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The decline of native freshwater mussels (Bivalvia: Unionoida) in California as determined from historical and current surveys

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Freshwater mussels are increasingly recognized as important components of aquatic ecosystems but paradoxically are one of the most critically imperiled faunal groups in North America. In California the conservation status of all three native genera had not been comprehensively evaluated in over 30 years. We determined the current distribution of freshwater mussels in California by resurveying historical sites of known occurrences and evaluating the relative change between historical and contemporary surveys. A total of 450 historical records were compiled and represented 116 unique, locatable sites. Nearly 70% of the historical sites were resurveyed, and freshwater mussels were found at 47% of the resurveyed sites. Of the three mussel genera (*Anodonta*, *Gonidea* and *Margaritifera*) known from California, *Anodonta* was historically the most commonly observed genus, but was only found at 33% of the resurveyed sites. Although *Margaritifera* and *Gonidea* were historically found at fewer sites than *Anodonta*, they were extant at 65% and 55% of the resurveyed sites, respectively. Mussel losses were especially apparent in southern California, with mussels extirpated from 13 of 14 resurveyed sites. The absence of mussels from many historical sites, especially in southern California, parallels the on-going decline of freshwater mussel populations nationally.

Keywords: *Anodonta,* California, freshwater mussels, *Gonidea angulata*, historical and current distribution, *Margaritifera falcata*

The native aquatic molluscan fauna of North America is extremely diverse relative to other continents, and over 60% of the world's known species of freshwater mussels (Bivalvia: Unionoida) occur there (Master et al. 1998). The decline of this fauna, especially in the eastern United States where the majority of species are found, has been well documented over the past two decades (Williams et al. 1993, Bogan 1993, Lydeard et al. 2004, Wilcove and Master 2005, Haag 2012). The degradation of freshwater environments (water diversions, loss of riparian vegetation, mining, road building, competition with invasive species, and climate change), a ubiquitous worldwide phenomenon, has been implicated in the loss of many aquatic species (Bogan 1993, Williams et al. 1993, Malmqvist and Rundle 2002, Hastie et al. 2003, Hovingh 2004, Lydeard et al. 2004, Strayer et al. 2004, Helmstetler and Cowles 2008, Regnier et al. 2009, Black et al. 2010, Strayer 2010). As a result, freshwater mussels have suffered precipitous declines in abundance and distribution and are considered, together with freshwater gastropods (Johnson et al. 2013), to be the most imperiled faunal group in North America, with about 71% of the 297 known species considered endangered, threatened, or of special concern (Williams et al. 1993, Lydeard et al. 2004, Wilcove and Master 2005). An additional 20 species (7%) of the fauna are considered extinct. As the vast majority of the freshwater mussel diversity in the United States occurs east of the Rocky Mountains, it is not surprising that there has been little focus on western species. Historically it was thought that only nine freshwater mussel species occurred west of the Rocky Mountains, but recent genetic evidence (e.g., Mock et al. 2010) suggests that the western mussel fauna may be more diverse than previously thought, and many taxonomic issues (e.g., species-level designations) remain unresolved. For example, in the previously single genus *Anodonta* there is genetic support to suggest that three distinct genera are present in the western United States, and that six distinct clades exist among those genera (Chong et al. 2008). The distribution of the clades conforms to major western river basins (Mock et al. 2010) and not necessarily to previous taxonomic designations. The two other genera of western freshwater mussels, *Margaritifera* and *Gonidea*, lack this genetic diversity (Mock et al. 2013), and their taxonomic positions remain congruent with historical and current taxonomic designations.

Mollusks are one of the better surveyed invertebrate groups largely because of the interest of shell collectors beginning in the 18th century (Wright 1897). Exploratory expeditions to the western frontier began soon after Lewis and Clark arrived in the Pacific Northwest in 1805. The English botanist Thomas Nuttall was the first to secure specimens of freshwater mussels from west of the Rocky Mountains. Nuttall later gave the specimens to Isaac Lea in Philadelphia, and Lea was the first to describe new species of freshwater mussels from the western United States, including the California floater, *Anodonta californiensis* (Lea 1852); western floater, *Anodonta kennerlyi* (Lea 1860); winged floater, *Anodonta nuttalliana* (Lea 1838); Oregon floater, *Anodonta oregonensis* (Lea 1838); and western ridged mussel, *Gonidea angulata* (Lea 1838). The western pearlshell, *Margaritifera falcata* (Gould 1850), Yukon floater, *Anodonta beringiana* (Middendorff 1851), and *Anodonta dejecta* (Lewis 1875) were also described in this period. After Lewis (1875) described *A. dejecta*, all of the currently recognized western freshwater mussel species with affinities to California had been described.

Despite the effort of early conchologists, information on western mussel populations has remained sparse and fragmented. The only synopsis of freshwater mussels in the state of California was published in 1981, and included general information on trends in abundance and distribution (Taylor 1981). In this assessment, Taylor considered the historical ranges

and current status of four species of freshwater mussels known to occur in California including *A. californiensis, A. wahlamatensis*, *G. angulata,* and *M. falcata*. Taylor noted *A. californiensis* historically ranged from southern British Columbia to northernmost Baja California and was likely extinct from most of the Central Valley and southern California; *A. wahlamatensis* historically ranged from central California to the Columbia River along the Oregon-Washington border, and was probably extirpated from most of its original range; *G. angulata* historically ranged from southern British Columbia to southern California and east to southern Idaho and northern Nevada, and was likely extirpated in most of its original range in California; and *M. falcata* historically ranged from southern Alaska to central California and eastward to western Montana, western Wyoming and northern Utah, and was probably extinct in the San Lorenzo River in California. Status of a fifth species, *A. oregonensis*, though mentioned as occurring in California by Taylor, was not assessed in the 1981 publication. An additional species, *A. dejecta,* historically known from California (Ingram 1948), was not included in Taylor's checklist. Subsequent to Taylor's checklist, *A. wahlamatensis* was placed in synonymy with *A. nuttalliana* (Williams et al. 1993).

Despite a number of ecological and distributional studies over the past decade regarding California freshwater mussels (Howard and Cuffey 2003, Howard 2004, Brim Box et al. 2005, Howard et al. 2005, Howard and Cuffey 2006a, 2006b; Spring Rivers 2007, ENTRIX 2007, Howard 2008, Howard 2010) knowledge of the distribution and conservation status of freshwater mussels in the state remains wanting. To provide a better understanding of freshwater mussel distribution in California, we compiled historical and spatial observations from museum specimens and published records. Using this information, we identified and surveyed a majority of known historical sites to better understand the current status and distribution of freshwater mussels in California.

Materials and Methods

Historical data collection.—We compiled historical observational data of freshwater mussels found in California freshwater systems from literature, museum collections, and personal communications. For this study, we define historical records as those recorded or collected before 1995; recent records are defined as post-1995. Bivalve collections at the California Academy of Sciences (CAS) in San Francisco, the Academy of Natural Sciences in Philadelphia (ANSP), and the United States National Museum (USNM) in Washington, D.C. (Smithsonian), were physically inventoried. This entailed searching the museum collections containing freshwater mussel shells, affirming identifications and recording accounts of all specimens documented from California.

We reviewed the published (Appendix I) and gray literature to obtain records for freshwater mussels from California. In addition, the USFS Freshwater Mollusk Database at Utah State University was queried to obtain published and unpublished records of freshwater mussel occurrences in California. This database contains over 1,000 records of historical occurrences of bivalves in the western United States, dating back to the 1830s.

Field survey – historical sites.—We categorized historical records by specificity of the site (i.e., how well the historical information described the site locality). Many records did not provide the information needed to locate historical sites. For example, many historical records list only a river or a county. Field surveys were designed to resurvey as

many historical sites as possible and to visit river systems where mussels were historically found to ensure representative coverage of all major river systems in California.

In the summers of 2008 and 2009 historical freshwater mussels sites were surveyed. We used timed searches, which are effective for detecting the majority of mussel species present at a site (Strayer and Smith 2003). All sites were surveyed by snorkeling or scuba diving, and by direct observation in shallow areas. At each site, we attempted to check habitats where mussels could occur, including stream banks and channel substrate, root and sedge mats, rock crevices, under woody debris (logs), and within aquatic vegetation. Each site was surveyed until no new species were found or potential habitats where freshwater mussels could occur were searched. A minimum of one-person hour was spent at each site. Despite current studies suggesting that one hour is not enough time to discover rare freshwater mussel species (Metcalf-Smith et al. 2000, Tiemann et al. 2009), timed searches are effective for detecting the majority of freshwater mussel species present at a site (Miller and Payne 1993, Strayer et al. 1997, Vaughn et al. 1997, Strayer 1999, Strayer and Smith 2003). The objective of our survey was to detect the presence of freshwater mussel species at a site, and therefore timed searches are considered an appropriate method.

In addition to our field surveys, we compiled recent records of freshwater mussel occurrences from previous field surveys (e.g., Brim Box et al. 2005; Howard 2008, 2010) and from a freshwater database compiled by The Xerces Society (2014). We included these records as current if they corresponded to historical sites.

Results

Historical data.—A total of 450 historical records were compiled from museum collections, and published and unpublished records. These records include drainages in California ranging from the southernmost part of the state to the Oregon border (Table 1, Figure 1). The historical records describe varying levels of specificity in site locations: some detail specific site localities (where sites can be located), others list rivers, and others only counties or simply “California”.

Table 1.—Museum and published sources documenting historical occurrences and the level of precision of those locations for freshwater mussels in California, USA.

Historical source	CAS	USNM	ANSP	Published reports
Specific site locality	116	35	15	76
River	18	31	15	64
General site locality	26	33	7	14

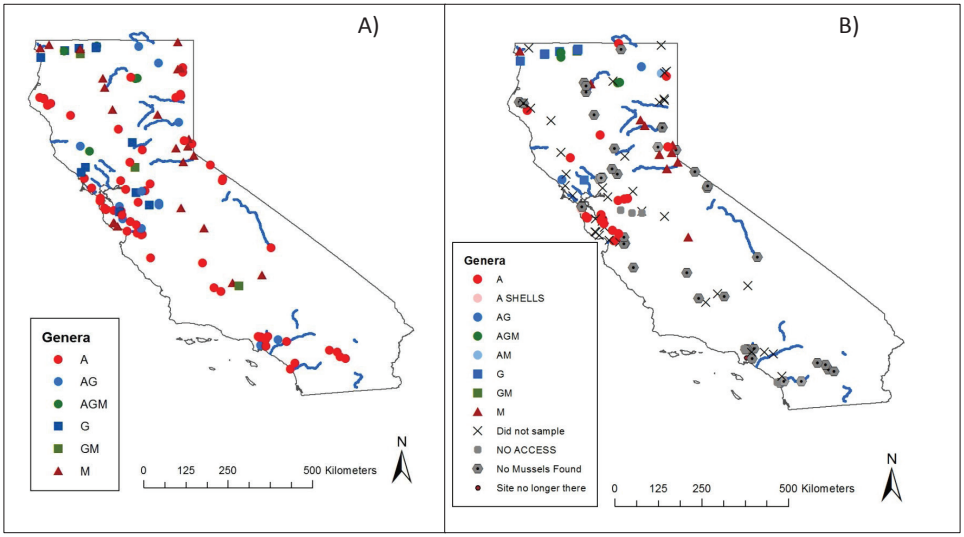

Figure 1.—Panel (A) Distribution of 116 historical locations of freshwater mussels in California. Colored symbols represent genera found at sites as follows: A=*Anodonta* spp.; AG = *Anodonta* spp. and *Gonidea angulata*; AGM = *Anodonta* spp., *G. angulata* and *Margaritifera falcata*; G = *G. angulata*; GM = *G. angulata* and *M. falcata*; M = *M. falcata*. Blue lines represent 24 additional rivers where mussels were historically found but where specific site localities were not recorded. Panel (B) Distribution of current locations of freshwater mussels in California based on surveys of 80 of 116 historical sites and 16 of 24 historical water bodies. Colored symbols represent species found at a site, and gray symbols with a center dot are sites where no mussels were found.

Of the three freshwater genera found in California, *Anodonta* was the most commonly observed or collected, historically constituting 64% (*n*=287) of the historical records; *Gonidea* were included in 20% of the records (*n*=88); and *Margaritifera* in 16% (*n*=75).

The oldest museum specimens we found date back to the 1800s. These include *M. falcata* found on May 17, 1877 in the McCloud River, Shasta County; *A. nuttalliana* dated 1877 from an unknown location in the Sierra Valley, Plumas County, and in 1892 from Mountain Lake in the Presidio in San Francisco, San Francisco County; *A. oregonensis* from the Pajaro River dated 1892, San Benito and Santa Clara counties; and *G. angulata* dated 1891 near Healdsburg, and in 1897 from the Russian River near Forestville (both in Sonoma County). Many of the museum specimens did not include specific collection dates or information but are likely very old (i.e., 19th century) based on the condition of tags, handwriting and shell preparation (tying shells with string). The oldest published California record is listed by Gould (1856), who described *M. falcata* as occurring in the Sacramento River in 1850.

Unfortunately, many museum tags did not contain specific locations or even county information. Of the total 450 historical records, only 242 provided enough information to locate the historical sites. Examples of historical records with adequate details to locate sites include CAS collections from Scott River at Kelsey Creek where *M. falcata* and *G. angulata* were found in 1924. Other examples of sites that could be located are those such as Clear Lake in Lake County, or Stow Lake in San Francisco's Golden Gate Park, San Francisco County.

We found that multiple observations or collections were often made from individual sites; therefore, these 242 records constitute a total of 116 unique sites from 80 ponds, lakes, creeks, rivers or reservoirs in California (Figure 1, Appendix II). For example, there are 18 records from Clear Lake over a period of >100 years — dating from 1870 to 1981. Therefore, we considered these 18 records as one site. Alternatively, it was possible to locate multiple locations on a particular creek or river as individual sites, and in these cases those sites were treated as separate entities. For example, five sites were identified from Coyote Creek in Santa Clara County. Of particular note are seven museum lots from the Smithsonian and CAS where *A. nuttalliana*, *A. oregonensis* and *A. californiensis* were collected from the now dry Tulare Lake in Kings County, which was drained in the 1930s. Unfortunately the Tulare Lake shells do not have dates associated with them.

In addition to the 242 records with specific site information, 128 (of the total 450 historical records) records provided enough information to identify specific rivers or water bodies from which the specimens were collected. Appendix II lists the 104 rivers, lakes, reservoirs and other water bodies where freshwater mussels were historically found in the state (80 which constitute unique site localities and 24 which include only river names), and Figure 1 maps the historical compared to current distributions.

The remaining historical records (n=80) provide only general information such as counties, locations such as "Borrego Springs, California from park naturalist" or "Central Valley, in the larger, slow streams only, as far south as the northern San Joaquin Valley" or simply list the state of California.

Field surveys of historical sites.—We attempted to survey as many historical sites and rivers as possible. Of the 116 historical sites with specific locality information, we surveyed or obtained recent information for a total of 80 sites (69%) (Figure 1). Of these sites, live mussels were found at 30 sites (38%), and shells only were found at one site. Five of the 80 sites we visited were inaccessible, such as Silverlake Reservoir in Los Angeles County; two lakes were dry (Owens Lake and Tulare Lake, Inyo and Kings counties, respectively); and one stream (Ballona Creek, Los Angeles County) had been moved from its historical location.

We attempted to sample 54 of the 80 sites where the genus *Anodonta* historically occurred, but could not access four sites, found one site no longer at the historical location, and two sites were dry (Table 2). Of the 47 sites we did survey, live *Anodonta* were found at 19 sites (40%) and shells only at one site. Since recent studies have found that genetic

Table 2.—Number of historical sites surveyed and results by genus. Parenthesis indicates where only shells were found. Composition change reflects shift in genus at sites (A to G = *Anodonta* to *Gonidea*; G to A = *Gonidea* to *Anodonta*; M to A = *Margaritifiera* to *Anodonta* and M to G = *Margaritifera* to *Gonidea*.

Current status of historical sites	*Anodonta*	*Gonidea*	*Margaritifera*
Total historical sites	80	31	31
Historical sites surveyed	47	26	22
No access to sites	7	3	0
Sites where genus was found	19 (1)	12	13
Number of sites now vacant	25	9	6
Number of sites where genus changed	2 (A to G)	5 (G to A)	1 (M to A) 2 (M to G)

subdivisions are incongruent with current taxonomic designations in western *Anodonta* (Chong et al. 2008), we identified *Anodonta* only to the genus level. We sampled 22 of the 31 sites where *M. falcata* historically occurred, and live *M. falcata* were found at 13 of those sites (59%) (Table 2). Twenty six of the 31 sites where *G. angulata* historically occurred were surveyed and live *G. angulata* were found at 12 sites (46%) (Table 2). We surveyed five sites where all three genera of mussels were historically documented and found all three genera at two of those sites—both located in the Pit River in Shasta County.

At a number of sites the genus of mussel found in the current survey was not the genus found in the historical surveys (Table 2). For example, *Anodonta* were found at a total of 19 sites in the current survey, and at six of these sites *Anodonta* were not recorded from the historical surveys. Similarly, we found *Gonidea* at 12 historical sites and at four additional sites where it was not historically recorded (Table 2).

In addition to the historical sites that could be spatially located, we also surveyed16 additional rivers where historical mussel records existed, but specific site information did not (Appendix II). We were unable to visit eight other rivers where general historical information existed. Where possible, multiple sites were surveyed within these 16 additional river systems. Live freshwater mussels were found in 12 (75%) of these river systems. In general, when mussels were found, individuals were widely dispersed and rarely found in dense beds. Five sites are noted exceptions: three sites on the main stem Klamath River (Siskiyou County), one site on the upper Pit River (Modoc County), where thousands of *G. angulata* individuals were densely packed near the channel banks; and one site on the South Fork Eel River in Mendocino County, where thousands of *Anodonta* spp. and *M. falcata* were found in a 100-meter-long meander bend.

Although 15 (13%) historical sites were surveyed in southern California, only one site contained live mussels. Live *Anodonta* spp. were found in the Bishop Creek Canal, a diversion of the Owens River in Inyo County.

Discussion

It is clear from museum records and published literature that freshwater mussels historically occurred throughout California. Given that multiple records were found from a wide variety of California sites and river systems, we suspect that in many cases mussels may have been extremely locally abundant at some sites. For example, there are numerous records for Clear Lake over a period of 100 years, and a similar number of records exist for the San Joaquin and Sacramento rivers over a period of 80 years. Early collectors were unlikely to have been snorkeling or scuba diving, and we therefore assume these collections or observations were made from the shore, and that mussels were conspicuous and visible in great numbers. In addition, many museum records contain numerous (e.g., 50) shells collected during a single visit.

Based on our survey of historical sites and multiple drainages throughout California, it appears that all three genera have undergone range restrictions within the state as compared to their historical distributions. This conclusion is consistent with Taylor's (1981) earlier observations for California, and with observations made on the conservation status of mussels found in other western states (Hovingh 2004). *Anodonta*, in particular, appears to be restricted to many fewer water bodies, and with far fewer individuals present at a site, as compared to historical records. This observation is consistent with the conservation status

some species in this genus have been given in California. For example, populations of *A. californiensis* are considered critically imperiled in southern California (Xerces Society 2014) and *A. californiensis* is a Sensitive Species on multiple national forests in California. The decline of freshwater mussels has been well established with causes linked to degradation of freshwater environments (Bogan 1993, Lydeard et al. 2004, Vaughn 2010, Strayer and Malcom 2012). In California, native fish species have suffered severe declines (Williams et al. 1985, Moyle 2002) with over 80% at risk of extinction (Moyle et al. 2011; 2013). Since fish serve as hosts for larval freshwater mussels, this degree of imperilment of fishes has the potential to depress mussel recruitment and hasten declines.

It appears that mussels have been extirpated from multiple historical sites in southern California. In our study, mussels were only found at one site, and earlier researchers (Taylor 1981, Coney 1993) also noted the disappearance of mussels from this part of California. Coney (1993), in particular, reached the conclusion that after eight years of searching for freshwater mussels, they were "...undoubtedly extirpated from all of Southern California." Our results demonstrate that historical data can play an important role in determining long-term trends in freshwater mussel distributions within defined geographic areas. Because mussels are well represented in museum collections and historical literature, their occurrence and distribution have been documented almost from the time of mass European colonization of the western United States. A comparison of these historical records to current distributions suggests freshwater mussel declines in California parallel those occurring nationally. To further our understanding of the status of freshwater mussels in California, future research should focus on resurveying the remaining sites and rivers in the state where freshwater mussels were historically found.

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Appendix II.—Number of Historical Locatable Sites by Water Body and Genera Found Historically and Currently in Those California Lakes, Rivers and Creeks

Where historical site equals 0, historical records refer only to the listed water body, not unique locations. Abbreviations for genera are as follows: A = *Anodonta* spp. G = *Gonidea angulata*, and M = *Margaritifera falcata*. Investigators recently have found that genetic subdivisions are incongruent with current taxonomic designations in western *Anodonta* (Chong et al. 2008); hence, we identified *Anodonta* only to the level of genus.

Water Body	Number of historical locatable sites	Genera found historically	Genera found currently
Alameda Creek	1	A	A
Arroyo Seco River	0	A	Not sampled
Ballona Creek	1	A, G	Site eliminated[a]
Big River	0	M	Not sampled
Blue Lake, Lassen Co.	1	A	A
Bridgeport Reservoir	1	A	None
Buena Vista Lake	1	A	Not sampled
Cedar Creek	1	M	Not sampled
Cerritos Lake	1	A	None
Chino Creek	2	A, G	Not sampled
Clear Lake, Lake Co.	1	A, G, M	A
Clear Lake, Modoc	1	A	Not sampled
Coyote Creek	5	A, G	A
Crystal Springs Reservoir	1	A	A
Delta Mendota Canal	1	A	No access
Donner Lake	1	A	A
Dry Creek, Yuba Co.	1	A	Not sampled
Dry Creek, Stanislaus Co.	1	A, G	Not sampled
East Branch North Fork Feather	1	M	M
Eel River	4	A, G, M	A, M
East Lake Park, Los Angeles	1	A	None
Elysian Park, Los Angeles	1	A	None
Feather River	2	A, G	M
Goose Lake	1	M	Not sampled
Guadalupe River	1	A, G	Not sampled
Irrigation ditch – Buttonwillow	1	A	None
Irrigation Ditch – Knights landing	1	A	M
Kern River	1	G, M	None
Klamath River	5	A, G, M	G, M
Lagunitas Creek	0	A	A, M
Lake Merced	1	A	A (Shells)
Long Valley Creek	1	A	Not sampled
Los Angeles River	0	A, G	None[b]

Appendix II.—Continued

Water Body	Number of historical locatable sites	Genera found historically	Genera found currently
Lost River	0	A, G	A
McCloud River	0	M	A, M
Merced River	1	M	M
Middle Fork American River	1	M	A
Middle Fork Feather River	0	A	M
Middle River	1	G	Not sampled
Mill Creek	1	M	M
Mojave River	0	A	Not sampled
Mountain Lake	1	A	None
Napa River	0	A	G
New River	0	A	Not sampled
Nicasio Lake	1	A	Not sampled
North Fork Feather	0	M	M
North Fork Mokelumne	1	A	M
Owens Lake	1	A	Dry lake
Owens River	0	A	A
Pacheco Creek	1	A, G	None
Pajaro River	0	A, G, M	A
Patricks Creek	1	M	Not sampled
Petaluma Creek	0	A	Not sampled
Pit River	4	A, G, M	A, G, M
Putah Creek	0	A, G	None
Quinto Creek	1	A	Not Sampled
Rio Hondo	1	A	Not Sampled
Rush Creek	0	A	Not Sampled
Russian River	2	G	A, G
Sacramento River	5	A, G, M	A, G, M
Salinas River	1	A	None
Salmon Creek	1	A	Not sampled
Salton Sea	1	A	None
San Benito	1	A	None
San Bernardino Creek	0	A	Not sampled
San Francisquito Creek	1	A	Not sampled
San Joaquin River	4	A, G, M	A, M
San Lorenzo River	3	M	Not sampled
San Luis Rey River	0	A	None
Santa Ana River	0	A, G	None
Santa Ana Creek – tributary to Pajaro River	1	A	Not sampled
Santa Margarita River	2	A	NONE

APPENDIX II.—Continued

Water Body	Number of historical locatable sites	Genera found historically	Genera found currently
Savannah Pond – Los Angeles	1	A	None
Scott River	2	G, M	A, G, M
Secret Creek	1	A	Not sampled
Sellick's Springs	1	A	Not sampled
Shasta Lake	1	A, M	None
Shasta River	2	A, G	G, M
Silver Fork South Fork American River	1	M	M
Silverlake Reservoir	1	A	No access
Smith Reservoir	1	A	Not sampled
Smith River	0	M	M
Soap Lake	1	A	A
South Fork American	0	M	M
South Fork Eel River	2	A	A, M
South Fork Kern River	1	M	Not sampled
South Fork Pit River	2	M	A, M
South Walker River	1	A	None
Spanish Creek	1	M	M
Stow Lake	1	A	None
Susan River	0	A	M
Tequesquite Creek	1	A	Not sampled
Topaz Lake	1	A	None
Truckee River	3	A, M	M
Tulare Lake	1	A	Dry lake
Tule Lake	1	A, G	None
Tuolumne River	2	A, G	M
Union Creek	1	A	Not sampled
Upper Blue Lake, Lake County	1	A, G	Not sampled
Upper Spring Lake	0	A	A
Upper Truckee River	1	M	M
Whitewater River	3	A	None
Willow Creek	1	A	A
Yuba River	0	A, M	M

[a] Site no longer located in area described historically
[b] No mussels present per Coney (1993)