Title

Short-term responses of freshwater mussels to floods in a southwestern U.S.A. river estimated using mark-recapture sampling

Author List

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Abstract

1. Floods can directly affect riverine organisms by displacing them, and population-level responses to floods can vary depending on flood magnitude and organism mobility. Benthic organisms can resist displacement until substrates become unstable, whereas mobile organisms are generally more resistant. Freshwater mussels are benthic organisms with low mobility, and there is limited research on their population-level responses to floods. This study provides novel insight to population-level responses of mussels to large floods (>500 m^3/s).

2. Population dynamics (i.e., abundance, survival, and site fidelity) and sampling efficiency (i.e. detection probability) were estimated in a robust design framework for four freshwater mussel species (*Cyclonaias petrina*, *C. pustulosa*, *Amblema plicata*, and *Tritogonia verrucosa*) from 2017 to 2019 at two sites (upper and lower sites) within riffle habitats in the Colorado River, Texas, USA. Individuals of each species were affixed with shellfish tags, with *C. petrina* and *C. pustulosa* individuals also being affixed with PIT tags. Changes in population dynamics related to the flood event at each site were directly tested. During sampling, a major flood occurred at each of the two study sites; the floods differed in magnitude but were in the 99^{th} percentile of historical flows at their respective gages.

3. There were site- and species-specific differences in estimated abundances, survival, and site fidelity during periods with the floods. Estimated abundances of *C. petrina*, *C. pustulosa*, and *T. verrucosa* were reduced 40 to 78% by the lesser flood magnitude (1,283 m^3/s) at the upper site. Estimated abundances of *C. petrina*, *C. pustulosa*, and *A. plicata* were reduced 93 to 95% by the greater flood magnitude (4,332 m^3/s) at the lower site. There was a reduction in survival of *C. petrina* at the upper site, while initially high survival at the lower site was reduced during the interval with the flood for all species. Finally, there was a reduction in site fidelity of *C. pustulosa* at the lower site.

4. Floods reduced the abundance of all species within riffle habitats at the two sites. Large floods, therefore, affect populations dynamics of mussels, but the fate of the displaced mussels is unknown, and with limited inference, reach-scale effects are unknown. This study adds to the growing body of knowledge on aquatic organism's response to large floods, although quantification of resiliency is needed to fully understand long-term fitness responses of mussels following large floods.

Introduction

Resistance and resiliency of riverine organisms to flooding are often-studied topics in population and community ecology (Power & Stewart, 1987; Grimm & Fisher, 1989; Flecker & Feifarek, 1994; Maltchik & Pedro, 2001; Franssen *et al.*, 2006; Robinson, 2012). Floods, generally defined as occurrences of water in usually dry areas (Jonkman & Kelman, 2005), indirectly affect riverine communities by altering physical (Peters *et al.*, 2016) and chemical (Talbot *et al.*, 2018) components of lotic systems. They also directly affect communities by displacing organisms (Cobb, Galloway & Flannagan, 1992), and generally have a variety of effects on ecosystem functions and services (Talbot *et al.*, 2018 and references therein). Additionally, they are considered essential components of the flow regime, maintaining ecological integrity of riverine communities (Poff *et al.*, 1997). Population-level responses of riverine organisms to floods vary widely and depend on several factors including flood magnitude, organismal biology (e.g., mobility), and instream habitats. Generally, populations are more resistant to small floods than large floods, though the effects depend on stream geomorphic features and hydraulic forces (Robinson, 2012). Mobile organisms (e.g., fish and mammals) are more resilient to flooding displacement effects (Crandall, Hayes & Ackland, 2003) due to their ability to escape or find appropriate refuge, whereas sessile and less mobile organisms (e.g., plants and some invertebrates) are particularly sensitive to flooding and resist displacement only until substrates become unstable (Cobb *et al.*, 1992).

Information about responses to floods is reported for only a few populations of freshwater mussels, a group of benthic organisms with limited mobility. A flood in one southwest (USA) desert river (maximum daily flow: 26 m^3/s, percentile: 99^{th}, median flow: 0.20 m^3/s, drainage area: 890 km^2; USGS Station 08405500) had no detectable effect on mussel population dynamics (i.e., survival, emigration, growth) over a 15-year period (Inoue *et al.*, 2014). Moreover, that flood event was considered beneficial for mussel survival because it displaced fine sediments that accumulated during low flow periods (Inoue *et al.*, 2014). Floods in two northeastern (USA) creeks, Tonawanda Creek (maximum daily flows: 163 m^3/s, percentile: 99^{th}, median flow: 6.8 m^3/s, drainage area: 900 km^2; USGS Station 04218000) and French Creek (maximum daily flows: 479 m^3/s, percentile: 99^{th}, median flow: 38 m^3/s, drainage area: 2,040 km^2; USGS Station 03023100), had no detectable effects on mussel survival, occurrences, or composition over two decades, despite bed sediment mobilization occurring during more frequent floods (<2 year intervals) (Sansom *et al.*, 2018). Conversely, a flood described as a 100-year flood event on an ungaged, upland river in Scotland (Hastie *et al.*, 2001) was a potential conservation concern for a mussel population. An estimated 50,000 mussels, representing 4 to 8% of the total population, were displaced, stranded, and then died. In other studies, the ability of freshwater mussels to resist floods depends on substrate stability and related hydraulic variables such as shear stress (Strayer, 1999; Morales *et al.*, 2006; Gangloff & Feminella, 2007; Zigler *et al.*, 2008; Allen & Vaughn, 2010; Randklev *et al.*, 2019), habitat type (Meador, Peterson & Wisniewski, 2011), channel geomorphology (Gangloff & Feminella, 2007), as well as shell morphology, behavior, and life-history strategies (Allen & Vaughn, 2009; Goodding *et al.*, 2019; Randklev *et al.*, 2019). To date, empirical studies that directly assess effects of floods on mussel population dynamics in rivers are lacking, particularly in relation to large floods (e.g. >500 m^3/s).

In spring and summer 2017, two mark-recapture sites located in the upper and lower Colorado River, Texas (USA) —henceforth referred to as “upper site” and “lower site”— were established within riffle habitats to quantify estimated abundance, survival, and site fidelity of mussel populations. Target species included *Cyclonaias petrina,* an endemic state-listed threatened species and a candidate species for listing by U.S. Fish and Wildlife Service, and *C. houstonensis*, another candidate species for listing, which was later synonymized with *C. pustulosa* (Johnson *et al.*, 2018). Additional target species were two common mussel species, *Tritogonia verrucosa* and *Amblema plicata*. Mark-recapture studies commonly use shellfish tags (Wisniewski *et al.*, 2013; Inoue *et al.*, 2014; Newton, Zigler & Gray, 2015) to estimate population dynamics such as abundance, immigration, emigration, and survival. However, burrowing tendencies of mussels can make them difficult to recapture in tactile surveys, leading to underestimates in population parameters (Strayer & Smith, 2003; Wisniewski *et al.*, 2013). Thus, to improve detectability in this study, passive integrated transponder tags (PIT tags) were used on candidate species, in addition to shellfish tags on all target species.

During the study period, in August 2017, precipitation from Hurricane Harvey inundated the lower site with a peak flow of 4,332 m^3/s (percentile: 99^{th}, median flow: 44 m^3/s, drainage area: 110,000 km^2; USGS Station 08161000). In October 2018, precipitation from a frontal boundary inundated the upper site with a peak flow of 1,283 m^3/s (percentile: 99^{th}, median flow: 5.6 m^3/s, drainage area: 51,000 km^2; USGS Station 08147000). Both floods were classified as greater than one per five-year events (Buzan *et al.*, 2011). This study opportunistically assesses initial population-level responses of four mussel species within riffle habitats following these large floods. The Floods were expected to reduce abundance, survival, and site fidelity of the four mussel species with greater reductions at a peak flow of 4,332 m^3/s at the lower site than a peak flow of 1,283 m^3/s at the upper site, unless site- (e.g., substrate differences) or species-specific (e.g., burrowing behavior) factors mediated reductions in abundance, survival, and site fidelity.

Methods

Field Sites— Two sites on the Colorado River with high densities of mussel species (Ruppel 2019) were chosen for mark-recapture locations. The upper site, located in the Colorado River near San Saba, Texas, was riffle habitat with a mixture of cobble (60%), sand (25%), and gravel (15%) on the standard Wentworth scale (Wentworth, 1922). Water quality parameters were measured with a multiprobe meter (YSI-85) during sampling. Water temperature ranged from 15.1 to 29.6°C, dissolved oxygen ranged from 7.2 to 10.5 mg/l, and specific conductance ranged from 501 to 711 μS/cm during the study. The lower site, located in the lower Colorado River near Columbus, Texas, was a riffle habitat with predominately cemented sandstone (70%) with interstitial pockets of sand (20%) and gravel (10%). Water temperature ranged from 20.8 to 31.7°C, dissolved oxygen ranged from 7.5 to 10.9 mg/l, and specific conductance ranged from 574 to 712 μS/cm during the study.

Field sampling— Robust design mark-recapture methods (Pollock, 1982; Nichols & Pollock, 1990) were used to estimate detection probability, abundance, survival, and site fidelity of freshwater mussels. Robust design methods consist of primary and secondary periods; populations are assumed closed between secondary periods (i.e., no mortality or migration), while populations are assumed to be open (i.e., mortality and migration can occur) during intervals between primary periods. At the upper site, mussels were initially captured and tagged in June 2017 and subsequently sampled during five primary periods over a three-year span (August and November 2017, April and August 2018, and April 2019). At the lower site, mussels were initially captured and tagged in March 2017 and sampled during five subsequent primary periods over two years (April, August, and November 2017; April and August 2018).

Primary periods, each consisting of three secondary periods (i.e., sampling events), were separated by three to four months; however, there were instances in which sampling had to be delayed several weeks for high flows to subside. Secondary periods were separated by about 24 hours. In total, there were five primary periods and four intervals at each sampling site.

For initial tagging and during subsequent primary and secondary periods, a 300-m^2 rectangular area was delineated within a riffle habitat at each site. The four corners were georeferenced so that the same area could be delineated during subsequent visits. During initial sampling, survey crews spread evenly across the downstream boundary and searched for mussels visually and tactilely while moving upstream by crawling, floating, or snorkeling. Detected mussels were removed and placed into mesh bags kept in the river. Upon completion of the survey, mussels were taken to a central processing station on the riverbank and identified morphologically to species. During the initial sampling and first primary period at each site, mussels were affixed with either one laminated vinyl shellfish tag (Floy®) or one shellfish tag and one PIT tag. During all remaining primary periods, newly encountered mussels were tagged with two shellfish tags or two shellfish tags and one PIT tag; the second shellfish tag was added to increase tag retention and thus increase detection. *Cyclonaias petrina* and *C. pustulosa* were affixed with a PIT tag (Biomark ®) affixed to a valve, whereas *T. verrucosa* and *A. plicata* were affixed with shellfish tags only. This gave us four tagging configurations which were incorporated into the parameter estimates to account for tag loss: 1 shellfish tag; 1 shellfish tag, 1 PIT tag; 2 shellfish tags; 2 shellfish tags, 1 PIT tag. Cyanoacrylic glue (Loctite Gel Control Super Glue®) was used to affix tags to the mussel valves (Young & Isely, 2008; Ashton, Tiemann & Hua, 2017). Mussels were returned to the same 300-m^2 rectangular areas at each site and placed in substrates with their posterior end in an upright position. For subsequent primary and secondary period sampling, the 300-m^2 rectangular areas were surveyed using a Biomark reader to locate PIT tagged individuals. After scanning, mussels were visually and tactilely captured, tagged, and returned as during initial tagging. For previously tagged mussels, the unique tag number per recaptured individual was recorded. Average person hours (p-h; calculated as total search time multiplied by number of people) ranged from 25.3 to 73.5 p-h at the upper site, and 4.6 to 36.0 p-h at the lower site.

Hydrology—Discharge at the upper site, measured from USGS gage 08147000, ranged from 0.06 to 1,283 m^3/s throughout the duration of the study (Figure 1A). Discharge at the lower site, measured from USGS gage 08161000, ranged from 13 to 4,332 m^3/s (Figure 1B). The flood at the upper site occurred during interval four, and the flood at the lower site occurred during interval two (Table 1). Median daily flow at the upper site (period of record: 1915–2017) was 5.6 m^3/s with a maximum peak flow of 5,409 m^3/s in 1938. Median daily flow at the lower site (period of record: 1915–2017) was 44 m^3/s with a maximum peak flow of 4,642 m^3/s in 1935.

Data Analysis—A Bayesian robust design model (Pollock, 1982; Nichols & Pollock, 1990) was used to estimate abundance, survival, and site fidelity while accounting for imperfect detection using code modified from Riecke *et al.* (2018). Specifically, detection probability (p_t) was estimated as the probability an individual available for detection during time t was in fact detected during at least one secondary occasion, abundance (N_t) was estimated as the number of individuals in the study area during each primary period, survival (ϕ_t) was estimated as the probability an individual in the population at time t survived to time $t + 1$ and did not permanently emigrate from the study area, and site fidelity (γ_t) was estimated as the probability an individual alive and in the area at time *t* remained in the area at time *t* + *1* and was available for detection. Survival estimates were converted to annualized survival (ϕ_a) by the following:

$$\phi_a = \phi_t^{52/nweeks_t}$$

where ϕ_t is the period specific survival estimate and $nweeks_t$ is the number of weeks between primary periods (i.e. length of interval *t*). Detection probabilities were allowed to vary between primary (p^*) and secondary periods (p) and individual mussels to account for differences in sampling effort, personnel, and tagging configuration. Uninformative priors were used for time-specific detection probabilities, each specified as a normal distribution with a mean of zero and a precision ($\tau = 1/\sigma^2$) of 0.001 on the logit-scale. For survival and site fidelity, weakly informative priors were used represented by a normal distribution with a mean of zero and τ of 1.00 ($\sigma^2 = 1$) on the logit scale. Each of these resulted in a broad, dome-shaped prior from zero to one on the real scale of the parameters with a mean of 0.50. The probability (Pr) of losing one PIT tag or shellfish tag (T_1) or both tags (T_2) was estimated as:

$$\Pr[T_1] = \frac{l}{N}(1 - \frac{l}{N})$$

$$\Pr[T_2] = T_1^2$$

where l is the number of mussels observed with tag loss and N is the total number of tagged mussels (Reinert *et al.*, 1998; Meador *et al.*, 2011). Using data from this study, the probability of losing a PIT tag was 0.053, the probability of losing a shellfish tag was 0.024, the probability of losing two shellfish tags was 0.00058, and the probability of losing a PIT and shellfish tag was 0.00127. The probability of not losing tags (1 - $\Pr[T_i]$) was calculated for each mussel and was used as a constant multiplier on detection probability depending on which type of tags were on each individual to account for tag loss in these estimates.

Species-specific abundance was estimated during each primary period by incorporating an n-mixture framework into the robust design model following the approach of Rossman *et al.*, (2016). For this study, the number of unique individuals collected in each primary period t for each species s ($C_{s,t}$) was modeled as the outcome of a binomial probability density function with probability of success equal to p^* and an unknown underlying population size representing estimated abundance for each species in each time period ($N_{s,t}$):

$$C_{s,t} \sim \text{Binomial}\left(p_t^*, N_{s,t}\right),$$

where abundance in each primary period from $t = 2$ to $t = 5$ was specified as the product of abundance in the preceding time period ($N_{s,t-1}$), survival ($\phi_{s,t-1}$) and site fidelity ($\gamma_{s,t-1}$) during the preceding interval, and was assumed to follow a Poisson density:

$$N_{s,\ t} \sim \text{Poisson}(N_{s,\,t\text{-}1} \cdot \phi_{\text{s},\,t\text{-}1} \cdot \gamma_{s,\ t\text{-}1}).$$

To initialize the count process model, abundance during primary period one for each species s ($N_{s,\,t\,=\,1}$) was assumed to be a function of the total number of unique individuals in species s that were ever observed during the study (MAX_S):

$$N_{s,\,t\,=\,1} \sim \text{Poisson}(\text{MAX}_S).$$

All model parameters were estimated using Markov Chain Monte Carlo methods in JAGS (Plummer 2003) written in the BUGS language, through R (R Core Team 2019) with the R2jags package (Su & Yajima, 2015). The JAGS model code is provided in Supplemental Information 1. For both sites, a total of 35,000 iterations were used with a burn-in period of 2,000 iterations, and a thinning rate of 10 for each of three Markov chains to ensure sufficiently large effective sample sizes. Effective sample sizes ranged from 1,300 to 9,900 with a mean of 8,375 for the upper site, and ranged from 690 to 9,900 with a mean of 8,292 for the lower site. Convergence was confirmed using visual inspection of trace plots and ensuring that the Gelman-Rubin statistic (Gelman & Rubin, 1992) was less than 1.10 for all parameters.

To test the effect of the flood directly at each site for each species, the estimates of abundance during pre-flood primary periods and post-flood primary periods, and survival and site fidelity between intervals with and without a flood were compared. At the upper site, pre-flood primary periods were 1 through 4, and post-flood was primary period 5; intervals without a flood were 1 through 3, and the flood interval was 4. At the lower site, pre-flood primary periods were 1 and 2, and post-flood were primary periods 3 through 5; intervals without a flood were 1, 3, and 4, and the flood interval was 2. Posterior estimates from each primary period or interval were combined and averaged for pre- or post-flood primary periods and for intervals with or without floods. For each MCMC iteration, the averaged posterior estimate of pre-flood or without flood parameter was subtracted from the averaged posterior estimate for post-flood or with flood parameter to represent increases (+) or decreases (-) in biological parameters due to the flood. Credible intervals (95% CRIs) were estimated around the differences, and if the CRI excluded zero, then the difference in estimates was considered statistically significant.

Results

A total of 1,595 mussels were tagged during this study. This included 563 *C. petrina*, 18 *C. pustulosa*, and 217 *T. verrucosa* from the upper site and 124 *C. petrina*, 308 C. *pustulosa*, and 365 *A. plicata* from the lower site (Table 2). Primary period detection probabilities were 0.871 for all primary periods at the upper site and ranged from 0.738 to 0.740 at the lower site (Table 3). Secondary period detection probabilities were 0.502 at the upper site and ranged from 0.363 to 0.365 at the lower site (Supplemental Table 1). Tagging configuration detection probabilities ranged from 0.855 to 0.876 at the upper site and from 0.723 to 0.742 at the lower site (Supplemental Table 2). Although variability between tagging configurations was minimal, detection probabilities were lower at both sites for single shellfish tags two shellfish tags, a PIT tag and a shellfish tag, or a single PIT tag.

Upper site

For *C. petrina*, mean estimated abundance was 285 (range: 226 - 316) during the pre-flood primary periods 1 through 4 (Table 4). Estimated abundance decreased to 169 during the post-flood primary period 5, a 41% decrease. The median difference in estimated abundance between pre- and post-flood primary periods was -115 (LB: -94, UB: -137; Figure 2). Mean survival was 0.919 (range: 0.840 - 0.960) during intervals 1 through 3 without the flood and decreased to 0.698 during the flood interval 4, a 24% decrease. The median difference in survival between intervals with or without the flood was -0.230 (LB: -0.395, UB: -0.011). Site fidelity was not statistically different between intervals with or without the flood. Annualized survival ranged from 0.475 to 0.908.

For *C. pustulosa*, mean estimated abundance was 7.5 (range: 6 - 12) during the pre-flood primary periods 1 through 4. Estimated abundance decreased to 3 during the post-flood primary period 5, a 60% decrease. The median difference in estimated abundance between pre- and post-flood primary periods was -4 (LB: -7, UB: -1). Survival and site fidelity were not statistically different between intervals with and without the flood. Annualized survival ranged from 0.156 to 0.507.

For *T. verrucosa*, mean estimated abundance was 54 (range: 22 - 91) during the pre-flood primary periods 1 through 4. Estimated abundance decreased to 12 during the post-flood primary period 5, a 78% decrease. The median difference in estimated abundance between pre- and post-flood primary periods was -42 (LB: -49, UB: -35). Survival and site fidelity were not significantly different between intervals with and without the flood. Annualized survival ranged from 0.048 to 0.691.

Lower site

For *C. petrina*, mean estimated abundance was 82 (range: 79 – 84) during the pre-flood primary periods 1 and 2 (Table 5). Estimated abundance decreased to 5 during post-flood primary periods 3 through 5, a 93% decrease. The median difference in estimated abundance between pre- and post-flood primary periods was -76 (LB: -86, UB: -67; Figure 2). Mean survival was 0.792 (range: 0.708 - 0.946) during intervals 1, 3, and 4 without the flood and decreased to 0.119 during the flood interval 2, an 85% decrease. The median difference in survival between intervals with and without the flood was -0.679 (LB: -0.801, UB: -0.512). Site fidelity was not significantly different between intervals with and without the flood. Annualized survival ranged from 0 to 0.800.

For *C. pustulosa*, mean estimated abundance was 207 (range: 203 – 210) during the pre-flood primary periods 1 and 2. Estimated abundance decreased to 14 during the post-flood primary periods 3 through 5, a 93% decrease. The median difference in estimated abundance between pre- and post-flood primary periods was -193 (LB: -208, UB: -178; Figure 2). Mean survival was 0.888 (range: 0.842 - 0.977) during intervals 1, 3, and 4 without the flood and decreased to 0.078 during the flood interval 2, a 91% decrease. The median difference in survival between intervals with and without the flood was -0.813 (LB: -0.879, UB: -0.722). Mean site fidelity was 0.894 (range: 0.842 - 0.977) during without flood intervals 1, 3, and 4 and was 0.634 during the flood interval 2, a 29% decrease. The median difference in site fidelity between intervals with and without the flood was -0.261 (LB: -0.494, UB: -0.035). Annualized survival ranged from 0 to 0.913.

For *A. plicata*, mean estimated abundance was 151 (range: 60 – 242) during the pre-flood primary periods 1 and 2. Estimated abundance decreased to 8 during the post-flood primary periods 3 through 5, a 95% decrease. The median difference in estimated abundance between pre- and post-flood primary periods was -144 (LB: -156, UB: -132; Figure 2). Mean survival was 0.599 (range: 0.499 - 0.731) during intervals 1, 3, and 4 without the flood and decreased to 0.100 during the flood interval 2, an 83% decrease. The median difference in survival between intervals with and without the flood was -0.499 (LB: -0.679, UB: -0.311). Site fidelity was not significantly different between intervals with and without the flood. Annualized survival ranged from 0 to 0.493.

Discussion

Estimated abundances, survival, and site fidelity were directly quantified for four species of mussels before and after large flood events, while accounting for imperfect detection. The expectations that large floods would result in reductions of mussel abundances and decreases in survival and site fidelity were largely supported. Estimated abundances of the four mussel species were reduced at both sites. Survival of one species (i.e., *C. petrina*) decreased with the lesser flood magnitude (i.e., 1,283 m^3/s) at the upper site, whereas survival of all three mussel species decreased with the greater flood magnitude (i.e., 4,332 m^3/s) at the lower site. Site fidelity of one mussel species (i.e., *C. pustulosa*) decreased at the lower site.

At both sites, the four mussel species persisted through floods, yet abundances decreased by as much as 41 to 95% following two large floods. To our knowledge, the floods reported in this study are the highest flows recorded in a study assessing influence of large floods on mussel populations. Combining these responses of different mussel species with two other studies (Inoue *et al.*, 2014; Sansom *et al.*, 2018) for a total of five flood events within drainage basins of different sizes and habitat types, mussel abundances have an apparent non-linear relationship with peak flow, ranging between 25 m^3/s and 4,332 m^3/s. Abundances were unaffected by smaller peak flows (25 to 470 m^3/s; Inoue *et al.*, 2014; Sansom *et al.*, 2018), yet, at 1,283 m^3/s in this study, abundances were reduced 41 to 78% among three species. At the highest flood magnitude, 4,332 m^3/s in this study, abundances were reduced 93 to 95% among three species. These findings, along with site- and species-specific responses reported in other studies (Meador *et al.*, 2011; Inoue *et al.*, 2014; Sansom *et al.*, 2018; Randklev *et al.*, 2019), suggest a complex relationship between mussel abundances and peak flow, which is likely influenced by site-specific substrate and hydraulic conditions.

Patterns in survival were largely congruent with patterns in estimated abundances; however, patterns in site fidelity were not always congruent with patterns in estimated abundances or survival. For example, *C. pustulosa* at the lower site was the only species for which a statistically significant decrease in site fidelity due to the flood was found. Decreases in survival were greater at the lower site (i.e., 83 to 91%) with the larger peak flow than at the upper site (i.e., 24%) with the smaller peak flow. These results suggest that peak flow magnitude influences survival and site fidelity similarly to estimated abundance. It is important to note that site fidelity is conditioned upon survival within these models and to recognize that survival and site fidelity could be confounded, along with the statistical parameters that represent them. However, regardless of the ultimate disposition of these animals (e.g., emigrated and alive or dead), we consider these individuals a loss to the local reproductive population within the study areas. This is supported because the influx of new mussels to the study area from upstream reaches following the flood was virtually zero at both sites. Regardless of fate, the results in this study suggest that depending on the magnitude of the flood, local habitat conditions, and species biology, there may be either reductions in survival or site fidelity as a result of extreme displacement, either of which can occur at a magnitude that has the potential to greatly reduce local population abundance and productivity. Focused research on this topic may help to further elucidate mechanisms underlying patterns in local and regional changes in population dynamics in the future.

There are several factors that, once quantified and replicated, could add robustness to explaining mussel population dynamics and peak flow relationships. These factors include site-specific attributes, such as basin size, stream geomorphology, substrate type and stability, and habitat types, and species-specific attributes such as shell morphology and burrowing behavior

(Strayer, 1999; Morales *et al.*, 2006; Gangloff & Feminella, 2007; Zigler *et al.*, 2008; Allen & Vaughn, 2010; Meador *et al.*, 2011; Randklev *et al.*, 2019). Observations during this study provide empirical support that substrate and shell morphology influence mussel population response to increased flow. Substrates at the upper site (i.e., sand, gravel, and cobble substrates) appeared to be less scoured than the substrates at the lower site (i.e., sand/gravel on top of cemented sandstone) following floods, suggesting a substrate-stability influence on mussel displacement. In addition, *T. verrucosa* and *A. plicata* have medial sculptured shells, which are thought to enhance anchoring ability compared to other shell sculptures types (e.g. *C. petrina*) and unsculptured species (typical central Texas form of *C. pustulosa*; Watters, 1994; Allen & Vaughn, 2009; Hornbach, Kurth & Hove, 2010; Howells, 2014; Goodding *et al.*, 2019), although the influence of shell morphology on dislodgment resistance needs further assessment (Levine, Hansen & Gerald, 2014). Thus, targeted investigation into the relationship between peak flood discharge in different sized rivers, habitats, substrate types, and among mussel species is warranted.

Notable limitations of this study, and other mark-recapture studies, are the unknown fate of the mussels displaced during flood events and the lack of power to infer mussel responses at the reach scale. Mussels displaced downstream have the potential to survive and establish new mussel beds (Hastie *et al.*, 2001), assuming they are deposited in suitable habitat. If deposited in non-suitable habitat, the fate is less certain given their low mobility. As for reach-scale inference, mussel responses to floods are heterogenous within a reach. In a 3-km reach of the Delaware River, USA, mussel aggregations were less persistent in areas with scour compared to areas with minimal scour following multiple floods (Maloney *et al.*, 2012). Therefore, 93% reductions in *C. petrina*, 93% reduction in *C. pustulosa*, and 95% reduction in *A. plicata* at the lower site with observed scour are likely overestimates relative to the entire lower Colorado River. This is also supported by field surveys taken in the lower Colorado River during the same period, although the surveys were not specifically designed to assess effects of the Hurricane Harvey flood on the mussel community. Prior to the flood, Ruppel (2019) reported 10.4 mussels per habitat surveyed (N = 179) with species relative abundances of 16% for *C. pustulosa* and 1.4% for *C. petrina* from a total of 1,859 mussels collected. After the flood, 6.2 mussels per habitat (N = 66) were reported with species relative abundances of 21% for *C. pustulosa* and 0.9% for *C. petrina* from a total of 441 mussels collected. Although comparability of community effects pre-flood (March – August 2017) and after the flood (September & October 2017) have limitations (e.g., unequal sampling effort, different seasons, taken at different sites within the reach), numbers of mussels per habitat and community structure suggest that reach-scale reductions noted by Ruppel (2019) were less than those reported from the mark-recapture site in the present study. In future studies, establishing a patchwork of mark-recapture sites within areas with various levels of scouring potential (e.g., numerous hydraulic and substrate types) would enable stronger inference about reach-scale effects.

Studies geared at understanding resistance and resiliency of aquatic organisms to flooding are partly driven by the distinctly human perception that floods are devasting (i.e., considered natural disasters due to destruction of human life and property). However, a differing ecological perspective has been forming through time based on the tenets of the Flow Pulse Concept (Junk, Bayley & Sparks, 1989) and the Natural Flow Paradigm (Poff *et al.*, 1997). Where floods are a component of the natural flow regime and not exacerbated by anthropogenic alterations (Konrad, 2003), labeling of floods as a conservation concern due to apparent localized mortality of mussels (Hastie *et al.*, 2001) might overlook long-term ecosystem services and functions of floods (e.g., removing accumulated sediment from interstitial spaces, maintaining channel complexity and habitat heterogeneity, providing nutrients from floodplains, and stimulating life-cycle cues; Poff *et al.*, 1997; Inoue *et al.*, 2014). Neither of the floods documented in this study were the highest flow peaks measured by USGS since 1915 in the Colorado River. Previous to 1915 and extending back to the beginning of the Holocene, flow magnitudes in western gulf slope drainages of Texas were estimated to be four to eight times greater than current magnitudes (Baker & Penteado-Orellana, 1977; Sylvia & Galloway, 2006), which is well within the likely timeframe of current freshwater mussel species radiation within the Colorado River (Inoue *et al.*, 2019). Therefore, despite evidence of reductions in abundance and survival in this and Hastie et al. (2001), contemporary floods might not be a threat to the long-term viability of mussel populations given that mussels have some level of resistance to displacement, can reestablish in suitable habitats, and the high-magnitude floods experience during this study are infrequent. However, more documentation is needed to quantify short-term mussel resistance (e.g., site-level and reach-level responses to floods while accounting for confounding factors), and more importantly, long-term quantification of mussel population resiliency is needed to fully understand ecosystem services and functions of large floods on the long-term fitness of mussel species.

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Data Availability Statement

Data and model code are available at https://github.com/vasotola/MusselMarkRecap

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Table 1. Discharge values (m^3/s) for each sampling site for each interval (i.e., the time between primary periods; the first interval occurred between primary period one and primary period two). Included are daily median discharge, minimum discharge, and maximum discharge.

Site	Interval	Minimum	Median	Maximum
Upper	1	0.60	1.10	2.10
	2	1.11	1.81	76.46
	3	0.09	0.79	31.89
	4	0.06	11.02	1,270.29
Lower	1	21.58	33.61	52.25
	2	19.03	29.34	4,336.50
	3	12.97	17.36	618.89
	4	22.63	32.85	87.16

Table 2. The number of mussels (N) sampled and tagged at each site for each tag configuration used as a covariate on detection probability (p) in the mark-recapture model.

Site	Species	Tagging Configuration	N
Upper	*C. petrina*	1 shellfish tag	69
		2 shellfish tags	3
		1 shellfish tag/1 PIT tag	313
		2 shellfish tags/1 PIT tag	178
	C. pustulosa	1 shellfish tag	1
		2 shellfish tags	0
		1 shellfish tag/1 PIT tag	12
		2 shellfish tags/1 PIT tag	5
	T. verrucosa	1 shellfish tag	99
		2 shellfish tags	118
		1 shellfish tag/1 PIT tag	0
		2 shellfish tags/1 PIT tag	0
Lower	*C. petrina*	1 shellfish tag	1
		2 shellfish tags	0
		1 shellfish tag/1 PIT tag	121
		2 shellfish tags/1 PIT tag	2
	C. pustulosa	1 shellfish tag	0
		2 shellfish tags	0
		1 shellfish tag/1 PIT tag	293
		2 shellfish tags/1 PIT tag	15
	A. plicata	1 shellfish tag	122
		2 shellfish tags	243
		1 shellfish tag/1 PIT tag	0
		2 shellfish tags/1 PIT tag	0

Table 3. Primary period detection probabilities ($p*$) for the upper and lower sites in the Colorado River. Presented are primary period detection probability estimates, along with 95% credible intervals (lower bound (LB), upper bound (UB)).

Site	Primary Period	Estimate	LB	UB
Upper	1	0.871	0.857	0.883
	2	0.871	0.855	0.878
	3	0.871	0.860	0.879
	4	0.871	0.853	0.879
	5	0.871	0.847	0.880
Lower	1	0.740	0.729	0.778
	2	0.738	0.686	0.762
	3	0.739	0.716	0.743
	4	0.738	0.719	0.765
	5	0.738	0.665	0.760

Table 4. Mark-recapture estimates and 95% credible intervals (lower bound (LB) and upper bound (UB)) of abundance (per 300 m^2), interval-specific survival, annualized survival, and site fidelity for *C. petrina*, *C. pustulosa*, and *T. verrucosa* from the upper site on the Colorado River during each period (primary periods for abundance, and intervals for survival, annualized survival, and site fidelity). The flood occurred between primary period 4 and 5 during interval 4.

Species	Parameter	Period	Estimate	LB	UB
C. petrina	Abundance	1	316	294	339
		2	226	207	247
		3	280	259	301
		4	316	292	341
		5	169	151	189
	Survival	1	0.842	0.800	0.882
		2	0.960	0.931	0.982
		3	0.956	0.925	0.981
		4	0.698	0.526	0.906
	Annualized Survival	1	0.475	0.381	0.579
		2	0.908	0.845	0.958
		3	0.845	0.749	0.930
		4	0.586	0.385	0.863
	Site Fidelity	1	0.731	0.672	0.788
		2	0.916	0.872	0.956
		3	0.977	0.956	0.992
		4	0.712	0.531	0.910
C. pustulosa	Abundance	1	12	8	16
		2	7	4	10
		3	6	3	9
		4	6	3	10
		5	3	2	6
	Survival	1	0.651	0.407	0.873
		2	0.749	0.492	0.931
		3	0.795	0.560	0.946
		4	0.633	0.328	0.896
	Annualized Survival	1	0.156	0.020	0.556
		2	0.505	0.187	0.845
		3	0.427	0.116	0.813
		4	0.507	0.191	0.849
	Site Fidelity	1	0.723	0.457	0.923
		2	0.746	0.482	0.933
		3	0.762	0.517	0.934
		4	0.633	0.336	0.900

T. verrucosa	Abundance	1	91	80	104
		2	55	45	66
		3	48	40	58
		4	22	16	28
		5	12	8	17
	Survival	1	0.794	0.651	0.923
		2	0.855	0.710	0.958
		3	0.441	0.295	0.655
		4	0.535	0.257	0.865
	Annualized Survival	1	0.369	0.156	0.706
		2	0.691	0.444	0.903
		3	0.048	0.011	0.208
		4	0.395	0.133	0.806
	Site Fidelity	1	0.507	0.385	0.645
		2	0.434	0.324	0.559
		3	0.571	0.352	0.794
		4	0.533	0.258	0.861

Table 5. Mark-recapture estimates and 95% credible intervals (lower bound (LB) and upper bound (UB)) of abundance (per 300 m^2), interval-specific survival, annualized survival, and site fidelity for *C. petrina*, *C. pustulosa*, and *A. plicata* from the lower site on the Colorado River during each period (primary periods for abundance, and intervals for survival, annualized survival, and site fidelity). The flood occurred between primary period 2 and 3 during interval 2.

Species	Parameter	Period	Estimate	LB	UB
C. petrina	Abundance	1	84	73	95
		2	79	67	91
		3	7	4	11
		4	5	3	8
		5	4	2	7
	Survival	1	0.946	0.887	0.983
		2	0.119	0.065	0.198
		3	0.708	0.425	0.922
		4	0.723	0.449	0.928
	Annualized Survival	1	0.800	0.619	0.934
		2	0.000	0.000	0.002
		3	0.458	0.145	0.832
		4	0.349	0.074	0.783
	Site Fidelity	1	0.948	0.892	0.984
		2	0.701	0.415	0.921
		3	0.731	0.452	0.927
		4	0.728	0.453	0.929
C. pustulosa	Abundance	1	210	192	227
		2	203	184	223
		3	13	9	18
		4	14	10	19
		5	14	9	19
	Survival	1	0.977	0.954	0.992
		2	0.078	0.050	0.114
		3	0.842	0.673	0.955
		4	0.843	0.677	0.955
	Annualized Survival	1	0.913	0.830	0.969
		2	0.000	0.000	0.000
		3	0.678	0.409	0.901
		4	0.574	0.281	0.861
	Site Fidelity	1	0.977	0.954	0.992
		2	0.634	0.408	0.851
		3	0.862	0.710	0.962
		4	0.842	0.670	0.955

A. plicata	Abundance	1	242	222	263
		2	60	50	71
		3	8	5	12
		4	10	6	14
		5	5	2	8
	Survival	1	0.499	0.285	0.785
		2	0.100	0.050	0.175
		3	0.731	0.477	0.923
		4	0.567	0.274	0.869
	Annualized Survival	1	0.062	0.007	0.380
		2	0.000	0.000	0.002
		3	0.493	0.188	0.833
		4	0.158	0.015	0.634
	Site Fidelity	1	0.412	0.233	0.664
		2	0.634	0.349	0.886
		3	0.763	0.522	0.935
		4	0.570	0.276	0.873

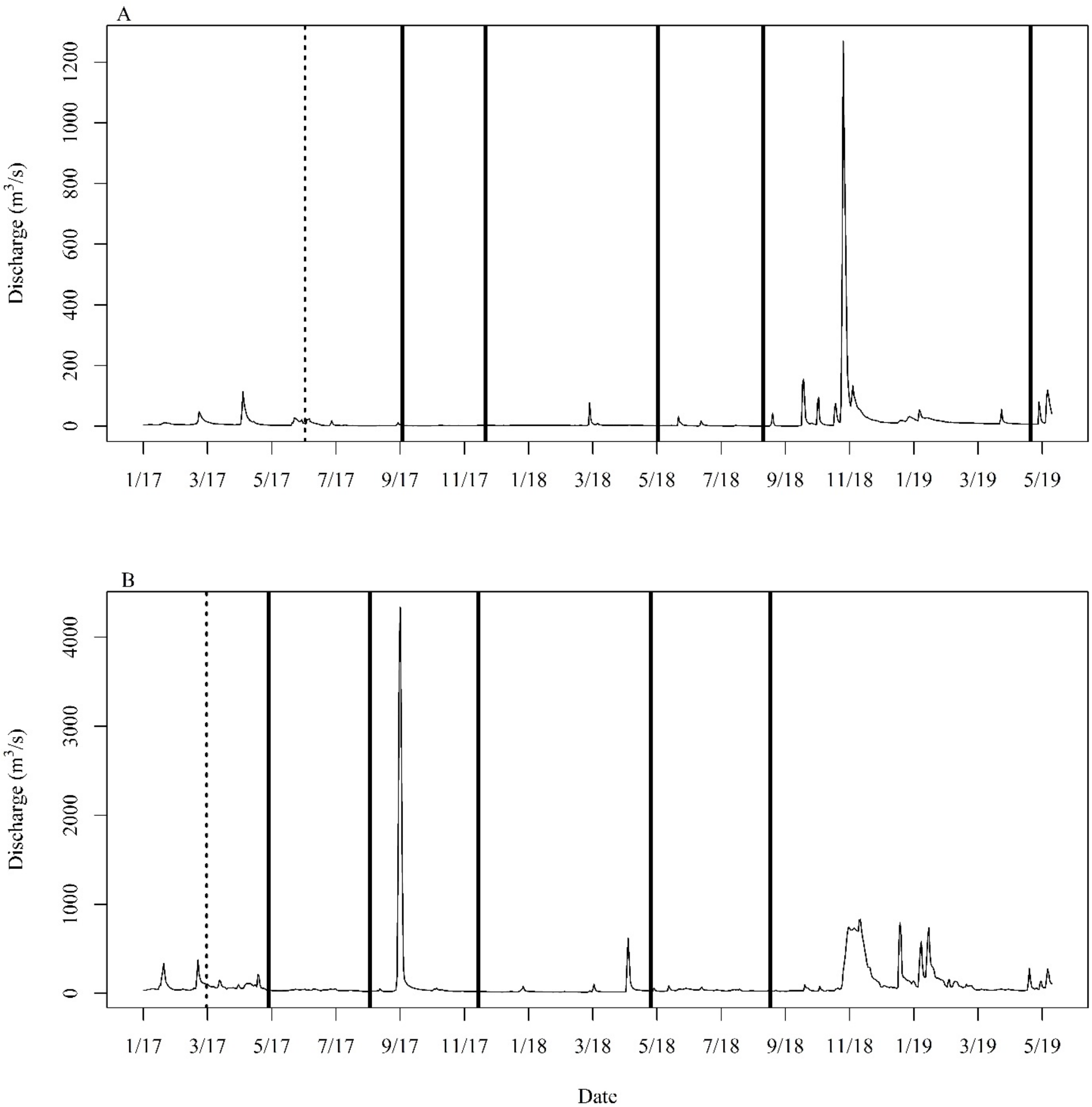

Figure 1. Discharge (m^3/s) plot of the upper (A) and lower (B) Colorado River throughout the duration of the study periods taken from USGS gages 08147000 (upper site) and 08161000 (lower site). Black dotted line denotes initial tagging event, black solid lines denote primary period sampling events.

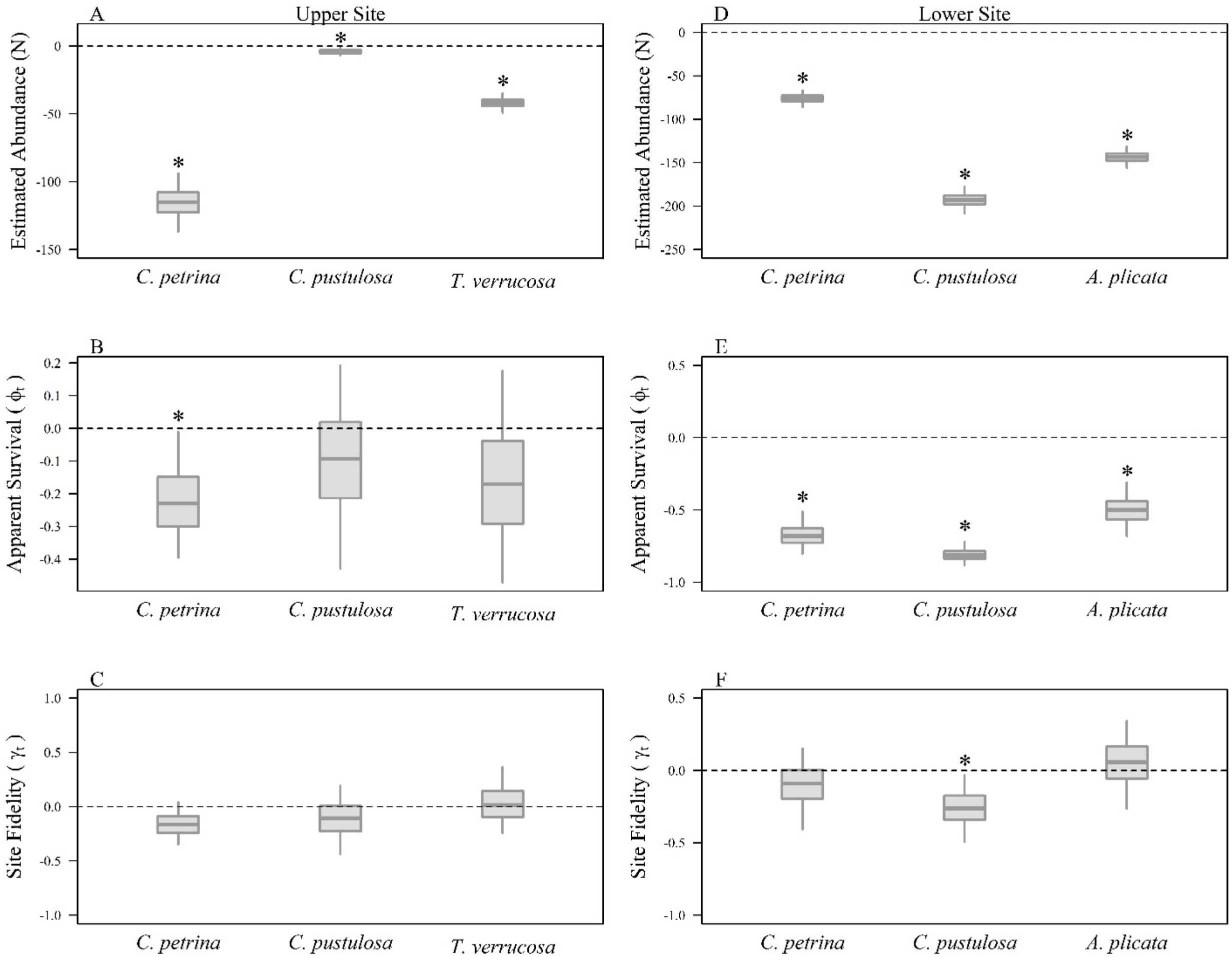

Figure 2. Boxplots depicting differences in parameter estimates between pre-flood and post-flood primary periods (estimated abundance per 300 m^2), and between without flood and with flood intervals (survival and site fidelity) of four mussel species at the upper and lower sites in the Colorado River. An * indicates a significant difference detected between pre-flood and post-flood primary periods or without flood and with flood intervals.