Refining Quagga Habitat Suitability Models

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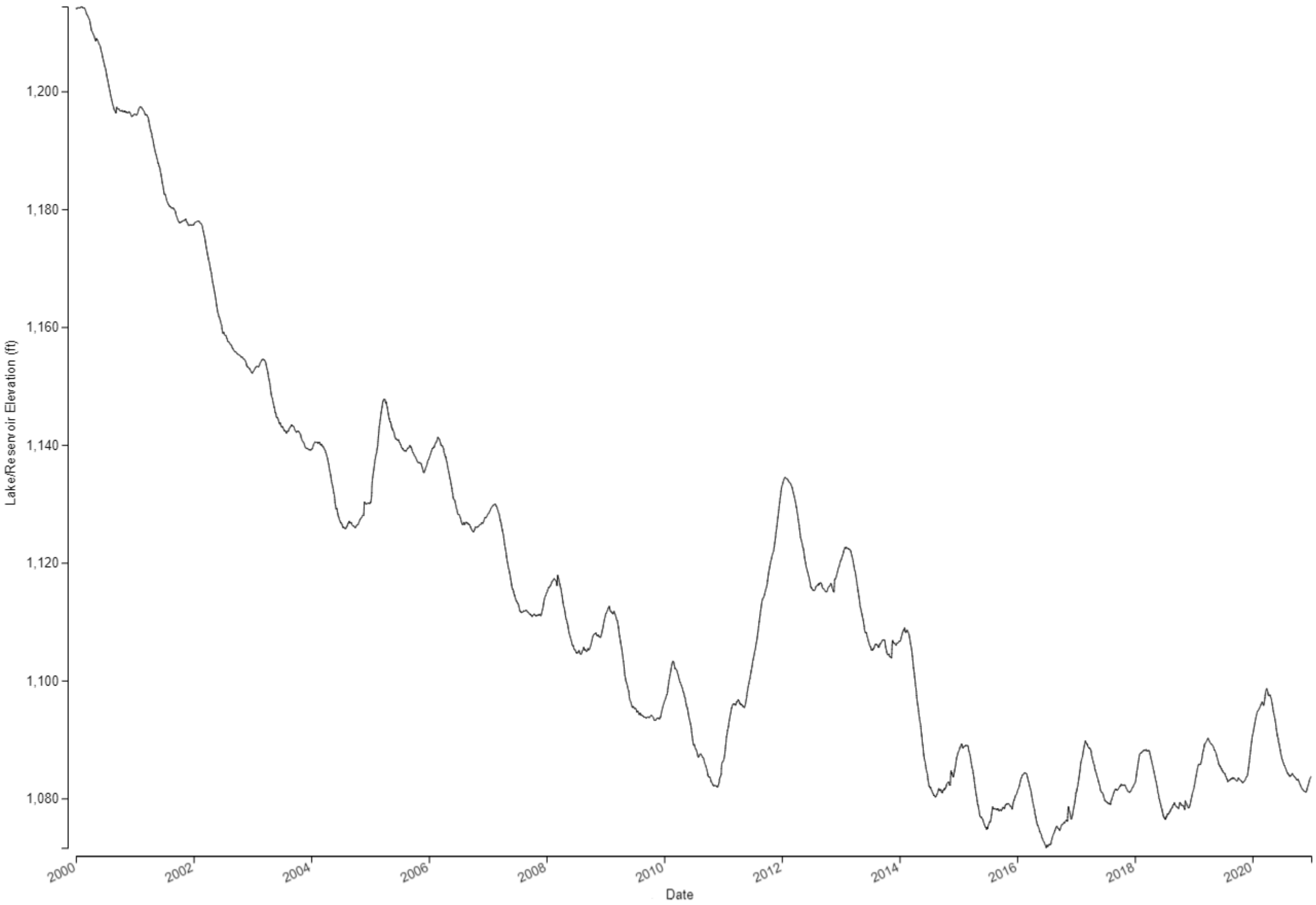

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14. ABSTRACT

The patterns of surface elevation changes were compared between waterbodies with and without infestations of quagga mussels. The frequency of drawdowns was higher in waterbodies with infestations, while the duration of drawdowns and absolute change in elevation were greater in waterbodies without infestations. Patterns from suspect waterbodies, where mussels have been observed but the population appears to have failed, were more comparable to negative waterbodies than to positive waterbodies. This suggests that patterns of water management in reservoirs may have implications for the potential that quagga mussels may become established.

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Acronyms and Abbreviations

χ^2	Chi-square statistic
d	day
DF	degrees of freedom
EcoLab	Reclamation Ecological Research Laboratory
no.	number
P	p-value
Reclamation	Bureau of Reclamation
RISE	Reclamation Information Sharing Environment
SRP	Salt River Project
y	year

Measurements

ft	feet
ft d^{-1}	feet per day (rate)
m	meters
no. y^{-1}	number per year (frequency)
%	percent

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Executive Summary

Quagga mussels (*Dreissena rostriformis bugensis*) present a risk to Reclamation operations, as they can increase operations and maintenance costs at facilities and present the potential to disrupt hydroelectric power generation. They also have broader impacts in waters where they become established, disrupting ecosystems, and limiting recreational opportunities. This invasive and damaging species has already become established in Lake Mead and Lake Powell, as well as in other reservoirs along the Lower Colorado River and the Salt River Project. Current habitat suitability models for the species suggest that many other Reclamation reservoirs may be susceptible to infestations should this species be introduced. Despite this, to date quagga mussels have not spread as widely in the Western U.S. as their proliferation in Lake Mead and Lake Powell suggested.

Extensive quagga mussel monitoring by Reclamation's Ecological Research Laboratory has evidenced that introductions have occurred in other reservoirs, but that these populations appear not to have persisted. Why mussel populations fail in some circumstances remains an open question. One factor that has not been previously investigated is the fact that water in the arid Western U.S. is heavily managed, with reservoirs in the region generally being much more dynamic systems than natural lakes that contain many of the invasive quagga mussel populations in the Eastern U.S. and Canada. To address how reservoir dynamics might relate to the success or failure of quagga mussel establishment, this study investigated patterns of surface elevation change across three classes of waterbody mussel infestation statuses: "established" waterbodies that have had sustained populations of quagga mussels for at least years, "suspect" waterbodies, where evidence of quagga mussels has been detected in the past but populations have not thrived/persisted, and "negative" waterbodies, where no evidence of quagga mussels has ever been detected.

We found that reservoirs with established quagga mussel populations were correlated with more frequent drawdowns than did suspect or negative waterbodies. In contrast, the duration of drawdowns was longer in suspect and negative waterbodies than it was in established waterbodies. The absolute change in surface elevation per drawdown event was also greater for suspect and negative waterbodies than it was in established waterbodies. Taken together, these results suggest that the duration and magnitude of drawdowns may be negatively associated with the ability of quagga mussel to establish in a novel environment. If these results are supported through further investigation it could provide an additional tool for reducing the risk of new quagga mussel infestations.

1. Introduction

Since the late 1980s, when the North America introduction of dreissenid mussels was identified from the Great Lakes, numerous studies have worked to predict the potential for their further spread. Much of this effort has focused on habitat suitability, identifying environmental parameters critical for the survival, colonization, reproduction, and population expansion of dreissenid mussels. A variety of chemical and physical characteristics have been analyzed and proposed to be important for dreissenid mussel to invade a new waterbody. Factors considered to be determinate for successful colonization by dreissenid mussels include the following: calcium, pH, alkalinity, dissolved oxygen, chlorophyll *a* (a proxy for food availability), the nutrients nitrogen and phosphorous, temperature, conductivity, salinity, and turbidity. (See Claudi & Mackie, 2010 for source references). For each of these parameters, attempts have been made to quantify the range of values that are expected to be permissive to, or exclusionary of, dreissenid mussel survival. Many of these values have been derived from observations of waterbodies where mussels have become established and those where mussels are absent. Values for some of these parameters have been supported by laboratory and field studies conducted under more controlled conditions (Claudi et al., 2012; Hincks & Mackie, 1997). Data on environmental parameters have been integrated into habitat suitability tables by a variety of sources (e.g., Claudi & Mackie, 2010; Cohen, 2007; Therriault et al., 2013). Such tables attempt to provide guidelines for environmental parameters, allowing for a risk assessment as to the likelihood a given waterbody is susceptible to colonization. Because there are a range of values of for each parameter from a variety of sources, and number of different habitat suitability tables have been devised. In addition, although quagga (*Dreissena rostriformis bugensis*) and zebra (*Dreissena polymorpha*) mussels show broad overlap in distribution, distinct tables have been devised for the two species to account for differences that have been observed in their physiological tolerances.

Despite the wide range of environmental parameters that have been proposed to play important roles in habitat suitability for dreissenids, a general consensus has arisen that calcium concentration and pH are of particular importance and can be used for initial screening of habitat suitability in waterbodies. Calcium is the major component of mussel shells and is required for growth (Hincks & Mackie, 1997; Whittier et al., 2008). While the precise values of calcium concentration required for mussel survival fluctuate between the various habitat suitability models, most models consider 10-12 milligrams/liter (mg/L) of calcium to be the lower limit for survival, while concentrations above 30 mg/L are general considered optimal and conducive the establishment of infestation-scale populations (Sprung, 1987; Neary & Leach 1992; Cohen & Weinstein, 1998; Whitter et al., 2008). pH interacts with calcium in that a basic environment is required for the precipitation of calcium carbonate ($CaCO_3$) in the shell, and therefore for growth and survival. In acid environments, deposition of new shell material cannot occur, and shells may even undergo degradation. As with calcium concentration, the specific values for pH vary between habitat suitability models. Generally, a pH value between 7-7.4 is considered the lower limit for survival, while values in the range of 8-8.8 are considered optimal (McMahon, 1996; Cohen, 2007; Claudi et al., 2012). There is also a higher limit for pH, with values above 9-9.5 considered unamenable to growth and survival (Mackie & Claudi, 2010). Physiologically this upper threshold for pH may be related to processes other than shell deposition and maintenance.

With regards to colonization of Reclamation reservoirs, quagga mussels have become established along the Lower Colorado River in Lake Mead, Lake Mojave, Lake Havasu, and in Lake Powell along the Upper Colorado River. Quagga mussel populations have also become established in three reservoirs along the Salt River Project in Arizona, Apache Lake, Canyon Lake, and Saguaro Lake. Beyond these established populations, analyses have suggested that the majority of large waterbodies in the Western U.S. have calcium and pH values in the ranges that should make them amenable to the establishment of dreissenid populations (Carrillo et al., 2020).

The Western U.S. contains large source populations in reservoirs that are actively used for boating, a primary vector for mussel introductions, and a large number of other lakes and reservoirs in the region appear to contain habitat suitable for colonization. Even so, comparatively few lakes and reservoirs in the Western U.S. have established populations of quagga or zebra mussels. The potential for successful introduction may be one factor limiting the spread of these mussels. Many Western states have undertaken efforts to inspect boats for the presence of mussels, and to fully decontaminate boats on which mussels are found. The significant number of "mussel boats" intercepted by Colorado, Montana, and Utah demonstrate the efficacy of these programs. Even so, there has been evidence of introductions of mussels to Western U.S. waterbodies in water samples analyzed by Reclamation's Ecological Research Laboratory (EcoLab). Since 2008, the EcoLab has analyzed over 17,000 samples for the early detection of dreissenid mussels, and among these have been a number of positive detections from waterbodies not known to have established mussel populations. In cases where subsequent sampling has not detected any evidence of mussels, it appears that an introduction occurred, but the population failed to persist. Despite these seemingly failed introductions, these waterbodies appeared to present a suitable habitat, at least with regards to calcium concentration and pH. In part, this could be related to populations having been derived from a single introduction event. In invasive species biology multiple introduction events are often thought to be an important factor in successful establishment in the novel environment. However, the fact that the EcoLab's detections are based on microscopic identification of veliger larvae supports the conclusion that these populations were reproducing successfully at the time of detection.

The identification of dreissenid populations that were likely reproductive, but which did not persist, suggests that some unidentified factors may have contributed to the extirpation of these mussels. One suite of environmental factors that have received comparatively little attention are the hydrological characteristics of waterbodies. In lotic systems there has been evidence that the turbulence and velocity associated with flowing water may limit mussel populations under some circumstances (Hasler et al., 2019). A recent study of lentic systems has proposed that lake morphometry may impact long-term population dynamics, although this study did not address initial colonization of lakes (Karatayev et al., 2021).

The hydrology of waterbodies in the Western U.S. appears to be quite different than that of the Eastern U.S. and Europe, where much of the research on habitat suitability for dreissenid mussels has been performed. In the Eastern U.S. and Europe many waterbodies that have been colonized by dreissenids are natural lakes. In contrast, nearly all the waterbodies of concern to Reclamation are man-made impoundments. These reservoirs are used for water storage and distribution, and in many cases for hydroelectric power generation. Due to the heavily managed nature of water in the Western U.S., these reservoirs tend to be much more dynamic systems than most natural lakes. Surface elevations in many reservoirs fluctuate significantly as hydroelectric power generation and delivery drawdowns remove water from reservoirs and transport of spring runoff from melting snowpacks subsequently refill them.

To date, the impact of these hydrological dynamics on the spread of dreissenids in the Western U.S. have not been investigated. Previous studies have generally focused on winter drawdowns on established populations of zebra mussels. In such cases it has been found that drawdowns, or even dewatering to 'dead pool' (in which the water level within the reservoir is so low that it cannot drain by gravity through reservoir outlets), has reduced but not eliminated established populations of zebra mussels (Gaarder, 2016; Hargrave & Jensen, 2012). The goal of the current study was to evaluate how dynamics in water surface elevation might correlate to the presence or absence of quagga mussels in Western U.S. reservoirs. In particular, we focused on comparing reservoirs with established populations of quagga mussels, reservoirs where introductions had occurred, but populations appear to have failed, and reservoirs where no introductions were detected. If drawdown properties or metrics strongly varied among reservoirs of differing statuses, these metrics could be used to devise benchmarks in future Reclamation reservoir management plans to prevent or combat quagga mussel infestation.

2. Methods

2.1 Data acquisition and quality check

Our previous report, ST-2021-19134-01, identifies several reservoirs of interest in predicting and understanding quagga mussel invasions dynamics. To understand the influence of reservoir water management on invasion status, we obtained daily water elevation data (ft, relative to mean sea-level) from the Reclamation Information Sharing Environment (RISE, data.usbr.gov; last accessed on April 20, 2021) for Reclamation managed reservoirs in the Western U.S. Data for reservoirs in the Salt River Project (SRP) were obtained from the SRP's engineering division. Upon initial acquisition, data were quality-checked for values that appeared to have resulted from instrumental or recording errors (e.g., changes >20 ft d^{-1}). These values were considered erroneous and were removed from the datasets. Water surface levels were rounded to the nearest foot.

For each of the 41 reservoirs (Table AA-1) quagga mussel infestation status (hereafter "status") was determined based on data from the EcoLab's early detection and monitoring. For each lake, status was categorized as either (a) established mussel population (i.e., "established"), (b) mussel introduction detected from microscopy and/or environmental DNA (eDNA) analysis, but subsequent sampling and analyses have all been negative (i.e., "suspect"), or (c) have never had detections by microscopy or eDNA; negative for mussel presence (i.e., "negative"). Six reservoirs were "established", twelve were "suspect", and twenty-four were "negative".

2.2 Drawdown definition and metric calculation

For the purposes of this study, we were interested in determining if periodic declines in reservoir water elevation, or drawdowns, were related to quagga mussel infestation statuses across reservoirs.

Drawdown events were defined by a magnitude and duration of changes in water elevation that are relevant to quagga mussel biology and ecology (Hoddle, 2019). Two conditions must be met for a drawdown to occur:

1) a minimum of 1 ft decrease in water level from the day prior, and
2) water level remains at that lower level, or continues to decrease, for five consecutive days.

Drawdowns ended when either of the following conditions were met:

1) the water elevation increased by a minimum of 1 ft, or
2) the elevation remained constant for a minimum of five days (past the initial five days).

This definition guaranteed that any mussels attached near the surface-level elevation at the start of a drawdown event would be exposed for a minimum of five days, which is the minimum emersion duration for mussel death (Hoddle, 2019).

We acknowledge three caveats for this operational definition of drawdown events:

1) it excludes instances of elevation decline with a duration of shorter than five days, regardless of the rate or magnitude of decline.
2) it identifies two drawdown events divided by a single day of 1-ft elevation increase, when ideally these would be considered a single event, and
3) once an event start is triggered, it does not consider the duration of potential mussel exposure while water elevation subsequently increases.

To address the first two caveats for the current study, we explored the average number of times <5-d events and intervals (durations between drawdown events) occurred per year in each reservoir (Table AA-2). We concluded that the conditions of these caveats were met rarely enough to warrant continuation with our current drawdown event definition. To address the third caveat, we intend to redefine the 'end trigger' of a drawdown event for future work with these data.

We calculated a family of eight metrics which describe various properties of individual events and annual patterns for each reservoir, such as: (1) number of events per year (no. y^{-1}), (2) percent of year spent in drawdown (%), (3) mean event duration (d), (4) mean interval duration (i.e., time between events) (d), (5) mean elevation change (ft), (6) mean rate of elevation change (ft d^{-1}), (7) mean percent change in elevation (%), and (8) mode season of drawdown occurrence. Broadly, these metrics can be used to describe event frequency (1, 2, and 4), duration (3), magnitude (5 and 7), rate (6), and seasonality (8). As a supplemental analysis, we also examined frequency (1) and magnitude (5) metrics for drawdown events with durations shorter than 5 d (Figure AA-1). Drawdowns and metric calculations were all performed in Python using Anaconda 1.10.0 Navigator (Anaconda Software Distribution, 2020) and Spyder (Raybaut, 2009).

2.3 Statistical analysis

We quantified the differences among reservoir statuses (a categorical predictor variable with three levels: established, suspect, negative) and our metrics of interest using eight individual (univariate, one-way) non-parametric tests described below.

We acknowledge that we used the same set of raw elevation data to calculate our eight drawdown event response metrics (see section 2.2) and therefore our analyses represent a family of multiple comparisons that can be used as a weight-of-evidence approach for inferring correlations among our metrics and lake status. P-values for each univariate analysis were not adjusted (Rothman, 1990), but were adjusted for post hoc test to find differences among reservoir statuses using the false discovery rate correction (Benjamini & Hochberg, 1995).

For statistical analysis, metrics were first pooled (averaged) to, or calculated at (in the case of frequency metrics), the year level for each reservoir, then the reservoir mean (averaged across years) was taken for each metric to ensure that all datapoints were independent (i.e., $n = 41$ independent reservoirs for each analysis). After reservoir means for each metric were calculated, we tested for normality and equality of variance. The distributions were not normal, and variances among statuses were often not equivalent. Therefore, we used non-parametric Kruskal-Wallis tests for all analyses with continuous response variables. For all tests that returned a significant result ($p < 0.1$), a post hoc Wilcoxon Rank Sum Multiple Comparison test was used to find differences among reservoir statuses.

To examine drawdown event seasonality, we first assigned a season category of spring (Mar-May), summer (Jun-Aug), fall (Sept-Nov), and winter (Dec-Feb) to each drawdown event based on the start month of the event. We then determined the mode (i.e., most common) season in which events occurred for each year in each reservoir. We then determined the mode season in which events occurred for each reservoir (by finding the overall mode of the annual mode-seasons). Because the drawdown event seasonality metric was categorical (i.e., season), we used a Chi-square test for this analysis. All statistical analyses were performed in R v4.0.3 (R Core Team, 2021).

3. Results

3.1 Drawdown event frequency, duration, and seasonality

Taken together, our examination of drawdown event frequency and duration metrics (Figure 1) indicate that reservoirs with established quagga mussel infestations generally have more frequent and shorter duration events than suspect or negative reservoirs. Further, suspect and negative reservoirs did not exhibit significant differences for any frequency or duration metric.

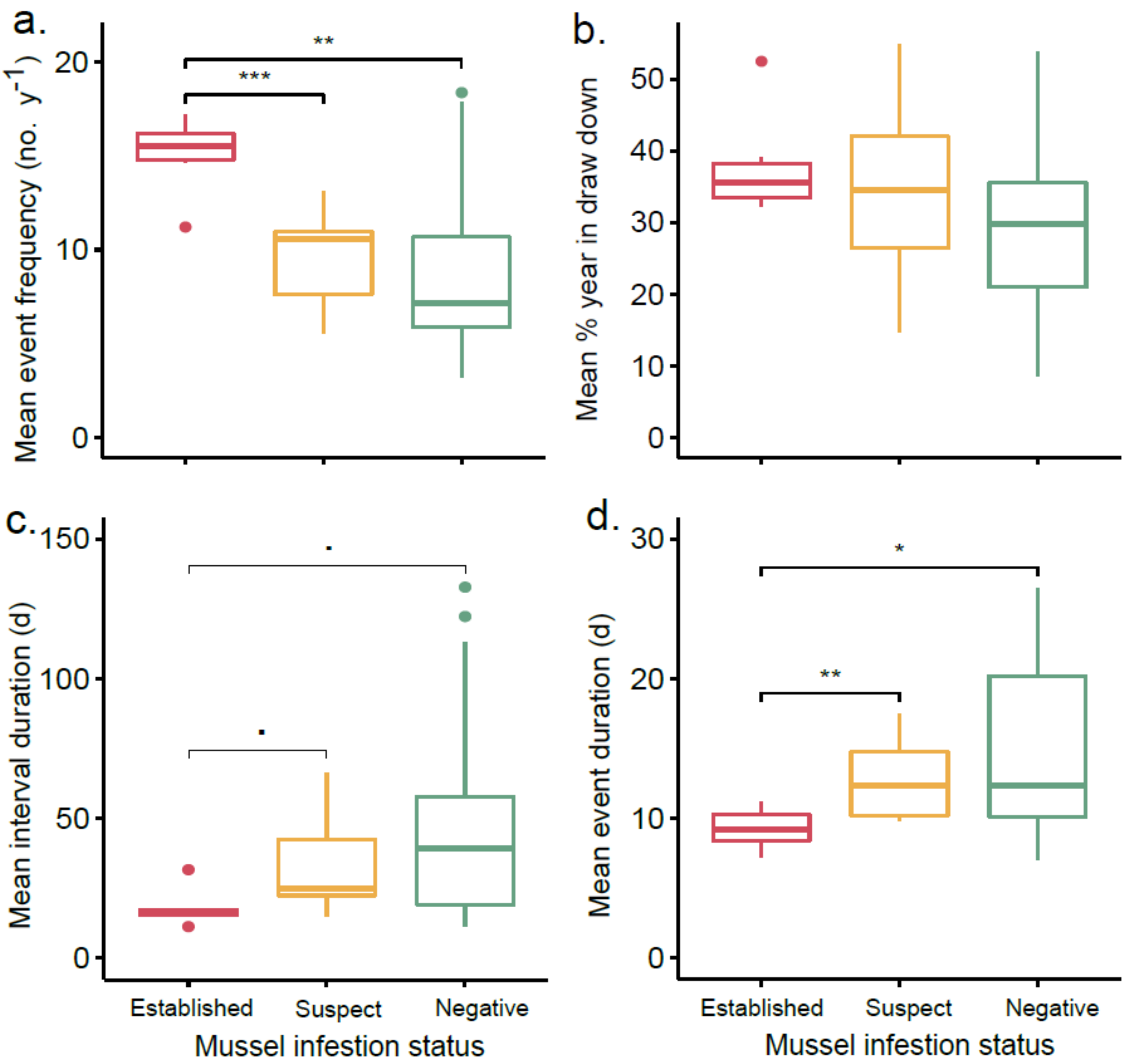

Figure 1. Drawdown event (a-c) frequency and (d) duration metrics across established (red), suspect (yellow), and negative (green) reservoirs. Event frequencies are summarized three ways: (a) the mean number of events per year, (b) the mean total percent of each year spent in a drawdown event, and (c) the mean duration of the intervals between drawdown events. Post hoc multiple comparison results are illustrated by horizontal brackets across significantly different statuses with the significance level noted (• = $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Our examination of event frequency, in terms of the mean number of events per year, revealed important differences among reservoir infestation statuses (Table 1). Established reservoirs exhibited significantly more events per year ($\bar{x} = 15.5\ \mathrm{y}^{-1}$) than both suspect ($\bar{x} = 10.6\ \mathrm{y}^{-1}$) and negative ($\bar{x} = 7.2\ \mathrm{y}^{-1}$) reservoirs, while the number of events seen for the latter two statuses were not different (Figure1a, Table2). While on its own this pattern appears counterintuitive in the context of quagga mussel exposure tolerances, the additional frequency and duration metrics (Figure 1b-d) bring clarity. Although established reservoirs have more events per year, the average overall percent of the year spent in a drawdown event is similar across reservoir statuses (30-35%; Table 1, Figure 1b). The lack of difference across statuses in this metric is explained by the patterns observed for both interval durations (i.e., days between events, Figure1c) and event durations (Figure 1d). The average duration of intervals between drawdown events was significantly different among reservoir statuses (Table 1). Established reservoirs had shorter mean interval durations (17 d) than both suspect (25 d) and negative (40 d) reservoirs (although our p-value adjustment for the post hoc multiple comparisons prevented these differences from meeting the threshold of $\alpha = 0.05$; Table 2). Further, the mean duration of drawdown events across statuses were significantly different (Table 1) with established reservoirs having, on average, significantly shorter events (9 d) than both suspect (12 d) and negative (12 d) reservoirs (Figure 1d; Table 2).

Table 1. Statistical analysis results summary examining differences among reservoir mussel infestation statuses. Results are from Kruskal-Wallis tests unless otherwise noted.

Response variable	**Units**	$\chi 2$	***DF***	***P***
Mean frequency of events	no. y^{-1}	11.163	2	**0.004**
Mean percent of year in drawdown	%	3.228	2	0.199
Mean event duration	d	6.550	2	**0.038**
Mean interval duration	d	6.240	2	**0.044**
Mean elevation change	ft	7.313	2	**0.026**
Mean rate of elevation change	ft d^{-1}	6.984	2	**0.030**
Mean percent change in elevation	%	6.101	2	**0.047**
Mode season of drawdown occurrence *	-	2.198	6	0.901

** = Chi-square test performed for this analysis*
Bold p-values = statistically significant ($\alpha \leq 0.05$)

Although drawdown event frequencies and durations varied between reservoir infestation statuses, the mode seasonality of events did not (Table 1; Figure 2). Across all three statuses, summer was the most common season in which drawdown events occurred, which is unsurprising since all these reservoirs are in the Western U.S., where the summer months see increased water deliveries for irrigation, decreased precipitation and runoff, and increased evapotranspiration. Further, fall was the least common season for events, while the rank order of spring and winter event frequency varied among statuses.

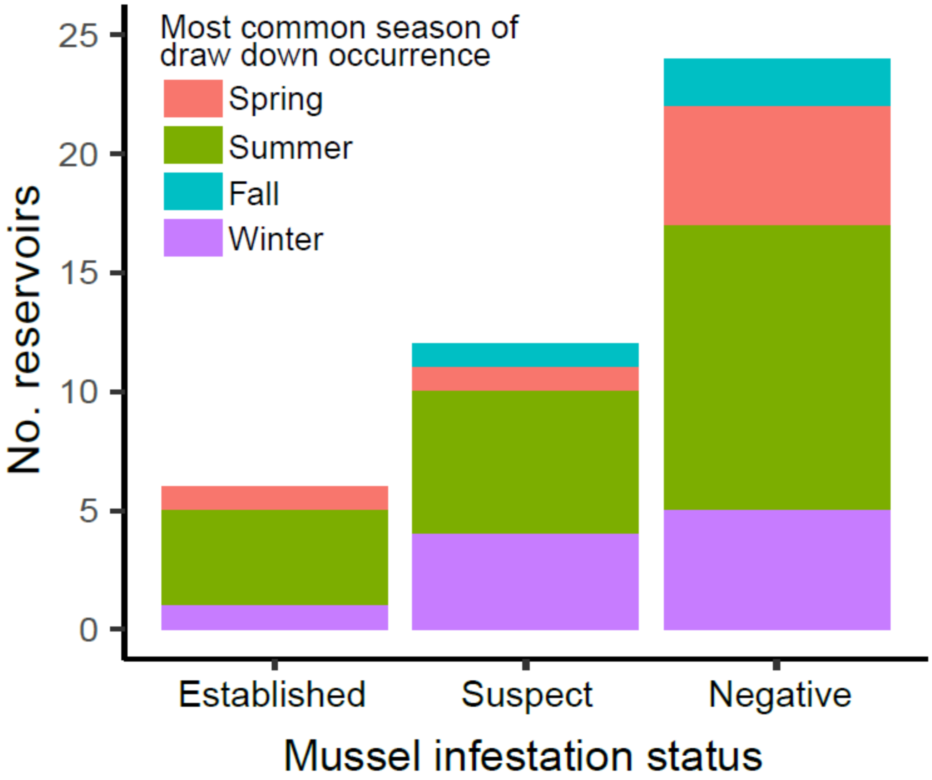

Figure 2. The mode (most common) season in which drawdown events occur in reservoirs with established, suspect, and negative statuses.

3.2 Drawdown event magnitude and rate

Each of our analyses of drawdown event magnitude (ft, %) and rate of change in water elevation (ft d^{-1}; Figure 3, revealed statistical differences among quagga mussel infestation statuses (Table 1).

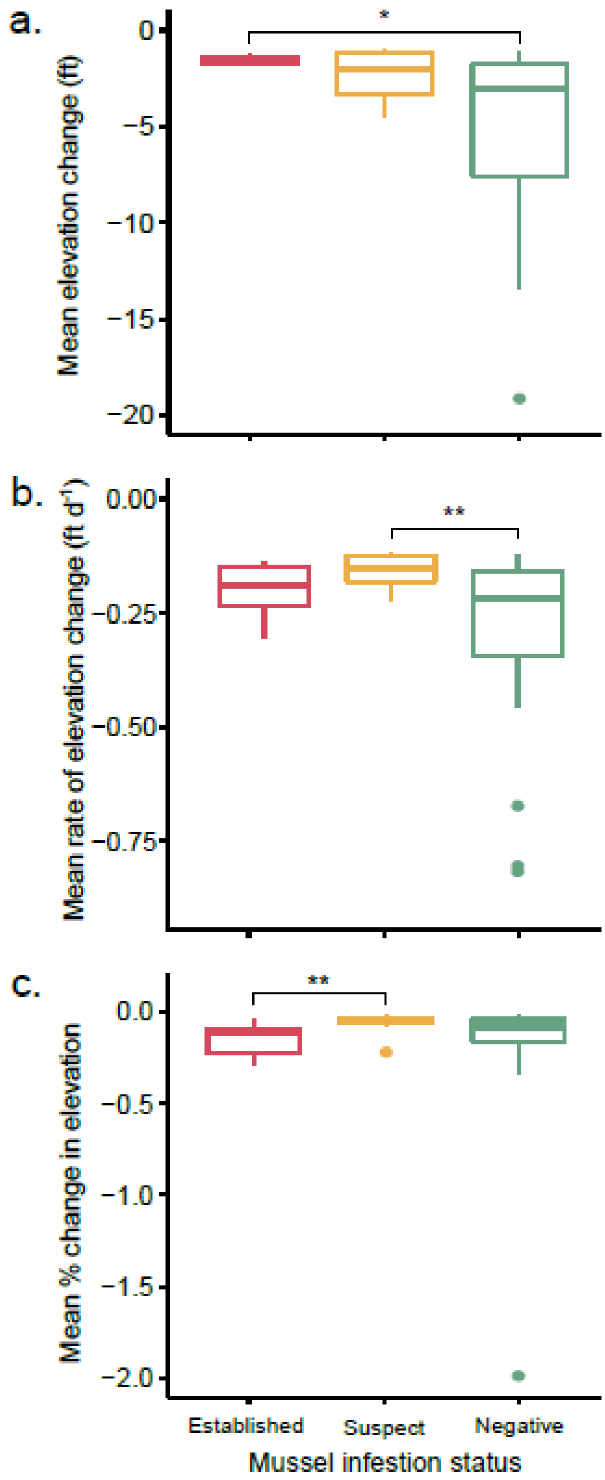

Figure 3. Drawdown event (a, c) magnitude metrics and (b) rate of change in elevation (ft d-1) across established (red), suspect (yellow), and negative (green) reservoirs. Event magnitude is summarized by (a) mean elevation change (ft) and (c) mean percent change in elevation (%). Post hoc multiple comparison results are illustrated by horizontal brackets across significantly different statuses with the significance level noted (* = p <0.05, ** = p <0.01).

Our examination of drawdown event mean change in elevation (ft) revealed that established reservoirs have smaller mean magnitude decreases in elevation (-1.6 ft) than negative (-3.0 ft), but not suspect (-2.2 ft) reservoirs (Figure 3a; Table 2). In contrast, the mean rate of change in elevation (ft d^{-1}) only significantly differed between suspect (-0.15 ft d^{-1}) and negative (-0.22 ft d^{-1}) reservoirs, while the established (-0.19 ft d^{-1}) reservoir rate differed from neither (Figure 3b; Table 2). Further, the mean percent (%) change in elevation (i.e., our metric for drawdown magnitude, standardized across reservoirs) only showed a significant difference between established (-0.12 %) and suspect (-0.04 %), but neither of these categories differed from the value for negative (-0.09 %) reservoirs (Figure 3c; Table 2).

Table 2. Adjusted P-values for post hoc Wilcoxon Rank Sum Multiple Comparison tests to compare response variable differences across reservoir statuses (i.e., established-suspect, established-negative, suspect- negative). Post hoc tests were only conducted for response variables with statistically significant ($\alpha \leq 0.05$) Kruskal-Wallis test results.

Response variable	**Est-Sus**	**Est-Neg**	**Sus-Neg**
Mean frequency of events	**0.001**	**0.005**	0.166
Mean event duration	**0.021**	**0.037**	0.728
Mean interval duration	0.062	0.062	0.311
Mean elevation change	0.437	**0.039**	0.117
Mean rate of elevation change	0.319	0.432	**0.026**
Mean percent change in elevation	**0.029**	0.347	0.126

Bold p-values = statistically significant ($\alpha \leq 0.05$)

4. Discussion

Our results indicate that seasonal drawdown dynamics could be an important driver for successful quagga mussel colonization in reservoirs in the Western United States. Drawdowns, which most commonly occur during summer months, likely provide the proper exposure conditions, such as high air temperatures and low humidity, which desiccate and kill exposed mussels (Bowers & de Szalay, 2005). More specifically, negative reservoirs generally had longer duration drawdowns than reservoirs with established populations. This could indicate that quagga mussels are more negatively impacted by longer exposure periods, either as adults or as settling juveniles (Grazio & Montz, 2002; Leuven et al., 2014).

Further, the absolute magnitude (ft) of drawdown events was roughly doubled in negative reservoirs relative to established reservoirs. In contrast, the percent changes in elevation were not different between established and negative reservoirs. While the percent change for suspect reservoirs was lower than for established or negative reservoirs, a difference of <0.1% in mean event elevation change may not be ecologically significant for infestation status. This suggests that, at least for deep waterbodies managed by Reclamation, the absolute decrease in elevation (by footage) is likely a more important driver of mussel infestation status than the drawdown magnitude relative to the total depth of the waterbody (i.e., percent change in elevation). However, we note that the percent change in elevation may be a more important determinant of mussel infestation for shallow waterbodies.

Although quagga mussels have been found growing at depths in excess of 90 m in the Great Lakes (Elgin et al., 2021), a study of artificial substrates in Lake Mead found settlement was highest in depths less than 20 m (Mueting et al., 2010). It may be that during the early stages of invasion in a new waterbody, the concentration of individuals near the surface makes the nascent population more vulnerable to the impacts of drawdowns. Therefore, our results suggest that less frequent drawdowns of longer duration (i.e., on average 12 days) and larger magnitude (i.e., on average 3 ft) may in part help to prevent mussel population establishment in currently negative reservoirs.

While these data do show trends in the relationship between quagga mussel presence and water level, specifically the frequency, duration, and magnitude of drawdowns, there were limitations with our analyses. First, we only used a small subsample of all the possible lakes in the Western U.S., so inference is constrained by the data used in these analyses. Second, we summarized drawdowns by time of year (annual means or seasons) and duration (e.g., 5 days). While summary values are useful for detecting general trends, we also could have missed any extreme events that might have impacted quagga mussel colonization. Finally, we did not consider other factors that might interact with a drawdown and impact habitat suitability (e.g., temperature, water quality). With respect to temperature, it could be that drawdowns do not need to result in full emersion of mussels, as exposure to warmer surface waters could be sufficient to cause physiological stress or mortality. Future efforts should consider integrating these results into the model developed by Carrillo et al. (2020), which indicated that quagga mussel distribution is a result of interactions between multiple factors including water quality (e.g., pH, calcium) and boater transport. However, quantifying the habitat space could be difficult if these factors interact non-linearly.

These results do, however, provide evidence that infrequent, long duration, large magnitude drawdown events are negatively correlated with quagga mussel presence. Natural resource managers can incorporate these results into strategies for predicting future dispersal and management of quagga mussels.

References

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

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*(1), 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bowers, R., & de Szalay, F. A. (2005). Effects of Water Level Fluctuations on Zebra Mussel Distribution in a Lake Erie Coastal Wetland. *Journal of Freshwater Ecology*, *20*(1), 85–92. https://doi.org/10.1080/02705060.2005.9664940

Carrillo, C. C., Altman, S., Swannack, T. M., Keele, J., Pucherelli, S., Passamaneck, Y., & Murphy, A. (2020). *Using constrained gravity models at large spatial scales to simulate invasive species colonization* (Final Report ST-2020-8110-01; p. 33). Bureau of Reclamation.

Claudi, R., Graves, A., Taraborelli, A. C., Prescott, R., & Mastitsky, S. (2012). Impact of pH on survival and settlement of dreissenid mussels. *Aquatic Invasions*, *7*(1), 21–28. https://doi.org/10.3391/ai.2012.7.1.003

Claudi, R., & Mackie, G. L. (2010). *Monitoring and control of macrofouling mollusks in fresh water systems*. CRC Press.

Cohen, A. N. (2007). *Potential distribution of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) in California* [Phase 1 Report]. California Department of Fish and Game. http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.573.1363&rep=rep1&type=pdf

Elgin, A. K., Glyshaw, P. W., & Weidel, B. C. (2021). Depth drives growth dynamics of dreissenid mussels in Lake Ontario. *Journal of Great Lakes Research*, S0380133021001726. https://doi.org/10.1016/j.jglr.2021.08.006

Gaarder, N. (2016, June 4). Zebra mussel larvae have been found again in Zorinsky Lake. *Omaha World-Herald*. https://www.omaha.com/news/metro/zebra-mussel-larvae-have-been-found-again-in-zorinsky-lake/article_333f2c46-3f08-11e6-975e-0b1ca96bf0e6.html

Grazio, J. L., & Montz, G. (2002). *Winter lake drawdown as a strategy for zebra mussel (*Dreissena polymorpha*) control: Results of pilot studies in Minnesota and Pennsylvania* (p. 15).

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* (Technical Report CENWO-ED-HA/WQSS/Zorinsky/2012). U.S. Army Corps of Engineers. http://www.dtic.mil/docs/citations/ADA581189

Hasler, C. T., Leathers, J., Ducharme, A., & Casson, N. J. (2019). Biological effects of water velocity and other hydrodynamic characteristics of flow on dreissenid mussels. *Hydrobiologia*, *837*(1), 1–14. https://doi.org/10.1007/s10750-019-03976-6

Hincks, S. S., & Mackie, G. L. (1997). Effects of pH, calcium, alkalinity, hardness, and chlorophyll on the survival, growth, and reproductive success of zebra mussel (*Dreissena polymorpha*) in Ontario lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(9), 2049–2057.

Karatayev, A. Y., Karatayev, V. A., Burlakova, L. E., Mehler, K., Rowe, M. D., Elgin, A. K., & Nalepa, T. F. (2021). Lake morphometry determines *Dreissena* invasion dynamics. *Biological Invasions*, *23*(8), 2489–2514. https://doi.org/10.1007/s10530-021-02518-3

Leuven, R., Collas, F., Koopman, K. R., Matthews, J., & van der Velde, G. (2014). Mass mortality of invasive zebra and quagga mussels by desiccation during severe winter conditions. *Aquatic Invasions*, *9*(3), 243–252. https://doi.org/10.3391/ai.2014.9.3.02

Mueting, S. A., Gerstenberger, S. L., & Wong, W. H. (2010). An evaluation of artificial substrates for monitoring the quagga mussel (*Dreissena bugensis*) in Lake Mead, Nevada–Arizona. *Lake and Reservoir Management*, *26*(4), 283–292. https://doi.org/10.1080/07438141.2010.540700

Rothman, K. J. (1990). No Adjustments Are Needed for Multiple Comparisons: *Epidemiology*, *1*(1), 43–46. https://doi.org/10.1097/00001648-199001000-00010

Therriault, T. W., Weise, A. M., Higgins, S. N., Guo, Y., & Duhaime, J. (2013). *Risk assessment for three dreissenid mussels (*Dreissena polymorpha*,* Dreissena rostriformis bugensis*, and* Mytilopsis leucophaeata*) in Canadian freshwater ecosystems* (p. 93). Fisheries and Oceans Canada.

Metric Conversions

Unit	Metric Equivalent
1 foot	0.3048 meters
1 foot per day	0.3048 meters per day

Appendix A

Table AA-1 Meta-data for 41 reservoirs of three quagga mussel infestation statuses included in our dataset. Daily water elevation (ft) data were available for each reservoir with the year range. Identifying information for suspect reservoirs has been omitted due to the confidential nature of these data.

Status	**Reservoir**	**State**	**Coordinates**	**Year range**
Established	Apache Lake	AZ	[33.584, -111.251]	2000-2020
Established	Saguaro Lake	AZ	[33.570, -111.524]	2000-2020
Established	Lake Havasu	AZ-CA	[34.478, -114.377]	1997-2020
Established	Lake Mead	NV-AZ	[36.150, -114.415]	1997-2020
Established	Lake Mohave	NV-AZ	[35.487, -114.644]	1997-2020
Suspect	Suspect 1	omitted	omitted	2004-2021
Suspect	Suspect 2	omitted	omitted	2000-2020
Suspect	Suspect 3	omitted	omitted	1998-2020
Suspect	Suspect 4	omitted	omitted	2004-2020
Suspect	Suspect 5	omitted	omitted	1998-2021
Suspect	Suspect 6	omitted	omitted	2001-2021
Suspect	Suspect 7	omitted	omitted	2001-2021
Suspect	Suspect 8	omitted	omitted	2006-2020
Suspect	Suspect 9	omitted	omitted	2001-2020
Suspect	Suspect 10	omitted	omitted	1998-2021
Suspect	Suspect 11	omitted	omitted	2000-2020
Suspect	Suspect 12	omitted	omitted	2007-2021
Negative	Calamus Reservoir	NE	[41.867, -99.254]	1997-2021
Negative	Carter Lake Reservoir	CO	[40.351, -105.192]	2003-2021
Negative	Currant Creek Reservoir	UT	[40.766, -110.987]	1997-2021
Negative	Davis Creek Reservoir	NE	[41.425, -98.758]	1997-2021
Negative	Flatiron Reservoir	CO	[40.370, -105.231]	2003-2021
Negative	Folsom Lake	CA	[38.683, -121.183]	1997-2021
Negative	Keith Sebelius Lake	KS	[39.807, -99.934]	1997-2021
Negative	Kirwin Reservoir	KS	[39.661, -99.144]	1997-2021
Negative	Lake Estes	CO	[40.373, -105.487]	1997-2021
Negative	Lake Tschida	ND	[46.596, -101.809]	1997-2021
Negative	Lost Creek Reservoir	UT	[41.188, -111.396]	1997-2021
Negative	Moon Lake Reservoir	UT	[40.574, -110.506]	1997-2021

Status	**Reservoir**	**State**	**Coordinates**	**Year range**
Negative	Newton Reservoir	UT	[41.899, -111.975]	1997-2021
Negative	Pactola Reservoir	SD	[44.072, -103.488]	1997-2021
Negative	Paonia Reservoir	CO	[38.944, -107.351]	1997-2021
Negative	Pinewood Reservoir	CO	[40.368, -105.286]	2003-2021
Negative	Platoro Reservoir	CO	[37.340, -106.564]	2016-2021
Negative	Ruedi Reservoir	CO	[39.363, -106.818]	1997-2021
Negative	Silver Jack Reservoir	CO	[38.232, -107.541]	1997-2021
Negative	Taylor Park Reservoir	CO	[38.832, -106.585]	1997-2021
Negative	Trinity Lake	CA	[40.801, -122.762]	1997-2021
Negative	Twin Lakes Reservoir	CO	[39.080, -106.313]	1997-2021
Negative	Webster Reservoir	KS	[39.391, -99.425]	1997-2021
Negative	Whiskeytown Lake	CA	[40.598, -122.537]	1997-2021

Table AA-1 Continued.

Table AA-2 Summary of the [Mean ± SD] number of events and intervals per year in each reservoir that not captured by our current drawdown event definition. Identifying information for suspect reservoirs has been omitted due to the confidential nature of these data.

Status	**Reservoir**	**No. <5-d events y^{-1}**	**No. <5-d intervals y^{-1}**
Established	Apache Lake	18.90 ± 6.43	5.57 ± 2.11
Established	Lake Havasu	7.96 ± 3.36	3.21 ± 1.91
Established	Lake Mead	2.39 ± 0.98	4.17 ± 2.66
Established	Lake Mohave	7.96 ± 3.18	4.50 ± 1.56
Established	Lake Powell	1.33 ± 0.58	9.00 ± 3.11
Established	Saguaro Lake	39.00 ± 11.52	4.33 ± 3.48
Suspect	Suspect 1	1.13 ± 0.35	2.88 ± 1.54
Suspect	Suspect 2	2.50 ± 1.58	4.29 ± 2.57
Suspect	Suspect 3	2.25 ± 1.86	6.17 ± 2.55
Suspect	Suspect 4	1.50 ± 0.53	2.35 ± 1.37
Suspect	Suspect 5	1.89 ± 0.93	0.26 ± 0.45
Suspect	Suspect 6	1.90 ± 1.20	6.00 ± 2.08
Suspect	Suspect 7	1.43 ± 1.13	3.53 ± 2.35
Suspect	Suspect 8	1.00 ± 0.00	1.67 ± 2.02
Suspect	Suspect 9	1.43 ± 0.79	3.20 ± 2.12
Suspect	Suspect 10	1.36 ± 0.50	4.30 ± 2.99
Suspect	Suspect 11	1.55 ± 0.69	5.19 ± 2.60
Suspect	Suspect 12	1.17 ± 0.41	0.43 ± 0.65
Negative	Calamus Reservoir	2.75 ± 2.18	2.44 ± 1.71
Negative	Carter Lake	1.56 ± 1.13	5.58 ± 5.94
Negative	Currant Creek Reservoir	2.14 ± 1.17	1.72 ± 1.34
Negative	Davis Creek Reservoir	1.64 ± 0.93	1.32 ± 1.57
Negative	Flatiron Reservoir	35.16 ± 11.31	5.11 ± 3.84
Negative	Folsom Lake	1.47 ± 0.77	4.00 ± 2.10
Negative	Keith Sebelius Reservoir	1.75 ± 1.16	0.35 ± 0.65
Negative	Kirwin Reservoir	1.36 ± 0.50	1.12 ± 1.27
Negative	Lake Estes	26.32 ± 13.61	3.84 ± 2.79
Negative	Lake Tschida	1.56 ± 0.73	0.83 ± 0.96
Negative	Lost Creek	3.00 ± 3.37	3.17 ± 1.90
Negative	Moon Lake	2.75 ± 2.24	1.71 ± 1.16

Status	Reservoir	No. <5-d events y^{-1}	No. <5-d intervals y^{-1}
Negative	Newton Reservoir	2.73 ± 3.44	1.54 ± 1.56
Negative	Pactola Reservoir	1.86 ± 0.69	1.70 ± 1.36
Negative	Paonia Reservoir	3.95 ± 2.98	1.68 ± 1.75
Negative	Pinewood Reservoir	17.32 ± 6.38	5.79 ± 3.14
Negative	Platoro Reservoir	1.75 ± 1.50	3.67 ± 1.97
Negative	Ruedi Reservoir	1.25 ± 0.46	6.72 ± 3.61
Negative	Silver Jack Reservoir	2.19 ± 1.17	1.44 ± 1.36
Negative	Taylor Park Reservoir	1.43 ± 0.65	3.52 ± 1.56
Negative	Trinity Lake	1.43 ± 0.53	3.38 ± 2.08
Negative	Twin Lakes Reservoir	11.38 ± 12.01	5.80 ± 3.80
Negative	Webster Reservoir	2.00 ± 1.05	1.35 ± 1.34
Negative	Whiskeytown Lake	7.52 ± 3.75	3.00 ± 1.73

Table AA-2 Continued.

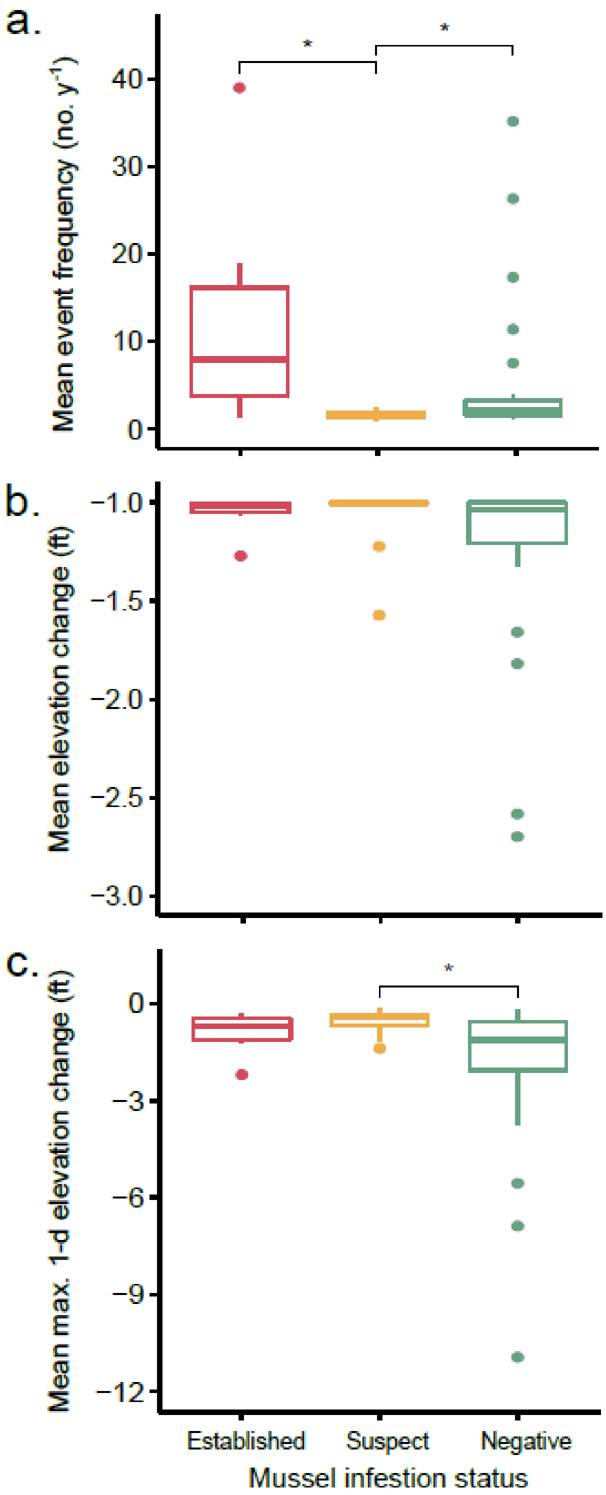

Figure AA 1. Less than 5-d duration drawdown event (a) frequency, and (b, c) magnitude metrics across established (red), suspect (yellow), and negative (green) reservoirs. Event magnitude is summarized by (b) mean elevation change (ft) and (c) the mean maximum change in elevation (ft) for a single day drawdown event. Post hoc multiple comparison results are illustrated by horizontal brackets across significantly different statuses (* = p <0.05).