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Authors: Lawrence, Andrew J., Matuch, Cindy, Hancock, Jacquelyn J., Rypel, Andrew L., and Eliassen, Laura A.

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Potential local extirpation of an imperiled freshwater mussel population from wildfire runoff

Andrew J. Lawrence[1,*], Cindy Matuch[2], Jacquelyn J. Hancock[3], Andrew L. Rypel[4], and Laura A. Eliassen[1]

[1]*Center for Environmental Management of Military Lands, Colorado State University, Fort Collins, CO 80524*
[2]*NOAA Center for Coastal and Marine Ecosystems, Applied Environmental Science Department, California State University, Monterey Bay, Seaside, CA 93955*
[3]*U.S. Army Garrison Fort Hunter Liggett, U.S. Army, Fort Hunter Liggett, CA 93928*
[4]*Department of Wildlife, Fish & Conservation Biology and Center for Watershed Sciences, University of California, Davis, Davis, CA 95616*

Abstract.—Effects of wildfire and subsequent hydric erosion on freshwater communities are of increasing interest. While freshwater biodiversity is in a global state of decline, examples of climate-driven wildfire impacts to freshwater mussel populations are especially limited. We discovered a population of native floater mussels (*Anodonta californiensis/nuttalliana*), documented fish species, and recorded data on river substrate characteristics before and after an influx of wildfire runoff in Monterey County, California, USA. Pre-wildfire runoff surveys documented robust and naturally reproducing populations of mussels and 3 species of native fishes (Monterey sucker, *Catostomus occidentalis mnioltiltus*; Monterey roach, *Lavinia symmetricus subditus*; and Sacramento pikeminnow, *Ptychocheilus grandis*). Post-wildfire, we did not detect live mussels using visual, tactile, and environmental DNA; and live fish observations included only Monterey roach and speckled dace (*Rhinichthys osculus*). River substrates shifted to sand, and thalweg depth decreased from 1.77 m to only 0.2 m. The potential for future extreme wildfire runoff to impact aquatic systems, and freshwater mussels specifically, should be more broadly evaluated. Increasing duration and severity of wildfire seasons in particular appear to be major future and additional challenges to freshwater mussels and ecosystems worldwide.

Resumen.—Los efectos de los incendios forestales y la subsecuente erosión hídrica en las comunidades de agua dulce son de creciente interés. Mientras la biodiversidad de agua dulce se encuentra en un estado global de declive, los ejemplos del impacto de los incendios forestales provocados por el clima en las poblaciones de mejillones de agua dulce son especialmente limitados. Descubrimos una población de mejillones flotantes nativos (*Anodonta californiensis/nuttalliana*), documentamos especies de peces y registramos datos acerca de las características del sustrato del río antes y después de una afluencia de escorrentía de incendios forestales en el condado de Monterey, California, EE. UU. Los estudios realizados antes de la escorrentía de incendios forestales documentaron poblaciones robustas de mejillones que se reproducían de forma natural y tres especies de peces autóctonos (Monterey sucker, *Catostomus occidentalis mnioltiltus*; Monterey roach, *Lavinia symmetricus subditus*; y el Sacramento pikeminnow, *Ptychocheilus grandis*). Posteriormente a los incendios forestales, no detectamos mejillones vivos y sólo observamos Monterey roach y speckled dace (*Rhinichthys osculus*). Los sustratos fluviales pasaron a ser arenosos y la profundidad del talud disminuyó de 1.77 m a sólo 0.2 m. El potencial de que futuras escorrentías extremas, producto de incendios forestales afecten a los sistemas acuáticos, específicamente a los mejillones de agua dulce, debe ser evaluado a mayor profundidad. El aumento de la duración y la gravedad de las temporadas de incendios forestales, en particular, podrían ser los principales desafíos en el futuro para los mejillones de agua dulce y los ecosistemas en todo el mundo.

Climate change will have broad effects on the fitness, abundance, and distribution of freshwater taxa (Woodward et al. 2010). Understanding impacts of climate change on freshwater resources is increasingly important in California, USA, where water drives the world's 5th largest economy and where related human water needs intersect with life cycles of highly endemic and endangered freshwater faunas (Moyle et al. 2011, Bork et al. 2020). Increasing frequency of wildfires and longer wildfire season durations due to extended dry periods and shifts in vegetation communities (Mann et al. 2016) have the potential to impact the persistence of aquatic organisms in particular because of their

*Corresponding author: Andrew.lawrence@colostate.edu

limited dispersal capabilities (Magoulick and Kobza 2003). Even though freshwater mussels have low dispersal capabilities as adults and are highly sensitive to aquatic pollution, the impacts of wildfires on these species have been poorly documented. Multiple freshwater mussel species in California and elsewhere in North America have already experienced significant declines or extinction due to habitat alterations and loss of native host fishes (Williams et al. 1993, Howard 2010). Therefore, climate-driven impacts of wildfire on freshwater mussels may be especially problematic from a conservation standpoint.

Several species of freshwater mussels in the genus *Anodonta* were formerly found in many of the major river systems in western North America (Blevins et al. 2017). The distribution of anodontine mussels has contracted considerably within California, and they are believed to be extirpated south of Monterey County, California (Howard 2010, Blevins et al. 2017). Two species that have been described in California, the California floater (*Anodonta californiensis*) and winged floater (*Anodonta nuttalliana*), have a complicated history of taxonomic revision and have previously been described as 2 separate species (Turgeon et al. 1998, Williams et al. 2017). Recent phylogenetic analyses of anodontine mussels in our study area (unpublished data) and others in the region have suggested that they represent a single clade that combines *A. californiensis* and *A. nuttalliana* (Chong et al. 2008, Mock et al. 2010), so we hereafter refer to mussels in our study as *A. californiensis/nuttalliana*. The primary objective of this study was to document the response of a newly discovered population of *A. californiensis/nuttalliana* to runoff and sedimentation resulting from a catastrophic wildfire and a subsequent extreme rainfall event. We evaluated whether wildfire runoff resulted in a decline or potential local extirpation of the mussel population and used this opportunity to describe this event's effects on sympatric fishes and aquatic substrates.

METHODS

Study Area

Our study site was located in a perennial pool of the San Antonio River on U.S. Army Garrison Fort Hunter Liggett, Monterey County, California, at approximately 121°22′2″W and 36°4′14″N. The elevation ranged from 369 m at the pool to 1785 m at the high point of the watershed. The San Antonio River is a 95-km-long, intermittent, seasonally flooded palustrine system dominated by woody vegetation <20 m tall (Fig. 2). The stream morphology varies from exposed sandstone and Monterey shale bedrock with moderately entrenched banks and deep pools to wide, sandy alluvial plains with braided channels. The average annual precipitation for the site is 48.2 cm, most of which occurs from late October to April. Stream flow is perennial in some reaches but is substantially reduced during summer and fall.

The study site pool had steep banks and fairly uniform water depth from the bank to stream center, with some undercutting of the banks. The primary bankside vegetation included western sycamore (*Platanus racemosa*), bigleaf maple (*Acer macrophyllum*), Fremont cottonwood (*Populus fremontii*), willows (*Salix* spp.), white alder (*Alnus rhombifolia*), and swamp carex (*Carex senta*). Dominant vegetation on surrounding hillsides included chamise (*Adenostoma fasciculatum*), oaks (*Quercus* spp.), Pacific poison oak (*Toxicodendron diversilobum*), foothill pine (*Pinus sabiniana*), and manzanita (*Arctostaphylos* spp.). Fish species that we observed during our mussel surveys included Monterey sucker (*Catostomus occidentalis mnioltiltus*), Monterey roach (*Lavinia symmetricus subditus*), speckled dace (*Rhinichthys osculus*), and Sacramento pikeminnow (*Ptychocheilus grandis*).

The region surrounding our study site experienced a catastrophic wildfire (hereafter, the "Dolan Fire") that began on 18 August 2020 and was not fully contained until 31 December 2020, at which point it had burned approximately 50,554 ha. The region received almost no precipitation until a slow-moving "atmospheric river" produced 38–51 cm of rain over the Dolan Fire burn scar from 26 to 29 January 2021, after which severe drought continued. On 1 February 2021, we visited the study pool and noted highly turbid water and substantial bankside sedimentation (Fig. 2). We visited the site again on 8 March 2021, when water levels had retreated, and discovered significant sedimentation of the study pool.

The total surface area burned upstream of the study pool was approximately 20,432 ha.

TABLE 1. Summary of river and substrate characteristics of a riverine pool in the San Antonio River, Monterey County, California, USA. Surveys were conducted on 15 October 2020 (preflood) and 17 August 2021 (postflood).

River characteristic	Preflood	Postflood
Thalweg	1.77 m	0.2 m
Water clarity	Clear	Clear
Wetted area	2537 m^2	2451 m^2
Estimated percent cover (%)		
Bedrock	5	0
Boulder	15	0
Cobble	15	0
Gravel	15	5
Sand	40	80
Sediment	5	15
Woody debris	5	0

We developed watershed boundaries and planar acreage from USGS 1/3 Arc Second digital elevation data using the ArcGIS Pro v 2.8.3 (Esri Inc.) Hydrology tool set. We estimated the surface area of the burn area by creating an interpolated surface using the Triangulated Irregular Network (TIN) method in ArcGIS Pro v 2.8.3.

Surveys

Before the sedimentation of the river, we conducted a 224-m-long snorkel survey of the pool and only counted individuals that we could visually observe (i.e., no substrate excavation) in order to limit disturbance. We recorded the survey time, wetted/surveyed area (m^2), catch-per-unit-effort (CPUE), number of live, dead, and juvenile mussels observed, and number of fish and other aquatic species observed. We also recorded river and substrate characteristics by estimating percent cover for each substrate type (Table 1). Although we did not take measures of water chemistry before or after the wildfire and flood, the relationship between wildfire runoff and increases of contaminants in waterways has been well established (Smith et al. 2011).

We conducted 3-person-hour postfire surveys for live and dead mussels and mussel remains on 13 May, 28 June, and 17 August 2021. We initially focused efforts on this single pool because it was the only pool we were able to formally survey in 2020. However, we extended the search area of surveys by approximately 125 m upstream to potentially increase the likelihood of detecting mussels. During surveys, we waded the length of the pool and conducted visual and tactile searches along the riverbank and within the center of the river channel. We used dive flashlights to illuminate sections of the riverbank that were shaded by vegetation. We searched under and along the bases of *Carex* sp., which grows along the water's edge and can provide microrefugia for aquatic organisms such as mussels (Howard and Cuffey 2003). We recorded observations of live or dead mussels, and of mussel remains (i.e., shells or shell fragments). We also recorded live or dead fish found within the pool or along its banks. We followed the same protocol as our initial survey for measuring river substrate characteristics. In the final survey, we measured water depth at 10 river sections spaced approximately 20 m apart from the downstream to upstream termini. We measured water depth 0.3 m from each riverbank and in the center of the river for a total of 30 measurements.

In addition to our visual and tactile surveys, we used environmental DNA (eDNA) to detect *A. californiensis/nuttalliana*. We sampled the study site pool and 2 downstream locations where we had previously observed mussels. We also sampled known extant mussel sites in Los Burros Creek, a tributary of the Nacimiento River (Fig. 1). We collected samples following the methods of Carim et al. (2016), using peristaltic pumps (Geotech, 91350103) to filter water through 1.6-μm glass microfiber filters (Whatman, 1820-047) and into outflow buckets. We lowered the filter holder into the water pointing in the upstream direction to minimize the chance of cross-contamination and filtered approximately 5 L of water or until the filter was clogged. We measured the total filtered volume using a graduated cylinder and recorded the value. Each filter was then stored and preserved in a 50-mL tube containing approximately 25 mL of silica-bead desiccant. Prior to collection activities, all materials were sterilized with a 20% bleach solution followed by a thorough rinse with deionized water.

We assayed the samples to determine the presence of *A. californiensis/nuttalliana* by using assay methods developed for *A. nuttalliana* by Rodgers et al. (2020). DNA was extracted from 1.6-μm glass microfiber filters (Whatman, 1820-047) using Qiagen DNeasy

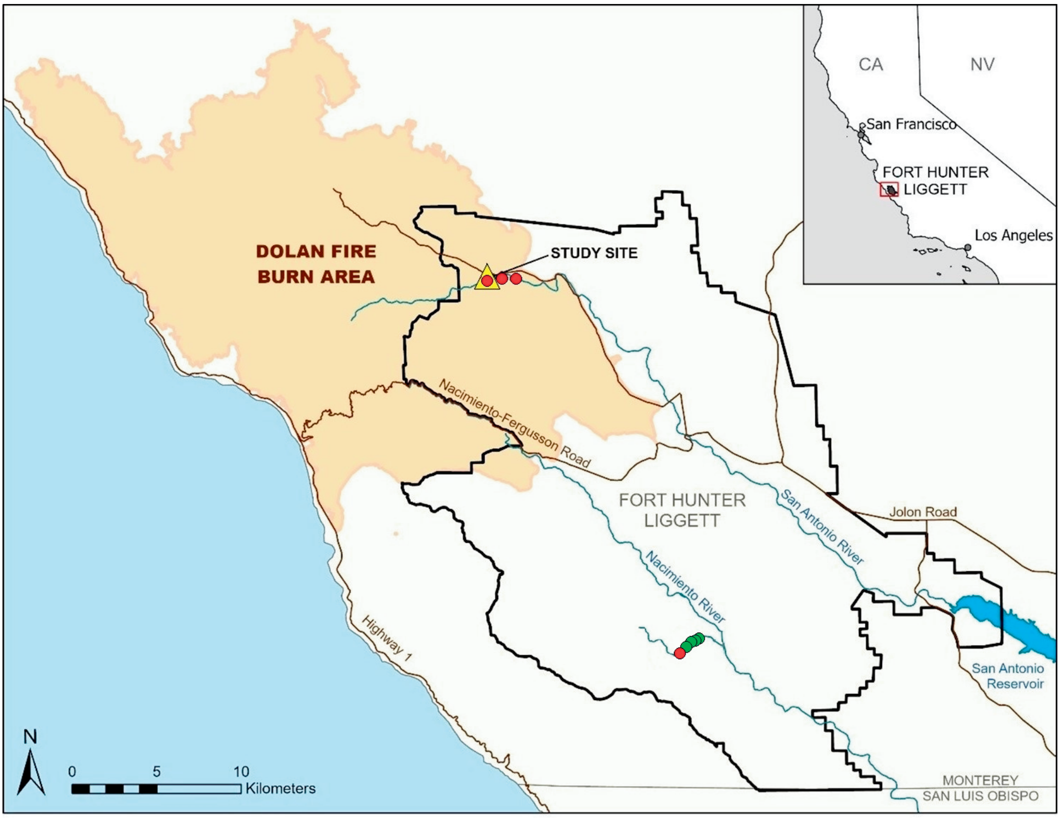

Fig. 1. Study site location (yellow triangle) in the San Antonio River, boundary of Fort Hunter Liggett (black line), and area burned by the Dolan Fire (orange) in Monterey County, California, USA, 2020. Green circles represent positive detection of *Anodonta californiensis/nuttalliana* from eDNA surveys, while red circles represent no detection.

Blood and Tissue and QIAshredder kits, following the manufacturer's protocol. We used a probe-based qPCR protocol that targeted *A. nuttalliana* sequences identified by Rodgers et al. (2020). F: GATCTCCTGGTTTGGTCGCT; R: ACGATCCGTCAACAGCATTG; P:ATTGGTTGCTGCTTTAC. All reagents and cycling protocols followed Rodgers et al. (2020). Each eDNA extraction (from a third of a filter) was run in triplicate using a 96-well plate (Neptune Scientific, San Diego, CA) and plate cover in a Bio-Rad CFX96 system.

Results

Our initial survey on 15 October 2020 provided the first record of *A. californiensis/nuttalliana* (Fig. 2) in the San Antonio River, Monterey County, California, USA. We counted 546 substrate surface–level mussels during our 2-person-hour survey of the pool on 15 October 2020. During a cursory shoreline survey on 8 March 2021 (1.5 person-hours), we documented 4 dead but complete *A. californiensis/nuttalliana* shells (no internal soft tissue present) on the bank directly adjacent to the water. We did not document any live mussels during our 3-person-hour surveys on 13 May, 28 June, or 17 August 2021, although we did document the incomplete shell remains of 1 juvenile *A. californiensis/nuttalliana* on the substrate surface on 28 June 2021. Of the 8 eDNA sample locations, 4 were positive for *A. californiensis/nuttalliana* presence, and all positive detections were from Los Burros Creek (Fig. 1). We did not detect mussel eDNA in the San Antonio River. The positive locations in Los Burros Creek had an average of 154.6 copies (range 25.5–425.3) of the target gene. We documented 2 dead mature Monterey suckers (*Catostomus occidentalis mnioltiltus*) following river sedimentation and did not detect any

Fig. 2. Photos of the San Antonio River in Monterey County, California, USA. ***A***, Before wildfire in July 2020 (photo credit: Andrea Adams). ***B***, The study pool after wildfire and flood in February 2021. ***C***, Sedimentation of entire study pool and growth of algae and new vegetation within the river in August 2021. ***D***, A live floater mussel (*Anodonta californiensis/nuttalliana*).

live larger-bodied fish during our 3 mussel surveys. We observed 3 and 4 mixed schools (approximately 20 individuals) of small-bodied (<6 cm) Monterey roach (*Lavinia symmetricus subditus*) and speckled dace (*Rhinichthys osculus*) on 28 June and 17 August 2021, respectively.

Water depth and substrate cover changed substantially following sedimentation. We estimated pool thalweg at 1.77 m before sedimentation, and the thalweg measured 0.2 m post-wildfire (substrate survey results in Table 1). The wetted area did not change substantially, as most of the original river channel still had surface water flow at the time of our final survey. Substrate types shifted to predominantly sand, whereas the dominant substrates prior to sedimentation were coarse sand and gravel (Table 1). Water depth during our final survey on 17 August 2021 ranged from 0 to 20 cm ($\bar{x}$ = 3.35 cm, SE = 0.58 cm). Although we did not take multiple measurements during our first survey on 15 October 2020, we estimate that the mean depth of the pool was approximately 1 m.

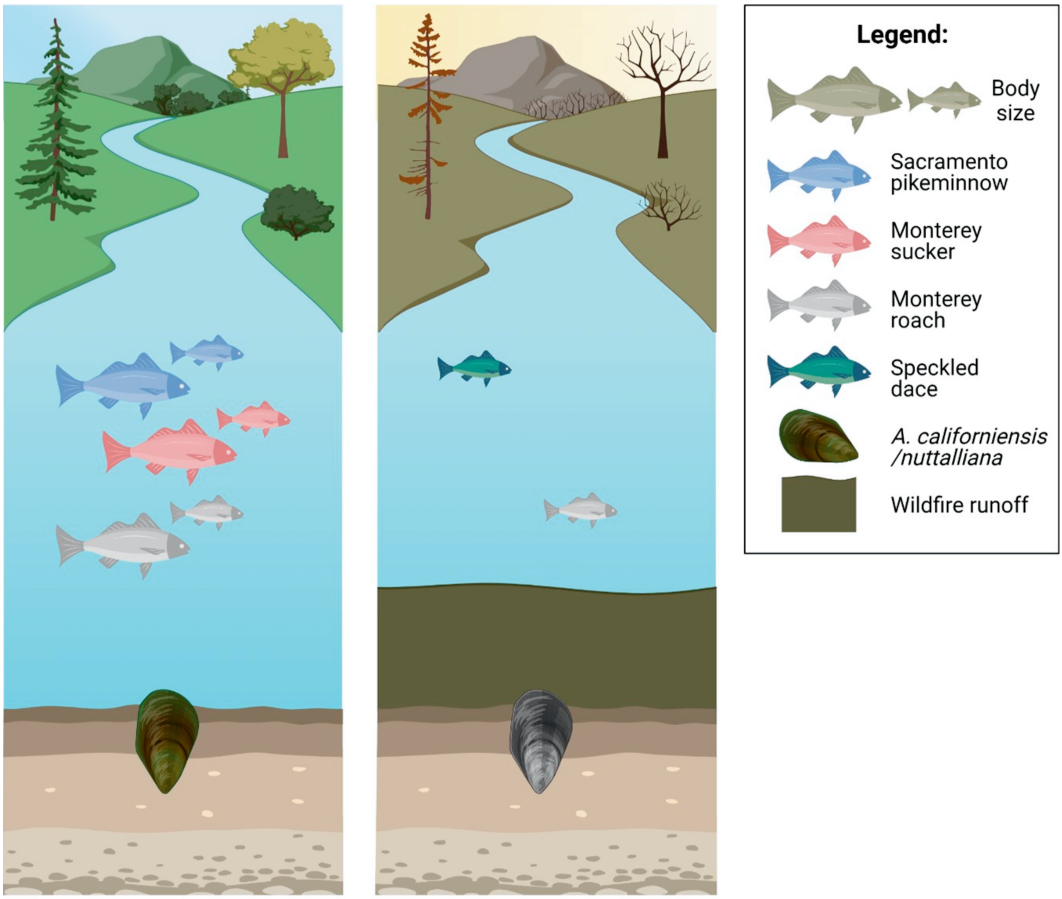

Fig. 3. Graphical overview of substantial sedimentation from wildfire runoff in the San Antonio River, Monterey County, California, USA, 2021, that resulted in the potential extirpation of a population of native freshwater mussels (*Anodonta californiensis/nuttalliana*) and altered assemblages of native fishes and river substrates.

DISCUSSION

Our study documents the potential local extirpation of a native freshwater mussel population due to wildfire and subsequent runoff following heavy rainfall. Furthermore, we document a substantial decline and potential loss of large-bodied native fishes, survival and/or recolonization by small-bodied fishes, and substantial changes to river substrates (Fig. 3). Large, catastrophic wildfires represent an increasingly pervasive ecological disturbance throughout California and western North America (Holden et al. 2018, Burke et al. 2021). While there is growing recognition that wildfires are impacting western landscapes, considerably less attention has been focused on impacts to sensitive aquatic taxa and ecosystems.

The apparent loss of a previously productive freshwater mussel population provides strong evidence that wildfires and subsequent ash and sediment runoff were the proximate cause for potential local extirpation of the mussels in our study site. Although we focused our survey efforts on one site, we observed similar patterns of sedimentation in other regions of the San Antonio River where mussels were present before the influx of wildfire runoff. Notably, we did not detect mussels in eDNA surveys for these other sites. It is possible that surviving mussels were undetected during our surveys because of relatively low detection probabilities for visual, tactile, and eDNA surveys when mussels have patchy distributions and when densities are low (Barbour et al. 1999, Smith et al. 2001, Preece et al. 2021). Regardless, even if surviving mussels were missed during our surveys, the population and available habitat have been substantially reduced to such a degree that population persistence is threatened.

Opportunities for mussel populations to recover in areas with frequent and substantial changes to aquatic environments can be limited by host-dependent dispersal and slow growth rates for some species (Haag and Rypel 2011, Kappes and Haase 2012). Although *A. californiensis/nuttalliana* generally live <25 years, other freshwater mussel species can obtain advanced longevity (Hastie and Toy 2008, Haag and Rypel 2011). Taken together, it is fair to suggest that some mussel communities may take decades to centuries to recover from disruptions. Furthermore, when mussels are lost, ecosystem services also disappear in parallel (Vaughn 2018). These ecological changes may indirectly promulgate or even generate regime shifts in the function of streams, independent of any direct effects of wildfire (Rocha et al. 2018).

Although some species of fish persisted after the sedimentation, their roles as host fish for *A. californiensis/nuttalliana* have yet to be determined. The status of fishes in our study area deserves additional investigation, as our observations were primarily opportunistic and did not include standardized surveys. In order to support recolonization of the river by mussels, habitat conditions would need to improve for native fish hosts to facilitate larval mussel development and dispersal (Williams et al. 1993, Haag and Warren 2003). While current conditions may support some small-bodied fishes, it is less likely that these systems will provide habitat for large fishes. This problem further increases the likelihood of additional declines, extirpation, and failure of *A. californiensis/nuttalliana* recolonization if fishes are unable to reproduce in degraded and wildfire-scarred streams.

The potential for relatively stable aquatic habitats, such as the San Antonio Reservoir, to act as refugia and source populations for both mussels and native fishes requires further investigation. While our study provides initial information on the lack of resistance and resilience of freshwater mussels to wildfire effects, this pattern may or may not be general. Additional studies are needed to track the response of other native western freshwater mussel populations and communities to wildfire impacts in the western USA and globally. The recovery time for aquatic systems impacted by wildfire and how subsequent natural or anthropogenic changes influence recolonization by mussels and fishes are important components to conservation that warrant further investigation.

Climate change is increasing precipitation volatility in California (Swain et al. 2018, Huang et al. 2020) and inducing massive shifts in the occurrence, intensity, and duration of wildfires across the western USA (Abatzoglou and Williams 2016, McCullough et al. 2019, Goss et al. 2020). Impacts of shifting climates and wildfire regimes on aquatic ecosystems and taxa are largely unknown but have been identified as a topic that should be of interest to most aquatic ecologists and managers. If results of this case study are broadly applicable, increased wildfires and wildfire runoff will drastically alter the abundance and distribution of freshwater mussels across the western USA. Freshwater mussel diversity is naturally low in California (3–4 native species), but mussels can be quite abundant locally, as seen in this study, and they can play important roles in food webs (Limm and Power 2011). These animals play underappreciated roles in our ecosystems, and continued losses of native mussels will lead to massive alterations to the ecosystem services they provide (Atkinson et al. 2013, Vaughn 2018).

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LITERATURE CITED

ABATZOGLOU, J.T., AND A.P. WILLIAMS. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences 133:11770–11775.

ATKINSON, C.L., C.C. VAUGHN, K.J. FORSHAY, AND J.T. COOPER. 2013. Aggregated filter-feeding consumers alter nutrient limitation: consequences for ecosystem and community dynamics. Ecology 94:1359–1369.

BARBOUR, M.T., J. GERRITSEN, B.D. SNYDER, AND J.B. STRIBLING. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish. 2nd edition. EPA 841-B-99-002, Office of Water, U.S. Environmental Protection Agency.

BLEVINS, E., S. JEPSEN, J. BRIM BOX, D. NEZ, J. HOWARD, A. MAINE, AND C. O'BRIEN. 2017. Extinction risk of western North American freshwater mussels: *Anodonta nuttalliana*, the *Anodonta oregonensis/kennerlyi* clade, *Gonidea angulata*, and *Margaritifera falcata*. Freshwater Mollusk Biology and Conservation 20:71–89.

BORK, K., P. MOYLE, J. DURAND, T.-C. HUNG, AND A.L. RYPEL. 2020. Small populations in jeopardy: a delta smelt case study. Environmental Law Reporter 50: 10714.

BURKE, M., A. DRISCOLL, S. HEFT-NEAL, J. XUE, J. BURNEY, AND M. WARA. 2021. The changing risk and burden of wildfire in the United States. Proceedings of the National Academy of Sciences 118: e2011048118.

CARIM, K.J., K.S. MCKELVEY, M.K. YOUNG, T.M. WILCOX, AND M.K. SCHWARTZ. 2016. A protocol for collecting environmental DNA samples from streams. General Technical Report RMRS-GTR-355, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO. 18 pp.

CHONG, J.P., J. BRIM BOX, J. HOWARD, D. WOLF, T. MYERS, AND K. MOCK. 2008. Three deeply divided lineages of the freshwater mussel genus *Anodonta* in western North America. Conservation Genetics 9:1303–1309.

GOSS, M., D.L. SWAIN, J.T. ABATZGOLOU, A. SARHADI, C.A. KOLDEN, A.P. WILLIAMS, AND N.S. DIFFENBAUGH. 2020. Climate change is increasing the likelihood of extreme autumn wildfire conditions across California. Environmental Research Letters 15:04016.

HAAG, W.R., AND A.L. RYPEL. 2011. Growth and longevity in freshwater mussels: evolutionary and conservation implications. Biological Reviews 86:225–247.

HAAG, W.R., AND M.L. WARREN JR. 2003. Host fishes and infection strategies of freshwater mussels in large mobile basin streams, USA. Journal of the North American Benthological Society 22:78–91.

HASTIE, L.C., AND K.A. TOY. 2008. Changes in density, age structure and age-specific mortality in two western pearlshell (*Margaritifera falcata*) populations in Washington (1995–2006). Aquatic Conservation: Marine and Freshwater Ecosystems 18:671–678.

HOLDEN, Z.A., A. SWANSON, C.H. LUCE, W.M. JOLLY, M. MANETA, J.W. OYLER, D.A. WARREN, R. PARSONS, AND D. AFFLECK. 2018. Decreasing fire season precipitation increased recent western US forest wildfire activity. Proceedings of the National Academy of Sciences 115:E8349–E8357.

HOWARD, J.K. 2010. Sensitive freshwater mussel surveys in the Pacific Southwest Region: assessment of conservation status. Report prepared for the U.S. Forest Service, Pacific Southwest Region.

HOWARD, J.K., AND K.M. CUFFEY. 2003. Freshwater mussels in a California North Coast Range river: occurrence, distribution, and controls. Journal of the North American Benthological Society 22:63–77.

HUANG, X., D.L. SWAIN, AND A.D. HALL. 2020. Future precipitation increase from very high resolution ensemble downscaling of extreme atmospheric river storms in California. Science Advances 6:eaba1323.

KAPPES, H., AND P. HAASE. 2012. Slow, but steady: dispersal of freshwater molluscs. Aquatic Sciences 74:1–14.

LIMM, M.P., AND M.E. POWER. 2011. Effect of the western pearlshell mussel *Margaritifera falcata* on Pacific lamprey *Lampetra tridentata* and ecosystem processes. Oikos 120:1076–1082.

MAGOULICK, D.D., AND R.M. KOBZA. 2003. The role of refugia for fishes during drought: a review and synthesis. Freshwater Biology 48:1186–1198.

MANN, M.L., E. BATLLORI, M.A. MORITZ, E.K. WALLER, P. BERCK, A.L. FLINT, L.E. FLINT, AND E. DOLFI. 2016. Incorporating anthropogenic influences into fire probability models: effects of human activity and climate change on fire activity in California. PLOS ONE 11:e0153589.

MCCULLOUGH, I.M., K.S. CHERUVELIL, J.-F. LAPIERRE, N.R. LOTTIG, M.A. MORITZ, J. STACHELEK, AND P.A. SORANNO. 2019. Do lakes feel the burn? Ecological consequences of increasing exposure of lakes to fire in the continental United States. Global Change Biology 25:2841–2854.

MOCK, K.E., J.C. BRIM BOX, J.P. CHONG, J.K. HOWARD, D.A. NEZ, D. WOLF, AND R.S. GARDNER. 2010. Genetic structuring in the freshwater mussel *Anodonta* corresponds with major hydrologic basins in the western United States. Molecular Ecology 19:569–591.

MOYLE, P.B., J.V.E. KATZ, AND R.M. QUIÑONES. 2011. Rapid decline of California's native inland fishes: a status assessment. Biological Conservation 144: 2414–2423.

PREECE, E.P., M. BRYAN, S.M. MAPES, C. WADEMAN, AND R. DORAZIO. 2021. Monitoring for freshwater mussel presence in rivers using environmental DNA. Environmental DNA 3:591–604.

ROCHA, J.C., G. PETERSON, Ö. BODIN, AND S. LEVIN. 2018. Cascading regime shifts within and across scales. Science 362:1379–1383.

RODGERS, T.W., J.C. DYSTHE, C. TAIT, T.W. FRANKLIN, M.K. SCHWARTZ, AND K.E. MOCK. 2020. Detection of 4 imperiled western North American freshwater mussel species from environmental DNA with multiplex qPCR assays. Freshwater Science 39:762–772.

SMITH, D.R., R.F. VILLELLA, D.P. LEMARIÉ, AND S. VON OETTINGEN. 2001. How much excavation is needed to monitor freshwater mussels? Freshwater Mollusk Symposium Proceedings. Ohio Biological Survey, Columbus, OH.

SMITH, H.G., G.J. SHERIDAN, P.N.J. LANE, P. NYMANN, AND S. HAYDON. 2011. Wildfire effects on water quality in forest catchments: a review with implications for water supply. Journal of Hydrology 396:170–192.

TURGEON, D.D., J.F. QUINN, A.E. BOGAN, E.V. COAN, F.G. HOCHBERG, W.G. LYONS, P.M. MIKKELSEN, R.J.

NEVES, C.F.E. ROPER, G. ROSENBERG, ET AL. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks.

SWAIN, D.L., B. LANGENBRUNNER, J.D. NEELIN, AND A. HALL. 2018. Increasing precipitation volatility in twenty-first century California. Nature Climate Change 8:427–433.

VAUGHN, C.C. 2018. Ecosystem services provided by freshwater mussels. Hydrobiologia 810:15–27.

WILLIAMS, J.D., A.E. BOGAN, R.S. BUTLER, K.S. CUMMINGS, J.T. GARNER, J.L. HARRIS, N.A. JOHNSON, AND G.T. WATTERS. 2017. A revised list of the freshwater mussels (Mollusca: Bivalvia: Unionida) of the United States and Canada. Freshwater Mollusk Biology and Conservation 20:33–58.

WILLIAMS, J.D., M.L. WARREN, K.S. CUMMINGS, J.L. HARRIS, AND R.J. NEVES. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18:6–22.

WOODWARD, G., D.M. PERKINS, AND L.E. BROWN. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2093–2106.

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