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Research Article

Distinct reservoir surface elevation patterns characterize quagga mussel habitat suitability

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Abstract

A prolific aquatic invasive species, the quagga mussel (*Dreissena rostriformis bugensis*), broadly impacts freshwater systems by altering ecosystem structure and function, damaging infrastructure, and limiting recreational boating opportunities. Quagga mussel populations have become established in several Western U.S. reservoirs which feed hydroelectric power facilities. Impacted facilities incur increased operational and maintenance costs and are at risk of power generation disruption. Current habitat suitability models suggest additional reservoirs are susceptible to successful invasion should introduction occur. The U.S. Bureau of Reclamation has detected additional quagga mussel introductions to numerous reservoirs, yet these populations appear not to have persisted. To further refine quagga habitat suitability models, we examined how reservoir surface elevation patterns, or storage dynamics, vary across reservoirs of three quagga mussel population statuses: established (i.e., established population confirmed), suspect (i.e., introduction detected without population establishment), and negative (i.e., no introduction detected). For this work, "drawdown events" or periodic water surface elevation declines, were operationally defined based on relevance to quagga desiccation mortality. Our comparisons of reservoir drawdown properties revealed that water-level declines were typically greater in suspect and negative reservoirs than in reservoirs with established quagga populations. Further, suspect reservoirs typically had less frequent, yet in many cases longer duration drawdown events than established reservoirs. Therefore, the magnitude and duration of drawdowns potentially have negative impacts on quagga population establishment in a novel environment. Managed large-magnitude and long-duration drawdowns may serve as a risk-reduction strategy for quagga invasion prevention.

Key words: bivalve, Dreissenidae, emersion, invasion ecology, risk management, water resource management

Introduction

Invasive species spread has increased in rate, intensity, and species diversity during the era of globalization (Hulme 2009). Aquatic invasive species (AIS) have become particularly widespread through increased shipping traffic, aquarium trade, and overland transport of small vessels (Johnson et al. 2001; Padilla and Williams 2004; Streftaris et al. 2005). AIS can incur intangible ecosystem costs by acting as autogenic or allogenic engineers (Emery-Butcher et al. 2020), disrupting food webs (Richardson and Bartsch 1997), and altering habitats, water quality, hydrology, and biochemical cycling (Gallardo et al. 2016; Strayer 2010). Conservative estimates suggest that AIS have cost the global economy $345 billion USD in damages, management, and prevention since 1971 (Cuthbert et al. 2021). Some of the most well-founded AIS cost estimates have been derived from direct observation of sessile invaders in water industry infrastructure (Harrison et al. 2021); causing pipe and filter blockages, pipe corrosion, and altering oxygen and nutrient concentrations (Gallardo and Aldridge 2020; Nakano and Strayer 2014). Moreover, the most common invaders of water infrastructure, dreissenid mussels (*Dreissena polymorpha* Pallas, 1771; *D. rostriformis bugensis* Andrusov, 1897), account for 16% of total global AIS incurred costs (Cuthbert et al. 2021).

Since dreissenid mussels were first detected in the North American Great Lakes in 1988 (Griffiths et al. 1991; Hebert et al. 1989), methods to anticipate and mitigate the risk of spread have been extensively researched (Bossenbroek et al. 2007; Cole et al. 2019; Karatayev et al. 2015). Considerable efforts have identified chemical and physical properties required for dreissenid colonization, reproduction, survival, and range expansion (Mackie and Claudi 2009; Locklin et al. 2020; Rolla et al. 2020). Widely recognized habitat suitability factors include calcium, pH, dissolved oxygen, alkalinity, temperature, chlorophyll a, nitrogen, phosphorous, conductivity, salinity, and turbidity. Most of these parameters were identified from observation of invaded European and Eastern U.S. natural lakes (Bossenbroek et al. 2007; Karatayev et al. 2015). However, these well-studied lentic systems are substantially hydrologically different from waterbodies in the Western U.S., where dreissenid invasion is also a growing concern. Many vulnerable Western U.S. waterbodies are man-made impoundments managed by the U.S. Bureau of Reclamation (hereafter “Reclamation”) and primarily used for hydroelectric power generation, water storage, and distribution (Harrison et al. 2021). As such, these reservoirs are more heavily managed and highly dynamic systems compared to natural lakes. Reclamation-managed reservoir water levels decline substantially due to hydroelectric power generation and operational “drawdowns”. Reservoirs are then refilled by water transport and springtime runoff from snowmelt.

Reclamation manages numerous reservoirs within which quagga mussel populations (*Dreissena rostriformis bugensis*) have become established, including Lakes Powell, Mead, Mohave, and Havasu along the Colorado River, as well as Apache, Canyon, and Saguaro Lakes along the joint Arizona state and public utility cooperative Salt River Project (SRP). Water quality monitoring further suggests that most large waterbodies in the Western U.S. exhibit calcium and pH levels within suitable ranges for dreissenid colonization (Carrillo et al. 2023). Quagga invasion of these reservoirs could cost hydropower programs several million USD annually through infrastructure maintenance, repair, and population establishment prevention measures (Harrison et al. 2021). A better understanding of the hydrological characteristics that put reservoirs at a risk of quagga population establishment remains critical to direct future efforts and funds for prevention.

Among the suite of environmental factors favorable to dreissenids, hydrology has received comparatively little attention (see Balogh et al. 2008; Bowers and de Szalay 2005). In lotic systems, water velocity and turbulence can impose limitations on mussel growth, abundance, and larval recruitment (Hasler et al. 2019; Kozarek et al. 2018). In lentic systems, lake morphometry can impact long-term population density and dynamics (Karatayev et al. 2021). However, the influence of hydrology in managed Western U.S. reservoirs has yet to be extensively investigated. Previous work in these systems has primarily examined how established populations of zebra mussels (*D. polymorpha*) are impacted by winter drawdowns (Karatayev et al. 1998; McMahon et al. 1993). These studies revealed that even reservoir dewatering to "dead pool" (i.e., the low level at which water can no longer passively drain through gravity-driven outlets; Hargrave and Jensen 2012) can diminish but not reliably eradicate zebra mussel populations (Leuven et al. 2014). This current study aimed to assess correlations between water level dynamics and quagga mussel population presence or absence using Reclamation-managed reservoirs in the Western U.S. as a study system. We investigated whether certain properties of "drawdown events", or intermittent water level declines, characterize reservoir quagga population statuses. We compared reservoirs with (a) established quagga populations, (b) detected quagga introductions, yet apparent population failures, and (c) no detected quagga introductions. If drawdown event properties vary across quagga population statuses, Reclamation may be able to use these metrics to devise benchmarks for future reservoir management plans, prevent novel quagga invasions, or combat existing populations.

Materials and methods

Study system

Since the first introductions in the region were recorded in 2007, several Western U.S. reservoirs have harbored large dreissenid source populations (Figure 1), while many others appear to have suitable pH and calcium levels for colonization (Whittier et al. 2008). Risk of quagga mussel spread among these reservoirs is high, as many are actively used by recreational boaters who regularly visit multiple waterbodies (Bossenbroek et al. 2007). Still, comparatively few Western U.S. lakes and reservoirs have established populations of dreissenid mussels. The declining rate of successful mussel colonization of novel U.S. waterbodies may be in large part due to protocols

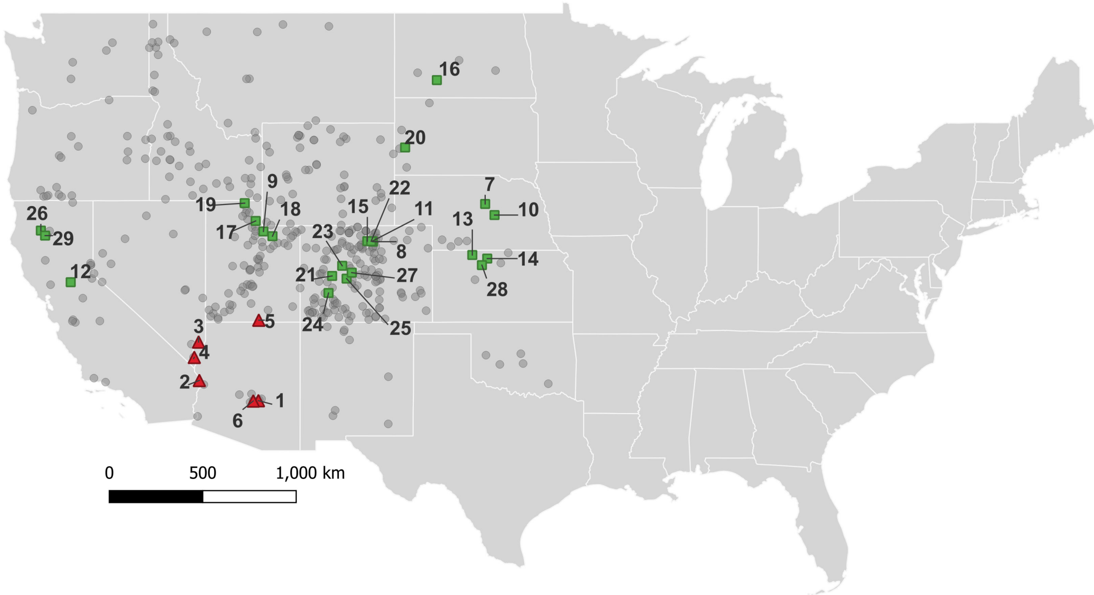

Figure 1. Map of 402 freshwater inland western United States reservoirs managed by the Bureau of Reclamation. Reservoirs included in this study with "established" (n = 6, red triangles) or "negative" (n = 23, green squares) mussel population statuses are shown. Reservoirs of "suspect" mussel population status (n = 12) are anonymized among the remaining reservoirs (gray points) in accordance with Reclamation protocols. Numbers correspond to reservoir IDs in Table S1.

states have enacted to inspect and decontaminate recreational boats of dreissenid mussels. In 2021, Colorado, Montana, and Utah intercepted 181, 61, and 46 "mussel boats" respectively, illustrating the effectiveness of these state programs (Duncan 2022; Montana FWP 2021; Utah DNR 2023). Even so, Reclamation's Ecological Research Laboratory (EcoLab) has detected evidence of quagga introductions to uninvaded waterbodies. Since 2008, the EcoLab has analyzed approximately 26,800 water samples for the early detection of dreissenid mussels. This sampling protocol (Bureau of Reclamation 2022) returned several positive detections of dreissenids from previously negative waterbodies by environmental DNA (eDNA) or microscopy (Supplementary material Table S1). Positive detections of mussel larvae or veligers were confirmed by microscopy, suggesting that reproductive mussel populations were present. In cases where subsequent sampling detected no evidence of more veligers or adult mussels, it is presumed that the population failed to persist. These apparent population failures may be derived from single introduction events, as multiple introduction events are often required for successful establishment of an invasive species in a novel environment (Dlugosch and Parker 2008). The identification of population failures further suggests that unknown factors may contribute to the eradication of nascent populations.

Data acquisition and quality check

To investigate the relationship between reservoir water storage patterns and mussel population statuses, we acquired daily water level information (feet elevation, relative to mean sea-level) for Western U.S. reservoirs from the Reclamation Information Sharing Environment (RISE) (available at data.usbr.gov; Bureau of Reclamation 2021) and the SRP's engineering division (obtained on or before April 20, 2021). Selected reservoirs had elevation data available for 2007 through 2020, though many had data available for complete years as far back as 1997 (Table S1). Elevation values were converted from feet to centimeters, and initial data quality-checks were performed to remove any instrumental errors (i.e., elevation changes > 610 cm d^{-1}, > 20 ft d^{-1}) from the datasets. One reservoir (Canyon Lake, AZ) was excluded from our dataset because it was directly hydraulically influenced by another reservoir upstream (Apache Lake, AZ) and elevation data were not independent.

For each of the 41 remaining reservoirs (Figure 1; Table S1) quagga population status (hereafter "status") was defined by state designation and suspect detections by Reclamation sampling results. Each reservoir was categorized as having a status of (a) "established", denoting an established quagga mussel population, (b) "suspect", indicating one or more mussel introductions were detected by eDNA analysis or microscopy, yet subsequent samples were all negative, or (c) "negative" for mussel presence, meaning there have never been quagga mussel detections by microscopy or eDNA. Out of 41 reservoirs, six were categorized as "established", twelve as "suspect", and twenty-three as "negative".

Drawdown definition and metric calculation

Reservoir water levels can fluctuate due to natural processes such as upstream influences, evaporation, or snowmelt, as well as management practices including actively managed drawdowns. However, managed drawdowns typically have much larger magnitudes than natural water level declines and therefore likely have greater impacts on quagga population survival (Hargrave and Jensen 2012; Leuven et al. 2014). Our datasets did not distinguish between natural and managed of water level fluctuations. Therefore, for this work we operationally defined "drawdown events" by daily water surface elevation change magnitudes and durations pertinent to quagga biology (Mackie and Claudi 2009) rather than management practices. We acknowledge that within our operational definition relatively small water level fluctuations were likely natural, while larger fluctuations were likely managed. The minimum threshold of water elevation decline chosen for our drawdown definition was 6 cm (or ~ 0.20 ft). This threshold matched the precision of our dataset and surpassed the average maximum lengths of adult quagga mussels (i.e., 2–4 cm) (Benson et al. 2023; Pathy and Mackie 1993), therefore guaranteeing that adult mussels at the surface would be exposed. Two conditions were required for a drawdown event to occur (Figure 2):

(1) the water surface level decreased by at least 6 cm from the day prior (which was denoted as Day 0),

and

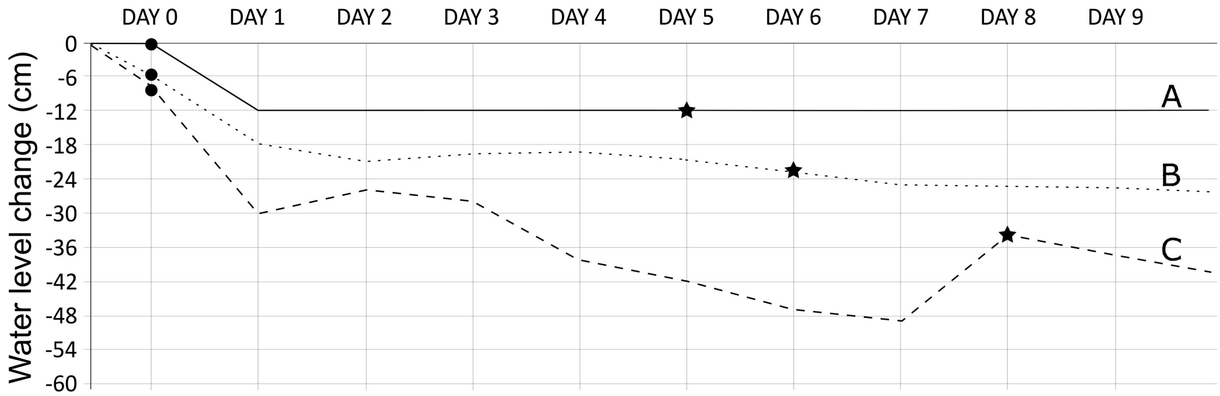

Figure 2. An illustration of three example drawdown events. All example events (labeled A through C) begin on Day 0 (solid circles) and end on the day denoted by a solid star. (A) From Day 0 to Day 1 the water level decreases by exactly 6 cm and remains constant for more than five consecutive days. The event ends on Day 5 because the water level is within 6 cm of the water level of the fifth day prior (i.e., Day 0). (B) From Day 0 to Day 1 the water level decreases by exactly 6 cm then remains at or below the threshold of Day 0−6 cm for more than five consecutive days. The event ends on Day 6 because it is the first instance when the water level is within 6 cm of the fifth day prior (i.e., Day 1). (C) From Day 0 to Day 1 the water level decreases by >6 cm then remains below the threshold of Day 0−6 cm for more than five consecutive days. The event ends on Day 8 because it is the first instance when the water level is within 6 cm of the level of the fifth day prior (i.e., Day 3).

(2) remained at or below that minimum decline threshold (i.e., the level of Day 0 minus 6 cm) for five or more consecutive days.

If both conditions were met, the date of initial 6-cm elevation decrease became Day 1 of the drawdown event and the date prior to this decrease was denoted as Day 0. Therefore, days of the drawdown event were counted as days elapsed since the water level was last within 6-cm of level of Day 0. Beyond the initial five days which were required to trigger an event, the end of a drawdown event was triggered on Day 5 or beyond if the water level elevation was within 6-cm of or surpassed the level of five days prior. The day this threshold was met became the final day of the event (Figure 2). For example, if the elevation level of Day 8 was within 6-cm of the level Day 3, Day 8 became the end of the drawdown event (Figure 2, example C).

This definition guaranteed that during a drawdown event, any mussels located near the starting surface elevation would be emersed for at least five days, as this is considered to be the minimum duration of aerial exposure for dreissenid mortality (McMahon et al. 1993; Ricciardi et al. 1995). This drawdown definition excluded any potential drawdown cases with durations less than five days. However, preliminary analyses revealed that these short duration events were generally rare. In addition, they likely had little biological relevance to mussel emersion-related deaths (Bowers and de Szalay 2005; Ricciardi et al. 1995).

We calculated eight related summary metrics for each reservoir, which described various drawdown event properties as reservoir means or annual patterns (i.e., n = 41 reservoirs for each metric):

(1) mean annual event frequency (no. y^{-1}),
(2) mean interval (i.e., between-event) duration (d),

(3) mean event duration (d),
(4) mean percent of year spent in drawdown (%),
(5) mode season of drawdown occurrence,
(6) mean elevation change (cm),
(7) mean elevation percent change (%), and
(8) mean rate of elevation change (cm d^{-1}).

These metrics broadly described drawdown event frequency (1, 2, and 4), duration (3), seasonality (5), magnitude (6 and 7), and rate (8). Drawdowns were identified and metrics were calculated using Python coding with the Anaconda 1.10.0 Navigator (Anaconda Software Distribution 2020) and Spyder (Raybaut 2009).

Statistical analysis

We quantified statistical differences in water surface elevation patterns among three categorical reservoir statuses (i.e., established, suspect, or negative). We acknowledge that we derived eight drawdown event metrics from a singular dataset, rendering these analyses as a family of comparisons. This approach enabled us to use these related metrics as a weight-of-evidence for inferring relationships between drawdown properties and reservoir statuses. *P* values obtained from the primary eight analyses were left unadjusted (Rothman 1990), while *P* values from post hoc tests were adjusted (*adj-P*), using the false discovery rate correction, to find pairwise differences between reservoir statuses (Benjamini and Hochberg 1995).

A non-parametric approach was used for all statistical analyses. For seven out of eight metrics, which were continuous variables, we used Kruskal-Wallis tests and post hoc pairwise comparisons using Wilcoxon rank sum tests to examine differences between reservoir statuses. Therefore, median values (M) and interquartile ranges (IQR) are reported to approximate shifts in distributions of reservoir-level summary metrics (i.e., means, annual patterns) across statuses. For the remaining categorical metric, we used a Chi-square test to examine differences in the mode (i.e., most common) season of event occurrence for each reservoir. Event seasons were defined by their start month: spring (March–May), summer (June–August), fall (September–November), and winter (December–February).

Drawdown metrics for each reservoir were calculated for the full timeframe of available data (i.e., 14 to 24 years) and for a standardized timeframe from 2007 through 2020 (i.e., 14 years). Statistical analysis results were virtually identical for these examined timeframes. Therefore, to fully leverage these long-term datasets, we present the results for the complete timeframe of available data for each reservoir. All statistical analyses were executed in the R coding environment (R v4.2.0; R Core Team 2022) with a significance level of $\alpha = 0.05$.

Table 1. Significant differences in reservoir-level drawdown metrics (for each n = 41) across quagga population statuses were determined by Kruskal-Wallis tests unless specified otherwise (α = 0.05).

Drawdown metric	Units	χ2	DF	P
Mean annual event frequency	no. y^{-1}	7.104	2	0.029
Mean interval duration	d	7.544	2	0.023
Mean event duration	d	4.755	2	0.093
Mean percent of year in drawdown	%	4.042	2	0.133
Mode season of event occurrence*		3.354	6	0.763
Mean elevation change	cm	5.064	2	0.080
Mean percent change in elevation	%	0.273	2	0.872
Mean rate of elevation change	cm d^{-1}	5.398	2	0.067

* = Chi-square test performed for this analysis

Results

Drawdown frequencies, durations, and seasonality across quagga population statuses

Patterns in drawdown event frequency, or the number of events per year, significantly differed between reservoir statuses (*P* = 0.029; Table 1). In general, reservoirs with established quagga populations exhibited a more than six-fold higher median frequency of drawdown events (M = 16.5 y^{-1}, IQR = 13.8 y^{-1}) than reservoirs with suspect (M = 1.6 y^{-1}, IQR = 2.0 y^{-1}) (*adj-P* = 0.055) or negative statuses (M = 2.5 y^{-1}, IQR = 5.1 y^{-1}) (*adj-P* = 0.112) (Figure 3A; Table 2; Table S2). The duration of intervals between drawdown events differed across reservoirs statuses (*P* = 0.023; Table 1). Established reservoirs had significantly shorter interval durations (M = 13 d, IQR = 77 d) versus suspect reservoirs (M = 171 d, IQR = 336 d) (*adj-P* = 0.029). There was also a seven-fold difference in median interval duration between established and negative reservoirs (M = 88 d, IQR = 153 d) (*adj-P* = 0.110) (Figure 3B; Table 2; Table S2). Further, drawdown event durations per status showed a similar pattern, though with greater variability (*P* = 0.093; Table 1). Established reservoirs had shorter events (M = 9 d, IQR = 23 d) than negative (M = 25 d, IQR = 33 d) (*adj-P* = 0.212) and even more so than suspect reservoirs (M = 38 d, IQR = 34 d) (*adj-P* = 0.159) (Figure 3C; Table 2; Table S2). Relatively similar percents of year were spent in drawdown for establish (M = 39.0%, IQR = 9.7%), suspect (M = 24.3%, IQR = 25.6%), and negative (M = 30.4%, IQR = 29.8%) reservoirs (Figure 3D; Tables 1, 2; Table S2).

Although event frequencies and durations showed varied patterns across reservoir population statuses, drawdown event seasonality did not (Table 1).

Among the 41 reservoirs, summer was the most common mode season of event occurrence, followed by spring, for all three statuses. Further, only two reservoirs commonly exhibited drawdown events during fall. Winter was the mode season of events for three negative and one suspect reservoir, but no established reservoirs (Figure 4).

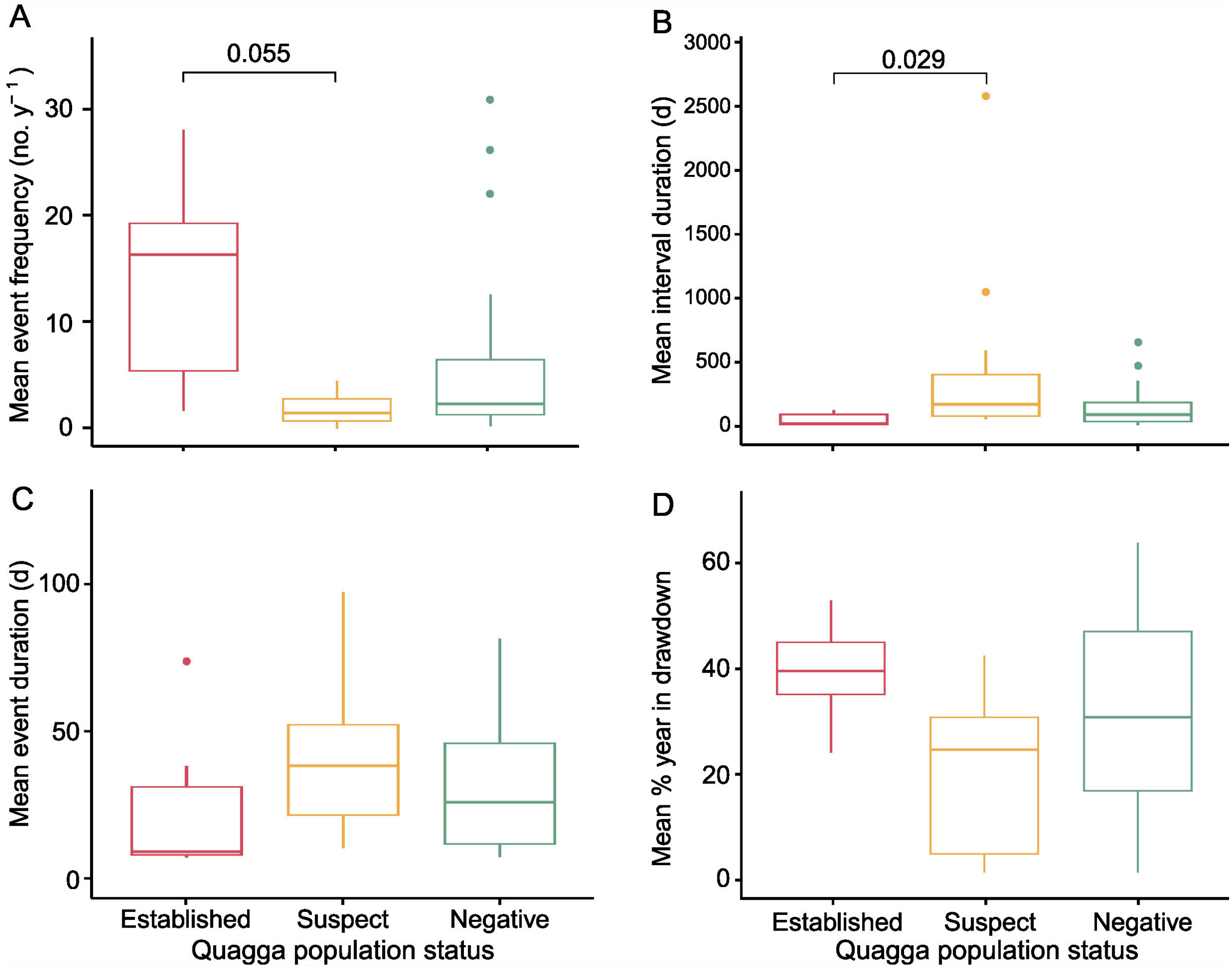

Figure 3. Boxplots illustrate the distributions (i.e., median, quartile ranges, outliers) of reservoir-level drawdown metrics (n = 41) across quagga population statuses. Metrics are reservoir means for (A) annual event frequency, (B) duration of the intervals between drawdown events, (C) duration of drawdown events, and (D) percentage of each year spent in drawdown. Adjusted *P* values ≤ 0.1 and horizontal brackets across different statuses are shown for post hoc multiple comparison tests.

Drawdown magnitudes and rates across quagga population statuses

Patterns of drawdown magnitude, or absolute changes in surface elevation, showed some evidence of differences among statuses (*P* = 0.080; Table 1). Established reservoirs in general had a smaller median magnitudes of water level decline (M = −47.4 cm, IQR = 77.8 cm) than both negative (M = −259.6 cm, IQR = 392.6 cm) (*adj-P* = 0.079) and suspect reservoirs (M = −247.2 cm, IQR = 253.9 cm) (*adj-P* = 0.079) (Figure 5A; Table 2; Table S2). In contrast, the median value of percent change in elevation (i.e., standardized drawdown magnitude relative to the starting elevation) was not different among established (M = −0.23%, IQR = 0.13%), suspect (M = −0.17%, IQR = 0.25%), and negative reservoirs (M = −0.19%, IQR = 0.19%) (Figure 5B; Table 1; Table S2). Finally, there was some evidence of differences in rates of elevation change among statuses (*P* = 0.067; Table 1); particularly between negative (M = −9.3 cm d^{-1}, IQR = 8.2 cm d^{-1}) and suspect reservoirs (M = −6.3 cm d^{-1}, IQR = 1.5 cm d^{-1}) (*adj-P* = 0.070), but not established reservoirs (M = −6.5 cm d^{-1}, IQR = 4.2 cm d^{-1}) (Figure 5C; Table 2; Table S2).

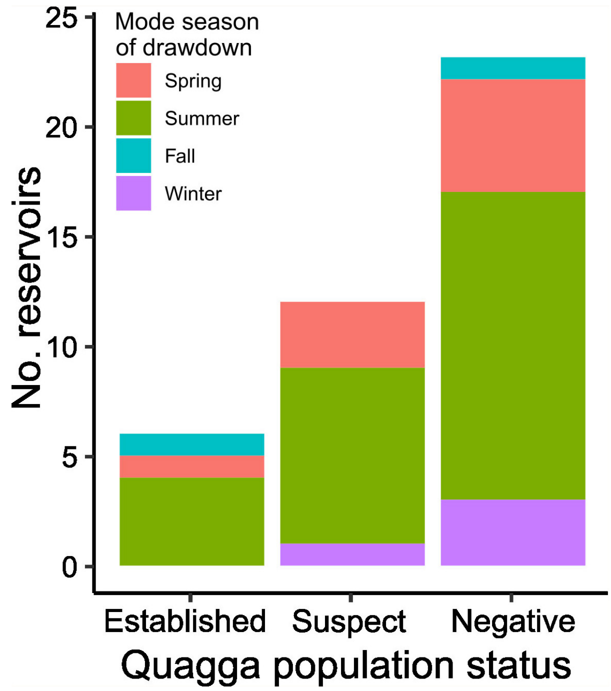

Figure 4. Mode (i.e., the most common) season per reservoir (n = 41) of drawdown event occurrence across quagga population statuses.

Table 2. Post hoc multiple comparisons using Wilcoxon rank sum tests (α = 0.05) examining statistical differences in reservoir-level drawdown metrics across quagga population statuses.

Drawdown metric	Established-Suspect			Established-Negative			Suspect-Negative		
	W	*r*	*adj-P*	*W*	*r*	*adj-P*	*W*	*r*	*adj-P*
Mean annual event frequency	61	0.552	0.055	99	0.300	0.112	190	0.305	0.110
Mean interval duration	9	0.596	0.029	39	0.300	0.114	86	0.305	0.110
Mean event duration	15	0.464	0.159	45	0.240	0.212	96	0.247	0.212
Mean percent of year in drawdown	58	0.486	0.124	91	0.220	0.263	171	0.194	0.263
Mean elevation change	57	0.464	0.079	109	0.400	0.079	139	0.006	0.986
Mean percent change in elevation	33	0.662	0.986	58	0.110	0.986	139	0.006	0.986
Mean rate of elevation change	33	0.066	0.820	91	0.220	0.381	72	0.382	0.070

**adj-P* = adjusted *P* value

Discussion

Our investigation of hydrological influences on quagga habitat suitability suggests that managed seasonal drawdowns may be critical disturbance events effective in the prevention of quagga colonization of Western U.S. reservoirs. Differences in water level fluctuation patterns between suspect and established reservoirs indicate that long-duration and large-magnitude spring or summer drawdowns may play a role in inhibiting quagga population establishment (McMahon et al. 1993). Drawdowns observed in suspect reservoirs may provide sufficient areal and temporal exposure to hot and dry conditions that can cause pervasive desiccation mortality in emersed dreissenids (Bowers and de Szalay 2005).

As a method for quagga mussel invasion prevention, control, or eradication, drawdowns can be considered a "habitat management" strategy,

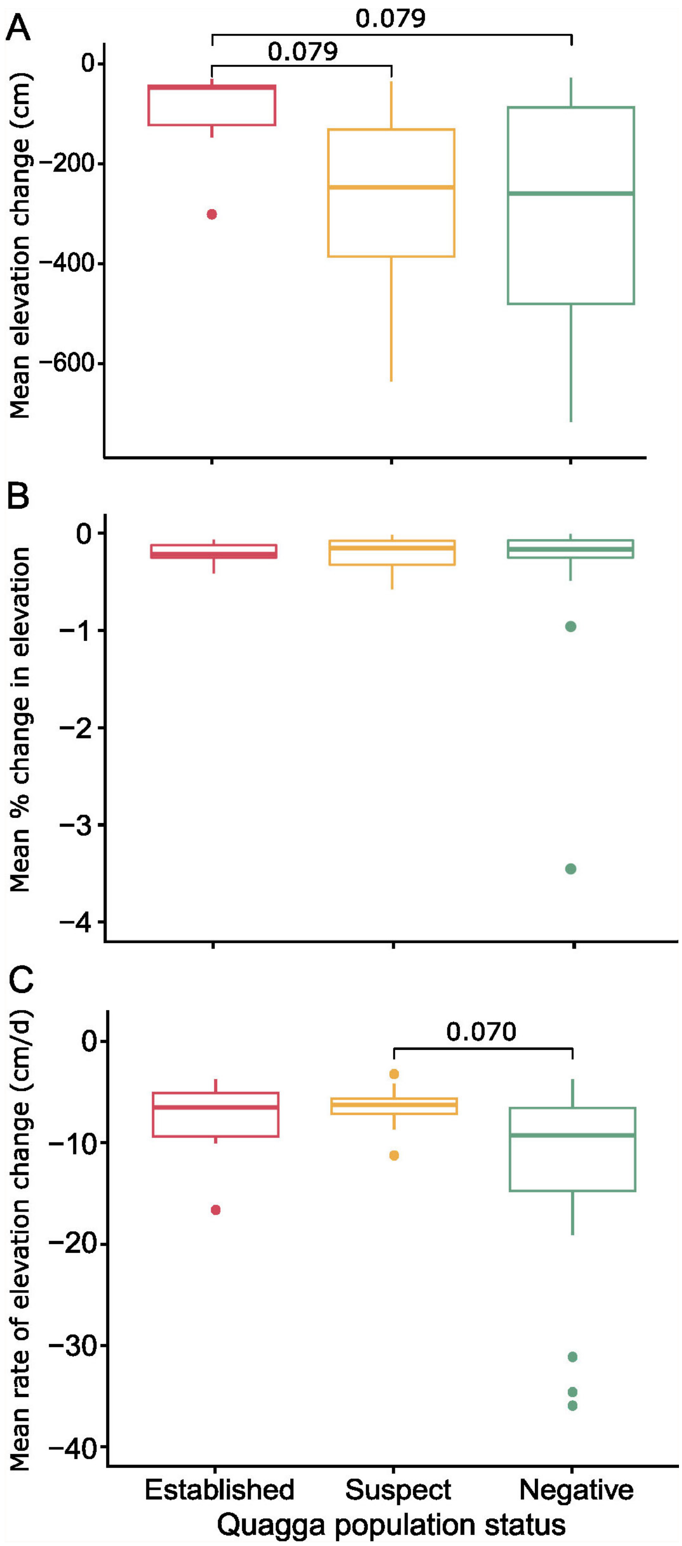

Figure 5. Boxplots illustrate the distributions (i.e., median, quartile ranges, outliers) of reservoir-level drawdown metrics (n = 41) across quagga population statuses. Metrics are reservoir means for (A) elevation change, (B) percent change in elevation, and (C) rate of change in elevation. Adjusted *P* values ≤ 0.1 and horizontal brackets across different statuses are shown for post hoc multiple comparison tests.

which makes the habitat undesirable for the invasive species (Gherardi and Angioloni 2009). Among the eight examined drawdown event metrics, it appears that magnitude, or the change in water surface elevation (cm;

Figure 5A), may be the most ecologically impactful property that differentiates reservoirs of established versus suspect and negative statuses. Two-thirds of reservoirs with established quagga populations had average drawdown magnitudes less than 50 cm, while roughly three-quarters of each of suspect and negative reservoirs had average drawdown magnitudes of greater than 100 cm. The disparity between establish and suspect reservoirs, may be an important driver of whether quagga introductions lead to population establishment or failure. Comparably, in wetlands of the Great Lakes region, dreissenids appeared not to settle in locations where water levels fluctuate on average more than 56 cm (Sherman et al. 2013). The impacts of large water level fluctuations on nascent quagga mussel populations are likely two-fold. First, larger drawdowns like those occurring on average in suspect reservoirs, expose more reservoir benthos and thus disturb a greater proportion of mussel suitable habitat (Balogh et al. 2008). Second, although quagga mussels can be found deeper than 90 m, veliger settlement densities tend to peak within the littoral zone, then decline with increasing depth (Balogh et al. 2008; Elgin et al. 2022; Karatayev et al. 2021; Mueting et al. 2010). Therefore, larger drawdowns potentially expose the majority of quagga settlers and adults, which may ultimately lead to population extinction. Because negative reservoirs experienced drawdown magnitudes more similar to suspect than established reservoirs (Table 2, Figure 5A), mussel populations may also have greater probabilities of establishment failure in these reservoirs, should an introduction occur.

Beyond the magnitude of surface elevation declines, the duration of drawdown events may also be ecologically important to impeding quagga population establishment. The median suspect reservoir had drawdown events on average more than four-times longer than the median established reservoir (Figure 3C). Negative reservoirs had average event durations that spanned an intermediate range between those of established and suspect reservoirs. As such, if quagga mussels were introduced to negative reservoirs, the probability of population establishment would likely vary based on the average drawdown magnitude and duration of the individual reservoir. While dreissenid desiccation death is generally considered to occur after five days of emersion, population percent mortality and mortality rates also depend on the air temperature and humidity during the exposure period (McMahon et al. 1993; Ricciardi et al. 1995). Studies in the Eastern U.S. and Europe have suggested that drawdowns during either extreme low or extreme high temperatures are effective management tools for dreissenid control (Grazio and Montz 2002; Leuven et al. 2014). From patterns observed in suspect reservoirs, where presumably complete quagga population mortality occurred, longer exposure periods during spring or summer months of on average 10–150 d (Table S2), can substantially negatively impact quagga mussel populations. While exposure durations of 150 d might seem unnecessary, we note that water levels were not stable during drawdowns of this length. Continual water level declines expose additional reservoir benthos and more mussels through time, increasing the proportion of the population ultimately affected.

Considered independently of other drawdown metrics, the fact that drawdown events occurred more frequently in established than suspect reservoirs (Figure 3A) appears counterintuitive. However, established reservoirs also typically experienced smaller drawdown magnitudes, shorter drawdown durations, and shorter interval durations (Figures 5A, 3B, C). Taken together, this may indicate that the signal of natural water level fluctuations was stronger than managed drawdowns in established reservoirs, or that managed drawdowns were more common in suspect and negative reservoirs. Regardless of the underlying cause, small drawdowns in established reservoirs likely only exposed a small portion of the quagga population during each event, leaving a sufficient proportion of the population unaffected, allowing for rebound (Balogh et al. 2008). Further, depending on the air temperature and humidity, short duration drawdowns may have resulted in sub-lethal periods of exposure, therefore not effectively reducing existing mussel populations (Ricciardi et al. 1995). Alternatively, because small and short drawdown events occur frequently in established reservoirs, over time quagga populations may have become established entirely below the level of frequent surface elevation decline (Bowers and de Szalay 2004, 2005).

Water level fluctuation patterns in suspect reservoirs indicated that 1–2 spring or summer drawdown events per year, with an average magnitude and duration of ≥ 250 cm and ≥ 40 d respectively (Table S2), may be effective at preventing quagga population establishment should introduction occur. Despite recent improvements to predictive models of dreissenid spread risk (Carrillo et al. 2023; Cole et al. 2019), uncertainty remains in predicting future introduction locations and timing. Further, delays in detection are common (Ahmed et al. 2022) due to sampling frequencies, sampling method minimum detection thresholds, and because introduced quagga populations can be initially highly localized, potentially leading to false negatives (Bureau of Reclamation 2022). Therefore, regularity in drawdown management patterns similar to those occurring in typical suspect reservoirs may be crucial to combat future quagga introduction events. However, whether these benchmarks can be appropriately and effectively incorporated into existing Reclamation management plans requires discussion with appropriate management groups.

Among the remaining metrics examined, percent of year spent in drawdown and percent change in elevation, did not provide additional insight into differences between quagga population statuses. The lack of difference among statuses in percent of year spent in drawdown can be explained by the counterbalancing patterns observed for the durations of drawdown events (Figure 3C) and durations of intervals (i.e., days between events, Figure 3B). Despite differences in pattern seen for absolute drawdown magnitudes (cm), it appeared that standardized magnitudes (i.e., percent change in elevation, Figure 5B) had no impact on quagga populations. Finally, although there is some evidence of differences in drawdown rates between suspect and negative reservoirs (Figure 5C), negative reservoirs have no known introductions, therefore it remains unclear how even the most extreme rates of drawdown would impact quagga populations. Further, drawdown rates seen in established reservoirs are similar to those seen in both negative and suspect reservoirs, indicating that the rate of drawdown may not be an important ecological factor in determining quagga population status.

Notably, the introduction and establishment of a zebra mussel (*Dreissena polymorpha*) population in Pactola Reservoir was confirmed during the summer of 2022 (Bureau of Reclamation *unpublished data*). Because our analyzed dataset concluded at the end of 2020 and was analyzed for relevance to quagga mussels only, we denoted the Pactola Reservoir status as “negative” for this study. Further, we note that Pactola Reservoir drawdown metrics have historically been either more dissimilar to established reservoirs than most negative reservoirs, or well within the IQRs of the drawdown metrics observed in suspect and negative reservoirs (Table S3). This supports evidence that zebra mussels may be less susceptible to emersion mortality than quagga mussels (Ricciardi et al. 1995). Furthermore, although quagga and zebra mussel geographic distributions broadly overlap, distinct physiological tolerance thresholds for environmental parameters have been established for each species to accommodate for observed differences (Spidle et al. 1995; Quinn et al. 2014). As such, separate management plans for zebra and quagga mussel control and prevention in the Western U.S. may be warranted.

While this work reveals meaningful relationships between quagga mussel presence and reservoir surface elevation patterns, specifically magnitudes and durations of drawdown events, our research had certain constraints. First, we utilized a limited subset of the available Western U.S. waterbodies. Consequently, the scope of inference may be confined to the reservoirs examined in this study. Next, we examined drawdown properties at the reservoir level. While summary metrics are valuable for detecting general spatial trends, these values do not capture extreme events or temporal variation within reservoirs that may impact quagga colonization. In particular, the characteristics of drawdowns occurring concurrently with or shortly after quagga introduction events are likely the most important to prevent population establishment. In general, eradication measure effectiveness decreases and associated costs increase with time from invasion detection (i.e., the invasion curve, Ahmed et al. 2022; Sakai et al. 2001). Finally, we did not consider temperature or chemical water quality characteristics which might interact with drawdown properties and influence habitat suitability. For example, it is possible that at extreme temperatures, complete emersion may not be required for mussel morality. Subjection to extreme surface water temperatures may be adequate to induce physiological stress and death (Locklin et al. 2020). Incorporating these findings into the model established by Carrillo et al. (2023), is a logical future step to further refine our understanding of quagga habitat suitability. This model indicated that quagga mussel distribution in the Western U.S. results from intricate interactions between water quality parameters, particularly pH and calcium concentration, as well as cross-land boater conveyance. Further parameterization of sophisticated modeling approaches is needed to quantify the quagga habitat suitability space, because important environmental factors that influence population dynamics often interact non-linearly.

This study provides evidence that (even infrequent) large-magnitude and long-duration drawdown events negatively relate to quagga population presence. Managers of natural resources can integrate these findings into management plans and strategies control, anticipate, and mitigate the future spread of quagga mussel populations.

Authors' contribution

AHY: Research conceptualization; sample design and methodology; data analysis and interpretation; writing – original draft. CCC: Research conceptualization; data analysis and interpretation; writing – review and editing. SA: Research conceptualization; writing – review and editing. ERR: Data analysis and interpretation. JAK: Research conceptualization; writing – review and editing. SFP: Research conceptualization; writing – review and editing. YJP: Research conceptualization; sample design and methodology; investigation and data collection; writing review and editing. ACM: Research conceptualization; writing – review and editing. TMS: Research conceptualization; writing – review and editing.

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References

Ahmed DA, Hudgins EJ, Cuthbert RN, Kourantidou M, Diagne C, Haubrock PJ, Leung B, Liu C, Leroy B, Petrovskii S, Beidas A, Courchamp F (2022) Managing biological invasions: the cost of inaction. *Biological Invasions* 24: 1927–1946, https://doi.org/10.1007/s10530-022-02755-0

Balogh C, Muskó IB, G.-Tóth L, Nagy L (2008) Quantitative trends of zebra mussels in Lake Balaton (Hungary) in 2003–2005 at different water levels. *Hydrobiologia* 613: 57–69, https://doi.org/10.1007/s10750-008-9472-3

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society*: *Series B (Methodological)* 57: 289–300, https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bossenbroek JM, Johnson LE, Peters B, Lodge DM (2007) Forecasting the expansion of zebra mussels in the United States. *Conservation Biology* 21: 800–810, https://doi.org/10.1111/j.1523-1739.2006.00614.x

Bowers R, de Szalay FA (2004) Effects of Hydrology on Unionids (Unionidae) and Zebra Mussels (Dreissenidae) in a Lake Erie Coastal Wetland. *American Midland Naturalist* 151: 286–300, https://doi.org/10.1674/0003-0031(2004)151[0286:EOHOUU]2.0.CO;2

Bowers R, de Szalay FA (2005) Effects of water level fluctuations on zebra mussel distribution in a Lake Erie coastal wetland. *Journal of Freshwater Ecology* 20: 85–92, https://doi.org/10.1080/02705060.2005.9664940
Bureau of Reclamation (2022) Standard Operating Procedure: Field Sampling Methods for Invasive Mussel Early Detection. Version 7 EcoLab-F436A-2022-01, 2022, Ecological Research Laboratory, U.S. Bureau of Reclamation, Denver, CO
Carrillo CC, Charbonneau BR, Altman S, Keele JA, Pucherelli SF, Passamaneck YJ, Murphy AC, Swannack TM (2023) Patterns of dreissenid mussel invasions in western US lakes within an integrated gravity model framework. *Journal of Environmental Management* 332: 117383, https://doi.org/10.1016/j.jenvman.2023.117383
Cole E, Keller RP, Garbach K (2019) Risk of invasive species spread by recreational boaters remains high despite widespread adoption of conservation behaviors. *Journal of Environmental Management* 229: 112–119, https://doi.org/10.1016/j.jenvman.2018.06.078
Cuthbert RN, Pattison Z, Taylor NG, Verbrugge L, Diagne C, Ahmed DA, Leroy B, Angulo E, Briski E, Capinha C, Catford JA, Dalu T, Essl F, Gozlan RE, Haubrock PJ, Kourantidou M, Kramer AM, Renault D, Wasserman RJ, Courchamp F (2021) Global economic costs of aquatic invasive alien species. *Science of The Total Environment* 775: 145238, https://doi.org/10.1016/j.scitotenv.2021.145238
Dlugosch KM, Parker IM (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology* 17: 431–449, https://doi.org/10.1111/j.1365-294X.2007.03538.x
Duncan T (2022) Keeping Invasive Mussels Out Of Colorado. Colorado Outdoors https://coloradooutdoorsmag.com/2022/05/19/keeping-invasive-mussels-out-of-colorados/
Elgin AK, Glyshaw PW, Weidel BC (2022) Depth drives growth dynamics of dreissenid mussels in Lake Ontario. *Journal of Great Lakes Research* 48: 289–299, https://doi.org/10.1016/j.jglr.2021.08.006
Emery-Butcher HE, Beatty SJ, Robson BJ (2020) The impacts of invasive ecosystem engineers in freshwaters: a review. *Freshwater Biology* 65: 999–1015, https://doi.org/10.1111/fwb.13479
Gallardo B, Aldridge DC (2020) Priority setting for invasive species management by the water industry. *Water Research* 178: 115771, https://doi.org/10.1016/j.watres.2020.115771
Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology* 22: 151–163, https://doi.org/10.1111/gcb.13004
Gherardi F, Angioloni C (2009) Eradication and control of invasive species. In: Gherardi F, Gualtieri M, Corti C (eds), Biodiversity Conservation and Habitat Management, Encyclopedia of Life Support Systems (EOLSS). EOLSS Publications, pp 271–298
Grazio JL, Montz G (2002) Winter Lake Drawdown as a Strategy for Zebra Mussel (*Dreissena polymorpha*) control: Results of Pilot Studies in Minnesota and. In: Proceedings 11th International Conference on Aquatic Invasive Species. US Army Engineer Research and Development Center, US Army Engineer Research and Development Center, pp 207–217
Griffiths RW, Schloesser DW, Leach JH, Kovalak WP (1991) Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes Region. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1381–1388, https://doi.org/10.1139/f91-165
Hargrave J, Jensen D (2012) Assessment of the Water Quality Conditions at Ed Zorinsky Reservoir and the Zebra Mussel (*Dreissena polymorpha*) Population Emerged after the Drawdown of the Reservoir and Management Implications for the District's Papillion and Salt Creek Reservoirs: CENWO-ED-HA/WQSS/Zorinsky/2012, Fort Belvoir, VA, April 23, 2012, https://doi.org/10.21236/ADA581189
Harrison AB, Heinz SD, Slack WT (2021) The Costly Impact of Zebra and Quagga Mussels in United States Waterways: Hydropower, Navigation, and Other Industries. Technical Note, United States Army Corps of Engineers
Hasler CT, Leathers J, Ducharme A, Casson NJ (2019) Biological effects of water velocity and other hydrodynamic characteristics of flow on dreissenid mussels. *Hydrobiologia* 837: 1–14, https://doi.org/10.1007/s10750-019-03976-6
Hebert PDN, Muncaster BW, Mackie GL (1989) Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1587–1591, https://doi.org/10.1139/f89-202
Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18, https://doi.org/10.1111/j.1365-2664.2008.01600.x
Johnson LE, Ricciardi A, Carlton JT (2001) Overland dispersal of aquatic invasive species: A risk assessment of transient recreational boating. *Ecological Applications* 11: 1789–1799, https://doi.org/10.1890/1051-0761(2001)011[1789:ODOAIS]2.0.CO;2
Karatayev AY, Burlakova LE, Padilla DK (1998) Physical factors that limit the distribution and abundance of *Dreissena polymorpha* (Pall.). *Journal of Shellfish Research* 17: 1219–1235
Karatayev AY, Burlakova LE, Mastitsky SE, Padilla DK (2015) Predicting the spread of aquatic invaders: insight from 200 years of invasion by zebra mussels. *Ecological Applications* 25: 430–440, https://doi.org/10.1890/13-1339.1

Karatayev AY, Karatayev VA, Burlakova LE, Mehler K, Rowe MD, Elgin AK, Nalepa TF (2021) Lake morphometry determines *Dreissena* invasion dynamics. *Biological Invasions* 23: 2489–2514, https://doi.org/10.1007/s10530-021-02518-3

Kozarek JL, Hondzo M, Kjelland ME, Piercy CD, Swannack TM (2018) Effects of turbulence exposure on zebra mussel (*Dreissena polymorpha*) larval survival. *Aquatic Sciences* 80: 1–10, https://doi.org/10.1007/s00027-017-0563-y

Leuven R, Collas F, Koopman KR, Matthews J, Velde G van der (2014) Mass mortality of invasive zebra and quagga mussels by desiccation during severe winter conditions. *Aquatic Invasions* 9: 243–252, https://doi.org/10.3391/ai.2014.9.3.02

Locklin J, Corbitt D, McMahon RF (2020) Settlement, density, survival and shell growth of zebra mussels, *Dreissena polymorpha*, in a recently invaded low latitude, warm water Texas reservoir. *Aquatic Invasions* 15: 408–434, https://doi.org/10.3391/ai.2020.15.3.04

Mackie GL, Claudi R (2009) Monitoring and Control of Macrofouling Mollusks in Fresh Water Systems, Second ed. CRC Press, Boca Raton, FL, https://doi.org/10.1201/9781439804414

McMahon RF, Ussery TA, Clarke M (1993) Use of emersion as a zebra mussel control method. Contract Report EL-93-1, U.S. Army Waterways Experiment Station, Vicksburg, M.S.

Montana FWP (2021) Montana Fish, Wildlife and Parks. Watercraft Inspection Report 2021. https://fwp.mt.gov/binaries/content/assets/fwp/conservation/ais/reports/watercraft-inspection-final-report-2021_final.pdf

Mueting SA, Gerstenberger SL, Wong WH (2010) An evaluation of artificial substrates for monitoring the quagga mussel (*Dreissena bugensis*) in Lake Mead, Nevada-Arizona. *Lake and Reservoir Management* 26: 283–292, https://doi.org/10.1080/07438141.2010.540700

Nakano D, Strayer DL (2014) Biofouling animals in fresh water: biology, impacts, and ecosystem engineering. *Frontiers in Ecology and the Environment* 12: 167–175, https://doi.org/10.1890/130071

Padilla DK, Williams SL (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment* 2: 131–138, https://doi.org/10.1890/1540-9295(2004)002[0131:BBWAAO]2.0.CO;2

Pathy DA, Mackie GL (1993) Comparative shell morphology of *Dreissena polymorpha*, *Mytilopsis leucophaeata*, and the "quagga" mussel (Bivalvia: Dreissenidae) in North America. *Canadian Journal of Zoology* 71: 1012–1023, https://doi.org/10.1139/z93-135

Quinn A, Gallardo B, Aldridge DC (2014) Quantifying the ecological niche overlap between two interacting invasive species: the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena rostriformis bugensis*): the ecological niche of zebra and quagga mussels. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24: 324–337, https://doi.org/10.1002/aqc.2414

Ricciardi A, Serrouya R, Whoriskey FG (1995) Aerial exposure tolerance off zebra and quagga mussels (Bivalvia: Dreissenidae): implications for overland dispersal. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 470–477, https://doi.org/10.1139/f95-048

Richardson WB, Bartsch LA (1997) Effects of zebra mussels on food webs: interactions with juvenile bluegill and water residence time. *Hydrobiologia* 354: 141–150, https://doi.org/10.1023/A:1003048431234

Rolla M, Consuegra S, Hall DJ, Garcia de Leaniz C (2020) Seasonal and spatial variation in growth and abundance of zebra mussel (*Dreissena polymorpha*) in a recently invaded artificial lake: implications for management. *Frontiers in Ecology and Evolution* 8: 1–14, https://doi.org/10.3389/fevo.2020.00159

Rothman KJ (1990) No adjustments are needed for multiple comparisons. *Epidemiology* 1: 43–46, https://doi.org/10.1097/00001648-199001000-00010

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The Population Biology of Invasive Species. *Annual Review of Ecology and Systematics* 32: 305–332, https://doi.org/10.1146/annurev.ecolsys.32.081501.114037

Sherman JJ, Murry BA, Woolnough DA, Zanatta DT, Uzarski DG (2013) Assessment of remnant unionid assemblages in a selection of Great Lakes coastal wetlands. *Journal of Great Lakes Research* 39: 201–210, https://doi.org/10.1016/j.jglr.2013.03.001

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

Strayer DL (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* 55: 152–174, https://doi.org/10.1111/j.1365-2427.2009.02380.x

Streftaris N, Zenetos A, Papathanassiou E (eds) (2005) Globalisation in Marine Ecosystems: The Story of Non-Indigenous Marine Species Across European Seas. In: Streftaris N, Zenetos A, Papathanassiou E (eds), Oceanography and Marine Biology. CRC Press, pp 429–464, https://doi.org/10.1201/9781420037449-10

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

Web sites, online databases and software

Anaconda Software Distribution (2020) Anaconda Documentation. Anaconda Inc, https://docs.anaconda.com/

Benson AJ, Richerson MM, Maynard E, Larson J, Fusaro A, Bogdanoff AK, Neilson ME, Elgin A (2023) *Dreissena bugensis* Andrusov, 1897: U.S. Geological Survey, Nonindigenous Aquatic Species Database, https://nas.er.usgs.gov/queries/FactSheet.aspx?speciesID=95 (accessed 6 February 2024)

Bureau of Reclamation (2021) Reclamation Information Sharing Environment (RISE). Release 2.4.0. https://data.usbr.gov/ (accessed 20 April 2021)

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/

Raybaut P (2009) Spyder-documentation, https://pythonhosted.org/ (accessed 25 May 2023)

Utah DNR (2023) Utah Department of Natural Resources, Division of Wildlife Resources Inspection Statistics. Utah Aquatic Invasive Species Inspections Dashboard. https://stdofthesea.utah.gov/ais/species-stats/ (accessed 28 August 2023)

Supplementary material

The following supplementary material is available for this article:

Table S1. Meta-data for 41 reservoirs of three quagga mussel population statuses.
Table S2. Drawdown metric summary statistics for continuous variables.
Table S3. Drawdown metric values for Pactola Reservoir from 1997–2020.

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