



Invasion dynamics of quagga mussels within a Southern California reservoir and its spatially intermittent watershed

Michael T. Booth · Carolynn S. Culver

Received: 16 November 2022 / Accepted: 11 April 2023
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Abstract Since its discovery in Lake Mead, Nevada in 2007, the invasive quagga mussel (*Dreissena rostriformis bugensis*) spread throughout the lower Colorado River drainage and into connected Southern California water systems. In December 2013, quagga mussels were found in Lake Piru, California, a reservoir with no connection to the Colorado River drainage. An initial “boom” period occurred in the first year after colonization. High densities and settlement rates continued for three years while lake water levels were low and relatively stable, despite periodic removals of mussels from lake infrastructure. Mussels were initially restricted to hard substrates but were regularly found on soft sediments within two

years of colonization. Storms in 2017 dramatically increased the lake level and deposited substantial sediment, which eliminated mussels on soft sediments and reduced the overall mussel population. Reproduction and juvenile settlement rebounded within 6 months, despite the low population of adult mussels in the lake. Environmental conditions, particularly fill status and water temperature, rather than adult density, appear to be the primary driver of veliger abundance in this system, while recruitment was primarily explained by veliger abundance. Elevated water releases from the reservoir increased the flux of veligers downstream and led to mussel recruitment > 15 km downstream. Sustained establishment of quagga mussels downstream has not occurred in the Santa Clara River and seems unlikely due to the unstable habitat conditions. However, periodic downstream colonization increases the likelihood for the infestation to spread and impact agricultural and municipal water systems that receive water from the river.

Handling editor Télesphore Sime-Ngando.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10452-023-10025-x>.

M. T. Booth (✉)
Department of Biological Sciences, University
of Cincinnati, Cincinnati, OH 45221-0006, USA
e-mail: michael.booth@uc.edu

C. S. Culver
California Sea Grant Extension Program, Scripps
Institution of Oceanography, University of California,
San Diego, CA 92093, USA

C. S. Culver
Marine Science Institute, University of California,
Santa Barbara, CA 93106, USA

Keywords Dreissenid mussels · Population dynamics · Veligers · Invasive species · Reservoir management

Introduction

The invasive quagga mussel (*Dreissena rostriformis bugensis*) has rapidly spread throughout the

southwestern region of the USA, particularly in water conveyance structures and reservoirs throughout southern California that receive water from the Colorado River (Wong and Gerstenberger 2011; Benson et al. 2021). The introduction to Lake Mead, Nevada, a major source of the western infestations, is thought to be a result of mussel-infested bilge water transported via a recreational boat from the Laurentian Great Lakes (Brown and Stepien 2010), with the rapid spread throughout the region undoubtedly due to the transport of planktonic mussel larvae via the artificially connected waterways (Wong and Gerstenberger 2011). In December 2013, quagga mussels were first observed at Lake Piru, a reservoir in the Santa Clara River watershed of Ventura County, California, and their introduction was attributed to transfer via a recreational vessel. Lake Piru is the first known invasion and established population of quagga mussels in the state not associated with water transfers from the Colorado River.

As with other quagga mussel invasions (Western Regional Panel on Aquatic Nuisance Species 2010), there was great initial concern about the potential impacts of the mussel invasion at Lake Piru. Anticipated were substantial costs for maintenance of water infrastructure that supports downstream agriculture, as well as recreational activities at the lake, since the lake is a popular boating and fishing destination and lake water is used to provide potable water to surrounding camp grounds. In addition, preventing further spread of the species into downstream sites was expected to be operationally challenging. Knowing dreissenid mussels invasions could have negative ecosystem-level impacts (e.g., nutrient and oxygen dynamics, harmful algal blooms; Nalepa 2010; Turner 2010), particularly during the initial “boom” phase when populations first establish, stakeholders raised concerns about potential impacts to recreational fishing. While long-term effects are less predictable and have been predominantly focused on lakes and reservoirs and not their associated watersheds (Karatayev et al. 2015), management of sport fishes and endangered species (Western Regional Panel on Aquatic Nuisance Species 2010) are frequently identified as a cause for concern. The presence of critical habitat for the endangered Southern California Steelhead (*Oncorhynchus mykiss*) downstream of Lake Piru (National Marine Fisheries Service 2012) made this invasion

of particular management concern and greatly complicates potential management options (e.g., changes in stream flow from the lake or application of molluscicides).

Although population persistence of quagga mussels requires lentic environments for reproduction (Hasler et al. 2019), concerns over the downstream spread of mussels were further heightened by the potential for colonization of agricultural and drinking water infrastructure downstream of Lake Piru and Santa Clara River watershed. However, large portions of the mainstem Santa Clara River and its tributaries are spatially and seasonally intermittent (i.e., no longer have surface water) potentially limiting the spread, while other reaches are typically perennial due to upwelling groundwater (Beller et al. 2011) and could harbor new colonists.

Since first detecting mussels at Lake Piru, United Water Conservation District (UWCD), with guidance from the authors and an advisory committee and consultants, has taken many measures to monitor and manage the infestations both within the reservoir and the downstream Santa Clara River watershed (Culver et al. 2014a, b). These efforts were conducted as part of their state-mandated monitoring and control plan (United Water Conservation District 2016, 2017, 2018a, 2019, 2020) to maintain recreational operations and fulfill requirements of the U.S. Endangered Species Act and California Invasive Species program. Here we describe the primary monitoring and removal efforts during the first eight years of the invasion to better understand how both natural and anthropogenic factors have influenced the mussel population. Our objectives were to (1) evaluate population dynamics within Lake Piru post-invasion, (2) assess environmental drivers of mussel reproduction and recruitment, (3) and investigate how management of affected infrastructure and water releases from the dam influence mussel populations in the lake and their downstream spread.

Methods

Study system

Lake Piru, constructed in 1955, is a warm, monomictic, mesotrophic lake and water storage reservoir formed by Santa Felicia Dam on Piru Creek in the

upper Santa Clara River watershed of Southern California (Fig. 1). Although the reservoir is primarily operated for surface water capture and downstream groundwater recharge, the lake is also a popular destination for boating and fishing. At design storage capacity, the maximum depth is 41 m and surface area is approximately 500 hectares. From 2005 to 2014, calcium levels ranged from 57 to 110 mg/L, pH from 7.9 to 8.8, and salinity was less than 5 ng/L (United Water Conservation District 2017). The shoreline is characterized by rocky cliffs and steep coarse substrates (gravel to boulders) which extends into the certain parts of the lake and the lake bottom is a mixture of fine sediments (silt and clay) and rock outcrops. Typically, the reservoir fills during the winter from precipitation, but it also receives limited out-of-season water releases from upstream Pyramid Lake as part of the State Water Project storage and delivery system. Water from Lake Piru is conveyed downstream to Piru Creek and the Santa Clara River during the dry season through out-of-season water releases (September–December) which are used to fulfill UWCD's water management role of recharging aquifers and delivering water resources to downstream municipalities, industry, and farms. The water intake tower is in the deepest section of the lake (40 m at capacity) and is approximately 5 m above the lake bottom. Water releases vary seasonally and are mandated to provide flow in critical habitat for endangered steelhead downstream from the lake. The dam contains two turbine units in its small hydro-power facility, which was recommissioned in November 2016. The turbines can be operated when flows exceed about 0.3 m³/s and their total capacity is about 0.7 m³/s, with additional flow routed through other outlets.

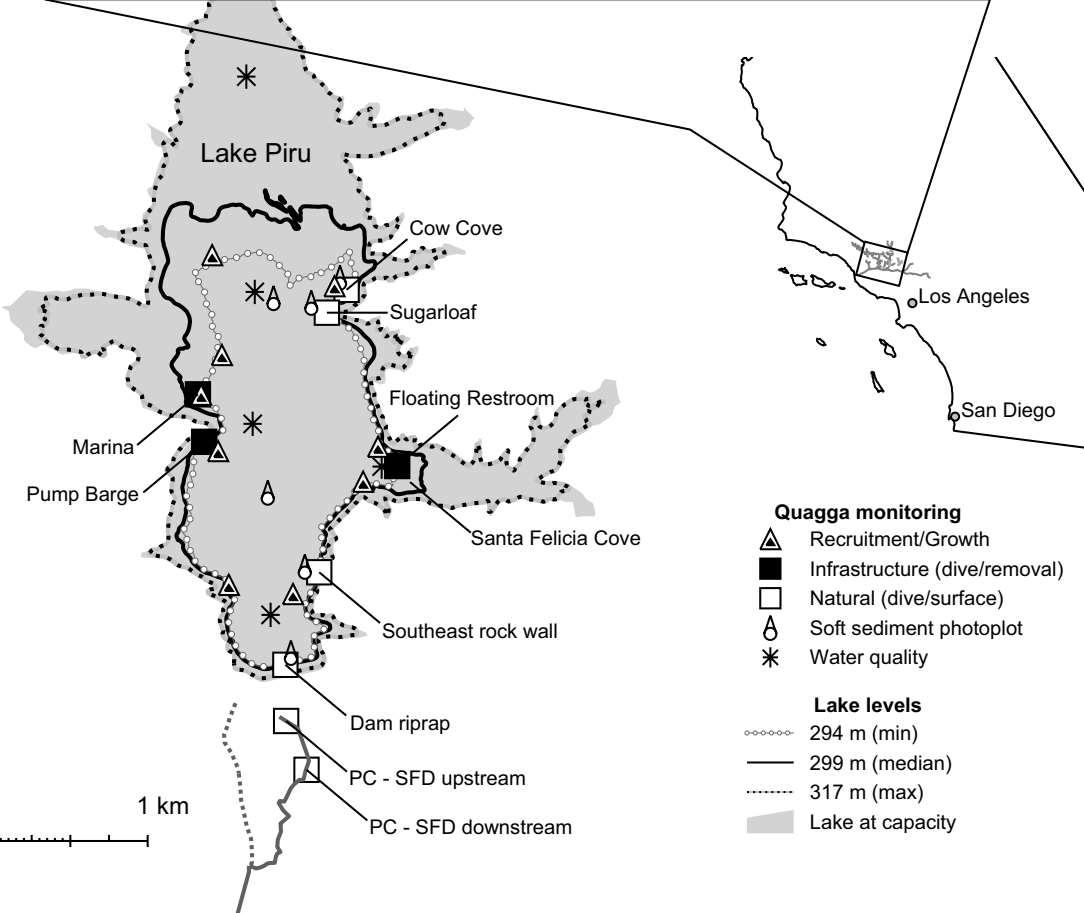
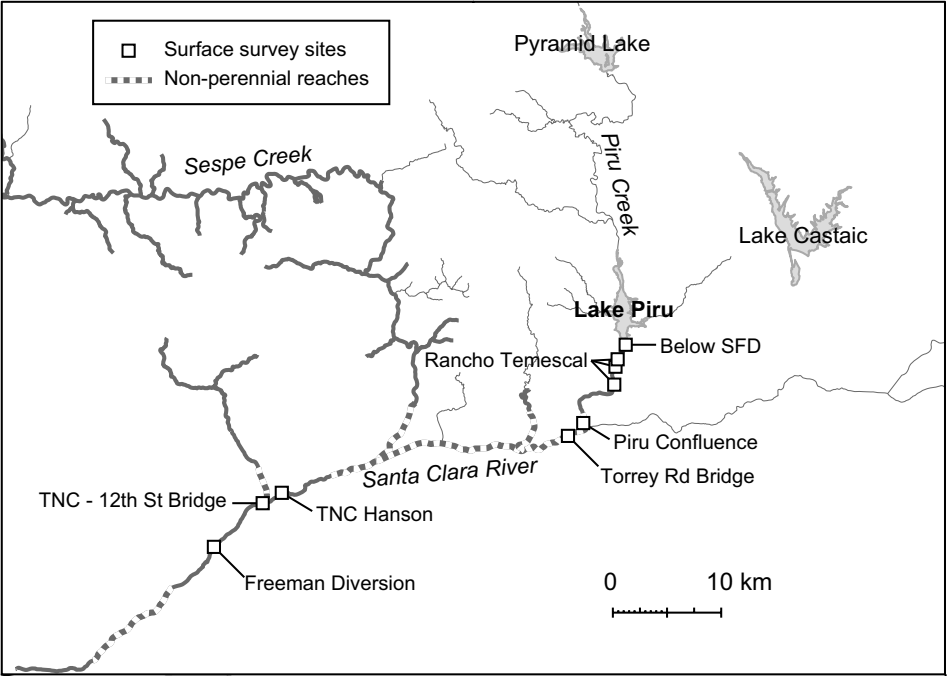
Physical and chemical property measurements

Water quality vertical profile data were collected throughout the study using a multi-parameter water quality meter every two weeks at five locations in Lake Piru (Fig. 1). Temperature, dissolved oxygen, turbidity, specific conductance and pH were measured at 0.6–1.2 m depth intervals from the surface to 35 m depth. The mussel hypoxia threshold of $PO_2 > 2.13$ kPa (Garton et al. 2014) was estimated as 0.85 mg/L, assuming salinity of 500 ppm, 1 atm, and 25 °C. Lake level and creek flow data were collected

from USGS gages (#11,109,700 and #11,109,800, respectively) using the dataRetrieval package (De Cicco et al. 2018) in Program R. Mean temperature for the epilimnion, hypolimnion, and whole lake, as well as the thermocline depth and Schmidt stability were calculated using the rLakeAnalyzer package (Winslow et al. 2019) in Program R. We calculated the thickness of the hypoxic zone as the difference between the depth of the shallowest DO measurement ≤ 0.85 mg/L and the total depth at the site at the time of observation. Bathymetric data for 2005, 2015, and 2020 were provided by UWCD.

Lake mussel density and biomass

Mussel density and biomass were measured on natural and artificial hard substrates, as well as surface coverage of fine sediment regions during routine maintenance activities. [See supplemental material and Figure S1 and S3 for timing and methods of maintenance-associated management activities.] Beginning in 2014, divers collected mussels 3–5 times per year (Figure S1) from a 0.125 m² quadrat at 7 sites (Fig. 1) containing hard substrates prior to mechanically removing mussel from the site. Four of the sites had natural hard substrate with varying topography: steep vertical rock walls and ledges (Sugarloaf), gentle sloping cobble areas with interspersed with large boulders and walls and ledges (Cow Cove, SE rock wall), or interspersed rock habitat (dam rip rap). The three other sites contained infrastructure surfaces (docks, pump barge and floating restrooms). Depending on site topography and lake level, depths for dive sampling varied. In general, divers collected quadrat samples at each site in the depth zone where mussels were most prevalent (characterized as more than one per meter square). For each quadrat sample, either the entire sample or a subsample of approximately 300 mussels were weighed (to the nearest g) and measured (shell height from umbo to midpoint of shell valve to the nearest 5 mm using a caliper) to determine biomass, density and size structure. When subsamples were taken, the entire sample was also weighed to determine the total biomass, and used to calculate the total number of mussels. Since mussels were grouped into 5 mm size classes, mussels were considered reproductive at sizes ≥ 5 mm (Vailati et al. 2001).



◀**Fig. 1** Location of Lake Piru and the Santa Clara River watershed in southern California. The inset shows sites in Piru Creek and the Santa Clara River surveyed for quagga mussels (monthly or quarterly). Monitoring locations within Lake Piru and relevant locations of infrastructure or repeated sampling. Lake shorelines at various lake levels are shown to highlight the dramatic changes in inundated area during the course of the study. Monitoring sites were only sampled when inundated

To quantify recruitment on soft sediments, beginning in November 2015, fixed photoplots were designated at six locations on the lake bottom in fines habitat using a central rebar stake and a dive compass for orientation. Photoplot locations ranged in depth from 13 to 3.4 m at minimum lake level (296 m) and 35 m to 25.4 m at the highest lake level (318 m). The protruding rebar stake was located and then a 0.5 m×0.5 m quadrat was placed on the bottom and a digital image was captured at 3 non-overlapping locations adjacent to the rebar stake when visibility was sufficient to collect a clear image. Images were de-fisheyeed using the wide-angle correction tool in Adobe Photoshop CS6 and percent cover of mussels was estimated within each quadrat using digital imaging software (Fiji/Image J; Schindelin et al. 2012).

Recruitment and growth

Monthly assessments of mussel recruitment and growth also began in January 2015. Lines containing artificial substrates (herein called “samplers”) were deployed throughout the lake (Fig. 1). The number of locations with samplers varied over time, ranging from 4 to 9 locations with a median of 7 sites, due to loss of samplers from weather or vandalism. The samplers were deployed 1–2 m from the lake bottom at sites shallower than 7–9 m total depth (Marina, North), and at approximately 8 m below the water surface in deeper areas (Dam, Pump Barge, Cow Cove, Sugar Loaf, Santa Felicia Cove), i.e., the epi- and metalimnion when the lake is stratified. Samplers were composed of three 0.2 m×0.2 m polyvinyl chloride plates—one for recruitment, two for growth—suspended on a threaded rod. A grid was engraved on the two growth plates dividing them into six equal-sized cells each ($n=12$ cells). Each month, mussels were carefully removed from the entire surface of the recruitment plate (0.08 m²) using a plastic putty knife to avoid damaging the shells

and then frozen until processed. Mussels also were collected from a single grid cell of one of the growth plates monthly, with previously sampled cells scraped to remove any newly recruited mussels. Mussel settlement and growth also was assessed from the data generated by the previously described quarterly dive surveys.

In the laboratory, frozen samples were thawed, washed on a 153 μm sieve, and mussels were measured to the nearest 5 mm using a ruler or caliper and counted. For both dive surveys and artificial substrates, recruitment was calculated as the number of mussels per m² of sampled area and divided by the number of days since last sampled. For mussels collected during quarterly dive surveys, maximum growth was estimated as the 90th percentile size class divided by the number of days since removal. For artificial substrates, a random subset of 75 mussels > 5 mm were measured to the nearest 0.01 mm using digital calipers, all mussels < 5 mm were counted, and additionally the 10 largest mussels were measured. Growth for mussels > 5 mm was estimated as the difference in modal lengths within the sample. Modes, i.e., cohort mean size, were identified by taking the second derivative of the probability density function of mussel size in Program R (R Core Team 2022). Modes were not always clearly defined and so probability density plots were visually examined to remove or estimate the value of extraneous modes. Growth was estimated as the difference between mean cohort size in the subsequent month.

Veliger abundance

Veliger abundance was first measured in February and April 2016 at four sites within Lake Piru, with monthly measurements implemented in May 2016 at five locations (Fig. 1). Depth-integrated vertical tows (2 m less than total water column depth) were performed at each site using a plankton net (63 micron mesh, 30 cm diameter) to achieve a minimum of 1000 L total tow volume (total tow length ≥ 15 m). When multiple tows were required to achieve the sample volume (i.e., sites < 17 m depth), all tows were combined into a single sample for analysis. Unpreserved, unbuffered samples were transported on ice to the laboratory. From April 2016 to June 2018, samples were shipped on dry ice to the Burton Lab

at Scripps Institution of Oceanography, University of California, San Diego. Samples were refrigerated until analysis and processed within 1–2 days of delivery. From May 2018 to present, veliger samples were processed at the UWCD laboratory within 72 h of collection. Samples were processed following the Reclamation Detection Laboratory for Invasive and Native Species protocol (2013). In brief, samples were poured into Imhoff cones and allowed to settle for 18 h. Five 15 mL subsamples were collected from the settled sample, and for each subsample, 1 mL was placed into a Sedgewick Rafter slide and all veligers were enumerated using a polarizing filter. To account for potential differences in handling and processing between the two labs, during May and June 2018 seven replicated samples were processed independently in each lab and UWCD's veliger counts were rescaled using a linear regression ($\text{Veligers}_{\text{Scripps}} = 14.45 * \text{Veligers}_{\text{UWCD}} + 0$; adjusted $R^2 = 0.86$ $t = 6.568$, $p < 0.001$).

Downstream mussel densities

Monthly surface surveys were conducted on lower Piru Creek (1) 0–500 m downstream of Santa Felicia dam (beginning February 2016), (2) on Rancho Temescal at sites 0.8 km, 2.3 km, and 3.3 km downstream (beginning February 2018) and (3) 14.5 km downstream, at the confluence of Piru Creek and the Santa Clara River (beginning February 2016). Based on locations with access and typically perennial flow, an additional four sites along the Santa Clara River were surveyed quarterly. Surveyors collected a minimum of 10 to 20 randomly selected cobble-sized substrates (surface area mean \pm s.d., 0.02 ± 0.05 m²), measured their size along the intermediate axis, assessed presence/absence of quagga mussels, and, when present, recorded the estimated number of quagga mussels visually determined to be in one of three size classes (<5 mm, 5–10 mm, >10 mm) and noting if any mussels were >20 mm. The surface area of individual cobbles was calculated as the rock intermediate axis squared.

Population and environmental controls on reproduction and recruitment

To examine the relationship between (1) reproductive mussels (>5 mm) and veliger abundance and (2)

veliger abundance and recruitment in the lake, we constructed a set of linear mixed effects models using the lmer function in the lme4 package (Bates et al. 2015). Data used in the modeling effort was from dive sampling of hard substrates (see Lake Mussel Density and Biomass) and recruitment settlement plates (see Recruitment and Growth). Observations on mussel in soft sediments were not included because these habitats typically did not contain mussels. Not all sampling efforts (e.g., water quality, recruitment, veligers) occurred at identical locations, so sites were grouped by lake region and named according to geography or pertinent infrastructure in the area (North, Santa Felicia Cove, Marina, Pump Barge, Dam). Lake region was included in models as a random effect and a variety of environmental covariates were considered as fixed effects, including metalimnion water temperature (7.3 to 9.8 m), Specific Conductivity, Turbidity, DO% saturation, lake elevation, and lake fill status (years where lake filled in winter and was drained in summer/fall). Prior to defining potential models, model parameters were assessed for evidence of collinearity using linear regression. For each pairwise regression, we calculated Variance Inflation Factor (VIF) equivalent to $1/1 - R^2$. Values greater than 3 indicate strong collinearity (Zuur et al. 2010). Specific conductivity, lake elevation, and lake fill status were significantly correlated and had VIF higher than 3. Although we expect that both lake elevation and specific conductivity could influence reproduction and recruitment for different reasons, high conductivity only occurred during dry years when the lake elevation was low. Instead, we used binary annual lake fill status as a proxy for specific conductivity and lake elevation. Since mussels were frequently removed from infrastructure and veligers were spatially variable within the lake but not consistently different among sites, only the density of reproductive mussels on natural substrates was included in analysis 1.

To account for the lifecycle of quagga mussels, we incorporated temporal lags into the model for veliger abundance and recruitment in the lake. Autocorrelation and cross-correlation functions require equally spaced data with no missing values. As described previously in the recruitment section, some recruitment plates were lost or vandalized. To assess suitable lags for veligers, we used only

a subset of the data from the marina and Santa Felicia Cove to generate time-series, and used the “acf” and “ccf” functions in Program R to generate autocorrelation and cross-correlation plots. For model generation, we used the complete dataset (all recruitment plate sites), but omitted missing values (i.e., where lagged values were not available).

We used an Information Theoretic Model Comparison procedure to identify best performing models (Burnham and Anderson 2004). Model comparison was performed using the “dredge” function in the MuMIn package (Barton 2022). We used the Akaike information criterion, adjusted for small sample size (AICc) and ΔAICc to rank models. Where $\Delta\text{AICc} < 2$, all models were considered functionally similar and parameter importance was compared by the proportion of top ranked models that included each term, as well as each term’s explanatory power. To assess the overall explanatory power of the models and predictors, we computed generalized and partial R^2 for mixed models following the framework of Jager et al. (2017) and Nakagawa and Schielzeth (2013) using the r2beta function in the r2glmm package (Jaeger 2017).

Results

Physical and chemical property measurements

Lake elevation was consistently low during the initial invasion period (300 ± 5.7 m, mean \pm s.d.; spillway elevation 321.5 m) and remained below the spillway elevation throughout the study period (Fig. 2a). Lake Piru filled rapidly and substantially (≈ 10 – 20 m) during storms in early 2017, 2019, and 2020 and was drawn down (≈ 8 – 15 m) and released into Piru Creek for groundwater recharge purposes during those same years. Lower Piru Creek flows are regulated releases from Lake Piru and typically base flow was held constant at $0.2 \text{ m}^3 \text{ s}^{-1}$. In years with substantial winter rainfall, monthly base flow was elevated (0.3 – $0.6 \text{ m}^3 \text{ s}^{-1}$) depending on prescribed rainfall triggers, which occurred in 2017, 2019, and 2020. During the steelhead migration season (January 1–May 31) occasional short duration higher flows (< 1 week, $5.7 \text{ m}^3 \text{ s}^{-1}$) occurred (2017, 2019, 2020). Extended (weeks–months), high magnitude ($< 14.6 \text{ m}^3 \text{ s}^{-1}$) out-of-season water releases occurred during fall 2015,

2017, 2018, 2019, 2020 to replenish downstream groundwater basins (Figure S2 and Fig. 2b). Except during winter storms and the extended high magnitude out-of-season releases, water from Piru Creek naturally percolated subsurface at the confluence with the Santa Clara River and upstream of the Torrey Rd bridge (Fig. 1).

Whole lake temperatures remained relatively consistent during the study, ranging from 9 to 26 °C (Fig. 2c). Lake temperatures were always greater than the lower spawning threshold for quagga mussels (9 °C; Garton et al. 2014), but lake temperatures slightly exceeded the upper spawning limit (24 °C) during several months each year. Temperatures were always below the upper thermal limit for mussel survival (28 °C; Garton et al. 2014). The metalimnion typically formed between 7.3 to 9.8 m and the lake remained stratified from March to September, though the strength and duration of stratification varied substantially among years, as shown by variation in Schmidt stability (Fig. 2e), with weak stratification in 2015 and 2016. Bottom DO levels ranged from 0 to 12 mg/L (6.5 ± 3.0 , mean \pm s.d.), but typically were greater than the mussel hypoxia threshold of 0.85 mg/L (Fig. 2d) except later during strongly stratified periods. Shallow sites were above the hypoxia threshold except on two monitoring dates (Fig. 2d, e) when these sites were stratified and relatively deep due to elevated lake levels in 2019 and 2020. Turbidity typically ranged from 0 to 135 ntu lake wide, but was higher (4.6 ± 10.7 ntu, mean \pm s.d.) in shallow sites than in deep sites when the lake level was low (3.8 ± 9.5 , mean \pm s.d., Figure S2). Turbidity briefly spiked in August 2016 (≈ 100 ntu), coinciding with a breakdown in stratification (Figure S2). Comparison of lake bathymetry between 2015 and 2020 showed patches of 0.3 to > 3.3 m of sediment deposition along the southeast shoreline, adjacent to the marina, within Santa Felicia Cove, and within the delta formed as Piru Creek enters the reservoir. Dive surveys indicated that this deposition occurred during the periods of rapid lake filling in 2017 and 2019, and that deposition of sediment occurred throughout the lake, even in patches where the bathymetric survey did not report measurable sediment accumulation.

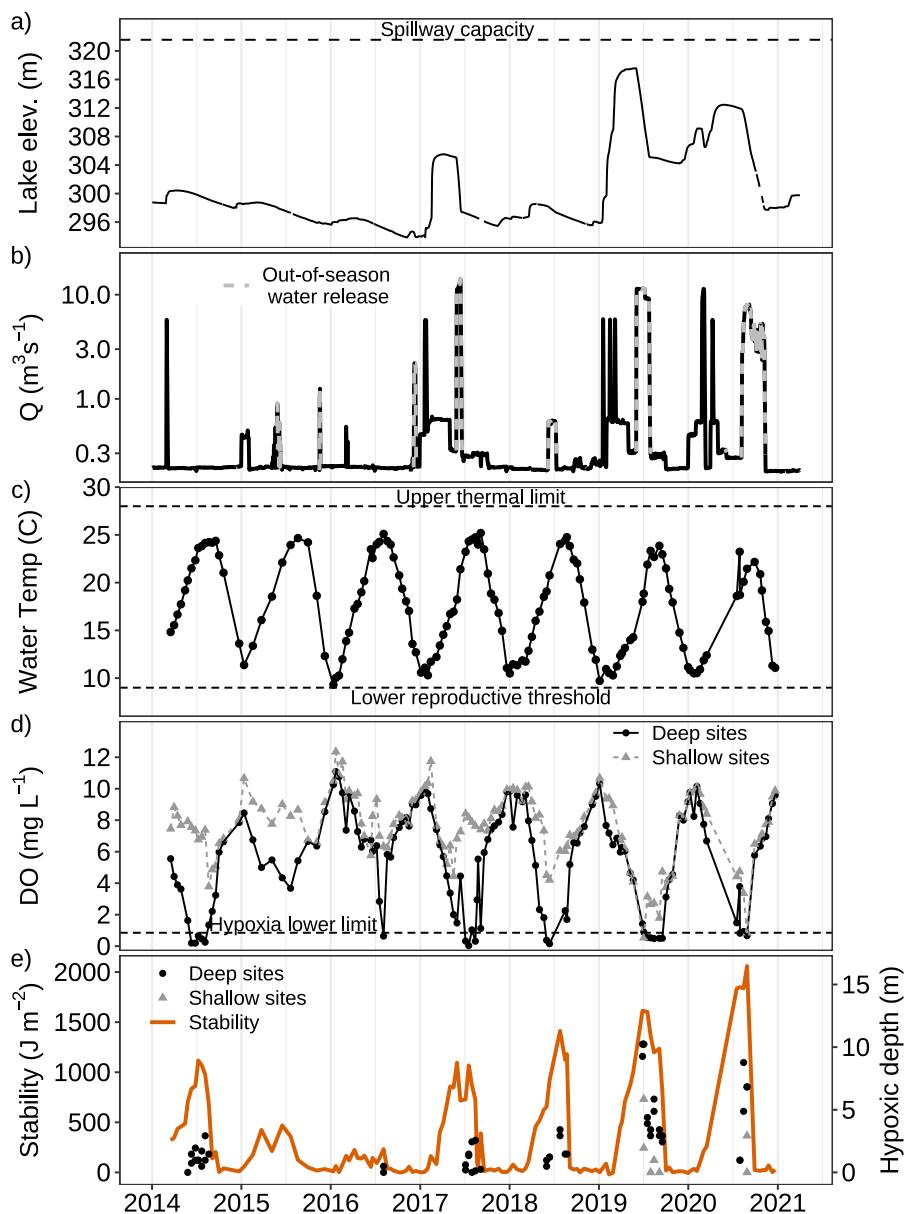
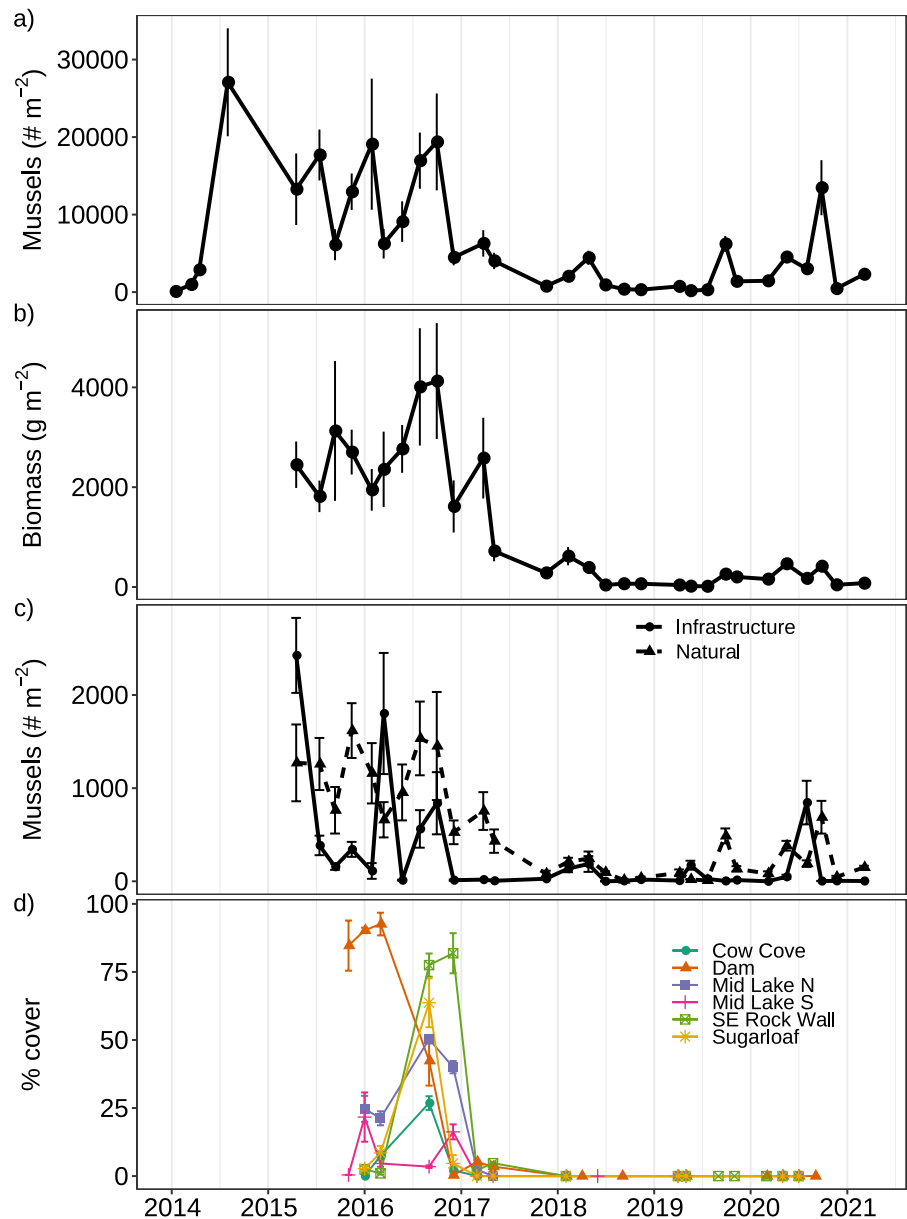


Fig. 2 Environmental parameters for Lake Piru and Piru Creek. **a** Lake water surface elevation (mean sea level datum) as reported at USGS gage #11,109,700. **b** Discharge in Piru Creek below Santa Felicia dam, USGS gage #11,109,800. The solid line indicates standard flow operations, including those intended for steelhead migration and linked to regional rainfall, while the dashed line indicates water releases intended to convey water downstream for water resource purposes and occur outside of the rainy season. Note that the y-axis is log scale to highlight periods of elevated baseflow. **c** Whole lake mean temperature calculated from vertical temperature profiles using RLakeAnalyzer, and **d** mean dissolved oxygen levels adjacent

to the bottom of the lake (bottom 3 m) for monitoring sites in deep and shallow regions of the lake. **e** Schmidt stability calculated from vertical temperature profiles using RLakeAnalyzer shown with the black solid line and points reflecting the depth (relative to the bottom of the lake at the sampling site) where conditions became hypoxic ($< 0.85 \text{ mg/L}$) in deep and shallow regions of the lake. For **d** and **e**, deep and shallow sites qualitatively describe relative site depth for sampling locations when lake levels was low (2014–2016), with shallow sites including only the epilimnion and deep sites including all lake layers. In 2019 and 2020, shallow sites were of sufficient depth to include all lake layers

Fig. 3 **a** Mussel density on natural hard substrates, **b** mussel biomass on natural hard substrates, **c** Density of potentially reproductive mussels (> 5 mm) on infrastructure and natural hard substrates. All mussels were removed from infrastructure subsequent to the sampling, but mussels were not managed on natural surfaces. **d** Percent surface cover of mussels on fine sediments estimated from fixed photoplots at six locations throughout the lake. All points are mean \pm s.e. Values are separated by location to highlight differing trajectories among sites (e.g., percent cover at the dam peaked and crashed several months prior to all other sites. For **a**, **b**, **c** samples were collected at depths less than 9 m and are likely reflective of epi- and metalimnetic conditions during stratified periods. For **b**, **c**, **d**, sampling did not begin until 2015



Lake mussel density and biomass

Mussels were present on all hard substrates within the lake in 2014. Mussel density on hard natural substrates rapidly increased and peaked in late July/early August 2014 (Fig. 3a; $27,069 \pm 6964$ mussels m^{-2} , mean \pm s.e.). Mussel density fluctuated, but remained high through September 2016, then dramatically declined during 2017 and since has remained at approximately 24% of initial mean mussel density. Mussel biomass on natural substrates,

which was not measured until 2015, peaked in mid-2016 (4126 ± 1161 g m^{-2} , mean \pm s.e.; Fig. 3b), then declined during 2017 to approximately 13% of the 2015–2016 level. The density of reproductive mussels (> 5 mm) on infrastructure was initially reduced to low levels after mussel removals (see Supplementary material) were implemented, but peaked again in mid-2016, before returning to low abundance (Fig. 3c). Reproductive mussel density on natural substrates was 2–10 times higher than on infrastructure until late 2017, when density crashed and remained low

relative to the initial invasion period (Fig. 3c), with the exception of a short-lived spike in summer 2020.

Mussels were occasionally observed in fine sediment areas of the lake primarily attached to debris or shells of Asian clam or dead quagga mussels during dive surveys in 2014 and 2015, but were not quantified. Only one site (dam) had high percent cover (66–94%) of mussels on fine sediments during the initial surveys in November 2015 and January 2016, however this site also rapidly declined while the other locations were increasing (Fig. 3d). For all other sites, mussel cover within fixed photoplots rapidly increased in 2016 and reached approximately 25–75% cover during the fall and winter of 2016 (Fig. 3d). Starting in early 2017, mussels were no longer observed within the fixed photoplots of fine sediment, or areas outside the photoplots, throughout the rest of the study.

Recruitment and growth

Mussel settlement rates were seasonally variable over several orders of magnitude (Fig. 4). Note that because the samplers were placed at depths < 9 m, during the stratified period the reported settlement rates likely reflect patterns within the epi- and metalimnion, rather than the hypolimnion. Settlement peaked in July 2015 (Fig. 4b; 6368 ± 5226 mussels $m^{-2} d^{-1}$, mean \pm s.e.) on the plates and total biomass accumulation on infrastructure (Fig. 4b; $14.2 g m^{-2} d^{-1}$). Settling rates were lowest in March 2017 on artificial substrates (none detected), however, settlement was observed on all other sample dates, and settled mussels were observed during the removal efforts on infrastructure in March and May 2017 (Fig. 4b). On infrastructure, the lowest settling rates occurred prior to November/December dive removal efforts in 2016, 2017, 2018, 2019, and 2020. Although recruitment rates varied spatially over time, there was no significant difference in rates among the lake regions sampled (ANOVA, $df=4$, 529 , $F=2.161$, $p=0.07$).

The size structure of mussels on natural substrates declined significantly over time (Fig. 5; ANOVA, $df=1$, $64,791$, $F=3393$, $p<0.0001$), with the most dramatic change occurring between 2017 and 2018 (-4.17 ± 0.09 mm, $t=48.1$, $p<0.001$). Mussels greater than 30 mm were rare (13 out of 117,161 measured, 0.01%) and completely absent subsequent to the first fill event in 2017. After mussel removal maintenance measures began in 2015,

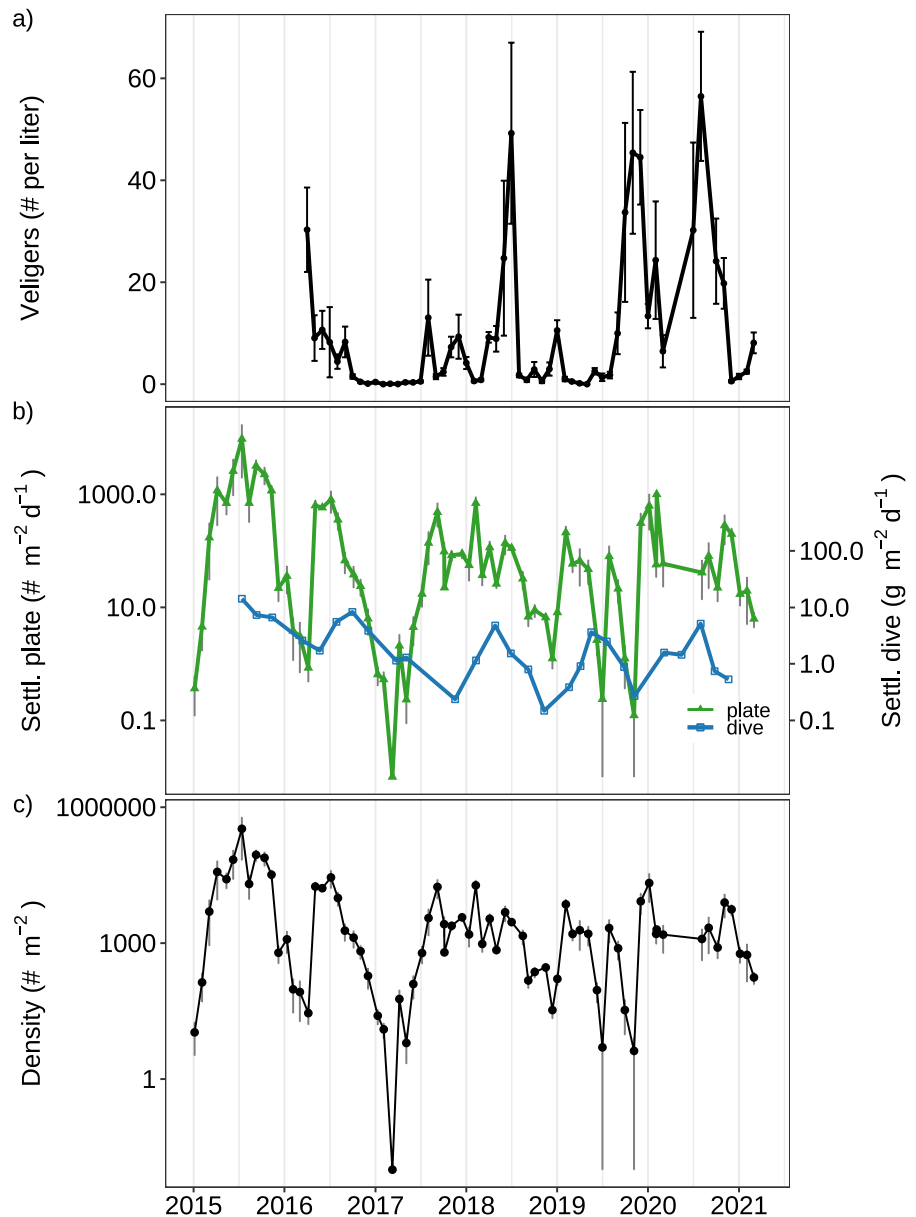
mussels > 10 mm were rarely found on infrastructure and composed $1.4 \pm 0.34\%$ (mean \pm s.e.) of the total mussels removed.

Maximum shell growth rates, estimated from mussels removed from infrastructure, were 0.17 ± 0.02 mm d^{-1} (mean \pm se). Mean cohort shell growth rates, estimated from artificial settling plates, were 0.095 ± 0.006 mm d^{-1} (mean \pm se). Growth was not significantly related to month (ANOVA, $df=10$, 24 , $F=0.915$, $p=0.54$), however, there was a trend towards increased growth rates between January and June, and measured growth rates were highly variable from August to December (Fig. 6).

Veligers

Veligers were continuously present in the lake during the monitoring period, but abundance was temporally and spatially variable within the lake and watershed. Veliger abundance significantly varied throughout the year (Fig. 4a and 7a), with peaks occurring at different times depending on the year: in April (2016, 30.3 ± 8.2 , mean \pm se), August (2017, 13.1 ± 7.5 ; 2020, 3.9 ± 0.9), May (2018, 7.7 ± 2.9), and November (2019, 3.9 ± 1.1 veligers). There were no significant differences in veliger abundance among sites within Lake Piru (ANOVA, $df=4$, 275 , $F=0.128$, $p>0.05$). However, veliger abundance in Piru Creek below Santa Felicia Dam was typically much lower than in the lake ($15.7\% \pm 19.8\%$ of lake abundance, mean \pm s.d.) and frequently below detection in at least one of the sites (Fig. 7b). However, during two sampling periods when the lake was not stratified, veligers were more abundant downstream of the dam than in the lake. In December 2016, maximum veliger abundance in Piru Creek was 4.7 veligers L^{-1} while lake abundance was 0.1 veligers liter $^{-1}$ during operational testing of the hydropower infrastructure and occurred when water was released from the dam penstock (a large pipe which only has flow when dam releases exceed approximately $0.7 m^3 s^{-1}$) which also included a population of mussels within it. In February 2017, multiple sites in the lake were below detection while veliger abundance in Piru Creek below SFD was 0.03 veligers liter $^{-1}$. Veliger abundance was higher immediately below the dam (SFD upstream) than at the site 500 m downstream (SFD downstream), except on two dates (Fig. 7b). In Piru Creek near the confluence with the Santa Clara River (14.5 km downstream of

Fig. 4 Patterns of veliger abundance and mussel settlement in Lake Piru. **a** Mean veligers abundance from vertically integrated tows of at least 1000L at multiple sites ($n=4$ or 5) within the lake, **b** Settling rates of mussels on artificial plate samplers and as biomass, estimated from mussel removals from infrastructure, and **c** mussel density on artificial plate samplers. Data from veliger samples and plate samplers are means \pm s.e., while dive samples in **b** are single point estimates. The y-axis for **b** and **c** are logarithmic. Note that recruitment was not quantified prior to 2015



SFD), veligers were only detected in 2020 and at low abundance (0.15 to 0.03 veligers liter⁻¹). All positive detections at the confluence site were subsequent to periods of elevated flow releases (relative to typical 0.2 m³ s⁻¹ base flows from Lake Piru), and 4 out of 5 positive detections occurring during the fall out-of-season flow releases for groundwater recharge (Fig. 7b, c; August to November 2020).

Downstream mussel densities

Mussel abundance varied with distance downstream. Mussel densities in the 500 m reach below Santa Felicia Dam (SFD) were similar to and broadly tracked the trends observed on natural substrates within the lake (Figs. 4, 8), declining dramatically in 2018 and remaining low until late 2019, then rebounding to earlier (2016) levels. However, mussels downstream

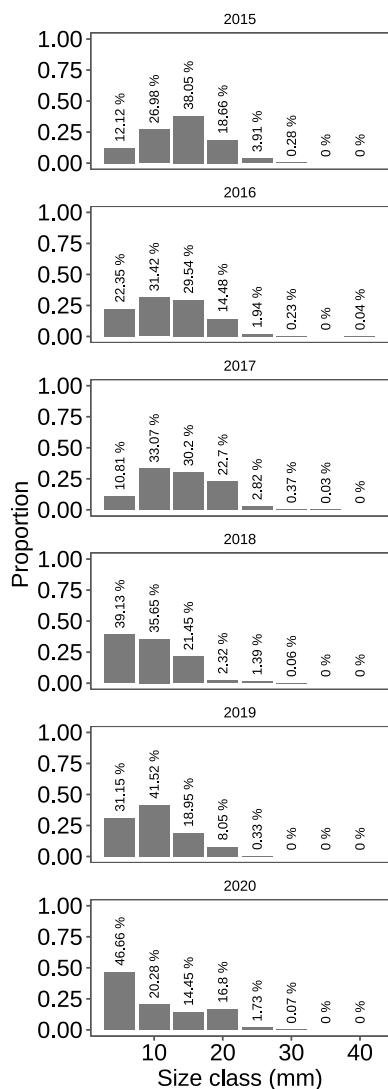


Fig. 5 Overall size distribution of mussels collected from natural substrates in Lake Piru for each year. Value labels over the bars represent the percent of the sample observed within the size class (e.g., 0–5 mm, 5–10 mm) because some bars are too small to be visualized

of the lake were consistently small, with only 217 mussels > 20 mm out of 187,309 mussels counted. Mussels under 10 mm were most abundant until 2017, when both size classes were at low density and equally abundant in the reach immediately below the dam until rebounding sometime in 2020 (exact timing unclear due to limited sampling in 2020; Fig. 8a).

Three sites were monitored in Rancho Temescal (0.8 km, 2.3 km and 3.3 km downstream of SFD).

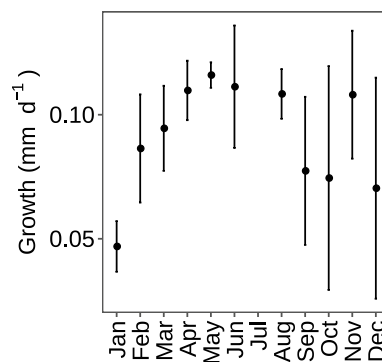


Fig. 6 Seasonal variation in individual growth rate for quagga mussels in Lake Piru estimated as the difference in mean shell length for a cohort between subsequent months. Data shown are means \pm s.e

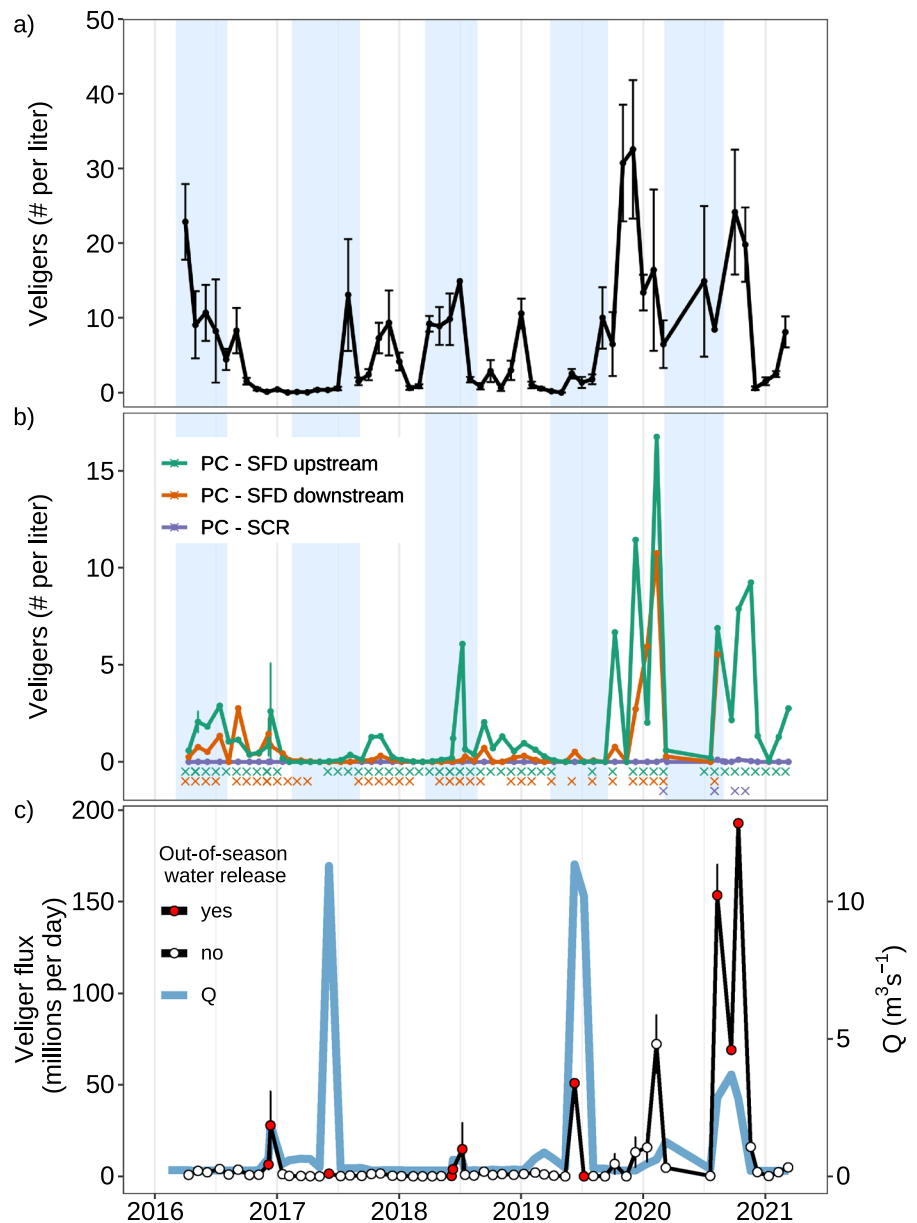
Monitoring at the two most upstream Rancho Temescal sites (0.8 km and 2.3 km downstream of dam) did not begin until 2018, and mussels were present at low abundance (6.1 ± 3.9 mussels m^{-2} , mean \pm s.d.) throughout the monitoring period (Fig. 8b, c). Mussels were not observed in Piru Creek at the Rancho Temescal site 3.3 km downstream. Mussels were not observed at the confluence of Piru Creek and the Santa Clara River (14.5 km downstream of SFD) until October 2017 (Fig. 8c). Mussel density at the confluence peaked in fall 2017 and spring 2018 (primarily composed of mussels < 10 mm), but mussels were consistently present once established (14.1 ± 49.6 mussels m^{-2} , mean \pm s.d.).

Mussels were only found in sites along the Santa Clara River downstream of the confluence with Piru Creek during two monitoring periods in 2017, all on cement bridge abutments (Table 1; Torrey Rd Bridge (16.7 km downstream): one mussel observed in August 2017, 12th St Bridge in Santa Paula (40 km downstream): < 15 mussels observed in August and September, 4 mussels in November). Mussels were never observed on natural substrates at either bridge site or at the Hanson property.

Population and environmental controls on reproduction and recruitment

For model 1, assessing the relationship between reproductive mussels (> 5 mm) and veliger abundance the two top models ($\Delta AICc < 2$) both included lake fill status, temperature, and dissolved oxygen,

Fig. 7 Mean veligers abundance from **a** vertically integrated tows of at least 1000L at multiple sites ($n=4$ or 5) within Lake Piru and **b** timed drift net deployments of at least 1000L at 3 sites in Piru Creek (PC). Santa Felicia Dam (SFD) upstream is 100 m below the outlet works, SFD downstream is approximately 500 m downstream of the dam, and the Santa Clara River (SCR) is approximately 10 km downstream of SFD. Water released into Piru Creek is taken from approximately 5 m above the lake bed. Data shown are means \pm s.e., however, for most dates in Piru Creek, only a single sample was collected from each site. X marks below the graph indicate dates when veligers were detected (to highlight dates with low abundance, but positive detection.). **c** Mean veliger flux (concentration * discharge) and stream discharge (Q m^3/s) below Santa Felicia Dam, with both SFD locations combined. Due to lack of available analytical facilities, veliger quantification did not begin until 2016. In **a** and **b** light blue boxes show the approximate periods of stratification based on Schmidt stability (see Fig. 2)

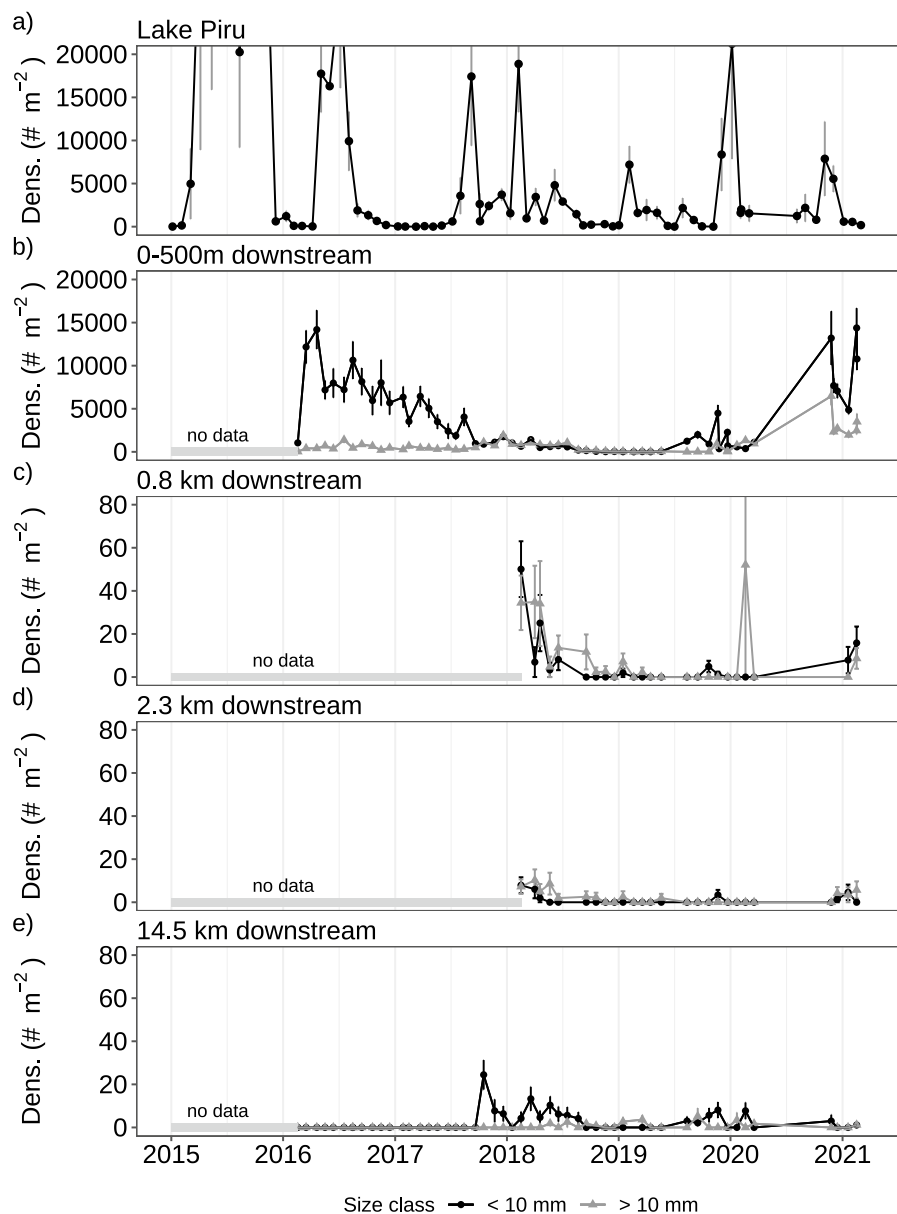


but the simplest model did not include reproductive mussel density (Table 2). For model 1, no strong relationship was found between environmental factors and mussel reproduction and recruitment: For the model with the least parameters ($\log_{10}.$ Veliger.per.Liter \sim DOsat + Fill + Temp.C) the full model $R^2=0.335$ (95% confidence limits, 0.431–0.248), with partial $R^2=0.208$ (0.302–0.124) for fill status, 0.161 (0.252–0.084) for temperature, and

0.023 (0.077–0.001) for dissolved oxygen percent saturation.

For model 2, the relationship between veliger abundance and recruitment in the lake was significantly autocorrelated (i.e., ACF greater than the confidence interval) with a lag of one month, and significant cross-correlation with recruits with a lag of 2 months in the subset of data from the marina and Santa Felicia Cove. Since values lagged by 1 month were correlated, including both current and lagged

Fig. 8 Comparison of settled mussel density within **A** Lake Piru (complete data shown in Fig. 4B) and surface surveys (enumeration of mussels on the surface of ≥ 10 cobbles) at sites downstream of Santa Felicia Dam **B** 0–500 m from Santa Felicia Dam to the Rancho Temescal property boundary, **C** 0.8 km downstream in Rancho Temescal, **D** 2.3 km downstream in Rancho Temescal and **E** 14.5 km downstream at the confluence of Piru Creek and the Santa Clara River. Data shown are means \pm s.e. Note that surveys were also completed in Rancho Temescal at 3.3 km downstream, however, no mussels were observed during the study period



values would result in models with confounded variables. Thus, we used a 3 month rolling average instead, consisting of current veliger abundance, 1 month, and 2 month lagged values. All of the top 5 models included the 3 month rolling average of veliger abundance, with two models including dissolved oxygen percent saturation or temperature, and one model including turbidity (Table 2). The simplest model included only the 3 month rolling average of veliger abundance as a fixed effect, with a full model $R^2 = 0.303$ (95% confidence limits, 0.419–0.193). Full

model R^2 was between 0.305 and 0.317 for models including water quality parameters, with partial R^2 for individual water quality parameters ranging from 0.002 to 0.018.

Discussion

Our investigation of the quagga mussel infestation at Lake Piru provides new insight into the influence of natural events and human-mediated activities on the

Table 1 Combined results of semiquarterly supplemental surface surveys at sites on the mainstem Santa Clara River downstream of Piru Creek. Distances for each site listed are relative to Santa Felicia Dam. Q1 is January–March, Q2 is April–June, Q3 is July–September, Q4 is October–December

Site	2017				2018				2019				2020				2021						
	Q3	Q4	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4	
Torrey Rd Bridge (15.7 km)	Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected
TNC-Hanson (38 km)	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected
TNC-12th St. Bridge (40 km)	Detected	Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected	Not Detected

invasion, its spread, and potential control. Although densities were quite low when first assessed in January 2014 (Culver et al. 2014a), the mussel population rapidly expanded within just 3 months and eventually reached high densities and settlement rates similar to those reported by Strayer et al. (2019) for other long-term population datasets across Europe and North America. The population continued to increase and remained high over the next 2 ½ years. This “boom” period occurred during an extreme drought with very mild winter conditions and weak summer stratification. The lake level remained consistently low with minimal level fluctuations due to a lack of winter precipitation within the watershed. Although the lake stratified during this period, dissolved oxygen levels remained well above the hypoxia lower limit for mussels for nearly the entire time. These conditions likely provided a prolonged period of optimal environmental conditions for the mussels leading to the rapid increase and persistent high mussel infestation.

The mussel infestation followed patterns documented in other waterbodies. The substantial lake infrastructure (docks, pumphouse, floating restrooms) and rocky habitat were colonized first, presumably because it provided the hard substrate that mussels prefer and was adjacent to the site of introduction. However, as the population continued to flourish over the next few years, mussels colonized soft sediments, attaching to debris and each other. Initially, the peak settlement rate (June 2015, 1.9×10^5 mussels m^{-2} month $^{-1}$) in Lake Piru was within the range observed in Lake Mead (1×10^4 – 1×10^6 mussels m^{-2} month $^{-1}$), but on average settlement was 10–100 times lower than rates observed in Lake Mead. Despite these lower settling rates, within 2 years of detection (late 2015), mussels were regularly found on soft sediments, similar to patterns observed in Lake Erie (Dermott and Munwari 1993; Dermott and Kerec 1997) and Lake Mead (Wittmann et al. 2010). Such high mussel settlement in this less suitable habitat represented a vast expansion of the infestation and was likely due to weak stratification when the lake level was low, which functionally eliminated seasonal hypoxic conditions from the lake bottom.

Throughout the study, growth rates in Lake Piru were similar to those observed in Lake Mead (Wong et al. 2012). However, our sampling approach primarily focused on relatively small mussels (5–10 mm) and growth rates were highly variable during fall

Table 2 Linear mixed models parameterized to relate 1) the relationship between reproductive mussels (> 5 mm) and veliger abundance and 2) the relationship between veliger abundance and mussel recruitment in Lake Piru. The top 10 or 11 models are shown, in order of the best fit model from AIC criteria. Upper and lower 95% confidence intervals for model R^2 are shown in []

Fixed effects										
	df	AICc	Δ AICc	Model R^2	Intercept	log ₁₀ Reprod_Mussels_m2	DOsat	Fill	Temp.C	Turbidity.ntu
<i>Reproductive mussels (> 5 mm) and veliger abundance</i>										
log ₁₀ .Veliger.L ~ DOsat + Fill + Temp.C	6	731.34	0.00	0.335 [0.248–0.431]	0.26		-1.66	+	0.12	
log ₁₀ .Veliger.L ~ log ₁₀ .Reprod_Mussels_m2 + DOsat + Fill + Temp.C	7	732.25	0.91	0.337 [0.253–0.435]	0.50	-0.054	-1.68	+	0.12	
log ₁₀ .Veliger.L ~ DOsat + Fill + Temp.C + Turbidity.ntu	7	733.47	2.13	0.335 [0.251–0.432]	0.27		-1.66	+	0.12	0.0001
log ₁₀ .Veliger.L ~ log ₁₀ .Reprod_Mussels_m2 + DOsat + Fill + Te mp.C + Turbidity.ntu	8	734.27	2.93	0.338 [0.256–0.437]	0.56	-0.059	-1.69	+	0.12	0.0003
log ₁₀ .Veliger.L ~ Fill + Temp.C	5	734.56	3.22	0.317 [0.229–0.412]	-1.35			+	0.14	
log ₁₀ .Veliger.L ~ log ₁₀ .Reprod_Mussels_m2 + Fill + Temp.C	6	735.60	4.26	0.319 [0.233–0.416]	-1.14	-0.051		+	0.14	
log ₁₀ .Veliger.L ~ Fill + Temp.C + Turbidity.ntu	6	736.66	5.32	0.317 [0.231–0.414]	-1.36			+	0.14	-0.0001
log ₁₀ .Veliger.L ~ log ₁₀ .Reprod_Mussels_m2 + Fill + Temp.C + Turbidity.ntu	7	737.70	6.36	0.319 [0.236–0.418]	-1.12	-0.054		+	0.14	0.0002
log ₁₀ .Veliger.L ~ DOsat + Fill + Turbidity.ntu	6	767.03	35.68	0.222 [0.142–0.321]	3.73		-3.38	+		0.0019
Fixed effects										
	df	AICc	Δ AICc	Model R^2	Intercept	log ₁₀ .veligers	DOsat	Temp.C	Turbidity.ntu	
<i>Veliger abundance and recruitment in the lake</i>										
log ₁₀ .recruits ~ log ₁₀ .veligers	4	669.38	0.00	0.294 [0.184–0.41]	4.39	1.81				
log ₁₀ .recruits ~ log ₁₀ .veligers + DOsat + Temp.C	6	670.55	1.16	0.308 [0.205–0.429]	0.77	1.81	3.06	0.071		
log ₁₀ .recruits ~ log ₁₀ .veligers + DOsat	5	670.65	1.27	0.298 [0.192–0.417]	3.29	1.85	1.33			
log ₁₀ .recruits ~ log ₁₀ .veligers + Turbidity.ntu	5	671.02	1.64	0.296 [0.19–0.415]	4.39	1.79			0.00019	
log ₁₀ .recruits ~ log ₁₀ .veligers + Temp.C	5	671.20	1.81	0.295 [0.189–0.414]	4.07	1.79		0.021		
log ₁₀ .recruits ~ log ₁₀ .veligers + DOsat + Turbidity.ntu	6	672.29	2.90	0.3 [0.198–0.422]	3.27	1.82	1.35		0.00019	

Table 2 (continued)

Fixed effects	df	AICc	ΔAICc	Model R ²	Intercept	log ₁₀ .veligers	DOsat	Temp.C	Turbidity.ntu
log ₁₀ .recruits ~ log ₁₀ .veligers + DOsat + Temp.C + Turbidity.ntu	7	672.65	3.26	0.308 [0.209–0.432]	0.92	1.80	2.96	0.066	0.0009
log ₁₀ .recruits ~ log ₁₀ .veligers + Temp.C + Turbidity.ntu	6	673.02	3.63	0.297 [0.194–0.419]	4.14	1.77		0.016	0.0016
log ₁₀ .recruits ~ Temp.C	4	718.56	49.17	0.02 [0–0.087]	4.76			0.075	
log ₁₀ .recruits ~ Turbidity.ntu	4	718.59	49.20	0.02 [0–0.086]	5.91				0.0054
log ₁₀ .recruits ~ Temp.C + Turbidity.ntu	5	718.93	49.55	0.032 [0.003–0.116]	4.94			0.060	0.0043

and winter, likely due to different rates of cooling among years. Based on these growth rates, settled mussels can reach reproductive size (> 5 mm) within 3–5 months and conditions permit continued growth throughout the year.

The mussel infestation at Lake Piru eventually underwent a dramatic decrease (“bust” phase). The bust period was associated with a major storm event, rapid lake level rise, and subsequent sedimentation. Lake Piru is a relatively small waterbody that is located in a highly eroding watershed. The lake typically experiences localized sediment deposition during storm-related fill events. The fill event in 2017 dramatically increased water levels (about 12 m within a month), and the combination of low initial lake level and high inflows lead to substantial sediment deposition. This, in turn, smothered many of the mussels on soft sediments and dramatically reduced the overall mussel population relative to the lake volume. In addition, the increased lake level led to greater stability of stratification and thus hypoxic conditions near the lakebed persisted for longer periods and impacted zone was larger (up to 10 m above the lakebed). After lake levels rose in 2017, recolonization of the soft sediments on the lake bottom did not reoccur during the study period, indicating the substantially reduced population is now recruiting only in habitats containing preferred substrate. The significant effect of this natural event has not been documented in other infested southwestern systems, including Lake Mead which has relatively low sedimentation rates after the closure of Glen Canyon Dam (Rosen et al. 2012).

The major flow event and lake level rise also influenced the mussel population on natural hard substrates. While sedimentation may explain some of the reduction in mussel density and biomass in these habitats, it does not explain the return of only low numbers of mussels (compared to the initial invasion period), or the lack of large mussels and remaining bias towards small size classes after the event through the end of the study. The continued observed reduction in mussel density and changes in size structure may be explained by more stable stratification during summer and associated hypoxia in the hypolimnion as well as the fluctuating water levels, both the rapid water level rise in spring and rapid draw down in fall during out- of-season water releases. These changes in water level may result in large adults being below

the thermocline during the summer with growth rates undoubtedly reduced (Karatayev et al. 2018) and mortality likely increased (Jones and Ricciardi 2014; Culver et al. 2015), particularly given the size and duration of the hypoxic zone within the hypolimnion when lake levels were high. Lake level reductions in the fall then dewater new colonists that recruited over the summer to the consistently oxygenated epilimnion. This pattern is consistent with the observed change in size structure (greater abundance of small size classes). The continued lack of large mussels since the lake first filled suggests that mortality rates are high for large mussels, though the cause is not clear.

Veliger abundance and juvenile recruitment were clearly disrupted by the first fill event, but returned and remained seasonally variable, but relatively stable from year to year. The relatively stable levels of larval production and mussel recruitment suggest that these parameters were not strongly impacted by the greatly reduced adult population and smaller size structure of mussels following the fill event. This lack of correlation is consistent with the findings of Strayer et al. (2019), which found that the temporal dynamics of particular life stages cannot generally be accurately predicted from the dynamics of other life stages. However, one potential explanation is that since rapid growth rates lead to reproductive-size mussels within three months, the high abundance of small, but mature mussels could negate the loss of large and potentially more fecund mussels. Importantly, while we did not specifically sample veligers in the hypolimnion, we believe contributions from this layer are generally low. We base this on the fact that post fill event, no mussels were found in this layer during dive surveys and veligers generally were not detected during release events when the lake was stratified. Studies examining reproductive and larvae condition could shed light on potential mechanisms explaining the disconnect between adult abundance and veliger abundance and recruitment.

We anticipated that environmental conditions (e.g., water temperature, dissolved oxygen) would play a role in population dynamics for quagga mussels in Lake Piru, influencing mussel reproduction and recruitment, and there were broad seasonal patterns in veliger abundance, recruitment, population density, and growth. Our models supported the hypothesis that environmental conditions, particularly a full

lake and warm water temperatures, are the primary drivers of veliger abundance in this system rather than adult density on hard substrates. Seasonal controls on veliger production have been observed for dreissenids in other systems (Churchill 2013; Balogh et al. 2018; Churchill and Quigley 2018), so it is not surprising that temperature would explain veliger abundance in Lake Piru. It seems biologically reasonable to expect some connection between adult and veliger abundance, however, in a broad review of long-term dreissenid monitoring datasets, Strayer et al. (2019) found that clear relationships among life stages were rare. In Lake Piru, we suspect that two factors may play into this finding: (1) veliger abundance was spatially and temporally variable within the lake, making patterns difficult to observe and (2) there is likely a disconnect between density and total population size in the lake as water levels fluctuate. The interplay between increased available habitat at higher lake levels (a significant factor in the model) and lower mussel density could result in similar magnitude of veliger production at the lake scale. Thus overall production of veligers may be sustained even during periods when adult abundance is relatively low. In contrast, our modeling suggests veliger abundance was the primary driver for recruitment, while environmental factors did not consistently explain much of the variation in settlement and juvenile survival. This is potentially because temperature was a control on veliger abundance, but recruitment was only monitored in the epi- and metalimnion, where environmental conditions were always suitable for mussel recruitment. It is likely that mussels in the hypolimnion would be differentially impacted, given extended periods of hypoxia near the end of the stratified period. During strongly stratified periods, veliger abundance in Piru Creek (which receives hypolimnetic water) was much lower than the lake, suggesting that veliger abundance near the bottom of the lake was also low. It is worth noting that both models had substantial unexplained variance, suggesting that additional factors control both reproduction and recruitment in Lake Piru.

Veliger densities in Lake Piru (0–30 veligers L^{-1}), which were similar to those observed in Lake Mead (Gerstenberger et al. 2011), undoubtedly lead to the transfer and spread of the infestation downstream. Compared to the lake, veliger densities

were much lower downstream in Piru Creek, and declined with increasing distance as found in other systems (Horvath and Lamberti 1999; Churchill and Quigley 2018). One potential explanation for the substantial reduction in veliger density downstream is that the penstock for the reservoir draws water near the bottom and so during stratified periods would likely draw primarily hypolimnetic water. Our veliger samples were depth-integrated and so cannot differentiate density with respect to lake layer. However, surveys in another southern California reservoir found maximal veliger density above the thermocline and lower abundance in the hypolimnion (Anderson and Taylor 2011). Low veliger abundance in the creek typically occurred when the lake was stratified, while high abundance occurred during mixed periods or when substantial outflows occurred, which may entrain water from the metalimnion. On some occasions, no veligers were observed in the creek immediately below the dam, but were observed 500 m downstream of the dam outlet, suggesting that flow or habitat complexity in streams may influence detection probability, particularly at low veliger densities. Although veliger density was generally low in the creek relative to the lake, by early 2016 settled mussel densities in Piru Creek immediately below the dam were similar to those observed in the lake. This finding was likely due to the high flux of new colonists relative to the stationary waters of the lake (i.e., although densities were lower in the creek, potential colonists are consistently replenished by the flowing water).

A key objective of this project was to determine how water management influenced the downstream spread of mussels. Mandated water management activities likely led to the spread of veligers and associated mussel recruitment on a few occasions at the Piru Creek–Santa Clara River confluence 14.5 km downstream of Santa Felicia Dam. Under typical summer base flow conditions, very little surface water arrives at the confluence due to diversion, percolation, and evaporation. However, in-stream flow requirements triggered by winter rainfall (Santa Felicia Dam Federal Energy Regulatory Commission license P-2153), resulted in several years (including 2017) with continuously elevated base flows for much of the year. Mussels were first observed at the Piru Creek–Santa Clara River confluence in late 2017, suggesting that this extended period of elevated

flows facilitated recruitment at downstream sites. Consistent with this hypothesis, in two years with elevated baseflow (2017 and 2020), mussels were found at downstream sites in the Santa Clara River and/or veligers were observed at the confluence, concurrent with the highest veliger densities in the lake and in Piru Creek.

Both veliger abundance and water flows may have influenced adult mussel densities downstream from the lake. Adult densities immediately below the dam dropped dramatically during 2017, concurrent with high water flow velocities due to water releases, hypolimnetic water releases, and reduced veliger flux from the lake. Changes in discharge and velocity can impact quagga mussels in a variety of ways, with high turbulence reducing veliger survival (Horvath and Lamberti 1999) and modifying spatial distribution, abundance, and feeding efficiency (Hasler et al. 2019). In contrast, recruitment 14.5 km downstream at the Piru Creek–Santa Clara River confluence did not begin until late 2017, indicating that periods of increased discharge both reduces colonization and survival immediately below the dam, but allows greater dispersal within the stream. The mussel size distribution in the creek has remained skewed towards small mussels, suggesting that although recruitment consistently occurs, there is relatively high mussel mortality in the creek. An additional possibility is that growth rates (which were not measured in the creek) are lower in the creek because water temperature there is typically 1–3 C (mean) cooler and up to 7.5 C (max) colder than the lake epilimnion as the dam's water intake is near the bottom of the lake.

Our findings raise questions about the efficacy of the standard veliger sampling methods used in this study and others (e.g., Gerstenberger et al. 2011, Churchill and Quigley 2018) in flowing waters. The methods were not sensitive enough to detect veligers at a time when recruitment occurred in downstream habitats. In particular, in 2017, no veligers were detected at the confluence when veligers were 0.5–1 veliger/L at the dam, but recruitment occurred at the confluence during this period. This highlights the need for further investigation of appropriate sampling volumes and sample replication to adequately estimate when and how far veligers are transported downstream in this watershed.

Management implications

While site-specific, not lakewide, mussel control has been a focus of management efforts at Lake Piru in order to maintain lake operations, the activities undertaken provide information useful for evaluating potential population control strategies. Since being implemented, routine mussel removals have been a critical and successful maintenance measure enabling ongoing use of lake infrastructure. The removals generally have kept mussel densities low on infrastructure, even during the ‘boom’ period, with only a few substantial increases in mussels observed on single monitoring dates over the years. It is likely that such increases could have been reduced with adaptive modifications to the maintenance schedule that better tracked peak spawning and recruitment periods. Alternatively, the application of site-specific biocontrol agent that reduces recruitment (Culver et al. 2019), such as Bluegill sunfish (*Lepomis macrochirus*), just prior to high periods of settlement may serve as a more effective measure than physical removals. This option may be particularly useful if peak spawning and recruitment periods vary year to year such that quickly modifying the maintenance schedule proves difficult and the critical periods are missed.

The potential impact of adaptively managed mussel removals from infrastructure on the total lake population remains unknown. However, because infrastructure comprises a relatively small portion of the total hard surfaces in the lake (<1%), in Lake Piru impacts are likely limited in scope at the lake scale but are critical for the ongoing use of infrastructure. Management activities have removed a substantial quantity of mussels and generally have kept reproductive populations low on infrastructure. Unfortunately, these removals and application of other methods (e.g., benthic mats; Wittmann et al. 2012) in natural hard substrate locations are not feasible at larger scale given the total area and complexity of the natural habitat. There is currently little evidence to suggest these removals impacted lake-wide reproduction or recruitment in the lake as a whole. Despite regular and substantial removals of quagga mussel biomass, the population remained relatively stable until the lake filled in 2017 and settlement rates on infrastructure generally have followed overall settlement patterns within the lake.

However, some of the infrastructure (e.g., docks) are located in areas that are predominantly soft sediment and adjacent to boat launch ramps, so at least in the short term, removals potentially minimize the colonization of soft sediments and transfer of mussels out of the lake. Similarly, initial positive detections for dreissenid mussels typically occur at marinas/boat launches (Hosler 2017), indicating that these regions are of particular relevance for minimizing the spread. Conducting removals on infrastructure when densities are low on natural habitat—such as after a fill event that results in sedimentation—could help to further reduce the mussel population overall.

In contrast to direct mussel removals, lake level fluctuations and storm-associated sediment deposition were much more effective at reducing the mussel population throughout the lake. Elsewhere, extended manipulation of water levels has resulted in mass mortality and resulted persistently low population levels for 1–2 years (Leuven et al. 2014), suggesting that it could be a potential tool for population management. However, Lake Piru water level is dictated by seasonal rainfall which varies dramatically from year to year, and leads to high uncertainty in water availability. Normal lake operations would include annual fill during winter/spring and water release in fall, and under such conditions, lake level modifications could be considered as an important tool to control the mussel population. Water level modification could also be combined with other management strategies (e.g., chemical treatment) to reduce or attempt to eradicate the overall population. Unfortunately, rainfall in the region has been exceptionally low during the historic megadrought (Williams et al. 2022) and the lake has not reached its full capacity since mussels were detected. As a result, the limited inflows as well as permitting and engineering constraints on dam operations have restricted the broad potential for lake level fluctuations as a management tool.

With current infrastructure, lowering lake levels requires extended periods of elevated base flow as well as out-of-season water releases. These elevated water releases expand the distribution of veligers into the creek and lead to downstream recruitment, particularly when veliger abundance is high or the lake is not stratified (e.g., Fall 2017, 2019, 2020). It seems relatively unlikely that quaggas will establish and reproduce in the Santa Clara River itself due to the unstable bed, highly fluctuating flows, and lack

of lentic habitat needed for reproduction. However, extended periods of connectivity transport veligers downstream (e.g., high flux in 2020), allowing periodic colonization within the river, and potentially leading to infestations in water systems that directly take in raw river water. Importantly, colonization was not consistent longitudinally downstream. This is clearly evident in the absence of mussels at the most downstream survey site in Rancho Temescal (3.3 km downstream of Santa Felicia Dam) and their presence downstream at the Piru confluence, as well as the observations of mussels on the bridge abutments at two sites, 16 and 40 km downstream on the Santa Clara River (but not on natural substrates in those areas or at sites between the bridges). Veligers can be transported long distances by flowing waters (Wong and Gerstenberger 2011) and thus have potential to colonize new habitats (e.g., off channel reservoirs) even if they do not establish within the river system. In the near term, collecting more information regarding depth-specific recruitment and growth to directly assess the potential impact of lake level fluctuations on the population would be useful for determining the most effective timing and magnitude of fluctuation when such operations are feasible.

The mussel invasion at Lake Piru highlights the challenges that arise from conflicting government mandates, specifically the need to manage invasive species while also meeting requirements for maintaining water sources and endangered species. For example, out-of-season water releases required to replenish groundwater and aquifers undoubtedly contributed to the spread of mussels downstream. Likewise, the timing and duration of mandated elevated base flows that are intended to provide suitable habitat conditions in lower Piru Creek for endangered Southern California Steelhead (United Water Conservation District 2012) also created opportunities for spreading the invasive mussel within the watershed. While the focus of many regulatory discussions, ceasing water releases from the dam into Piru Creek to contain the mussel in the lake is not permitted under the current FERC license (United Water Conservation District 2018b) and modification of the flow release plan likely would require evaluation of potential impacts to Steelhead under the federal Endangered Species Act. Similar evaluations would be required for any management activities within the lake that could impact Steelhead critical

habitat in Piru Creek (e.g., addition of molluscides, filtration of released water).

Modeling suggests that infrastructure elements, particularly the Santa Felicia Dam hydropower facility may generate levels of shear stress that kill veligers at some flows (United Water Conservation District 2017, 2018a) thereby providing a strategy for controlling the spread of mussels downstream. Such impacts were not observed, however, during initial operation of the facility. In fact, veliger output was higher downstream than in the lake at that time. It is believed that the limited flow capacity of the hydropower infrastructure and challenges associated with flow transitions between outlet pipes as discharge volume changed limited the sheer stress generated and potentially released veligers from the dam penstock. Although such operations cannot be avoided due to engineering constraints, under some conditions the hydropower facility may have the potential to control veliger fluxes downstream and further work should explicitly measure the impact of the facility operations.

The quagga mussel infestation at Lake Piru is unique in that it is the first known reservoir in California to be colonized by quagga mussels without having received water from the Colorado River. It is also one of the few systems that did not continually receive mussel larvae from another source. This may have changed though, with the relatively recent finding of mussels in upstream reservoirs, Pyramid Lake (2016) and Castaic Lake (2021). It remains unknown whether mussel populations have established there and where those populations originated, given their proximity to Lake Piru and shared user base. If a population establishes in Pyramid Lake, it could contribute to the population in Lake Piru. Determining whether this input is occurring is critical to considering potential lakewide management actions. If Lake Piru is still isolated from other sources of veligers, it may be possible to further reduce the population in the lake through lake-focused efforts. Recognizing and taking advantage of natural events that reduce mussel densities as documented here, and applying adaptive strategies for removing mussels that maximize removal of mussels before they reproduce, are steps that would undoubtedly further help control the mussel population at Lake Piru.

Acknowledgements All data collection efforts were funded and implemented by United Water Conservation District as part of their Quagga Mussel Management and Control Plan. We thank Kimo Morris and Mike Anghera of Ecomarine Consulting for their dive surveys. Special thanks to UWCD employees who collected or provided data: Evan Lashly, Katherine Ayres, Cherie Windsor, Dan Detmer, Greg DeJarnette, and many others. We thank two anonymous reviewers for their insightful comments which clarified and improved the manuscript.

Author contributions Michael Booth contributed to conceptualization, methodology, formal analysis, investigation, data curation, writing—original draft, review and editing, and visualization.Carolynn Culver contributed to conceptualization, methodology, investigation, writing—review and editing.

Data availability Data are available on the Environmental Data Initiative (Booth 2023) (<https://environmentaldatainitiative.org/>).

Declarations

Conflict of interest M. Booth is a former employee of United Water Conservation District (UWCD). M. Booth and C. Culver have received financial support from UWCD for research on monitoring and managing quagga mussels. No funding was received to assist with the preparation of this manuscript.

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