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Notes from the Editor

With this issue comes the close of volume 99 of *California Fish and Game*, California's longest-running continuously published scientific journal. In 1914, when *California Fish and Game* first appeared, I doubt that the then editor considered the possibility that the journal would still be published 100 years later; I am pleased to see that it is, and I trust that Leadership appreciates the effort that has gone into producing it over the past century. Surely the initial editor, H. C. Bryant, did not envision a time in which the journal would be produced electronically and become available immediately to researchers throughout the world.

California Fish and Game was first published electronically as Volume 99 (3), earlier this year. With electronic publication, the journal also became one of "open access" and is available at no cost to interested researchers. There are many advantages to open access journals, among which are unrestricted access to research publications. Open access provides a worldwide audience larger than that of any subscription-based journal and, thus, increases the visibility and impact of published works. Open access also enhances indexing and retrieval power, and eliminates the need for permissions to reproduce and distribute content. I think it is safe to announce that *California Fish and Game* is fully committed to free, international access to all articles as soon as they are published.

With the close of volume 99, I want to thank Paul Hofmann, who has resigned after serving as an Associate Editor for nearly 20 years. I also want to acknowledge the willingness of several incoming Associate Editors that will be responsible for processing manuscripts in their respective areas of expertise, and who will be announced in the first issue of Volume 100. All Associate Editors serve in a volunteer capacity, and without their dedication and desire to help *California Fish and Game* be the successful journal that it is, publication could not continue.

I also want especially to acknowledge the contributions of Ms. Debra Hamilton, who handles all of the layout work for the journal (in addition to her regular responsibilities in the Audio Visual Unit), and those of Ms. Kirsten Macintyre, who has handled the mailing list, invoicing for page charges, complaints from subscribers, and the distribution of back issues, as well as supporting requests from the editor for better equipment, compatible software, and occasional travel expenditures. The amount of effort put forth by Debra and Kirsten in producing *California Fish and Game* is not readily apparent, and it is essential that their efforts be recognized.

During 2014, the California Department of Fish and Wildlife will publish the 100th volume of *California Fish and Game*. Several special issues are planned to commemorate this occasion, with the plan that each special issue will follow a particular theme. I look forward to the publication of volume 100, and to continuing the fine tradition that has been the flagship of this publication over the past 100 years.

Vernon C. Bleich
Editor-in-Chief

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Barotrauma related mortality of Florida-strain largemouth bass from winter tournaments in Diamond Valley Lake, California

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Fish captured and retained during fishing tournaments can experience initial or delayed mortality from barotrauma caused by the rapid elimination of hydrostatic pressure that occurs when a fish is brought from depth to the surface. Florida-strain largemouth bass (FLMB), (*Micropterus salmoides floridanus)* in Diamond Valley Lake, California are vulnerable to barotrauma-related stress when caught, due to their consistent habitation in depths that result in barotrauma (9 to 27 meters; personal observations). Bass tournaments are held on Diamond Valley Lake (DVL) up to 85% of all weekends annually. The small size of the reservoir, large number of tournaments and the vulnerability of FLMB to barotrauma-related stress can potentially affect the fishery. Eight bass tournaments were sampled for the incidence of barotrauma-related symptoms and 36-hour delayed mortality rates of bass with and without physical signs of barotrauma, caught as part of catch-and-release fishing tournaments during winter. The 36-hour delayed mortality rates of manually deflated FLMB with barotrauma were determined to be significantly lower than those that were not deflated following capture in winter tournaments. Florida-strain bass caught in tournaments with physical symptoms of barotrauma were also more likely to die than those asymptomatic. Bass tournament organizations that manually deflate barotrauma afflicted FLMB by knowledgeable and qualified staff would reduce 36-hour mortalities.

Key words: barotrauma mortality, Diamond Valley Lake, California, largemouth bass tournaments, *Micropterus salmoides floridanus*

Largemouth bass angling in freshwater is a popular recreational and competitive activity that is growing in popularity, with many thousands of tournaments held in North American inland waters annually that target black bass, including Florida-strain largemouth bass (FLMB; *Micropterus salmoides floridanus*) (Schramm et al. 1991, Kerr and Kamke 2003). Of the 1.35 million freshwater anglers in California, 33% spent 6.69 million days pursuing black bass (U.S Fish and Wildlife Service 2013). Additionally, California Department of Fish and Wildlife (CDFW) issued 835 black bass tournament permit applications statewide in 1991, and that number increased to 1,989 in 2012 (Krogman 2013). Tournament angling is an important part of fishing activities (Schramm et al. 1991) and is most often associated with catch-and-release fishing. However, compared with non-competitive catch and release fishing, fish caught by tournament anglers may suffer higher mortality due to stressors applied during a tournament. These stressors include relocation, air exposure, extensive handling (Hartley and Moring 1995, Killen et al. 2003, Edwards et al. 2004), prolonged retention time (Neal and Lopez-Clayton 2001, Graeb et al. 2005), livewell anoxia or hypoxia (Carmichael et al. 1984, Furimsky et al. 2003), livewell crowding, weigh-in procedures (Suski et al. 2004), and barotrauma (Siepker et al. 2007).

Barotrauma can affect any fish brought out of deeper water to the surface (Wilde 2009), although physoclistous fish, including largemouth bass, are most often visibly affected due to the expansion of their gas bladder (Shasteen and Sheehan 1997, Gravel and Cooke 2008) and a consequential increase in partial pressure of dissolved gases that can form bubbles (i.e., emboli) within the fish's organs and fluids. Resulting emboli can form in the eyes, brain, heart, arteries, gills, spleen, fins, musculature, and skin beneath the scales (Feathers and Knable 1983, Parrish and Moffit 1993, Kerr 2001, Brown et al. 2007, Wilde 2009).

Physical signs resulting from barotrauma include a distended or ruptured gas bladder, abnormal swimming behavior, protruding eyes, protrusion of internal organs through the mouth, internal and external hemorrhaging, cloacal protrusions, and death (Feathers and Knable 1983, Kerr 2001, Gravel and Cooke 2008). The extent and severity of the physiological and physical symptoms of barotrauma increase with increased depth of capture (Feathers and Knable 1983, Gitschlag and Renaud 1994) beyond the minimum of 3.5 meters (Shasteen and Sheehan 1997).

Recognition of barotrauma as an important physiological consequence of catch-and-release bass tournaments is increasing. Bass caught and released during tournaments held on reservoirs where a majority of the bass population resides in deeper water are particularly vulnerable to barotrauma (Morrissey et al. 2005). Per the California Code of Regulations (Lee 1992a), bass tournaments in California must require that "all fish shall be returned to the water alive and in good condition." This requirement is successful only if released bass survive. Therefore, artificial deflation (deflation) of an overinflated gas bladder or deep water release (crating) is required by CDFW during tournaments as part of the conditions of a permit, and generally is promoted throughout California inland waters (Lee 1992b).

Crating is the lowering of barotrauma afflicted bass to be released with a weighted basket or clip attached to the fish to a depth (generally 30 feet or more) of re-acclimatization to regain neutral buoyancy. Deflation of an expanded gas bladder is accomplished by inserting a hypodermic needle into the gas bladder to release the excess pressure. Although the release of excess gas from an over-inflated gas bladder cannot rectify all decompression trauma, it can allow bass that are positively buoyant and suffering from barotrauma-associated stress the opportunity to swim to a depth of neutral buoyancy, and potentially increase survival (Lee 1992a, Keniry et al. 1996). Only nine U.S. states, and no Canadian provinces, advocate deflation (Kerr 2001, Myers 2012). Further, deflation of bass caught in tournaments is likely discouraged in many states because insertion of a needle to relieve pressure can potentially miss the intended target and puncture other vital organs or vascular tissue. The ability of personnel applying technique is highly variable and, in some instances may actually increase mortality if not properly carried out. For these reasons, Wilde (2009) suggested that management agencies discourage or prohibit deflation techniques on fish exhibiting evidence of barotrauma. It is important to recognize that there may be substantial variation in response to angling induced stressors like barotrauma among various black bass species (Siepker et al. 2007) or, in this case, sub-species. Therefore, my objective was to determine barotrauma incidence of FLMB during winter tournaments (December–February) and if deflation by entities conducting tournaments is a meaningful requirement. Further, I describe the results of an assessment of barotrauma-related tournament mortality of FLMB from Diamond Valley Lake (DVL), a 1,983 ha reservoir in Riverside County, California.

METHODS

Study area.—Diamond Valley Lake is an off-stream storage reservoir built by Metropolitan Water District of Southern California, and is located 6.4 kilometers (km) southwest of Hemet in western Riverside County, California. The mean depth at full pool (elevation 535 m) is 61 m, 49 m at the East Dam, and 79 m at the West Dam. The lake has approximately 40 km of shoreline including the three dams. DVL is subjected to annual water level fluctuations of approximately 10 m, with the maximum drawdown to the emergency supply level at 27 m below full pool.

Diamond Valley Lake was selected due to the large number of tournaments and the number of FLMB caught from depths that result in symptoms of barotrauma. Tournaments are held on up to 85% of all weekends annually, with 63 contests held on DVL in 2011 and 52 contests held in 2012 (Krogman 2013). A large quantity of the bass caught, retained and brought in to be weighed at this reservoir are caught from depths from 9 to 18 m, as determined from interviews with participating anglers and from personal observations.

Methods.—Bass were collected at DVL during eight bass tournaments from December 2012 through February 2013, when bass within the reservoir are typically captured from the greatest depths and the risks of barotrauma and mortality are greatest. All tournaments during this period were subjected to a 3-fish bag limit per boat to reduce potential non-barotrauma-related stressors associated with tournaments, and to minimize mortality from untreated barotrauma. Bass were collected after the weigh-in process at a release-boat, where the bass were segregated by CDFW staff into (1) individuals showing external physical signs of barotrauma; (2) those not showing external physical signs of barotrauma; or (3) initial mortalities. Bass were held in an aerated, 500-l holding-tank filled with ambient lake water adjacent to the release boat. External physical signs of barotrauma were classified as (1) positive buoyancy or abnormal swimming; (2) external hemorrhaging; (3) bulging eyes; or (4) gas-bladder distention.

Dead or moribund bass brought to the release boat were evaluated for physical signs of barotrauma, recorded and set aside as initial mortalities. Moribund bass are those that underwent the weigh-in process and were deemed "alive" by tournament staff, which were beyond resuscitation. Half of the bass not exhibiting physical signs of barotrauma were measured, tallied, tagged with a blue Floy© anchor-tag below the second dorsal fin, recorded, and placed into a 1,000-l release tank equipped with 5,500 l/hr water inflow system on the release boat. The other half not exhibiting external physical signs of barotrauma were measured, tallied, not tagged, recorded, and placed in the same release tank. Bass exhibiting external evidence of barotrauma were alternately segregated into two study groups (treatment [yellow anchor-tag] and control [red anchor-tag]), and marked accordingly. Fish in each of these groups were then measured, tallied, recorded, and placed into the same release tank after tagging. Tournament personnel treated bass with obvious signs of barotrauma by deflation (treatment group); no fish in the control group were treated. Surface water temperature was recorded the day of each tournament using a digital thermometer.

All live bass collected from each tournament were transferred to a mesh-covered floating net-pen (1.2-m x 1.2-m x 3.0-m deep, with 10 mm nylon mesh) for approximately 36 hours to assess delayed mortality. A 36-hr holding period was selected due to logistical constraints, and previous investigators (Schramm et al. 1987) reported that highest incidence of mortality was most likely to occur within 24 hours. The net-pen was tied to the lee side of a floating wave attenuator approximately 300 m from the boat-launching facility. Bass in the net-pen were checked for mortalities the following morning, and again 24 hrs. later. Dead bass were checked for the presence or absence of an anchor-tag. A dead bass without an anchor-tag was assumed to have died from a stressor independent of the application of the anchor tag or tournament handling. Mortality of bass marked with a blue anchor tag was assumed to be the result of a stressor independent of barotrauma, but possibly related to tagging or handling. Mortality of bass in the control group (red anchor-tag) was assumed to be the result of stressors associated with untreated barotrauma or untreatable barotrauma afflictions. Mortality of bass in the treatment group (yellow anchor-tag) was assumed to be the result of untreatable barotrauma afflictions or improper gas bladder deflation. All bass still alive and suitable for release following the second morning mortality check were released.

Statistical analysis.—I used Cochran-Mantel-Haenszel chi-squared tests for *k* strata, wherein each tournament represented a different stratum, and set $\alpha = 0.05$. Similar to a general chi-squared test, this test detects differences between groups using 2x2 contingency tables (Hollander and Wolfe 1999). Differences in mortality were tested between (1) FLMB with and without physical signs of barotrauma; (2) artificially deflated-barotrauma and non-barotrauma FLMB; and (3) deflated and non-deflated barotrauma FLMB.

Results

Reservoir surface water temperatures ranged from 14° to 17° C during tournament sampling. Bass ($n = 655$) were collected and examined for physical signs of barotrauma following eight bass tournaments held between December 2012 and February 2013. Of the total, 214 bass (33%) exhibited physical signs of barotrauma, 413 (63%) exhibited no apparent signs of barotrauma, and 28 (4%) were moribund. All moribund FLMB had severe symptoms of barotrauma, including bulging eyes or gas bladder distention. Tournament workers present at all eight tournaments deflated 107 (50%) of the 214 bass that exhibited signs of barotrauma. The other 107 FLMB exhibiting external signs of barotrauma received no treatment.

Thirty-four (34) of the 107 FLMB (32%) that were not deflated died, while 15 of the 107 FLMB (14%) that were deflated were mortalities. The mortality rates for the eight tournaments ranged from 25 to 56% for un-deflated fish and from 0 to 29% for those that were deflated (Figure 1). Mortality rates of FLMB without signs of barotrauma ranged from 0 to 14% ($\bar{x} = 2\%$, $s = 3.88$). Regardless if deflation treatment occurred, the mortality rate of FLMB exhibiting symptoms of barotrauma, was significantly greater than that of FLMB exhibiting no signs of barotrauma ($P < 0.001$, 1 *df*, $MH = -8.68$). Furthermore, the mortality rate of deflated FLMB with barotrauma was still significantly greater than the mortality rate of FLMB without barotrauma ($P < 0.001$, 1 *df*, $MH = -5.43$). However, deflated FLMB with barotrauma displayed significantly lower mortality than un-deflated FLMB with barotrauma ($P = 0.001$, 1 *df*, $MH = 3.06$). Tagging did not have a significant effect on 36-hour mortality during this study ($P = 0.5$, 1 *df*, $MH = 0.013$).

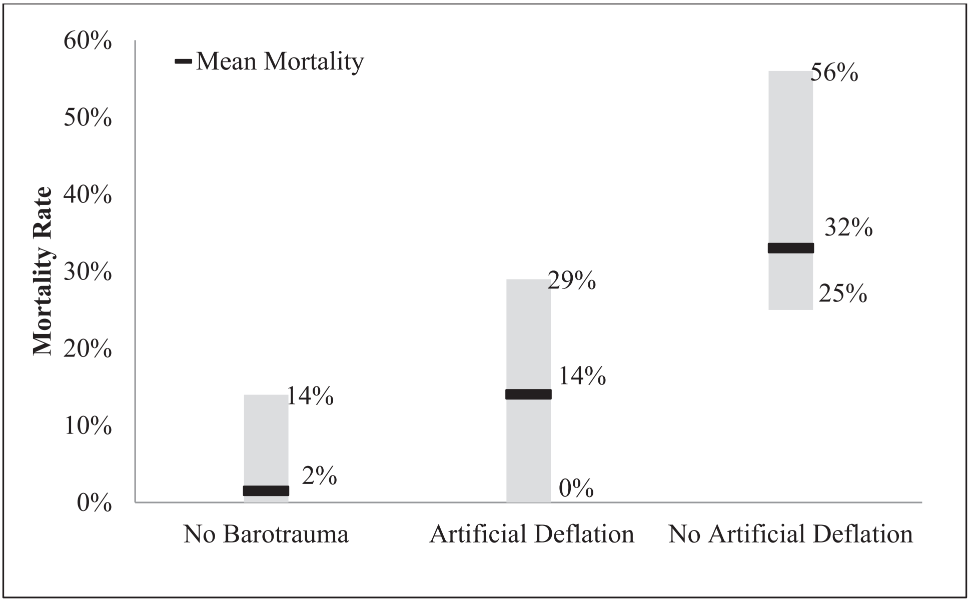

Figure 1.—Thirty-six hour delayed mortality rates of Florida-strain largemouth bass (*Micropterus salmoides floridanus*) caught during winter tournaments at Diamond Valley Lake, Riverside County, California, 2012–2013

Discussion

This study evaluated winter (December – February) tournament mortality rate over 36 hours, comparing FLMB with physical signs of barotrauma and those without, and of bass exhibiting symptoms of barotrauma that undeerwent air bladder deflation and those that were not deflated. Other studies evaluating barotrauma on freshwater species have focused on yellow perch, (*Perca flavescens)* (Keniry et al. 1996), smallmouth bass, (*Micropterus dolomieu)* (Morrissey et al. 2005, Gravel and Cooke 2008), black crappie, (*Pomoxis nigromaculatus)* (Childress 1987), walleye, (*Sander vitreus)* (RL&L 1995, Talmage and Staples 2011), or largemouth bass, (*Micropterus salmoides)* (Feathers and Knable 1983, Lee 1992a, Shasteen and Sheehan 1997). The effects of barotrauma and deflation, specifically on FLMB in California reservoirs have not been evaluated. This study was conceived as a retult of the increased recognition of barotrauma as a significant issue affecting the survival of tournament caught fish and a lack of information on the incidence of barotrauma and associated mortality rates of FLMB occurring in DVL. These data are necessary to recommend prudent and effective management measures to reduce the potential adverse impacts resulting from fish captured at barotrauma-inducing depths during tournaments.

Barotrauma is a factor affecting the condition and survival of black bass captured at depth and subsequently released, particularly during live-release angling tournaments (Morrissey et al. 2005, Siepker et al. 2007, Gravel and Cooke 2008). The FLMB population in DVL is particularly vulnerable to barotrauma-related tournament mortality due to the small size of the reservoir, large number of tournaments held annually, and the tendency of the FLMB to be captured from 9 to 27 m during winter. Tournaments occur at DVL on up to 85% of the weekends annually, and resulted in 3,836 FLMB reported caught in 2012. A FLMB population estimate conducted at DVL during 2012 ranged from ~5,971-8,199 ($\bar{x}$ =6,910, α=0.05; Schnabel estimate) tournament legal FLMB greater than 380 mm in length (California Department of Fish and Wildlife, unpublished data). The number reported caught represents a large portion of the available population (47–64%) within the lake. The number reported caught does not include fish caught and released during competitions prior to weigh-in (culling), fish captured by tournament anglers on non-tournament days (pre-fishing) or fish caught and released by non-tournament anglers.

External symptoms of barotrauma were evident in 27– 40% ($\bar{x}$ =34%) of all of the FLMB caught during this study. DVL water levels were high and relatively stable with abundant inundated woody habitat in the littoral zone during the study period. This could have kept more fish shallower than in prior years with lower water levels when shallow woody habitat was not as prevalent. Barwick (2004) reported higher bass abundance in littoral areas with coarse woody debris than other habitats. Abundant woody habitat in the littoral zone during this study could have resulted in barotrauma incidence at the low end of the range witnessed in other studies with smallmouth bass (29–66%; Morrissey et al. 2005), (32–76%; Gravel and Cooke 2008), and largemouth bass (34–68%; Myers 2012).

FLMB with barotrauma had a significantly higher mortality rate than those without barotrauma, regardless of deflation. However, deflation significantly reduced mortalities from >30% to ~15%. Consistent with other studies (Feathers and Knable 1983, Lee 1992a, Keniry et al. 1996, Shasteen and Sheehan 1997), my results demonstrated that deflating FLMB exhibiting signs of barotrauma can improve survival rate. Deflation of FLMB can significantly reduce mortality, but deflation cannot rectify the physiological effects other than an overinflated gas bladder. Morrissey et al. (2005) reported that deflation may provide some benefits to decompressed fish by allowing them to return to depth, but it would probably have little impact on any tissue damage that already had occurred. Virtually every organ in the body of a fish is affected by barotrauma and up to 70 different types of injuries have been documented (Feathers and Knable 1983, Rummer and Bennett 2005, Wilde 2009). Gas emboli, protruding eyes, protrusion of internal organs through the mouth, cloacal protrusions, and internal or external hemorrhaging cannot be addressed after the fact. Although the potential long-term survival of FLMB caught may have been reduced due to internal and physiological damage, the effects of which were not assessed in this study, and potentially explained why deflated bass still suffered higher mortality than non-barotrauma FLMB despite treatment.

This study evaluated only the 36-hour mortality rate, and it is possible that a percentage of bass that survived to be released did not survive. Mortality observed in this study was likely the result of relatively acute injuries resulting from barotrauma, severe tournament-related stress, errors in deflation technique, or all of the above. Mortality from severe injury or acute stressors should result in rapid death, whereas cumulative effects of sub-lethal stressors are more likely to result in delayed mortality (Kwak and Henry 1995). Less acute barotrauma-induced mortality would likely occur beyond the 36-hour retention time of this study. The cumulative and interactive effects of sub-lethal stressors can eventually lead to death, even if the individual factor alone does not exceed physiological tolerances (Carmichael et al. 1984, Wedemeyer et al. 1990). Other investigators (Morrissey et al. 1995, Gravel and Cooke 2008) reported stress indicators (i.e. blood glucose and lactate levels) in post-mortem bass with barotrauma were significantly higher than fish with negligible barotrauma, and bass that survived with severe barotrauma had intermediate glucose or lactate levels. Coupling the potentially acute physiological effects of barotrauma with the stressors associated with tournaments, it becomes paramount that participants and organizers of tournaments are aware of the signs and conditions likely to cause, severe barotrauma, the increased risk of mortality, and institute proper care and handling to maximize the survival of fish collected and retained (Shasteen and Sheehan 1997).

Organizations conducting tournaments at DVL are required to have staff proficient in artificial deflation on hand at the release location as a condition of the requisite permit, although the level of expertise likely varies. Mortality rates of deflated FLMB ranged from 0 to 29% during the study period, and variability in proficiency likely contributed to the variation in mortality rate because success of deflation depends on the training and experience of the individual performing the procedure (Kerr 2001). Education and training directed at tournament organizations and participants concerning techniques to properly alleviate an over-inflated gas bladder also are needed. During this study, the most common potential error committed by tournament staff was the release of most — or all — of the air from the gas bladder, such that the fish became negatively buoyant. Another common potential error posing a risk to fish health and survival is the inability to consistently hit the gas bladder, thereby requiring repeated punctures resulting in possible damage to other vital organs. The method of depressurization could also affect the success of deflation. Some chose to go through the side of the fish, which allows a greater margin of error to find the gas bladder to release air. Texas Parks and Wildlife recommends anglers attempt deflation through the side within the first hour of capture (TPW Magazine 2011) to minimize potential error in missing the gas bladder. Though the side method may be preferred, the fish is typically kept out of the water, and often times flops itself onto the ground, further contributing to handling stress. A second technique is to puncture the air bladder through the mouth, a method that decreases the margin for error. Greater precision is required, but the fish can be restrained and held in the water, which can minimize additional handling stress. The bass can also be held vertically, thereby allowing air to escape when the fish is submerged after the bladder has been punctured. However, Myers (2012) reported that deflation through the mouth led to 14% lower survival than side-deflation.

My objective was to determine the incidence of barotrauma occurring during winter tournaments and if tournament staff were increasing survival at tournaments by deflating bass, per the conditions of their permit. It was not an objective to assign a deflation method to tournament staff fulfilling their permit requirement or evaluate between the different methods available to address barotrauma following weigh-in. Cumulatively, using either method showed improved survival of bass. Crating fish to a desired depth with barotrauma is an alternative to alleviate barotrauma and is not invasive; however, it was not utilized or evaluated in this study. Crating appears more logistically practical while anglers are on the water when individual fish need assistance to depths of re-acclimatization, rather than at the end of a tournament when numerous fish with barotrauma need to be addressed following weigh-in.

Water temperature taken the day of each tournament (14 – 17°C) did not affect mortality based on studies that reported consistently low mortality at temperatures ≤20°C (Bennett et al. 1989, Schramm et al. 1987). Further, Hartley and Moring (1995) reported no correlation between the numbers of fishes held in live cages and delayed mortality. Tranquilli and Childers (1982) reported minimal effect on mortality rates from tagging with Floy© anchor-tags, which was confirmed in this study. Therefore, confinement likely had no effect and tagging had no effect during this study. It is not known if any FLMB were treated for barotrauma by the competitors during the tournaments at DVL prior to weigh-in. Myers (2012) reported only 6–24% of participants treated their catch for barotrauma prior to weigh-in. In this study, the number of fish treated prior to weigh-in is likely comparable, as the primary objective of tournament anglers is to catch the biggest limit of bass possible in the limited amount of time allotted to do so. Time taken to address barotrauma-afflicted bass already captured and retained detracts from the tournament angler's primary objective of catching fish. However, it is also unknown if fish immediately treated for barotrauma following capture have lower mortality than fish that have barotrauma treatment addressed after weigh-in, and is an issue requiring further study.

Deflation of FLMB is most prudent on smaller waters with bass populations that experience large amounts of tournament fishing pressure such as DVL, which had ~47–64% of the estimated legal FLMB population (CDFW, unpublished data) reported caught during tournaments in 2012. Artificial deflation of barotraumatized FLMB can significantly reduce mortality rates of bass captured at depth from DVL, contributing support of CDFW's requirements for deflation of bass following a tournament. In addition to deflation, managing the number of tournaments could also be useful on waters with vulnerable FLMB populations by managing the opportunity for mortalities to occur on high-use, high-barotrauma incidence waters. Since mortalities associated with barotrauma are probably greatest during fishing tournaments in which fish are retained by anglers for some period of time, a shortened tournament duration (6 h; Lee 1992a) conducted when FLMB are in deeper water may reduce mortality. Also, because stress is cumulative in fish (Gravel and Cooke 2008), a reduced bag limit could minimize stress on all fish in the livewell resulting from confinement (Kwak and Henry 1995) and reduce stress associated with handling during weigh-in by shortening bagging time. Further study is needed to evaluate how immediate or delayed deflation, the two artificial deflation methods, shortened tournament duration, or a reduced bag limit affect FLMB barotrauma mortality to provide sound scientific recommendations to fisheries managers.

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Checklist of inland aquatic Isopoda (Crustacea: Malacostraca) of California

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We present the first comprehensive checklist of Isopoda in Californian inland waters. Isopod distribution records were based upon a thorough literature review, unpublished data of colleagues, and collections of the authors. We present 17 species in 12 genera and 7 families, with additional potentially new taxa awaiting formal description. Six species are exotic and five species are California endemics. At least four of the native species are subterranean obligates. Conservation status rank revisions are offered in order to update the California Natural Diversity Database and IUCN Red List.

Key words: biodiversity, conservation, endemic, estuarine, freshwater, invasive species, stygobiont

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Aquatic isopods, commonly known as water slaters or aquatic pill bugs, are conspicuous components of aquatic biodiversity and function as important links in aquatic foodwebs by processing detritus and serve as an important dietary component for many predators (Vainola et al. 2008, Rogers et al. 2010). Assembled here for the first time is a comprehensive checklist of the stenohaline, freshwater inland isopod crustaceans of California. Although the marine fauna is not considered here, California hosts a diverse marine assemblage of approximately 190 named species from thirty-six families in eight suborders (see Brusca et al. 2010). The lack of a swimming phase may limit dispersal in the nonparasitic taxa and may explain high levels of isopod endemism (Brusca et al. 2010).

For a checklist limited to freshwater habitats, transitional habitats such as littoral, estuarine, and dunal ponds constitute problematic ecotones, and euryhaline taxa challenge the ability to separate freshwater (less than 500 ppm dissolved salts) from marine. Lake Merced on the San Franciscan peninsula, for example, has a diverse malacostracan assemblage tolerant of brackish water, where two amphipods (*Americorophium spinicorne*

[Stimpson, 1857] and *Hyalella* sp.), two isopods (*Caecidotea tomalensis*, *Gnorimosphaeroma oregonensis*), and a mysid shrimp (*Neomysis mercedis* Holmes, 1896) are sympatric (Miller 1958, White 2005). Likewise, California terrestrial isopods, including semi-aquatic forms such as *Ligidium* and *Ligia* (Ligiidae), are not considered here, nor are symbionts such as the commensal isopod *Phyllodurus abdominalis* Stimpson, 1857, which attaches to mud shrimps (*Upogebia* and *Callianassa*) (MacGinitie 1935). See Miller (1938) and Muchmore (1990) for a general summary of terrestrial isopoda.

METHODS

We conducted an exhaustive literature review and examined private collections and gray literature for occurrences reported from Californian freshwaters. The following sources were consulted: California Academy of Sciences (CAS) Department of Invertebrate Zoology and Geology's Invertebrate Collection Catalog Database; California Department of Fish and Wildlife's (CDFW) Natural Diversity Database (CDFW 2011); CDFW's Aquatic Bioassessment Laboratory (ABL) database, which includes data from the State Water Board's Surface Water Ambient Monitoring Program, US Environmental Protection Agency's Environmental Monitoring and Assessment Program, and regional agency and citizen monitoring programs; California Department of Water Resources' (CDWR) Bay Delta and Tributaries Project, Interagency Information Systems Services Office and Bay-Delta Monitoring and Analysis Section (CDWR 2010); Sierra Nevada Aquatic Research Laboratory (SNARL); unpublished data of the Southwestern Association of Freshwater Invertebrate Taxonomists and of C. Barr and W. Shepard (Essig Museum of Entomology); University of California at Davis Bohart Museum of Entomology (BME); the United States Geologic Survey (USGS) Nonindigenous Aquatic Species Database (USGS 2010); and the collections database of the National Museum of Natural History, Smithsonian Institution (NMNH) as well as NMNH's World List of Marine, Freshwater and Terrestrial Isopod Crustaceans (Internet database available from: http://invertebrates.si.edu/Isopod/about.html).

All records not directly attributed to others are new records of the authors. Many of the specimens referenced in this checklist are, or will be, deposited in CAS or NMNH. Taxonomic keys consulted included Williams (1972), Iverson (1982), Smith (2001), Rogers (2005), Lewis (2009a), Carlton (2007), and Rogers et al. (2010).

Any aquatic species not found in strictly marine habitats were included in this checklist. Exotic and naturalized taxa are identified and ecological associations mentioned where known. Of special interest were the cold stenotherms that rely upon groundwater and display high specialization (i.e. troglomorphy) and narrow endemism (Figure 1) (Rogers et al. 2010). The term *stygobiont* was used for cavernicoles that are limited to, or adapted to, subterranean streams, while *phreatobiont* was applied to taxa occupying phreatic zones (or *nappe phréatique*), and are accessible only by sampling springs, seeps, wells, and bore holes, but not normally caves (Motas and Serban 1965, Holsinger 1967). This speleological term should not be equated with the phylogenetic term *phreatoicidean*, although there is some overlap in functional group and niche (see Wilson and Keable 2001). Lotic interstitial habitats, or hyporheos, are typically separated from these subterranean (or hypogean) classifications because interaction with surface waters introduces nutrient pulses, predators, and temperature fluctuations not typically experienced in subterranean habitats.

Troglomorphic isopods typically associated with hypogean streams may be found in epigean streams, either from accidental displacement from the subterranean environment, or because the epigean stream functions as an extension of the subterranean environment. This is especially so where the epigean stream is influenced by groundwater and creates analogous habitat (e.g. rheocrene, hyporheos) (Barr 1960, Minckley 1961).

RESULTS

Family ASELLIDAE Latreille, 1802

***Asellus hilgendorfii* Bouvallius, 1886** (exotic)

Records.—**Contra Costa, Sacramento, San Joaquin, and Solano counties**. Sacramento River-San Joaquin River Delta: Sacramento River, Sherman Lake, Frank's Tract, Old River, 53 sampling events from 1978 to 2006, over 300 specimens, collection by ponar grab (CDWR database); Mandeville Island, Mildred Island, and Venice Cut, 1998 (Toft 2000, Toft et al. 2002). **Contra Costa Co**. Pittsburgh Freshwater Marsh at Dow Chemical Plant, D. C. Rogers, 24 February 1998.

Comments.— Introduced into the Delta probably by ballast discharge, but native to Asia (Magniez and Toft 2000, Toft et al. 2002, Schotte et al. 2009). The palearctic genus *Asellus* is not currently known from North America except for one species—*Asellus alaskensis* Bowman and Holmquist, 1975—endemic to Alaska (Bowman 1975a, Lewis 2009b).

***Bowmanasellus sequoiae* (Bowman, 1975)** (stygobiont)

Records and Comments.—**Tulare Co.** Lilburn Cave, type specimens collected by S. Shimek and P. Hara on 13 October 1974, described as *Caecidotea sequoiae* by Bowman (1975b), and confirmed as still present by Krejca (2006); additional Sequoia National Park sites discovered by J. Krejca et al. during 2003–2004 — Big Spring Cave, Crystal Cave, Hurricane Crawl Cave. Endemic to karst aquifers in Sequoia National Park (Krejca 2006, Lewis 2008).

***Caecidotea communis* (Say, 1818)** (exotic)

Records.—**Alameda Co.** "Berkeley, Court Pond, Life Sciences Building on U. of California Campus", 2 and 14 December 1994, 23 specimens, C. Hand and W. Burbank (NMNH database). **Marin Co.** "Tomales Bay, Paper Mill", 10 specimens (NMNH database).

Comments.—Introduced into the Pacific Northwest (California, Colorado, Oregon, Idaho, Washington, British Columbia), but native to eastern North America east of the Continental Divide (Richardson 1905, Mackin and Hubricht 1938, Hatch 1947, Williams 1970, 1972; Bowman 1975b, Robison and Schram 1987, Sovell and Guralnick 2005, Graening et al. 2007 2012a).

***Caecidotea occidentalis* (Williams, 1970)** (epigean)

Records.—**Humboldt Co.** Fern Lake outfall, 29 October 2006. J. Lee [det. D. C. Rogers]. **Lassen Co.** "drowned spring", near town of Karlo, 27 August 1979, L. Eng and J. Landye (CAS) [det. A. Baldinger]. East shore of Eagle Lake at elevation of 5,113 feet, 1 male, 3 ovigerous females (CAS) [det. J. Lewis]; Eagle Lake at Pelican Point, 21 May 1988, D. C. Rogers.

The following records are from D. C. Rogers' unpublished data and the ABL database from benthic sampling from 2002 to 2010, and may represent a significant range extension of this species: **Fresno Co**. San Joaquin and Kings River Canal. **Humboldt Co.** Bear Canyon, end of Bear Canyon Road, upstream of Eel River; Cooper Canyon Creek above Myrtle Ave.; South Fork Eel River, above Briceland Bridge. **Lake Co.** Bear Creek about 1.5 miles above Rice Fork Creek; Rice Fork Creek below Bear Creek. **Lassen Co.** Ash Creek W.A.; Lower Willow Creek. **Mendocino Co.** Navarro River about 0.7 miles below Indian Creek. **Merced Co**. El Capitan Canal. **Monterey Co.** Little Sur River above dam impoundment. **Napa Co**. Pickle Creek about 2.5 miles above Redwood Rd. **San Joaquin Co.** Port of Stockton. **Santa Clara Co.** Chestnut Picnic Area; Guadalupe Creek above reservoir; Los Gatos Creek below reservoir. **Santa Cruz Co.** San Lorenzo River at Crossing Street. **Shasta Co.** Pit River County Route 404, at Pittville; Sacramento River at Redding, north of Highway 44, 21 July 1990, D. C. Rogers; Sacramento River at Anderson River Park, 1 August 1992, D. C. Rogers; Cow Creek at Palo Cedro, just below Old Highway 44 Bridge, 6 June 1988, D. C. Rogers; Clear Creek above Seltzer Dam, 20 June 1991, D. C. Rogers; Battle Creek below Coleman Fish Hatchery, 26 May 1988, D. C. Rogers; Dog Creek, Old Shasta, 16 April 1989, D. C. Rogers. **Siskiyou Co**. Mt Shasta City Park, headwaters of the Sacramento River, 19 June 1994, D. C. Rogers. **Solano Co**. Putah Creek, below Monticello Dam, 8 September 1999, D. C. Rogers. **Sonoma Co.** Mark West Creek. **Stanislaus Co**. Orestimba Creek above Morris Rd; Orestimba Creek above Orestimba Rd.; Tuolumne River at Roberts Ferry. **Tehama Co**. Big Chico Creek at Chico State University, 5 April 1992, D. C. Rogers; Sacramento River at Dog Island, 12 June 1994, D. C. Rogers. **Trinity Co**. Brown's Creek, north of Sugar Loaf Peak, Brown's Creek Road, 2 July 1991, D. C. Rogers **Tuolumne Co.** Woods Creek below Hwy 49.

Comments.—*C. occidentalis* is also known from Oregon, Washington, and British Columbia (Williams 1970, 1972; Bowman 1974; Lewis 2001).

***Caecidotea racovitzai* (Williams, 1970)** (exotic)

Records.—**Contra Costa, Sacramento, San Joaquin, and Solano counties**. Sacramento River-San Joaquin River Delta, sampling events from 1995 to 2006, collection by ponar grab (CDWR database); Brown's Island, Lindsey Slough, Mildred Island, Old River, Sherman Island, Sand Mound Slough, Mandeville Island, Venice Cut, and West Canal at Clifton Court Forebay intake (Toft 2000, Toft et al. 2002, CAS database, CDWR database). **Merced Co**. Merced River (dredger tailing ponds), 12 September 2007, collected by Stillwater Sciences (2008) [det. J. Lewis].

Comments.—Introduced into the Pacific Northwest (California, Washington British Columbia), but native to eastern North America east of the Continental Divide (Williams 1970, Bowman 1975a, Lewis 2001, Toft et al. 2002). Established in the Sacramento-San Joaquin Delta probably by ballast water discharge (Toft 2000, Toft et al. 2002). Williams (1970) differentiated populations in the southern United States as *C. r. australis* and all others as *C. r. racovitzai.*

***Caecidotea tomalensis* (Harford, 1877); Tomales Bay Isopod** (epigean)

Records.—Graening et al. (2012a) provided a detailed analysis of the current distribution of this taxon; an abbreviated version is presented here. **Del Norte Co.** Lagoon Creek (NMNH database). Unnamed tributary of upper Lopez Creek, 4.3 km northwest of the town of Smith River (Graening et al. 2012a). **Humboldt Co.** “A well” (Holmes 1904); Ferndale, 10 males, 2 females (CAS) [det. J. Lewis]. **Marin Co.** Tomales Bay-Bolinas Lagoon area: a freshwater habitat described only as “Tomales Bay and vicinity” (type locality) (Harford 1877); “Tomales Bay, Dillon Beach, Rolland Pond, in mud . . . about 500 km N of Tumaco” (NMNH database); “In small creek on S side Dillon Beach Road, approx. 1 mile E of beach” (NMNH database); “Offshoot of Lagunitas Creek near Point Reyes Station” (NMNH database); lower Olema Creek (Graening et al. 2012a); “shallow pond adjacent to nearby Bolinas Lagoon” (Bowman 1974); “shallow freshwater pond on Audubon Canyon Ranch, Volunteer Canyon” (Bowman 1974; Serpa 1984, Graening et al. 2012a); “Polio Pond” at Stinson Beach (Graening et al. 2012). Point Reyes Peninsula: “pool in creek in Tomales Bay State Park” (NMNH database); lower Home Ranch Creek (Graening et al. 2012a); pond in Glenbrook Creek at Estero Trail bridge (Lobianco and Fong 2003, Graening et al. 2012a). Marin peninsula (Golden Gate National Recreation Area): Backdoor Pond, lower Elk/Tennessee Creek, Tennessee Cove Pond, Rodeo Creek, and Rodeo Lake (Graening et al. 2012a). **Mendocino Co**. Point Arena (Holmes 1904); “Pygmy Forest Preserve, in stream falls among decaying leaves” (NMNH database). Records from the Post (2010) study: Hans Jenny Pygmy Forest (University of California Natural Reserve System); Van Damme State Park; Mendocino Pygmy Forest (Jug Handle State Nature Reserve); “Pygmy Forest off Gibney Lane”; “Nature Conservancy Pygmy Forest near Ltl R. Airport”. **Monterey Co**. Pacific Grove (NMNH). **San Francisco Co.** Lake Merced (Bowman 1974, Serpa 1984). **San Mateo Co.** “under boards in sag pond on east side of Skyline Blvd., 100 yards S. of Kings Drive, Sierra Monte development” (Bowman 1974, Serpa 1984); Pillar Point Marsh upstream of West Point Avenue (Graening et al. 2012a); Huddart Park, McGarvey Gulch (Graening et al. 2012a). **Sonoma Co**. “Cheney Gulch, 3 miles SE Bodega Bay, Highway 1” (NMNH); “Marshall Gulch, in stream” (NMNH); “Stempe Creek, about 2.5 km upstream of Walker Road” (NMNH); “Portuguese Beach - spring near N Parking Lot - E side Highway #1” (NMNH); “Schoolhouse Beach, spring at end of culvert” (NMNH); Fairfield Osborn Preserve, in Courtship Creek and Frog Heaven pond (Serpa 1984, Graening et al. 2012a).

Comments.—The Tomales Bay Isopod is restricted to California’s northern Coast Ranges in perennial, shallow lentic habitats (e.g. sag ponds, springs, coastal lakes, acidic forest pools), but it can be found in ephemeral pools and moist mud where it burrows into the substrate during drought (Bowman 1974, Graening et al. 2012a).

***Caecidotea* sp.**

Records.—**Merced Co**. Merced River near Oakdale Road Bridge, 14 November 2002, R. Bottorff (unpublished data). **Stanislaus Co**. Tuolumne River, stations R4 and R23, 2000 and 2002, various collections from benthic sampling, N. Hume (unpublished data) [det. R. Bottorff].

Comments.—Wang and Holsinger (2001) reported that stygobiotic isopods of the genus *Caecidotea* were collected from a flooded chamber in Empire Cave (Santa Cruz Co.) during the collection of *Calasellus californicus* and *Stygobromus mackenziei* Holsinger, 1974 on 4 December 1983 by T. Briggs.

***Calasellus californicus* (Miller, 1933)** (phreatobiont)

Records.—**Alameda Co.** Livermore, Wente St. (Concannon St.), 5 November 2011 (ABL/SWAMP unpublished data). **El Dorado Co.** Unnamed spring tributary to Knickerbocker Creek near Cool, 1 mile west of Highway 49, 7 February 1988, R. Bottorff (unpublished data)[det. J. Lewis]; same locale, collections in 1976 and 2010, R. Bottorff (unpublished data). **Lake Co.** Near Kelseyville, unnamed well on W. Tuttle's ranch, syntypes collected by E. Essig in 1931, additional specimens in 1932, described as *Asellus californicus* by Miller (1933). **Marin Co.** 40 cm deep in gravel bed of Cronair [sic] Creek, 15 July 1997, Rosalie del Rosario (Lewis 2001). **Mendocino Co.** Sugar Creek, Angelo Coast Range Reserve, 30 January 1984, L. Serpa (Serpa 1984, NMNH Invertebrate Zoology Collections database), and also 31 May 2003 (C. Barr, unpublished data); Garcia Creek, coll. by L. Serpa. **Napa Co.** "Napa, mouth of spring under house" (Bowman 1975b); Napa River at Bale Lane, 18 April 2008 (ABL/SWAMP unpublished data); unnamed spring, 9 miles north of Napa, W. Shepard, 23 February 1991, prob. *C. longus* (CAS record). Benthic macroinvertebrate sampling in Napa River and tributaries, 2001-2003, Friends of Napa River and Institute for Conservation Advocacy, Research, and Education [det. R. Wisseman]: Bell (Canyon) Creek, 19 April 2002 and 15 May 2003, 1 female each; Cyrus Creek, 24 May 2003, 1 male; Diamond Mountain Creek, 23 April 2002, 1 male, 2 juveniles; Heath Canyon, 29 April 2004, 2 females; Milliken Creek at Westgate, 17 April 2001, 3 males, 1 juvenile; upper Napa River at Tubbs Lane (Calistoga), 20 April 2001, 1 male, 1 female; Nash Creek, 17 April 2002, 2 males, 1 female; Pickle Creek, 30 April 2003, 1 male, and 30 April 2006, 2 males; Rector [Canyon] Creek, 25 April 2001, 1 male, 1 female, 28 February 2002, 1 male and 1 juvenile, 28 April 2002, 1 male; Ritchey Creek, 25 April 2004, 1 male, 26 April 2006, 1 female; Soda Creek, 1 May 2002, 1 male, 11 females, 13 May 2002, 1 juvenile **Santa Clara Co.** "springs of Black Creek, on slope of Black Mountain" [SW of Los Gatos], 25 June 1967, R. Kenk (Bowman 1975b); Coyote Creek at Gilroy Hot Springs, 29 January 2005, S. Fend [det. D. C. Rogers]; Los Gatos Creek below reservoir, 3 February 2009, S. Fend and P. Weissich [det. D. C. Rogers]. **Santa Cruz Co.** UCSC Preserve, Empire Cave, 22 April 1979, D. Rudolph, B. van Ingen, and D. Cowan (NMNH Invertebrate Zoology Collections database), and 4 December 1983, 2 females, T. Briggs (Lewis 2001); Wilder Ranch State Park, Stump Spring, 26 July 2010, G. O. Graening.

***Calasellus longus* (Bowman, 1981)** (phreatobiont)

Records and Comments.—**Fresno Co.** "Shaver Lake, in Sierra National Forest about 35 miles (56 km) northwest [sic] of Fresno, elevation 3500 ft (1068 m)…in spring box", April 1977 (Bowman 1981). This is a single-site endemic (Lewis 2001).

***Calasellus* sp.**

Records and Comments.—**Madera Co.** Rock Creek Spring, adjacent to Minarets Road near Rock Creek Campground, 1 male, 1 December 1998, C. Popelish; either *Calasellus* sp. nov. or a juvenile of *C. longus* (J. Lewis, unpublished data).

Genus undet.

Records.—From the ABL database, benthic sampling from 2002 to 2009: **Glenn Co**. Stoney Creek, Olive Rd. **Humboldt Co**. Eel River below Allen Creek. **Monterey Co**. Willow Creek at Highway 1. **Sonoma Co**. Felta Creek; Sheephouse Creek. **Stanislaus Co**. Orestimba Creek above River Rd.

Family CIROLANIDAE Dana, 1852

***Excirolana linguifrons* (Richardson, 1899)** (euryhaline)

Records and Comments.—**Contra Costa Co.** San Pablo Bay near Pinole Point, 25 April 2006, 1 specimen from ponar grab (CDWR database). This species ranges from Monterey Bay to southern California, and is primarily intertidal on sandy beaches (Richardson 1905, Brusca et al. 2007).

Family IDOTEIDAE Samouelle, 1819

***Synidotea laticauda* Benedict, 1897** (euryhaline)

Records.—**Contra Costa, Sacramento, San Joaquin, and Solano counties.** Grizzly Bay, San Pablo Bay, Suisun Bay, Sherman Lake, Sacramento River, San Joaquin River (reported as *S. laevidorsalis* in the CDWR database; specimens also in BME). Aldrich (1961) reported *Synidotea* from benthic samples in the San Joaquin River between Bradford and Twitchell Islands and also near the Antioch bridge. **Sonoma Co**. Sonoma Boat Harbor at mouth of Sonoma River, 13 January 1992, J. Chapman; Port Sonoma, 3 October 1993, J. Chapman et al. (Chapman and Carlton 1994, Poore 1996); Petaluma River, under pier, August 1967, A. Kuris and J. Born (BME).

Comments.—*Synidotea laticauda* is common in the San Francisco Bay, especially in warmer waters with reduced salinity; in contrast, *S. laevidorsalis* (Miers, 1881) occurs subtidally in marine algal and seagrass communities (Lee and Miller 1980, Poore 1996) in the northwest Pacific Coast (Kwon 1986).

Family JANIRIDAE Sars, 1897

Iais californica (Richardson, 1904) (exotic)

Records and Comments.—Distribution in California is identical to *Sphaeroma quoyanum*, with which it is ectocommensal; it is probably native to New Zealand (Rotramel 1972, 1975).

Family MUNNIDAE Sars, 1897

***Uromunna* sp.** (euryhaline)

Records and Comments.—**Contra Costa, Sacramento, San Joaquin, and Solano counties.** Franks Tract, Grizzly Bay, Old River, Sacramento River, Sherman Lake, Suisun Bay, West Canal at Clifton Court Forebay intake (CDWR database). This family is typically marine, although *Uromunna* has been reported from freshwater in the lower Sacramento and San Joaquin Rivers near the Delta and other large rivers around the world (Rogers 2005; G. Wilson, Australian Museum, Sydney, Australia, pers. comm. 2013).

Family PARANTHURIDAE Menzies and Glynn, 1968

***Paranthura elegans* Menzies, 1951** (euryhaline)

Records and Comments.—Primarily intertidal, this species has been reported from San Pablo Bay near Pinole Point and at mouth of Petaluma River (CDWR database); its range is Marin County and south (Brusca et al. 2007).

Family SPHAEROMATIDAE Latreille, 1825

***Gnorimosphaeroma insulare* (Van Name, 1940)** (euryhaline)

Records.—**Contra Costa, Sacramento, San Joaquin, and Solano counties**: Suisun Bay, Grizzly Bay, Sherman Lake, Sacramento River, Frank's Tract, Old River, San Joaquin River, and West Canal at Clifton Court Forebay intake; over 100 sampling events from 1978 to 2006, over 250 specimens collected from ponar grab (CDWR database). **Contra Costa Co.** Brown's Island (Toft 2000); Pittsburgh Freshwater Marsh at Dow Chemical Plant, 24 February 1998, D. C. Rogers. **Marin Co**. Millerton Gulch at Tomales Bay, 3 May 2004, D. C. Rogers and E.C.L. Rogers. **Mendocino Co**. Jug Handle Creek, 9 September 1998, D. C. Rogers. **San Joaquin Co.** Mildred Island, Mandeville Tip (Toft 2000). **San Luis Obispo Co**. Santa Rosa Creek at Highway 1, 23 July 2007, G. Challet [det. D. C. Rogers]. **Ventura Co.** San Nicolas Island, freshwater, reported as *Exosphaeroma insulare* (Van Name 1940, Menzies 1954).

***Gnorimosphaeroma oregonensis* (Dana, 1853)** (euryhaline)

Records.—**Alameda Co.** Berkeley Beach, Berkeley (Menzies 1954). **Contra Costa, Sacramento, and Solano counties**: San Pablo Bay, Suisun Bay, Grizzly Bay, Sacramento River, and Old River, numerous specimens collected from ponar grab from 1986 to 2006 (CDWR database). **Marin Co.** Point San Quentin (Menzies 1954); Walker Creek and Stemple Creek (Menzies 1954); Glenbrook Creek, 10 January 2010, Guy Graening and G. O. Graening; Shell Beach (Tomales Bay State Park), intertidal brackish water (Menzies 1954); and Schooner Creek, spring 2000, J. Lee and D. Fong (Jon Lee Consulting, unpublished data). **Monterey Co.** mouth of Salinas River, as *Neosphaeroma oregonensis* (Smith 1953, Filice 1958); Monterey Bay and Pacific Grove (Richardson 1905). **San Francisco Co.** Angel Island, San Francisco Bay (Dana 1852, Richardson 1905); Lake Merced (Johnson 1903, Menzies 1954, this study). **San Joaquin Co.** San Joaquin River at mouth of Mokelumne River (Menzies 1954); San Joaquin River estuary (Filice 1958, Aldrich 1961). **San Luis Obispo Co.** Oso Flaco Lake, as *G. o. lutea* (Eriksen 1968); Sweet Springs at Morro Bay, 18 June 2008, D. C. Rogers and M. Hill. **San Mateo Co.** La Honda (Menzies 1954). **Solano Co.** "Napa River at Mare Island, bridge on Black Point Road" (Menzies 1954). **Sonoma Co**. Goat Rock Beach estuary, 22 Oct 2007, D. C. Rogers.

Comments.— *G. oregonensis* is distributed along the Pacific Coast from California to Alaska (Richardson 1905, Eriksen 1968, Hoestlandt 1973, Lee and Miller 1980, Wones and Larson 1991). The taxonomy of this species has been greatly confused in the literature. Many forms were described that were subsequently synonymized under *G. oregonensis* (Riegel 1959, Hoestlandt 1973, Brusca et al. 2007). Menzies' (1954) *Gnorimosphaeroma oregonensis lutea* was actually *G. insulare* (Riegel 1959). Hoestlandt (1973) changed *G. oregonensis* to "*G. oregonense*" either by error or design: if the latter, no reasons were given. This unjustified emendation was followed by Brusca et al. (2007).

***Gnorimosphaeroma* sp.** (euryhaline)

Records.—**Contra Costa Co**. San Pablo Creek at 3rd Ave. Bridge, 2 June 2005, A. Madrone [det. R. Bottorff]. **Mendocino Co.** Irish Gulch Creek below Highway 1, collections by Bottorf and Bottorf (2007) during 2004 - 2006. **Santa Cruz Co**. Collections by K. Orr in 2001 in Baldwin Creek, Dairy Creek, Majors Creek, Peasley Creek, Sandy Flat Creek, and Wilder Creek [det. R. Bottorff].

The following are from the ABL database, benthic sampling from 2000 to 2009: **Mendocino Co**. Garcia River at Hathaway Creek. **Monterey Co**. Big Sur River; Carmel River; Salinas River at Davis Road. **San Mateo Co**. Headwaters; Jones Gulch; Oil Creek; Peters Creek; Tarwater Creek; Water Lane; Waterman Creek. **San Luis Obispo Co**. Arroyo de la Cruz at Highway 1; Arroyo De La Cruz; Arroyo Grande River; Pico Creek; Pismo Creek above Highway 101, Frady Lane Bridge; San Simeon Creek; Santa Rosa Creek; Scott Creek, at Swanton Ranch and at lagoon at Highway 1. **Santa Barbara Co**. Arroyo Burro at Cliff Drive; Carpinteria Creek; Refugio Creek at Refugio State Beach; Jalama Creek at County Park at railroad trussels; Tecolote Creek at Bacara Resort access road. **Santa Clara Co**. Alviso Slough about 0.5 miles below Highway 237 at Alviso. **Santa Cruz Co**. Aptos Creek at Spreckles Drive; Majors Creek about 0.9 miles below Smith Grade Rd.; Pajaro River; San Lorenzo Estuary at Laurel Street; Soquel Creek; Soquel Creek Lagoon at railroad trussels; Waddell Creek; Waddell Creek Lagoon at Highway 1.

***Sphaeroma quoyanum* Milne-Edwards, 1840** (euryhaline; exotic)

Records and Comments.—Humboldt Bay, Bodega Bay, Tomales Bay, Bolinas Lagoon, San Francisco Bay, San Pablo Bay (Carlton 1979); Grizzly Bay at Dolphin near Suisun slough (CDWR database). Also found in Baja California and may be native to New Zealand and Australia; it burrows in sediments, rock, wood, and other substrates of protected bays and estuaries (Rotramel 1972, 1975; Lee and Miller 1980). It is often found in the same burrows with *Gnorimosphaeroma* spp.; tiny species of the genus *Iais* (Janiridae) are ectocommensal with these sphaeromatids (Rotramel 1972, 1975).

***Pseudosphaeroma campbellensis* Chilton, 1909** (exotic, euryhaline)

Records and Comments.—An invasive species from New Zealand, reported from estuaries along the Pacific coast from Coos Bay, Oregon, south to San Francisco Bay (Brusca et al. 2007).

Discussion

California is not particularly rich in non-marine aquatic isopod diversity, having only 9% of the approximately 130 species known from freshwaters in the United States (Smith 2001). Seventeen species in 12 genera and 7 families are listed here, with several potentially new taxa to be determined. Five species are known only from California, and 4 of them are subterranean obligates. Six species are exotic introductions. Exotic isopods, such as *Asellus hilgendorfii*, not only threaten native biodiversity but may serve as intermediate hosts of a number of parasites that affect fish, including salmonids (reviewed by Toft 2000). *Lirceus* (Asellidae) is not known to occur naturally in western North America (Hubricht and Mackin 1949, Lewis 2001), but introductions or invasions are predicted by Rogers (2005). Rogers (2005) suggests (1): the genus *Sphaerolana* (Cirolanidae), known only from cave streams in Mexico, may be detected in the southwestern USA, when the hyporheic and phreatic zones are better inventoried; and (2) *Thermosphaeroma* (Sphaeromatidae), endemic to hot springs in the southern deserts of North America (Cole and Minckley 1972), may be detected west of the Continental Divide when these habitats are better inventoried.

The native freshwater isopod fauna is still under-inventoried, especially in springs and other subterranean habitats. The shortage of taxonomists, a global crisis (Agnarsson and Kuntner 2007), hampers the identification of additional, novel Californian taxa as well as the enumeration of true alpha richness. Based upon our current understanding of the distribution of isopods in California's inland waters, and the conservation status assessment criteria established by the International Union for Conservation of Nature and Natural Resources (IUCN 2001) and NatureServe (Master et al. 2012, Faber-Langendoen et al. 2012), new and revised conservation rankings are recommended (Appendix I) for the California isopod taxa. Based upon the IUCN criteria, several taxa are globally rare or endangered. We assumed that all locales were intrinsically vulnerable to the threat of hydromodification and habitat loss in their watersheds, and to competition and predation pressure from invasive species.

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Appendix I. Current IUCN Red List and Natural Heritage Program conservation status ranks and suggested revisions for those freshwater taxa having sufficient data, and notes on endemism and population trends.

The full rationale and explanation for these conservation status ranking systems is detailed in IUCN (2012) for the Red List and in Faber-Langendoen et al. (2012) for the Natural Heritage Program, but briefly, for the Red List, VU = vulnerable to extinction, CR = critically endangered, and for the Heritage Program, G = global rank, S = subnational rank, and the numbers range from 1 = critically impaired to 5 = secure. Exotic species (not listed here) should be assigned the Red List category "LC" (i.e., of least conservation concern) and Natural Heritage rank "SNA" to indicate that they have no applicable conservation status in California.

Taxon	Current Red List Rank	Suggested Red List Rank	Current Heritage Rank	Suggested Heritage Rank	Notes
Bowmanasellus sequoiae	not listed	VU-B2	G1S1	no change	known from only 4 locales globally: restricted to karst aquifers in Sequoia Nationa Park
Caecidotea tomalensis	not listed	VU-B2,D1	G2S2	no change	see Graening et al. (2012a) for details
Calasellus californicus	not listed	VU-D2	G2S2	no change	20 locales in 8 counties
Calasellus longus	not listed	CR-B2,D1	G1S1	no change	single-site endemic dependent upon a single groundwater resurgence

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The historical range of beaver (*Castor canadensis*) in coastal California: an updated review of the evidence

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The North American beaver (*Castor canadensis*) has not been considered native to the watersheds of coastal California or the San Francisco Bay Area. These assertions form the basis of current wildlife management policies regarding that aquatic mammal, and they date to the first half of the 20th century. This review challenges those long-held assumptions based on verifiable (physical) and documented (reliable observational) records. Novel findings are facilitated by recently digitized information largely inaccessible prior to the 21st century. Understanding that beaver are native to California's coastal watersheds is important, as their role in groundwater recharge, repair of stream channel incision, and restoration of wetlands may be critically important to the conservation of threatened salmonids, as well as endangered amphibians and riparian-dependent birds.

Key words: beaver, California, *Castor canadensis*, fur trade, historic range, San Francisco Bay

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The currently recognized historic range of the beaver (*Castor canadensis*) in California, according to the California Department of Fish and Wildlife (CDFW) (California Department of Fish and Game 2005, Zeiner et al. 1990) includes only the Central Valley, the Pit, McCloud and Klamath River drainages of far northern California, and the lower Colorado River in the extreme southeastern corner of the State. This limited range appears to be based on monographs by early twentieth century zoologists Joseph Grinnell (1937) and Donald Tappe (1942). Both authors excluded the San Francisco Bay Area from the beaver's confirmed native range except where the delta of the Sacramento and San Joaquin Rivers (Delta) reaches the easternmost portion of Suisun Bay. Those authorities also concluded the range of beavers did not extend into southern California except along the lower Colorado River. Grinnell et al. (1937) also excluded all coastal watersheds from the early 20th century range except the upper Klamath River from the Scott River and east. Tappe (1942) extended the historical range relative to Grinnell to include the lower Klamath and Trinity Rivers and other coastal streams, but only as far south as the Little River, about 57 km south of the Klamath. Tappe (1942:14) speculated that, south of these northernmost California coastal streams, beaver were absent because the climate was more arid, and that coastal "stream beds are for the most part rocky and steep with but little beaver food growing along them, conditions which limit their suitability for this animal."

Tappe's description of coastal stream geomorphology is inaccurate for many watersheds south of the Klamath River, where numerous streams pass through low-gradient alluvial valleys rich with silt, creating habitat conditions quite suitable for beaver. While far south of the Klamath River precipitation does appreciably decrease, the notion that aridity limits beaver populations conflicts with the well-established historic and contemporary occurrences of beaver in the lower Colorado River, and the Alamo River in the Imperial Valley (Grinnell et al. 1937), the Mojave River (Lovich 2012), the Virgin and Humboldt Rivers of Nevada, Arizona's Gila and San Pedro Rivers (the latter known to fur trapper James Ohio Pattie as "Beaver River") (Allen 1895), and watersheds in the Mexican States of Sonora and Tamaulipas (Morgan 1868, Naiman 1988).

Casting further doubt on Tappe's speculation that more southerly coastal streams are unsuitable for beaver are observations that numerous colonies have for decades thrived in coastal streams. For example, beaver are reportedly present along the Big River in Mendocino County (Hall 1966), Pescadero Creek in San Mateo County, Meadow Creek in San Luis Obispo County (Christopher 2004), the Salsipuedes Creek tributary to the Santa Ynez River in Santa Barbara County, San Mateo Creek in San Diego and Orange Counties, and Tucalota Creek in Riverside County (Longcore et al. 2007) and Temecula Creek in San Diego County (Atkinson et al. 2003), both tributary to the Santa Margarita River.

Grinnell et al. (1937) and Tappe (1942) also excluded the Sierra Nevada, opining that beaver did not occur above 305 meters (1,000 feet) in the rivers draining into the California Central Valley. However, recent physical evidence indicates that beaver lived in the Sierra Nevada until at least 1850 (James and Lanman 2012). In addition, Lanman et al. (2012) reported multiple reliable observer records of beaver in streams in watersheds from the western and eastern slopes of the Sierra Nevada, extending from the northern to southern boundaries of that mountain range. These findings prompted our search for evidence that might extend the historic range of beaver to coastal California watersheds.

In this paper, we review available verifiable (physical) and documented (reliable observational) records of the historic presence of beaver in California coastal watersheds and tributaries to San Francisco Bay, facilitated by relatively open access to recently digitized archival materials. Supplementary evidence is also reviewed and includes ethnographic information, reviews of geographic place names, and historical newspaper accounts, all of which serve primarily to support the higher order levels of evidence. We hypothesize that beaver were native to the streams and rivers of California's coast and San Francisco Bay and that the exclusion of these areas in the early 20th century range maps proposed by Grinnell et al. (1937) and Tappe (1942) were primarily a result of the near extirpation of beaver from most of California prior to their research, the absence of pre-20th century specimens from California museums, and limited access to historic records, which at the time (unlike today) were widely dispersed, uncatalogued and not yet digitized.

Materials and Methods

Study areas and time period.—To organize the geographic breadth of the evidence, we divided our study area into five regions: (1) coastal watersheds in Del Norte, Siskiyou, and Humboldt counties including the Klamath River west of (and inclusive of) the Scott River; (2) coastal watersheds of Sonoma and Marin counties; (3) tributaries to San Francisco Bay (parts of Marin, Sonoma, Napa, Solano, Contra Costa, Alameda, Santa Clara, San Mateo and San Francisco counties) including San Pablo Bay but not Suisun Bay; (4) coastal watersheds of Monterey, San Luis Obispo, Santa Barbara, Ventura and Los Angeles counties; and (5) coastal watersheds of Riverside, Orange and San Diego counties (Figures 1–3). With the exception of archaeological beaver remains from the Subatlantic Holocene (< 2,400 years BP), the time period of the evidence investigated to support the historic presence of beaver in California begins with the Spanish settlement of San Diego in 1769 and ends before 1923, when a 28-year long state-wide program of beaver translocations program began (Hensley 1946, Lynn and Glading 1949, Anonymous 1950).

Specimen and records search.—We searched for specimens of beaver prior to 1923 in all museum collections participating in the Mammal Networked Information System (MaNIS) (http://manisnet.org/) and the Arctos Multi-Institution and Multi-Collection Museum Database (http://arctos.database.museum/) via Boolean searches. In addition, we contacted curators of mammal collections at the California Academy of Sciences (CAS), Natural History Museum of Los Angeles County (NHMLAC), Moore Laboratory of Zoology, Museum of Vertebrate Zoology (MVZ), San Diego Museum of Natural History, Santa Barbara Museum of Natural History, Santa Cruz Museum of Natural History, National Museum of Natural History (USNM), and the UCLA Dickey Collection. We used Web of Knowledge, Google, and Google Scholar to search for historical fur-trapper records and ethnographic evidence of beaver. We queried FAUNMAP (http://www.ucmp.berkeley.edu/neomap/search.html) for *Castor* remains found in late Holocene archaeological sites, and contacted eight county historical societies for relevant source material. We also identified references from citations in other publications that reviewed the historic ranges of other California mammals (Schmidt 1991; Bockstoce 2005), and searched historical newspaper accounts at the Library of Congress digitized "Historic American Newspapers" (1836-1922) (http://chroniclingamerica.loc.gov/) , the California Digital Newspaper Collection (1847-present) (http://cdnc.ucr.edu/cdnc), and NewspaperArchive (1847-present) (http://newspaperarchive.com/). Further, we searched geographic place names using the United States Geological Survey (USGS) Geographic Names Information System (GNIS) (https://geonames.usgs.gov/pls/gnispublic) and toponomastic references (Gudde and Bright 2004, Durham 1998).

Evidence was ordered into three categories of decreasing reliability in accordance with a classification scheme modified from Aubry et al. (2007). We considered physical evidence of beaver such as specimens in museum collections and zooarchaeological evidence to be the highest level of evidence (hereafter, verifiable records); documented first person

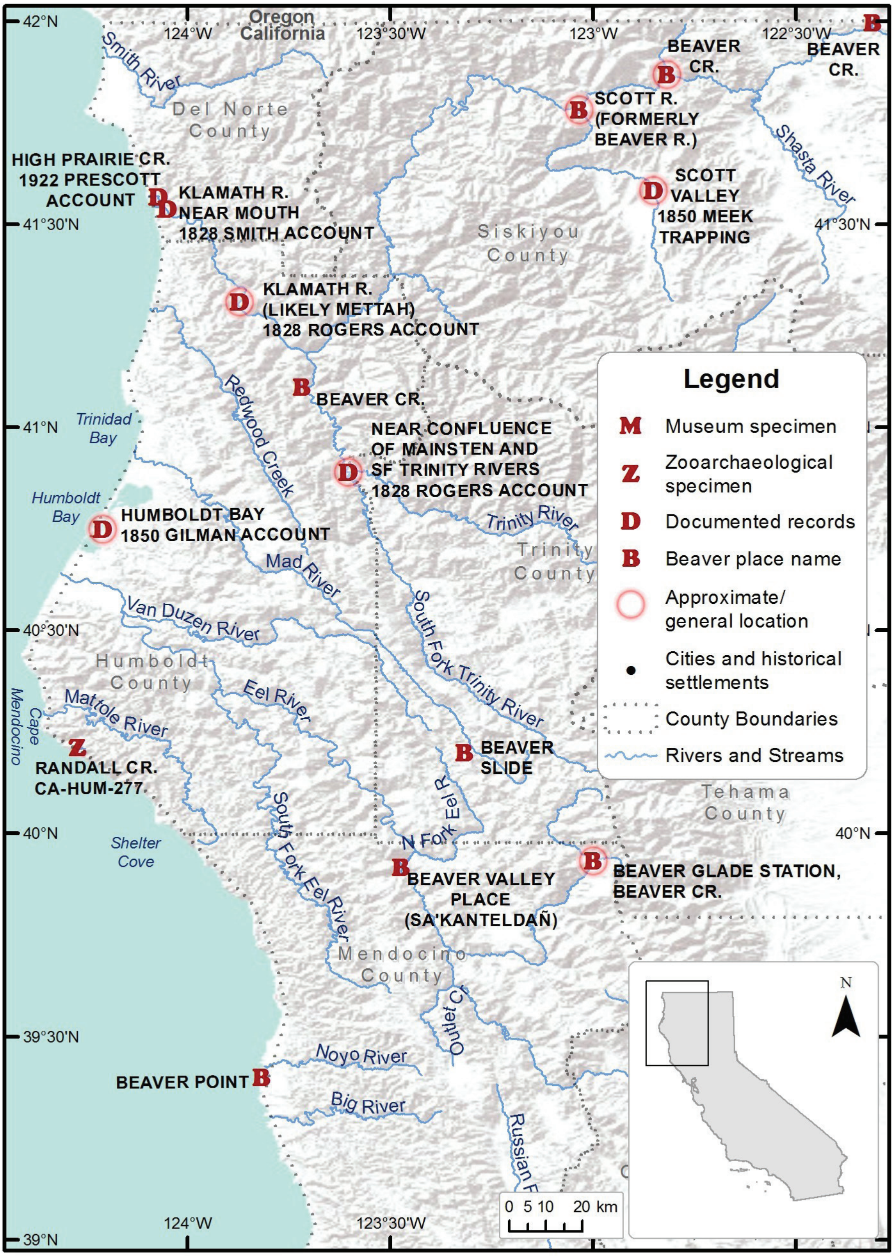

FIGURE 1.—Verifiable records (collection locations for museum specimens and zooarchaeological specimen locations) and locations for historical documentary records (reliable observers) and geographic place names including the word "beaver" for study region 1 (coastal watersheds in Del Norte, Siskiyou and Humboldt counties, including the Klamath River west of the Shasta Valley, and extreme northern Mendocino County), California, September 2013.

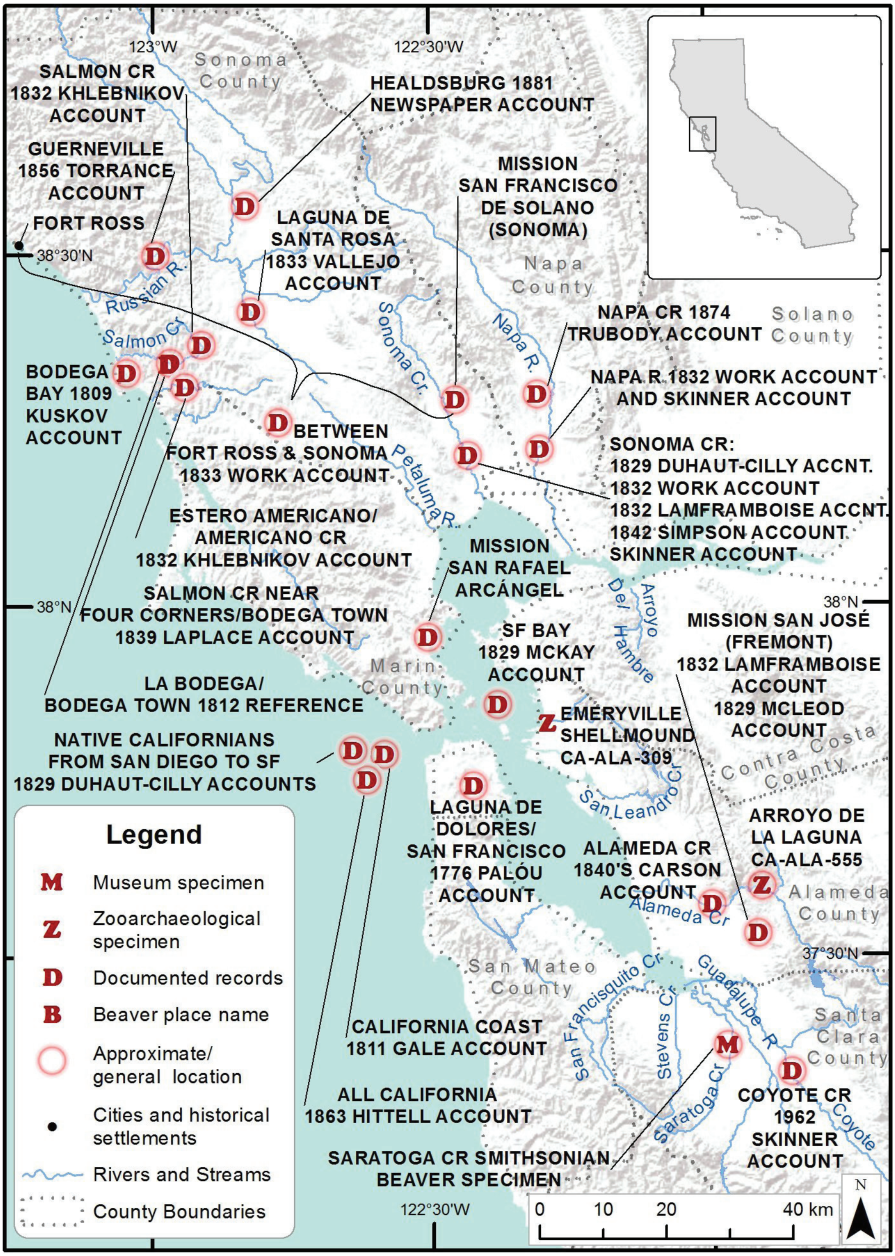

FIGURE 2.—Verifiable records (collection locations for museum specimens and zooarchaeological specimen locations) and locations for historical documentary records (reliable observers) and geographic place names including the word "beaver" for study region 2 (coastal watersheds in western Sonoma and Marin counties) and study region 3 (all counties with tributaries to San Francisco Bay west of the Carquinez Strait), California, September 2013.

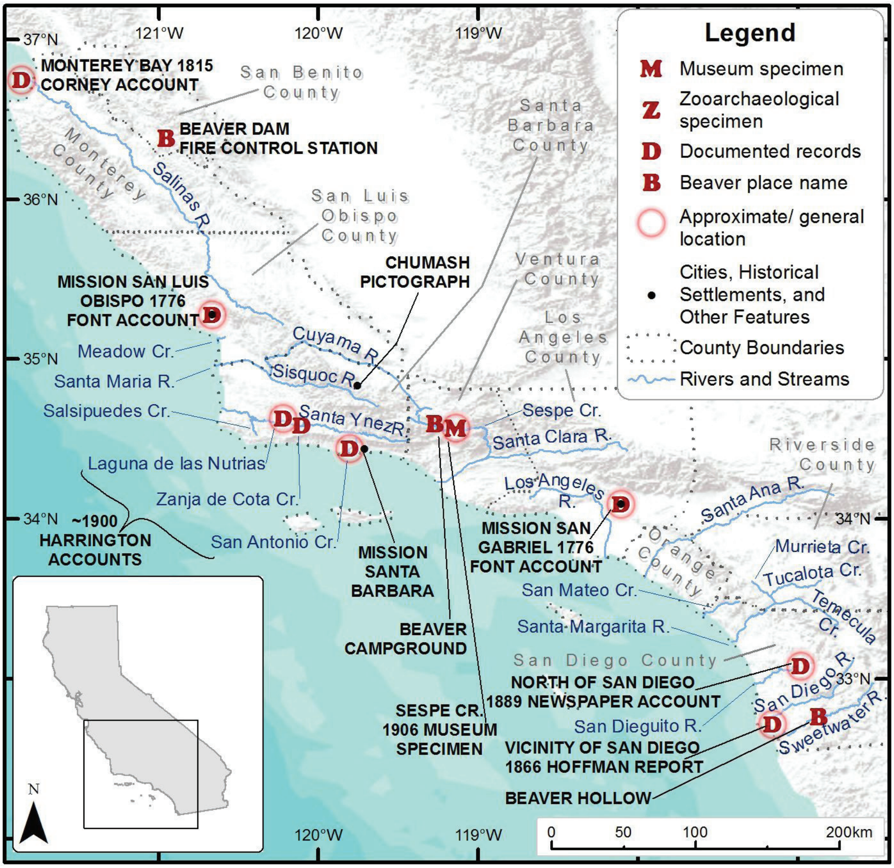

FIGURE 3.—Verifiable records (collection locations for museum specimens and zooarchaeological specimen locations), and locations for historical documentary records (reliable observers) and geographic place names including the word "beaver" for study region 4 (coastal watersheds in Monterey, San Luis Obispo, Santa Barbara, Ventura and Los Angeles counties), and for study region 5 (coastal watersheds in Orange, Riverside and San Diego Counties), California, September 2013.

accounts of the historical occurrence of beaver by reliable observers such as scientists, trappers, or rangers as the next highest level of evidence (hereafter, documented records); and evaluation of habitat suitability, ethnolinguistic and ethnographic information, and geographic place names as a lower level of evidence (hereafter, supplementary evidence). Aubry et al. (2007) referred to his third order level of evidence as "anecdotal" but narrowly defined this as visual observation made at a distance or tracks; therefore, we prefer the term "supplementary" to include our expanded definition of this categorization. Historical newspaper accounts were counted as documentary records if an animal was killed or captured as per Aubry et al. (2007), or as supplementary evidence if the article merely mentioned a beaver sighting.

RESULTS

Verifiable evidence, all five coastal regions.—The FAUNMAP query revealed no late Holocene *Castor* remains in archaeological sites in any of the regions studied. However, independent investigations identified beaver remains in the excavations of the Emeryville Shellmound, located on Temescal Creek, 37 m from San Francisco Bay in Alameda County (Figure 2). A "beaver [*C. canadensis*] tooth" from AD 300-500 (1500–1700 years Before Present (BP)) was found in the Emeryville Shellmound, CA-ALA-309 (Bennyhoff 1986; Uhle 1907). In addition, Cope (1985) identified three beaver bones, dating to 700 to 2600 radiocarbon years BP. Further, Broughton (1995: Table E8) identified an incisor tooth from Uhle's stratum 8. Associated material from that stratum is 2070 radiocarbon years BP.

On Arroyo de la Laguna Creek west of Interstate 680 in Pleasanton, Alameda County, a beaver lower incisor was found at the CA-ALA-555 site (Figure 2). The tooth was not radiocarbon dated, but was located in the lower part of the site that dates to 2200–1650 BP (Wiberg 1986). Arroyo de la Laguna is a low gradient, perennial stream in the Alameda Creek watershed and drains to San Francisco Bay.

Archaeologists uncovered a beaver molar at CA-HUM-277 on the southern coast of Humboldt County (Levulett 1985) (Figure 1). This site, located on coastal Randall Creek, just south of the Mattole River, dates to between 1000 and 500 years BP based on the depth at which it was found (W. Hildebrandt, Far Western Anthropological Research Group, personal communication, 2013). However, the specimen has not undergone radioisotopic analysis.

Museum specimens, all five coastal regions.—A MaNIS search combined with direct inquiries to California museums for pre-1923 *Castor* specimens located only a single vouchered specimen. That specimen, a beaver skull (catalogued MVZ Mammals 4918) was collected by John Hornung on 19 May 1906 on Sespe Creek, a tributary of the Santa Clara River, Ventura County. Grinnell (1937) was hesitant to accept the provenance of this specimen and placed a question mark by its location on his range map. Hornung, an NHMLAC zoologist, had collected many specimens for the MVZ as well as the American Museum of Natural History (Loomis 1901, Osborn 1910) and CAS (Howell 1923). Recently digitized correspondence between Grinnell and Hornung has become available and settles this longstanding question. When Grinnell wrote Hornung asking for further details regarding the specimen; Hornung (1914:1-2) wrote back: "... In reference to the beaver, I will say that I murdered the specimen in question 3 miles east of Cold Springs. I was on horseback and saw on the river, enormously swollen as the date which you have [19 May 1906], what appeared to me as a dead large dog surrounded by branches of a big stump. This stump was swimming in the water, but anchored in a tangled mass of some kind of a vine. After some maneuvering I could reach this animal with a stick. As soon as I touched it, it showed its teeth, and I knew then what unexpected find I had made…A shot ended the animal's sufferings, and I secured the skull which you have…". Hartman Cold Springs Ranch (34° 33' N, 119° 15' W) is located on upper Sespe Creek in the Sierra Madre Mountains at 1,025 m elevation and the creek along this stretch is quite low gradient, i.e. suitable beaver habitat. Interestingly there is a Beaver Camp on the USGS GNIS at 1,000 m elevation about 1 km east of Hartman Cold Springs Ranch, although its toponomastic origin is not known (Figure 3). In addition to the 1906 Sespe Creek beaver specimen, Hornung (1914:2) told Grinnell: "There are still quite a few beaver in Southern California, myself being so lucky as to get hold of one as late as Dec. 24, 1913, 3 weeks ago."

A search of museums outside of California for pre-1923 beaver specimens revealed a beaver skull identified as *C. c. subauratus* (USNM 580354) collected in December 1855 in Santa Clara, Santa Clara County, California by John Graham Cooper. Cooper lived in Mountain View, California from 19 October to 1 December 1855 and collected specimens for the USNM in Arroyo Quito (now Saratoga Creek) (Coan 1982), which flows to south San Francisco Bay and was, until the 1870s, tributary to the Guadalupe River watershed (Figure 2). This is the probable site of collection of the Santa Clara beaver specimen.

Documented records and supplementary evidence of beaver from the California maritime fur trade.—James Cook's discovery of sea otter (*Enhydra lutris*) on the west coast of North America in 1778 led quickly to American ships from Boston dominating the maritime fur trade south of Russian America (Alaska) (Bockstoce 2005). In addition, Vicente Vasadra y Vega instructed California's Mission Indians to procure otter pelts for Spain beginning in 1786 (Ogden 1932). Evidence that American ships also took beaver from California's coastal watersheds is suggested by the log of the ship *Albatross*, which states that while hunting and trading for fur seals (*Callorhinus ursinus* and *Arctocephalus townsendi*) and sea otter on the Columbia River and California coast, the ship also obtained 248 beaver pelts (Bancroft 1886). Another example of sea otter hunters taking coastal beaver is the Russian American Fur Company ship *Kodiak*, piloted by Ivan Kuskov who sailed into Bodega Bay in 1809 and returned to Novoarkhangelsk (Sitka, Alaska) with beaver skins and otter pelts (Thompson 1896). When French sea captain Auguste Bernard Duhaut-Cilly visited the coastal settlements of Alta California [Upper California as opposed to Baja California] in 1827–1828 on the ship *Heros*, he described the Indians hunting beaver: "For the skin of a rabbit or a beaver the bow is bent, and the lethal arrow does not fly through the air with impunity…To prevent the sound of the string from warning the game, they wrap a small part of it with a sleeve of beaver skin" (Duhaut-Cilly 1834).

Decades before Jedediah Smith led California's first overland beaver hunt and reached the Klamath River mouth in Del Norte County in 1828 (Dale et al. 1918, Smith et al. 1834) and before Peter Skene Ogden sent Hudson's Bay Company parties to the area from Oregon (Warner 1966), coastal Native Americans had apparently provided beaver, along with sea otter pelts, to the visiting oceanic fur hunters: "From their rocky lookouts the Indians of this remote coast had seen ships of many nations come and go, had even traded for knives and trinkets, the beaver and otter skins being so plentiful that they wore them for clothing" (Maloney 1940). In 1831 the Hudson's Bay Company at Fort Vancouver (on the Columbia River) complained that American ships had caused the price of beaver to rise fivefold on the coast and, after plying the coastal fur trade on the West Coast, Captain John Dominis of the *Owhyhee* returned to Boston with 8,000–9,000 beaver pelts (Gibson 2000).

Documented records and supplementary evidence of beaver in coastal watersheds: Del Norte, Siskiyou, and Humboldt Counties, including the Klamath River west of the Scott River.— Documented records for this region begin with the accounts of Jedediah Smith's 1828 journey from the Sacramento Valley near Red Bluff (Tehama County) northwest across the mountains to the Pacific Ocean. Smith's party observed beaver sign along the Trinity River near the border of Humboldt and Trinity counties and traded with Yurok Indians for beaver pelts while crossing the Klamath River at Met-tah as well as on the ridge between the Klamath River and Redwood Creek in Humboldt County (Dale et al. 1918, Lewis 1943). Smith also noted beaver sign on 5 June 1828 near the mouth of the Klamath River in Del

Norte County: “In the vicinity I saw some Beaver sign but the tide setting up interfered with the design of trapping” (Smith et al. 1934:96). These are the first reports of beaver on the lower Klamath River watershed, and the first record of beaver in the tidal zone of a California stream. Grinnell noted that beaver were plentiful on upper Klamath River tributaries such as the Shasta River and Scott River in Siskiyou County until 1911 (Grinnell et al. 1937). Fur trapper Joseph Meek took 1,800 beaver from the Scott River in 1850 (Tappe 1942). A letter written to Grinnell 29 January 1922 by Fish and Game Deputy H. S. Prescott documents observation of beaver sign “up-river of Requa” in 1915–1916, and explains that these lower Klamath River beaver were extirpated in 1917. In 1922, Prescott also noted beaver sign (willow cuttings) on High Prairie Creek, near the mouth of the Klamath River at Requa (Prescott 1922). Grinnell et al. (1937) remained skeptical of this record and placed a question mark on their map of MVZ beaver records near the confluence of the Trinity and Klamath Rivers labeled “*C. c. shastensis.”* Tappe’s later report (1942) cited additional take of beaver on the lower Klamath in February 1827 by Peter Skene Ogden’s Hudson’s Bay Company (Ogden and Elliot 1910). Based on the totality of the Smith and Ogden reports, Tappe (1942) and Hensley (1946) extended Grinnell’s historic range map for beaver all the way to coastal Del Norte and Humboldt counties.

California’s north coast was hunted by American and Hudson’s Bay Company fur brigades in 1832–1833, and beaver were encountered in small numbers. In 1832, Ewing Young’s American fur brigade ascended Putah Creek from the Sacramento River and reached the coast about 120 km north of Fort Ross. From there they trapped up the coast to the Umpqua River in Oregon “with little success” (Warner 1907:187, Hill 1923:32). In 1833, Michel Laframboise trapped from Bodega up the coast to Fort Vancouver in Oregon “along the ridge that runs parallel to the sea” (Nunis 1968a:153). Although we could not determine how many beaver Laframboise took from the North Coast Range, Hudson’s Bay Company records indicate that his hunt was successful (Nunis 1968a). In April 1850, the *Laura Virginia* entered Humboldt Bay and Charles Gilman (1901:40) wrote then of the fauna of the Humboldt Bay area, “…what exceeds all I ever saw is the quantity of game and fish. Elk, deer, black bear, and grizzly bear, beaver, otter, geese, ducks, curlews, snipe, robin, partridge are without number...”.

Supplementary historical evidence of beaver from the watersheds of the North Coast includes multiple toponomastic references including the word “beaver.” The Scott River was formerly known as the Beaver River by nineteenth century trappers (Gudde and Bright 2004). Several additional geographic place names are found in this region, including two Beaver Creeks in Humboldt County and another Beaver Creek as well as a Beaver Point in Mendocino County (Table 1). One of the Humboldt County “Beaver Creeks” could be ascribed to a Mr. Jacob Beaver, who lived in 1890 at the Beaver Creek that meets Redwood Creek at Beaver Flat, and is one mile from Beaver School (Turner and Turner 2010). However, the other Beaver Creek in Humboldt County flows into the Trinity River in a valley separated from the Beaver residence by 14.3 km as well as 1,200 m elevation Pine Ridge-Hupa Mountain. In addition, no eponymous origin for the Beaver Creek and Beaver Glade Station on the Middle Fork of the Eel River could be found. Whether Beaver Point referred to sea otter which were sometimes called “sea beaver” is unknown. Ethnolinguistic records of North Coast Indian tribes are replete with the respective words for beaver (Table 2) including *sa’kAntEłdAn* (Beaver Valley Place) and is located on the Eel River mainstem upstream of Bell Springs Creek and just south of the Trinity County-Mendocino County line (Baumhoff 1958).

Table 1.—Geographic place names in coastal watersheds incorporating the word “beaver” (including the Klamath River watershed west of the Scott River). All place names are from USGS GNIS except Beaver Valley Place (Baumhoff 1958:172) and Laguna de los Nutrias (Harrington 1981), California, September 2013.

Name of Geographic Feature	County	GPS (DMS) Coordinates of Feature or Stream Mouth	Coastal Watershed
Scott River (formerly Beaver River)	Siskiyou	41° 47’ N, 123° 02’ W	Klamath River
Beaver Creek	Humboldt	41° 06’ N, 123° 43’ W	Trinity River to Klamath River
Beaver Creek, Beaver Ridge, Beaver Butte, Beaver Flat, Beaver School	Humboldt	41° 01’ N, 123° 52’ W	Redwood Creek
Beaver Slide	Trinity	40° 12’ N, 123° 19’ W	Mad River
Beaver Valley Place	Mendocino	39° 55’ N, 123° 28’ W	Eel River
Beaver Creek, Beaver Glade Station	Mendocino	39° 56’ N, 123° 00’ W	Middle Fork Eel River to Eel River
Beaver Point	Mendocino	39° 24’ N, 123° 49’ W	South of mouth of Noyo River
Beaver Dam Fire Control Station	San Benito	36° 23’ N, 120° 56’ W	San Benito River to Pajaro River
Laguna de las Nutrias or Tsəpək isiyo (Chumash for Beaver Lake)	Santa Barbara	34° 37' N, 120° 17' W	Santa Ynez River
Beaver Campground	Ventura	34° 36’ N, 119° 15’ W	Sespe Creek to Santa Clara River
Beaver Camp	Ventura	34° 33’ N, 119° 15’ W	Sespe Creek to Santa Clara River
Beaver Hollow	San Diego	32° 46’ N, 116° 51’ W	Sweetwater River

Documented records and supplementary evidence of beaver in coastal watersheds: western Sonoma and Marin Counties.—After Ivan Kuskov’s first visit to Bodega Bay in 1809 (and return to Sitka with beaver pelts), he returned in 1811 on the schooner *Chirikof*, and explored the Russian River for 80 km upstream. Next, Kuskov established the Russian

Table 2.—Tabulation of words for beaver used by Native American tribes inhabiting California’s coastal watersheds, 2013.

Tribe	Counties from North to South	Coastal Watershed or Bay/Channel	Indian Word	Source[1]
Tolowa	Del Norte	Smith River (Crescent City)	*sah’-hot*	Merriam
Karok	Siskiyou	Klamath River (Happy Camp)	*sah’-peneetch* *sa-pin·itch*	Merriam Powers
Coast Yurok	Humboldt	Trinidad Bay	*tes-a’r*	Heizer
Wiyot	Humboldt	Humboldt Bay	*he-wo’-li*	Merriam
Whilkut	Humboldt	Redwood Creek	*tch’wah’-i*	Merriam
Lolangkok/ Sinkyone	Humboldt	South Fork Eel River	*ba-chen’-tel*	Merriam
Huchnom	Mendocino	Eel River (Round Valley)	*tik-keh*	Powers
Pomo	Mendocino	Eel River (Round Valley)	*kat-si-keh'*	Powers
Northern Pomo/ Tabate	Mendocino	Navarro River (Anderson Valley)	*kah-ke’*	Merriam
Central Pomo/ Yokaia/Yukai	Mendocino	Russian River (Ukiah)	*kah-ke’* *ka-tai-u-ki’ah* *ko-o’*	Merriam Powers Powers
Northern Pomo/ Kaiyu	Lake	Tule Lake, Blue Lakes	*chin-nor* *chi-nor*	Merriam Powers
Central Pomo/ Shanel	Mendocino	Russian River (Hopland)	*kaht’-ka*	Merriam Powers
Wappo	Sonoma	Russian River (Alexander Valley)	*ma’-nah ow’-we*	Merriam
Pomo/ Gallinomero	Sonoma	Russian River (Healdsburg)	*tek’-keh*	Powers
Southern Pomo/ Makahmo	Sonoma	Russian River (Cloverdale Valley)	*tek’-ke* *tek’-keh*	Merriam Powers
Kashaya Pomo/ Venaambakaiia/ Chwachamaju	Sonoma	Russian River (Fort Ross)	*ikh-shi* *khavena* *ṱ’ek:e*	Powers Powers Walker
Bodega Miwok/ Olamentke	Sonoma	Bodega Bay	*poo*	K&VW

Table 2.–Continued.

Tribe	Counties from North to South	Coastal Watershed or Bay/Channel	Indian Word	Source[1]
Mutsun Costanoan/ Tcho-ko-yem	Sonoma	Mission Sonoma (Sonoma Creek)	*timis* *ti-mis*	Powers Powers
Coast Miwok	Marin	Tomales Bay	*kah-ka’*	Merriam
Mutsun Costanoan	Santa Cruz	San Lorenzo River	*ha-mi-h’l, gupi* *gupi*	Heizer Powers
Rumsen Costanoan	Monterey	Salinas River	*sur-ris*	Heizer
Chumash Ineseno	Santa Barbara	Santa Ynez River	*che-puk’* *c’ɨpɨk* *tsəpək*	Merriam Applegate Harrington
Chumash Barbareño	Santa Barbara	Santa Barbara Channel	*ol-ko-osh* *c’əpək*	Powers Henry
Chumash Ventureno	Ventura	Santa Clara River Ventura River	*tsə’pək*	Henry
Gabrieleno/ Tongva	Los Angeles	Santa Ana River, Los Angeles River	*tooleva'che',* *toliiva'chi'* *'eveenxar*	Merriam
Luiseño	San Diego	San Luis Rey River	*'eveeenxal*	Harrington
Kumeyaay (Diegueno)	San Diego	San Diego River, Tijuana River	*epín*	Ware

[1] Applegate 2007, Harrington 1981, Heizer 1974, Henry 2012, Kostromitinov and Von Wrangell 1974 (K&VW), Merriam 1979, Powers 1877, Walker 2012, Ware 1968

colony of Fort Ross 26 km north of Bodega Head in today’s Sonoma County (Thompson 1896). G. K. Blok (1933:189-190) described the natural resources of the Russian settlement near “La Bodega”: “The rich, fertile soil and the abundance of seal, otter and beaver were the principal factors which favored this colonization.” Fort Ross official Kyrill T. Khlebnikov reported that, “…although it happens rarely, nonetheless one does sometimes see close to the American settlements American lions and amphibious animals such as river beavers and otters” (Dmytryshyn and Crownhart 1976:142). The “American settlements” were lands granted by Mariano Vallejo to three Americans to prevent Russian expansion southwest of Bodega (Gudde and Bright 2004). These lands included the coastal watersheds of Salmon Creek (Sonoma County), Americano Creek (Sonoma and Marin counties) and Russian River tributary Atascadero Creek (Sonoma County). In August 1839, Captain Cyrille Laplace of the *Artemise*, while travelling with Fort Ross manager Alexander Rotchev to the Khlebnikov Ranch (now the town of Bodega), reported unmistakable beaver sign. Laplace (Farris and Laplace 2006:54) said, “…we had stopped a moment by a little river [Salmon Creek] on the banks of which my traveling companion pointed out to me the former habitations of beaver, probably destroyed by the Indians to catch the rich prize that lay within.” Rotchev then explained how the Indians close the entrance to beaver lodges in order to catch and club them.

Alexander McLeod of the Hudson’s Bay Company’s reported in 1829, “The Country to the northward of Bodega is said to be rich in Beaver and no encouragement given to the Indians to hunt” (Nunis 1968b:34). In 1833, John Work led a Hudson’s Bay Company fur brigade from Fort Vancouver, Oregon to the Sonoma Mission (then Mission San Francisco Solano). On 5 April, Work writes of some American trappers who said that between the Russian establishment (Ft. Ross) and the Mission at Sonoma they “caught very few beaver” (Maloney and Work 1944:19). Although Maloney (1943) reports that John Work found no beaver on the coast from Fort Ross to Cape Mendocino, he turned east probably around Shelter Cove, and on crossing the Russian River on the way to Clear Lake wrote that there “are supposed to be beaver in the lower part of this Russian river” (Maloney 1944:30). This report is consistent with another Sonoma County account regarding S. H. Torrance, who settled on the Russian River across from Guerneville in 1856, and “engaged in trapping beaver and in hunting,” dressing the skins and making them into gloves for sale (Lewis Publishing Company 1889:573). Mariano Vallejo, on a return trip from Fort Ross to Mission Sonoma, provided another report of beaver in the Russian River watershed: “Four leagues away, more or less one finds Livantuligueni [Laguna de Santa Rosa], which forms in its basin great tulare lakes teaming with beaver. One can find here, as well as in other places, some vestiges [left by] the foreigners who hunted these animals” (Vallejo 2000:6). Vallejo (2000:5-6) described seeing Indians who by the “many hundreds were coming down from their hill country to bring to the fort [Ross] the hides of wild animals which they traded for tobacco, kerchiefs and liquor.”

Supplementary evidence of beaver in this region includes an historic newspaper account and also places beaver in the Russian River watershed: “Beavers are being trapped near Healdsburg” (Sacramento Daily Union 25 February 1881). The Southern Pomo, who inhabited the lower half of the Russian River, had a word for beaver: *ṱ’ek:e* (N. Alexander Walker, UC Santa Barbara, personal communication, 2011) and beavers in their oral legends (Luthin 2002). In addition there are words for beaver for virtually all the coastal tribes in this region (Table 2).

Documented records and supplementary evidence of beaver in coastal watersheds: San Francisco Bay Area counties.—Although Grinnell et al. (1937) and Tappe (1942) concluded that beaver were not present historically in the watersheds of the San Francisco Bay Area downstream /west of the Carquinez Strait, more recent reviews indicate that beaver “was one of the most valued of the animals taken,” and found in abundance (Skinner 1962:157). The earliest documentary record is from the second Anza Expedition sent to found the Presidio at San Francisco. When the expedition halted on the banks of the Laguna de los Dolores (the site of the future Mission Dolores) on 22 June 1776, Father Francisco Palóu wrote of the Indians, “The men go totally naked, although here and there one covers his shoulders with a sort of a little cape of beaver skins and pelican feathers” (Bolton and Palou 1930:390). Over fifty years later, in August 1827, Duhaut-Cilly (1834:243) observed the Indians at Mission Sonoma, “the young men are letting fly their arrows at the beaver...”.

In 1829, Alexander R. McLeod reported on the progress of the first Hudson’s Bay Company fur brigade sent to California, “Beaver is become an article of traffic on the Coast as at the Mission of St. Joseph [Fremont] alone upwards of Fifteen hundred Beaver Skins were collected from the natives at a trifling value and sold to Ships at 3 Dollars” (Nunis 1968b:34). Skinner (1962) cited Thomas McKay’s statement that in one year [1829] the Hudson’s Bay Company took 4,000 beaver skins on the shores of San Francisco Bay. In 1832, fur trapper Michel Laframboise travelled from the “Bonaventura River” (Sacramento

River) to San Francisco and then the missions of San Jose (Fremont), San Francisco Solano (Sonoma) and San Rafael Arcangel (San Rafael). La Framboise stated that the Bay of San Francisco abounds in beaver and that he "made his best hunt in the vicinity of the missions" (Maloney and Work 1943:343). While staying with General Vallejo, Sir George Simpson of the Hudson's Bay Company wrote in 1842, "Beaver and otter have recently been caught within half a mile of Mission San Francisco de Solano [Mission Sonoma]" (Simpson 1847:313). In 1840, the port of Alviso, Alameda County, shipped beaver pelts, cattle hides and tallow to San Francisco (Mehaffy 1999). In the 1840s Kit Carson was granted rights to trap beaver on Alameda Creek in the East Bay where they "abounded...from the mouth of its canyon to the broad delta on the bay" (MacGregor 1976:13, Gustaitis 1995:69). Skinner (1962:162) wrote that there is evidence that beaver were found historically "in small numbers at least" in Coyote Creek (Santa Clara County), and Sonoma Creek (eastern Sonoma County) and the Napa River (Napa County), although he did not provide primary sources. This is consistent with John Work's 1832 Hudson's Bay Company expedition account of beaver on Sonoma Creek in April (Maloney 1944), and on the Napa River in May (Maloney 1944, Grossinger 2012). Also William Trubody, who arrived in California in 1849, wrote of catching beaver on Napa Creek (upper Napa River) (Trubody and Camp 1937). Supplementary evidence of beaver in the San Francisco Bay Area include words for beaver in the Coast Miwok and Mutsun Costanoans at Mission San Rafael and Mission Santa Cruz (Table 2), but toponomastic references to beaver were not found.

Documentary records and supplementary evidence of beaver in coastal watersheds: Monterey, San Luis Obispo, Santa Barbara, Ventura and Los Angeles counties.—There are several reliable observer records of beaver in these watersheds, complementing the MVZ specimen from Sespe Creek. Before citation of accounts from the 18th century Spanish explorations up coastal California, the translation of the Spanish word for beaver merits discussion. The early diaries of the Spanish padres refer to both sea otter and beaver as "nutria," which in modern Spanish means "otter." However, the historian Herbert Eugene Bolton generally translates "nutria" as beaver, unless the words "nutria marinas" meaning sea otter, are used (Bolton and Font 1930, Bolton and Palou 1930). Further evidence of the use of the word "nutria" for beaver may be found in other records of the Spanish padres and government officials in the late 18th century (Garces and Coues 1900, Barrows and Wolfskill 1902). The misuse of "nutria" instead of "castor" for beaver by the late 18th century Spanish in the American southwest occurred because both Eurasian otter (*Lutra lutra*) and beaver (*Castor fiber*) were extirpated in Spain by the 17th century (Halley et al. 2012). The third possible translation of "nutria" as meaning river otter (*Lontra canadensis*) is unlikely in the accounts below, as this latter species' range is not considered to extend south of the Pajaro River watershed either historically or currently (Grinnell et al. 1937, Morejohn 1969, Zeiner et al. 1990).

On the second Anza Expedition, Father Pedro Font, on 24 February 1776, described coastal Chumash women wearing beaver capes (Bolton and Font 1930). Next, Font visited the San Luis Obispo Mission on 2 March 1776 and wrote of the Indians, "…the women wear capes of deer and beaver skin" (Bolton and Font 1930:272). Visiting the mission again on 23 April 1776, Font says that Father Cavaller "gave Senor Ansa…thirty-odd beaver skins…and gave me personally two choice beaver skins" (Bolton and Font 1930:454). In October 1818, English explorer Peter Corney sailed into

Monterey Bay on the *Santa Rosa*. He described the fauna of the Monterey area: “There are many bears, wolves, foxes, deer, beavers, etc…” (Corney and Alexander 1896:44).

John Peabody Harrington (1981) provided three documentary records (circa 1900) of beaver in two coastal watersheds of Santa Barbara County: Zanja de Cota Creek, a perennial tributary of the Santa Ynez River downstream from the modern day Cachuma Dam, and San Antonio Creek’s Los Alamos Valley in Los Alamos. Harrington also wrote that on the historic Rancho Santa Rosa on the Santa Ynez River, “There is Otter lake, commonly called in Sp. “Laguna de las Nutrias”… Otter lake is called in Indian “tšəpək isiyo,” meaning “Laguna de los Castores.” These animals are sometimes called las nutrias but incorrectly for they are really beavers. The otter is an ocean creature. The Indians call otter ’ukpaaš. The Sp. speaking people, however, Laguna de las nutrias. It should be called, however, Laguna de los Castores.” The modern Spanish word for beaver is “castor.”

In addition to the above documented observer records, there is significant ethnographic evidence that beaver lived in the region. On the Montgomery Potrero, the divide between the upper watersheds of the Cuyama and Sisquoc Rivers in eastern Santa Barbara County, a Chumash pictograph appears to represent a beaver (Lee and Horne 1978) (Figure 3). Additionally, the Hearst Museum in Berkeley has a Ventureno Chumash shaman’s rain-making kit, collected in 1948 when it was estimated at 100 years old by archaeologists Frank Fenenga and Francis A. Riddell. The kit was made from the skin of a beaver tail and kept in a tobacco sack. The shaman, Somik, was elderly when he lived at Fort Tejon in the 1870s (Phoebe Hearst Museum of Anthropology 1-84666). Timbrook (2007:180) relates a Chumash story where “a willow stick that had been cut by a beaver was thought to have the power to bring water. The Chumash would treat the stick with ‘ayip (a ritually powerful substance made from alum) and then plant it in the ground to create a permanent spring of water.” In addition the Barbareno and Ventureno Chumash had a Beaver Dance (Timbrook 2007). Finally, the coastal Chumash tribes had words for beaver or *Chipik*, spelled *č’əpək’* in Barbareno and *tšə’pək* in Ventureno (Timothy Henry, California State Fullerton, personal communication, 2012), and *č’ɨpɨk* in Ineseño (Samala) (Applegate 2007).

A documentary record of historic beaver presence on the Los Angeles River is Father Pedro Font’s description of the Beneme (Mojave) and Jeniguechi (San Jacinto branch of the Cahuilla) Indians of Mission San Gabriel Arcangel on 5 January 1776, “…the women wear a bit of deer skin with which they cover themselves, and likewise an occasional cloak of beaver or rabbit skin” (Bolton and Font 1930:178-179). In addition, the Tongva or Gabrieleno Indians of Mission San Gabriel had words for beaver *tooleva’che’, toliiva’chi’, ‘eveenxar* (Merriam 1979) (Table 2). Although not coastal watersheds, we found Indian words for beaver in the arid Antelope and Mojave Valleys, the Kitanemuk words *cɨpɨʔkɨ* and *hurist* (Anderton 1988), and the Mojave word *‘apen* (Munro et al. 1992), respectively.

Documentary records and supplementary evidence of beaver in coastal watersheds: Riverside, Orange and San Diego counties.—We found two documented historic records of beaver in San Diego County. The first is contained in an 1864 report on the region’s geography, geology, flora and fauna by David Hoffman, an early San Diego physician (Graves 1964). Hoffman (1864:154) stated, “Of the animal kingdom we have a very fair variety. The grizzly bear, the mountain sheep, the antelope, the black bear, the deer, the pole-cat, the beaver, the wild-cat, the otter, the fox, the badger, the hare, the squirrel, and cayotes[sic] innumerable.” The second record is contained in a 20 January 1889 historical newspaper article, "A beaver weighing forty pounds was on exhibition on Fifth street yesterday, having been trapped by Joe McCord, who lives north of the city. It was the largest specimen ever taken in this section" (San Diego Union 20 January 1889). The phrase "largest specimen" suggests that other beavers had previously been caught.

Supplementary evidence of beaver in San Diego County includes a creek named Beaver Hollow, tributary to the Sweetwater River (Durham 2001) (Figure 3). Beaver Hollow is named on the historical USGS Topo Map for Cuyamaca in 1903, 20 years before CDFG began beaver re-introductions in California (Goode 1903). The Kumeyaay (Diegueno) people had a word for beaver *epín* (Wares 1968).

DISCUSSION

Surprisingly few contemporary studies have been conducted with the primary goal of determining the historical geographic range of a particular species (Schwartz et al. 2007). As with the recent discovery of physical evidence of beaver in the Sierra Nevada (James and Lanman 2012), we located verifiable records extending the known historic range of beaver to the North Coast, the San Francisco Bay Area, and a coastal watershed in southern California. These records include museum specimens collected from Sespe Creek in Ventura County in 1906 and from Saratoga Creek in Santa Clara County in 1855, both collected by highly reputable zoologists. Additional physical evidence in the form of zooarchaeological specimens was located near coastal Randall Creek, south of the Mattole River in Humboldt County, and on Temescal and Alameda creeks, two San Francisco Bay tributaries in northern and southern Alameda County, respectively.

In four of the five study regions, we also found many documented records indicating that beaver were native historically. In contrast, only two reliable historical observer records were located in San Diego County. Similarly, many geographic place names including the word "beaver" were found but only one, Beaver Hollow Creek, located on the Sweetwater River watershed, was located in San Diego County. Cox et al. (2002) reported that faunal place names have high fidelity to their historical ranges and may be important indicators of their historical distribution. The relative lack of toponomastic references to beaver in San Diego County could relate to low species density, or the near extirpation of beaver prior to American colonization. Using the USGS GNIS to search for Spanish place names for "beaver" in coastal California using the contemporary Spanish "castor" or early colonial Spanish "nutria" (Garces and Coues 1900, Bolton and Font 1930, Bolton and Palou 1930) words for beaver yielded no references. We note that there is only a single beaver place name in the Central Valley of California, "Castoria", which is the historical name for La Framboise's 1832 "French Camp" in the San Joaquin Valley (Gudde and Bright 2004). This near absence of toponomastic beaver references in Central Valley watersheds occurs despite the fact that beaver have always been recognized as both native and numerous there. Aybes and Yalden (1995) posited that faunal place names are more common for charismatic species and noted that there are 200 places in Britain containing "wolf" but only 20 for "beaver."

Although not definitive evidence, we did find Indian words for beaver in two separate San Diego County tribes. In addition, the fact that beaver translocated in the 1940s still thrive on the San Mateo Creek and Santa Margarita River coastal watersheds suggest that habitat is quite suitable for beaver in San Diego County. In a documented record even farther south, Eugene Duflot de Mofras, the 19th century naturalist and explorer, described Baja California's mammalian fauna in 1841 as, "The wildcat, bear, coyote, maneless

American lion, wild goat, deer, polecat, ground squirrel, beaver, and fresh-water otter are the principal quadrupeds of Old [Baja] California" (Wilbur and De Mofras 1937:154). However, de Mofras' attribution of beaver and river otter to the Baja Peninsula may have been in reference to the Colorado River delta.

Evidence of habitat suitability for beaver in California's coastal watersheds includes the ongoing survival of the species in coastal watersheds since state-sponsored translocations 70–80 years ago. The 1923–1950 CDFG translocations to three quarters of California's 58 counties resulted in increases in the state's beaver population from 1,300 in 1942 (Tappe 1942) to 20,000 in 1950 (Anonymous 1950). Counties with coastal and Bay

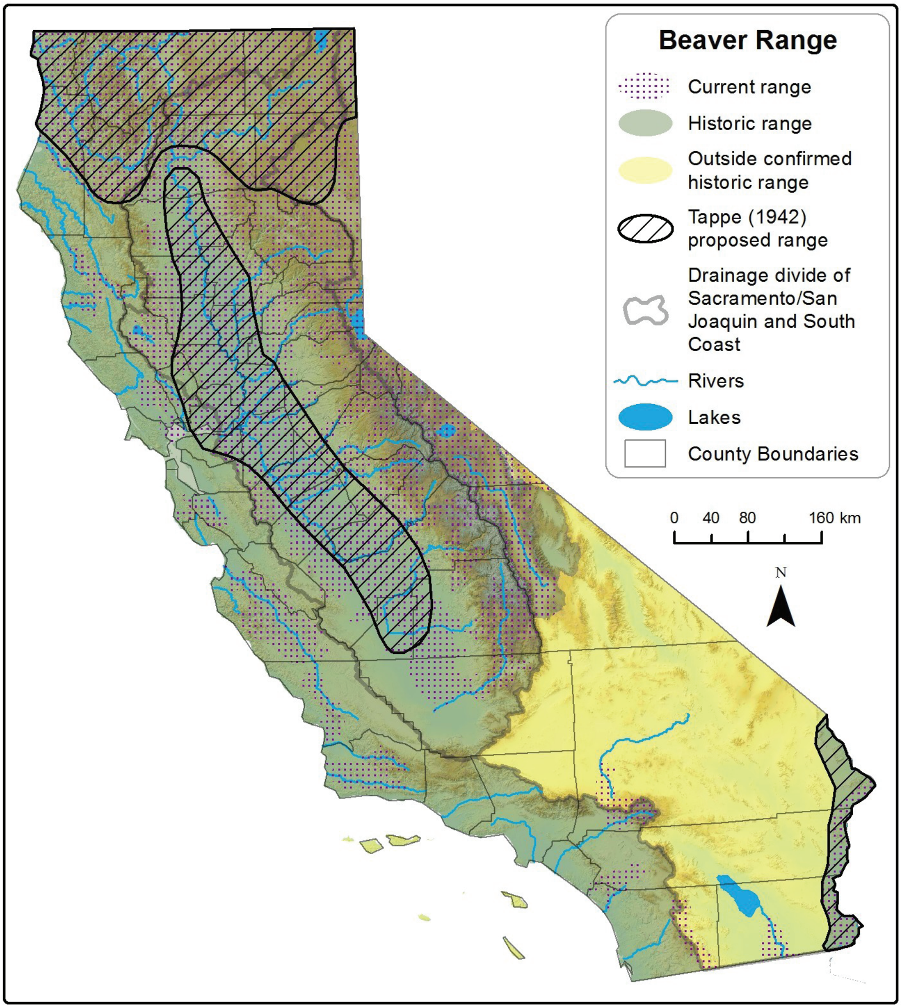

FIGURE 4.—Updated historical range map and current distribution of Castor *canadensis* in California. The current distribution was derived by combining ranges from CDFG (2005) and Asarian (2013) and conversion to 5th-field hydrologic units (watersheds) — except along the Mexican border where original CDFG polygons were retained — and removing Noyo River population in Mendocino County shown in the CDFG (2005) map, which has been extirpated; September 2013.

Area watersheds that received these beaver translocations included (north to south) Del Norte, Siskiyou, Humboldt, Mendocino, Marin, Napa, Contra Costa, Alameda, San Mateo, Santa Cruz, Monterey, San Benito, San Luis Obispo, Santa Barbara, Ventura, Los Angeles, Riverside, Orange and San Diego (Hensley 1946, Lynn and Glading 1949). Maps (CDFG 2005, Asarian 2013) of current beaver populations show that descendants of the translocated beavers or of undiscovered relict beaver populations continue to thrive in most of these coastal and Bay Area counties (Figure 4).

Although we found several important archaeological sites with subfossil beaver remains, the zooarchaeological record for beaver in California was relatively sparse. It is possible that beaver are not common in Indian middens because it was difficult to hunt the aquatic mammal. Although Indians hunted beaver from east to west across North America, beaver still thrived until the Indians were availed of steel traps from the American, Russian and European fur traders. Shimkin (1947: 268) wrote: "Originally, he [the beaver] could not be killed off at will, but the introduction of steel traps and tough axes made his defense of water, mud house, and ice quite vain." Bettinger (2010) noted that, "Although the beaver was fairly common all over western North America, it was not a key Native American resource (at least not west of the Mississippi) until historic times. The data show that beaver do not appear much in the archaeological records as a major element in the fauna. It begins to occur with increasing frequency in historic times undoubtedly as the result of western technology, most notably axes and Newhouse style beaver traps." The following report supports the idea that beaver were not a major food source although they were considered valuable to the Yuki tribe of the Middle Fork Eel river in Mendocino County. Anthropologist George Foster (1944:6) wrote, "A rich man owned hides of beaver, otter, mink, panther, bear and occasionally elk." Foster also included beaver in his list of animals not killed or eaten by the Yuki, suggesting that they were either difficult to catch, rare, or obtained only by trade. The nearby Huchnom tribe, who lived upstream of the Middle Fork Eel River along the mainstem Eel River and its tributaries, did consume beaver (Foster 1944:Appendix I): "netted in water, shot with bow; good eating; skin saved for quivers," although it is not clear if the aquatic mammal was a major food item. Difficulty hunting beaver would have ceased once maritime fur traders provided iron traps and guns to coastal tribes. The maritime fur trade stripped California's coast and the San Francisco Bay Area of fur-bearing mammals for four decades prior to the arrival of the first overland fur brigades led by Jedediah Smith in 1828 and John Work, Ewing Young and Michel Laframboise in 1832–1833. Therefore, the short interval between the arrival of the white man and the decimation of California's Indians would have left little time for beaver bones to be accumulated in Indian villages.

Why were documented observational records of coastal beaver difficult to find? As noted above, there was a maritime "California Fur Rush" that began 40 years before the Hudson's Bay Company and its meticulous diarists reached coastal California (Wikipedia Contributors 2013). Along with the Mission padres, ships from New England and Russia solicited the coastal Indians for furs, including beaver as well as otter, perhaps as early as the arrival of the first Boston ship to the West Coast in 1787 (Bolton and Font 1930, Nunis 1968b, Thompson 1896). Over a year before Jedediah Smith reached the mouth of the Klamath River in 1828, Peter Skene Ogden reported that his trappers encountered Indians four days from there who had "various trading articles from the American ships" (Ogden and Elliot 1910:215). While the furs lasted, the employment of Native Americans to obtain pelts was a continent-wide phenomenon (Dolin 2010). The Pilgrims began trading for beaver in 1621 and "The Bible and the Beaver were the two mainstays of the Plymouth Colony in its early years" (Dolin 2010:xiv). Just as the early colonies on the eastern seaboard employed the Indians in the rapid eradication of beaver, the maritime fur traders and European populations of California's earliest settlements likely provided the native population with the tools and the motive to hunt beaver to near extirpation on the West Coast. Thus, a largely unrecorded beaver hunt scoured California's coastal watersheds well before the first American and British overland fur hunters arrived with diaries in hand. It does not take long to exhaust a region of its furs. For example, sea otter and other fur bearing mammals were so depleted along the California's coast by 1841 that the Russian American Fur Company abandoned and sold Fort Ross just 30 years after it had been established (Thompson 1896).

Because the Spanish and Russian early settlements were limited to a relatively thin strip along California's coast and shipborne fur seekers could only trade with coastal Indians, beaver populations sufficiently inland from the coast were relatively unscathed until the American and Hudson's Bay Company overland fur brigades arrived. The widely travelled explorer Captain Thomas Farnham wrote in 1840 that beaver were very numerous in the Delta's "hundreds of small rushcovered islands" and that, "There is probably no spot of equal extent in the whole continent of North America which contains so many of these muchsought animals (Farnham 1857:383)." It seems probable that these superabundant inland beaver could have colonized coastal watersheds historically.

Although we could not demonstrate a uniform and homogeneous distribution of beaver throughout all of California's coastal watersheds, there is no reason to believe they would not have been able to occupy any suitable habitat. Traversing between watersheds is not difficult for beaver, since two- to three-year-old beavers may naturally disperse over 30 km by land or 50 km by stream (Muller-Schwarze and Sun 2003). This has been recently demonstrated in coastal northern California by the apparent overland recolonization of beavers from the Sonoma Creek watershed into the Russian River basin (Santa Rosa Creek) in 2011 and from the Outlet Creek watershed to the South Fork Eel River sub-basin in 2012 (Asarian 2013). It is also likely that beaver in California have, or will, use saltwater, i.e., San Francisco Bay and the Pacific Ocean, to move from one coastal stream to another, since beaver are well known to travel along coastlines and cross saltwater to colonize new territory such as islands off Alaska, British Columbia, and Washington (Anderson et al. 2009), or in Norway (Halley et al. 2013). This hypothesis is supported by recent reports of beaver constructing dams and lodges in oligohaline tidal marsh in the Skagit River delta of Puget Sound, and at higher densities than beaver in fluvial systems (Hood 2012).

While a great deal of historical information is presently digitized and our review of that material was exhaustive, additional information might be obtained with further research. More historical records of beavers may be located in California and Nevada state archives, college or university special collections, newly digitized historical newspapers, as well as Hudson Bay Company archives in Canada and the National Academy of Sciences in St. Petersburg, Russia. Naturalist collectors from various European countries visited California in the 19th and early 20th centuries (Beidleman 2006), but we did not search for North American beaver specimens in foreign museum collections. Searching archaeological specimens collected from sites associated with historical accounts and grossly catalogued as "small mammal" could yield additional physical evidence. Also, ground-penetrating radar (Kramer 2012) and radiocarbon dating of buried ancient beaver dams exposed by eroding, incised streams (James and Lanman 2012) are novel approaches to finding physical evidence of historic beaver yet to be employed in coastal watersheds. Additional research analyzing undigitized zooarchaeological records in California could provide additional evidence.

Using modern data acquisition and investigative techniques, we have extracted and synthesized multiple lines of evidence (physical, ethnographic, historical, as well as habitat suitability) indicating that beaver were historically widely distributed from extreme northern to southern coastal California, probably as far south as San Diego County. Deciphering the historical ecology of California is particularly challenging given that the State's first museum, the CAS, was not founded until 1853. The only California museum with a 19th century zoology collection, it was destroyed (except for a single cartful of specimens) in the 1906 San Francisco earthquake and fire (Lanman et al. 2012).

Grinnell et al. (1937) and Tappe's (1942) research was initiated almost 100 years after the Hudson's Bay Company in 1843 stopped sending fur brigades to California (Nunis 1968a:169) and the Russians abandoned Fort Ross for lack of furs in 1841 (Thompson 1896). Before statewide translocations of beaver from the 1920s to 1950s, California beaver were nearly extinct except for their last refuges, the great marshes of the Central Valley's Sacramento-San Joaquin River Delta, the Colorado River in southeastern California, and the Pit River in northeastern California. These factors likely limited the abilities of Grinnell et al. (1937) and Tappe (1942) to accurately reconstruct the historical distribution of beaver. In addition, it is not clear whether Grinnell was trying to determine the historical range of beaver, or simply trying to establish the current range of beaver in the early 20th century, since he relied heavily on local MVZ records plus observations from trappers and rangers mainly within the decade prior to his 1937 publication, *Fur-bearing Mammals of California*. Consistent with our findings, recent investigations significantly extended the historical ranges established by Grinnell et al. (1937) for other mammals in California, such as the ringtail (*Bassariscus astutus*) (Orloff 1988) and gray wolf (*Canis lupus*) (Schmidt 1991).

Neither Grinnell et al. (1937) nor Tappe (1942) explored coastal watersheds looking for evidence of beaver, even when presented with physical evidence that beaver were present in these systems (e.g., Sespe Creek). Tappe (1942) limited his field surveys to areas where beaver were known to exist. Most beaver observation points in Tappe's (1942) range map are based on direct personal observation or observations of his living colleagues. Thus Tappe's (1942) range map is perhaps more accurately described as a map of the remnant strongholds of California beaver in the early 20th century, after more than 100 years of unregulated commercial trapping and conversion to agriculture of alluvial valley bottoms where prime beaver habitat was located.

Considering the role of beavers as allogenic ecosystem engineers (Jones et al. 1994), establishing the aquatic mammal as native to California's coastal and San Francisco Bay watersheds may be of particular importance. Studies conducted and reviewed by Pollock et al. (2003, 2007) in semi-arid Western habitats, have found that re-introduction of beaver can rapidly aggrade stream sediments, elevating incised channels and reconnecting them to their floodplains, ultimately converting formerly incised xeric valleys into gently sloping ones with more abundant riparian vegetation.

There has been a tendency to underestimate the influence of beaver on ecosystems (Pollock et al. 1994). The presence of beaver has been shown to increase bird, fish, invertebrate, amphibian and mammalian abundance and diversity (Naiman et al. 1988, Rosell et al. 2005). As an integral part of the ecosystem of historic California, beaver may have benefitted many threatened species. Colonization of southern California streams by beaver is associated with increased riparian habitat, especially dense shrubby willow, which is critical habitat for federally endangered southwestern willow flycatcher (*Empidonax traillii extimus*) (Finch and Stoleson 2000) and least Bell's vireo (*Vireo bellii pusillus*) (Muller-Schwarze and Sun 2000) populations. There is evidence that beaver dams provide important refugia for endangered California red-legged frogs (*Rana draytonii*) (Alvarez et al. 2013) and western pond turtles (*Actinemys marmorata*) (Alvarez et al. 2007, Lovich 2012). Similarly, beaver ponds and bank burrows appear to provide refugia for endangered tidewater goby (*Eucyclogobius newberryi*) (USFWS 2005). In a historical ecology study of the San Gabriel River in southern California, it was estimated that since 1870, 86% of historical wetlands have been lost especially in the lower floodplain (Stein et al. 2010). In contrast, in the tidal Copper River delta beaver activity has been shown to increase freshwater surface area and to prevent seasonal drying of the floodplain (Cooper 2007). Allowing beaver to recolonize their historic range could reverse the ongoing loss of wetland habitat in California's coastal watersheds.

Documenting that beaver were historically extant in California's coastal streams may have important implications for declining salmonid populations. Pollock et al. (2003) reviewed reports of beaver "perennializing" formerly seasonal streams, and Tappe (1942) noted summer flows in several streams in northern California increased after beaver colonized upstream reaches. Gallagher et al. (2012) reported on limiting factors for coho salmon (*Oncorhynchus kisutch*) populations in coastal northern California streams and concluded that winter habitat was critically important, recommending adding substantial amounts of large wood to increase pool habitats, improve stream shelter in high winter flows, and reconnect the stream to floodplain habitats. Beaver impoundments also increase winter habitat, and whereas large woody debris may be associated with coho salmon smolt production (SPP) of 6-15 individuals, SPP per beaver dam ranges from 527 to 1,174 fish, indicating that promotion of beaver populations may have an 80-fold more positive impact (Pollock et al. 2004). Salmon from Alaska to Oregon have clearly evolved in sympatry with beaver and these anadromous fish ascend coastal streams with beaver dams, the latter often overtopped or breached by high winter flows. Coho salmon can jump dams as high as 2 meters (Bryant 1984, Powers and Orsborn 1986). Gard (1961) showed that rainbow trout (*Oncorhynchus mykiss*) can also cross beaver dams and in both directions, with some accounts of trout crossing a series of 14 dams (Pollock et al. 2003). Hood (2012) reported that beaver dams tripled juvenile Chinook salmon (*Oncorhynchus tshawytsha*) survival in brackish tidal marshes in the Skagit River delta of Puget Sound. Today California's coastal beaver are widely regarded as the non-native survivors of twentieth century translocations, and when they cause flooding problems or fell trees, depredation permits are often provided. Understanding beaver as native to coastal ecosystems may impact this decision-making.

Based on the results of our study, coupled with the recent evidence of historic beaver in the Sierra Nevada (James and Lanman 2012, Lanman et al. 2012), and the long-established nativity of beaver to the Central Valley, the Colorado River and California's northern rivers (Tappe 1942, Grinnell et al. 1937), we conclude that the historic range of beaver included most of California, except the streamless portions of the southern deserts (Figure 4). We consider the historic presence of beaver in the perennial streams in California's deserts (e.g., the Mojave River) unverified, but highly probable, given their current presence in these systems (Lovich 2012) and the historic and current presence of beaver in similar desert streams in Arizona (Allen 1895).

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Desert tortoise road mortality in Mojave National Preserve, California

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Direct impact by motor vehicles is a known threat to the federally- and California state-listed Agassiz's desert tortoise (*Gopherus agassizii*). Tortoise sign adjacent to paved roads is depressed, indicating that roads can have a population-level effect extending up to 400 m away from the road edge. We found that temporarily erected warning signs equipped with flashing lights had no effect on driver awareness of a potential tortoise on the road and that population depression adjacent to roads with lower speeds and greater driver awareness was similar to roads with heavier traffic traveling at higher speeds and lower driver awareness. The management implications are that slowing traffic with lower posted speed limits and increased law enforcement and improving driver awareness may not reduce impacts to tortoise populations.

Key words: desert tortoise, *Gopherus agassizii,* Mojave Desert, Mojave National Preserve, mortality rate, road ecology, road kills

Approximately 216 km of paved, two-lane roads bisect 312,605 ha of critical habitat designated for the desert tortoise (*Gopherus agassizii*) in Mojave National Preserve. Sections of Kelbaker, Kelso-Cima, Morning Star Mine, and Ivanpah roads (Figure 1) form a route between Las Vegas, Nevada, and inland cities in Southern California. Direct impacts by motor vehicles are among known causes of mortality for desert tortoise. In the central Mojave Desert, Boarman and Sazaki (1996) estimated at least one tortoise killed per 3.2 km of road per year along a heavily traveled road. They also reported a zone of depressed tortoise density extending outwards up to 800 m from the road edge. Other work has indicated that the depressed densities can extend 1,600 m (Nicholson 1978), 3.2 km (Karl 1989), or even 4.6 km (von Seckendorff et al. 2002). A road-edge effect of depressed tortoise density occurs along the paved roads through Mojave National Preserve, similar to the heavily traveled California State Route 58 studied by Boarman and Sazaki (1996), but with the additional finding that roads with more traffic can also have a demographic consequence (Nafus et al. 2013). Comparing roads with 60 or fewer vehicles per day with those carrying several hundred or more vehicles per day, Nafus et al. (2013) reported that live tortoises tended to be significantly smaller adjacent to the heavily traveled roads. Loss of adult tortoises to road mortality at an unsustainable rate could severely impact and, ultimately, drive local populations to extinction (Congdon et al. 1993).

Tortoise barrier fencing constructed parallel to roads is effective in reducing mortalities of tortoise and other species, while culverts under roads appear to mitigate the effects of habitat fragmentation (Boarman 1995). Construction and maintenance costs, however, often preclude barrier fencing as an attainable action by resource management agencies. Additionally, concerns have been raised about tortoises becoming trapped by barrier fencing (Wilson and Topham 2009). Roadside fencing detracts from the aesthetics of areas set aside for scenic beauty, such as national parks, whereas fences built farther from roads may result in substantial new disturbance during construction and loss of habitat. Other management actions have been suggested for reducing the impact of roads, including increased law enforcement to reduce traffic speeds, posting warning signs, and education to heighten public awareness with the intent of improving driver attention (National Park Service 2002, U.S. Fish and Wildlife Service 2011).

Our first objective was to estimate the loss of desert tortoise to motor vehicle impacts on paved roads and determine if larger-scale effects, such as road-edge population depression, were occurring in the Preserve. Our second objective was to investigate the effectiveness of management actions other than construction of barrier fencing, such as improving driver awareness through warning signs. Specifically, we looked for an improvement in driver response to a model tortoise at the road edge after installation of warning signs and compared road edge effects between heavily and moderately traveled paved roads. Traffic on the less-traveled road also proceeded at a lower speed, allowing us to infer, *a posteriori*, potential improvements to be obtained by slowing traffic.

Materials and Methods

Study area.—Mojave National Preserve is located in northeastern San Bernardino County, California, and contains portions of the Ivanpah and Fenner Desert Wildlife Management Areas (DWMA), designated as critical habitat for the desert tortoise (U.S. Fish and Wildlife Service 2011), and that are separated by a north-south trending mountain range. A series of two-lane paved roads carry heavy traffic between Las Vegas, Nevada, and the Palm Springs, California, area through the Ivanpah DWMA, whereas paved roads in the Fenner DWMA dead-end or convert to gravel surfaces. We selected a straight section of Morning Star Mine road in the Ivanpah DWMA and Essex road in the Fenner DWMA (Figure 1) as representative heavily and moderately traveled roads in desert tortoise habitat, respectively. Both sections were in creosote bush mixed scrub habitat (Thomas et al. 2009) ranging in elevation between 950–990 m and 810–850 m, respectively. Gravel roads between Kelso-Cima Road and Essex Road and between Ivanpah Road and Lanfair Road are the only connections between these two areas, which we treated as independent.

Traffic monitoring.—We collected data on traffic density and speed using a traffic radar device (StealthStat, Kustom Signals, Inc., Chanute, KS) mounted on a pole on the northwest side of Morning Star Mine road and on a post on the southwest side of Essex road. The traffic monitoring device was mounted along a straight and fairly level stretch of highway and data were collected for 2,515 hours on Morning Star Mine road and 2,143 hours

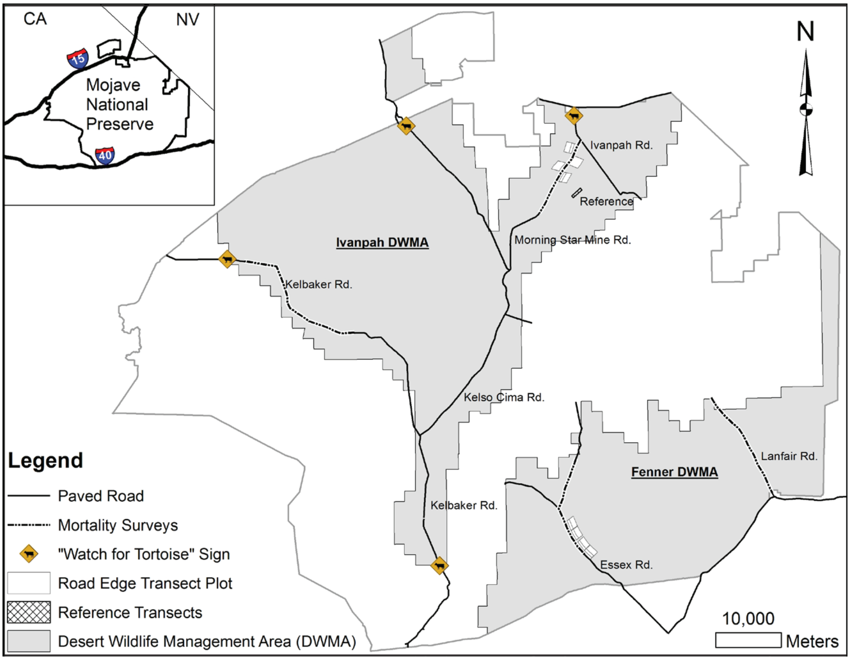

FIGURE 1.—Mojave National Preserve is shown with the Ivanpah and Fenner Desert Wildlife Management Areas (DWMA) that are designated critical habitat for the threatened desert tortoise. Plots for transects 0, 400, 800, and 1,600 m from road edge are shown in white on Morning Star Mine and Essex roads along with reference transects 3.3 km from Morning Star Mine Road. Sections of roads that were surveyed for evidence of road mortalities are indicated by a dashed line. The location where temporary, seasonal warning signs with flashing yellow lights were erected are indicated where paved roads enter designated tortoise habitat. San Bernardino County, California, 2008–2010.

on Essex road during the months of April and May, and September, and October, which are the desert tortoise active seasons. Speed was recorded for each passing vehicle and the number of vehicles counted per 15 minute interval, but with no discrimination of travel direction. Thus, the data indicate speed distribution and traffic density in both directions combined. Density of vehicles on each road was estimated by averaging over days after omitting partial days from the beginning and end of each sampling period.

Road edge effect.—We implemented transect surveys for tortoise sign following the method of Boarman and Sazaki (2006) at 0, 400, 800, and 1600 m from pavement edges at four plots each along Morning Star Mine and Essex roads plus four reference transects in the Ivanpah DWMA approximately 3.3 km from Morning Star Mine road, the nearest paved road (Figure 1). On each transect the Global Positioning System (GPS) coordinates were recorded for tortoise burrows, scat, carcasses, and live tortoises. Tortoise sign was corrected by combining adjacent sign (e.g. live tortoise inside a burrow) according to the methodology of Boarman and Sazaki (2006). We then used R 2.14.1 (R Development Core Team 2011) to conduct analysis of covariance on square root transformed total corrected tortoise sign with distance, road, and plot as potentially explanatory variables. We also analyzed the untransformed total sign on each transect using the generalized linear model procedure in R 2.14.1 (R Development Core Team 2011) with quasipoisson errors to account for overdispersion.

Effect of road signage.—We investigated the effect of warning signs by observing the response of motorists to a model tortoise placed at the road edge (Figure 2). Two concealed observers noted any behavior indicating that the driver of the vehicle, or the first in a closely spaced group of vehicles, had noticed the tortoise model, such as brake lights, slowing, swerving or stopping. Both observers were close enough to see head movements of the driver. "Watch for Tortoise" warning signs (Figure 3) were erected on all paved roads entering the Ivanpah DWMA boundary (Figure 1) in the spring of 2009, and were equipped with flashing yellow lights in the spring of 2010. We observed motorists for 37.2 hours on Essex road and 13.8 hours on Morning Star Mine road during the desert tortoise active seasons prior to setting up the warning signs; 13.7 hours on Essex road and 6.4 hours on Morning Star Mine road after signs were erected; and 26.9 hours on Essex road and 4.5 hours on Morning Star Mine road after the warning signs were equipped with flashing yellow lights. The longer observation times on Essex road were required to observe a comparable number of vehicles. Proportion of drivers responding to the tortoise model was analyzed by two-way factorial analyses of deviance with road and year as potentially explanatory factors using the generalized linear model procedure in R (R Development Core Team 2011) with binomially distributed errors.

FIGURE **2.**—Placement of the tortoise model was in a visible location at the pavement edge along a straight and relatively flat stretch of paved road. The tortoise model was sufficiently realistic as to be mistaken for a real tortoise at close range. Mojave National Preserve, San Bernardino County, California, 2008–2010.

Figure 3.—"Watch for Tortoise" warning signs were erected along paved roads at the entrance to desert tortoise critical habitat in 2009 and equipped with flashing yellow lights in 2010. Mojave National Preserve, San Bernardino County, California, 2008–2010.

Road mortality surveys.—Paved roads in the Ivanpah and Fenner DWMAs were divided into sections, each 1,610 m in length, for a total of 9 on Essex road, 13 on Kelbaker road, 10 on Lanfair road, and 8 on Morning Star Mine road. The difference in the number of sections per road was related to the length of road intersecting tortoise habitat and past experience of where tortoises were most commonly seen. At the beginning of each of 31 field-days over the course of 3 years, the road to be surveyed was randomly selected then sections along that road were randomly selected and surveyed according to the time available in the day. Selected stretches were inspected by walking, and we searched from the centerline to 5 m away from each road edge on both sides of the road for evidence of road mortalities of tortoise and other species. If the section had been previously surveyed, only evidence of new mortalities was recorded. We used the generalized linear model procedure in R 2.14.1 (R Development Core Team 2011), with quasipoisson errors to account for overdispersion, to conduct analysis of deviance with number of mortalities per transect as the dependent variable and road class with four levels of traffic density (i.e., vehicles per day) as a potential explanatory factor.

RESULTS

Traffic patterns.—Morning Star Mine road receives heavier traffic than Essex road because it connects Las Vegas, NV, to inland communities of Southern California, such as Palm Springs, Yucca Valley, and the Marine Corp Air Ground Combat Center at 29 Palms. Essex road intersects an isolated stretch of I-40 and ends at Mitchell Caverns State Park. Traffic also turns north off Essex road to reach the Hole in the Wall Visitor Center, Campground, and Interagency Fire Center. Mean speed on Morning Star Mine road was 112.8 ± 0.09 km/h (1 *SE*, $n = 38{,}830$) with a maximum recorded speed of 193.1 km/h compared to a mean speed of 96.4 ± 0.18 km/h (1 *SE*, $n = 8{,}241$) on Essex road with a maximum recorded speed of 180.2 km/h. The difference in means was significant ($t = 80.0$, $df = 12{,}839$, $P < 0.001$). The mean traffic density on Morning Star Mine road (370.6 ± 15.1 vehicles per day, 1 *SE*, $n = 91$) also differed ($t = 17.9$, $df = 108$, $P < 0.001$) from the mean traffic density on Essex road (87.6 ± 4.8 vehicles per day, 1 *SE*, $n = 88$). Over this period of observation, traffic densities were higher than data available from the County of San Bernardino (2013), which reported 325 vehicles/day on Morning Star Mine road and 59 vehicles/day on Essex road. County of San Bernardino traffic data for Kelbaker road was 183 vehicles/day south of Interstate 15 near Baker, California. Data on Lanfair road north of Goffs, California, was not available from the County of San Bernardino, but our observations indicated a low traffic volume, similar to the estimate of Nafus et al. (2013), of 35 vehicles per day.

Road edge effect.—Analogous to other work (e.g. Boarman and Sazaki 2006, Nafus et al. 2013), we saw a significant decrease in tortoise sign with proximity to roads (distance from road effect: $F_{1,34} = 21.2$, $P < 0.001$ for square root transformed data, and $F_{1,34} = 19.8$, $P < 0.001$ for total sign), including the background reference transects located 3.3 km from Morning Star Mine road (Figure 4). When the reference transects were omitted from the analysis, the distance effect was weak using the square root transformation ($F_{1,30} = 3.0$, $P = 0.09$), and not significant analyzing the counts directly ($F_{1,30} = 1.7$, $P = 0.2$). The difference in tortoise sign depression between Morning Star Mine and Essex roads was not significant ($F_{1,30} = 0.4$, $P = 0.55$).

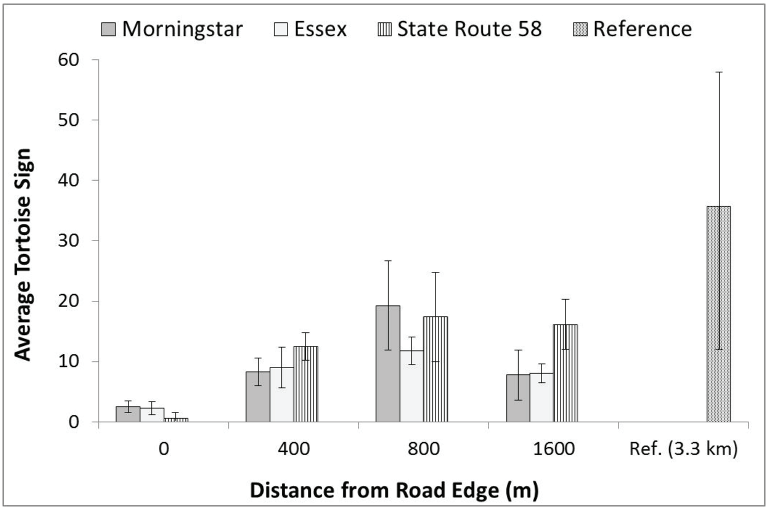

FIGURE 4.—Average tortoise sign (total count corrected by combining adjacent sign) for transects 0, 400, 800, and 1,600 m from road edge are shown comparing results from Morning Star Mine Road, Essex Road, California State Route 58, and reference. Error bars are one standard error ($n = 4$). Data for State Route 58 are from Boarman and Sazaki (2006) and are shown for comparison with data from Mojave National Preserve, San Bernardino County, California, 2008–2010.

Effect of road signage.—There was no noticeable change in driver behavior after erection of warning signs at the entrance to the DWMAs on Morning Star Mine road (year category effect: $\chi^2_{15} = 41.3$, $P = 0.4$). With no warning signs on Morning Star Mine road, 7 out of 195 (3.6%) motorists responded to the model; when warning signs were erected, 6 out of 104 responded (5.8%); and when the warning signs were equipped with bright flashing yellow lights, 7 out of 206 (3.4%) responded. Driver behavior did, however, differ significantly between Morning Star Mine and Essex roads (road category effect: $\chi^2_{16} = 10.8$, $P < 0.001$). On average 4% of the motorists on Morning Star Mine road reacted to the tortoise model compared to 14% on Essex road, with no significant variation year to year or with or without warning signs.

Road mortality surveys.—The first survey of each of the 40 sections distributed along 4 roads showed evidence of road mortalities such as animal remains, bloodstains on asphalt, scattered plastron and carapace bones and scutes per transect of 0.7 ± 0.24 (1 *SE*, $n = 9$) on average for Essex road, 1.0 ± 0.42 (1 *SE*, $n = 13$) on Kelbaker road, 0.2 ± 0.13 (1 *SE*, $n = 10$) on Lanfair road, and 1.0 ± 0.38 (1 *SE*, n = 8) on Morning Star Mine road. The difference between roads was not significant (road class effect: $F_{3,36} = 1.76$, $P = 0.17$). Over the course of 3 years, 135 surveys were completed on transects randomly selected from the 40 sections, which resulted in an average per transect of 0.66 ± 0.13 (1 *SE*, $n = 41$) on Essex road, 0.81 ± 0.36 (1 *SE*, $n = 16$) on Kelbaker road, 0.69 ± 0.19 (1 *SE*, $n = 36$) on Lanfair road, and 0.76 ± 0.16 (1 *SE*, $n = 42$) on Morning Star Mine road. Again, the difference between roads was not significant (road class effect: $F_{3,131} = 0.11$, $P = 0.95$). Given that the time interval between surveys of the same road section was typically several months and road mortality evidence disappeared over a period of a few days to weeks, these repeated surveys did not give any indication of the temporal rate of road mortalities. Anecdotal observations by park visitors and staff, however, indicated that between 0 and 10 tortoises were killed on roads per year in the Preserve from 2002 through 2012 (average = 5.3 ± 1.1 tortoises per year, 1 *SE*, $n = 11$).

DISCUSSION

Desert tortoise population depression adjacent to roads has been well-studied and the effect found to extend from less than 175 m (Baepler et al. 1994) up to 4.6 km (Von Seckendorff Hoff and Marlow 2002). The results presented here (Figure 4) show a pattern of depressed tortoise sign similar to California State Route 58 (Boarman and Sazaki, 1996), extending outwards from the road edge to less than 400 m (Nafus et al. 2013). Our small sample size likely weakened the significance of the road-edge effect as compared with Nafus et al. (2013) and limitation of reference transects to only one area of the Ivanpah DWMA failed to adequately characterize the undisturbed background level. When compared to the results from California State Route 58 and the work of Nafus et al. (2013) on roads with high and intermediate traffic volume (M. Nafus, University of California, Davis, personal communication) in the Preserve, however, the similar patterns suggest an important management implication. Zones of desert tortoise population depression can apparently form along roads with moderate traffic density and lower speeds similar to those with heavier traffic and higher speeds. Thus, slowing traffic with lower speed limits and increased law enforcement may not benefit the adjacent tortoise population.

Much of the published literature on automobile and wildlife impacts involves deer, likely due to the danger posed to motorists. Lehnert and Bissonette (1997) found permanent passive and active signs located at mule deer crosswalks had no influence on long-term driver response. Though drivers slowed down initially, immediately after installation of signs, they quickly grew accustomed to their presence. Many of the drivers were commuters that traveled the road every day. Curtis and Hedlund (2005) found that temporary passive signs and active signs (e.g. with flashing lights) were promising methods for which more information was needed. They also indicated that general education, long-term passive signs, and lower speed limits appear to be ineffective. A comprehensive review of the literature (Danielson and Hubbard 1998) for the Iowa Department of Transportation concluded that passive warning signs were ineffective because drivers became complacent (Putman 1997). Pojar et al. (1975) found that lighted, animated signs did slightly reduce vehicle speed. Strongly enforced lower speed limits may reduce deer-vehicle collisions (Romin and Bissonette 1996). Intermittently lighted warning signs were recommended by Bruinderink and Hazebroek (1996), but Danielson and Hubbard (1998) found no scientific evidence of their effectiveness. We were motivated to undertake this study by recommendations in the Preserve's General Management Plan (National Park Service, 2002). The plan suggested that entrance signs and information kiosks, temporary signing, staffing of heavily used entrances on busy weekends, and temporary adjustment of speed limits would heighten awareness and slow traffic with the implication that heightened driver awareness and slower traffic would reduce tortoise mortality. Initially we set out to see if warning signs, temporarily erected during the tortoise active season and equipped with flashing yellow lights to improve their visibility, would have any noticeable effect on driver behavior. They did not and, in the absence of not improving driver awareness, they are unlikely to reduce tortoise impacts in any other way. Drivers on Essex road were on average about 3.5 times more likely to notice the tortoise model on the edge of the road than drivers on Morning Star Mine road, suggesting that they were more aware. Traffic on Morning Star Mine road proceeded at a mean speed 16.3 km/h faster than traffic on Essex road, yet the difference in depression of tortoise sign adjacent to the two roads and the difference in encounter rate of mortality remains between the two roads were not significant. This suggests that, even if warning signs and other measures did improve driver awareness and traffic was slowed, the effect on tortoise populations might not be noticeable.

Over a period of 11 years on average 5.3 tortoises were reported killed annually on paved roads in the Preserve. These observations were anecdotal and depended upon an observer being in that particular place at the right time. Inspections of recent road kills indicated that remains are rapidly scavenged and most evidence effectively disappears within a few days. During a survey in late April along Lanfair road, for instance, a freshly crushed carcass was encountered on the road centerline. Since the surveyor had been at this location earlier in the day, the time of mortality was known to have occurred between 1400 and 1515 Pacific Daylight Time. The carcass was revisited approximately 21 hours later and found to be mostly pieces scattered within a radius of 2 m from the point of impact. A small section of carapace scutes was found approximately 11 meters away. Approximately 92 hours after death the only evidence remaining on the road was a faded stain at the point of impact, two withered limbs approximately 8 meters from the point of impact, and a handful of centimeter-sized pieces of carapace and plastron. The remains were scattered over a radius of approximately 12 m from the point of impact and a piece of carapace dome was found approximately 22 m away. A recently (same day) killed adult male tortoise was encountered on Morning Star Mine Road during a mid-April survey the following year and a somewhat older carcass was found along the same road the previous year, both scavenged and the remains scattered over a period of a few days. Thus, the estimate of 5.3 tortoise road mortalities per year should be considered a minimum.

Modeling work by Congdon et al. (1993) showed that, because of delayed sexual maturity and high neonatal mortality, long-lived chelonians are unable to sustain increased mortality above natural levels and that an adult female mortality rate above 2% per year over natural deaths is not sustainable. Tortoise density in the Ivanpah DWMA may be in the range estimated for the Eastern Mojave Recovery Unit ($0.75 < 2.2 < 6.67$ tortoises/km^2, 95% *CI*) and Fenner DWMA in the range of the Colorado Desert Recovery Unit ($1.45 < 2.4 < 3.95$ tortoises/km^2, 95% *CI*) (U.S. Fish and Wildlife Service 2012). For the area of the Ivanpah DWMA (1,943 km^2) and Fenner DWMA (1,133 km^2) within the Preserve, using the lower 95% confidence interval bound, we could expect an estimated 1,550 adult female tortoises to be present. Two percent above the unknown natural mortality rate would be approximately 31 adult females per year. These rough estimates, assuming equal sex ratios in the population and killed on roads, suggest that direct motor vehicle impacts may account for 9% of the sustainable non-natural mortality rate.

Our results corroborate previous work indicating that motor vehicle traffic on paved roads through Mojave National Preserve poses a threat to the desert tortoise. In addition, we present new results showing that warning signs have no noticeable effect on driver behavior and that slowing traffic and raising driver awareness may be inadequate mitigations. Road barrier fencing, as prescribed in the Revised Recovery Plan for the Mojave Population of the Desert Tortoise (U.S. Fish and Wildlife Service 2011) may introduce other concerns (Nafus et al. 2013) and be too costly to be used effectively at the scale of the entire Preserve. Monitoring should be continued and mitigation, including construction of barrier fencing, should be implemented in an experimental framework with adequate controls. Management actions, such as road barrier fencing should, however, only be implemented with a period of monitoring before construction sufficient in order to allow for testing of hypotheses that address both the potential adverse as well as beneficial effects. Future research questions of interest to managers will likely address optimizing the location of road segments for barrier fencing; location and utilization of culverts or underpasses by numerous species; effectiveness of shorter segments of barrier fencing entirely within tortoise habitat; and, how to deal with the end of barrier fencing within tortoise habitat to avoid trapping animals on a fenced road. Additional considerations include construction techniques to minimize maintenance, minimization of the visual presence of fencing, and minimizing habitat disturbance during construction.

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Observations on the ectoparasites of elasmobranchs in San Francisco Bay, California

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There has been considerable documentation of the ectoparasites of elasmobranchs along the Pacific Coast (Moore 1952; Cressey 1966, 1967, 1968; Russo 1975; Robinson 1982; Love and Moser 1983; Moser and Sakanari 1985; Deets and Dojiri 1989; Benz et al. 2002, 2003). While some of this information is specific to leopard shark (*Triakis semifasciata*) and brown smoothhound shark (*Mustelus henlei*) along the California coast, little is known concerning frequency of occurrence of ectoparasites on these and other inshore sharks in San Francisco Bay.

Between 1970 and 1996, I captured 3,790 sharks and rays through the use of long-line, otter trawl, and rod and reel fishing efforts, primarily from South San Francisco Bay. All sharks captured were sexed and measured, and most were checked for parasites over the full length of the body including gill tissues, and buccal and nare cavities, noting location of attachment for each species of parasite. Parasites initially were separated into labeled vials and preserved in 70% ethyl alcohol for later identification by R. Cressey (copepods), E. Burreson (leeches), and J. Sakanari (isopods) who presumably deposited the specimens in their respective collections. I retained a duplicate set to aid field identifications.

Following publication of initial observations of ectoparasites (Russo 1975; *n*=900), I focused on an analysis of an additional 575 sharks between 1976 and 1996, including leopard sharks (*n*=362), brown smoothhound sharks (*n*=130), soupfin sharks (*Galeorhinus galeus*) (*n*=41), and spiny dogfish sharks (*Squalus suckleyi*) (*n*=42). All sharks examined appeared normal in body form and coloration, with no apparent relationship between the number and species of parasites present and the general health of the host sharks.

Male leopard sharks were infected more often than females, with 130 (58.8%) of the 221 males infected compared to 45 (31.9%) of the 141 females with parasites. Conversely, 91 of the male leopard sharks (41.2%) and 96 of the of the female leopard sharks (68.1%) were without parasites. On average, 51.7% of the 362 leopard sharks examined had no ectoparasites.

The copepods *P. bicolor* and *A. oblongus* were the most common crustacean ectoparasites, occurring on 106 male and 54 female leopard sharks. The order of frequency of parasites on leopard sharks (Table 1) was *A. oblongus* (27.3%), *B. lobata* (24.1%), *P. bicolor* (16.8%), *E. coleoptratus* (9.4%), *L. galei* (3.6%). Some individual leopard sharks supported more than 20 *P. bicolor* on both sides of the caudal edges of the first dorsal fin, and occupied nearly every attachment site available.

Table 1.—The occurrence of external parasites *Branchellion lobata* (Bl), *Achtheinus oblongus* (Ao), *Pandarus bicolor* (Pb), *Echthrogaleus coleoptratus* (Ec), and *Lernaeopoda galei* (Lg) on leopard sharks and brown smoothhound sharks from San Francisco Bay, California, 1976–1996.

	Leopard sharks (*n*=362)				Brown smoothhound sharks (*n*=130)			
	Females (*n*=141)		Males (*n*=221)		Females (*n*= 92)		Males (*n*=38)	
Parasite	# sharks	%	#sharks	%	# sharks	%	# sharks	%
Bl	16	11.3	71	32.1	35	38.1	20	52.6
Ao	40	28.4	59	26.7	13	14.1	4	10.5
Pb	14	9.9	47	21.3	7	7.6	1	2.6
Ec	7	5.0	27	12.2	11	12.0	-	-
Lg	7	5.0	6	2.7	-	-	2	5.3
None (Clean)	96	68.1	91	41.2	37	40.2	12	31.6

Brown smoothhound sharks (*n*=130) showed slightly less frequency of copepods in males than females and higher overall rates of infection, as well as fewer individuals free of ectoparasites than did leopard sharks. Forty-nine (37.7%) of male and female brown smoothhound sharks were designated free of external parasites (Table1). Numerous "clean" sharks examined, however, had circular attachment scars thought to have been caused by leeches, but since no live parasites were found, these individuals were categorized as clean. Of the 38 male brown smoothhounds examined, none were found to support *E. coleoptratus*, while none of the 92 females supported *L. galei*.

While *P. bicolor* and *A. oblongus* are typically found on the body, fin edges, and soft tissues around the cloaca and claspers, *L. galei* and *E. coleoptratus* were found on gill arches and, occasionally, in buccal and nare cavities of leopard sharks and brown smoothhound sharks. Although *L. galei* was uncommon among all elasmobranchs examined during this study, they appeared more on leopard sharks than other sharks in South San Francisco Bay and are limited to just a few species of elasmobranchs (Love and Moser 1983).

Male leopard sharks and male brown smoothhound sharks had higher infestation rates of the leech *Branchellion lobata* than did females, with male brown smoothhound sharks (52.6%) and male leopard sharks (32.1%) having the highest infestation rate of all four elasmobanchs (Table 1). Sharks infested with this leech often had several leeches in various locations around male claspers, near the cloaca in females, in the nare cavities, at the caudal-basal attachment of dorsal and pectoral fins, or directly attached to eyes. Males of leopard sharks and brown smoothhound sharks showed substantially higher rates of infection, especially by young leeches, than females, which is possibly due in part to the increased availability of the soft tissues of the spermatic sulcus of male claspers. On 15 April 1977 an all-male aggregation of 29 leopard sharks was captured, and leeches were attached to the spermatic sulcus of 21 (72.4%) of those individuals. Leeches were also attached to one or both eyes of juvenile and adult leopard sharks and brown smoothhound sharks and, in one incident, several leeches completely covered the right eye of an adult female brown smoothhound shark (46.9 cm TL). No copepods were ever found attached to the eyes of any shark species in this study, in contrast to the report of Benz et al (2002) involving Pacific sleeper sharks (*Somniosus pacificus*). The common isopod *Lironeca vulgaris*, which is often found on teleosts, was also found on gill tissues and in buccal cavities of some leopard sharks subsequent to Russo (1975), but the number of specimens found was not included in this report, due to the mobility of the isopod (Robinson 1982, Moser and Sakanari 1985).

Soupfin sharks (*n*=41) and spiny dogfish sharks (*n*= 42) varied in infestation rates involving leeches and the copepods *A. oblongus*, *P. bicolor* and, to a lesser extent, *E. coleoptratus* and *L. galei*. Indeed, the latter was practically non-existent among those species (Table 2), when compared to levels of infestation among leopard sharks and brown smoothhound sharks (Table 1).

Table 2.—The occurrence of external parasites *Branchellion lobata* (Bl), *Achtheinus oblongus* (Ao), *Pandarus bicolor* (Pb), *Echthrogaleus coleoptratus* (Ec), and *Lernaeopoda galei* (Lg) on soupfin sharks and spiny dogfish sharks from San Francisco Bay, California, 1976–1996.

	Soupfin sharks (*n*=41)				Spiny dogfish sharks (*n*=42)			
	Females (*n*=28)		Males (*n*=13)		Females (*n*=31)		Males (*n*=11)	
Parasite	# sharks	%	# sharks	%	# sharks	%	# sharks	%
Bl	6	21.4	3	23.1	5	16.1	2	18.2
Ao	8	28.6	2	15.4	3	9.7	1	9.1
Pb	9	32.1	5	38.5	9	29.0	1	9.1
Ec	4	14.3	2	15.4	2	6.5	-	-
Lg	-	-	-	-	-	-	1	9.1
None (Clean)	7	25.0	3	23.1	18	58.1	7	63.6

Soupfin sharks had the highest rates of infestation by *P. bicolor* among shark species considered in this report. One female soupfin shark (81.3 cm TL) had 52 *P. bicolor* on various parts of the body. Neither male brown smoothhounds (*n*=38) nor male of spiny dogfish sharks (*n*= 11) were determined to be infested by *E. coleoptratus*. This parasite appeared on female (14.3%) and male (15.4%) soupfin sharks, but only female spiny dogfish sharks (6.5%) supported any specimens.

No male or female soupfin sharks (*n*=41 total) and no female spiny dogfish sharks (*n*=31) were infested by *L. galei*, but one of 11 male spiny dogfish sharks had several *L. galei*. Finally, males of both soupfin sharks and spiny dogfish sharks had only slightly higher rates of infection by leeches than females (Table 2), compared to leopard and brown smoothhound sharks (Table 1). Leopard shark females (68.1%), spiny dogfish males (63.6 %), and spiny dogfish females (58.1 %) exhibited the highest parasite-free rates, respectively.

Finally, eight of 13 big skates (*Raja binoculata*) that were examined were infested with two additional copepods (*Pseudocharopinus dentatus* and *Trebius latifurcatus*) that I had not previously found on other elasmobranchs in San Francisco Bay. Both of these copepods are known to occur only on a few other hosts along the Pacific coast (Love and Moser 1983, Deets and Dojiri 1989), but *R. binoculata* represents a new host record for *T. latifurcatus*. Both these parasites have the ability to rapidly move over the skin of their hosts to different attachment sites making them difficult to count or collect them.

The disparate rates of infection by leeches and copepods shown here raise several questions regarding host selection, frequency of occurrence, and ease of attachment as they relate to the behavior of host sharks. This is especially so concerning the abundance of leeches on leopard sharks and brown smoothhound sharks, and *P. bicolor* on soupfin sharks. The frequency and distribution of the parasites identified in this study should be examined on these same hosts in additional geographic areas for a more complete understanding of those relationships.

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Orange coloration in a black-and-yellow rockfish (*Sebastes chrysomelas*) from central California

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Key words: abnormal coloration, black-and-yellow rockfish, *Sebastes chrysomelas*

In November 2010 an orange colored rockfish (*Sebastes* sp.) was caught by hook and line off Avila Beach, San Luis Obispo County, California (35º 14' N, 120º 64' W) at a depth of 6 m near the Point San Luis Lighthouse. The fish initially was not identifiable with any of the shallow-water rockfishes, yet had the general conformation of a member of the *Pteropodus* rockfish complex. Through analysis of morphological characters the specimen was determined to be either a black-and-yellow rockfish (*S. chrysomelas*) or gopher rockfish (*S. carnatus*). Both are considered as shallow-water species with gopher rockfish generally found deeper than black-and-yellow rockfish (Larson 1980, Love et al. 2002) and we initially assumed that the orange colored rockfish was a black-and-yellow rockfish. Within aquarium conditions, the fish demonstrated behavioral characteristics similar to those of both black-and-yellow rockfish and gopher rockfish by hiding in cracks in rocks covered with invertebrates such as California hydrocoral (*Stylaster californicus*), strawberry anemone (*Corynactis californica*), sponges (Porifera), and algae (Figure 1). As coloration is the primary character used to separate these species, we incorporated genetic techniques to confirm identification.

To date, no orange black-and-yellow rockfish or gopher rockfish have been reported. Xanthic coloration has been observed off the California coast in what likely was one of those two species (Medlin 2012), but was not confirmed as the fish was not landed. Additionally, xanthism has been reported in other rockfish species, including the China rockfish (*S. nebulosus*; Ueber 1989) and grass rockfish (*S. rastrelliger*; Cripe 1998).

Figure 1.—Orange colored black-and-yellow rockfish on display at Monterey Bay Aquarium. The fish has been continuously maintained and on exhibit from November 2010 to date (January 2014).

Morphological, morphometric, and meristic characteristics, following Phillips (1957), aided in placing the specimen within the *Pteropodus* clade and into the black-and yellow and gopher rockfish complex. The relevant characteristics are as follows: total length 305 mm; standard length 255 mm; head length 97.5 mm; orbital width 21.6 mm; interorbital width 13.5 mm; longest dorsal spine 34.1 mm; dorsal fin XIII,12; anal fin III, 6; pectoral fin L 9/17, R 9/17; interorbital space concave; cranial spines upright and strong; caudal fin rounded; anal fin rounded. The counts and measurements were taken while the fish was under anesthesia.

To genetically identify the specimen, DNA was extracted from a piece of fin tissue using a Chelex-based boiling method (Hyde et al. 2005). The mitochondrial cytochrome b gene was amplified and sequenced using methods described by Hyde and Vetter (2007). The resultant sequence was compared to reference sequences in order to determine species identity. The sequence indicated that the fish in question was either a gopher rockfish or black-and-yellow rockfish. These spec ies are not reciprocally monophyletic at mitochondrial loci, and examination of the highly divergent nuclear DNA locus *Sch*-18 was necessary. The *Sch*-18 locus was amplified and digested with the restriction enzyme *Alu*I, using methods described by Buonaccorsi et al. (2011). The resultant genotype was homozygous for black-and-yellow rockfish diagnostic alleles, providing an unambiguous species identification.

Sebastes rockfishes are known for their high evolutionary diversity, and are considered a marine species flock (Johns and Avise 1998, Love et al. 2002). The occurrence of visually striking within-species color polymorphisms, such as that described herein, may affect mate selection and, therefore, could have evolutionary implications (Gray and McKinnon 2007). For example, if two subgroups of black-and-yellow rockfish were in the process of ecological divergence, a genetic color polymorphism that arose within one subgroup could result in assortative mating, reduce gene flow between populations, and facilitate divergence.

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KIRKWOOD, S., AND E. MEYERS. 2012. America's national parks: an insider's guide to unforgettable places and experiences. Time Home Entertainment, Inc., New York, New York, USA. 208 pp. $24.95 (hard cover).

LOVE, M. S. 2011. Certainly more than you want to know about the fishes of the Pacific coast: a postmodern experience. Really Big Press, Santa Barbara, California, USA. 650 pp. $29.95 (soft cover).

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