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Research Article

Mussel squeeze: dissolved oxygen and temperature can "squeeze" zebra mussels out of invaded reservoirs

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Abstract

Zebra mussels (*Dreissena polymorpha*) are an aquatic invasive species that cause extensive economic and ecological impacts and are a management priority in areas outside of their native range. Survivorship and distribution of zebra mussels within a waterbody are thought to be influenced by temperature and dissolved oxygen conditions, but detailed information to confirm the importance of these environmental controls is necessary to inform management efforts. We measured planktonic zebra mussel veliger density and adult survivorship in San Justo Reservoir in central California to determine distribution and timing of spawning in relation to temperature and dissolved oxygen throughout winter, spring, and summer. We found seasonal patterns in adult survivorship, with high mortality late in the summer and higher than expected survivorship during the spring when dissolved oxygen concentrations were approximately 1 mg/L. Veliger abundance peaked several meters above the thermocline from June to August. Dissolved oxygen concentrations limited veliger distribution, with few to no veligers collected in the anoxic hypolimnion. Veliger settlement out of the water column appears to be possible in San Justo Reservoir at any time of year. A better understanding of how veligers, juveniles, and adult mussels respond to fluctuating dissolved oxygen and temperature conditions will further knowledge of timing and duration of water drawdowns or other control methods for managing this harmful invasive species.

Key words: dreissenids, aquatic invasive species, biological invasions, lakes, freshwater, hypoxia, temperature

Introduction

Zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. rostriformis bugensis*) (hereafter dreissenids) are invaders that can cause extensive economic and ecological impacts in areas outside of their native range (Connelly et al. 2007; Higgins and Vander Zanden 2010; Strayer 2010). Filter feeding by large populations can change energy flow in freshwater ecosystems through bottom-up effects in the food web, alteration of light penetration, and an increase in dissolved nutrients via excretion of feces and pseudofeces, which may subsequently lead to increases in toxic

cyanobacteria (Nalepa et al. 2010; Strayer 2010; Higgins and Vander Zanden 2010). Dreissenids attach to hard, submerged surfaces, such as rock and concrete, using byssal threads, which can create operational problems for hydroelectric and irrigation facilities (Claudi and Mackie 1994; Hosler 2011).

Dreissenid population abundance is dependent upon initial population size and demographics, as well as environmental interactions, which are often context specific (Ramcharan et al. 1992; Strayer et al. 2019a, b). Dreissenids occupy different parts of a water body during their life cycle. Water currents and wind conditions are likely to distribute larvae (i.e., veligers) throughout the water column both vertically and by concentrating them horizontally in downwind bays (Nalepa et al. 2010). Veligers can swim during development (Raven 1958) and in low mixing conditions may concentrate near the thermocline (Mackie and Schloesser 1996). Veligers in later developmental stages actively settle out of the water column onto a variety of submerged substrates, where they secrete a single byssal thread and undergo metamorphosis (Ackerman et al. 1994; Sprung 1993). Mussels are considered juveniles once the siphons and shells are fully formed. They reach sexual maturity when shell lengths are between 5 and 12 mm (Nichols 1996). Juvenile and adult mussels translocate year-round to preferred areas, and are found in epilimnetic, littoral, and profundal areas (Claudi and Mackie 1994).

Dreissenids do not thrive in all parts of a water body. Short-term studies have found multiple causes for population declines, leading to valuable information relevant to management and control. Larval settlement and recruitment are reduced at oxygen concentrations < 2.0 mg/L (McMahon 1996; Karatayev et al. 2007). Settlement and recruitment are also reduced at higher water velocities (> 1.8 m/s: Claudi and Mackie 1994) and in areas with high sedimentation (Sprung 1993). Temperature strongly influences reproduction (Nalepa et al. 2010), and larval density peaks when water temperatures are between 16–19 °C (McMahon 1996). Mussel development is also affected by food availability (Sprung 1993; Strayer et al. 2019a). Predation and competition (intra- and interspecific) have been found to naturally reduce population abundances, but long-term data on these phenomena are scarce (Carlsson et al. 2011; Strayer et al. 2019a). Poor water quality, particularly from increased nutrient inputs, can also reduce abundance (Ramcharan et al. 1992; Strayer et al. 2019a). Dreissenids can rapidly rebound following population declines (Ramcharan et al. 1992).

Once established, dreissenids can quickly spread within hydrologically connected systems via planktonic larvae (Strayer 2009). In addition, dreissenids can spread via human transport, surviving as larvae in water-filled boat compartments or as adults attached to boat hulls or other equipment (Strayer 2009). In 2008, zebra mussels were discovered in San Justo Reservoir, California, and this remains the only known established

population west of the Continental Divide. The likelihood of the successful transport and introduction of dreissenids into additional areas makes development of effective management options critical.

Dreissenid control efforts have typically focused on using chemicals, heat, manual removal, treatment of surfaces with artificial coatings, and reservoir drawdown. Control or eradication in large open waterbodies has rarely been achieved (Strayer 2009; Catita et al. 2020; Invasive Mussel Collaborative, https://invasivemusselcollaborative.net/). Many factors determine the type of control method used, including extent of the mussel invasion and size and characteristics of the invaded water body (Cohen 2008; Invasive Mussel Collaborative, https://invasivemusselcollaborative.net/). Water drawdowns and forms of mechanical control have been employed in hydropower facilities but are labor, cost and resource intensive (Bureau of Reclamation 2015). In lakes and reservoirs, drawdowns increase exposure of mussels to ambient air, increase water temperature, and minimize chemical use due to the decreased water volume (Cohen 2008; Bureau of Reclamation 2018; Invasive Mussel Collaborative, https://invasivemussel collaborative.net/). Winter drawdown was attempted in three lakes in Minnesota, Pennsylvania, and Nebraska, but was only effective at eradication in Nebraska with full winter drawdown (Invasive Mussel Collaborative, https://invasivemusselcollaborative.net/). Additional eradications have occurred with chemical control, using either mined potassium (i.e., potash) (Cohen 2008) or chlorine (Catita et al. 2020). Potash is considered safer for non-bivalve organisms and is currently proposed as a method of control in conjunction with water drawdown in San Justo Reservoir, California (Bureau of Reclamation 2018).

The overall objective of our study was to gain a better understanding of the spatial and temporal patterns of dreissenids in a dynamic reservoir system to inform management and eradication efforts in San Justo Reservoir and similar systems. Our specific objectives were: (1) To determine the timing and spatial distribution of dreissenid spawning (as measured by the presence of early-stage veligers) and veliger settlement out of the water column (as measured by the presence of late-stage veligers); (2) To determine adult mussel survivorship at different water depths and across time; (3) To relate temperature and dissolved oxygen to the vertical distribution of veliger stages in the water column, as well as adult survival. A better understanding of the timing and spatial distribution of veliger spawning and settlement out of the water column, as well as the factors affecting juvenile and adult mussel survival and growth, could inform where and when particular control technologies are used to prevent veliger settlement within facilities and improve the effectiveness of early detection monitoring.

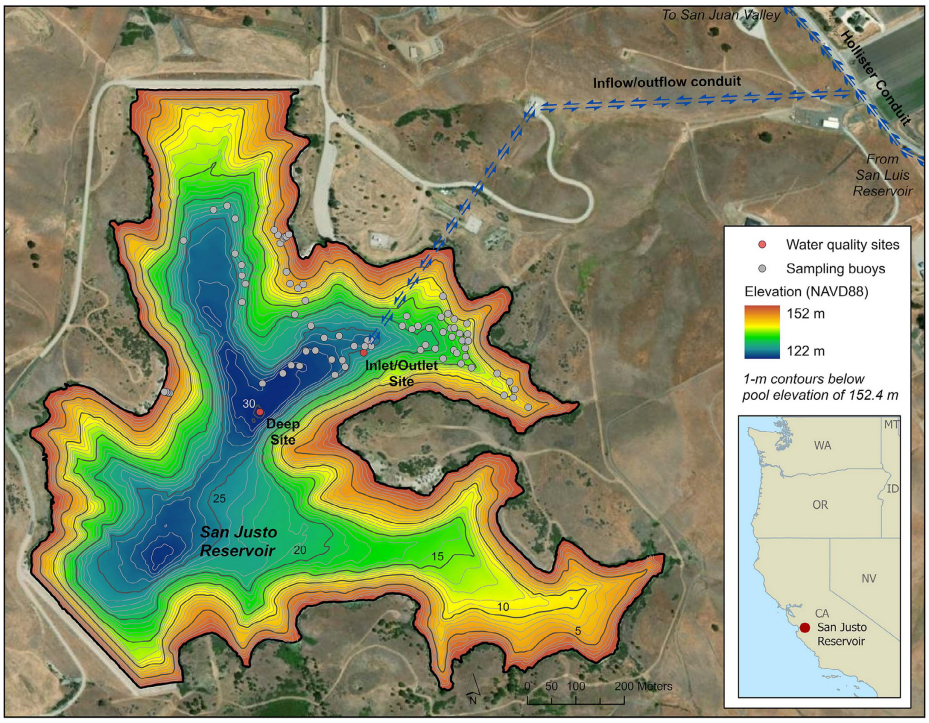

Figure 1. Map of San Justo Reservoir interpolated from hydroacoustic surveys conducted by Portland State University during 2015 and terrestrial Lidar data (USGS Lidar Point Cloud, ARRA-CA_CentralCoast-Z4_2010_000269, 2014-08-27). Contour elevations in 1-m intervals, NAVD 88. Full pool elevation is 152.4 m. Water quality sites were sampled for water quality monthly from January to August 2015. Sampling buoys contained mussel cages and were visited at various sampling dates.

Materials and methods

Study site

San Justo Reservoir is a ~ 81-ha, warm monomictic, meso- to eutrophic reservoir located in central California near the town of Hollister (Figure 1). The reservoir is operated by US Bureau of Reclamation (USBR) and San Benito County Water District (SBCWD) as an off-channel storage facility used to irrigate the San Juan Valley. Source water is received from the California Aqueduct via O'Neill Forebay, San Luis Reservoir, and a series of conduits terminating with the Hollister Conduit. San Justo Reservoir is connected to the Hollister Conduit via a pipe that serves as an irrigation supply outlet or a water storage inlet depending on water supply and irrigation demand. The water levels change throughout the year due to regional uses, mostly during the peak period of June to September (Cohen 2008) and are measured by SBCWD (Supplementary material Figure S1). The reservoir was closed to the public in 2008 after zebra mussels were found by an angler. Given the size and density of mussels, it is thought that they were present for at least two years prior to discovery (Cohen 2008).

Physical characteristics

Veliger and water quality sampling were conducted at two locations: 1) the deepest portion of the reservoir; and 2) the inlet/outlet structure, located

near where water enters and leaves the lake (Figure 1). The location of the deepest sampling site was determined in the field during the initial sampling event using a depth sounder. Both sampling sites were marked by a GPS unit and moored buoys. Sampling occurred at these two locations approximately monthly from January to August 2015. Water surface elevation was measured biweekly by the SBCWD. Water levels on sampling dates were interpolated between measurement dates assuming a linear change between dates.

Water quality data profiles were acquired using a calibrated YSI ProDSS multiparameter sonde. Water temperature and dissolved oxygen were measured at 1-m depth intervals from the water surface to 1 m above the reservoir bottom using the YSI concurrently with dreissenid veliger sampling at the two locations identified in Figure 1. MiniDOT dataloggers (Precision Measurement Engineering, San Diego, California) were deployed at 1 m below the surface at the deepest location, 1 m from the sediment at the deepest location, and 1 m from the sediment at the inlet/outlet pipe location to record dissolved oxygen and temperature at 15-min intervals. The presence and depth of the thermocline was determined from *in situ* temperature data and defined as the depth at which the maximum change in temperature is observed between adjacent 1-m measurements.

Veliger sampling

We collected depth-specific pumped plankton samples to determine the periodicity, density, size, and developmental stage of veligers. We used a peristaltic pump and silicone tubing to directly sample a specific volume of water at 1-m depth intervals. The silicone tubing was attached to a weighted and marked rope that was used to lower the tubing into the water column and maintain vertical position during sampling at each depth. At each depth, 3 L of reservoir water was pumped through the tubing (approximately 2.5 times the volume of the tubing) to rinse the tubing with water from each depth, and then 5 L of water was pumped and passed through a 64-µm mesh filter. The filtered particulate collected on the 64-µm mesh was rinsed into 50-mL centrifuge tubes and preserved to a final concentration of 70% ethanol, which was buffered using tris(hydroxymethyl)aminomethane (Tris) to maintain pH > 7.5.

Adult mussel survivorship

A total of 95 moored buoy stations were deployed at various depths (approximately 1-m intervals with at least two stations per depth interval, see Figure 1, Table S1) with cages containing marked adult dreissenid mussels to evaluate adult mussel survivorship at different water quality conditions over time. The mussel cages were located approximately 0.5 m above the buoy anchor, and each cage (6 × 12-inch, 800-µm polyester bag, Drs. Foster

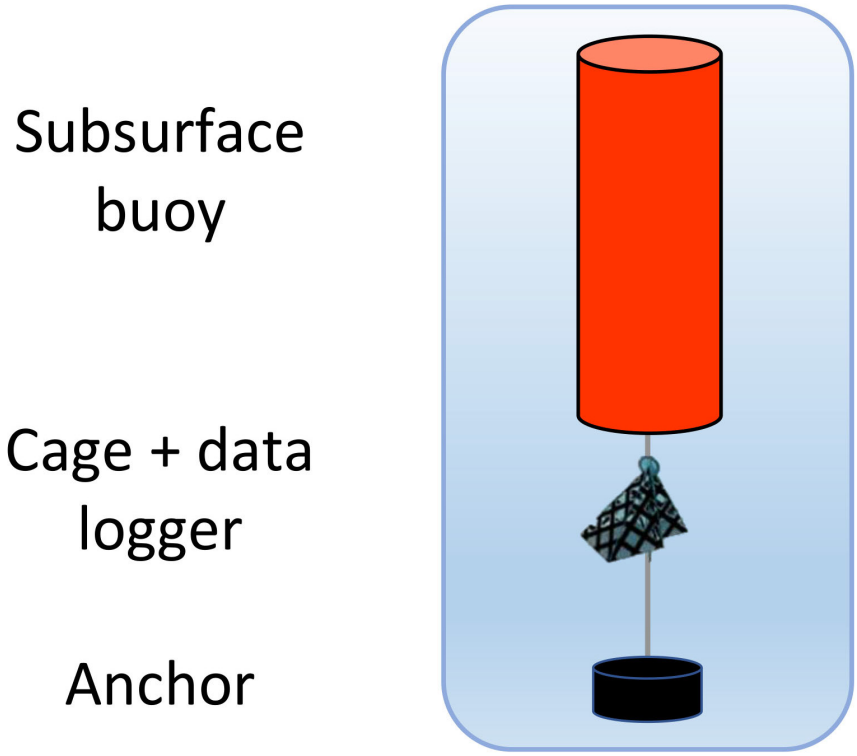

Figure 2. Design of the adult mussel survivorship experiment. The cage containing adult mussels was placed at 0.5 m from the anchor on each of the 95 buoys.

and Smith) contained 10 adult zebra mussels collected randomly from the reservoir, measured using digital calipers, and numbered using a waterproof paint pen (Figure 2). The mussels included in each bag were chosen from a stratified random distribution of shell length: 2 mussels each of < 10, 10–15, 15–20, 20–25, and > 25 mm. The caged and marked mussels were retrieved approximately monthly, except for a data sampling gap in March, and the mussels were evaluated for survivorship (visible tactile response = alive) and measured for shell length. Live and unknown status mussels were then redeployed in the same reservoir position. Shallow buoys that became dry were removed from the list of buoys for selection during the following trip. Due to logistic constraints, we were not able to sample all 95 buoys on each sampling trip, nor were we able to sample more frequently than monthly (or bimonthly in one instance). More buoys were sampled on the first and last trips (95, 75 respectively), with 37–40 buoys sampled on the intervening trips. We randomly selected buoys to sample after it became clear that we would not be able to sample all buoys on each trip (i.e., after Event 1; Figure S2) and included buoy as a random factor in the model to account for variability across space.

Since the water level dropped over the course of the study, we accounted for changes in the recorded depth of the caged mussels. The elevation of the water quality measurements was based on the depth from the surface and the water surface elevation on the date of measurement; measurements were interpolated (linearly) to 0.1-m elevation increments between the 1-m

intervals to link with mussel bag elevations. We therefore converted temperature and dissolved oxygen profile depths from the deep station to elevations based on the water surface elevation on each sampling date, then converted the caged mussel depths to elevations. We then had estimates of temperature and dissolved oxygen for each mussel bag at each buoy for each sampling event. On a few dates the water quality profile data did not reach all the way down as far as the deepest buoy. For those dates water quality profiles were linearly extrapolated as temperature and dissolved oxygen were stable at deeper depths in the hypolimnion.

Laboratory methods

The veliger samples were concentrated in the sample containers by centrifuging for 5 minutes at 1,000 RPM in preparation for analysis. Samples were analyzed with a compound microscope (Leica DM750, DME or DM1000 LED) under cross-polarized light (Johnson 1995) to identify dreissenid veligers, measure their shell dimensions, and determine their larval developmental stage (Nichols and Black 1994; Wells and Sytsma 2013). Cross-polarized light microscopy aids in the detection of bivalve larvae in plankton samples (Johnson 1995). Identification of preserved specimens was based on shell dimensions, overall shape, shell surface features and visible internal tissues, e.g., velum and foot (Ackerman et al. 1994; Nichols and Black 1994; Wells and Sytsma 2013).

Planktonic dreissenid veligers were assigned to one of three larval developmental stages: 1) straight-hinge (Figure S3-1), 2) umbonal (Figures S3-2, S3-3), or 3) late-umbonal/pediveliger (Figure S3-4). Straight-hinge veligers were defined as those veligers possessing a straight hinge where the umbo did not protrude beyond the shell line, and an overall shell shape resembling a capital D (Figure S3-1). Concentric growth lines on the periphery of the shell margin were not always visible. Straight-hinge veligers possessed a velum although this was typically withdrawn within the shell and not visible using preserved specimens. As a veliger grows, the overall shape changes from D-shape to round, i.e., the umbonal larval stage (Figures S3-2, S3-3). Umbonal stage veligers (Figure S3-3) were characterized by an umbo beginning to protrude beyond the shell line giving the veliger an overall rounded shape, with both the anterior and posterior ends of the shell being relatively symmetrical. Umbonal veligers do not possess a functional foot. The development of a functional foot marks the transition to the pediveliger larval stage. The pediveliger stage is the settling stage and is defined by a distinct umbo, asymmetrical anterior and posterior ends, and well-developed foot (Figure S3-4; Carriker and Palmer 1979). The foot was retracted on preserved specimens and was difficult to see; therefore, our classifications of veliger stage did not use the presence of a functional foot to separate pediveligers from older umbonal stage veligers. While shell size can be a diagnostic factor in determining the pediveliger stage, there can be

Table 1. Results for the top generalized mixed models for each life stage grouping of pumped plankton samples. Each model included the random effects depth and event, with events as approximately monthly sampling occurrences from June to August (low densities precluded analyses of earlier sampling events). DO residuals are the residuals of dissolved oxygen ~ temperature. The DO threshold is a binary variable splitting dissolved oxygen values between 0 (< 2 mg/L) and 1 (≥ 2 mg/L). * $p < 0.05$.

	Model	AIC	ΔAIC	Predictor	Est.	SE	z	p
Straight-hinge	Temp * DO residuals + DO threshold + (1|Depth) + (1|Event)	522	0	Intercept	−12.760	1.468	−8.693	< 0.001*
				Temperature	0.888	0.105	8.473	< 0.001*
				DO residuals	1.948	0.879	2.215	0.027*
				DO threshold	−2.112	0.873	−2.420	0.016*
				Temp * residuals	−0.071	0.043	−1.661	0.097
	Temp + DO residuals + DO threshold + (1|Depth) + (1|Event)	522.8	0.8	Intercept	−11.707	1.271	−9.207	< 0.001*
				Temperature	0.807	0.089	9.120	< 0.001*
				DO residuals	0.499	0.082	6.065	< 0.001*
				DO threshold	−1.367	0.713	−1.916	0.055
Umbonal	Temp * DO residuals + DO threshold + (1|Depth) + (1|Event)	470.1	0	Intercept	−7.709	1.574	−4.899	< 0.001*
				Temperature	0.441	0.110	4.006	< 0.001*
				DO residuals	2.103	1.167	1.802	0.072
				DO threshold	2.227	0.937	2.377	0.017*
				Temp * residuals	−0.084	0.058	−1.439	0.150
	Temp + DO residuals + DO threshold + (1|Depth) + (1|Event)	470.2	0.1	Intercept	−7.394	1.713	−4.316	< 0.001*
				Temperature	0.418	0.120	3.497	< 0.001*
				DO residuals	0.426	0.091	4.693	< 0.001*
				DO threshold	2.457	0.992	2.478	0.013*
Pediveliger	Temp * DO residuals + DO threshold + (1|Event)	351	0	Intercept	−19.735	4.725	−4.177	< 0.001*
				Temperature	1.105	0.290	3.810	< 0.001*
				DO residuals	12.055	3.997	3.016	0.003*
				DO threshold	−1.396	1.957	−0.713	0.476
				Temp * residuals	−0.577	0.193	−2.996	0.003*
	Temp * DO residuals + DO threshold + (1|Depth) + (1|Event)	353	2	Intercept	−19.735	4.725	−4.177	< 0.001*
				Temperature	1.105	0.290	3.810	< 0.001*
				DO residuals	12.055	3.997	3.016	0.003*
				DO threshold	−1.396	1.957	−0.713	0.476
				Temp * residuals	−0.577	0.193	−2.996	0.003*

variation in this metric (Ackerman et al. 1994; Wells and Sytsma 2013). We also relied upon overall shell shape, hinge development, and symmetry of the posterior and anterior ends to classify the pediveliger stage.

Data analysis

For the veliger analysis, we applied a negative binomial generalized linear mixed effects model using the R Software package *glmmTMB* (v. 1.0.2.1; Brooks et al. 2017) to test for a difference in density and depth distribution of individuals of each life stage (straight-hinge, umbonal, pediveliger) relative to environmental conditions at each of the last four events ranging from early June to early August 2015 (Table 1). The negative binomial distribution is appropriate for over-dispersed count data, that is, when the conditional variance exceeds the conditional mean. We excluded data from January through May from the model because veliger densities were very low. We analyzed data from the deep station as results from the inlet/outlet station were similar.

Temperature and dissolved oxygen were significantly correlated over the last four sampling events (i.e., the events we were analyzing; $r = 0.91$, $p < 0.001$), so we used the residuals of the linear model of dissolved oxygen

~ temperature, as well as temperature, as fixed effects, with event and depth as random effects. Because residuals are the difference between the observed and predicted relationship of dissolved oxygen ~ temperature, we hypothesized that any significance of dissolved oxygen residuals in the model might point to how density might be impacted by dissolved oxygen as opposed to temperature. This positive relationship between temperature and dissolved oxygen is common in stratified eutrophic systems, where dissolved oxygen is being driven more by plankton dynamics (e.g., photosynthesis, respiration) than by physical processes. We also created a dissolved oxygen threshold variable to classify whether samples were hypoxic (< 2 mg/L dissolved oxygen; assigned a value of 0) or oxic (≥ 2 mg/L dissolved oxygen; assigned a value of 1); this was a fixed effect in the models. Performance of the model was determined using AIC. Only models with ΔAIC < 2 were reported (Symonds and Moussalli 2011). All veliger life stages were also combined and analyzed with a generalized linear mixed effects model (as above) to examine overarching trends.

We evaluated survivorship of individual mussels in each cage at each buoy using a binomial generalized linear mixed model (Bates et al. 2015). The binomial generalized linear mixed model is appropriate because it allows response variables from different distributions, such as binary responses (here: alive vs dead). We included the initial length measurement for each mussel to see if size influenced survivorship ability. Temperature and dissolved oxygen variables were included in the models in two ways: 1) the measured values at each sampling event; and 2) averaged between the measured values at each sampling event and the previous sampling event. Both methods were tested in models, and we used AIC to determine which method explained the most variance. The best model included the averages of temperature and dissolved oxygen measurements. Because temperature and dissolved oxygen were also significantly correlated for events 5–8 for this analysis ($r = 0.46$, $p < 0.001$), the final model included the residuals of the linear model of dissolved oxygen ~ temperature (as in the veliger analysis), as well as temperature and length as fixed effects, with buoy identification number and event as random effects. Buoy was included as a random factor to capture spatial variation and the effects of sampling different buoys during different sampling events. Event represents the progression of development of veliger populations (density and developmental stage) over the course of the growing season. A dissolved oxygen binary variable similar to that in the plankton analysis was also a fixed effect (Table 2).

All analyses were performed in R (R Core Team 2020, Version 4.0.2). Model assumptions were verified by plotting the residuals against the fitted values and inspecting the output to ensure there were no patterns (Zuur et al. 2009).

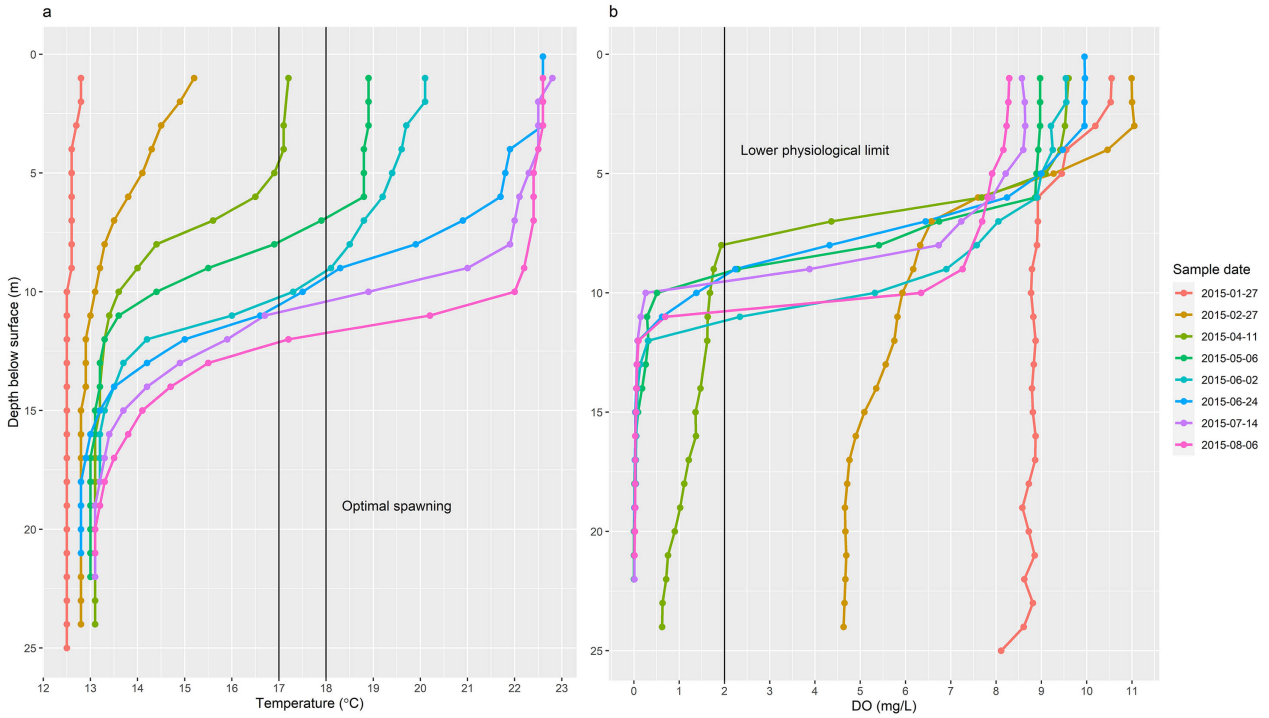

Figure 3. a) Water temperature (°C) and b) dissolved oxygen DO (mg/L) throughout the water column at the deep location in San Justo Reservoir. Optimal spawning temperatures (17–18 °C) indicated with vertical lines in a); lower physiological limit for dissolved oxygen (2 mg/L) indicated with the vertical line in b).

Results

Thermocline and water quality

San Justo Reservoir stratified by early April 2015 (Figure 3). The sampling event in late January was the only sampling period when the water column was mixed and relatively isothermal. Strong stratification began in May 2015 as indicated by the slope of the profiles in the metalimnion (Figure 3). Water temperatures were above the lower limit for mussel spawning (i.e., ≥ 17–18 °C) during all sampling events (Figure 3a; McMahon 1996). Water temperatures between 17 and 18 °C are associated with peak spawning (McMahon 1996), and epilimnion water temperatures during the April, May, and early June sampling events were in this temperature range (Figure 3a). Similarly, dissolved oxygen concentrations in the epilimnion were well above the lower physiological limits throughout the project period (e.g., < 2 mg/L; McMahon 1996). Dissolved oxygen concentrations, however, declined at water depths approximately 10 m below the surface, with moderate hypolimnetic dissolved oxygen declines in February and a hypoxic hypolimnion from April through August (< 2 mg/L; Figure 3b).

Veliger spawning, settlement, and spatio-temporal distribution

We used veliger developmental stage as a proxy of two key components of mussel life history: spawning was inferred from the presence of early-stage veligers (i.e., straight-hinge and umbonal), while settlement out of the water column was inferred from the presence of late-stage veligers (i.e.,

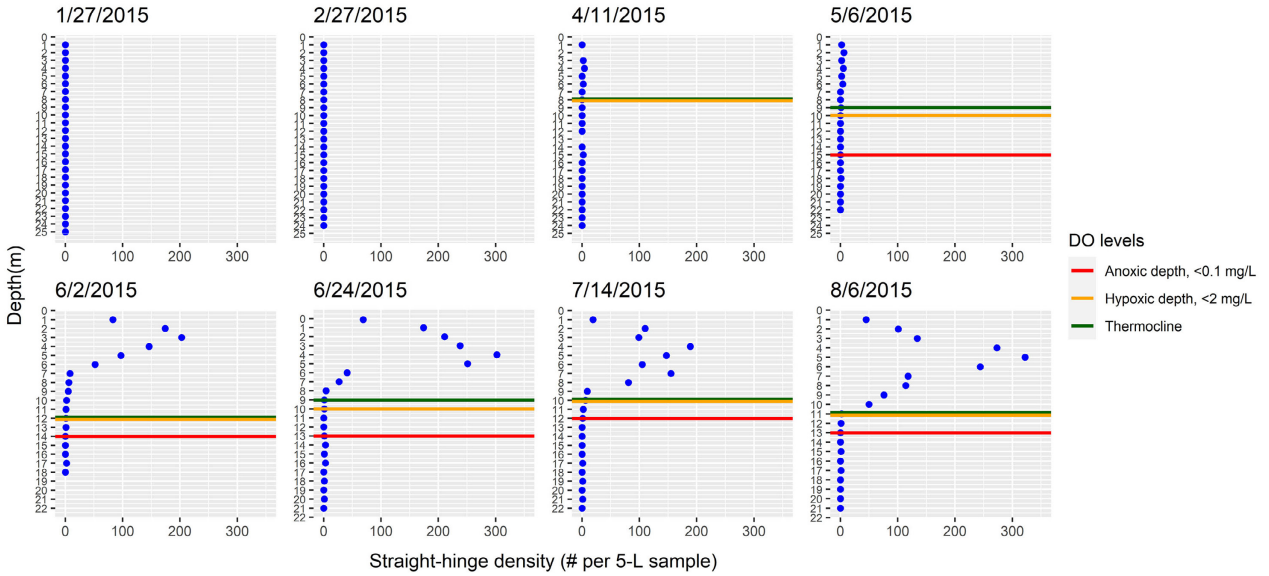

Figure 4. Straight-hinge veliger densities (per 5-L sample) across all sampling events (events 1–8) at depth (m). Veliger densities ranged from 0 to 6 in sampling events three and four. Thermocline is the lowest water depth at which the maximum change in temperature is observed between adjacent 1-m measurements.

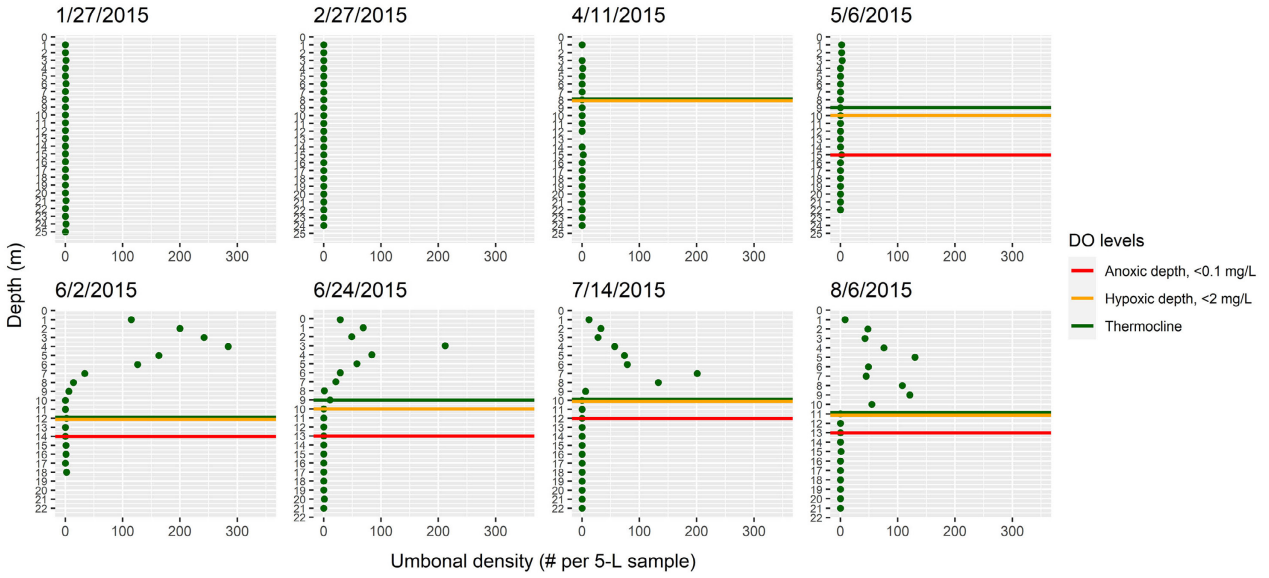

Figure 5. Umbonal veliger densities (per 5-L sample) across all sampling events (events 1–8) at depth (m). Veliger densities ranged from 0 to 3 for the first four sampling events. Thermocline is the lowest water depth at which the maximum change in temperature is observed between adjacent 1-m measurements.

pediveligers). There were two distinct periods in the veliger population between January and August: one characterized by low densities of veligers in the water column (January to May), and another characterized by much higher veliger densities for all larval stages (June to August) (Figures 4, 5, 6). The pediveligers found during the January sampling event, and possibly those found during the April and May sampling events, may represent overwintering veligers from the prior year that are finally settling out of the water column. Accordingly, the absence or very low densities of young veligers in the water column from January to May suggests that the population ceased spawning for some period after the previous summer and resumed

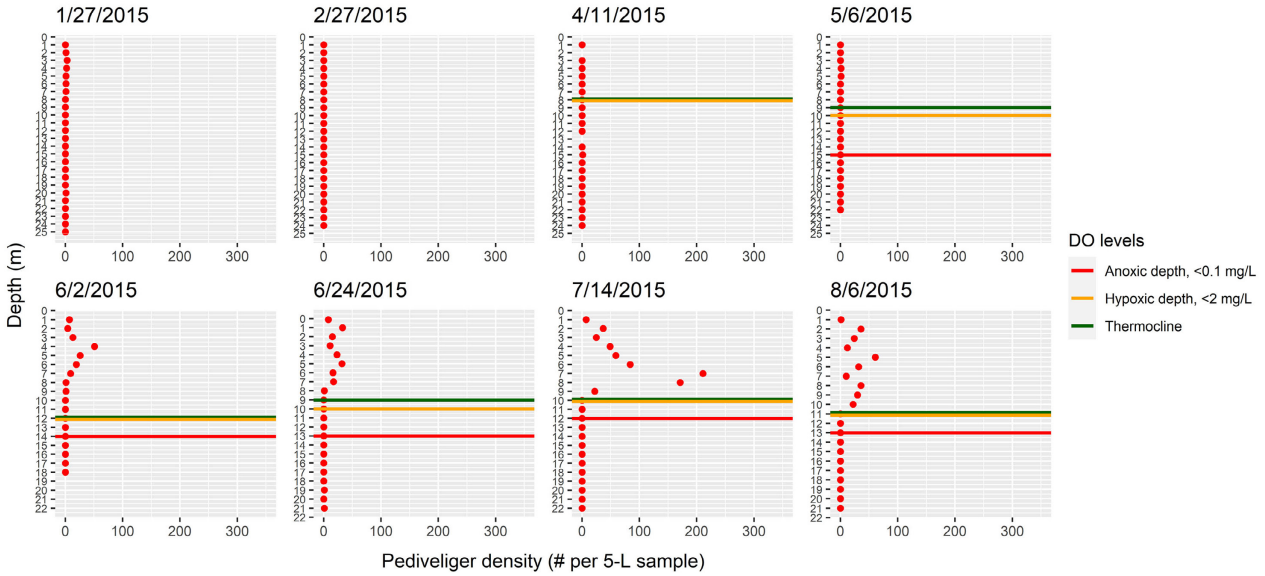

Figure 6. Pediveliger densities (per 5-L sample) across all sampling events (events 1–8) at depth (m). Veliger densities ranged from 0 to 3 for sampling events one, three, and four. Thermocline is the lowest water depth at which the maximum change in temperature is observed between adjacent 1-m measurements.

spawning during our spring sampling events. Straight-hinge and umbonal stage veligers represented a large proportion of the veliger community composition in the late spring and summer periods, with straight-hinge as the most abundant life stage for all events.

Straight-hinge veligers were first collected in April and densities increased rapidly starting in early June. These younger veligers in the water column did not substantially decrease during the summer as the densities of older veligers increased. In general, straight-hinge veligers were found throughout the epilimnion and densities peaked several meters above the thermocline (Figure 4). Temperature and dissolved oxygen had significant relationships with straight-hinge veliger densities in late spring and summer: densities were highest in the epilimnion and above the zone of hypoxia (Table 1, Figure 4). Temperature and dissolved oxygen residuals had significant positive effects on densities (Figure 4). Conversely, the dissolved oxygen threshold variable had a significant negative relationship with density: when dissolved oxygen was < 2 mg/L, densities were high (Figure 4). This result seems counter-intuitive; however, temperature had a stronger relationship with straight-hinge density than dissolved oxygen at concentrations > 2 mg/L. For example, when temperatures were low, but dissolved oxygen was high, densities were lower than expected.

The umbonal stage veligers increased rapidly starting in early June. Umbonal veligers, similar to the straight-hinge veligers, were found throughout the epilimnion with densities peaking several meters above the thermocline (Figure 5). Temperature also had a significant positive relationship with umbonal-stage densities (Table 1, Figure 5). Unlike the straight-hinge veligers, the umbonal densities showed a significant positive relationship with the dissolved oxygen threshold variable, indicating that densities

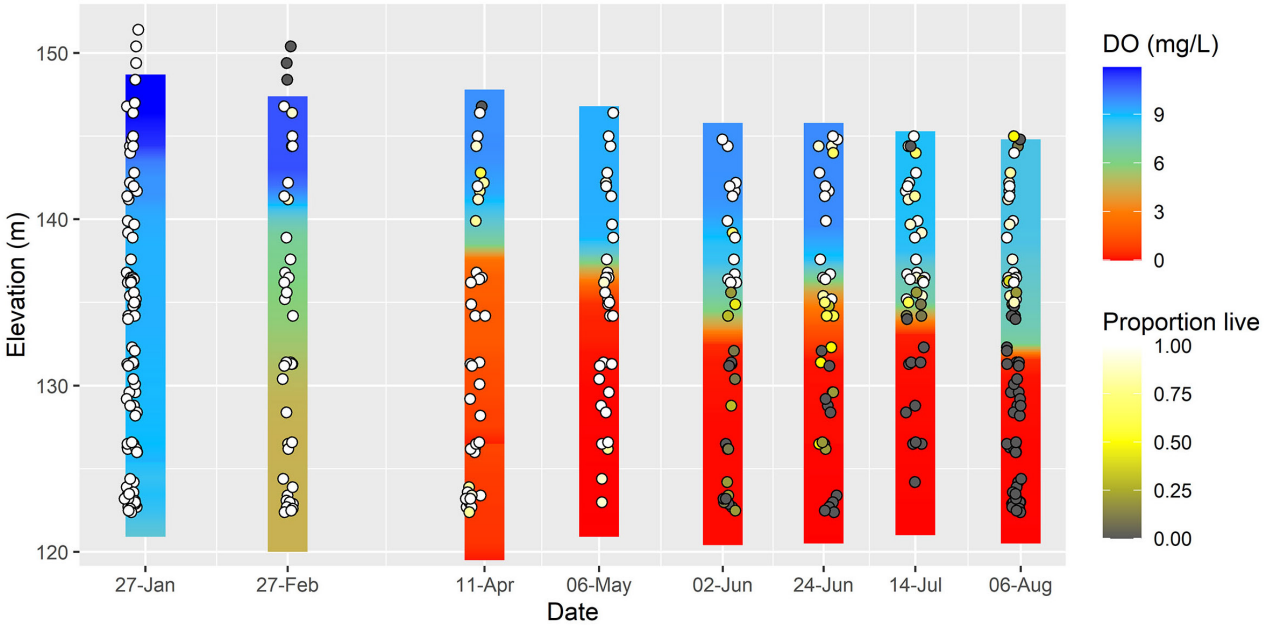

Figure 7. Survival percentage of surveyed adult mussels across all of the sampling events. Dissolved oxygen (mg/L) measurements represent the initial dissolved oxygen concentration at each event that corresponded to the survivorship assessment for each mussel. Points above the bars (January and February) represent buoy measurements above the water level; water levels did not rise as expected at these sites due to drought.

increased above 2 mg/L (Table 1). Dissolved oxygen residuals also had a positive effect on densities in the second-best model, similar to the straight-hinge life stage.

The densities of older veligers (i.e., pediveligers) increased from the onset of spawning in the spring into the summer, peaking in mid-July. Similar to both straight-hinge and umbonal veligers, pediveligers were found throughout the epilimnion and density peaked several meters above the thermocline (Figure 6). Temperature and dissolved oxygen residuals had a significant positive relationship with pediveliger densities in late spring and summer; however, the dissolved oxygen threshold did not (Table 1, Figure 6). Both top models also included an interaction between temperature and dissolved oxygen residuals. When temperature was low and dissolved oxygen residuals were high, pediveliger densities were low; conversely, when temperature was high and dissolved oxygen residuals were low, pediveliger densities were high. All veliger life stages were also combined, and we found that temperature and dissolved oxygen residuals had a significant positive relationship with veliger densities; however, the dissolved oxygen threshold variable was not significant (Table S2).

Mussel survivorship

Adult mussel survivorship above the thermocline was high, whereas the adult mussels located below the thermocline largely died in the summer. Adult survivorship was very high during the first four sampling events (January–May) at all water depths, with less than 3% of all individuals dead (Figure 7, Table S3). Adult mussels in the hypolimnion survived low dissolved oxygen concentrations (< 2 mg/L) for several weeks in events 3 and 4 (April

Table 2. Results of general linear mixed effects models for mussel cage survivorship for the top models, which included buoy identification number and event as random effects. Event represents approximately monthly sampling occurrences from January to August. DO residuals are the residuals of dissolved oxygen ~ temperature. The DO threshold is a binary variable splitting dissolved oxygen values between 0 (< 2 mg/L) and 1 (≥ 2 mg/L). * $p < 0.05$.

Model	AIC	Predictor	Est.	SE	z	p
Temp + DO residuals + DO threshold + Length + (1| buoy ID) + (1| Event)	426.4	Intercept	−12.514	4.260	−2.937	0.003*
		Temperature	0.955	0.256	3.727	< 0.001*
		DO residuals	1.259	0.295	4.275	< 0.001*
		DO threshold	−0.416	0.918	−0.453	0.650
		Length	0.095	0.022	4.290	< 0.001*

and May). Adult survivorship below the thermocline, however, began to decline in the late spring and into the summer (Figure 7). The top model included temperature averaged between events (Table 2). Length, temperature, and dissolved oxygen residuals were significantly positively related to mussel survivorship. The best model included both random effects (i.e., buoy identification number and event).

Discussion

Our study details several key findings in line with our three main objectives. In particular, we found seasonal patterns in adult survivorship, with high mortality late in the summer and higher than expected survivorship during the spring. Additionally, we discovered a significant positive relationship between initial adult length and survivorship. Mussels with larger body size at the beginning of the survey were more likely to survive through the season (Table 2). We found a peak for all veliger life stages (straight-hinge, umbonal, and pediveliger) during June to August. In the hypolimnion, dissolved oxygen concentrations were limiting to veliger distribution, with few to no veligers collected below the thermocline. We had mixed results for objective one; while we found periods of peak spawning for all life stages, veliger settlement out of the water column appears to be possible in San Justo Reservoir when veligers of any developmental stage are present including the spring, summer, and winter. We do not have data for fall, but another spawning event could be possible as the temperatures are likely above the lower temperature limit for spawning (e.g., ≥17–18 °C, McMahon 1996). In Lake Mead, Nevada, dreissenid pediveliger abundance relative to total veligers in the water column peaked in the October to January period (Gerstenberger et al. 2011). Peak spawning temperatures preceded peaks in total veliger density for each life stage. These results have important implications for when and where to monitor for veligers, as well as for management tactics to control invasion and spread of this harmful invasive species, which we discuss below.

We separated the various veliger life stages to investigate spawning frequency and settlement out of the water column. We were then able to relate each life stage to temperature and dissolved oxygen to determine if there were differences in abundance and vertical distribution over time.

Previous studies have not distinguished larval stages and this information is important for determining what factors may contribute to abundance and spatial distribution in a water body (Strayer et al. 2019a). Veliger spawning started in the spring and spawning was underway by early June. Veliger densities for all life stages were concentrated in the epilimnion several meters above the thermocline, and veliger densities declined significantly below the thermocline where dissolved oxygen reached the 2 mg/L threshold for hypoxia in the late spring and summer sampling events (Figures 4, 5, 6). Increased veliger density above the thermocline during strong stratification is likely due to physical conditions such as density gradients at the thermocline that make it more difficult for veligers to move out of the epilimnion during this time as well as favorable dissolved oxygen and temperature conditions. Veliger swimming behavior, however, may also contribute to veliger depth distribution within the epilimnion as veliger densities peaked several meters above the thermocline. Interestingly, the straight-hinge veliger stage had lower than expected densities where dissolved oxygen was above 2 mg/L, as indicated by the negative dissolved oxygen covariate (Table 1). This could be due to the somewhat steep gradient between high and low dissolved oxygen that occurs within approximately a meter in the 8–10 m depth range depending upon sampling date (Figure 3b). Swimming veligers could have migrated during the sampling period, or measurement error is possible in this small range. The density of pediveligers increased from the onset of spawning in the spring into the summer, with peak density occurring in mid-summer throughout the epilimnion (Figure 6). Fluctuations in depth distribution are an important consideration for monitoring planktonic veligers and veliger sampling in stratified water bodies should be focused in the epilimnion when there are depleted dissolved oxygen conditions below the thermocline.

The pediveliger model indicated a significant interaction between temperature and the dissolved oxygen residuals. The dissolved oxygen residuals (i.e., the deviation of observed from predicted values in a linear relationship of dissolved oxygen and temperature) are important to evaluate because many systems have highly correlated temperature and dissolved oxygen values across depths. When temperature was lower and dissolved oxygen residuals were higher, pediveliger densities were relatively low; however, when temperature was higher and dissolved oxygen residuals were lower, densities were relatively high (Table 1). Lower temperature and higher dissolved oxygen residuals were likely observed because temperatures were not low enough to limit density even if dissolved oxygen concentration was relatively high. This result may simply reflect the seasonal development of veliger life stages. Higher temperature and lower dissolved oxygen residuals could be explained by dissolved oxygen being less than what would be expected at the corresponding temperature, though potentially not low enough to restrict veliger presence, resulting in high densities.

Given the strong correlation between temperature and dissolved oxygen in the last four sampling events, it is difficult to disentangle the proximate driver of pediveliger densities, thus, we can only conclude that both temperature and dissolved oxygen are influencing pediveliger densities, and that dissolved oxygen becomes most influential at low concentrations (i.e., hypoxic). As with the straight-hinge densities at low dissolved oxygen concentration, it is important to consider fluctuations in depth distribution in sampling. This consideration should extend to all veliger life stages, particularly when densities are at their peak. Drawdown as a management strategy should consider temperature as well as dissolved oxygen concentration given the propensity of the pediveliger life stage to obtain higher densities at higher temperatures.

Adult zebra mussel mortality was high at low dissolved oxygen concentrations in the summer sampling events (June to August) (Figure 7). As San Justo Reservoir stratified, the dissolved oxygen concentrations below the thermocline declined. In April and May, the hypolimnion developed hypoxic conditions (i.e., < 2 mg/L), and yet surprisingly, adult mussel mortality in the hypolimnion was relatively low during the April and May sampling events. This period spanned from April 11 to May 6, indicating that some adults may have survived hypoxic conditions for at least three weeks. Additionally, mussels that started at a larger size at the beginning of the sampling events were more likely to survive by the end of the season. By the beginning of June, however, adult mussel mortality in the hypolimnion increased, and adult mussels in the hypolimnion were dead by the summer. While zebra mussels are generally more intolerant of anoxic or hypoxic conditions and exposure to ambient air compared to other bivalve species, they have been found to exhibit hypoxia tolerance for varying lengths of time depending upon temperature (Matthews and McMahon 1995; McMahon 1996; Yu and Culver 1999). In laboratory experiments, Matthews and McMahon (1995) tested anoxia tolerance and found mean survival of 17.8 days at 15 °C, with lower tolerance at higher temperatures. In a lake study, the threshold oxygen level for survival was between 1.0–1.7 mg/L when water temperature was at about 17–18 °C (Yu and Culver 1999). These studies align with our findings of hypoxia tolerance, where dissolved oxygen was approximately 1 mg/L in April and early May. In addition to hypoxic conditions in water, zebra mussels have the ability to survive outside of water for periods of time. McMahon (1996) estimated maximum survival of adults in air at ~ 3 weeks at low temperature (i.e., < 5 °C) and high relative humidity (> 95%). However, other studies have found that higher air temperatures (~ 20 °C) and lower relative humidity (~ 50%) restricted survival to 3–5 days (Ricciardi et al. 1995; Johnson et al. 2001). Our study provides further evidence zebra mussels can survive in conditions with reduced oxygen for fairly long periods of time.

The particular conditions of San Justo Reservoir's management could have influenced survivorship results (Figure 7). One hypothesis is that mussels were receiving oxygenated water into the hypolimnion periodically through water operations in the June to September time period. Water is pumped into San Justo Reservoir through the inlet/outlet structure located near the reservoir bottom at the deepest part of the water body during the night, and water is then pumped out during the day to meet water use demands (Cohen 2008). We do not have dissolved oxygen data on the water flowing into the lake. However, dissolved oxygen loggers placed at the bottom of the deep station and at the inlet/outlet station during our study did not register dissolved oxygen fluctuations, and oxygen concentrations at the bottom depths were very low (Figure S4). Internal seiches driven by wind events could also result in vertical shifts in oxygenated waters. Logger data from the hypolimnion did not provide any indication that seiches occurred during our study, but metalimnetic seiches cannot be ruled out. Overall, these factors indicate that our mussel survivorship results in hypoxic conditions were robust.

Our study results provide some important guidelines for management and monitoring. Adult dreissenid mussels are susceptible to low dissolved oxygen, but adult mussels may need to be deprived of oxygen for at least three weeks to achieve high levels of mortality. To result in total eradication, this time period may need to be longer, given how long adults survived at low dissolved oxygen in the spring. Other studies show congruent results with ours and align with this recommendation (Matthews and McMahon 1995; Yu and Culver 1999). Based on the timing of our results, adult mussels that colonize the hypolimnion the prior year during isothermal conditions may reproduce prior to dying from the low dissolved oxygen formed after thermal stratification in the subsequent spring and summer (the viability of eggs and sperm released in hypolimnetic waters are unknown). Given that few veligers were found in May, when temperatures ranged from ~ 16–19 °C above the thermocline, followed by much higher veliger densities in early June, when temperatures ranged from ~ 18–23 °C, monitoring efforts could conservatively set the threshold for suitable temperatures around 15–16 °C as a starting point for veliger monitoring and likely capture of any individuals in the water column. For management purposes, this might be an opportune time for drawdown and/or chemical control, since an optimal number of individuals could be targeted. However, several factors such as water use, or other logistic concerns may be a factor in decision making for particular reservoirs. While it may not be plausible to practice control methods at the most optimal spawning or survivorship peaks, information on these factors could help to identify water depths and locations to focus early detection monitoring sample collection efforts and control.

In this study, we gained a more complete understanding of temporal patterns in veliger densities and abiotic factors influencing veliger and adult mussel survival. Additional studies could include longer term monitoring, particularly to understand periodicity of spawning and how veliger density varies from year to year. A better understanding of how veligers, juveniles, and adult mussels respond to fluctuating dissolved oxygen concentrations would inform timing and duration of water drawdowns or other control methods. Ultimately the results presented here will enable better prediction of where and when different mussel life stages thrive within a water body given certain environmental parameters. Successful monitoring and control of this highly damaging invasive species is dependent on a better understanding of its population dynamics and interactions with its ambient environment.

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Authors' contribution

CG led the data analysis, interpretation and writing; RM contributed to research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, and writing; SW contributed to research conceptualization, sample design and methodology, investigation and data collection, and writing; MDS contributed to research conceptualization, sample design and methodology, funding provision, and writing; ALS contributed to research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, funding provision, and writing.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. San Justo Reservoir water surface elevation measurements.
Figure S2. Buoys sampled by buoy identity and date throughout the study.
Figure S3. Dreissenid veliger stages found in plankton.
Figure S4. Dissolved oxygen (mg L^{-1}) values from MiniDOT dataloggers.
Table S1. Targeted buoy depths at the start of the study and numbers of buoys deployed at each depth.
Table S2. Results for the top negative binomial generalized mixed models for combined life stages of pumped plankton samples.
Table S3. Number of individuals sampled from each mussel bag and buoy and cumulative survivorship at each event.