVBH), Callville Bay Marina (CBM) and Lake Mead Marina (LMM), all in the Boulder Basin of Lake Mead, and Katherine Landing Marina (LMM) in lower Lake Mohave.

distributions (Figure 2). Sample SL distributions were visually examined for the presence of distinct size cohorts presumed to represent annual generations resulting from successive seasonal episodes of spawning and juvenile settlement.

Results

Shell lengths of quagga mussels ranged from 2.1-21.2 mm across a total of 2,014 measured individuals in all five samples. All five samples were numerically dominated by a distinct size cohort presumed to consist of individuals resulting from mussel spawning and settlement in 2006 (Figure 2). In the Boulder Basin of Lake Mead, the SL range of this 2006 cohort was 2.1-13.4 mm in LVBH, 2.8-15.9 mm in CMB-1, 3.5-17.0 mm in CBM-2, and 5.3-19.2 mm in LMM. In the Lake Mohave KLM sample, the SL range of the 2006 cohort was 4.0-18.3 mm (Figures 2 and 3). Four of the samples also contained a few individuals distinctly large enough to be assigned to a cohort resulting from juvenile settlement in 2005 (Figure 2). These 2005 cohorts included one individual (SL = 17.5) mm in the LVBH sample, four individuals (SL range = 18.2-19.8 mm) in the CBM-2 sample, one individual (SL = 21.2 mm) in the KLM sample, and five individuals (SL range = 19.9-20.9 mm) in the LMM sample (Figures 2 and 3). No individuals in the CBM-1 sample were large enough to form a 2005 cohort (Figures 2 and 3).

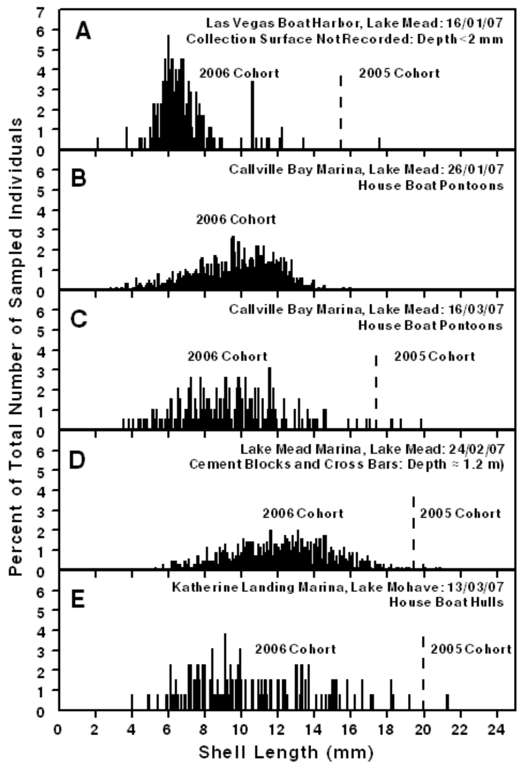

Figure 2. Percent size-frequency distributions of individual shell lengths for five samples of quagga mussels (*Dreissena rostriformis bugensis*) collected in the lower Colorado River at depths <2 m from Las Vegas Boat Harbor (A), Callville Bay Marina (B and C), and Lake Mead Marina (D) in the Boulder Basin of Lake Mead and Katherine Landing Marina (E) in lower Lake Mohave. Surface sampled is indicated for each sample site. In each panel the designation "2006 Cohort" indicates a mussel cohort presumed to have settled during spring-fall of 2006 and the "2005 Cohort", a cohort presumed to have settled during spring-fall of 2005. The size-frequency distributions of the 2006 and 2005 annual cohorts are separated by dashed vertical lines.

The mean shell lengths of the 2006 cohorts from the LVBH, CBM-1, CBM-2, KLM and LMM samples were 6.86 mm (s.e. = ±0.126), 9.59 mm (±0.080), 9.31mm (±0.194), 10.49 mm (±0.287) and 12.15 mm (±0.105), respectively (Figure 3). While the number of individuals in the 2006 cohorts varied among samples from 129 (KLM) to 833 (CBM-1), all sample sizes were large enough (n ≥129) to accurately determine mean SL values with 95% confidence limits ranging from ± 0.173 mm for the CBM-1 2006 cohort to ± 0.438 mm for the KLM 2006 cohort. When parametrically analyzed by ANOVA, mean 2006 cohort SL was significantly different among sites (n = 2018, F = 195.84, p = <0.00001). An *a posteriori* Schefee's test revealed that the mean SL of the 2006 cohorts was significantly different (p <0.05) among the LVBH, KLM and LMM samples (Figure 3). In contrast, those of the CBM-1 and CBM-2 2006 cohorts were not different (p >0.05), but both were different from those of the other three sampled sites (Figure 3). Similarly, a nonparametric Kruskal-Wallis ANOVA on ranks yielded essentially similar results with significant differences in SL distribution among sites (H = 559.8, p < 0.00001). A nonparametric *a posteriori*, Dunn's multiple pairwise comparison test indicated that the SL distributions of the 2006 cohorts where significantly different (p < 0.05) among sites with the exceptions of the CBM-1 vs. CBM-2 and CBM-1 vs. KLM comparisons (p >0.05) (Figure 3). The mean shell lengths of the 2005 cohort in the LVBH, CBM-2, KLM and LMM samples were 17.5 mm (n = 1), 18.9 mm (n = 4), 21.2 mm (n = 1) and 20.1 mm (n = 4), respectively (Figures 2 and 3). Small sample sizes (n ≤4) precluded estimation of standard deviations and standard errors of SL means for the 2005 cohorts.

Discussion

Sample SL distributions suggested that two size-age cohorts existed at all four sampled sites. At all sites, mussel populations were numerically dominated by a distinct cohort of smaller-sized individuals referred to as the 2006 cohort. At all four sites, this cohort greatly outnumbered the 2005 cohort consisting of a relatively few, distinctly larger individuals (Figure 2). These cohorts appear have resulted from settlement of juveniles produced by annual spawning events in 2005 and 2006. The lack of individuals representing the 2005 cohort in the CMB-1 sample (Figure 2) appeared to be an indication of their relative rarity in the population.

The general temperature range for successful development and settlement of zebra mussel larval stages is 12-24°C (Sprung 1987, 1993) with spawning inhibited at >27°C (Fong et al. 1995). Based on the assumption that temperature ranges for spawning and successful larval development in quagga mussels are likely to be similar to those of zebra mussels, it is possible

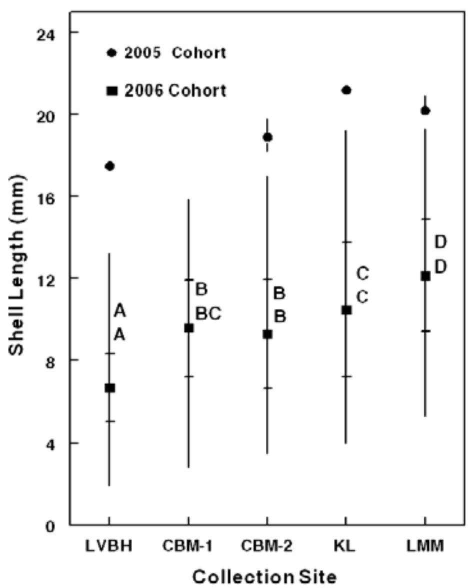

Figure 3. Mean shell lengths (SL), standard deviations and range (vertical axis) of the 2006 cohort (solid squares) and mean SL and SL range of 2005 cohorts (solid circles) for samples of quagga mussels (*Dreissena rostriformis bugensis*) collected from Las Vegas Boat Harbor (LVBH), Callville Bay Marina (CBM-1 and CBM-2) and Lake Mead Marina (LMM) in the Boulder Basin of Lake Mead and Katherine Landing Marina (KLM) (horizontal axis) in lower Lake Mohave on the lower Colorado River. Vertical bars around SL means for the 2006 cohorts indicate standard deviations (inner lines with caps) and SL ranges (outer lines without caps), respectively. Due to low sample size precluding accurate estimation of standard deviation, vertical bars about SL means for the 2005 cohorts only represent SL range. Those 2005 cohort SL means without SL range bars were based on the SL of a single individual. The CMB-1 sample contained no individuals representing the 2005 cohort. Dissimilar letters above 2006 cohort means indicate sample SL distributions were significantly different ($p < 0.05$) based on parametric Schefee's (upper set of letters) and nonparametric Dunn's (lower set of letters) multiple comparison tests.

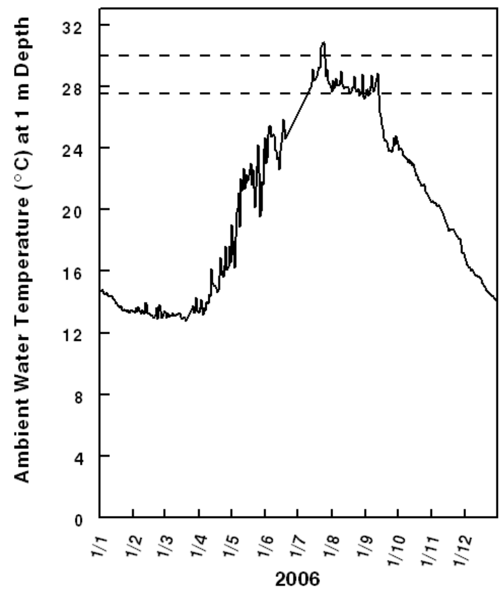

Figure 4. Mean daily water temperatures developed from continuous ambient water temperature data recorded at a depth of 1 m from a water quality monitoring station off Sentinel Island in the Boulder Basin of Lake Mead (USGS Nevada Water Science Center 2010). The upper and lower horizontal dashed lines represent estimates of the incipient upper thermal limit of quagga mussels (*Dreissena rostriformis bugensis*) at 30°C (Spidle et al. 1995) and 27.5°C (Morse 2009), respectively. Note that ambient surface water temperature approached or exceeded the 27.5°C estimated incipient upper thermal limit of quagga mussels (Morse 2009) from 12/07/2006 through 13/09/2006 and the 30°C estimated incipient upper thermal limit (Spidle et al. 1995) from 22/07/2006 through 25/07/2006.

that summer ambient surface water temperatures approaching or exceeding 30°C in Lake Mead (USGS Nevada Water Science Center 2010) (Figure 4) could have inhibited spawning and settlement leading to development of separate spring and fall cohorts as modeled by Griebeler and Seitz (2007) for *D. polymorpha*. However, in all five quagga mussel samples, the 2006 cohort SL distributions appeared unimodal (Figure 2) indicating that they resulted from a single spawning period or that a mid-summer suppression of spawning and settlement did not last long enough to result in a bimodal SL distribution. The size range and distributions of the 2006 quagga mussel cohorts after growth through the summer and fall at all four sites were within the range reported for zebra mussels over roughly the same time period in North America (Strayer and Malcom 2006) and Europe (Dall and Hamburger 1996).

The relative ratios of individuals assigned to the 2006:2005 cohorts in the, LVBH, CBM-2, LMM, and KLM samples were 174:1, 95:1, 172:1 and 65:1, respectively. The high level of numerical dominance exhibited by the most recently settled cohort in all four sites suggested that, at the time of sampling, the *D. rostriformis bugensis* populations in the Boulder Basin of Lake Mead and lower Lake Mohave were exponentially expanding in density with high levels of juvenile settlement occurring during successive annual spawning events. Massive dominance of the most recently settled cohort appears characteristic of newly established populations of quagga mussels in North America (Mills et al. 1993; Dermott et al. 2003) and Europe (Bij de Vaate and Jansen 2006). Similarly, dominance of the most recently settled cohort has also been reported in newly established zebra mussel populations in North America (Nalepa et al. 1995; Cope et al. 2006) and Europe (Millane et al. 2008). In contrast, older generations tend to make up a greater demographic proportion of longer established zebra mussel (Bij de Vaate 1991; Martel 1995; Sprung 1995; Dall and Hamberger 1996; Jantz and Schöll 1998; Chase and Bailey 1999) and quagga mussel populations (Roe and MacIsaac 1997; Orlova and Scherbina 2002; Kalayda 2004). Similarly, the size distributions of the Lake Mead and Mohave 2006 cohorts, ranging in SL from 2.1-17.5 mm at LVBH to 5.5-21.2 mm at LLM, were similar to that reported for one year old annual cohorts during the early stages of population establishment for both quagga (Mills et al. 1993; Dermott et al. 2003) and zebra mussels (Nalepa et al. 1995; Cope et al. 2006). Lack of larger individuals (i.e., SL > 21.2 mm) from all four sites suggested that adult mussels from cohorts earlier than 2005 were missing in the samples. Cohorts three or more years old containing individuals with SL > 25 mm are characteristic of long-established quagga (Orlova and Shcherbina 2002; Kalayda 2004) and zebra mussel (Jantz and Schöll 1998; Chase and Bailey 1999; Orlova and Panov 2004; Strayer and Malcom 2006) populations. Samples of quagga mussels taken during spring 2010 from LVBH, CBM and the Temple Bar Marina in the Temple Basin of Lake Mead were less dominated by the most recently settled 2009 cohort relative to 2006 cohort domination of the 2007 samples described herein (McMahon unpublished data). This suggests that the rate of density increase in Lake Mead quagga mussel populations may be slowing relative to that which occurred in the earlier stages of quagga mussel invasion.

Based on boater survey data (Britton and McMahon 2005, 2006) and molecular genetic evidence (Wilson et al. 1999; Morse 2009) it can be hypothesized that quagga mussels were introduced to Lake Mead via overland transport of a mussel-infested boat from a water body in the Great Lakes/St Lawrence River drainage to which they had been previously restricted (USGS 2010c). By the time of its initial discovery in the Boulder Basin of Lake Mead on 06/01/2007 quagga mussels appeared to be already established in downstream portions of the lower Colorado River including populations in Lakes Mohave and Havasu (Nevada Department of Wildlife 2007; USGS 2010b). It is possible that quagga mussels could have been rapidly spread throughout the lower Colorado River via movement of infested boats as hypothesized to have occurred during recent rapid dreissenid dispersal in the interconnected, contiguously navigable portions of the Shannon, Boyle and Erne River drainages of Ireland (Minchin 2000; Minchin et al. 2003), especially because infested large recreational and commercial vessels may move long distances in contiguously navigable waterways (Keevin and Miller 1992; Minchin 2000). However, recreational boat movements appear to have been less of a factor in early quagga mussel dispersal in the lower Colorado River because of delayed establishment of quagga mussel populations in portions of Lake Mead upstream of the Boulder Basin (Figure 1) (USGS 2010b) in spite of extensive inter-basin boat movements. In addition, infested boats would have had to be transported overland around navigational barriers including dams to establish quagga mussel populations downstream of Lake Mead (Figure 1). Because successful introduction of aquatic invasive species via overland transport between water bodies appears to be a relatively rare event (Padilla et al. 1996; Buchan and Padilla 1999) and mussel colonization upstream of the Boulder Basin was delayed in Lake Mead, it seems far more likely that quagga mussels were established via a single introduction to the Boulder Basin of Lake Mead in the relatively large numbers required to successfully found a reproducing population (Claereboudt 1999; Morse 2009).

Stoeckel et al. (1997) estimated that dreissenid veligers reached densities $>250 \cdot l^{-1}$ in the Illinois River (IL) such that 75 10^6 veligers·sec^{-1} were being carried by a fixed point to generate annual downstream veliger fluxes of 1.935 10^{14} and 2.131 10^{14} yr^{-1} in 1994 and 1995, respectively. Veligers were estimated to be transported at least 306 km downstream before settlement (Stoeckel et al. 1997). Thus, once a reproducing population of quagga mussels had been established in the Boulder Basin of Lake Mead, planktonic veliger larvae could have been hydrologically transported in massive numbers long distances downstream (Carlton 1993; Mackie and Schloesser 1996) leading to rapid establishment of mussel populations throughout the lower Colorado River by the end of 2007 (USGS 2010b).

Since members of the initially settled Lake Mead cohorts were likely to be too rare to appear in the 2007 samples it can be hypothesized that initial quagga mussel introduction to the Boulder Basin must have occurred no later than 2004, but more likely occurred prior to that time. The basis of this supposition is that a reproducing population of mussels must been introduced somewhere in the Boulder Basin of Lake Mead in 2003 in order to generate enough adults in 2004 to produce enough veliger larvae to settle as relatively wide-spread members of the 2005 cohort during spring and fall of 2005 and be transported downstream to establish the 2005 cohort at KLM in the lower reaches of Lake Mohave. Because the three sites sampled in the Boulder Basin essentially had similar cohort structures (i.e., containing 2005 and 2006 cohorts), it is impossible to speculate where quagga mussels first became established in the Boulder Basin of Lake Mead. Since the cohort structure of quagga mussels in the lower Lake Mohave (KLM) sample was also similar to those from the Boulder Basin (Figures 2 and 3), and because mussel infestations were found on Hoover Dam intake structures, in the Colorado River below Hoover dam, and at KLM in lower Lake Mohave within a month of the initial discovery of mussels in LVBH it appears most likely that quagga mussels became established in Lake Mohave by downstream transport of veligers and juveniles soon after a reproducing mussel population was established in the Boulder Basin of Lake Mead. Since all four sampled sites contained well-developed populations with essentially the same cohort structure, it can be hypothesized that the original successful introduction of quagga mussels to the Boulder Basin of Lake Mead was likely to have occurred during or before 2003, but no later than 2004.

The mean SL of the 2006 cohorts was significantly different among the sampled sites (Figure 3) suggesting that mussel growth rates and/or settlement times were variable among these sites and, by inference, throughout Lakes Mead and Mohave. In contrast, the mean shell lengths of the CBM 2006 cohorts were not different on 16/01/07 and 16/3/07 reflective of lack of shell growth during cooler winter months when Lake Mead surface water temperatures are generally <15°C (Figure 4) (USGS Nevada Water Science Center 2010). The appearance of a few large individuals of the 2005 cohort on shallow water substrata (i.e., boat hulls and cement blocks) in the LVBH, CMB-2, LMM, and KLM samples suggested that these individuals survived in Lakes Mead and Mohave during the summer of 2006 even though ambient surface water temperatures (Figure 4) approached or periodically exceeded the incipient upper thermal limit this species estimated to range from 27.5°C (Morse 2009) to 30°C (Spidle et al. 1995) (Figure 4). Exposure to near lethal summer surface water temperatures in infested water bodies on the lower Colorado River (Figure 2) could lead to eventual selection for a thermally tolerant race of quagga mussels. Evolution of a thermally tolerant race of quagga mussels in water bodies on the lower Colorado River could, in turn, allow this species to further invade warm water bodies in the southwestern US once considered thermally resistant to dreissenid invasion (Drake and Bossenbroek 2004). Morse (2009) determined the incipient upper thermal limit of quagga mussels collected during May 2007 from Sentinel Island in the Boulder Basin of Lake Mead to be 27.5°C. Retesting of the incipient upper thermal limits of Lake Mead quagga mussels appears warranted now that they have experienced over three years of thermal selection in the lake's warm surface waters and are rapidly expanding in distribution and density within the lower Colorado River and other southwestern water bodies (USGS 2010c).

Differences in the mean SL and size distributions of the 2006 cohorts suggest that there may have been shell growth rate and/or juvenile settlement timing differences among the sampled sites. Growth rates in zebra mussels have been shown to be positively correlated with temperature both in the field (Stańczykowska 1976; Walz 1978a, 1978b; Smit et al. 1992;

MacIsaac 1994; Sinicyna and Zdanowski 2007) and laboratory (Walz 1978a, 1978c). Similarly, quagga mussels of 5 and 15 mm SL enclosed in the warmer western basin of Lake Erie exhibited elevated shell growth rates compared to those concurrently enclosed in the cooler eastern basin (MacIsaac 1994). A similar differential in shell growth rates was obtained in mussels of the same two size classes grown at 15°C relative to 6°C in the laboratory (MacIsaac 1994).

Based on hourly mean surface water temperature monitoring from 27/05/2010 through 06/06/2010 the mean daily water temperature at CMB (19.96°C) was 1.31°C higher ($p < 0.05$) than that of LVBH (18.64°C) (McMahon unpublished data). The mean shell length of the 2006 cohort at CBM-1 (9.59 mm, s.e. = ±0.080) was 2.73 mm greater than that at LVBH (6.86 mm, s.e. = ±0.126) (Figure 3) suggesting that ambient water temperature differences may have, in part, accounted for the recorded differences in the size frequency distributions and mean shell lengths recorded among mussel samples from the four sampled sites.

The concentration of phytoplankton food available to mussels has also been demonstrated to be positively correlated with shell growth rate both in the laboratory (Walz 1978b) and natural habitats (Walz 1978c). Thus, differences in phytoplankton density could also be partially responsible for the differences in 2006 cohort mean shell lengths and size distributions recorded among the four sampling sites. Based on these preliminary results, the relationship between surface water temperature, phytoplankton density and population dynamics among *D. rostriformis bugensis* populations infesting the water bodies of the lower Colorado River appears to warrant investigation.

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References

Bij de Vaate A (1991) Distribution and aspects of population dynamics of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), in the Lake IJsselmeer area (The Netherlands). *Oecologia* 86: 40–50, doi:10.1007/BF00317387

Bij de Vaate A, Jansen EA (2006) De verspreiding van de quagga mussel in de rijkswatern. *Spirula Correspondentieblad van de Nederlandse Malacologische Vereniging* no. 351: 72–77

Bossenbroek JM, Kraft, CF, Nekola JC (2001) Prediction of long-distance dispersal using gravity models: zebra mussel invasion of inland lakes. *Ecological Applications* 11: 1778–1788, doi:10.1890/1051-0761(2001)011[1778:POLDDU]2.0.CO;2

Britton DK, McMahon RF (2005) Analysis of trailered boat traffic and the potential westward spread of zebra mussels across the 100th Meridian. *American Malacological Bulletin* 20: 147–159

Britton DK, McMahon RF (2006) Assessment for potential range expansion of zebra mussels on the western edge of their distribution in the United States. *Aquatic Invaders* 17: 1–7

Buchan LAJ, Padilla DK (1999) Estimating the probability of long-distance overland dispersal of invading aquatic species. *Ecological Applications* 9: 254–265, doi:10.1890/ 1051-0761(1999)009[0254:ETPOLD]2.0.CO;2

Carlton JT (1993) Dispersal mechanisms of the zebra mussel (*Dreissena polymorpha*). In: Nalepa TF, Schloesser DW (eds), Zebra Mussels: Biology, Impacts, and Control. Lewis Publishers, Boca Raton, Florida, USA, pp 677–697

Chase ME, Bailey RC (1999) The ecology of the zebra mussel (*Dreissena polymorpha*) in the lower Great Lakes of North America: I. Population dynamics and growth. *Journal of Great Lakes Research* 25: 107–121, doi:10.1016/S0380-1330(99)70720-3

Claereboudt M (1999) Fertilization success in spatially distributed populations of benthic free-spawners: a simulation model. *Ecological Modeling* 121: 221–233, doi:10.1016/S0304-3800(99)00080-0

Cope WG, Bartsch MR, Hightower JE (2006) Population dynamics of zebra mussels *Dreissena polymorpha* (Pallas, 1771) during the initial invasion of the Upper Mississippi River, USA. *Journal of Molluscan Studies* 72: 179–188, doi:10.1093/mollus/eyi063

Dall PC, Hamburger K (1996) Recruitment and growth of *Dreissena polymorpha* in Lake Esrom, Denmark. *Limnologica* 26: 27–37

Drake JM, Bossenbroek JM (2004) The potential distribution of zebra mussels in the United States. *BioScience* 10: 931–941, doi:10.1641/0006-3568(2004)054[0931:TPDOZM]2.0.CO;2

Dermott R, Bonnell R, Carou S, Dow J, Jarvis P (2003) Spatial distribution and population structure of the mussels *Dreissena polymorpha* and *Dreissena bugensis* in the Bay of Quinte, Lake Ontario, 1998 and 2000. Fisheries and Oceans Canada. Canadian Technical Report of Fisheries and Aquatic Sciences No 2479, 58 pp

Domm S, McCauley RW, Kott E, Ackerman JD (1993) Physiological and taxonomic separation of two dreissenid mussels in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2294–2297, doi:10.1139/f93-253

Fong PP, Kyozuka K, Duncan J, Rynkowski S, Mekasha D, Ram JL (1995) The effect of salinity and temperature on spawning and fertilization in the zebra mussel *Dreissena polymorpha* (Pallas) from North America. *Biological Bulletin* 189: 320–329, doi:10.2307/1542149

Griebeler EM, Seitz A (2007) Effects of increasing temperatures on population dynamics of the zebra mussel *Dreissena polymorpha*: implications from an individual–based model. *Oecologia* 151: 530–543, doi:10. 1007/s00442-006-0591-0

Jantz B, Schöll F (1998) Size and age structure of a riverine zebra mussel population (Rhine River, Rh-km 168-861). *Limnologica* 28: 395–413

Kalayda ML (2004) *Dreissena polymorpha* (Pall.) and *Dreissena bugensis* (Andr.) (Mollusca, Bivalvia) in the upper part of the Kuibyshev Reservoir. *Biologiya Vnutrennikh Vod* 3: 60–67

Keevin TM, Miller AC (1992) Long-distance dispersal of zebra mussels (*Dreissena polymorpha*) attached to the hulls of commercial vessels. *Journal of Freshwater Biology* 7: 437

MacIsaac HJ (1994) Comparative growth and survival of *Dreissena polymorpha* and *Dreissena bugensis*, exotic mollusks introduced to the Great Lakes. *Journal of Great Lakes Research* 20: 783–790, doi:10.1016/S0380-1330(94)71196-5

Mackie GL, Schloesser DW (1996) Comparative biology of zebra mussels in Europe and North America: an overview. *American Zoologist* 36: 244–258

Martel A (1995) Demography and growth of the exotic zebra mussel (*Dreissena polymorpha*) in the Rideau River (Ontario). *Canadian Journal of Zoology* 73: 2244–2250, doi:10.1139/z95-266

McMahon RF (1996) The physiological ecology of the zebra mussel, *Dreissena polymorpha*, in North America and Europe. *American Zoologist* 36: 339–363

Millane M, Kelly-Quin M, Champ T (2008) Impact of the zebra mussel invasion on the ecological integrity of Lough Sheelin, Ireland: distribution, population characteristics and water quality changes in the lake. *Aquatic Invasions* 3: 271–281, doi:10.3391/ai.2008.3.3.2

Mills EL, Dermott RM, Roseman EF, Dustin D, Mellina E, Conn DB, Spidle AP (1993) Colonization, ecology, and population structure of the “quagga” mussel (Bivalvia: Dreissenidae) in the lower Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2305–2314, doi:10.1139/f93-255

Minchin D (2000) Dispersal of zebra mussels in Ireland. *Verhandlungen des Internationalen Verein Limnologie* 27: 1576–1579

Minchin D, Maguire C, Rosell R (2003) The zebra mussel (*Dreissena polymorpha* Pallas) invades Ireland: human mediated vectors and the potential for rapid international dispersal. *Biology and Environment: Proceedings of the Royal Irish Academy* 103B: 23–30, doi:10.3318/BIOE.2003.103.1.23

Morse JT (2009) Thermal tolerance, physiologic condition, and population genetics of dreissenid mussels (*Dreissena polymorpha* and *Dreissena rostriformis bugensis*) relative to their invasion of waters in the western United States. PhD Dissertation, The University of Texas at Arlington, Arlington, Texas, USA, 280 pp

Nalepa TF, Wojcik JA, Fanslow DL, Lang DA (1995) Initial colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron: population recruitment, density and size structure. *Journal of Great Lakes Research* 21: 417–434, doi:10.1016/S0380-1330 (95)71056-5

Nevada Department of Wildlife (2007) Quagga chronology January 30, 2007. Nevada Department of Wildlife, 2 pp. http://www.ndow.org/boat/exotic/Quagga%20Chronology.pdf (Accessed 18 June 2010)

Orlova MI, Shcherbina GKh (2002) On distribution of *Dreissena bugensis* (Dreissenidae, Bivalvia) in reservoirs of the Upper Volga River Basin. *Zoologicheskii Zhurnal* 81: 515–520

Orlova MI, Panov VE (2004) Establishment of the zebra mussel, *Dreissena polymorpha* (Pallas), in the Neva Estuary (Gulf of Finland, Baltic Sea): distribution, population structure and possible impact on local unionid bivalves. *Hydrobiologia* 514: 207–217, doi:10.1023/B:hydr.0000018220.44716.8c

Padilla DK, Chotkowski MA, Buchan LAJ (1996) Predicting the spread of zebra mussels (*Dreissena polymorpha*) to inland waters using boater movement patterns. *Global Ecology and Biogeography Letters* 5: 353–359, doi:10.2307/2997590

Roe SL, MacIsaac HJ (1997) Deepwater population structure and reproductive state of quagga mussels (*Dreissena bugensis*) in Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2428–2433, doi:10.1139/cjfas-54-10-2428

Sinicyna OO, Zdanowski B (2007) Development of the zebra mussel, *Dreissena polymorpha* (Pall.), population in a heated lakes ecosystem. II. Life strategy. *Archives of Polish Fisheries* 15: 387–400

Smit H, Bij de Vaate A, Fioole A (1992) Shell Growth of zebra mussels (*Dreissena polymorpha* (Pallas)) in relation to selected physico-chemical parameters in the Lower Rhine and some associated lakes. *Archiv fuer Hydrobiologie* 124: 257–280

Spidle AP, Mills EL, May B (1995) Limits of tolerance to temperature and salinity in the quagga mussel (*Dreissena bugensis*) and the zebra mussel (*Dreissena polymorpha*). *Canadian Journal of Fisheries and Aquatic Sciences* 52: 2108–2119, doi:10.1139/f95-804

Sprung M (1987) Ecological requirements of developing *Dreissena polymorpha* eggs. *Archiv für Hydrobiologie Supplement* 79: 69–86

Sprung M (1993) The other life: an account of present knowledge of the larval phase of *Dreissena polymorpha*. In: Nalepa TF, Schloesser DW (eds), Zebra Mussels: Biology, Impacts, and Control. Lewis Publishers, Boca Raton, Florida, USA, pp 39–53

Sprung M (1995) Physiological energetics of the zebra mussel *Dreissena polymorpha* in lakes I. Growth and reproductive effort. *Hydrobiologia* 304: 117–132, doi:10.1007/BF02579417

Stańczykowska A (1976) Occurrence and growth of *Dreissena polymorpha* Pall. in lakes included in a cooling system. *Roczniki Nauk Rolniczych Seria H Rybactwo* 97: 109–122

Stoechel JA, Schneider DW, Soeken LA, Blodgett KD, Sparks RE (1997) Larval dynamics of a riverine metapopulation: implications for zebra mussel recruitment, dispersal, and control in a large-river system. *Journal of the North American Benthological Society* 16: 586–601, doi:10.2307/1468146

Strayer DL, Malcom HM (2006) Long–term demography of a zebra mussel (*Dreissena polymorpha*) population. *Freshwater Biology* 51: 117–130, doi:10.1111/j.1365-2427.2005.01482.x

United States Geological Survey (USGS) (2010a) NAS – nonindigenous aquatic species, Specimen information, *Dreissena rostriformis bugensis*, Collection info, Specimen ID 236384, http://nas.er.usgs.gov/queries/SpecimenViewer.aspx?SpecimenID=236384 (Accessed 30 June 2010)

United States Geological Survey (USGS) (2010b) NAS – nonindigenous aquatic species, Specimen information, *Dreissena rostriformis bugensis*, Collection info. http://nas.er.usgs.gov/queries/collectioninfo.aspx?SpeciesID=95 (Accessed 30 June 2010)

United States Geological Survey (USGS) (2010c) NAS – nonindigenous aquatic species, Specimen information, *Dreissena rostriformis bugensis*, Point Maps. http://nas2.er.usgs.gov/viewer/omap.aspx?SpeciesID=95 (Accessed 30 June 2010)

United States Geological Survey Nevada Water Science Center (2010) Water-quality monitoring at Lake Mead, Arizona and Nevada, Sentinal Island, Historic quality-assured data. http//Nevada.usgs.gov/water/Imqw/data_sentinel.htm (Accessed 10 July 2010)

Walz N (1978a) Growth rates of *Dreissena polymorpha* Pallas under laboratory and field conditions. *Internationale Vereinigung fuer Theoretische und Angewandte Limnologie* 20: 2427–2430

Walz N (1978b) The energy balance of *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. IV. Growth in Lake Constance. *Archiv für Hydrobiologie*, Supplement 55: 142–156

Walz N (1978c) The energy balance of *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. III. Growth under standard conditions. *Archiv für Hydrobiologie Supplement* 55: 121–141

Whittier TR, Ringold PL, Herlihy AT, Pierson SM (2008) A calcium-based invasion risk assessment for zebra and quagga mussels (*Dreissena* spp). *Frontiers in Ecology and the Environment* 6: 180–184, doi:10.1890/070073

Wilson AB, Naish K-A, Boulding EG (1999) Multiple dispersal strategies of the invasive quagga mussel (*Dreissena bugensis*) as revealed by microsatellite analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2248–2261, doi:10.1139/f99-162

Zhulidov AV, Pavlov DF, Nalepa TF, Schierbina GH, Zhulidov DA, Gurtovaya TYu (2004) Relative distributions of *Dreissena bugensis* and *Dreissena polymorpha* in the lower Don River System, Russia. *International Review of Hydrobiology* 89: 326–333, doi:10.1002/iroh.200310727