THE IMPACT OF SUMMER MORTALITY OF INVASIVE ZEBRA MUSSELS ON NUTRIENT CYCLING IN A TEXAS RESERVOIR

by

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ABSTRACT

Large mortality events can cause nutrient pulses that affect nutrient cycling within a system and ecosystem functioning. Invasive zebra mussels (*Dreissena polymorpha*) in Canyon Lake, Texas occur at the southern edge of their North American distribution and hot temperatures during summer can lead to high mortality. The goal of this study was to examine nutrient release in decaying mussels in the laboratory and to combine this with field observations of zebra mussel density and mortality to estimate the amount of nutrients released during summer mortality events. Zebra mussels were collected from Canyon Lake and decayed at 30°C in lab to determine mass loss and nutrient release rates. Dive surveys along several transects in July and October 2019 and 2020 were used to estimate population size of zebra mussels at different depths throughout the lake. Cages with smaller (<15mm) and larger (> 15mm) zebra mussels were placed at three marinas and monitored bimonthly to determine mortality rates. The decline of zebra mussels in summer 2019 was larger compared to 2020, which was associated with a longer period of high water temperatures (27 vs. 17 days over 30°C respectively). Mortality in the cages varied with mussel size, depth and location. Temperature was likely the most important driver, but other factors such as total suspended solids and dissolved oxygen also played a role. Nitrogen and carbon were lost more quickly from the decaying tissue than phosphorus. Estimated nutrient releases for the lake with low to high summer mortality over a month ranged between 1.2 and 47t for nitrogen and 0.04 to 14t of phosphorus. This would mean zebra mussel mortality could release nitrogen into

Canyon Lake by 52 to 2, 000% and phosphorus by 6 to 240% compared to inputs from the Guadalupe River. The potential impacts on ecosystem processes remain to be studied.

I. INTRODUCTION

Zebra mussels (*Dreissena polymorpha*) originate from Western Asia/Eastern Europe and are prolific freshwater bivalves that were first found in 1988 in the North American Great Lakes (Benson 2013). Within 3 years of establishment, they were found throughout the Great Lakes region. From this region they subsequently and quickly spread to the Mississippi, Arkansas, Cumberland, Illinois, Missouri, Ohio and Tennessee river basins (Benson 2013). Beyond these connected waterways, invasion of zebra mussels from one unconnected water body to another has been facilitated by transfer of both planktonic larva in ballast water and adult individuals attached to boats (Bossenbroek et al. 2001, Johnson et al. 2006, Bossenbroek et al. 2007, Strayer 2009, Kelly et al. 2013, Robertson et al. 2020).

Once introduced, zebra mussels cause a variety of ecological and economic problems. Zebra mussels are known to be a virulent bio-fouler and have caused damage to industry, recreation and drink water infrastructure (Bobat et al. 2004, Connelly 2007 et al., Strayer 2009). Between 1993 and 1999, the economic impact of zebra mussels was estimated to have totaled more than $5 billion (De Leon 2008), and in 2013 annual economic costs across eastern North America were estimated at $100 million (Benson 2013). Furthermore, zebra mussels act as ecosystem engineers by altering the environments they invade (Karatayev 2002 (add to references), Sousa 2009). Their efficient filter feeding can cause declines in phytoplankton (Raikow 2004 et al., Caraco et al. 2006) which results in increased water clarity (Caraco et al. 1997, Strayer 2009). This increase in water clarity increases benthic photosynthesis and alters submerged macrophyte densities and composition (Chambers et al. 1984, Vanderploeg et al. 2002,

Zhu et al. 2006). In addition, zebra mussel beds often increase benthic macroinvertebrate densities (Stewart et al. 1998, Ricciardi et al. 1997, Vanderploeg et al. 2002, Mortl and Rothhaupt 2003). These alterations to invaded ecosystems can result in "benthification," a shift of energy production from the pelagic zone to the benthic region (Vanderploeg et al. 2002). Finally, studies have shown zebra mussels can affect nutrient cycling in aquatic systems, leading to large scale changes in ecosystem processes (Arnott et al. 1996, Li et al. 2021).

Nutrient cycling through animals can increase primary productivity, recycle nutrients within habitats, and translocate nutrients across habitats (Arnott and Vanni 1996, Vanni 2002, Vanni et al. 2006). Animals can also be a source of nutrient pulses, which can have significant impacts on nutrient cycling (Polis et al. 1997, Yang et al. 2008, Hsieh et al. 2012). For example, the massive mortality event following salmon spawning can introduce large quantities of nutrients directly into the surrounding environment (Gende et al. 2002), spread nutrients significant distances through connected water ways (Cak et al. 2008), and even influence a system for months or years later (Verspoor et al. 2011). While mass mortality of salmon after their spawning is a regular annual event, mass mortality of native unionid mussels only occurs during drought or periods of high water temperatures (Dubose et al. 2019, Mitchell et al. 2019) In the short-term such mortality events increase ammonium and phosphorus (soluble reactive phosphorus (SRP)) and the shells of dead mussels could have significant impacts on long term nutrient release (Dubose et al. 2019). Mass mortality events of invasive mussels, e.g., *Corbicula fluminea*, can also increase nutrients in a system (McDowell et al. 2016), and represent a new source of pulsed nutrient input into an ecosystem, which has the

potential to alter nutrient cycling withing a system.

Zebra mussels in Texas are at the southern edge of their distribution range and were first reported in Canyon Lake, TX in 2017. Zebra mussels can experience high mortality during summer in this southern range which has been linked to extended periods of high summer temperatures (White et al. 2015). A large mortality event was observed in Canyon Lake in late summer 2018, indicated by a considerable decline in mussel densities observed by both dive surveys throughout the lake and mortality on artificial substrate installed at the JBSA Marina to monitor cumulative settlement rates (Robertson and Schwalb 2019). The goal of this study was to examine how much nutrient was release from summer mortality of zebra mussels in Canyon Lake. To accomplish this goal we 1) estimated zebra mussel densities and size distribution in Canyon Lake; 2) quantified summer mortality with *in situ* cage experiments; 3) examined with lab experiments how much carbon, nitrogen, and phosphorous was released from zebra mussel mortality and whether nutrient release rates and ratios varied with mussel size; 4) and estimated the amount of nutrients released in Canyon Lake from summer mortality of zebra mussel based on findings from objectives 1-3; and examined how estimates changed with different population sizes and mortality rates. Specifically, I wanted to test the following hypotheses and predictions (Table 1):

1a) Water temperatures are higher closer to the surface. As higher temperatures are expected to cause higher mortality, densities of zebra mussels in shallower water should be lower.

1b) Summer mortality reduces the number of zebra mussels, however spring and fall spawning results in large number of offspring, resulting in a high proportion of

smaller mussels (<15mm) in the lake.

2a) Large mussels (>15mm) have thicker shells and are expected to be more resistant to thermal stress, therefore should have lower mortality rates compared to smaller mussels.

2b) Environmental conditions at different marinas in Canyon Lake based on previous observations were presumed to be similar, thus mortality rates should not differ significantly between marinas.

3) Zebra mussel soft tissue sequesters nutrients equally across size classes (Arnott and Vanni 1996), therefore nutrient release of decaying mussels should be proportional to their body size resulting in higher release rates (nutrient/individual/day) from larger mussels compared to smaller mussels.

II. METHODS

Canyon Lake and Cage Locations: Canyon Lake is a reservoir in the Texas Hill country fed by the Guadalupe River with a surface area of ~33 km^2 and a volume of ~0.471 km^3. Canyon Lake is a monomictic lake, stratifying in the summer months and mixing between late fall and early spring. Cages for the *in situ* mortality experiments were placed at the JBSA, Canyon Lake, and Crane's Mill marinas (Fig. 1). JBSA and Canyon Lake marinas are situated in relatively deep parts of the north shore (compared to Crane's Mill). JBSA is the smallest marina and is closest to the dam, Canyon Lake Marina is the largest marina and is the second closest to the dam, and Crane's Mill Marina is the furthest away. Crane's Mill Marina is situated on the south shore of Canyon Lake and is much closer than the other two marinas to the river/lake interface. All three marinas have boat slips for long-term storage of boats and are heavily trafficked during the summer.

Environmental Data: All environmental data was collected from the mortality cage locations (Fig. 1). Onset pendant temperature loggers were attached to cages at 1 and 9 m depths, and recorded temperatures every two hours from June 16th to October 11th. Monthly (twice in September, with the second sample taken during additional field work related to surveys of dive site locations) water samples were collected in 1000 mL opaque sampling bottles and were kept on ice or in a fridge and filtered within 72 hours of collection. Samples were taken at cage locations (1 and 9 m) over the course of the summer and tested for both chlorophyll-*a* (chl-*a*) and total suspended solids (TSS). Crane's Mill and Canyon 9 m locations were not sampled in July. Chl-*a* was calculated by measuring the relative fluorescence units (RFU) using a Trilogy Fluorometer model

7200-000, then converting RFU into chl-*a* concentration using a predetermined regression relationship between the two methods (Robertson and Schwalb 2019).

To calculate TSS, water was filtered through pre-weighed glass microfiber filters until the filter noticeably changed color. The filter was then placed in an oven and heated to 101°C for one hour. Filters were allowed to cool to room temperature then were measured again for a final weight value. TSS was then calculated using initial weight of the filter, final weight after filtration and drying and total volume of water filtered (Standard Methods for the Examination of Water and Wastewater 1998).

Marina profiles were taken at all three marinas during each sampling event with a YSI model ProDDS, where temperature, dissolved oxygen (mg/L and % saturation), specific conductance and pH were measured every meter from 1 to 9 m.

Field Survey Methods: To estimate population densities and size frequency distributions (Objective 1), scuba surveys were conducted in July and October of 2019 and 2020 at 8 established transect sites that ranged from 0.5 to 14.7 rkm from the dam at Canyon Lake (Fig. 1). The transects were located perpendicular to the Canyon Lake shore line along a depth gradient, where three replicate quadrats (0.25 x 0.25 m) were placed every 3 m until a depth of 20 m was reached or no zebra mussels were found. Mussels were counted in each quadrat. A subsample of 50 mussels were collected to determine the size distribution at each depth at all sites in July 2020, and at three sites (close to the dam, middle of lake and closer to the lake/river interface) in October 2020. Mussels collected for size frequency distribution estimates were measured from the anterior to the posterior end to the nearest tenth of a millimeter with vernier calipers. Mussels were grouped in two size classes, smaller (<15 mm) and larger (>15 mm)

mussels and the proportion of each size class was computed for each sampling depth and location. To determine total nutrient release from summer mortality of zebra mussels, a total population value was calculated by taking the highest and lowest average site densities from July 2020 and multiplying them by the total surface area of Canyon Lake to get high and low population values. The high and low population values were then averaged to get an average population value for Canyon Lake. This average was multiplied by the average shell distribution frequency of the entire lake (Small: 70.7%; Large: 29.3%) to determine the total number of small and large individuals. Zebra mussel population estimates were then used in scenario modeling below to estimate total nutrient release from summer mortality.

To determine mortality rates of zebra mussels in Canyon Lake (Objective 2), cages were suspended in the water column at two depths (1 and 9 m) and at each of 3 sites (JBSA, Canyon Lake and Crane's Mill marinas in Canyon Lake, TX). Preliminary cage experiments were run from September to October 2019 and April to May 2020. Summer mortality of zebra mussels was determined from cage experiments that ran from June to October 2020. Zebra mussels were removed by hand from marina substrates within arm's reach at the JBSA marina. Mussels were sorted into larger and smaller size classes and placed inside mesh bags (9 x 6.5 x 5 cm). Two bags containing smaller zebra mussels (5-15 mm) and two containing larger mussels (15-25 mm) were then placed inside conical mesh cages (40 cm long, 10 cm diameter, 1 cm wide holes). These cages were monitored every 2 weeks during the 2019 and June to October 2020 periods, however cages were only monitored once a month during the April to May 2020 period due to COVID-19 complications. At each sampling event, dead zebra mussels were

counted and removed from cages.

Laboratory Methods: Decay experiments (Objective 3) followed methods similar to those describe by Pray et al. (2009). Live zebra mussels were collected from the JBSA marina in Canyon Lake, TX, and transported back to the lab and placed in the incubator on the same day as collection. Lake water filtered through 70 µm mesh was collected and transported on the same day as mussel collection to serve as the medium in which to conduct experiments. Mussels were separated into 2 size classes (5 to 15 mm and 15 to 25 mm shell lengths), and 5 replicates were used for each size class. Beakers consisted of five individuals (n = 25 for each size class) and 275 mL of filtered lake water. Beakers were sealed with parafilm and placed in an incubator at 30° C with no light exposure. Treatments were pulled from the incubator at 1, 2, 4, and 8 days, and shells were removed after vigorous shaking to dislodge any particulate matter stuck to the shell. The beaker was then homogenized with a stir bar and plate, after which the water in the beakers was filtered through pre-weighed, ashed glass microfiber filters (47 mm diameter, 1-µm nominal pore size Pall A/E filters) to catch remaining mussel tissue. The captured tissue was dried at 60°C for 24 h to determine dry mass and then analyzed for C, N and P content. P content of captured mussel tissue was measured with a particulate phosphorus analysis involving an HCl digestion and an ascorbic acid/molybdenum blue spectrophotometric method modified from Vanni Lab methods written by Annie Bowling, 3 August, 2009. Spectrophotometry was performed in a Varian UV-Visible Spectrophotometer.C and N content of captured mussel tissue was analyzed using a FlashEA 1112 Series NC Soil Analyzer. Mass loss rates of zebra mussels during decay experiments were estimated from plots of the natural log-transformed % initial dry mass

remaining as a function of time (days). Initial dry mass of each size class of zebra mussel was determined from additional sets of zebra mussels (n = 5 for each size class).

Total nutrient release from summer mortality (Objective 4) was estimated with the estimated total number of zebra mussels in the lake (see above, Objective 1), the nutrient release rates of N and P (Objective 3, for both smaller and larger mussels) and three different mortality scenarios (high, moderate and low) across three different population sizes (high, average and low). The highest mortality rate (88% over 16 days), was based on mortality observed in cages with larger mussels at 9 m depth at Crane's Mill, the low mortality rate (8% over 16 days) had been observed JBSA, and an in intermediate was value was assumed as 48% mortality (i.e., moderate mortality)

Data Analysis: Cage mortality data, mass loss data and nutrient ratio data were tested for normality and homogeneity of variances with a Shapiro-Wilks test and a Bartlett test respectively. If data was not normally distributed, it was log-transformed to improve normality. All tested data met the assumption of homogeneity of variances.

To determine what factors had significant impacts on mortality, a linear mixed effects model was run with survival as the dependent variable, time (days), size class (larger vs. smaller), depth (1 m vs. 9 m), and the number of degree days over 30°C as fixed factors and location (marina) as a random factor. Temperature data at the 9 m location at the Crane's Mill marina was lost as water infiltrated the logger and corroded the electronics. Temperature regimes between Canyon Lake and Crane's Mill marinas were similar, with an average difference of 0.29 ± 0.22°C so temperature for Crane's Mill 9 m was substituted with Canyon Lake 9 m temperature data. In addition, a repeated measures analysis of variance was run with temperature as the dependent variable and

depth as the independent variable to determine if temperature regimes differed between depths.

To assess potential differences in decomposition of the size classes in the laboratory experiments, percent initial dry mass remaining of both size classes was plotted as a function of time (d) and an exponential decay model was fitted to the data to produce a decay constant (k) (Prey et al. 2009) for both size classes. To determine whether mass loss rates differed between size classes, percent initial dry mass remaining was ln-transformed and compared with a repeated measures ANCOVA. Percent dry mass remaining was the dependent variable, size was the independent (categorical) variable and time was the covariate.

Changes of C:N ratios over time were analyzed with ordinary least squares regression, and an exponential decay model was fitted to C:P and N:P ratios. Rates of change in nutrient ratios of the 2 size classes (slopes of the regressions) were compared over the course of the experiment with ANCOVA. Ratio data was the dependent variable, size was the independent (categorical) variable, and time was the covariate).

Changes in mass and nutrient content of both size classes were used to calculate release rates (mg/d) of C, N, and P as:

$$RR\ (mg/d) = [(DM_0 * Nut_0) - (DM_f * Nut_f)]/d$$

where DM is the dry mass (mg) of items on the first (DM_0) and last (DM_f) days of the experiment and Nut is the proportional nutrient content (C, N, or P µg/mg dry mass) on the same days. Initial dry mass concentrations for nutrient release calculations were derived from previously derived shell-mass relationships (Robertson and Schwalb, 2019).

Total Nutrient Release from Summer Mortality: Different mortality scenarios were used: low, medium and high. The highest mortality in this study was found at 9 m at Crane's Mill, where 87.5% of large mussels died within 16 days (between sampling events). Lowest mortality was found 1m JBSA, where 7.5% of large mussels died over the same time period (16 days). Percent mortality was multiplied by the estimated population size in the lake (for both smaller and larger mussels, see above) and then multiplied by the nutrient release per individual mussel from laboratory decay experiments to determine the amount of nutrient (metric tons) released by mortality of each size class. Nutrient release from zebra mussel mortality was then compared to nutrient loading from the Guadalupe River. Average monthly values of nitrogen and phosphorus from river inputs were calculated using flow data from USGS gage 08167500 and water quality data from a 2018 TCEQ report on Canyon Lake. Average daily flow of the Guadalupe was taken from USGS gage 08167500 and multiplied by total P values reported by TCEQ to calculate average daily P inputs from the Guadalupe River, while the same flow data was multiplied by the combined values for ammonia and nitrate nitrogen from the same TCEQ report to calculate average daily nitrogen inputs. These daily values of P and N were then multiplied by 16 to arrive at the values used in the nutrient release scenarios (objective 4).

III. RESULTS

Environmental Data: Across the entire experiment, temperature at 1 and 9 m differed on average by 0.6 to 1.0 degrees (range 0.1 to 5.6°C). These differences were statistically significant (ANOVA: $F_{1,700} = 33.85$, $p < 0.001$). There were also difference in the number of degree days over 30 ranging between 17 (JBSA) and 40 (Canyon) at 1 m, and 0 (JBSA) to 4 (Canyon) at 9 m. In addition, the number of degree days over 30°C were nearly double in 2019 (27 days) compared to 2020 (17 days), but the number of degree days over 25°C (95 vs. 94 in 2019 and 2020 respectively) and 28°C (75 vs. 79 in 2019 and 2020 respectively) were similar in both years.

Crane's Mill 9 m had higher TSS values compared to all other sites, with an average of 9.1 ± 4.5 (mean ± SD) mg/L, whereas all other sites ranged between 2.0 ± 1.7 mg/L and 4.0 ± 2.0 mg TSS/L (Table A1). Chl-*a* concentrations from the same water samples taken showed little variation across all sites, including Cranes Mill 9 m, ranging on average from 0.9 ± 0.3 to 1.7 ± 1.3 µg/L (Table A2).

In 2020, average DO values at all cage sites were similar except at 9 m depth at Crane's Mill (Table A3), where average DO was considerably lower (5.8 ± 1.4 mg/L, minimum: 3.5 mg/L) compared to the other locations (range throughout summer: 7.3 ± 0.4 mg/L and 7.9 ± 0.3 mg/L, minimum 6.1-6.8 mg/L). In the Sep-Oct 2019 cage experiment, average DO values at all cage sites were similar except at 9m depth at Crane's Mill, where average DO was slightly lower (6.4 ± 0.8 mg/L, minimum: 5.80 mg/L) compared to other locations (range: 7.89 ± 0.69 and 7.53 ± 0.37 mg/L, minimum: 6.97 mg/L).

Objective 1 - Zebra mussel population estimates and size distributions: In July 2019, higher mussel densities were found closer to the dam and in deeper water, whereas higher densities were also found further away from the dam in both July and October 2020 (Fig 2.). In July 2019, average mussel densities across all depths ranged from 47 ± 22.47 (mean ± SE) to 1208 ± 279 ind/m^2, with average densities > 1,000 ind/m^2 occurring at 9, 15 and 18 m depths. Mussel densities in July 2020 were generally higher compared to July 2019; for example, densities of > 1,000 ind/m^2 were found at twice as many sampling points (at 6 m depth and deeper) when compared to July 2019. The spatial distribution of zebra mussels also changed between years: mussel densities were lower closer to the dam and in deeper water in 2020 (when compared to July 2019) and densities were greater in shallower depths and farther upstream from the dam (Fig. 2).

Summer mortality occurred in 2019 and 2020 but was more intensive and widespread in 2019 (Fig. 3) and the spatial distribution of mortality patterns in the lake differed between years. Between July and October 2019 mussel densities overall declined considerably, declining on average by -47 to -967 ind/m^2 (range: -35% to -100%) at depths ≥ 9 m (Fig. 3), whereas densities increased on average at 3 and 6 m depths (+ 82 and 199 ind/m^2 (+ 27 and 74 %) respectively) with most increases observed at sites farther upstream (> 5.1rkm from the dam). In contrast, mussel densities did not decline at most depths between July and October 2020. Declines occurred at 3, 6 and 12 m depths (-360, -299, -533 ind/m^2; -38, -24, -29% respectively), however densities increased at 9, 15, 18 and 20 m (84, 254, 774, 280 ind/m^2; + 5, 27, 105, 3% respectively). The larger decline in summer 2019 compared to 2020 was associated with a longer period of extremely high temperatures (27 days > 30°C in 2019; 17 in 2020).

Size frequency distributions taken from both 2020 sampling events showed the Canyon Lake population was composed of predominately smaller (<15 mm) sized individuals (Figs 3 and 4). As predicted (Table 1), overall, smaller zebra mussels comprised a larger proportion of the population. Across both sampling events, the average proportion of individuals <15 mm ranged from 65 ± 23% (mean ± SD) to 80 ± 19%. In July 2020, there was a higher proportion of larger individuals at some locations (BR 1: 3, 6, 9 m; Jacob's Creek: 3 m; BR 7: 3 m), and only at a few sites in October 2020 (BR 1: 3 m, Jacob's Creek: 3 m).

Objective 2 - Mortality: Similar to the dive surveys, higher zebra mussel mortality was detected during preliminary cage experiments in September to October 2019 (at 9 m depth) compared to the same time interval (42 days) in 2020 at two of the three marinas (declines in survival at JBSA: -92.5 ± 7.5 % in 2019 vs. -36.5 ± 6 % in 2020, and Canyon Lake: -50.0 ± 8 % in 2019 vs. -31.2 ± 17 % in 2020). At Crane's Mill survival declined quickly in both years (-92.5 ± 3 % decline 2019, 67.2 ± 25 % decline 2020).

In contrast, survival in spring (April to May 2020, 49 days) did not decline as quickly (-10% or less) in 20 out of 24 cages across all marinas (5 and 9 m depths). Highest declines were detected in three cages at JBSA 9m, where survival declined by -17.5 ± 10 to -25 ± 7% over 49 days.

For data collected in summer 2020, all tested variables (time, number of degree days over 30°C, size, and depth) had a significant effect on mortality (Table 5). At 1 m depth, survival decreased by -3.8% (Canyon) to -11.9% (Canyon and Crane) in the first 2 weeks, with similar decreases recorded at 9 m depth (-5% (Canyon) to -12.5% (JBSA)). The decline in survival accelerated at 1m depth after water temperature reached 30°C

(after 26 days (Canyon) to 27 days (Crane's Mill and JBSA). Although water temperature did not reach 30°C until later in the summer (75 days (Canyon)) at 9 m depth, survival declined most rapidly at 9 m at Crane's Mill. Large mussels declined -88% within the first sampling period (16 days) and smaller mussels declined -20 ± 15% per week. All larger mussels were dead by day 74 after deployment of cages and smaller mussels by day 54. The average decline at 9 m depth at Crane's Mill was (-4.6 ± 0.07 %/week vs -5.3 ± 0 %/week, at 1m depth). In contrast, at two of the three marinas, mussel survival declined faster at 1 m compared to 9 m depth, which was most pronounced between day 32 and 89, when survival declined by an average of -16.3 ± 3 (JBSA) to -21.3 ± 8% (Canyon) at 1m and -11.7 ± 3 (JBSA) to -20.0 ± 4% (Canyon) at 9m.

The average survival at the end of the experiment (October 11th, 2020) was low, but slightly higher for smaller mussels (11 ± 10 (mean ± SD) to 21 ± 18%) compared to larger mussels (3.0 ± 3.0 to 6.0 ± 5.0%). Higher survival of smaller mussels compared to larger mussels occurred at 4 out of 6 sampling points (JBSA: 1, 9m; Canyon: 9m; Crane's Mill: 1m) (Fig 5).

Objective 3 - Decay and Nutrient Release: Both size classes lost the majority (~65%) of soft tissue mass within the first 48 hours of the experiment. Multiple functions were fit to the relationships between time and % initial mass remaining (e.g., linear, quadratic, exponential) to see which function best described the data (exponential) (Fig. 6). Mass loss rates (based on % decline) did not differ significantly between size classes (small: k = -0.32, large: k = -0.28; ANCOVA: F = 0.047, p = 0.8345). The majority (~65%) of mass was lost within the first 48 hours for both larger and smaller mussels. Over the 8 days of decay, smaller mussels lost on average 4.4 ± 1.3mg of soft tissue per

individual and large mussels lost 12.1 ± 5.9mg of soft tissue per individual. Mass loss across multiple preliminary experiments was consistent with results presented here and decay constants ranged between -0.23 and -0.32.

Molar ratios relating to phosphorus (C:P, N:P) decreased over the course of the experiment, while molar C:N ratios first decreased slightly day 0 to day 1 and increased afterwards (Fig. 7). Thus, both N and C were lost at a faster rate from decomposing mussel soft tissue when compared to P. There were no significant differences detected in the rate of change of any nutrient ratio between the two size classes of mussel. (ANCOVA: $F_{1,7} = 0.131$, $p = 0.73$ (C:N), $F_{1,7} = 3.335$, $p > 0.11$ (C:P), $F_{1,7} = 1.804$, $p > 0.22$ (N:P)). In addition, the average P release rate calculated for both size classes showed similar rates of P release (Large: 2.53 ± 3.51 µgP/mussel/day, Small: 2.10 ± 0.90 µgP/mussel/day). Calculated P release rates of large mussels varied by orders of magnitude (39.55 to 0.21 µgP/mussel/day), with one of the five calculated rates suggesting P was sequestered by mussel tissue (net uptake of (-4.75 µgP/mussel/day). This large variation in large mussel P release rates (and net uptake value) likely resulted in the average release rate for large mussels being lower, and thus similar to the release rates of small mussels. Unlike P, N and C were found to be released faster from large zebra mussels when compared to small individuals (Large: 0.16 ± 0.11 mgN/mussel/day, 0.57 ± 0.46 mgC/mussl/day; Small: 0.07 ± 0.03 mgN/mussel/day, 0.26 ± 13 mgC/mussel/day).

Objective 4 - Summer Nutrient Release: Carbon release from summer mortality of zebra mussels (over 16 days) ranged from 5.4 to 240 t (metric tons) across all mortality scenarios (Table 3). Nitrogen release ranged from 1.2 to 47 t (52 to 2,000% increase

compared to river inputs) and was higher than river inputs in eight out of nine mortality scenarios (Low Population Low Mortality Scenario: 1.2 t; River Loading: 2.3 t) (Table 3). Phosphorus release ranged from 0.04 to 14 t (6 to 240% increase compared to river inputs) but was higher than river inputs in only three scenarios (High Population High Mortality: 14 t; Average Population High Mortality: 0.92 t; High Population Intermediate Mortality: 0.78 t; River Inputs: 0.58 t). Eight of nine mortality scenarios predicted that nitrogen released by decaying zebra over 16 days would be higher compared to nitrogen loading from the Guadalupe River into Canyon Lake over the same time span, with even low mortality in the average population value resulting in an increase of 120% compared to river inputs (Table 3).

IV. DISCUSSION

This study supported previous findings that zebra mussel summer mortality is correlated with higher water temperatures (White et al. 2015); however, the thermal limit was higher in Canyon Lake when compared to reports from more temperate lakes (Griebeler and Seitz 2007, Feng et al 2020), but similar to reports from other Texas lakes (Morse 2009, Locklin et al. 2020), where mussels occur at the southern edge of their distribution. Such mortality can cause considerable releases of nutrients while mussels die in large numbers and decay.

Although water temperature was linked to summer mortality of zebra mussel populations, the thermal threshold for populations may also depend on local adaptation. A study of zebra mussel mortality in Gull Lake, Michigan showed a relationship between zebra mussel mortality and the number of degree hours above 25°C (White et al. 2015). In contrast I found that the higher mortality in 2019 (detected in both the dive surveys and cage experiments) compared to 2020 was associated with a roughly double the number of days over 30°C in 2019. In 2020, when days over 30°C occurred less often compared to 2019 (17 vs 27 respectively), zebra mussel mortality was more restricted to shallower locations and sites near the river/lake interface, where water temperatures tended to be slightly higher than in the deeper parts of the lake. Similarly, the absence of days over 30°C at 9 m depth was associated with lower mortality at that depth especially between days 25 and 80) at two of the three marinas, when average daily temperatures often exceeded 30°C. Although actual temperature differences between 1 and 9 m depth were small (0.6 ± 0.5 to 1.1 ± 1°C), the differences in degree days over 30°C likely contributed to the higher mortality, as even small differences at high temperatures may be

relevant for zebra mussel mortality.

Apart from temperature, there are other factors that may potentially increase mortality. For example, mortality was higher at 9 m depth at Crane's Mill, which was associated with high values of total suspended solids (TSS) and lower DO, whereas chlorophyll-*a* showed little variation between sites. Studies have shown low levels of dissolved oxygen (DO) can result in mortality of zebra mussels (Karatayev et al. 1998, Garton et al. 2014, Robertson and Schwalb 2019) and larger values of total suspended solids (TSS) can have negative effects on zebra mussels, provided those higher TSS values do not represent higher concentrations of food particles (Madon et al. 1998, Allen et al. 1999, Chakraborti et al. 2002).

Summer mortality of zebra mussels may result in a nutrient pulse of nitrogen, phosphorus, or both, as large amounts of both nutrients can be released over a relatively short time span (16 days in our scenarios). Nitrogen release from summer mortality exceeded river inputs in eight out of nine scenarios, and even released half as much as river inputs in the lowest possible population and mortality estimates. If this nitrogen is released in the form of ammonia, summer mortality of zebra mussels could be especially relevant for juvenile unionid mussels, as even low levels of ammonia are known to be toxic (Newton et al. 2003: 93–165 µg, Cherry et al. 2005: 0.11-0.62 mg/L, Wang et al. 2007: 7.8-10.0 mg/L). Phosphorus release from summer mortality was predicted to exceed river inputs in only three scenarios: High Population High Mortality, High Population Intermediate Mortality, and Average Population High Mortality). While these scenarios estimated P release that exceeded river inputs, these values are unrealistic as high population and mortality values were not seen throughout Canyon Lake. Average

and low population values with intermediate mortality however, were predicted to release phosphorus equal to 38 and 86% of river inputs respectively, which may or may not affect primary productivity in the lake, as Lake productivity and algal growth is usually phosphorus limited (Holdren 2001, Kalf 2002, Wagner 2010).

It should be noted that all estimates from this study have a wide range of possible values due to the uncertainty connected with the estimated population size. As the population size was simply based on the total lake surface area, the estimated population size may be an underestimate of the actual population size, however zebra mussels were not found in parts deeper then 24 (July 2019 survey only, not used in any calculations presented here) meters and need hard substrate to settle, which could also lead to an overestimate of the populations size.

The estimated increase in phosphorus due to intermediate summer mortality in average and low population sizes in this study (38 and 86%) is similar to those found in other studies. For example, a mortality event of ~100 million Corbicula in Broad River in Georgia was estimated to increase phosphorus by 50% (McDowell et al. 2017) and mesocosm experiments with induced unionid mortality found a 38% increase in phosphorus (Dubose et al 2019). Extensive modeling in the Laurentian Great Lakes predicted zebra mussel soft tissue released roughly 0.5-1.0 µgP/L (Li et al. 2021), and intermediate mortality in average and low populations from this study predicted similar increases in water column P concentrations (0.5-1.0 µgP/L). Phosphorus release from the same scenarios as above fell within the range of P fluxes from zebra mussel excretion plus degradation of egesta found in the Great Lakes (Li et al. 2021: 0.05 to 9 $mg/m^2/day$; This study: 0.4 to 0.9 $mg/m^2/day$), but fell short of other rates found in the Mississippi

River (James et al. 2000: 3 mg/m^2/day) and laboratory experiments (James et al. 2001: 0.5-2 mg/L).

Despite the similarities to some studies, summer mortality of zebra mussels in Canyon Lake is less substantial when compared to mass mortality events of larger organisms, such as salmon spawning and mortality of bison and caribou during migrations. Studies performed on salmon spawning have reported increases of dissolved ammonium by 30-350% and SRP by 14-130% (Cak et al 2008), and inputs of 180 t of N and 24 t of P into systems (Gende et al. 2002). This study found increases in nitrogen and phosphorus similar to the lower range of increases from salmon spawning. Estimates of historic mass drownings during bison and caribou migrations have been calculated to total up to 50% of a river's annual P load, and introduce thousands of tons of C, N and P into aquatic systems across the ranges of these animals (Wenger et al. 2019). While zebra mussel mortality in Canyon Lake released fewer overall amounts of nutrients compared to larger native organisms, nutrient release from zebra mussel mortality represents a "new" source of inputs for systems such as Canyon Lake. In addition, the timing of these mortality events (both time of year (summer) and rate of release (can be quick, 16 days in scenarios) can potentially influence large scale ecosystem processes.

Provided P limitation exerts the strongest influence on system dynamics in Canyon Lake, the relatively small amount of P released by zebra mussel mortality may not have immediately noticeable impacts. However, when considered alongside other impacts of zebra mussels, mortality events may help accelerate the changes zebra mussels cause. For example, the small but relatively short-term P release by zebra mussel summer mortality may influence primary productivity, as higher levels of nutrient input have been

shown to increase primary productivity (Polis et al. 1997, Lurling et al 2018, Ferriera et al. 2020). This potential increase in primary productivity combined with the zebra mussels' selective consumption of phytoplankton (Caraco et al 2006, Fishman et al. 2010) could result in summer phytoplankton blooms dominated by grazing resistant and potentially toxic species.

In addition to the changes brought on by the zebra mussel invasion, climate change will modify the ecosystem as well, potentially altering the dynamics of zebra mussel mortality observed in this study. While mortality naturally occurs in any system, the "new" mortality from the invasive zebra mussel population will likely worsen as climate change progresses. Warming global temperatures will cause water temperatures to rise (Poff et al. 2002), resulting in more days during the summer where water temperatures reach or exceed 30°C. If the number of degree days > 30°C is an important factor for zebra mussel mortality in this region, as suggested by this study, an increase in the frequency of degree days > 30°C will likely increase both the frequency and magnitude of the mortality events, resulting in larger nutrient releases occurring more often and potentially a higher risk of toxic algal blooms.

Future studies will need to examine to what degree the warming climate will affect frequency and magnitude of mortality events to determine a trajectory for future nutrient release from zebra mussel mortality. Additional studies should also examine shell decomposition, as scenarios in this study estimate billions of dead individuals in one summer and research has shown nutrient release from shell decomposition can be a significant source of long-term (5-30 years) phosphorus release (Dubose et al 2019, Wenger et al. 2019). Finally, mortality events in bivalve populations have been show to

release significant amounts of ammonium (McDowell et al. 2016, Dubose et al. 2019), which is highly toxic to juvenile unionid mussels. All but one scenario from this study predicted large amounts of nitrogen would be released by zebra mussel mortality, and future studies should utilize laboratory or mesocosm experiments to determine how much nitrogen is released in the form of ammonium.

Table 1: Objectives, predictions and corresponding methods proposed to be used in my study.

Objective	**Hypothesis**	**Predictions**	**Method**
1. Estimate zebra mussel densities and population structure (size distribution) in Canyon Lake	1a) Water temperatures are higher closer to the surface and higher temperatures cause higher mortality 1b) Summer mortality reduces zebra mussels and spring and fall spawning results in large number of offspring, resulting in a high proportion of smaller mussels (<15mm)	1a) Populations in shallower water will have lower densities and 1b) smaller mussels (<15mm) will dominate the size distribution	Lake wide surveys and determinatio n of size distribution
2. Quantify summer mortality in Canyon Lake cages and how it varies with size and location	2a) Large mussels have thicker shells and so should be more resistant to thermal stress. 2b) Conditions at different marinas will not differ drastically (personal observations)	2a) Mortality will be higher in larger mussels compared to smaller mussels, 2b) but will not differ across locations	Monitoring of mortality of distinct size classes placed in cages at 1 and 9 m depth at 3 marinas in Canyon Lake
3. Determine release of nutrients from soft tissue of smaller (<15mm) and larger (>15mm) zebra mussels and the ratios of C, N and P in soft tissue	Zebra mussel soft tissue sequesters nutrients equally across size classes (Arnott and Vanni 1996). Thus, nutrient release of decaying mussels should be proportional to their body size	3a) Nutrient release will increase with size, 3b) ratios of C, N and P will not will not differ with size	Decay experiments in the laboratory

Table 2: *t* and *p* values of factors and interactions from the linear mixed effects model.

Factor/Interaction	***t* Value**	***p* Value**
Intercept	13.56	<0.001
Size	4.44	<0.001
Depth	-2.78	< 0.05
Deg. Days >30	-4.15	<0.001
Time	-7.76	<0.001
Time:Deg. Days >30	3.73	<0.001
Time:Depth	1.60	0.11
Depth:Deg. Days >30	-2.42	< 0.05

Table 3: Estimated amounts of C, N and P in tons released by decaying zebra mussels in Canyon Lake and how it would increase the loading from the Guadalupe River (%).

Estimated Population size		**Estimated release (t) due to mussel decay**			**Percentage of Guadalupe River loading**	
Total number of zebra mussels	Mortality	C	N	P	N	P
High	High (**88%**)	207	47	14	2,000	240
Average		133	30	0.92	1,300	160
Low		60	13	0.41	570	70
High	Intermediate **(48%)**	113	25	0.78	1,100	130
Average		73	17	0.50	700	86
Low		33	7.3	0.23	310	38
High		19	4.2	0.13	180	22
Average	Low **(8%)**	12	2.7	0.08	120	14
Low		5.4	1.2	0.04	52	6

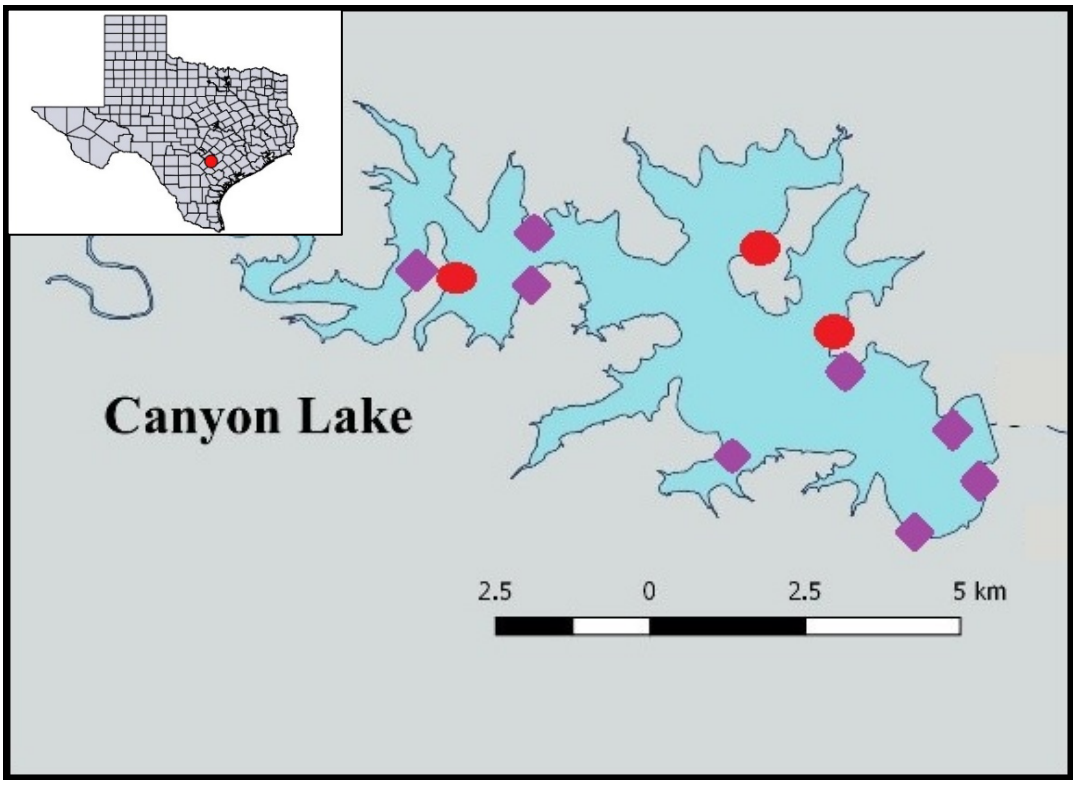

Figure 1. Map of settlement monitoring sites in Canyon Lake (red circles) and diving transects (purple diamonds).

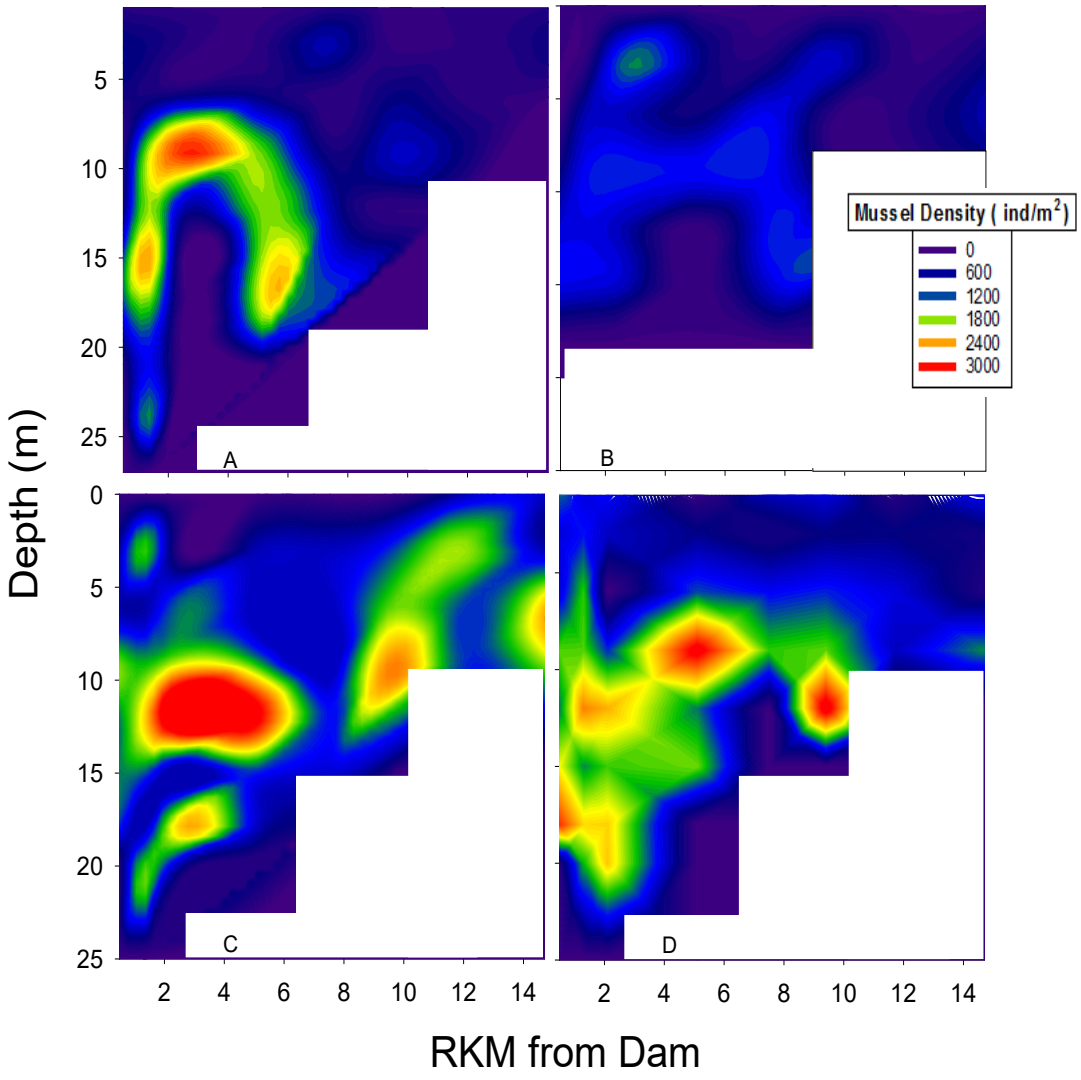

Figure 2. Density (ind. per m^2) distribution of zebra mussels surveyed via dive transects in A) July 2019, B) October 2019, C) July 2020, and D) October 2020. The July 2019 survey was conducted by Josi Robertson (Robertson and Schwalb 2019), the remaining dive surveys were collected specifically for use in this study.

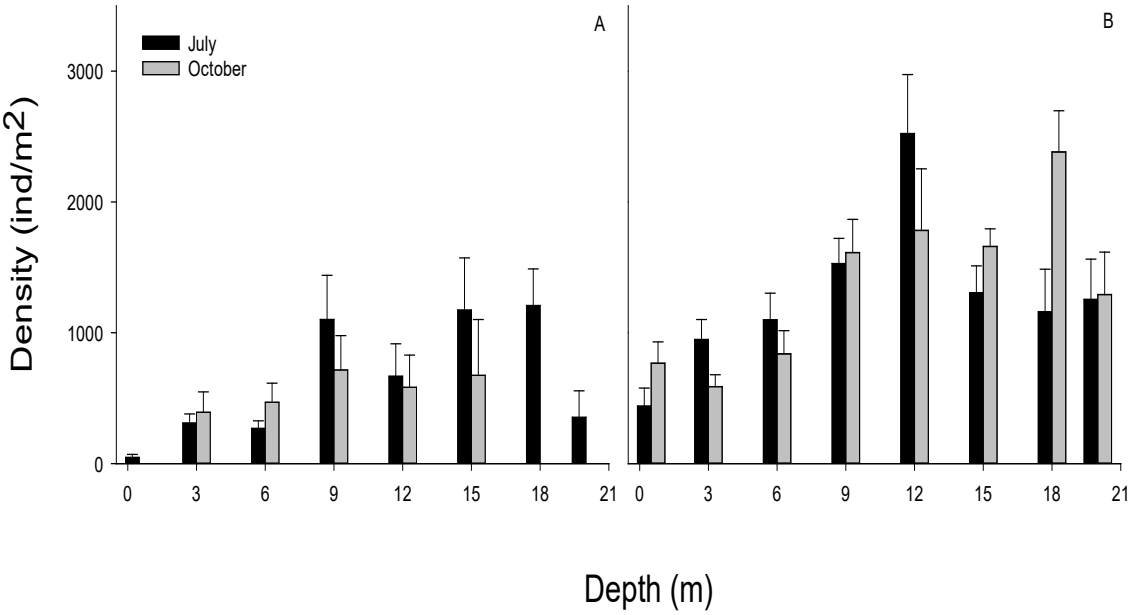

Figure 3. Densities (mean ± SE) at all sampled depths in A) July and October 2019 and B) July and October 2020.

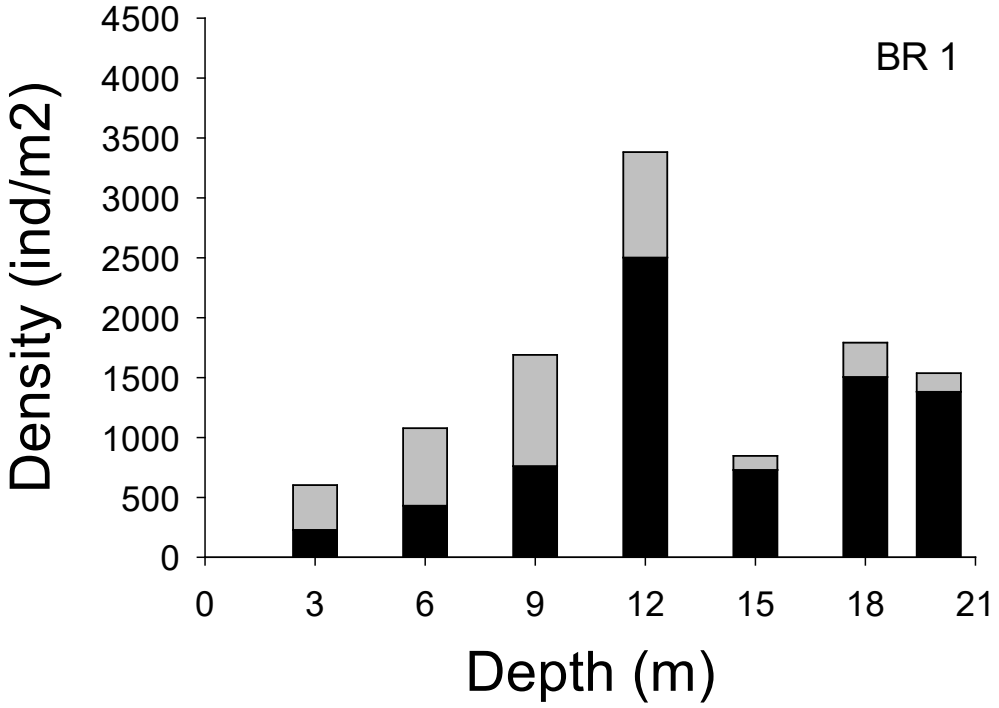

Figure 4. Size frequency distribution at Boat Ramp 1, 2.1rkm from the dam, presented as an average profile for near dam sites. Black bars represent the number of small individuals, grey bars represent the number of large individuals.

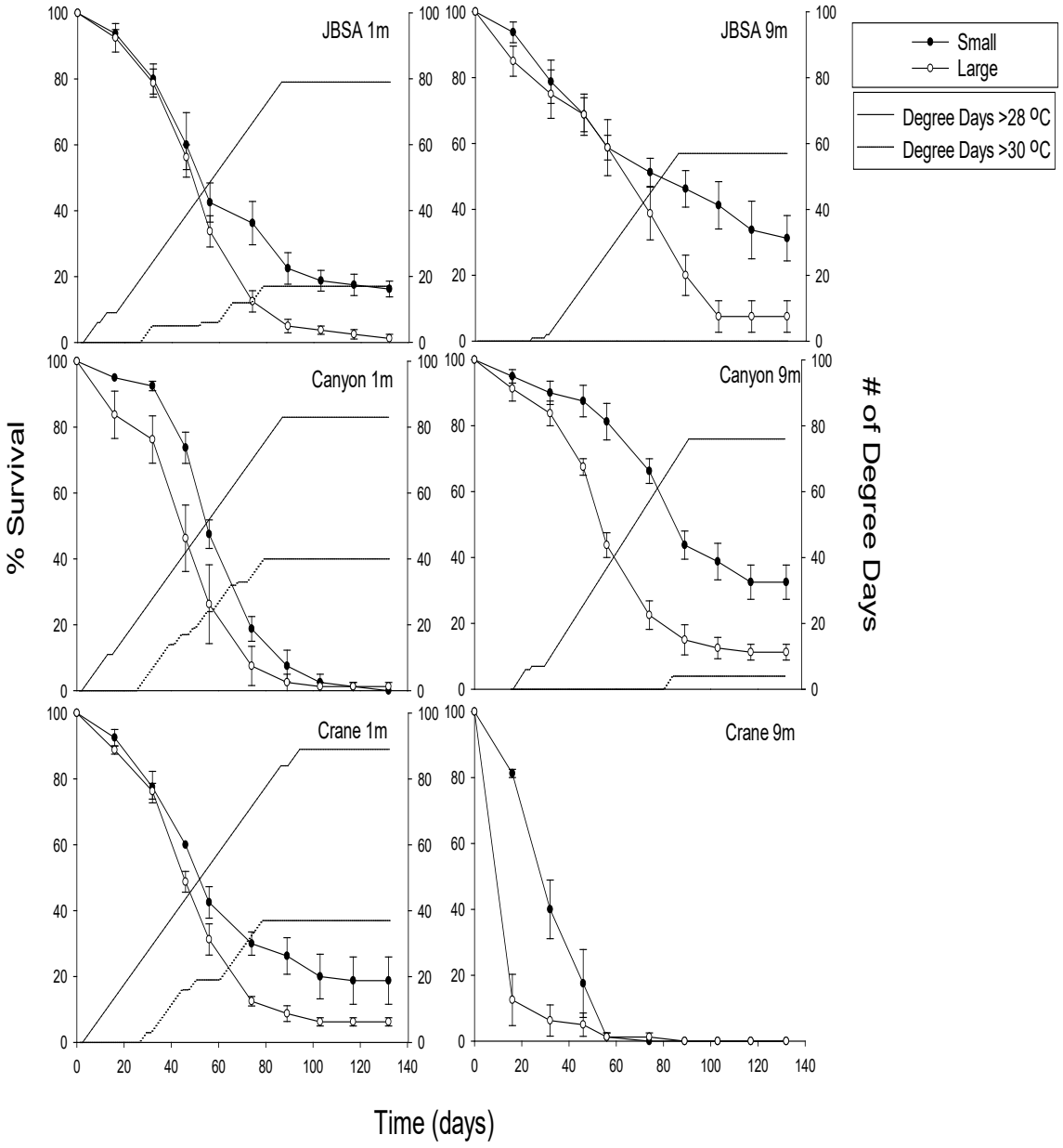

Figure 5. Percent survival (mean ± SE) of small (black dots) and large (white dots) mussels at each marina and each depth. Solid lines represent cumulative degree days over 28°C, dashed lines represent cumulative degree days over 30°C. No temperature data is available for Crane's Mill 9m as the logger was lost to corrosion near the end of the experiment.

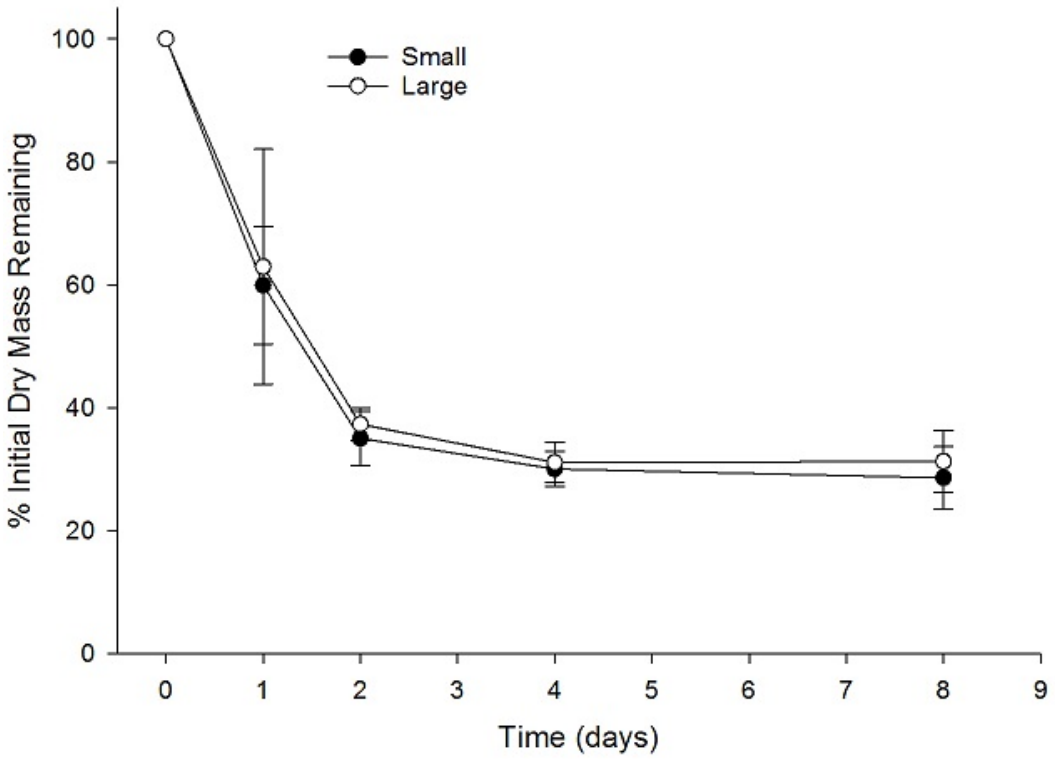

Figure 6. Percent initial dry mass remaining (mean ± SD) of large and small size classes of zebra mussels over 8 days of decomposition.

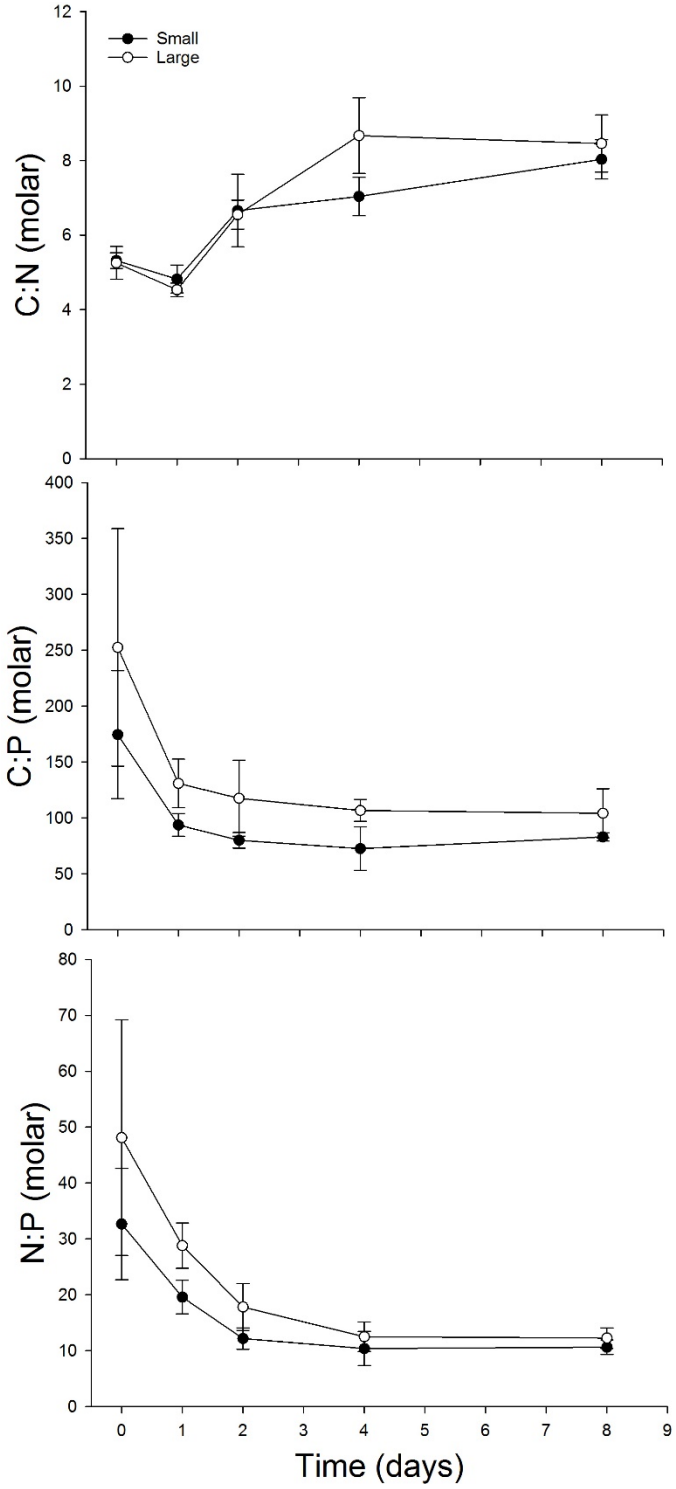

Figure 7. Ratios of C:N, C:P, and N:P (mean ± SD) in small and large mussel soft tissue over 8 days of decomposition.

APPENDIX SECTION

Table A1: Total suspended solid values (mg/L) from water samples taken across all marinas.

	TSS (mg/L)					
Date	JBSA 1m	JBSA 9m	Canyon 1m	Canyon 9m	Crane 1m	Crane 9m
6/17/2020	1.6	5.6	3.2	3.2	0.4	14
7/3/2020	3.6	7.6	4.8		3.6	
8/13/2020	2.4	3.2	2.4	3.2	4.8	7.2
9/13/2020	4.0	3.6	1.6	2.0	2.0	5.2
9/27/2020	0.8	3.6	1.2	4.4	1.0	14.4
10/11/2020	2.8	2.8	0.4	2.0	2.8	10.4
11/14/2020	1.0	1.6	0.8	0.8	1.6	3.6

Table A2: Chlorophyl-a values (µg/L) from water samples taken across all marinas.

	Chl-a (µg/L)					
Date	JBSA 1m	JBSA 9m	Canyon 1m	Canyon 9m	Crane 1m	Crane 9m
6/17/2020	0.16	0.02	1.05	0.84	0.0	14
7/3/2020	1.26	0.99	0.18		1.49	
8/13/2020	2.33	2.74	2.33	2.74	4.68	7.2
9/13/2020	1.79	2.0	0.99	0.55	1.47	5.2
9/27/2020	1.31	0.86	1.20	1.60	0.94	14.4
10/11/2020	0.77	0.65	1.14	2.18	0.86	10.4
11/14/2020	0.61	0.96	1.02	1.41	0.24	3.6

Table A3: Dissolved oxygen values (mg/L) from marina profiles.

	DO (mg/L)					
Date	JBSA 1m	JBSA 9m	Canyon 1m	Canyon 9m	Crane 1m	Crane 9m
6/1/2020	8.15	6.84	8.13	7.07	8.22	6.65
6/17/2020	8.15	6.84	7.93	7.58	7.66	3.5
7/3/2020	7.87	7.85	7.75	7.85	7.63	7.09
7/17/2020	7.67	7.07	7.61	6.02	7.80	7.51
7/27/2020	7.91	7.36	7.69	7.62	7.33	6.84
8/13/2020	7.69	7.28	7.52	7.54	7.42	5.05
8/29/2020	7.78	7.09	7.76	7.67	7.60	3.91
9/13/2020	7.60	7.42	7.37	7.23	7.24	6.59
9/27/2020	8.10	7.81	7.98	7.72	7.61	6.11
10/11/2020	8.50	8.13	8.96	7.79	8.32	5.05

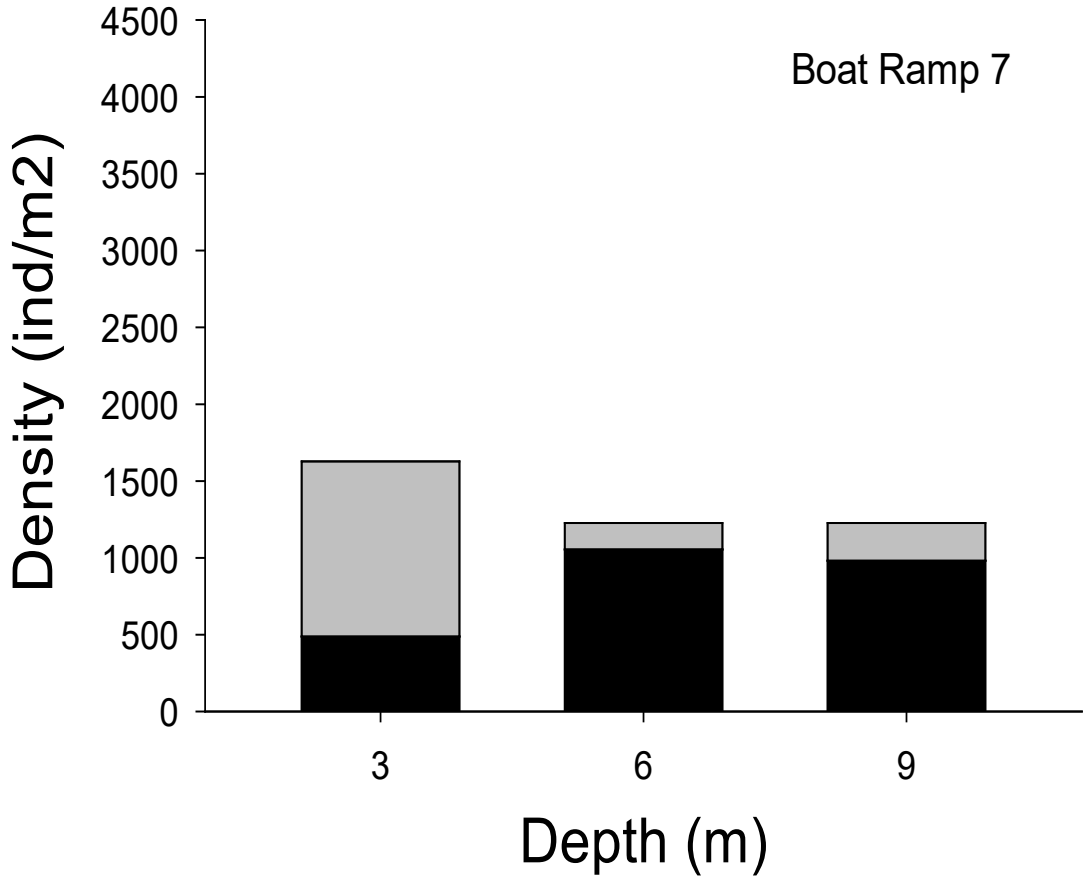

Figure A1: Size frequency distribution at Boat Ramp 7, 11.7rkm from the dam, presented as an average profile for sites closer to the river/lake interface. Black bars represent the number of small individuals, grey bars represent the number of large individuals.

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