Quagga Mussel Risk Assessment - An experiment test of quagga mussel survival and reproductive status using Lake Tahoe water with a prediction of invasion into Western water bodies

Lake Tahoe Aquatic Invasive Species Integrated Management Strategy

LAKE TAHOE WATERSHED, CALIFORNIA & NEVADA

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This Aquatic Invasive Species Quagga Mussel Risk Assessment is part of a multi-stakeholder collaborative effort to minimize the deleterious effects of nuisance and invasive aquatic species in the Lake Tahoe Basin. This specific product is authorized pursuant to Section 108 of Division C of the Consolidated Appropriations Act of 2005, Public Law 108-447 and in interagency agreement between the U.S. Army Corps of Engineers and the California Tahoe Conservancy.

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Risk of invasion or really no problem? An experiment test of quagga mussel survival and reproductive status using Lake Tahoe water with a prediction of invasion into Western water bodies

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Executive Summary
The recent establishment of non-native dreissenid mussel species (quagga and zebra) in the western United States is creating concern amongst regional water resource managers, scientists and other recreational and commercial users of waterways. These invasive species cause both ecological and economic damage to aquatic ecosystems, impacting native biodiversity and debilitating water conveyance systems. Since eradication of these species is not likely, agencies and other water resource managers in the western U.S. have installed preventative measures such as monitoring for juvenile forms, water drawdown to minimize the downstream spread, and recreational boat inspections and washes at entries to highly utilized lakes, rivers and reservoirs in an effort to keep these species out of waterways. In particular, at Lake Tahoe the Tahoe Regional Planning Agency (TRPA) has enacted regulations requiring mandatory boat inspection at each launch point. Agencies are also providing inspectors and boat washing stations which are available throughout the boating season as well as in the off-season. These agencies have also formed multiple aquatic invasive species working groups whose goals are to protect against and prevent the introduction of future aquatic invasive species to the lake. Despite these progressive efforts, Lake Tahoe is still at risk of invasion by quagga mussel and other aquatic invasive species such as the spiny waterflea and the New Zealand mudsnail. It remains unclear whether Lake Tahoe's physical habitat can support their establishment. Previous models for dreissenid mussel establishment are minimum threshold driven, based mostly on dissolved calcium levels. A majority of western reservoir and lake systems that have recently reported quagga mussel veliger presence have dissolved calcium levels that are much lower than previously determined minima. This study seeks to understand the potential for adult quagga mussel to survive when exposed to a Lake Tahoe conditions (i.e. low calcium, oligotrophic cold waters) in a laboratory setting. We tested the survival, growth and reproductive potential for quagga mussels collected from Lake Mead, NV-AZ when exposed to water from the Tahoe Keys marina of Lake Tahoe for a 51 day period. The laboratory experiment showed that quagga mussel had 87% survival with a positive growth rate over the experimental period. Reproductive status was variable with 43% of individuals (male and female) showing sperm and oocyte production, 14% were in a post-spawn phase, and 29% showed resorption. The regional invasion of dreissenid, and more specifically quagga mussel in the Western United States is currently not well understood due to data gaps for this particular species, and the lack of a clear relationship between water column calcium levels and the probability of establishment. This is the first study that addresses survivability and reproduction as it relates to water column characteristics for quagga mussel specifically in reference to western reservoirs, conveyance systems, and natural lakes.
While Lake Tahoe have previously been categorized as "low risk" for dreissenid mussel establishment because of its low dissolved calcium concentrations, findings from our study show survivability as well as a positive growth rate when exposed to these concentrations. While the positive growth rate decreased over the duration of the experiment, there is still evidence that adult quagga survival is possible despite the findings of previous models. We highly recommend continued monitoring and prevention efforts in Lake Tahoe for quagga mussel and other potential aquatic invasive species.

Scientific Abstract

The recent detection and establishment of quagga mussels in aquatic ecosystems of the Western United States is requiring a re-evaluation of dreissenid survivability and suitable-habitat range prediction. Models predicting dreissenid mussel establishment have been minimum-threshold driven, based mostly on dissolved calcium levels. However, the majority of western reservoir and lake systems in which quagga mussel veligers are present have dissolved calcium levels that are much lower than previously-determined minima. This laboratory study tested the survival, growth, and reproductive potential for quagga mussels collected from Lake Mead, NV-AZ when exposed to the low calcium, oligotrophic waters of Lake Tahoe for a 51-day period. Lake Tahoe has no known populations of quagga mussels and the purpose of this study was to determine whether growth and reproduction in a laboratory replicating Lake Tahoe conditions is possible. Quagga mussel showed 87 % survival with a positive growth rate over the experimental period. Reproductive status was variable with 43 % of individuals (male and female) showing sperm and oocyte production, 14 % in a post-spawn phase, and 29 % showing gonad resorption. Studies conducted to evaluate the short-term (≤48 h) effects from quagga establishment suggest reductions in algal biomass of up to 76 % and increases in the nutrient pools of bioavailable phosphorus and nitrogen. The regional invasion of dreissenid mussels, and more specifically quagga in the Western United States, is currently not well understood due to the unclear influence of water calcium concentrations on quagga establishment. This is the first study to address survivability and reproduction as it relates to water column characteristics for quagga mussel specifically, in reference to reservoirs, conveyance systems, and natural lakes in the Western United States.

Introduction

The introduction of non-native species is a leading threat to biodiversity and function of freshwater ecosystems (Sala et al. 2000). A major introduction pathway for aquatic invasive species to North America has been ship ballast water releases into the Laurentian Great Lakes and coastal waters. Once established, species can extend their range through natural waterways via passive or active transport. The long distance spread of these species far beyond neighboring watersheds increases over time predominantly due to human recreational activity (e.g. boating, fishing). Invasive dreissenid zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels (quagga and zebra) in particular have altered the ecology of lakes and rivers by coupling pelagic and benthic trophic pathways, increasing offshore clarity, stimulating benthic production and altering biodiversity (Makarewicz et al. 1999, Bially and MacIssac 2000, Ricciardi et al. 1998).

In recent years there has been a western range expansion in North America for a number of aquatic invasive species such as New Zealand mudsnail (*Potamopyrgus antipodarum*), dreissenid mussel species, and crayfish (*Procambarus clarki*). This spread has been of increasing concern to aquatic ecosystem managers in the western U.S. due to the high level of endemism in their waters (Sada and Vinyard 2002) as well as high costs often associated with the prevention, monitoring and control of introduced species. The Southern Nevada Water Authority has spent approximately $32 million (US dollars) to manage quagga biomass impacts on the water intake infrastructure of Lake Mead, a recently invaded reservoir in the western U.S. (Peggy Roefer, Southern Nevada Water Authority, pers. communication). While it is clear that many of these species can be viably transported to water bodies, the physical characteristics of these water bodies that are necessary for successful invasive establishment are poorly understood.

Dreissenid mussels have already invaded the mid-western and eastern regions of North America, with zebra mussels (*Dreissena polymorpha*) discovered in the Great Lakes region of North America in the mid-1980's (Hebert et al. 1989) and quagga mussels found there in 1992 (May and Marsden 1992, Mills et al. 1993). The quagga mussel first appeared in western U.S. in Lake Mead, AZ-NV in early 2007 (Stokstad et al. 2007) and has subsequently been found in other major western impoundments including Lakes Powell and Mohave. These recent invasions have spurred efforts to determine invasion risk posed by zebra and quagga mussels in western waters.

There are a large number of dreissenid mussel establishment risk assessment approaches that have been based on European and Eastern North American invasions that may or may not be appropriate for evaluations of western water ways. Risk assessment for the western U.S. should be based on these approaches, but with careful consideration of western water body characteristics such as differences in water temperature, calcium and other nutrient concentrations as well as food availability that may determine different parameters for western waterways. Water column calcium concentration is often used as an index for determining the potential for mollusk establishment, growth, and reproduction with variable requirements depending on the species (Ramcharan et al. 1992, Sousa et al. 2008, Whittier et al. 2008). Food availability is also an important variable for mollusk establishment, and is often the cause for massive dreissenid mussel population crashes after initial population explosions (Strayer et al. 1996). Since the recent establishments in Lakes Mead, Powell and Mohave, numerous studies are underway to determine zebra and quagga mussel invasion risk to Western waterways. Based on empirical information gathered from water quality databases and modeled systems, Whittier

et al. (2008) created a watershed-scale risk model for dreissenid species. This model is based on calcium requirements, primarily derived from zebra mussel due to limited experimental data on quagga mussel survival. Managers have used this model to determine the risk-potential of quagga mussel establishment from invaded water bodies such as Lake Mead. However, because quagga mussels appear to have different environmental tolerances than zebra mussels, (Baldwin et al. 2002, Stoeckmann 2003, Roe and MacIssac 1997, Zhulidov 2004), and possibly than quagga in other parts of their range (Domm et al. 1993, Antonov and Shkorbatov 1990), the potential risk of invasion of western water bodies may be underestimated by using zebra mussel-based risk assessments.

The objectives of this study were to experimentally determine a) survival, growth, and reproduction potential in Lake Tahoe, a large, oligotrophic ecosystem in the Western United States containing levels of calcium thought to be low risk for quagga mussel establishment (Whittier et al. 2008), b) potential short-term water quality impacts of adult establishment in this ecosystem, and c) potential invasive hot spots for adult quagga in waterways of the Great Basin/Lower Colorado River ecosystems.

Methods

A laboratory experiment using low calcium (~13 ppm), oligotrophic waters from Lake Tahoe was used to determine adult survival, relative individual growth, and potential reproduction of quagga mussels these conditions. Neither quagga nor zebra mussels have been found in Lake Tahoe. Water from the Tahoe Keys Marina (South Lake Tahoe, CA) was used since this area is the primary launch for public boats in the Tahoe Basin and was the location of interception by lake managers of a quagga-infected boat arriving from Lake Mead (Zabaglo pers. comm. 2008). Adult quagga mussels (4 females, 3 males, 1 unknown due to death) were obtained from Las Vegas Bay marina (2 m depth) in Boulder Basin, Lake Mead and transported under carefully monitored conditions back to the University of Nevada, Reno, where the subsequent experiments were carried out. To minimize a 'container effect' from depletion of food resources, each adult was placed individually in a 19 L container and provided a daily ration of 15 L of Lake Tahoe water for the duration of the experiment (51 days). To allow evacuation of stomach content material, mussels were held for 48 h before placement in their containers. Mean initial length and blotted wet-weight for the live mussels (n=7) was 8.0±0.40 mm and 44.0±6.4 mg, respectively. Water quality parameters (temperature, dissolved oxygen, conductivity) were measured approximately every 12 h for each of the 7 replicate using a YSI 85 multiprobe (YSI Incorporated, Yellow Springs, Ohio). Phosphorus (total, dissolved, reactive), nitrogen (ammonium and nitrate), and chlorophyll *a* (pheophytin corrected) were measured nearly daily from field water and analyzed using standard methods (Strickland and Parsons 1972, Marker et al. 1980, US EPA Methods 350.1, 353.1, 365.3, and SM4500-PE). Dissolved calcium was measured intermittently throughout the experiment from field water and analyzed using an Inductively Coupled Plasma Mass Spectrometer (ICP-MS) following standard methods used by UC Davis. The mussels in their containers were maintained in a temperature controlled chamber at 17 °C, on a 12 hour day-night light cycle. All 7 mussels survived the duration of the experiment, 51 days.

Mussel survival was determined daily by qualitatively noting gape size (Matthews and McMahon 1999). If gape size appeared abnormally large or mortality was suspected, the adult was gently tapped and shell closure was used as an indicatory of viability.

Growth rate was measured by the slope of the line during three periods (0-36 d, 36-51 d and 0-51 d) when mean wet weight of the mussels was plotted against time. Additionally, we plotted start- versus end weight compared to a 1:1 line, since a slope of 1 represents no growth (start = end weight); points falling above the 1:1 line were interpreted as weight gain, points below as weight loss, over the course of the entire experiment.

To determine the reproductive potential of each of the experimental mussels, gonad status was determined for each replicate. At the end of the experiment the soft tissue of each live mussel was removed from the shell, placed in 15 mL of 10 % neutral buffered formalin for 24 hours, and transferred to 70 % ethanol. Tissue from each replicate was then placed in a tissue cassette and processed for routine preparation of 5 µm, hematoxylin- and eosin-stained paraffin-embedded tissue sections. Due to their small size, three sections were cut from each mussel tissue block at different levels, thus sampling most of the embedded tissue. Each mussel was scored qualitatively for the presence of gametes with notes on the sex, gonad stage and the stage of resorption. The scoring were as follows for gonad development stage: 0, no gonad present, 1) early development, very immature sperm or egg precursors present, 2) between stages 1 and 3, 3) apparently mature sperm or oocytes present (in any volume), 4) post-spawn, empty gonad follicles present with some residual sperm or egg; and for gonad resorption stage: 0) no evidence of resorption, few or no hemocytes in gonad follicles, 1) small proportion of hemocytes present among reproductive cells, 2) between stages 1 and 3, and 3) follicles dominated by hemocytes with some residual sperm or egg.

The potential short-term impact of quagga mussel on Lake Tahoe water nutrient concentrations and algal biomass was determined by conducting a second experiment using adults that had survived the 51-day experiment (n=7). Adults were allowed to feed for 48 h without lake water replacement. Containers with lake water and no mussels were used as controls (n=7). As in the first experiment, each container was filled with 15 L of Lake Tahoe water, and all containers were maintained in a temperature controlled chamber at 17 °C on a 12 h diurnal light cycle. Initial conditions for the experiment were: chlorophyll *a*, 97.7±12.8 ppb; soluble reactive phosphorus (SRP), 5.3±2.6 ppb; total phosphorus (TP), 31.4±6.5 ppb; and ammonium, 3.6±1.3 ppb. These water quality parameters were compared at 24 h and 48 h after the initiation of the experiment. For both time periods, mussel treatment versus control were compared using a two-tailed, two-sample *t*-test for unequal variances. Relative change between control means and mussel treatment means were used to determine quagga mussel impacts on water quality. The experiment time was restricted to 48 h to avoid depletion of food resources that could have impacted reproductive status of the mussels.

Values obtained from the first experiment were used to assess the potential survival, growth and reproduction of adult quagga mussel in other Western Great Basin and Lower Colorado ecosystems. Water was collected for calcium analysis from 11 sites in the Western Great Basin, including boat launches at lakes and reservoirs, and common recreational access points on rivers, during two time periods (May and November 2008). To determine locations vulnerable to adult quagga mussel establishment in Lake Tahoe, water was collected approximately every 1.5 km around the lake perimeter, 0.5 m above the lake bottom in the nearshore environment. Special emphasis was placed on marinas and boat launch areas that may receive mussel-contaminated boats. Water at all sites was filtered with 0.45 µm membrane filters and analyzed for calcium as described for the laboratory experiment.

Results

Water quality parameters during the mussel growth experiment were relatively static with phosphorus and chlorophyll *a* concentrations varying the most over the 51-day duration of the experiment (Table 1). This is typical of nearshore conditions in the Lake Tahoe during late summer/early fall. Dissolved calcium levels in the containers varied little and fell within the very low- (<12 mg·L) to low- (12-20 mg·L) range of conditions for quagga mussel survival as presented in Whittier et al. (2008). During the experiment, quagga mussel adults were active and exhibiting strong diel movement such as migration from the bottom to the top of the experimental tank. After 51 days of exposure to ambient Lake Tahoe water, 86 % (6 of 7) of the adult quagga mussels survived.

Mussel growth in the overall experimental period (day 1-51) was positive (Figure 1), however, breaking the experiment into two periods (period 1, day 0-36; period 2, day 37-51) it is apparent that growth was not constant (Figure 2). Mussels exhibited stronger-than-overall growth in period 1 and static or negative growth in period 2 (Table 2, Figure 2). The positive growth in period 1 indicates that, for the short-term, quagga mussels were able to grow under ambient low-calcium conditions in water from the Tahoe Keys area of Lake Tahoe. The mean negative growth observed in period 2 suggests that the mussels experienced a shift in metabolic ability attributable to a number of possibilities ranging from environmental stress, a lack of calcium or appropriate food source, or a natural seasonal shift in growth period.

After the 51-day exposure to Lake Tahoe-Tahoe Keys water, the combination of male and female adults exhibited varying reproductive potential (Table 3). Two individuals were in early development or very immature in their reproductive cycle with nearly fully resorbed gonads, with follicles dominated by hemocytes with small volumes of residual immature oocytes. One mussel was intermediate in its reproductive cycle and displaying some resorption. Four individuals exhibited mature sperm or oocytes with one individual having spawned and two exhibiting little or no resorption of gonadal tissue or some residual resorption. We could not find tissues photos for quagga in the literature and have placed the tissues from this study for reference (Appendix I).

The second experiment, to determine potential short-term impacts from individual adult quagga mussels on water quality, yielded changes to nutrient and chlorophyll *a* concentrations of Lake Tahoe water. Chlorophyll *a* concentrations were lower in the mussel treatments than the control containers (24 h, $p=0.002$; 48 h $p=0.005$; Figure 3a), with a reduction in algal biomass of 16 % and 45 % over 24- and 48-h periods, respectively, in the mussel treatment. Total phosphorus did not significantly differ between control and mussel treatments for the 24- ($p=0.68$) and 48- ($p=0.96$) hour periods (Figure 3b). Soluble reactive phosphorus (SRP) increased in the mussel treatment compared to control, with increases of 76 and 30 % during 24- and 48 h, respectively (24 h, $p=0.004$; 48 h $p=0.042$; Figure 3c). Finally, ammonium increased in the mussel treatments compared to control (24 h, $p<0.001$; 48 hour $p<0.0001$; Figure 3d) by 132 and 540 % in the two time periods. Although SRP in the mussel-treated water showed a moderate increase compared to control (Figure 3c), ammonium showed a much larger increase (Figure 3d) relative to control, so ammonium:SRP was positive, and significantly different between treatment and control (24 h, $p=0.48$; 48 h, $p<0.001$; Figure 4).

The spring/fall mean calcium concentrations in Lake Tahoe's nearshore (9.3 ± 0.3 mg·L^{-1}) were relatively uniform, with highest concentrations (14.6 ± 1.4 mg·L^{-1}) in Tahoe Keys and lowest but variable concentrations in Meeks Bay Marina (5.3 ± 2.9 mg·L^{-1}; Figure 5, Appendix I). Emerald Bay, located in the southwest corner of Lake Tahoe and semi-isolated from the open

waters of Lake Tahoe showed slightly lower calcium levels (8.3±0.4 $mg \cdot L^{-1}$) than seen in the main lake. Sediment porewater from beds of Lake Tahoe's newest invasive species, Asian clam (*Corbicula fluminea*), had elevated calcium concentrations (Timber Cove 24.1±1.8 and Ski Run marina 16.0±1.8 $mg \cdot L^{-1}$) compared to other nearshore sites, and to sediment porewaters in locations without clams. Stormwater runoff collected during spring also had elevated calcium concentrations (14.5±2.5 $mg \cdot L^{-1}$) compared to nearshore water. In the greater Tahoe-Pyramid drainage, calcium concentrations varied broadly with the lowest concentrations of our study at Fallen Leaf Lake (2.8±0.1 $mg \cdot L^{-1}$) and highest concentrations (15.5±1.9 $mg \cdot L^{-1}$) in the Lower Truckee River that drains Lake Tahoe (Figure 5, Appendix I). Nevadan regional waterbodies outside of the Tahoe-Pyramid watershed also exhibited a large range of calcium concentrations, all higher than in Lake Tahoe: Lahontan Reservoir (28.2 $mg \cdot L^{-1}$), Walker River (27.1 $mg \cdot L^{-1}$), Walker Lake (44.0 $mg \cdot L^{-1}$); Lake Mead had notably the highest concentration (80.0 $mg \cdot L^{-1}$) of all sites that we examined (Figure 5, Appendix I).

Discussion

Our findings indicate a strong likelihood of short-term adult survival (51 days) with a positive growth rate in low-calcium (~13.5 ppm), oligotrophic waters. Similarly, Dietz et al. (1994) found that zebra mussels survived at least 51 days in water containing minimal concentrations of NaCl, potassium and magnesium but no calcium and suggested that the mussels survived by mobilizing calcium from shells to maintain critical levels of blood calcium for muscle function. Recent findings from other western aquatic ecosystems also indicate that dreissenid survival can occur under variable and lower calcium concentrations than used in this experiment. For example, there are currently 8 Coloradan limnetic ecosystems (some hydrologically connected) where dreissenids have been detected (Table 4). These systems exhibit varying calcium concentrations ranging from 3.5-75 $mg \cdot L^{-1}$. Five of the eight locations that have been invaded by quagga mussels (Willow Creek Reservoirs, Lake Granby, Shadow Mountain Reservoir, Grand Lake and Blue Mesa Reservoir) have similar calcium concentrations and water quality characteristics to the oligotrophic water bodies in the Tahoe basin.

Previous research suggests that in the Midwestern and eastern regions of North America, calcium can be a limiting factor for reproducing colonies of dreissenids (Cohen and Weinstein 2001). North American researchers show that the minimum calcium concentration required for establishment and reproduction is 20 $mg \cdot L^{-1}$, whereas studies conducted in European waters suggest that the calcium threshold for establishment is higher, 28 $mg \cdot L^{-1}$ (Ramcharan et al. 1992, Cohen and Weinstein 2001). Whittier et al. (2008) used literature-based calcium thresholds in create a broad scale, landscape-level approach to determine survival probability for dreissenid mussels in Western watersheds. Thresholds were established based on calcium limitations of zebra mussel, since little calcium-based survival information existed for quagga mussel. These authors assumed that zebra and quagga mussel requirements were similar because of the genetic proximity of these two closely related taxa. Their findings suggested Lake Tahoe and surrounding waters in the Truckee-Pyramid watershed have a very low (<12 $mg \cdot L^{-1}$) to low (12 $mg \cdot L^{-1}$ to 20 $mg \cdot L^{-1}$) risk of invasion by quagga mussels.

It is unclear whether the newly introduced populations in the Colorado lakes and reservoir system will be able to maintain long-term growth and population expansion given variable environmental conditions (e.g. calcium and nutrient concentrations, food availability), or whether these systems will act as a sink where short-term survival occurs but growth and

reproduction will be limited or nonexistent. This source-sink pattern has been noted in connected river aqueduct systems such as the St. Joseph River basin in Indiana-Michigan where lakes and reservoirs rich with adult zebra mussels act as sources of veliger larvae for river and stream portions of the system (sinks). There is little or no adult development in these "sink" areas due to poor food quality and high water velocity (Horvath et al. 1996). Additional zebra mussel research suggests that systems with calcium concentrations <20 $mg \cdot L^{-1}$ should have relatively low abundances and act as a population sink for this species (Whittier et al. 2008, Cohen and Weinstein 2001).

While the invasion of zebra mussel has been well studied in Europe and the North American Midwest, understanding the metabolic and life history processes specific for quagga mussels is necessary given recent and repeated establishments in water bodies that are outside of assumed values of mussel minimum temperature, nutrient and calcium thresholds in western aquatic ecosystems such as in Colorado and in the laboratory experiment described here. It has been shown in European and Midwestern American systems that quagga and zebra mussels have different requirements and responses to environmental cues; thus using estimates of zebra mussel performance in distant regions may no longer be a satisfactory index for quagga mussel invasion in the Western U.S. Specifically, because quagga mussels have advantageous physiological characteristics, they tend to out-compete zebra mussels in areas where ranges overlap for at least 3 and as much as 9 years (Zhulidov 2004, Kharchenko 1995, Mills et al. 1996, Mills et al. 1999). Quagga mussels have a higher assimilation efficiency than zebra mussels so they can achieve higher growth and fecundity rates given the same food intake (Baldwin et al. 2002). Quagga mussels also have a lower respiration rate which translates into a greater proportion of energy directed to soft body development and growth than zebra mussels at similar food levels (Stoeckmann 2003, Roe and MacIssac 1997). These attributes give quagga mussels strong competitive advantages during periods of low food and high temperature (Zhulidov 2004), which can occur in reservoir and lake systems in Western regions. There are metabolic differences between mussels in North American and European systems, but genetic profiles of invasive populations, and hence environmental tolerances, may be quite different from profiles of populations within their native range. In testing upper thermal tolerances of North American populations of both species, it was found that quagga mussels had a lower lethal temperature threshold than zebra mussels (Domm et al. 1993). Yet in similar tolerance tests with populations from the Dnepr River basin in Ukraine, quagga had a higher thermal tolerance than zebra mussels (Antonov and Shkorbatov 1990). The variability in regional field and laboratory studies suggests that relying upon thresholds determined for zebra mussels in Midwestern North America is not adequate for invasive zebra or quagga management and prevention in the western U.S.

Dreissenid reproduction can be largely controlled by temperature, with quagga mussels having a lower temperature requirement for developing mature gonads than zebra mussels (Waltz 1978, Roe and MacIsaac 1997). For zebra mussels, physiochemical cues produced from phytoplankton or presence of gametes in the water can also trigger spawning (Ram and Nichols 1993). In our study we found both males and females at variable stages of reproductive maturity with some individuals having mature sperm/oocytes or in a post-spawn condition, with spawning speculated to have occurred sometime after field collection and during the experimental period. Variable degrees of gonadal resorption were also present. The resorption of gonadal tissue prior to spawning may occur when conditions are sufficient to stimulate gonad development, but are, or become, insufficient to complete the production of mature gametes, or when there is a lack of

stimulation to release mature gametes. In such cases the gonad is cleared of gametes or gamete precursors by hemocyte phagocytosis. This may occur in animals exposed to metabolically adverse conditions or additional cues such as seasonal environmental change. Evidence of gonad resorption may be seen at any stage of gonadal development although under ideal conditions resorption is expected to occur only in animals after spawning (gonad development stage 4). Environmental calcium concentrations affect the developmental cycle of zebra mussels with gonadal development occurring even under low calcium conditions (2.5 $mg \cdot L^{-1}$), presumably due to utilization of calcium from shells (Cohen and Weinstein 2001); such conditions are lower than the concentrations measured in our study. Thus, it is possible that quagga gonads developed despite the low calcium levels in our experiment by using shell calcium, indicating their potential for reproduction in Tahoe waters. However, it is also possible that gonadal development carried over from the initial collection in Lake Mead. Given the establishment of quagga mussels in low-calcium Coloradan systems, we suggest further study to link calcium levels to reproductive ability of quagga mussels.

Our study has determined that it is possible for transplanted, viable adult quagga mussels to survive in oligotrophic, low-calcium waters for periods of at least 1-2 months, but that the potential for growth can be variable over time. However, this experiment was carried out in autumn, a population life-cycle phase in which quagga mussels typically are shifting into a post-spawning, non-growth period in order to direct metabolic processes toward development of gonadal structures and the upcoming spring reproductive event (Costa et al. 2008). Given the timing of field collection and subsequent laboratory experimentation (October through December) it is possible we observed a natural seasonal shift in growth rate. Alternatively, it is possible that the individuals collected from Lake Mead had sufficient reserves for survival, and even moderate growth, in any (non-toxic) environment for the 51-day duration of the experiment. The observation that one mussel appeared to have spawned during the experimental period indicates that gonad development and spawning proceeded in the low-calcium conditions, suggesting that this was not a stressful enough environment to halt the reproductive process.

We observed three important points: 1) adult quagga mussels survived 51 d in low-calcium and low-chlorophyll *a* waters, 2) the population showed positive growth during the first 36 d of the experiment, and 3) the population showed potential for reproduction. These three points support the observation that adults mussels can survive in the short-term, display growth, and possibly reproduce, but whether this population can continue to grow and produce a viable set of recruits in the long-term (i.e., >51 d) is uncertain. Thus, it is critical for accurate risk assessment in western waters to determine long-term growth and potential fecundity of adult quagga mussels, and survivability of veliger-stage quagga, in low-calcium conditions.

Our findings on the water quality impacts of quagga indicate that adult quagga mussels could decrease algal biomass and alter nutrient species available within the water column. While most calculations are made from either mixed- or zebra mussel populations rather than quagga mussel populations, there have been similar longer-term findings from Lake Superior, another oligotrophic ecosystem, where mussels remove chlorophyll at a higher rate than they remove total phosphorus (Nicholls and Standke, 1996). This removal-rate yielded a 60 % decrease in the summer chlorophyll:total phosphorus ratio, resulting in less phytoplankton food sources for primary consumers. The decrease in algal biomass is a results of the efficient filter-feeding capacity of dreissenids, using cilia to remove phytoplankton, bacteria, organic debris, microzooplankton, silt, and clay from >1 L of water per individual per day (MacIssac 1996).

Research from mussel populations in large lakes indicates that dreissenids can alter the

balance of nutrients and nutrient remineralization rates. The findings from our short-term study showed a decrease of pelagic algal biomass with a slight increase in soluble reactive phosphorus (SRP) and no change in total phosphorus. Ammonium increased dramatically over 51 days, with a significant increase in ammonium to soluble reactive phosphorus ratio after 48 hours (Figure 4). Johengen et al. (1995) found annual mean values of dissolved inorganic nitrogen (nitrate and ammonium) were greater but also variable during post- than pre-zebra mussel periods. As mussels filter organic material from the water, they release ammonium in their pseudofeces and feces, producing some of the highest nitrogen excretion rates of any animal (Bruesewitz et al., 2006). Zebra mussels also act as a sink for phosphorus in phosphate-limiting environments (Johengen et al., 1995) and only affect water column phosphorus when the phosphorus output of mussels is greater than 20 % of the lake's phosphorus loading (Mellina et al. 1995). Lake Tahoe has already shifted from nitrogen limitation to nitrogen and phosphorus co-limitation during most of the year due to anthropogenic influences (Hackley et al. 2007). Potential greater increases in nitrogen (as ammonium) than phosphorus (as soluble reactive phosphorus; Figure 4) by quagga mussels, if they were to establish in Lake Tahoe, could further shift the lake toward phosphorus-limitation. A disruption in the balance of nutrients, if sustained in the environment, could affect phytoplankton composition (Conroy and Culver 2005) and nutrient limitation in Lake Tahoe.

The replication in our study and duration of the experiment was relatively short to estimate the extent of mussel impacts on nutrient balance, and subsequent effect on the food web. However, given changes to water chemistry and food web dynamics due to both zebra and quagga mussel establishment observed in other lakes and waterways, and our evidence that the possibility exists for at least adult quagga to survive, grow and reproduce in the Lake Tahoe environment, the diligent monitoring of recreation vehicles (the major pathway for transfer of invasive mussels to inland lakes) putting in to western lakes-of-interest is prudent. The assumption that western oligotrophic waterbodies low in calcium are at very low- to low risk of quagga mussel invasion is not necessarily supported.

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Table 1. Water quality conditions (mean±sd) during the experiment. Temperature, dissolved oxygen, and specific conductivity were measured twice daily from each replicate container and pooled. Phosphorus, algal biomass (chlorophyll *a*), and calcium were measured from ambient water prior to addition into mussel containers.

Constituent	n	Reading or Concentration
Temperature (ºC)	707	15.6±2.7
Dissolved oxygen (ppm)	707	6.3±0.7
Specific conductivity (uS)	707	123.8±4.4
Total phosphorus (ppb)	43	21.8±8.8
Soluble reactive phosphorus (ppb)	49	2.0±1.6
Dissolved calcium (ppm)	15	13.5±0.3
Chlorophyll *a* (ppb)	49	2.9±2.0

Table 2. Start-, end-, and mean (sd) weights for 3 time periods (days 0, 36, and 51) for quagga mussels in Lake Tahoe water.

Mussel ID	Initial blotted wet weight (mg) Day 0	Blotted wet weight (mg) Day 36	Final blotted wet weight (mg) Day 51
Keys 5	47.664	60.369	60.647
Keys 6	44.936	58.085	57.621
Keys 7	46.359	44.869	38.058
Keys 8	44.039	61.794	49.420
Keys 3	56.252	62.539	62.310
Keys 1	41.825	51.425	51.783
Keys 2	37.109	45.787	40.533
Mean	45.45	54.98	51.48
(sd)	(5.88)	(7.55)	(9.52)

Table 3. Reproductive status of adult quagga mussel after 51 days of exposure to ambient Lake Tahoe water. See text for explanation of gonad stage and resorption indices.

Replicate number	Sex	Gonad stage	Gonad resorption
Keys 1	F	3-4	2
Keys 2	M	3	0
Keys 3	M	3	0
Keys 5	F	1	3
Keys 6	F	1	3
Keys 7	M	3	2
Keys 8	F	2	2

Table 4. Ecosystems in Colorado (USA) where dreissenids have been detected, their life stage at detection, and associated environmental parameters.

Ecosystem	Dressenid type	Life stage	Calcium ($mg \cdot L^{-1}$)	Chlorophyll *a* ($ug \cdot L^{-1}$)	Total P ($mg \cdot L^{-1}$)	Water quality references
Grand Lake	quagga, zebra	veliger	4.0-9.0	0.8-7.1	0.006-0.032	USGS CWSC
Shadow Mtn Res.	quagga	veliger	3.5-9.5	0.5-25.2	0.009-0.030	Stevens 2003, Crowfoot et al. 1995, USGS CWSC
Willow Creek Res.	quagga	veliger	10.4-19.1	5.6-8.3	0.009-0.012	USGS CWSC
Lake Granby	quagga	veliger	5.5-11.0	1.0-12.8	0.006-0.038	Stevens 2003, Crowfoot et al. 1995, USGS CWSC
Pueblo Res.	quagga, zebra	veliger	23-75	4.5-51.8	0.005-0.097	USGS CWSC
Jumbo Res.	quagga	veliger	26-47	0.5-102	<0.01-0.14	USGS CWSC, unpublished 2008 data
Tarryall Res.	quagga	veliger	N/A	N/A	N/A	N/A
Blue Mesa Res.	quagga	veliger	27.5-37.9	N/A	0.008-0.057	USGS CWSC

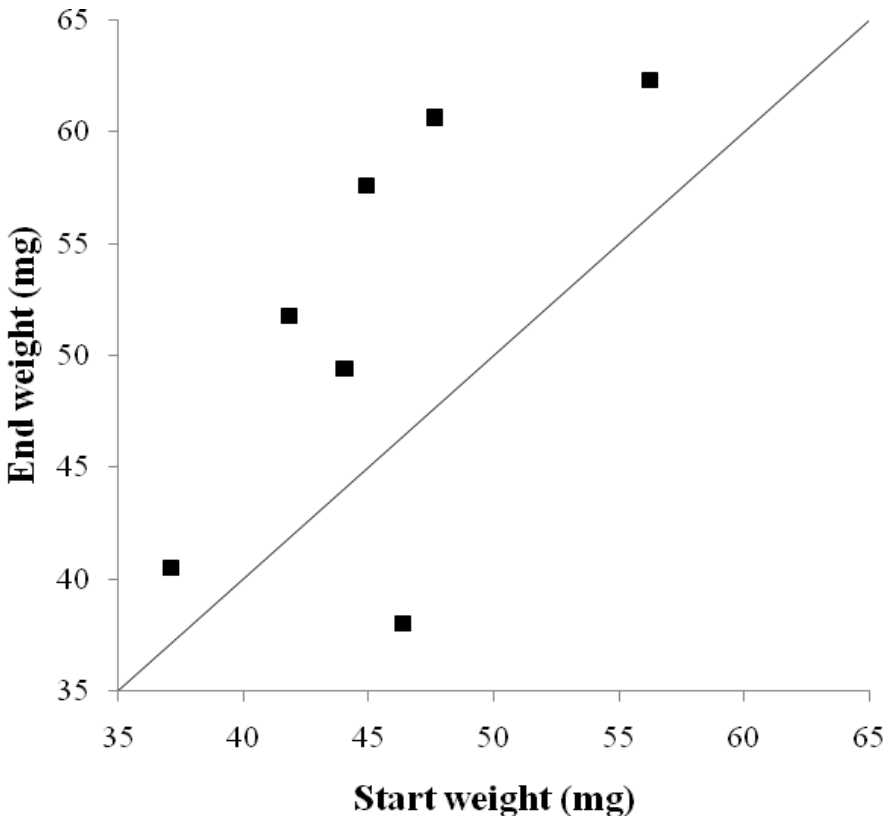


Figure 1. Start- and end (wet) weights of quagga mussels (n=7) for the overall experimental period (days 0-51). The line indicates a 1:1 relationship for reference; points falling above the line indicate positive growth, points below the line indicate negative growth.

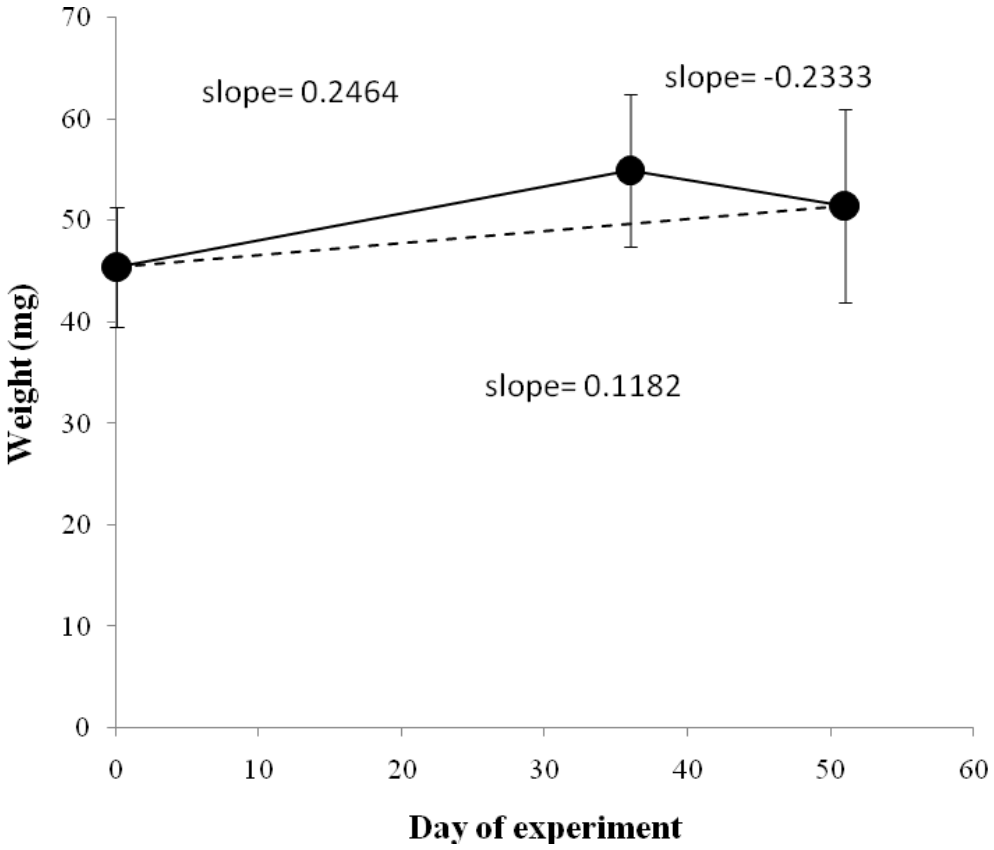


Figure 2. Mean blotted wet weight of quagga mussels at 0, 36, and 51 d. Average growth rates are indicated by the slope of lines between periods; while the overall 51-day growth was positive, growth in the second period, on average, was negative. We assumed linear growth rates for these relatively short time intervals. Error bars are standard deviation.

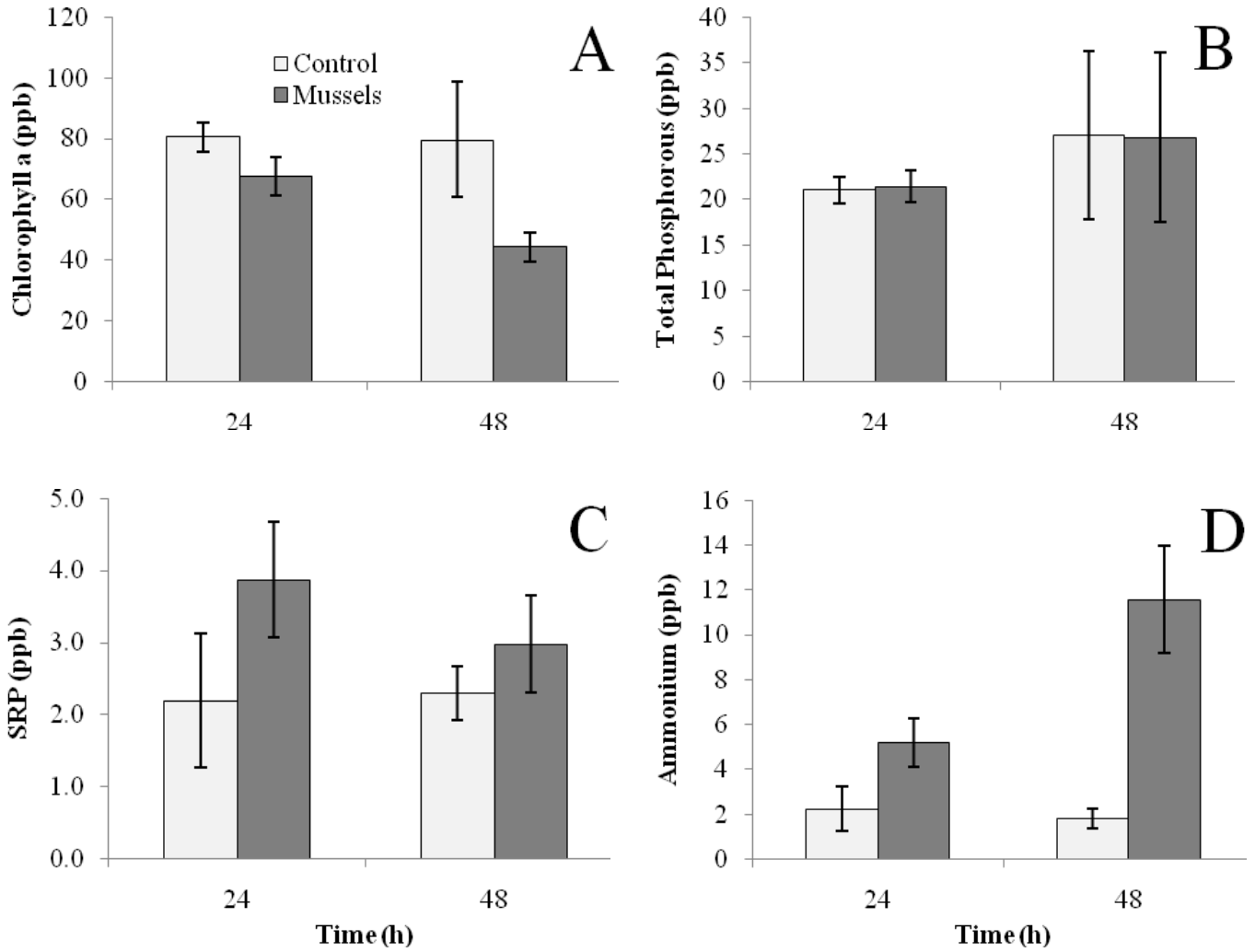


Figure 3. Short-term (24 and 48 h) changes in Lake Tahoe water quality due to adult quagga mussels: A) chlorophyll *a* , B) total phosphorus, C) soluble reactive phosphorus (SPR), and D) ammonium. Each treatment of 15 L of Tahoe water contained an individual mussel (n=7), with control containers (n=7) containing water only. Error bars are standard deviation.

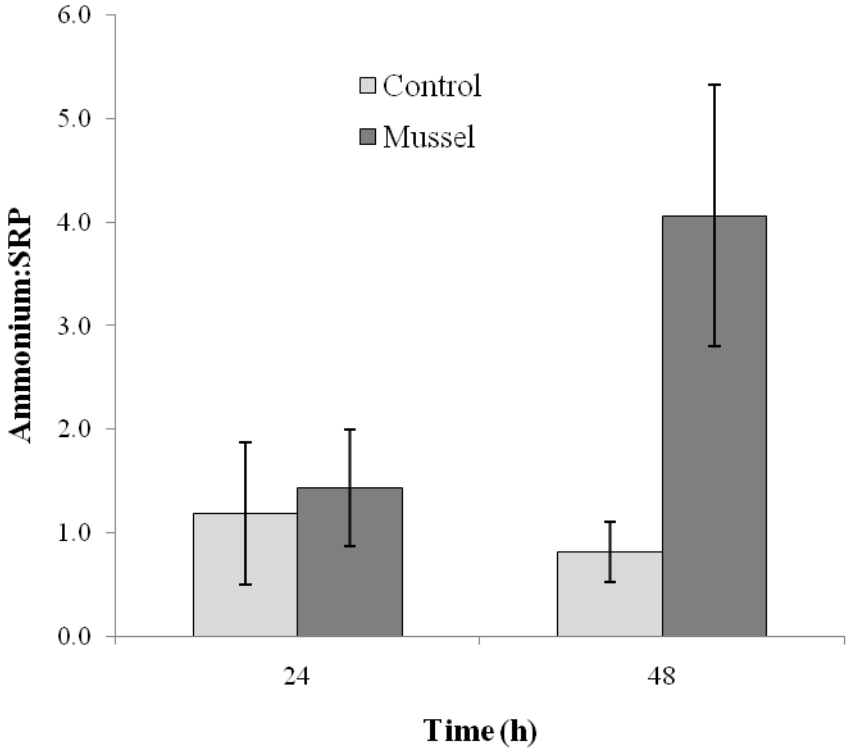
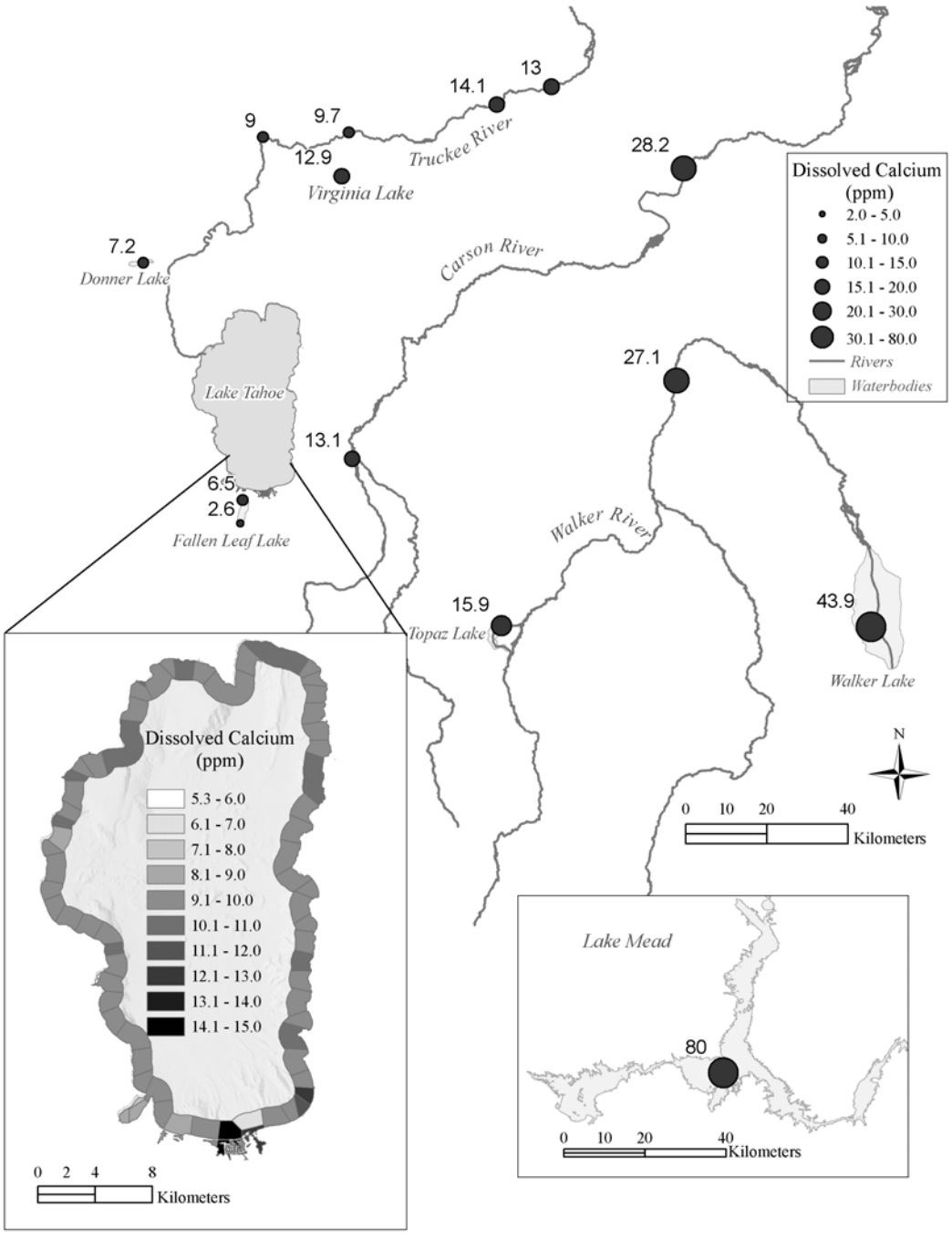


Figure 4. Ammonium:SRP ratios in mussel-treated water and control water after 24 h and 48 h.

Figure 5. Dissolved calcium concentrations from selected Western waterways of the Great Basin and Lower Colorado River ecosystems, as well as finer scale calcium concentrations from Lake Tahoe's nearshore zone.



Will Lake Tahoe's newest invader, the Asian clam, facilitate the invasion of quagga mussel? (Additional Analysis Unfunded)

Introduction

Recent studies indicate an expanding population of a new invasive species, the Asian Clam (*Corbicula fluminea*), in Lake Tahoe's littoral zone (Hackley et al. 2008, Wittmann et al. 2008). Of primary concern to research managers and scientists is the potential for these clams to promote quagga mussel establishment by 1) potentially increasing calcium levels in the bottom sediments in clam patches and 2) providing a hard substrate for growth. Observations from Lake Mead (NV-AZ), where quagga mussels and Asian clams coexist, suggest that mussels grow on dead and live Asian clams (Chandra and Wittmann, unpublished data). Moreover, in Lake Constance clams have been shown to act as ecosystem engineers, with dead clams shells providing substrate and live clams releasing pseudo feces and feces; therefore modifying the benthic environment and nutrients concentrations (Werner and Rothaupt 2007). The objective of this study was to conduct a pilot experiment to determine 1) the survival and growth rate of quagga mussel with Asian clams and 2) if there are elevated levels of calcium concentrations in Lake Tahoe's Asian clam beds.

Methods.

Methods were the same as those employed in the ambient water survival experiment (see above). However, in this pilot experiment, 1 grab sample of sediments from Marla Bay containing Asian clams (1000 to 3619 m^{-2}) was added to each 19 liter container. Grab samples were obtained using a Petite Ponar. Tahoe Keys water in each container was replaced daily. Pore water in two clam beds (Timber Cove and Ski Run Marina), pore water from outside the beds, and surface water was collected, filtered using 0.45 micron membrane filters, and analyzed as described in the ambient water survival experiment.

Results

After 51 days of incubation and water changes, quagga survival was 86% for the clam treatment, similar to the ambient water treatment. In contrast to the ambient Tahoe water survival experiment, individuals in the Asian clam treatment showed negative growth initially and maintained growth towards the end of the experiment (Figure 6). The individuals had slope values less than 1 for each time period as well as the combined entire experimental period. Period 1 showed a slope that was close to, but less than 1 ($b_1 = 0.951$, $p<0.001$). Period 2 also showed a slope that was less than one, but slightly higher than that for period 1 ($b_1 = 0.962$, $p<0.001$). Both periods combined showed an overall negative "growth rate" ($b_1 = 0.979$, $p<0.001$). Pore water in the Asian clam beds of Tahoe showed elevated calcium levels as compared with surface water and pore water in non-clam beds (Figure 7).

Discussion

While the quagga mussels exposed to Asian clams survived until the end of the experiment, there was a negative impact to quagga mussel growth rate in the presence of clams and their sediments. We believe this is likely due to an experimental effect where the amount of food supplied daily was not enough to support both the mussels and the

clams. Clam densities varied between the replicates and previous research combined with chlorophyll a data (not presented) suggests algal biomass was cleared every day in the experiment, resulting in food-limited conditions.

Elevated calcium concentrations in Asian clam beds in Lake Tahoe suggest the potential for clams to modify the benthic environment. Whether this modification will increase the potential for successful quagga mussel establishment is unclear since the ambient Tahoe water experiment suggests survival, growth, and possible reproduction at lower calcium concentrations than in the sediments. This data suggests that quagga mussels could survive and grow if they were not competing with Asian clams for resources. Although background calcium concentrations were elevated in clam beds, calcium levels in these beds are still with in the low survival range of a model that predicts dreissenid survival (Whittier et al. 2008). Thus, it is unclear how much Asian clam presence could potentially contribute to the probability of quagga establishment. Future experiments should be conducted to determine quagga mussel growth with a range of finer-scale calcium levels and enough food for maximum growth potential. If possible, different aspects of quagga mussel life history should also be analyzed such as adult survival, gamete production and quality, and veliger survival.

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Figure 6. Plots of start weight (wet) and end weight of the Asian clam and mussel treatment for three time periods: a) time period 1 (days 0 to 36), b) time period 2 (days 36 to 51), and c) overall (days 0 to 51). Lines in each panel indicate the 1:1 relationship for reference.

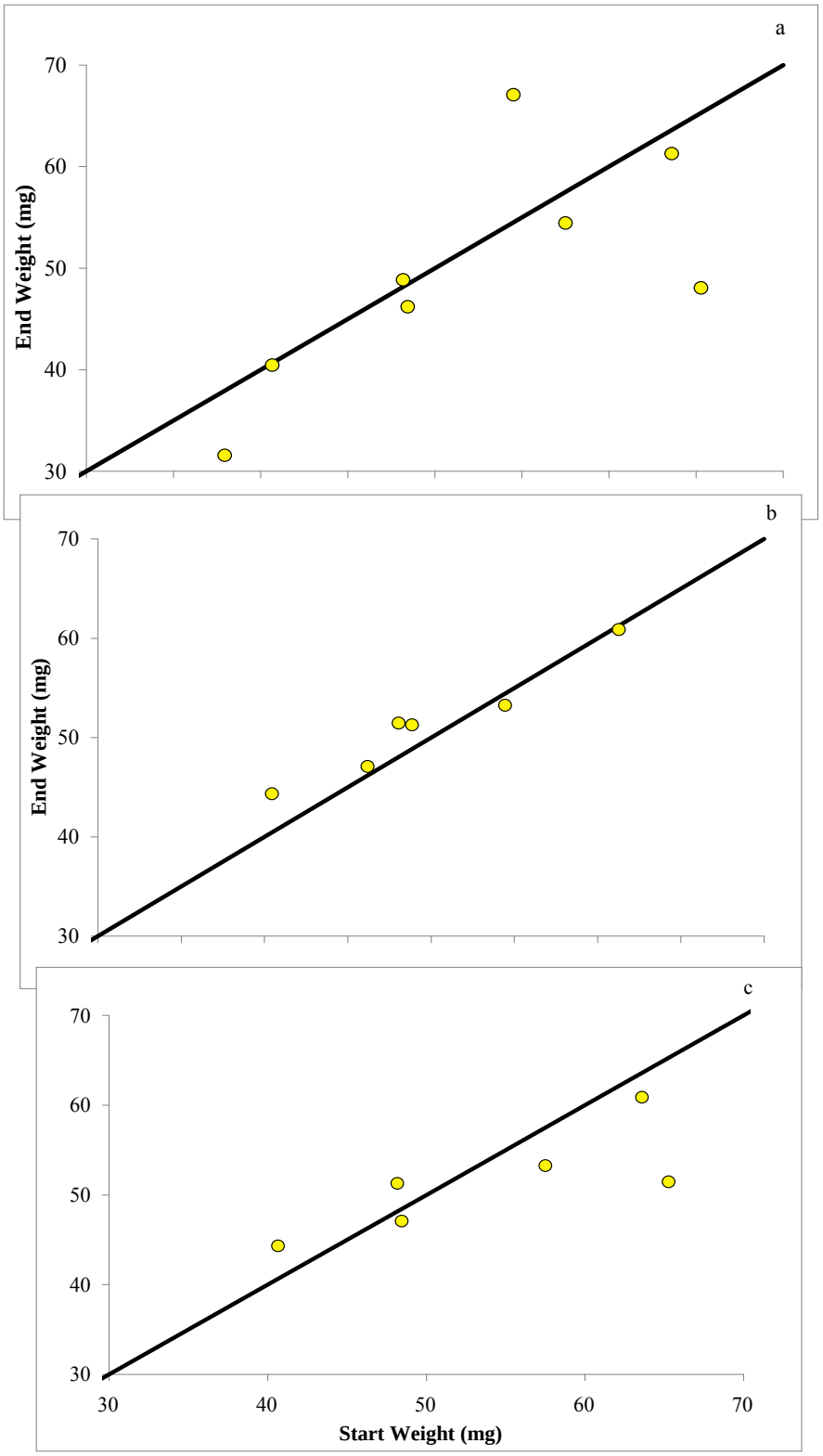
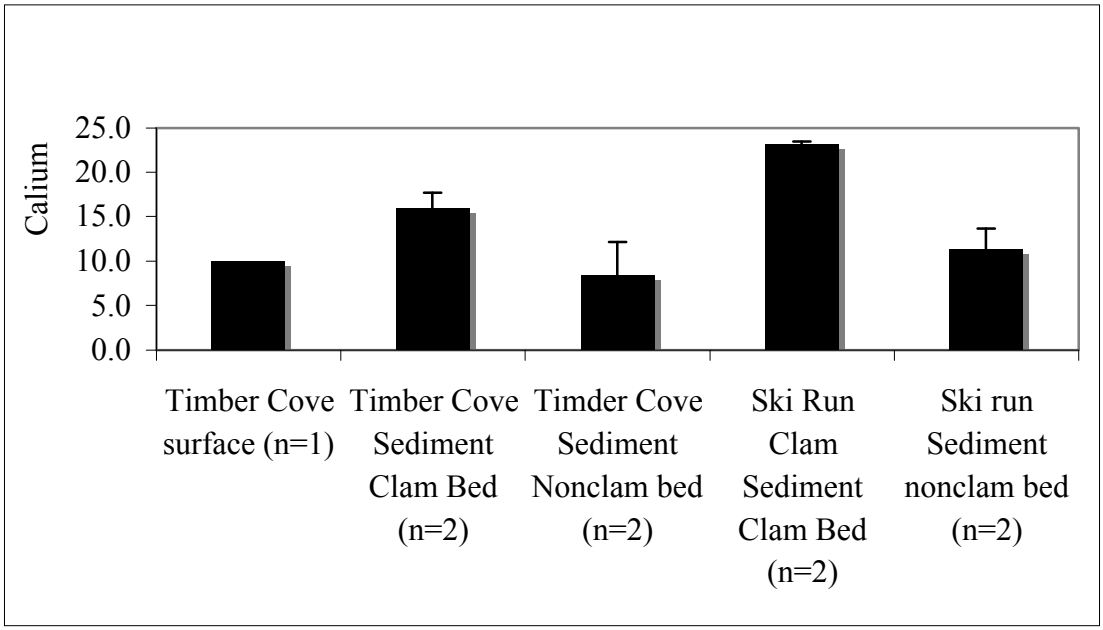


Figure 7. Calcium measured within sediment porewaters of clam beds, in sediment porewaters away from beds, and in the water column above the beds at two locations.



Appendix 1

Table 1. Dissolved calcium concentrations (ppm) from Lake Tahoe and other Western waterways in 2008.

Table 1. Calcium levels from Lake Tahoe and other Western waterways in 2008.

Ecosystem	Location	GPS (NAD27) Latitude	Longitude	Dissolved calcium concentrations (ppm) May	November	Mean±stdev
Lake Tahoe	Cave Rock boat launch	39.04362	119.94831	11.1	9.9	10.5±0.4
	Eldorado Marina boat launch	38.94526	119.97667	9.9	9.6	9.8±0.1
	Tahoe Keys marina	38.93560	120.00168	12.1	12.7	12.4±0.2
	Camp Richardson marina	38.93922	120.03839	10.0	9.8	9.946±0.1
	Zephyr Cove marina	39.00736	119.94844	9.7	9.6	9.7±0.0
	Sand Harbor boat launch	39.20066	119.92962	9.8	9.7	9.8±0.1
	Skyland subdivision (1 mi. south of Cave Rock)	39.03092	119.94879	9.7	9.9	9.8±0.1
	Dreyfus property	39.01843	119.95267	10.0	9.7	9.8±0.1
	Mouth of McFall creek	38.99384	119.95387	10.2	9.8	10.0±0.1
	Nevada beach	38.98233	119.95497	10.0	9.8	9.9±0.1
	Edgewood creek mouth	38.96853	119.94928	9.8	9.9	9.9±0.0
	Lakeside marina	38.95894	119.95044	12.5	11.8	12.1±0.2
	Timber Cove	38.94987	119.96647	8.5	9.9	9.2±0.5
	Trout Creek/Upper Truckee mouth	38.94316	120.00370	4.6	8.5	6.6±1.4
	Tahoe Keys Homeowner's Lagoon (West Channel)	38.93597	120.01341	12.7	16.6	14.7±1.4
	Cascade properties	38.95021	120.07551	9.1	9.6	9.4±0.2
	Eagle Point	38.96561	120.07780	9.1	9.0	9.0±0.1
	Emerald Bay (Viking's home pier)	38.95322	120.10528	8.5	8.4	8.4±0.0
	Emerald Bay (West shore)	38.95339	120.08966	8.3	8.4	8.3±0.0
	Emerald Bay (East shore boat camp)	38.95976	120.09434	7.5	8.5	8.0±0.3
	Emerald bay (north end)	38.96856	120.08591	9.6	9.7	9.6±0.0
	Emerald Bay (south of Bliss State Park campground)	38.98271	120.09197	9.5	9.8	9.7±0.1
	Rubicon Point	38.99934	120.09474	9.4	9.9	9.7±0.2
	South Rubicon Bay	39.00886	120.11077	9.5	9.2	9.4±0.1
	North Rubicon Bay	39.02286	120.11740	9.3	10.0	9.7±0.2
	Meek's Bay Vista	39.03510	120.11578	9.7	9.9	9.8±0.1
	Sugar Pine Point (Ehrman Mansion)	39.04665	120.11021	9.5	9.9	9.7±0.1
	General Creek mouth	39.05566	120.11159	10.3	9.8	10.1±0.2
	Sugar Pine Point	39.06151	120.11199	9.5	9.8	9.7±0.1
	Tahoma	39.06865	120.12632	9.6	10.0	9.8±0.1
	McKinney Creek mouth	39.07421	120.13965	9.8	9.9	9.8±0.0
	Kings Beach boat dock,	39.23530	120.02319	9.5	10.3	9.9±0.3
	North Tahoe marina	39.23739	120.04163	10.6	10.9	10.8±0.1
	Tahoe Vista recreational area boating facility	39.23882	120.04735	10.1	dry	-
	Sierra Boatworks Marina	39.22609	120.08013	10.3	10.4	10.4±0.0
	Lake Forest boat launch	39.18072	120.11868	9.5	10.1	9.8±0.2
	Tahoe City Marina	39.17194	120.13628	9.8	9.2	9.5±0.2
	Sunnyside Marina	39.13913	120.15185	10.4	9.9	10.1±0.2
	Obexer's Marina	39.08232	120.15641	9.7	10.0	9.8±0.1
	Meek's Bay Marina	39.03706	120.12151	1.1	9.5	5.3±2.9

	Madden Creek	39.09252	120.16075	9.3	9.1	9.2±0.1
	Blackwood Creek mouth	39.10647	120.15681	8.6	9.9	9.3±0.5
	Kaspian Beach	39.12323	120.16019	9.3	10.0	9.6±0.2
	Ward Creek mouth	39.12851	120.15465	7.9	9.7	8.8±0.6
	North of Sunnyside	39.14421	120.14874	9.6	10.1	9.9±0.2
	Tahoe Pines area	39.15576	120.14002	9.6	10.0	9.8±0.1
	Tahoe dam	39.16740	120.13923	10.5	9.9	10.2±0.2
	Dollar Point Homeowner's pier	39.18351	120.10397	10.6	9.9	10.3±0.2
	Chinquapin and Dollar Properties	39.19048	120.09360	10.4	10.1	10.2±0.1
	North of Dollar Properties, south of Watson Creek	39.20692	120.09049	9.4	9.8	9.6±0.1
	Northeast of Watson Creek	39.22074	120.08444	9.3	10.1	9.7±0.3
	Flick Point (Carneliean Bay)	39.22733	120.06823	9.3	9.9	9.6±0.2
	Tonopalo	39.23819	120.05347	9.5	10.1	9.8±0.2
	Cal Neva Beach	39.22202	120.00607	9.3	9.8	9.6±0.2
	Yont's house	39.23568	119.99918	9.4	9.9	9.7±0.2
	Western Crystal Bay Marina	39.24849	119.98291	10.2	10.0	10.1±0.1
	Birdseeder Beach	39.24329	119.96494	11.1	10.0	10.6±0.4
	Incline Creek and ramp	39.23831	119.94548	10.4	10.1	10.2±0.1
	Incline near Pinecone Circle	39.23074	119.93249	9.6	10.2	9.9±0.2
	Tunnel Creek mouth	39.22081	119.92802	9.4	10.0	9.7±0.2
	Memorial Point	39.21039	119.92964	9.6	10.0	9.8±0.1
	South of South Sand Harbor	39.18751	119.92733	9.2	10.2	9.7±0.3
	Beach at Thunderbird Lodge	39.17572	119.92787	9.3	10.2	9.7±0.3
	Chimney Beach	39.16500	119.93312	9.8	10.3	10.1±0.2
	Nude Beach	39.14820	119.93328	9.8	10.3	10.0±0.1
	Skunk Harbor (north)	39.13780	119.94531	9.5	10.2	9.9±0.2
	Skunk Harbor (south)	39.12552	119.95292	9.7	10.0	9.8±0.1
	Osprey nests	39.11028	119.95762	9.6	10.0	9.8±0.1
	North of Slaughterhouse Creek	39.10028	119.95097	9.3	10.3	9.8±0.4
	Glenbrook Creek	39.08799	119.94069	9.2	10.2	9.7±0.3
	Ledbetter's house	39.07720	119.94703	9.3	9.9	9.6±0.2
	Logan Schoals Marina	39.07120	119.94246	8.8	10.2	9.5±0.5
	North of Cave Rock	39.05245	119.94559	9.1	10.1	9.6±0.4
	Ski Run Marina	38.95104	119.95838	9.4	13.0	11.2±1.3
	Elk Point Marina	38.59043	119.57334	-	10.0	-
	Mean Lake Tahoe			9.5	10.0	9.8±0.3
Tahoe other	Stormwater runoff from 3 locations			11.8, 15.2, 16.6	dry location	14.5±2.5
	Timber cove porewater outside of Asian clam beds			-	5.7, 11.0	8.4±3.7
	Timber cover porewater inside of Asian clam beds			-	14.7, 17.2	16.0±1.8
	Timber Cove surface water above Asian clam beds			-	10.0	-
	Ski Run Marina porewater outside of Asian clam beds			-	9.6, 13.0	11.3±2.4
	Ski Run Marina porewater inside of Asian clam beds			26.1	22.8, 23.4	24.1±1.8
	Ski Run Marina surface water above Asian clam beds			9.1, 9.4	-	9.3±0.2
Fallen Leaf Lake	Taylor creek inflow	38.94182	120.05774	6.5	9.8	8.1±1.2
	Fallen Leaf Lake marina	38.87961	120.06486	2.6	3.0	2.8±0.1

Donner Lake	Publc boat launch ramp	39.19487	120.16948	7.2	6.5	6.9±0.5
Truckee River	Verdi bridge in Nevada	39.52424	119.99264	9.0	10.4	9.7±1.0
	Downtown Reno, Nevada bridge on Center St.	39.52720	119.80695	9.7	12.1	10.9±1.7
	Tracy Bridge in Nevada	39.56475	119.48582	14.1	16.9	15.5±1.9
	Painted Rock bridge in Nevada	39.59113	119.36633	13.0	17.2	15.1±3.0
Lahontan Res.	Boat launch	39.44507	119.08820	28.2	-	-
Virginia Lake	Urban lake in Reno, Nevada	-	-	-	13.0	-
Topaz Lake	Boat launch	38.69308	119.51890	15.9	-	-
Carson River	Genoa, Nevada	38.98153	119.83151	13.1	-	-
Walker Lake	Boat launch	-	-	44.0	-	-
Walker River	Mason Valley fish hatchery bridge	39.09119	119.12436	27.1	-	-
Lake Mead	US Bureau of Reclamation	-	-	80.0	-	-

Figure 1. Very early developing female gonad. Arrow points to developing gonad.

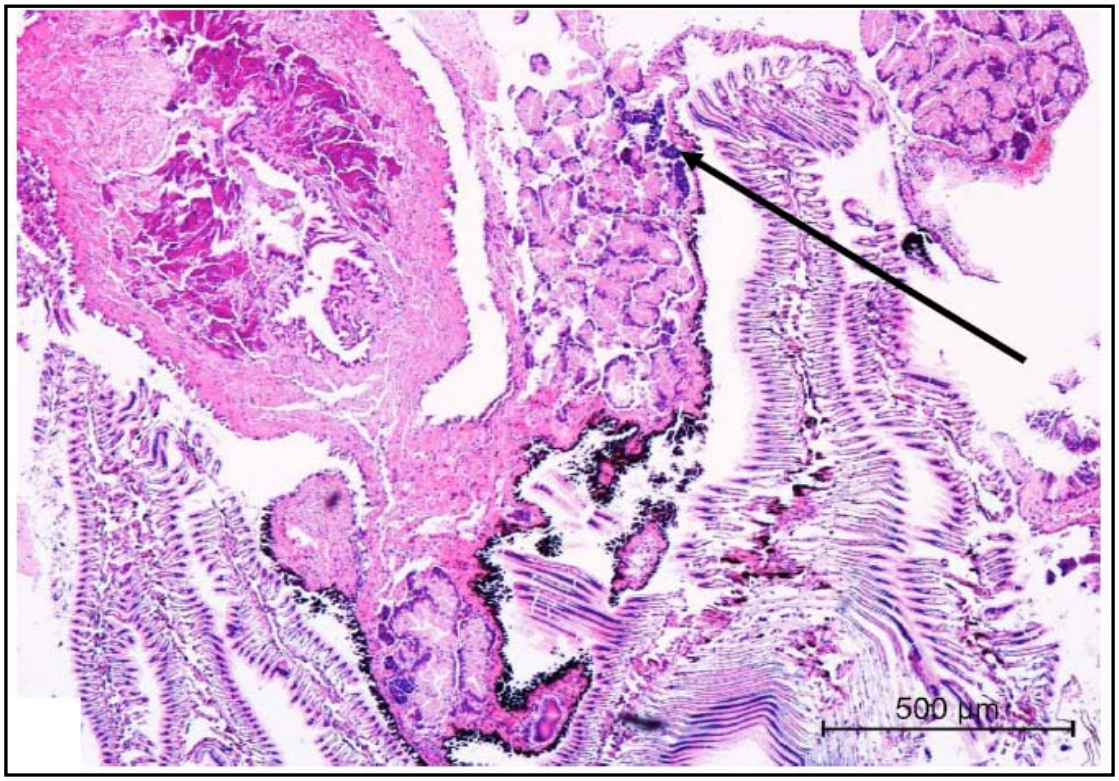


Figure 2. High magnification of small gonad follicle.

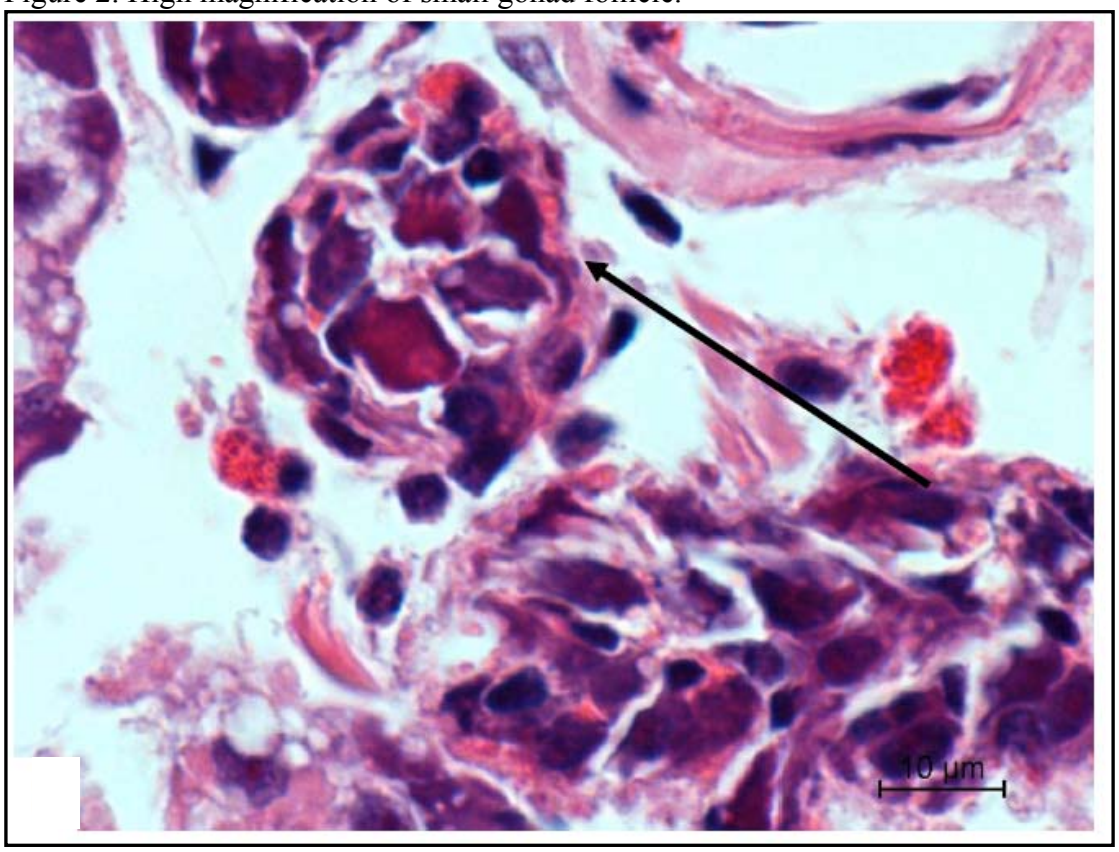


Figure 3. Female developing gonad with moderate resorption. Go = Gonad, DG = Digestive gland.

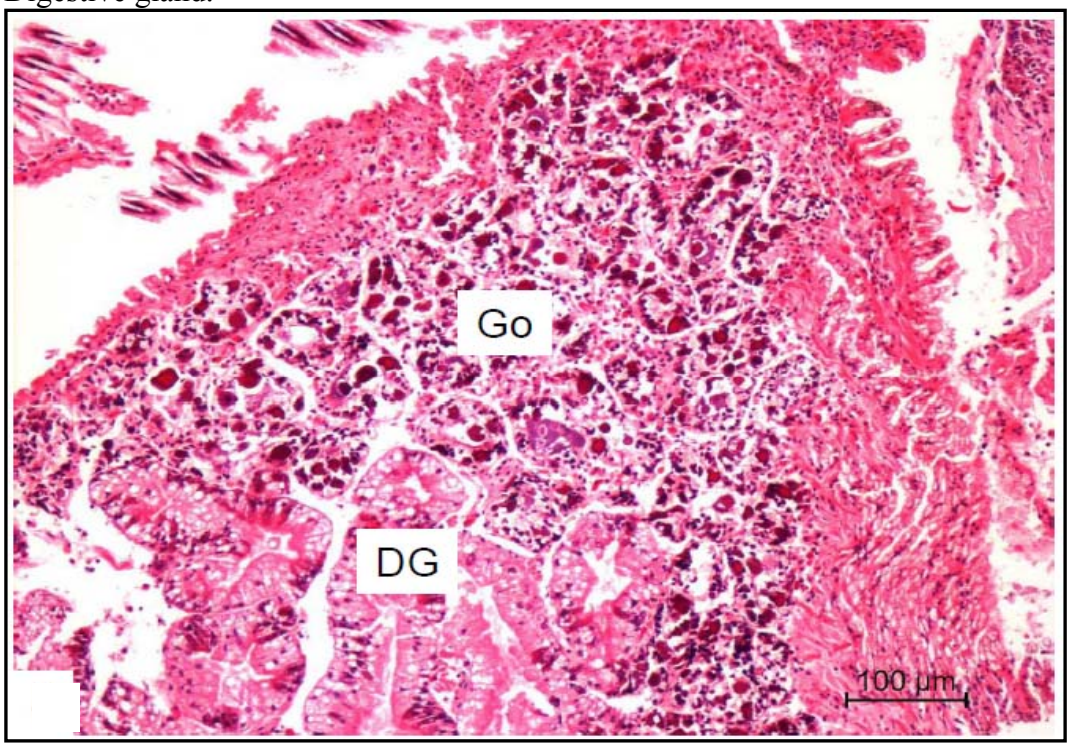


Figure 4. High magnification of gonad in Figure 3. Arrows point to different stages of oocytes.

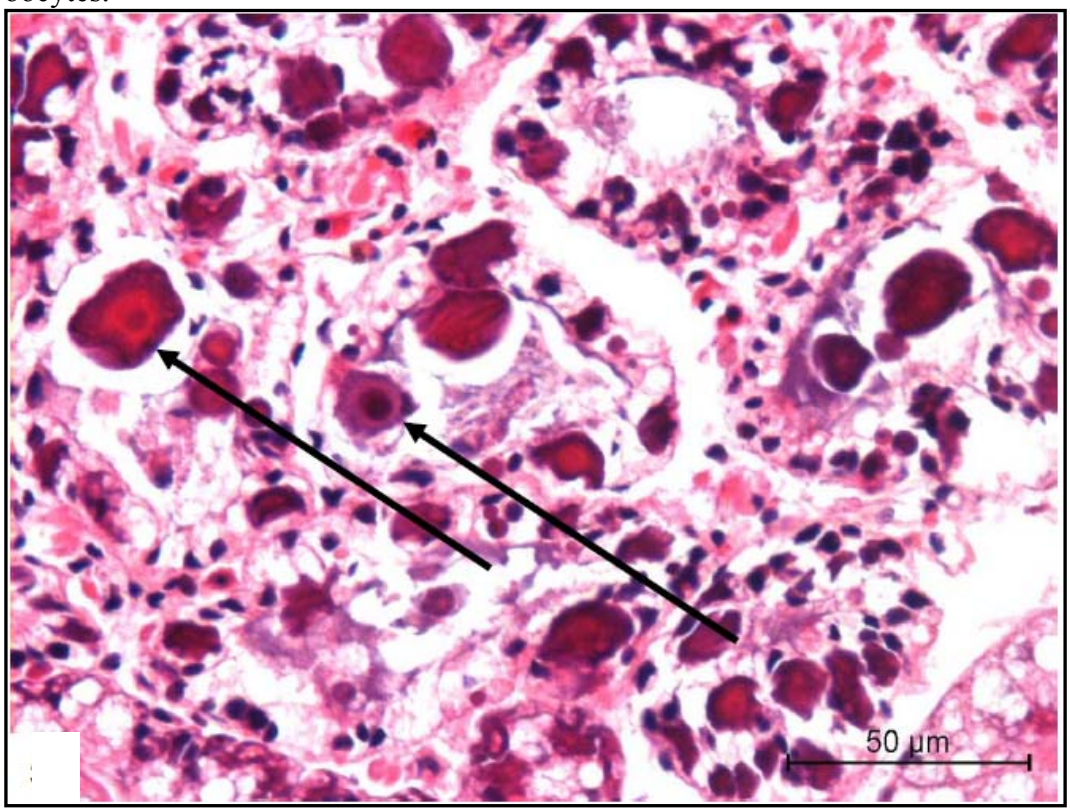


Figure 5. Mature male gonad with no resorption. Arrow points to portion of gonad. * = posterior adductor muscle.

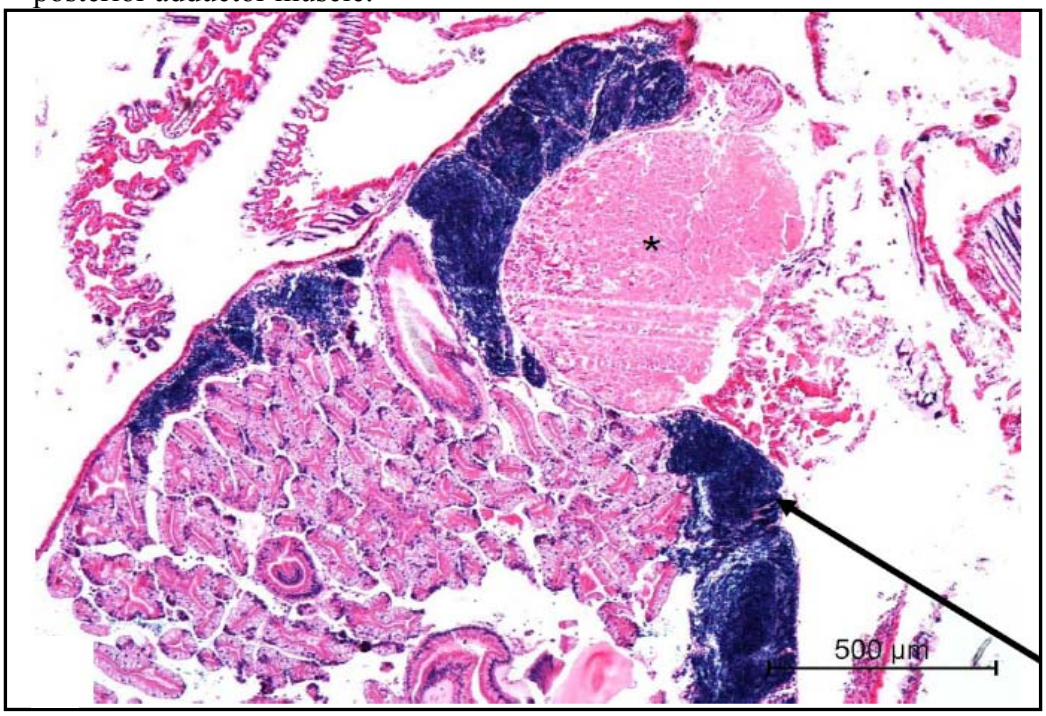


Figure 6. Mature male gonad with no resorption. Hemocytes are interspersed with mature or nearly mature sperm.

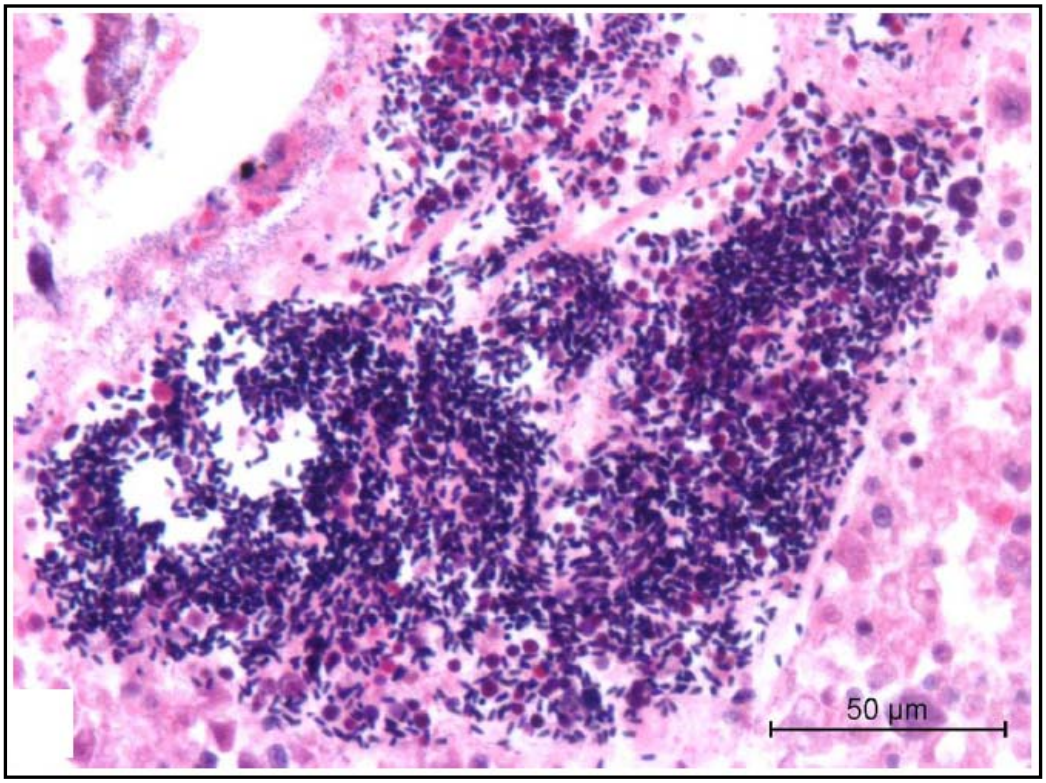


Figure 7. Putative partially spawned female with immature remaining eggs and moderate resorption.

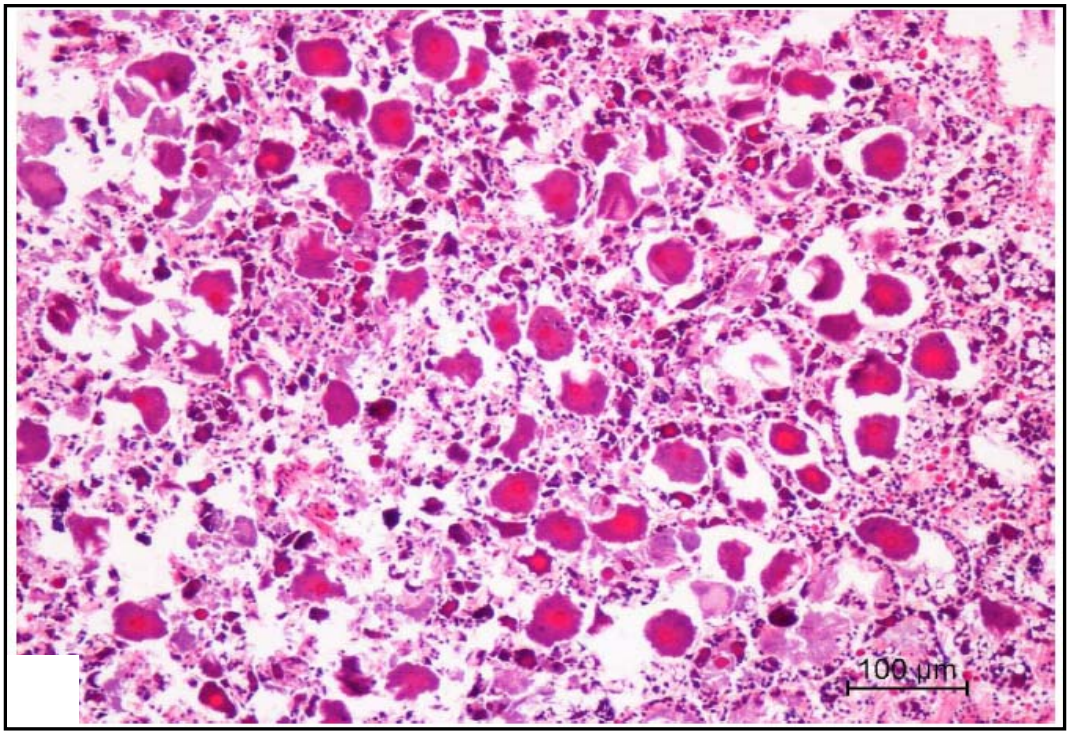


Figure 8. Mostly spawned female. Long arrow points to residual oocytes; short arrow indicates empty follicle.