

ORIGINAL RESEARCH

Post-fire species composition and abundance of a lentic-breeding amphibian assemblage: case study of Ledson Marsh

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Amphibians frequently inhabit wildfire-prone environments, but little is known how amphibians respond to fire. This study assessed the post-wildfire species composition and abundance of an amphibian assemblage in an 11.8-ha seasonal marsh. Pre-fire, four native amphibians occupied Ledson Marsh, including: California red-legged frog (*Rana draytonii*), Pacific treefrog (*Pseudacris regilla*), California newt (*Taricha torosa*), and roughskin newt (*Taricha granulosa*), in addition to the exotic American bullfrog (*Rana [Lithobates] catesbeiana*). Qualitative data revealed the California newt and Pacific treefrog were abundant species. In 2017, the Nuns Wildfire burned the majority of ground cover within the watershed. Nearly all marsh vegetation burned to charred and desiccated stubble. Renewal of substantial marsh vegetation occurred after one growing season, indicating a protected rootstock in a majority of perennial wetland plants. Post-fire, the same four native amphibians were still present. In addition, western toad (*Anaxyrus boreas*), a species previously undetected, also appeared. Appearance of western toad is consistent with its positive short-term response to fire, as described in other studies. The California newt and Pacific treefrog remained the two most abundant species post-fire. Over the short-term, the amphibian assemblage appeared resilient, or potentially benefitted, due to the temporary disturbance of wildfire within their lentic breeding habitat. The conclusion is based on the persistence of all pre-fire species, colonization by the western toad, and the return to an earlier successional stage, which may extend the longevity of the marsh. Since the rapid seasonal drying of habitat can increase the likelihood of fire under the current climate trajectory, we need a better understanding of the mechanisms that enable amphibians to cope with fire. This is particularly important over longer timelines and within wetland habitats that have the potential to burn.

Key words: amphibians, fire, frog, Ledson Marsh, newt, northern California, survival, toad, wetlands

Until recently, little was known about the effects of fire on amphibian ecology even though amphibians frequently inhabit wildfire-prone environments (Bury et al. 2002; Pilliod et al. 2003; Bury 2004). Fire can cause direct mortality, changes in diversity, and alterations in habitat, contributing to both immediate and long-term consequences (Pilliod et al. 2003;

Rochester et al. 2010). However, a series of fire–amphibian studies over the last 25 years has begun to alter this view. Most of these studies have evaluated wildfire or prescribed fire on primarily stream or terrestrial taxa (Kirkland et al. 1996; Keyser et al. 2004; Hossack et al. 2006; Greenberg and Waldrop 2008; Cano and Leynaud 2009; Sutton et al. 2013). The research does not emphasize lentic-breeding amphibian use of wetlands. Until recently, wetlands were less likely to burn because conditions were less conducive to fire (Jolly et al. 2015). Since the risk and severity of drought due to climate change (Allen et al. 2010) has increased the likelihood of large fires (Perry et al. 2011), there is greater potential to impact more wetland habitat not typically prone to fire. This phenomenon has led researchers to examine fire response among lentic-breeding amphibians using wetlands (Hossack and Corn 2007, 2008; Hossack et al. 2013).

Hossack and Pilliod (2011) reviewed amphibian responses to wildfire in the western United States, which have provided some perspectives on the response of lentic-breeding amphibians. The authors suggested wetlands would experience the smallest fire-related changes, in contrast to the stream and terrestrial habitats amphibians utilize that are the most likely to benefit amphibian larvae. The authors further opined that amphibians in larger lentic habitats would be less vulnerable than those in smaller lentic habitats because the larger habitats typically maintain longer hydroperiods and thus, are less likely to burn. Hossack and Pilliod (2011) also stated the high perimeter-to-surface ratio of small wetlands, which conjoins them more tightly to the terrestrial landscape, may make the amphibian populations more vulnerable. Hence, the type and degree of fire impacts on lentic-breeding amphibians will likely depend on the size of the aquatic habitat as well as the relative impact of the fire on the aquatic habitat versus the juxtaposed terrestrial habitat.

On 8 October 2017 and the days following, several wildfires ignited in eastern Sonoma County, California. These fires, collectively named the Nuns Wildfire, burned a combined 22,887 ha before they were contained on 30 October 2017 (Gabbert 2018). The Nuns Wildfire burned through Ledson Marsh, where David G. Cook (DGC) had been examining the amphibian assemblage since 1996. Although some of the pre- and post-fire surveys differed, the Nuns Wildfire afforded a rare opportunity to examine the changes in amphibian composition, abundance, and specific habitats. In this case study, the authors describe the following changes in Ledson Marsh prior to and following the Nuns Wildfire: 1) amphibian species composition; 2) adult amphibian breeding populations and reproductive effort; and 3) marsh vegetation and aquatic habitats. The authors provide data on herpetofauna survival within the post-fire watershed of Ledson Marsh to provide context on the survival of species that are similar ecologically to the Ledson-breeding amphibians in terms of terrestrial habitat use and mobility. The patterns illustrated by this case study, including the precipitation patterns, correspond with the suggestions made by Hossack and Pilliod (2011) regarding short-term lentic-amphibian response to fire and long-term changes due to climate conditions.

METHODS

Study area

Ledson Marsh is located on a hilly plateau in Trione-Annadel State Park, Sonoma County, California, USA (38.40°N, 122.60°W; WGS84; 476 m elevation). Every winter, rains fill the marsh in January or February and it typically dries in late summer. The current aquatic footprint of Ledson Marsh is approximately 11.8 ha at full inundation, and it maintains a maximum depth of approximately 1.3 m. The marsh was created in 1930 via construc-

tion of a small earthen and rock dam (Furtini 1976). Prior to 1930, aquatic habitat existed at the site, though its size was likely much smaller (P. Northen, personal communication). The >2000-ha Trione-Annadel State Park encompasses approximately 95% of the 84.8-ha Ledson Marsh watershed, and all of Ledson Marsh proper. The State Park encompasses six habitat types, including: oak (*Quercus* spp.) woodland, Douglas-fir (*Pseudotsuga menziesii*) forest, chaparral, grassland, meadow, and marsh (Cook and Jennings 2007). The primary habitats and related vegetation classifications (Klein et al. 2015) within the Ledson Marsh watershed include: freshwater marsh (*Schoenoplectus californicus* Alliance), Douglas-fir forest (*Pseudotsuga menziesii* Alliance), and oak woodland (*Quercus* spp. Alliance) with an understory dominated by California fescue (*Festuca californica*). The Ledson Marsh watershed is largely undeveloped. However, in the early 1900s, basalt for street cobble was quarried on a small scale (Whatford 1995); a few shallow pits and tailing mounds up to 2 m high that collectively cover approximately 0.09 ha attest to this historic activity.

Life history of Ledson Marsh amphibians

Nomenclature for the amphibians discussed follows Crother et al. (2017). Five amphibian species regularly breed at Ledson Marsh, including: the California red-legged frog (*Rana draytonii*; a California Species of Special Concern and listed as threatened by the Federal Endangered Species Act), Pacific treefrog (*Pseudacris regilla*), California newt (*Taricha torosa*; California Species of Special Concern), and roughskin newt (*Taricha granulosa*), in addition to the invasive American bullfrog (*Rana [Lithobates] catesbeiana*; Cook and Jennings 2007; Stokes et al. 2011; DGC, personal observation).

The native amphibian assemblage that breeds in Ledson Marsh is adapted to the summer drought imposed by California's Mediterranean climate (Storer 1925; Keeley and Swift 1995; CDFG 2003; Cook and Jennings 2007). Larvae of members of this assemblage typically metamorphose by mid-summer prior to the marsh drying. The dominant amphibians breed in winter and deposit eggs in shallows < 40 cm deep along the shoreline (Cook and Jennings 2007; DGC, personal observation). In this case study, the authors refer to egg cluster for species that typically deposit several groupings of eggs during oviposition (California newt, roughskin newt, Pacific treefrog) and egg mass for species that typically deposit a single group (California red-legged frog and American bullfrog). Winter breeders consist of the California red-legged frog, California newt, and Pacific treefrog (Table 1). Though the Pacific treefrog breeds primarily in winter, its breeding can extend from late-fall to spring. Prior to the Nuns Wildfire, the only spring-breeding amphibian in Ledson Marsh was the roughskin newt. A second spring-breeder, western toad (*Anaxyrus boreas*), was known within Trione-Annadel State Park. Prior to the wildfire, individual western toads had been observed at non-breeding sites near the Ledson Marsh watershed (DGC, personal observation). In addition to the native assemblage, the non-native American bullfrog, which breeds late spring into summer, is also present in Ledson Marsh (Cook and Jennings 2007). American bullfrog tadpoles frequently overwinter at least once before metamorphosis (Bury and Whelan 1984). However, at Ledson Marsh, metamorphosis has occurred within the same year tadpoles develop from eggs (Cook and Jennings 2007). This has been observed during wetter years and the longest hydroperiods (DGC, unpublished data). Except for the Pacific treefrog, all amphibian species at Ledson Marsh require at least two years to reach sexual maturity (Table 1).

Table 1. Breeding characteristics of amphibians at Ledson Marsh.

Species	Sexual Maturity (yr) ^a	Local Breeding Period (peak) ^b	Egg Mass or Clusters Produced ^c	Egg Clutch Size ^c
American bullfrog	2-3	Apr-Jul (May-Jun)	1	20,000
California newt	3	Jan-Feb	3-6	130-160
California red-legged frog	2-3	Jan-Apr (Feb)	1	2,100
Pacific treefrog	1-2	Nov-Jul (Feb-Mar)	9-80	400-750
Roughskin newt	4-5	Apr-Jul	200-300	No Data ^d
Western toad	4-6	Jan-Jul (Mar-Apr)	1	12,000

^aLannoo (2005)

^bCook and Jennings (2007); Stokes et al. 2011; Petranka 1998; DGC, personal observation

^cLannoo 2005; Cook 1997; Stokes et al. 2011

^dRoughskin newts deposit single eggs (Jones et al. 2005) in widely scattered patterns in soft aquatic vegetation (MPH, unpublished data)

Pre-fire surveys

The first author (DGC) conducted more than 250 Visual Encounter Surveys (VES) at Ledson Marsh, with the assistance of several others, following Heyer et al. (1994) since 1996 (Cook and Jennings 2007; DGC, unpublished data). Annual VES focused on enumerating California red-legged frogs in the egg, post-metamorphic, and adult life stages. We conducted the minimum number of seasonal site visits according to Heyer et al. (1994) between 1996 and 2016, as follows: three surveys in winter, three surveys in spring, and two surveys in summer. Since 2017, only the winter site visits were completed. Researchers recorded qualitative observations of California newt and Pacific treefrog breeding and the abundance of egg clusters. Researchers recorded maximum water depth during each site visit using a permanent gauge located in the deepest area of the marsh, near the dam.

Satellite imagery (2013) and Geographic Information System maps were used to delineate and quantify vegetation and habitat types present at Ledson Marsh prior to the 2017 Nuns Wildfire (Sonoma County 2019a). We estimated the dominant vegetation types according to surface area of the marsh and percentage of shoreline. Researchers confirmed pre-fire vegetation types based on field observations, recorded annually since 1996, and noted changes in plant species and mapped vegetation patterns.

Post-fire surveys

On 7 November 2017, one week after the Nuns Wildfire was contained, DGC investigated the severity and extent of damage in the watershed. This investigation consisted of a walk-through and visual inspection of the dry marsh and surrounding woodland and forest habitats. DGC also searched for unburned areas or areas that may have served as refuge for wildlife during the fire. The field observations confirmed the patterns illustrated on burn severity maps produced from satellite imagery (Sonoma County 2019b).

Researchers estimated wetland habitat and egg cluster/mass production of winter-breeding amphibians at Ledson Marsh in 2018 and 2019. The surveys were similar to the pre-fire surveys for CRLF, with an added stratified random approach (Heyer et al. 1994). The post-fire surveys served to effectively sample other lentic-breeding amphibians, particularly California newts that lay numerous egg clusters as conducting a total count can be unfeasible. Prior to the wildfire, we collected only qualitative estimates. To add the stratified random approach to surveys, researchers established 36 sample plots in 2018 along the 1604-m full-pool shoreline, where most amphibian oviposition occurs (DGC, personal observation). The number of plots were stratified based on the percent of pre-fire dominant vegetation types: 18% common spikerush (*Eleocharis palustris*), 67% broad-leaved cattail (*Typha latifolia*), 5% mixed spikerush/cattail, and 10% mixed cattail/California bulrush (*Schoenoplectus californicus*). These vegetation types occurred in 10 areas along the shoreline in 2013 (Sonoma County 2019a). Plot size was 3×5 m with the shorter side positioned approximately parallel to the shoreline. The longer sides were oriented into the marsh to accommodate fluctuating water levels. We marked plot borders with wooden stakes and string. Plots covered 6.7% of the shoreline perimeter length.

We sampled plots twice monthly during the winter (January to March). During one of the field visits, two investigators conducted a VES of each plot. All amphibian egg clusters/masses were identified to species and the developmental interval recorded using a four-category scale. The Gosner system (1960) was used to identify three categories between Gosner stages 1 and 22, described as follows: 1) spherical (1-12); 2) bean-shaped (13-18); or 3) banana-shaped (19-22). Hatching was the fourth category. Gosner stages (1960) are best applied to anurans (frogs and toads). However, the coarse categories made it useful for staging salamanders as well based on the similarity to salamander developmental stages proposed by Harrison (1969). Researchers recorded the maximum depth at each plot and the maximum depth of the marsh during each site visit. We conducted VES between plots to determine if a species was breeding but not detected within the sample plots. To estimate post-fire changes in habitat, DGC visually scored the percent cover of dominant wetland plants and open water habitat to the nearest 5% within each plot during the last site visit each winter. Open water habitat was categorized as either barren open water (if the substrate appeared burnt) or vegetated open water (if unburnt vegetation or organic material covered the substrate). Winter surveys ended when no newly deposited eggs since the last visit were observed. This equated to no eggs younger than Gosner (1960) stage 13 (i.e., no bean-shaped eggs), which requires approximately two weeks to develop at Ledson Marsh (DGC, unpublished data).

After completing the 2018 winter aquatic plot surveys, we conducted terrestrial VES within the marsh watershed to characterize the amphibian and reptile fauna that survived the wildfire. These surveys included visual inspection beneath rocks and logs that were not completely burned in the wildfire. Anecdotal observations of amphibians at Ledson Marsh's dam were obtained from a biological monitor during a dam repair project over a three-week period in August 2018.

On 10 May 2019, we conducted timed dipnet surveys to determine the larval amphibian composition at Ledson Marsh (Heyer et al. 1994). The surveys were designed to detect larvae produced from both winter and spring breeding as it was unlikely to detect spring-breeding amphibians during the winter plot sampling. A crew of six conducted dipnet surveys and sampled for six minutes in each of the ten vegetation areas. We identified all larval amphib-

ians to species and counted. These surveys allowed the researchers to determine the complete assemblage of amphibians breeding at Ledson Marsh.

Water quality and climatic data

Water-quality monitoring was conducted during the post-fire winter of 2018. On 19 January 2018, we used a YSI 85 digital meter to assess water samples from the 10 vegetation patches. A YSI Series 6600 data sonde was installed in the deepest area of the marsh near the dam and suspended approximately 30 cm above the bottom. The data sonde recorded at one-hour intervals from 22 January to 9 March 2018. Both instruments recorded temperature (°C), dissolved oxygen (DO in mg/L), and pH.

Precipitation data was obtained from the California Department of Water Resources, California Data Exchange Center weather station (SRO) located in Santa Rosa, California, approximately 14 km northwest of Ledson Marsh. We summarized data by water year (1 October through 30 September) for the 24-year period from 1996 to 2019.

Data analysis

The numbers of egg masses or clusters and adult breeding amphibians were estimated from winter plot data by multiplying the mean plot densities and shoreline area. Shoreline area was determined by the shoreline length (1,604 m) and plot length. We used the typical number or range of egg masses or clusters produced by females (Table 1) and a 1:1 sex ratio was assumed to estimate the adult breeding populations in Ledson Marsh.

Standard descriptive statistics (mean [\bar{x}], standard deviation [$\pm SD$]) were used to describe the variation within selected variables. We completed a regression of precipitation data per water year (October through September) using a general linear model. To assess long-term precipitation patterns, we determined whether the regressions had a non-zero slope. A two-tailed t-test was used to compare the annual (water year) data, the halves of the 24-year timeline, and the water depths along sample plots between two post-fire study years. In all cases, variables approximated normal distributions and were homoscedastic, so t-tests for equal variances were employed. We conducted all analyses using JMP™ version 13.0.

RESULTS

Pre-fire species composition and abundance

Pre-fire observations of amphibians at Ledson Marsh revealed four native species (California red-legged frog, Pacific treefrog, California newt, and roughskin newt) and one exotic species (American bullfrog) occupied the marsh every year for 22 water years leading up to the Nuns Wildfire (1996-2017; DGC, unpublished data). Evidence of recruitment, based on some individuals reaching metamorphosis, has been observed every year throughout the course of the study for all species except for the American bullfrog. In contrast, American bullfrog annual recruitment has been irregular with a 50% frequency between 1996 and 2016. These numbers reflect the combination of onset timing of annual breeding and the duration of aquatic habitat available for egg and tadpole development before marsh drying.

Pre-fire timeline observations of amphibians at Ledson Marsh provide qualitative data on abundance for most species and quantitative data for the California red-legged frog. Field observations revealed California newts and Pacific treefrogs were abundant (numbers in the tens of thousands), roughskin newts were common (in the hundreds), and American bullfrogs were relatively few. In 1996, Cook (1997) estimated the presence of 39 adult American bullfrogs in Ledson Marsh. Quantitative data on California red-legged frogs over the interval 1996 to 2017 estimate the adult breeding population ranged between 8 and 234 ($\bar{x} = 60.2 \pm 27.1$; Cook 1997; DGC, unpublished data). The California red-legged frog adult breeding population falls between the range of roughskin newts and American bullfrogs.

In 1996, approximately half of the Ledson Marsh vegetation consisted of large, dense, tall, and emergent (> 2 m) stands of California bulrush and broad-leaved cattail, particularly within the center. The remaining half was interspersed with open water and low-emergent (< 0.5 m) common spikerush, particularly along the shoreline (Cook and Currylow 2014; Figure 1). Primary changes in vegetation since 1996 demonstrate an increase in tall-emergent vegetation, mainly broad-leaved cattails invading open water and common spikerush areas. Additionally, the aquatic fern (*Azolla filiculoides*), first observed in 2005, covered much of the open water and large portions of the shoreline prior to the Nuns Wildfire. The small floating fern created dense mats, particularly on the downwind (eastern) side of Ledson Marsh. In 2013, Ledson Marsh was composed of 81% tall-emergent (bulrush/cattail) and 19% common spikerush, interspersed with other low-emergent plants, open water, and aquatic fern. Moist microhabitats, available during the dry season prior to the wildfire, consisted of dense thatch within stands of California bulrush, broad-leaved cattail, and thick mats of aquatic fern.



Figure 1. Pre-fire landscape of Ledson Marsh on 18 February 2010 looking northwest. Dormant broad-leaved cattail and California bulrush are in the background and new growth of common spikerush is in the foreground. The position and direction of the photograph are similar to the images in Figure 3.

Nuns wildfire effects on habitat

When the approximately 23,000 ha Nuns Wildfire burned through Sonoma Valley in October 2017, fire swept through all of southern Trione-Annadel State Park, encompassing a radius > 1 km around Ledson Marsh (Figure 2; Sonoma County 2019b). Nearly all of the Ledson Marsh watershed ($> 95\%$) sustained low to moderate severity fire. Visual inspection of the watershed in November 2017 indicated nearly all ground cover burned, including herbaceous material, shrubs, and downed trees. The exception to this were large logs (> 45 cm diameter) that did not burn entirely; these logs were rare in the watershed. In some areas, the fire burned below the soil surface as indicated by large voids at the base of once standing trees. Some tree trunks burned to nearly a meter below the soil surface, and lateral roots burned for several meters leaving hollow openings below ground (DGC, personal observation). These subsurface fires smoldered for days after the initial fire. In contrast, with few exceptions, the canopy of the oak woodland and Douglas-fir forest did not burn.

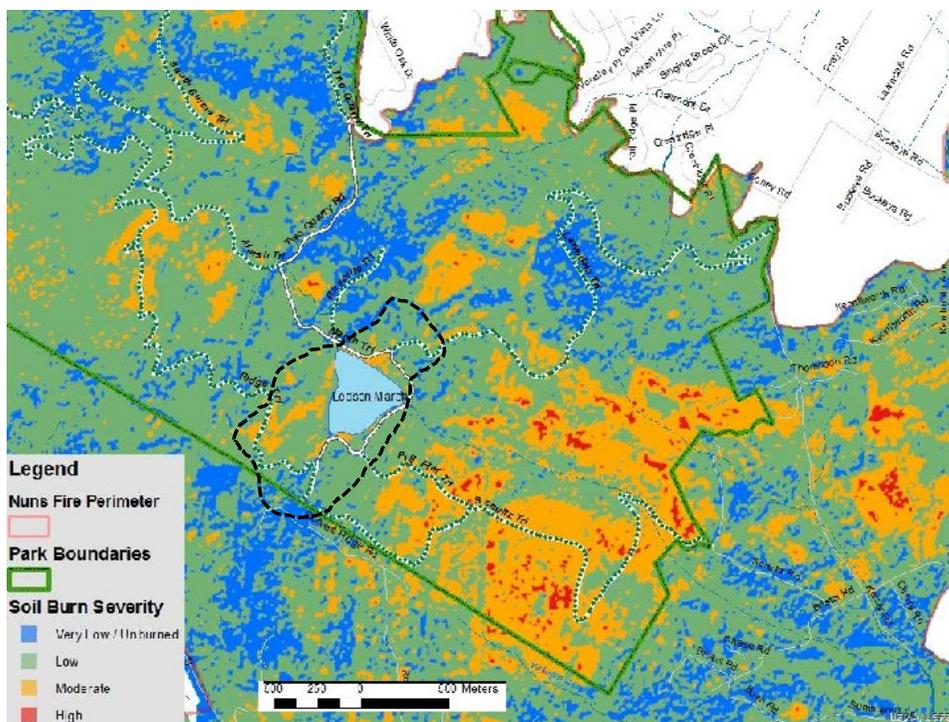


Figure 2. Nuns Wildlife soil burn severity map for southern Trione-Annadel State Park (Sonoma County 2019b). The black dashed line is the Ledson Marsh watershed boundary.

During the wildfire, Ledson Marsh was lacking any standing water and nearly all marsh vegetation burned to charred and desiccated stubble (Figure 3A). All the common spikerush and aquatic fern, and most stands of California bulrush and broad-leaved cattail, were dry enough to burn. The exception to this included three small patches of California bulrush and broad-leaved cattail collectively covering 0.14 ha in the central marsh and consisting of 1.2% of the surface area of the marsh.



Figure 3. Post-fire landscape of Ledson Marsh looking northwest: A) immediately post-burn (7 November 2017); and B) roughly 18 months post-burn (10 May 2019).

Weather patterns and amphibian breeding habitat

Over the 24-year study interval, the region has experienced generally declining precipitation with what appears to be an increase in variability (Figure 4). Annual (water year) precipitation levels reflect severe drought conditions to very wet conditions. The wettest year observed during the study (1998) maintained precipitation levels over 3.5 times compared to the driest year (2014). Over the first 12 water years (1996–2007), annual precipitation averaged 14 cm greater than the next 12 water years (2008–2019). Regressing precipitation for the entire time series revealed a significant (non-zero) negative slope for annual precipitation ($\beta = 0.70$; $P = 0.007$; Figure 4).

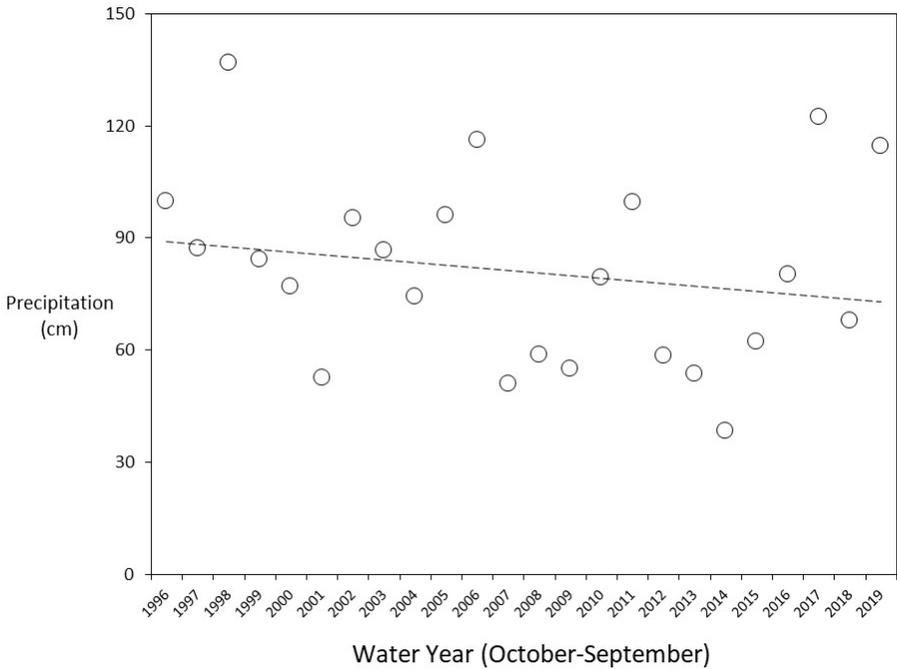


Figure 4. Variation in annual (water year) precipitation, 1996–2019. Precipitation data are from the California Data Exchange Center weather station located in Santa Rosa, CA. The trend line has a significant negative non-zero slope. See text for details.

The two years after the Nuns Wildfire were climatically and hydrologically very different. Severe drought characterized the 2018 winter (December to March) as compared to the wet 2019 winter. In particular, precipitation during winter 2018 was 36.0 cm or 64% of the 24-yr mean (56.0 cm). In contrast, 2019 winter precipitation was 83.3 cm or 149% of the 24-yr mean. Researchers recorded a 2.3-fold increase in winter precipitation and a 1.7-fold increase in water-year precipitation between 2018 and 2019. In 2018, amphibian breeding habitat was only partly inundated. For example, sample plot water depths in 2018 ($\bar{x} = 15.8 \text{ cm} \pm 14.1$) averaged less than half the depths in 2019 ($\bar{x} = 35.7 \text{ cm} \pm 15.5$), an unambiguous difference (t-test: $t = -18.368$, $df = 34$, $P < 0.001$).

Post-fire species composition and abundance

All five amphibian species known to occur at Ledson Marsh were detected after the Nuns Wildfire (Table 2). We also detected the western toad for the first time at Ledson Marsh after the wildfire. Post-fire, terrestrial surveys in the watershed found adult California newt, roughskin newt, and Pacific treefrog using the very sparse downed wood and rock cover available (Table 3). Two terrestrial salamander species (California slender salamander [*Batrachoseps attenuatus*], yellow-eyed salamander [*Ensatina eschscholtzii xanoptica*]), and four reptile species (western fence lizard [*Sceloporus occidentalis*], ring-neck snake [*Diadophis punctatus*], common gartersnake [*Thamnophis sirtalis*], and western pond turtle [*Actinemys marmorata*]) were also observed in the uplands surrounding Ledson Marsh.

Table 2. Estimates of amphibian egg production and adults at Ledson Marsh, 2018–2019. Estimates of egg clusters and masses are based on shoreline plots. Estimates of adults assume a one-to-one sex ratio.

Species	2018		2019	
	Egg Masses	Adults	Egg Masses	Adults
American bullfrog				1 ^a
California newt	3,089	1,030–2,059	29,585	9,862–19,723
California red-legged frog	3 ^b	6	2 ^b	4
Pacific treefrog	178	4–40	371	9–83
Roughskin newt				
Western toad		1 ^c		

^aAdult male heard vocalizing during spring dipnet survey.

^bEgg masses observed during winter VES between sample plots.

^cAdult male detected during winter VES between sample plots.

Table 3. Terrestrial herpetofauna observations in the Ledson Marsh watershed. Data are summarized observations from five single-pass Visual Encounter Surveys conducted between 19 January and 9 March 2018.

Species	Count
Amphibians	
California newt (<i>Taricha torosa</i>)	18
California slender salamander (<i>Batrachoseps attenuatus</i>)	436
Pacific treefrog (<i>Pseudacris regilla</i>)	66
Roughskin newt (<i>Taricha granulosa</i>)	2
Yellow-eyed salamander (<i>Ensatina eschscholtzii xanoptica</i>)	5
Reptiles	
Common garter snake (<i>Thamnophis sirtalis</i>)	1
Ring-neck snake (<i>Diadophis punctatus</i>)	1
Western fence lizard (<i>Sceloporus occidentalis</i>)	18
Western pond turtle (<i>Actinemys marmorata</i>)	1

For most species, amphibian egg clusters and masses were higher in 2019 when above-normal rainfall occurred, except for the California red-legged frog (Table 2). In winter 2019, California newt maintained the highest estimate of abundance with 29,585 egg clusters, reflecting an estimated 9,862 to 19,723 breeding adults. Pacific treefrogs ranked second in abundance with an estimated 371 egg clusters, reflecting 9 to 83 breeding adults. One adult male western toad was observed in Ledson Marsh during a winter 2019 survey.

California red-legged frog egg masses were not detected within the survey plots. However, we observed three egg masses in 2018 and two egg masses were observed in 2019 outside of the plots, indicating four to six breeding adult California red-legged frogs. More California red-legged frogs are known to have survived the fire than detected during winter surveys. During the Ledson Marsh dam repair from 22 August to 11 October 2018, C. Shafer (personal communication) made observations of 49 juvenile and 15 adult California red-legged frogs over 20 different days. The highest single-day observation of California red-legged frogs during this period was 13 juveniles and 1 adult.

Spring larval surveys detected four native amphibians, including: California newt, roughskin newt, Pacific treefrog, and western toad (Table 4). Pacific treefrogs maintained the largest complement of larvae at 58.9%, larger than the California newt (39.3%), though California newt egg clusters and adult estimates were much greater than Pacific treefrog estimates in winter (Table 2). A small proportion of larval amphibians from the spring surveys were roughskin newt (0.5%) and western toad (1.3%). California red-legged frog and American bullfrog tadpoles were not detected during the 2019 spring surveys. One male American bullfrog was heard calling during spring dipnet sampling and served as the only detection of this species during the post-fire surveys.

Table 4. Relative percentages of 4,468 observations of larval amphibians at Ledson Marsh, spring 2019 based on dipnet surveys conducted in May 2019.

Species	Percentage
American bullfrog	0
California newt	39.3
California red-legged frog	0
Pacific treefrog	58.9
Roughskin newt	0.5
Western toad	1.3

Habitat response to fire

Loss of marsh vegetation at Ledson Marsh resulting from the Nuns Wildfire was near complete (Figure 3A), though its regeneration was rapid (Figure 3B). In winter 2018, breeding areas were either dry (44.0%) or consisted of open water over charred substrate (46.5%) (Figure 5). After only one growing season (2019), substantial increases in broad-leaved cattail (44.1%) and to a lesser extent common spikerush (4.6%) were observed (Figure 5). Despite the increases, cover levels were lower than pre-fire conditions in 2013 (67% broad-leaved cattail and 18% common spikerush) based on 2013 shoreline vegetation types (Sonoma County 2019a).

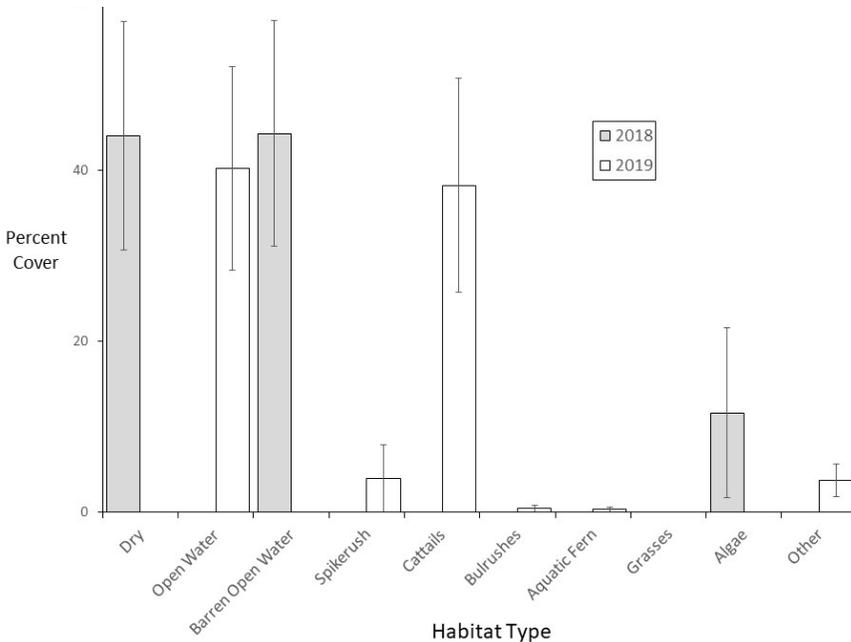


Figure 5. Habitat change in shoreline plots, Ledson Marsh, 2018 and 2019. Columns indicate mean values; whiskers are standard deviations. Barren open water is open water over charred ground.

Although the ranges in water quality parameters tolerated by amphibians in Ledson Marsh are not known, post-fire water quality revealed no unusual conditions that would likely effect the normal development of larval amphibians. Water on 19 January 2018 was cool ($9.0 \pm 0.8^\circ\text{C}$), near neutral pH (6.9 ± 0.5), and high in dissolved oxygen (9.4 ± 1.5 mg/L). Continuous winter monitoring near the dam in 2019 found similar temperature ($9.2 \pm 2.15^\circ\text{C}$) and pH (6.2 ± 0.1) conditions, and somewhat lower dissolved oxygen (5.6 ± 3.3 mg/L).

DISCUSSION

This case study contributes to our limited but growing understanding of amphibian response to the effects of wildfire, a condition that Hossack and Pilliod (2011) underscored. Overall, the amphibian assemblage at Ledson Marsh appeared resilient to or benefitted from the temporary disturbance caused by the Nuns Wildfire, at least through two years post-fire. This was demonstrated by the persistence of species detected prior to the wildfire, colonization by the western toad, and a return to an earlier successional stage that may prolong the marsh. The apparent relative constancy in species composition post-fire can be attributed to a combination of factors, including: 1) a short-term fire disturbance, 2) rapid vegetation regeneration, 3) affected amphibians with adult longevities longer than one year (assuming they could evade the fire), and/or 4) affected amphibians having a refuge from the fire. There is some data to support the first three points. However, the fourth point is speculative. Nevertheless, each merits a brief comment.

The Nuns Wildfire was clearly large in magnitude (Gabbert 2018) and fire movement was frequently fast and short in duration (Nauslar et al. 2018). Observations at Ledson Marsh and within the vicinity correspond with this perspective. Ground fire rapidly eliminated herbaceous and shrubby vegetation, crowning was rare, and pockets of more substantial fuel (large wood) were extremely dry due to preceding climate conditions (Nauslar et al. 2018), resulting in longer-term burning only locally. The authors speculate this pattern reduces the likelihood that fire, or the conditions resulting from a fire such as local temperatures and other air quality conditions, affected herpetofauna present in concealed refuges within the Ledson Marsh watershed. The terrestrial survey results correspond with little evidence of a fire effect. In addition, renewal of substantial vegetation in Ledson Marsh occurred after one growing season reflecting the protected rootstock of the perennial emergent plants (broad-leaved cattail, California bulrush, common spikerush) and their fire responsiveness (Rivard and Woodard 1989; Bowles et al. 1996). This rapidly re-established some vegetation structure, providing amphibian oviposition anchorage and refuge for larvae and post-metamorphic life stages during their rearing period.

Except for the Pacific treefrog, all native amphibian species that use Ledson Marsh typically live at least two years as reproductive adults and some live longer (Pimentel 1960; Watters and Kats 2006; Marc P. Hayes [MPH], unpublished data). Assuming they did not colonize from elsewhere, most adults that bred during the 2018-2019 survey period had to survive the Nuns Wildfire. Given the large footprint of the Nuns Wildfire, which encompassed the entire drainage basin around Ledson Marsh (Figure 2), and the known species range of movement in this amphibian assemblage (Pimentel 1960; Bulger et al. 2003; Smith and Green 2005; Fellers and Kleeman 2007), colonization from outside the fire area seems unlikely.

If Ledson Marsh amphibians did not colonize from elsewhere, a basic unknown is what refuges were used when the fire passed through the area. Native amphibian larvae within the marsh typically metamorphose by mid-summer (DGC, unpublished data) and two to three months prior to the marsh drying, so all life stages would have needed to find terrestrial refuge before the fire. Since most near-surface refugia (patches of unburned California bulrushes [rare], downed wood [rare], rock tailings from pit mining [limited]) had either burned or were likely too dry to provide refuge (the latter a basic reason for the rapid successful movement of this fire across the landscape), the authors suspect that refugia were largely not near the surface and/or concentrated in small areas. Understanding the refugia that amphibians and other herpetofauna might use to evade fire clearly merit study.

The exception to the lack of change in the species composition pattern, western toad, merits particular comment because the western toad had not been recorded at Ledson Marsh since monitoring began in 1996. Pre-fire, western toad had been observed outside the Ledson Marsh watershed but within the footprint of the 2017 wildfire. Western toad adults and tadpoles were detected post-fire, indicating successful breeding within Ledson Marsh. In Glacier National Park, Hossack and Corn (2007) found western toad colonized nine burned wetlands within two years post-fire in an area where no breeding had been detected and adults were rarely seen. Following the eruption of Mt. St. Helens in Washington State in 1980, western toad was the first amphibian colonizer of newly created ponds on the pumice plain (Crisafulli et al. 2005). Conditions that influenced western toad breeding habitat in these circumstances differ markedly (fire versus volcanic eruption), but both returned vegetation to an earlier successional stage. The Nuns Wildfire resetting of vegetation succession likely represents a parallel pattern for the response of western toad at Ledson Marsh. In addition,

the fire may have prolonged the natural conversion of the marsh to a wet meadow by returning the plant community to an earlier successional stage.

Larval California red-legged frogs were not detected during the spring of 2019, although egg masses were detected the previous winter. The cause may be due to one or more of the following: 1) dipnet sampling intensity, 2) low reproductive effort, and/or 3) low larval survival. The latter two reasons may not be an indication of decline of this threatened frog. The post-fire adult estimates were low, but similar to the range recorded since 1996. Also, the main habitat used for oviposition is common spikerush (Cook and Jennings 2007), which had a slower recovery post-fire as compared to the broad-leaved cattail (Figure 5). Adults may have been present and forgone breeding due to poor habitat conditions.

Climate projections indicate that temperatures across California will rise substantially (1 to 3°C) by 2050 (Cayan et al. 2008; Cayan et al. 2009). Increased evapotranspiration associated with higher temperatures is expected to exacerbate drier conditions (Matthews 2010) and the likelihood of drought (Mastrandrea and Luers 2012) may result in an increase in fire activity, including severity, area burned, ignitions, and season (Flannigan et al. 2000; Flannigan et al. 2005; Perry et al. 2011). The authors believe the Nuns Wildfire reflects this ascending trajectory. Though it may be tempting to speculate that maintenance of an early successional stage represents a benefit for western toad, increasing fire frequency may have complex interactive effects that include shifts in marsh vegetation seedbed, alteration of amphibian refuges to fire, and synergistic adverse impacts from environmental stress (e.g., reproductive and larval failure from prolonged and severe drought). This kind of complexity creates high uncertainty in terms of outcomes, not only for western toad but for the entire amphibian community within sites such as Ledson Marsh. The authors regard unambiguous understanding of species-specific refuges as among the most important data gaps needed to unravel potentially complex effects of fire on amphibians.

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Author Contributions

Conceived and designed the study: DGC

Collected the data: DGC

Performed the analysis of the data: MPH and DGC

Authored the manuscript: DGC and MPH

Provided critical revision of the manuscript: MPH and DGC

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