Zootaxa 4543 (2): 221–240
https://www.mapress.com/j/zt/
Copyright © 2019 Magnolia Press

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4543.2.3
http://zoobank.org/urn:lsid:zoobank.org:pub:0D3BBCE4-B836-417F-A293-6A93D155A0C7

A reappraisal of the California Roach/Hitch (Cypriniformes, Cyprinidae, *Hesperoleucus/Lavinia*) species complex

JASON BAUMSTEIGER[1,2,4] & PETER B. MOYLE[1,3,5]
[1]*Center for Watershed Sciences, University of California, Davis, One Shields Avenue, Davis, CA 95616*
[2]*Department of Animal Sciences, University of California, Davis, One Shields Avenue, Davis, CA 95616*
[3]*Department of Wildlife, Fisheries, and Conservation Biology, University of California, Davis, One Shields Avenue, Davis, CA 95616*
[4]*Current address: Department of Biological Sciences, University of the Pacific, 3601 Pacific Ave, Stockton, CA 95211*
[5]*Corresponding Author. E-mail: jbaumsteiger@ucdavis.edu; pbmoyle@ucdavis.edu*

Abstract

The California Roach (*Hesperoleucus symmetricus*) and Hitch (*Lavinia exilicauda*) form a species complex largely endemic to California (CA), USA. Using previous studies of this complex along with a recent comprehensive genomic analysis, we developed a highly supported taxonomic hierarchy of two genera, five species, four subspecies and multiple distinct population segments within two presently recognized species. The genera *Lavinia* and *Hesperoleucus* are supported as representing distinct lineages, despite occasional hybridization between them. While hybridization is one pathway to some speciation in this complex, hierarchical levels correlate nicely between genomic results and earlier morphological work. *Hesperoleucus symmetricus* is newly divided into four species (*H. parvipinnis*—Gualala Roach, *H. mitrulus*—Northern Roach, *H. venustus*—Coastal Roach, and *H. symmetricus*—California Roach) and two subspecies (*H. s. serpentinus*—Red Hills Roach, *H. s. symmetricus*—California Roach). Within *H. venustus*, two subspecies are identified (*H. v. navarroensis*—Northern Coastal Roach, and *H. v. subditus*—Southern Coastal Roach), which are supported by previous morphological studies but resolve discrepancies between those studies. Finally, six distinct population segments are identified within different species/subspecies: Kaweah, Russian River, Navarro River, Monterey, and Tomales Bay. Clear Lake Roach are introgressed between California and Coastal Roach, making them distinct but difficult to formally name. Results should greatly improve management and conservation of each taxonomic entity and help resolve past ambiguities. Additional studies are needed to improve range-wide boundaries and to investigate population structure within all species and subspecies identified in both *Lavinia* and *Hesperoleucus* lineages.

Key words: Genomics, Minnows, Endemic, DPS

Introduction

California Roach (*Hesperoleucus symmetricus*) and Hitch (*Lavinia exilicauda*) form a complex of small fishes in the minnow and carp family (Cyprinidae). Members of this complex are largely endemic to California and adapted for survival in streams experiencing extreme conditions brought on by the region's Mediterranean climate (Moyle 2002). The complex was first described as multiple taxa (Snyder 1913) but later merged into the two contemporary species (*H. symmetricus* and *L. exilicauda*) without formal taxonomic review, a decision generally accepted by fish biologists (e.g., Page *et al.* 2013). Unfortunately, most lineages within the complex are in decline and their declines appear to be accelerating with contemporary climate change (Moyle *et al.* 2013). Thus, the time has come for a formal taxonomic review of these taxa in order to identify and protect distinct lineages that might need listing under state and federal Endangered Species Acts (ESA).

We begin by reviewing the taxonomic history of the complex, followed by a brief description of the value of contemporary genomics for discerning difficult species complexes. Using a combination of contemporary genetic/genomic analyses and an exhaustive review of previous morphological and ecological studies, we then systematically describe the most strongly supported taxonomic lineages within this complex for the purpose of

Accepted by L. Page: 31 Aug. 2018; published: 7 Jan. 2019

Licensed under a Creative Commons Attribution License http://creativecommons.org/licenses/by/3.0

formal recognition. This includes demonstrating why the complex should remain two genera. Four species (excluding Hitch), four subspecies, and five distinct population segments (DPS) are properly described and assigned names (most based on former nomenclature). The DPS designation is adopted from the federal ESA, where it is used to protect organisms that are clearly different and/or isolated from other populations of the species but not to a point where they have formal taxonomic recognition. In California it is widely used for salmonid fishes (e.g., Moyle *et al*. 2017). We conclude with a brief summary addressing the taxonomic uncertainty surrounding Roach in the Clear Lake basin.

History of the California Roach/Hitch complex

The California Roach ("CA Roach") was originally described as *Pogonichthys symmetricus* by Baird & Girard (1854) from specimens collected from the San Joaquin River at Fort Miller, Fresno County (all locations are in California, USA, unless otherwise indicated). Jordan & Evermann (1896) then placed it in the same genus as the superficially similar European Roach (*Rutilus rutilus* Linnaeus 1758). Snyder (1913) erected the genus *Hesperoleucus* and described five additional species based on locality, isolation from other populations and morphological differences, giving a total of six species:

Hesperoleucus symmetricus from the Sacramento/San Joaquin River Basins.
Hesperoleucus mitrulus from tributaries to Goose Lake, Lake Co, Oregon.
Hesperoleucus navarroensis from the Navarro River, Mendocino Co., CA.
Hesperoleucus parvipinnis from the Gualala River, Sonoma Co., CA.
Hesperoleucus venustus from the Russian River and streams tributary to San Francisco Bay and Tomales Bay.
Hesperoleucus subditus from streams flowing into Monterey Bay (Pajaro and Salinas river systems).

The taxa were then recognized in a number of ensuing studies (Evermann and Clark 1931; Shapovalov & Dill 1950; Shapovalov *et al.* 1959). However, Miller (1945) examined Hitch and *H. subditus* from the Pajaro River and observed potential hybridization between them, leading him to posit Snyder's (1913) species only merited designation as subspecies of *H. symmetricus.* Murphy (1948), in an unpublished Masters' thesis, analyzed data from Snyder (1913) together with his own data and concluded Miller (1945) was correct and coastal forms of *Hesperoleucus* should be relegated to subspecies status based on their likely recent evolution. Although unpublished, Murphy's (1948) diagnosis was eventually adopted by subsequent studies (Hopkirk 1973; Hubbs *et al.* 1979; Moyle 2002; Page *et al.* 2013).

Hopkirk (1973) agreed with Murphy in placing all Roach into a single species but differed in his conclusions regarding which populations constituted subspecies. He recognized *H. s. symmetricus, H. s. parvipinnis,* and *H. s. subditus* as subspecies and suggested that Roach from the Russian River be grouped with *H. s. navarroensis* and that those from the Tomales Bay region be given subspecies status. He also concluded that former *H. venustus* from San Francisco Bay tributaries and Roach from the Clear Lake drainage are synonymous with *H. s. symmetricus* from the Central Valley. Hopkirk, however, cautioned that *H. s. symmetricus* probably consisted of several subspecies given the presence of morphological distinctiveness in some localities.

To test Hopkirk's assertion, Brown *et al.* (1992) examined morphometrics of Roach in streams flowing into the South Central (San Joaquin) Valley. This dry region contains some of the most extreme and isolated environments in which Roach are located. Brown *et al.* (1992) found populations from different drainages could be distinguished by multivariate analysis of 14 characters. Individuals from the Kaweah River (Tulare Co.) and the Red Hills Region (Horton and other small creeks in Tuolumne Co.) were particularly distinctive due to the high frequency of "chisel lip". Jones *et al.* (2002) found Red Hills individuals to be genetically distinct and the combination of morphological and genetic distinctiveness in Red Hills individuals led Moyle (2002) to consider it an undescribed subspecies.

In a more comprehensive genetic study of CA Roach and Hitch, Aguilar & Jones (2009) used nuclear microsatellites (nDNA) and mitochondrial DNA (mtDNA) markers to supply new insight into the taxonomy of the Roach/Hitch complex. Microsatellites clearly defined Gualala River, Pit River, Navarro River and Red Hills individuals as distinct genetic units and largely supported the subspecies proposed by Moyle (2002). Their analysis of mtDNA found Roach from the Pit and Gualala Rivers to be highly divergent from those from all other locations and reciprocally monophyletic for the haplotypes assayed, estimating the two populations had been isolated for 3–6 million years. In addition, mtDNA results showed Tomales Bay, Red Hills, Russian River and Clear Lake locations were distinct evolutionary lineages. Three distinct lineages of Hitch were also identified, supporting long-standing subspecies designations: *L. e. exilicauda*, *L. e. harengus* and *L. e. chi* (Hopkirk 1973).

Genomics

The recent advent of genomic analyses has allowed for a more comprehensive, genome-wide assessment of species (Seehausen *et al.* 2014). Specifically, the use of restriction site-associated DNA sequencing (RADseq) has allowed for exploration of closely related lineages in non-model organisms (Andrews *et al.* 2016). In a recent publication, we employed this technique on samples from the CA Roach/Hitch complex (Baumsteiger *et al.* 2017). Using hundreds of thousands of single nucleotide polymorphisms (SNPs) over 22,000 loci (> 300 bp in length), we applied this powerful dataset to identifying each evolutionary lineage from the genus-level down to the population-level. Support was spread over three independent analyses (Principal Component-PC, Admixture, and F_{ST}) and all conclusions were based on agreement among the three analyses, unless otherwise stated. These results demonstrated the need to re-examine the taxonomic status of all members of the Hitch–Roach complex.

Taxonomy

The following taxonomic hierarchy represents the culmination of available data from all studies currently available (morphological, ecological, genetic/genomic). Our designation of species is consistent with the Unified Species Concept (de Queiroz 2007), which seeks to find agreement among as many 'species concepts' as possible for its designations. Subspecies designations were also made for the following reasons: (a) there is a large amount of structure within each Roach species and subspecies, both genomically and morphologically; (b) the structure is highly distinct; (c) many subspecies were considered to be species at one time. Our designations provide the highest level of clarity for management and conservation and can be defended quantifiably with the genomic data. Institutional abbreviations follow Fricke and Eschmeyer (2018).

Lavinia and *Hesperoleucus*

One conundrum within the Hitch–Roach species complex is uncertainty regarding whether species should be placed in one genus or two genera. While the complex was originally divided between *Lavinia* and *Hesperoleucus,* multiple examples of hybridization between the genera suggest they are more closely related than separate genera designations would normally indicate. For example, CA Roach are known to hybridize with Hitch in the Pajaro and Salinas rivers in Monterey Bay drainages (Miller 1945), in Coyote, Alameda, and Walnut Creeks in the San Francisco Bay region (Miller 1963; Leidy 1984, 2007, pers. comm.), and in Sacramento-San Joaquin drainages (Avise *et al.* 1975; Jones 2001). Hybrids were fertile in the Pajaro River; Avise *et al.* (1975) found 8% of Hitch examined to be F_1 hybrids and 5% to be backcrossed. Since it is unusual for two genera to be interfertile and because other endemic species in California do not appear to exhibit this behavior (Avise *et al.* 1975; Avise & Ayala 1976; Moyle & Massingill 1981; Moyle 2002), it has been proposed these two species belonged in a single genus.

Aguilar & Jones (2009) found the two genera are closely related mtDNA lineages that could be considered to be one genus. Schönhuth *et al.* (2012), however, noted that while their mtDNA analyses supported this close relationship, their limited nuclear DNA results did not. Our recent study (Baumsteiger *et al.* 2017) found the strongest genomic signal coincided with splitting samples into two genera. We discovered, however, that samples from the Pit River (Northern Roach) were a confounding factor, having mixed historical ancestry with both genera. It was estimated in one analysis that approximately 80% of the Northern Roach genome clustered with Hitch whereas only 20% clustered with CA Roach. But all subsequent analyses found Northern Roach to be a distinct species, on par with currently identified species. Thus Northern Roach appears to be the result of an ancient hybrid speciation event (Mallet 2007) between ancestral Hitch and CA Roach but it is currently genomically different enough to warrant species status.

It is our conclusion that despite hybridization between individuals in the different genera, the distinctiveness of each genus is still strongly maintained and prevalent throughout the genomes interrogated. If results were more admixed, the argument for a single genus would be more plausible. We recognize admixture between genera is uncommon but note that not all mutations lead to post-zygotic barriers (Abbott *et al.* 2013). Additionally, hybridization has been proposed between Roach/Hitch and other members of the subfamily Leuciscinae including Speckled Dace (*Rhinichthys osculus)*, Arroyo Chub (*Gila orcuttii*), and the now extinct Thicktail Chub (*Gila crassicauda*) (Greenfield & Deckert 1973; Hopkirk 1973). Thus the frequency of hybridization suggests reproductive barriers are poorly developed in the endemic minnows of California. Secondly, although Northern Roach represent an ancient hybridization event and cluster primarily with individuals from the *Lavinia* genus (~80% but only in the admixture analysis), we cannot definitively say they are *Lavinia*. Northern Roach still strongly resemble CA Roach in appearance (see below), but this may simply be the result of natural selection for the CA Roach morphotype. Future phylogenetic analyses between all genera within the family may provide the solution but it remains, as yet, unavailable. Thus, without universal agreement between genomic analyses or improved criteria for taxonomically delineating hybrids, we default to the original genus assignment by Snyder (1913). Therefore, the species of *Hesperoleucus* are as described below.

***Hesperoleucus symmetricus* (Baird & Girard, 1854)**

California Roach

Lectotype: USNM 191, present designation. This species was originally described as *Pogonichthys symmetricus* by Baird & Girard (1854) from specimens collected in the San Joaquin River at Fort Miller, Fresno Co., CA. Paralectotypes: USNM 440410; ANSP 5330–33; MCZ 1961; MNHN 0000–0353.

The benchmark California Roach is based on Baird & Girard (1854). Individuals primarily occupy streams/rivers flowing into California's Central Valley, most of which are isolated to some degree. Groups of California Roach appear to become easily isolated from one another and adapted to local conditions, particularly following anthropomorphic changes to the landscape (Brown *et al.* 1992). Many of these isolated groups are distinguishable both morphologically (Brown *et al.* 1992) and genetically (Aguilar & Jones 2009; Baumsteiger *et al.* 2017). In fact, Baumsteiger *et al.* found every sample location of CA Roach within our study was distinctive, including support for a new subspecies and a distinct population segment (see below). Baumsteiger *et al.* (2017) also found California Roach from the Central Valley to be genomically distinct from those along the coast. All analyses show a clear break between these two species. Our conclusion is CA Roach *sensu stricto* should be limited to individuals from Central Valley drainages and the following formal description reflects this new delineation.

Description. CA Roach (*H. symmetricus*) are small, stout-bodied cyprinids with narrow caudal peduncles and deeply forked tails. Adult individuals usually have total lengths less than 100 mm, although fish up to 150 mm TL have been observed (Moyle 2002). The head is large and conical, with large eyes and a mouth that is slightly sub-terminal and slants downward. Individuals in some locations, especially those in streams of the Sierra Nevada, develop a keratinous plate on the lower jaw, referred to as a "chisel lip". The dorsal fin is short (8–10 rays) and is positioned behind the insertion point of the pelvic fin while the anal fin is also short, with 7–9 rays (Table 1). Pharyngeal teeth (0,5,4,0) have curved tips, which overhang grinding surfaces of moderate size. CA Roach are dark on the upper half of their bodies, ranging from a shadowy gray to a steel blue, while the lower half of the body is much lighter, usually a dull white/silver color. Scales are small, numbering 47–62 along the lateral line. Individuals tend to exhibit general (non-nuptial) sexual dimorphism (Snyder 1908; Murphy 1943).

California Roach are highly variable in most of their characteristics across their range. Brown *et al.* (1992) measured 14 morphometric variables from eight watersheds around the San Joaquin Valley, including the southern end of the range (Table 1). Using these variables, a discriminant analysis correctly assigned 76% of the individuals to the watershed from which they were collected, suggesting locations were sufficiently isolated from one another to have local adaptations or phenotypic divergence.

TABLE 1. Original morphometric and meristic counts for proposed taxonomy covering the five primary studies to date.

	California Roach *H.symmetricus*					Coastal Roach *H. venustus*				Hybrid
						Southern Coastal Roach *H.v. subditus*		Northern Coastal Roach *H.v. navarroensis*		
	California Roach *H.s.symmetricus*	Red Hills Roach *H.s. serpentinus*	Kaweah Roach	Northern Roach *H. mitrulus*	Gualala Roach *H. parvipinnus*	Monterey Roach	Tomales Bay Roach	Russian/Eel Roach	Navarro Roach	Clear Lake CA x Coastal
SNYDER (1913)										
Fins	long	NA	NA	lower, shorter	short, rounded	shorter	long	long	rounded	NA
Dorsal fin rays	9	NA	NA	8	8	8	9	9	8	NA
Anal fin rays	8	NA	NA	7	7	7	8	8	8	NA
Caudal peduncle	narrow	NA	NA	NA	deep	deep,heavy	slender	slender	deep	NA
Body	symmetrical	NA	NA	deeper	robust	robust	trim	trim	robust	NA
Head	long	NA	NA	NA	NA	NA	shorter	shorter	NA	NA
Snout	pointed	NA	NA	short, round	short	rounded	pointed	pointed	short	NA
Eyes	large	NA	NA	NA	NA	NA	smaller	smaller	NA	NA
Gill rakers	NA	NA	NA	9	8	9	10	NA	8	NA
Scales	larger	NA	NA	cup–like,small	smaller	larger	varied	varied	spatulate	NA
Apical radii	13–22	NA	NA	13–20	11–24	12–25	8–21	8–21	14–24	NA
Lateral radii	usually absent	NA	NA	3–9	1–4; weak	1–8	absent	1–5	1–5; weak	NA
Basal radii	absent	NA	NA	8–17	absent	absent	absent	absent	absent	NA
Lateral line scales	47–53	NA	NA	54–61	54–59	48–59	50–61	50–61	51–59	NA
Above LL	13	NA	NA	12–15	14–16	NA	NA	NA	11–13	NA
MURPHY (1948)										
Scales on LL	NA	NA	NA	NA	54–65 (59)	50–60 (54)	49–63 (54)	44–60 (52)	49–63 (54)	NA
Scales above LL	NA	NA	NA	NA	12–17 (14)	12–15 (13)	12–15 (13)	11–14 (12)	11–15 (13)	NA
Scales below LL	NA	NA	NA	NA	8–12 (9)	7–12 (8)	7–11 (8)	6–9 (7)	7–11 (8)	NA
Dorsal scales	NA	NA	NA	NA	25–31 (29)	24–30 (27)	22–30 (26)	22–29 (25)	23–29 (26)	NA
Ventral scales	NA	NA	NA	NA	23–34 (27)	22–31 (25)	22–30 (25)	20–27 (23)	23–29 (26)	NA
Scales around body	NA	NA	NA	NA	50–67 (58)	47–60 (53)	47–61 (53)	45–56 (50)	47–61 (52)	NA
Scales before dorsal	NA	NA	NA	NA	28–38 (33)	26–37 (31)	28–36 (32)	27–36 (30)	25–34 (30)	NA
Dorsal rays	NA	NA	NA	NA	7–8 (8)	8–9 (8)	8–10 (9)	8–9 (9)	8–9 (8)	NA
Anal rays	NA	NA	NA	NA	6–8 (7)	6–8(7)	7–8 (8)	7–9 (8)	7–9 (8)	NA
Diameter of eye (mm/100)	NA	NA	NA	NA	20–28 (24)	21–28 (25)	20–27 (23)	23–30 (27)	20–28 (24)	NA
Snout length (mm/100)	NA	NA	NA	NA	26–34 (29)	24–31 (28)	25–33 (29)	24–31 (28)	27–33 (30)	NA
Caudal depth (mm/100)	NA	NA	NA	NA	38–54 (43)	43–57 (49)	39–55 (47)	31–50 (41)	44–55 (49)	NA

……*continued on the next page*

TABLE 1. (Continued)

	California Roach *H.symmetricus*					Coastal Roach *H. venustus*				Hybrid
						Southern Coastal Roach *H.v. subditus*		Northern Coastal Roach *H.v. navarroensis*		
	California Roach *H.s.symmetricus*	Red Hills Roach *H.s. serpentinus*	Kaweah Roach	Northern Roach *H. mitrulus*	Gualala Roach *H. parvipinnus*	Monterey Roach	Tomales Bay Roach	Russian/Eel Roach	Navarro Roach	Clear Lake CA x Coastal
HOPKIRK (1973)										
Dorsal rays	8–10 (9)	NA	NA	NA	7–8 (8)	7–9 (8)	8–10 (9)	8–9 (9)	8–9 (8)	8–10 (9)
Anal rays	7–9 (8)	NA	NA	NA	7–8(7)	6–9 (7)	6–7 (7)	7–9 (8)	7–9 (8)	7–9 (8)
Gill rakers	7–10 (9)	NA	NA	NA	NA	7–11 (9)	NA	8–11 (9)	NA	8–11 (10)
Lateral line scales	49–62 (53)	NA	NA	NA	54–65 (59)	47–65 (54)	47–63 (54)	47–60 (53)	49–63 (54)	47–58 (53)
BROWN ET AL (1992)										
n	298	49	40	NA	NA	NA	NA	NA	NA	NA
SL	59.7	52.3	60.1	NA	NA	NA	NA	NA	NA	NA
Head length	16.5	15.4	16.1	NA	NA	NA	NA	NA	NA	NA
Head width	9.3	9.9	9.1	NA	NA	NA	NA	NA	NA	NA
Body depth	14.9	15.0	14.7	NA	NA	NA	NA	NA	NA	NA
Body width	10.3	10.4	10.4	NA	NA	NA	NA	NA	NA	NA
Trunk shape	24.8	25.6	24.5	NA	NA	NA	NA	NA	NA	NA
Caudal peduncle length	12.6	12.2	12.4	NA	NA	NA	NA	NA	NA	NA
Caudal peduncle depth	6.8	7.1	6.6	NA	NA	NA	NA	NA	NA	NA
Pectoral fin length	12.6	10.2	13.1	NA	NA	NA	NA	NA	NA	NA
Pectoral fin width	6.4	4.8	6.6	NA	NA	NA	NA	NA	NA	NA
Pelvic fin length	9.6	7.7	9.9	NA	NA	NA	NA	NA	NA	NA
Eye diameter	4.2	3.6	4.4	NA	NA	NA	NA	NA	NA	NA
Interorbital distance	6.0	5.3	6.5	NA	NA	NA	NA	NA	NA	NA
Pectoral fin rays	12.6	12.2	12.8	NA	NA	NA	NA	NA	NA	NA
Pelvic fin rays	8.1	8.1	8.1	NA	NA	NA	NA	NA	NA	NA
Percent chisel lip	13	94	77	NA	NA	NA	NA	NA	NA	NA

Distribution. Individuals were historically found in most tributaries to the Sacramento and San Joaquin Rivers, including tributaries in the extreme southern San Joaquin Valley (e.g. Kern River), as well as in fringe habitats (backwaters with dense riparian cover) along the main rivers (Moyle 2002; Fig. 1). Fish were rarely found in streams above 1000 m in elevation, presumably restricted by high gradients and natural barriers. In the Tuolumne River, the upstream limit was historically (and still is) Preston Falls at 885 m elevation. The historic distribution in the upper Sacramento River is poorly understood.

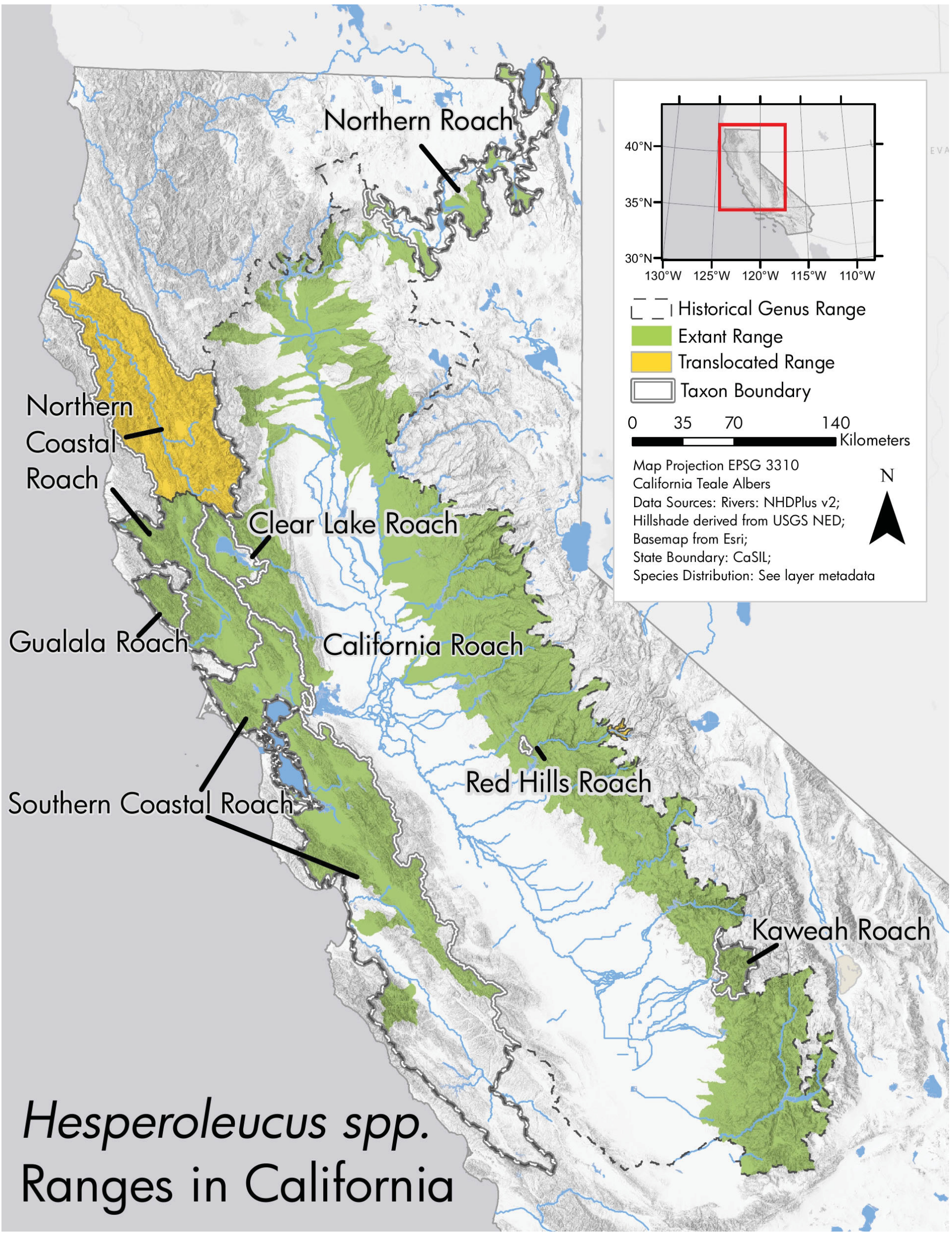

FIGURE 1. Historic, present, and translocated ranges of *Hesperoleucus* taxa in California. The range of the Northern Roach in Oregon is largely omitted. Overall range of each taxon is based on watersheds, so are only approximate, and should not be used for precise locational information. Representatives of each taxon may occasionally occur in areas from which they were historically present but are now shown as absent, such as low elevation regions of the Central Valley. The Cuyama River (southern California) apparently supports a population of *Hesperoleucus,* but its origins and relationships are unknown so it is omitted from this map.

Today CA Roach are absent from many streams as the result of habitat change and invasions of alien predators. For example, Moyle & Nichols (1973) and Brown & Moyle (1993) found they were absent from the Fresno River (Fresno Co.) and other tributaries to the San Joaquin River. They were also once common in the mainstem San Joaquin River but are absent today. Moyle (2002) documented their consistent presence in the river at Friant

(Fresno Co.) until the construction of Friant Dam in the 1940s. CA Roach are absent from most of their historic range in the Cosumnes River watershed due to the invasion of piscivorous Redeye Bass, *Micropterus coosae* (Moyle *et al.* 2003). In the upper Yuba River watershed, they are largely absent as the result of 19th century hydraulic mining, with the exception of one small tributary to the South Fork Yuba, Kentucky Ravine (Gard & Randall 2004).

The range of CA Roach has also been expanded, presumably through 'bait bucket' introductions by anglers. For example, Hetch-Hetchy Reservoir (1,162 m) on the upper Tuolumne River, well above a series of natural barriers, supports a large pelagic population (P. Moyle, unpublished observations). This is unusual because CA Roach do not generally live in reservoirs, especially those with predatory fishes. Interestingly, individuals from this location were found to be admixed with Hitch (Baumsteiger *et al.* 2017), a factor which may explain their persistence. Soquel Creek and the Cuyama River in southern California support presumed introduced populations, although their origins are also uncertain (Moyle 2002).

It is possible that the ancestor of the widely-distributed CA Roach gave rise to most other Roach species and subspecies but this has not yet been investigated phylogenetically. The ability of these fish to persist in small, often intermittent tributaries presumably led to their colonization of adjacent drainages in a number of areas through capture of interior headwater streams by erosion or tectonic movements (Snyder 1908, 1913; Murphy 1948; Moyle 2002). Because they are relatively intolerant of saline waters, dispersal to coastal streams could not have occurred through ocean waters. However, connections at low elevations may have been possible in some cases when sea levels were lower and estuaries joined the mouths of rivers (Moyle 2002). Similarly in the giant San Francisco Estuary, exchange between salt-water intolerant populations likely occurred during flood years when river outflows were high enough to create freshwater lenses in the surface waters of the estuary (Ayres 1854; Snyder 1905; Murphy 1948; Leidy 2007). During high water periods, fish may also have been able to disperse through flooded marshes on the fringes of the estuary. Today such opportunities for dispersal are largely absent (Moyle *et al.* 2012).

Status. Moyle *et al.* (2015) list California Roach as a Species of Special Concern, with an IUCN status of Near–threatened. If CA Roach were a single interbreeding taxon, there would be little danger of immediate extinction because they occur in many streams over a wide area. However, the discovery that CA Roach comprise multiple lineages, some of which are under immediate threats, is of conservation concern. After all, the small, isolated populations that are the most likely to be extirpated also tend to be the most distinctive (Brown *et al.* 1992). Emerging appreciation for the variation within the taxon (Moyle *et al.* 1989; Brown *et al.* 1992; Jones 2001; Jones *et al.* 2002; Aguilar & Jones 2009; Baumsteiger *et al.* 2017) has highlighted the need to preserve populations endemic to specific watersheds. On a broader scale, Moyle *et al.* (2013) regarded the entire taxon as highly vulnerable to extinction in the next century due to massive changes to smaller streams brought on by climate change, the continuing effects of anthropogenic land and water use, and the spread of invasive species.

***Hesperoleucus symmetricus symmetricus* (Baird & Girard, 1854)**
Central California Roach

This subspecies is consistent with the descriptions and distribution of the species itself, minus the Red Hills region. According to Baumsteiger *et al*. (2017), population structure is available within the subspecies, but only one lineage (see below) stood out in the genomic analyses and therefore would rise to the level of a DPS by our estimation. However, the presence of population structure and morphological differences (Brown *et al*. 1992) within the subspecies indicates isolation/adaptation among locations that, if fully investigated, may warrant additional DPS designations. We would argue this should be investigated on a case-by-case basis to evaluate the level of isolation and potential threat to each population so as to not overuse the DPS designation within the U.S. Endangered Species Act.

Kaweah Roach. The current population of Kaweah Roach is highly isolated in the Kaweah River system, at the southern end of the CA Roach range. Some morphometric characters are distinctive in Kaweah Roach, including a high prevalence of chisel-lip (Brown *et al.* 1992). Although found to be genetically (Aguilar & Jones 2009) and genomically distinct (Baumsteiger *et al.* 2017), these determinations were only discovered once analyses were restricted to CA Roach samples. Therefore, we believe Kaweah Roach is a unique evolutionary lineage within CA Roach, representing a distinct population segment (DPS) that should be managed accordingly.

Description. Kaweah Roach are largely similar to the description for CA Roach, with slightly different morphometric and meristic mean counts reported (Brown *et al.* 1992). This includes a higher prevalence of chisel-lip, similar to Red Hills Roach.

Distribution. This distinct population segment appears to be isolated in the Kaweah River above Kaweah Reservoir. Historically it may have occurred on the Valley floor, in places such as Tulare Lake or in the lower reaches of nearby river systems such as the Kings River. Such access is now denied by dams, diversions, and altered habitats.

Status. This DPS is reasonably safe, at least in the short run (50 years). The upper half of the range within the Kaweah River is bounded by Kings Canyon National Park and as such receives special protection. The lower half, which flows mostly through private lands before ending up in Kaweah Reservoir, is less secure. Individuals here may be at risk from upstream movement of invasive species such as Largemouth Bass, *Micropterus salmoides*, a factor which will intensify with climate change and warmer temperatures.

Hesperoleucus symmetricus serpentinus **Baumsteiger and Moyle, new subspecies**
Red Hills Roach
(Fig. 2)

Holotype: Museum of Wildlife and Fish Biology, University of California, Davis, WFC3050, 51.8 mm SL, Horton Creek, Tuolumne County, CA, July 16, 2010.

Paratypes. WFC3241–3244, 30.4—40.4 mm SL, same location and date as the holotype, The Red Hills Roach has strong support for a subspecies designation (e.g. Brown *et al.* 1992; Jones *et al.* 2002; Moyle 2002), especially given its increased isolation from other populations by New Don Pedro Reservoir (constructed in 1971), unique environmental constraints, and the prevalence (~97%) of the chisel-lip morphotype. Genetic and genomic analyses (Aguilar & Jones 2009; Baumsteiger *et al.* 2017) also found Red Hills Roach to be highly distinct, easily distinguishable from other CA Roach. In fact, our genomic study indicated a clear break between Red Hills Roach and all other CA Roach sampled in every analysis. With so many lines of support, subspecies status is clearly warranted.

Diagnosis. Distinguished from other subspecies of *H. symmetricus* by their flattened body profile, smaller interorbital distance and fewer pectoral and pelvic rays (Jones *et al.* 2002; Table 1). The holotype has 8 dorsal rays, 8 anal rays, 12 pectoral rays, and 8 pelvic rays.

Description. The Red Hills Roach is a genetically and morphologically distinct minnow adapted for living in small streams flowing through serpentine outcrops. They are typically small, less than 60 mm SL (Brown *et al.* 1992; Jones *et al.* 2002) and resemble CA Roach in their general appearance. Red Hills Roach exhibit an elevated frequency of "chisel-lip", a keratinous projection on the lower lip used for scraping algae (Brown *et al.* 1992). However there is substantial temporal variation in frequency of the chisel-lip condition amongst CA Roach (Jones *et al.* 2002).

Spawning coloration appears to be similar to that of CA Roach but is more intense. W. J. Jones (pers. comm.) describes it as follows: "The body is dark brown to brassy above, dark black lateral band, and brilliant white below, splashed with black blotches on the sides. Dorsal and caudal fins [are] dark olive-brown to reddish-brown, with the rays often deep-olive and with the nearly clear inter-radial membranes faintly flushed with brassy color; pectoral fins [are] yellowish with orange-red axils and very strong orange coloration at base; anal and pelvic fins [are] bright orange-red at the base with lessening coloration towards the rays. Cheeks and operculum with strong gilt reflections; strong orange coloration is found on the edges of the mouth (especially in males) with some blending into the upper mouth region. A lateral band is more strongly gilt than adjacent parts of body, thus often obscuring the lateral line. In females, the coloration is similar but less intense except for the orange coloration at the base of the paired fins that appears equally intense in both sexes. Males can be distinguished primarily by breeding tubercles on the top of the head."

Distribution. The Red Hills Roach is confined to Six Bit Gulch and its tributary streams: Amber Creek, Horton Creek, Minnow Creek and Poor Man's Gulch in Tuolumne Co. (Jones *et al.* 2002). Six Bit Gulch, during rainy periods, flows into the western arm of New Don Pedro Reservoir on the Tuolumne River. In July 2010, Roach were observed in three discontinuous wetted reaches of Horton Creek, which covered approximately 500 meters in total wetted length (P. Moyle, unpublished observations). However, only the lower reach, which extends about 200 meters upstream from the confluence with Six Bit Gulch, appeared to be perennial (as indicated by lush growth of sedges and other riparian vegetation). A natural fish barrier approximately 1.2 km upstream from the confluence likely inhibits Roach from accessing upper Horton Creek. Roach have also been observed in Six Bit Gulch where it is forded by Six Bit Ranch Road and in a pool in Roach Creek.

Status. Red Hills Roach merit protection as a threatened or endangered subspecies and rate as an IUCN status of Critical Concern (Moyle *et al.* 2011, 2015). They have an extremely limited distribution in a very harsh environment and less than 1,000 individuals persist in isolated summer pools (Jones *et al.* 2002). Their persistence is threatened by fire, depleted stream flows, lack of protection on private lands, and most notably, from invasive fishes. While some habitat is protected in the Red Hills Area of Critical Environmental Concern, much is on private land along a road and remains unprotected. Red Hills Roach has persisted only because of its physiological capacity to endure the extreme environmental conditions found in these small exposed streams.

Etymology. Both the common and subspecies name reflect the nature of the rocks through which these small creeks flow. The Red Hills region is named for the color of the soils created by weathering one of the largest outcroppings of serpentine rocks in the Sierra Nevada. Serpentine soils are high in magnesium and other minerals and create conditions in which few species can live. The landscape has a sparse but highly endemic flora (Anacker & Harrison 2012, Harrison 2013) and streams are small and largely unshaded.

FIGURE 2. Holotype of *Hesperoleucus symmetricus serpentinus*, Red Hills Roach. Photo courtesy of Irene Engilis.

Hesperoleucus venustus **Snyder, 1913**
Coastal Roach

Holotype: USNM 74476. Originally described from Coyote Creek, Santa Clara Co., CA. *Paratypes*: CAS-SU 22492, 24282; USNM 75335.

Snyder (1913) originally split this species into three species: *H. navarroensis* (from the Navarro River), *H. venustus* (from the Russian River), and *H. subditus* (Monterey region). These populations were later considered to be subspecies within the single species CA Roach, as suggested by the unpublished study of Murphy (1948). Aguilar & Jones (2009) did not find strong support for these species or subspecies with their mtDNA analysis although their microsatellite analysis found some structure among regions. As mentioned above, Baumsteiger *et al.* (2017) found clear evidence for populations in all coastal draining watersheds belonging to a single species. Subspecies were also detected but more broadly distributed than previously thought. Watersheds extending from the Russian River north to the Eel River (excluding the Gualala River) clustered as one subspecies and watersheds south of the Russian River (Tomales Bay to the Monterey region) clustered as a second.

Description. Based on previous morphological work, the Coastal Roach species has a mixture of characters (Table 1). For a cyprinid, the head is large and conical, the tail deeply forked, the eyes large, and the mouth sub-terminal, slanting at a downward angle. However, the body can be stout or slender, the snout short or more pointed, the caudal peduncle narrow or thick, and the fins small and rounded or long and narrow. Individuals are typically less than 120 mm total length. The dorsal fin is short (7–10 rays) and positioned behind the insertion point of the pelvic fin. The anal fin has 6–9 rays. Pharyngeal teeth (0,5—4,0) have curved tips which overhang grinding surfaces of moderate size. Gill rakers number 8–11. The scales are small, numbering 47–63 along the lateral line and 32–38 before the dorsal fin. Individuals are usually dark on the upper half of their bodies, ranging from a shadowy gray to a steel blue, while the lower half of the body is much lighter, usually a dull white/silver color. A light lateral stripe approximately two scales wide extends from upper edge of the gill opening to the base of tail and entirely above the lateral line. Below this line is a somewhat wider dark stripe and then several narrower and very distinct dark stripes which grow lighter ventrally.

Distribution. Coastal Roach are restricted to coastal watersheds, largely west of the coastal mountain range. The northernmost native population is in the Navarro River, although introduced Coastal Roach exist in the Eel River. Excluding the Gualala River (see below), watersheds south of the Navarro River do not support any Roach populations until the Russian River. Populations are then found intermittently from the Russian River south to the Tomales Bay region. Scattered Coastal Roach are found in streams around San Francisco Bay but are once again absent from coastal watersheds to the south until the Salinas and Pajaro river watersheds of the Monterey region. The population in Soquel Creek (Santa Cruz Co.) is probably introduced from the Salinas River, while the origin of the population in the Cuyuma River (San Luis Obispo and Santa Barbara counties) is uncertain but may be native (Moyle 2002). Coastal Roach are widespread in the Eel River, from an introduction in the early1970s. This introduction was noted by Moyle (2002) and Jones (2002) and is now confirmed by Baumsteiger *et al.* (2017) and A. Kinziger (pers. comm. 2017). Studies show that Eel River fish originated from the Russian River mainstem and not the recently connected East Fork (via the Potter Valley Project - Power *et al.* 2015).

Status. Due to its wide distribution throughout northern California coastal drainages, the species appears to be in little danger of extinction. However, subspecies or distinct population segments (see below) may be at risk within their particular watershed(s).

Hesperoleucus venustus navarroensis **Snyder, 1913**
Northern Coastal Roach

Holotype: USNM 74477. Originally described as *Hesperoleucus navarroensis* from Navarro River, near Philo, Mendocino Co., CA. *Paratype*: CAS-SU 22488.

Snyder (1913) described two species as occurring within the range of this subspecies: *H. navarroensis* from the Navarro River basin, and *H. venustus*, from a mixture of Russian River, Tomales Bay, and San Francisco Bay regions. Hopkirk (1973) disagreed with Snyder, placing Russian River individuals within the subspecies *H. s. navarroensis* and downgrading Tomales and San Francisco Bay individuals to population status. Aguilar & Jones (2009) found genetic distinctiveness for a Navarro/Russian grouping and a Tomales/SF Bay grouping within their microsatellite analyses. They also found some mtDNA distinctiveness for each location proposed (Navarro, Russian, and Tomales/SF Bay). Baumsteiger *et al.* (2017) found clear genomic distinctions between Navarro/Russian and Tomales/SF Bay individuals, consistent with other studies, supporting our assertion of two subspecies within the Coastal Roach species.

Description. Like other Coastal Roach, members of this subspecies are relatively trim, with a slender caudal peduncle, short, pointed snout, and variable length fins (dependent on which region is sampled). Individuals are typically 80-120 mm total length, with a large, conical head. Eyes are large and the mouth is sub-terminal. The dorsal fin has 7–9 rays (average 8) and the anal fin has 6–9 rays (average 8). Most pharyngeal teeth (0,5—4,0) have curved tips which overhang slightly. Scales are small, numbering 47–63 (average 54) along the lateral line. Fish appear darker on the upper half while the lower half is much lighter. Northern Coastal Roach differ from Gualala Roach in having fewer anal rays (Hopkirk 1973) and one less row of scales above the lateral line (Snyder 1913).

Distribution. Northern Coastal Roach are generally restricted to the Navarro River and Russian River basins. There are no records of Roach being found in watersheds between these basins. The exact distribution within the two watersheds is poorly documented but they appear to be present wherever water quality is suitable and alien predators are absent. The introduced population in the Eel River constitutes a major range expansion north.

Status. Because this subspecies is restricted to just two watersheds in its native range, it is highly subject to localized effects of farming, ranching, water diversions, dams, and other perturbations. However there are no reports of dwindling numbers in these systems, suggesting that, for now, populations of this subspecies are relatively robust.

Russian River Roach. The Russian River Roach was originally described as a population of *H. venustus* by Snyder (1913), along with populations in streams flowing intoTomales and San Francisco bays. Following the downgrading of this group to subspecies status, Russian River Roach were later lumped with Navarro Roach as *H.*

s. navarroensis by Hopkirk (1973). This move was confirmed genetically by Aguilar & Jones (2009). The recent analysis by Baumsteiger *et al*. (2017) found them to be part of the Northern subspecies of Coastal Roach but as a distinct population segment (DPS). Hierarchical genomic analyses revealed Eel River individuals cluster (are synonymous) with Russian River individuals in all analyses. An analysis using only fish from the two watersheds showed population structure at each of three sampling locations within the Russian River whereas within the Eel River there was no population structure among the four locations sampled. This means that the Eel River population is derived from a very recent introduction from the Russian River.

Description. Russian River Roach have a trim, slender body, a somewhat pointed snout, a slender caudal peduncle. The fins are somewhat longer than those of other Coastal Roach. They have 8–9 dorsal rays (average 9) and 7–9 anal rays (average 8); there are 8–11 gill rakers (average 10) and 47–60 scales in the lateral line (average 53) (Hopkirk 1973). Individuals rarely exceed 120 mm total length. Minor morphological differences were observed between Russian River and Navarro Roach by Snyder (1913) and Murphy (1948). Differences included a higher prevalence of individuals with 9 dorsal rays in the Russian rather than the 8 generally seen in Navarro (see Table 1).

Distribution. Russian River Roach are restricted to the Russian River and its tributaries in Sonoma Co. as well as to the Eel River watershed. They are common in the middle sections of many tributary creeks, including Mark West, Santa Rosa, Maacama, Austin, and Big Sulphur and Pieta (Moyle *et al.* 2015). Individuals are also present in the main stem Russian River (Pintler & Johnson 1958; Cook 2005). They become increasingly rare in the lower sections of the main river, where their downstream limit appears to be Duncan's Mill, just above the main estuary (Moyle *et al.* 2015). However, Goodwin *et al.* (1993) found that Roach seemed to move down into the estuary during the summer and return upstream in the fall. Within the Eel River watershed, fish are widespread and abundant, with Brown & Moyle (1997) finding individuals at 230 of 412 (56%) sampling locations in the watershed.

Status. Little is known of Russian River Roach abundance trends in their native habitat because few recent, systematic surveys have been conducted in tributary streams where they are most abundant. In the Russian River, gradual loss of tributary populations through dewatering and other factors, combined with mainstem river changes that reduce connectivity among tributaries may limit distribution and reduce abundance. The DPS is currently listed as a state Species of Special Concern (IUCN, Near-threatened) because of a limited distribution, the presence of dams and diversions in the Russian River watershed, and a poorly understood status (Moyle *et al.* 2015). Eel River fish were not included in the designation. The increasingly stressful conditions in the Russian River and its tributaries led Moyle *et al.* (2013) to rate the Russian River Roach as "highly vulnerable" to extinction in its native range as the result habitat loss due to climate change, if present trends continue.

Navarro Roach. Hopkirk (1973) was the first to suggest that the original species/subspecies described by Snyder (1913) should include Russian River individuals. Aguilar & Jones (2009) and Baumsteiger *et al.* (2017) later found genetic distinctiveness between individuals from the Navarro and Russian rivers, prompting their recognition as distinct population segments of Northern Coastal Roach.

Description. Like other Coastal Roach, Navarro Roach are small, stout-bodied cyprinids with a narrow caudal peduncle, deeply forked tail, short snout, and small, rounded paired fins. They are typically less than 100 mm total length. The head is large and conical, the eyes large and the mouth is sub-terminal and slants downward. The dorsal fin is short (7–9 rays; average 8) and is positioned behind the insertion point of the pelvic fin. The anal fin has between 6–9 rays. Pharyngeal teeth (0,5–4,0) have curved tips which overhang grinding surfaces of moderate size. Scales are small, numbering 47–63 along the lateral line and 32–38 before the dorsal fin. Individuals are usually dark on the upper half of their bodies, ranging from a shadowy gray to a steel blue, while the lower half is much lighter, usually a dull white/silver color. Snyder (1913) described them as having a light lateral stripe approximately two scales wide extending from upper edge of the gill opening to the base of tail and entirely above the lateral line. Below this line is a somewhat wider dark stripe and then several narrower and very distinct dark stripes which grow lighter ventrally. As mentioned previously, small morphological differences are found between Russian and Navarro populations (Table 1).

Distribution. Navarro Roach are confined to the Navarro River and its tributaries within Mendocino Co. (including Greenwood Creek) but are widely distributed within the watershed, from the mouth throughout the river and its tributaries (Feliciano 2004).

Status. The Navarro Roach, through its original lumping with CA Roach, was a state Species of Special

Concern with an IUCN status of Near-threatened (Moyle *et al.* 2015). However with its new taxonomic status, a re-evaluation will eventually be necessary, despite being widespread and abundant within its limited range. Most of the Navarro River watershed was logged and converted to orchards and vineyards in the 20th century. While removal of big trees created more of the warm-water habitat preferred by Navarro Roach, diversion of water has greatly reduced flows, presumably countering the effects of tree removal. Because of these factors, Moyle *et al.* (2013, 2015) considered it highly vulnerable to extinction in the next century from climate change and other factors.

Hesperoleucus venustus subditus **Snyder, 1913**
Southern Coastal Roach

Holotype: USNM 74475. Originally described as *Hesperoleucus subditus* from Pajaro Basin, San Benito and Santa Clara Cos., CA. *Paratypes*: BMNH 1900.9.29.176; CAS-SU 22489; USNM 49579, 75338–40, 75342–43, 75345–50.

Unlike previous listings by Snyder (1913), Tomales Bay (*H. venustus*) and Monterey Bay (*H. subditus*) species are genomically part of a southern subspecies of Coastal Roach (Baumsteiger *et al.* 2017). Previous works have recognized these individuals as distinct lineages both morphologically and genetically (Murphy 1948; Hopkirk 1973; Aguilar & Jones 2009). So while their distinctiveness seems consistent, their taxonomic level has not been properly defined till now.

Description. Adult total length is typically 55–100 mm, up to 125 mm. Roach typically have 7–10 dorsal rays (average 9), 6–8 anal rays (average 7), and 47–62 lateral line scales (average 54) (Hopkirk 1973). The remaining characters vary between different DPSs proposed within this subspecies (see below), including thickness of caudal peduncle, fin length, body size, and snout shape (Snyder 1913; Murphy 1948; Hopkirk 1973).

Distribution. Southern Coastal Roach are restricted to the drainages of Tomales Bay/northern SF Bay in the north and Monterey Bay in the south. There are no records of Roach being present in watersheds between these two systems but thorough sampling is needed to be sure of their absence.

Status. Although both DPSs within this subspecies are considered to be Near-threatened (see below), the subspecies as a whole seems fairly abundant in their native ranges (Moyle *et al.* 2015). However, this is still probably a small subset of the original range of this subspecies, given the current geographic divide between the two DPSs within the subspecies. Both are found in areas where freshwater sources are limited and human use is high, making them candidates for decline through water manipulation. Additionally, most locations with this subspecies are relatively small, isolated creeks, making climate change an increasing problem for their persistence.

Tomales Roach. Snyder (1913) described *Hesperoleucus venustus* from the Russian River, Tomales Bay tributaries, and San Francisco Bay tributaries. Hopkirk (1973) recognized that Roach from these three regions were different from each other but similar enough to California Roach that he declared *H. venustus* to be a synonym of *H. s. symmetricus.* He did suggest, however, that individuals in Tomales Bay tributaries were distinct enough to be recognized as a subspecies. The genetic studies of Jones (2001), Aguilar & Jones (2009) and Baumsteiger *et al.* (2017) indicated that populations from Tomales Bay tributaries are distinct, which we recognize here. Jones (2001) found populations of Tomales Roach from Lagunitas and Walker creeks shared nuclear DNA allele frequencies but were reciprocally monophyletic for mitochondrial DNA haplotypes. Aguilar & Jones (2009) determined from the mtDNA analysis of fish from Lagunitas and Walker Creeks that they were clearly a distinct lineage from CA Roach. Microsatellites, however, were not as definitive, with one analysis finding weak support for Tomales Roach as a distinct lineage, while another analysis found that, although distinguishable, individuals from Lagunitas and Walker Creeks clustered with Monterey Roach. Our genomic analysis (Baumsteiger *et al.* 2017) provided further clarity, showing that Tomales Bay locations are clearly definable within the Southern Coastal Roach subspecies, as a distinct population segment.

Description. Tomales Roach look similar to other members of the CA Roach complex but are most similar to Russian River Roach (Table 1). Adult total length is typically 55–100 mm, up to 125 mm. Like Russian River Roach, Tomales Roach differ from CA Roach in having a more trim, slender body, a more pointed snout, a more slender caudal peduncle, and longer fins. Tomales Roach have 8–10 dorsal rays (average 9), 6–7 anal rays (average 7), and 47–62 lateral line scales (average 54) (Hopkirk 1973).

In tributaries to San Francisco Bay, Snyder (1905, 1908) demonstrated that sex could be established by using the ratio of pectoral fin length to body length. Males exhibited a ratio of > 0.21 while females bore pectoral fins between 0.16 and 0.20 the length of their body. Both sexes exhibit bright orange and red breeding coloration on the operculum, chin and the base of the paired fins. Males may also develop numerous small breeding tubercles (pearl organs) on the head (Murphy 1943).

Distribution. Tomales Roach are restricted to the Lagunitas Creek and Walker Creek drainages of western Marin County. Roach of uncertain taxonomic affinity have also been reported from Pine Gulch Creek, tributary to Bolinas Lagoon (Murphy 1948) and Salmon Creek, Marin Co. (Moyle 2002). However, a 1997 survey of Pine Gulch Creek recorded no Roach present (Fong 1999).

Status. There is no indication that Tomales Roach in Walker and Lagunitas Creeks are in decline, but no regular surveys exist. Dams and diversions, however, have altered flows and habitat. They are currently listed as a state Species of Special Concern (IUCN Status, Near-threatened) but do not appear to be in immediate danger of extinction as a DPS. Fragmentation of populations, along with habitat alterations, may be limiting distribution and abundance (Moyle *et al.* 2015). Increasing urban water demands, coupled with predicted climate change impacts, are likely to lead to more widespread drying of stream segments and elimination of Roach populations. As a result, Moyle *et al.* (2013) considered Tomales Roach as "highly vulnerable" to extinction by 2100 from the effects of climate change. Moyle *et al.* (2015) considered it to be a species of "moderate concern", not facing immediate extinction threats.

Monterey Roach. The Monterey Roach has been of interest because of its frequent hybridization with Monterey Hitch (*L. e. harengus*) (Miller 1945; Avise *et al.* 1975) but it retains its identity as a distinct taxon (Baumsteiger *et al.* 2017). Its isolation from other populations within the subspecies is of note, indicating that should be managed as a distinct population segment.

Description. Monterey Roach are similar in appearance to CA Roach (see description) but can be distinguished by having fewer dorsal (7–9; average 8) and anal fins rays (6–8; average 7), fewer scales in the lateral line, slightly shorter fins, a slightly more robust body and a thicker caudal peduncle (Snyder 1913; Murphy 1948; Hopkirk 1973).

Distribution. Monterey Roach are widely distributed in the Pajaro, Salinas, and San Lorenzo River systems as well as Soquel Creek, all tributaries to Monterey Bay on the central coast of California. Pescadaro Creek, just north of Monterey Bay, also contains Monterey Roach. Within the Pajaro watershed, Monterey Roach no longer occur in the mainstem but are present in Uvas Creek, Llagas Creek upstream of Chesbro Reservoir, the North Fork of Pacheco Creek upstream of Pacheco Reservoir, Arroyo Dos Picachos and in the San Benito River and its tributaries, including Tres Pinos, Laguna, and Clear Creeks (Smith 2007). In the Salinas River system, Roach also have been extirpated from the mainstem and now occur primarily in tributaries such as Arroyo Seco (J.J. Smith, pers. comm. 2009) and Gabilan Creek, although recent survey information is lacking.

Status. Monterey Roach are apparently still numerous and widely distributed in smaller streams in much of their native range, but the DPS has been largely extirpated from the mainstem Pajaro and Salinas River systems due to habitat alteration, degraded water quality and quantity and alien species (Smith 1982, 2007). Long-term trends are not known but populations are likely fewer and more fragmented than historically. Moyle *et al.* (2015) listed them as a state Species of Special Concern (IUCN status of Near-threatened) and noted they were "highly vulnerable" to climate change due to potential reductions in stream flow throughout the watersheds (Moyle *et al.* 2013).

***Hesperoleucus mitrulus* Snyder, 1913**
Northern Roach

Holotype: USNM 74474. Originally described from Drew Creek, Lake Co., OR. *Paratypes*: CAS-SU 22491; UMMZ 139019.

Northern Roach were first collected in 1898 by C. Rutter as *Rutilus symmetricus* (Rutter 1908). Rutter (1908: 139) stated "We have but few small specimens of this form, the longest being but 3 inches long. They were taken in North Fork Pitt (sic) River near Alturas and at the mouth of Joseph Creek, several hundred miles from where any other specimens of *symmetricus* have been taken. The form may prove to not to be *symmetricus*, but we cannot identify it otherwise with the material at hand." In 1913, Snyder described the Goose Lake drainage fish as *Hesperoleucus mitrulus.* The first inclusion of Roach from the Pit River as part of *H. symmetricus* was by Hubbs *et al.* (1979). Genetically, Aguilar & Jones (2009) found that individuals from these locations were distinct from all other CA Roach. Our genomic study (Baumsteiger *et al.* 2017) also found all individuals collected from these locations to be distinct at the species-level in every analysis.

Description. Northern Roach are small (adult size typically 50–100 mm TL) bronzy cyprinids, similar in appearance to the California Roach (Moyle 2002; Fig. 3). They have a robust body, deep caudal peduncle, short snout and short rounded fins. Northern Roach differ from CA Roach in having short rounded fins and "cup-like" scales (Snyder 1913; Table 1). Snyder (1908) examined 20 fish from Drew Creek, Oregon and all individuals had 8 dorsal rays and 7 anal rays. Snyder found that males had longer, larger fins than did females, especially pectoral fins; the sexes could be differentiated by the ratio of pectoral fin length to body length.

FIGURE 3. *Hesperoleucus mitrulus,* Northern Roach. Ana River, Lake Co., Oregon. September 27, 2010. Photo by Stewart Reid

Distribution. The original collections by Rutter (1908) consisted of the North Fork of the Pit River and the mouth of Joseph Creek. Snyder (1908) collected widely in the upper Pit River, Goose Lake basin of California and Oregon, and in the Summer, Abert, Harney and Warner basins of Oregon but only found Roach in tributaries to Goose Lake, Lake Co., Oregon. The first inclusion of individuals from the Pit River as part of this species was by Hubbs *et al.* (1979). While no mention is made of a range extension for the taxon, it is assumed this change was precipitated by the 1934 collection of 19 roach in the North Fork Pit River near Alturas, Modoc County (unpublished field notes and collections of Carl Hubbs at the Univ. of Michigan as reported in Reid *et al.* 2003).

In the most comprehensive sampling of the Pit system in California to date, Moyle and Daniels (1982) found Roach at only 8% of 261 collection sites. Northern Roach were found in only three widely separated drainages: (1) Ash–Rush–Willow Creek drainage, Lassen/Modoc Co., (2) Bear Creek, tributary to the Fall River, Shasta Co. and (3) Beaver Creek, Lassen Co. All locations are above Pit River Falls (Shasta Co.) which divides the Pit River Basin into upper and lower drainages. The falls are a barrier to fish movement (Kinziger *et al.* 2016). Historically, the waterfall was the northern range limit for some Sacramento River fishes, such as Tule Perch, *Hysterocarpus traskii* (Moyle 2002). Roach below the falls had unimpeded access to the Sacramento River system and are assumed to be *H. s. symmetricus*. However, genetic and morphometric studies have not been conducted and relationships remain uncertain.

Status. Northern Roach have been uncommon in California ever since they were first collected in 1898, although by that time much of the Pit River drainage had been heavily altered by grazing, agriculture and logging (Moyle & Daniels 1982). Subsequently, alien fish species that compete with or prey on Northern Roach (e.g. Green Sunfish, *Lepomis cyanellus*) became widely introduced. Their absence from some streams, however, may be the result of specific habitat requirements. Northern Roach prefer spring pools and swampy stream reaches, unlike the intermittent stream habitats where other species of Roach are found (S. Reid, pers. comm.). Thus in Lassen/Modoc Co., Roach are found in small numbers, inhabiting the weedy margins of streams and, in one case, an isolated spring pond (Moyle & Daniels 1982; S. Reid, pers. comm.). However a fairly recent survey of fishes in the Oregon portion of the Goose Lake watershed found Northern Roach to be relatively abundant in six small creeks (Scheerer *et al.* 2010).

Moyle *et al.* (2015) rated the Northern Roach as a Species of Special Concern in California and the

International Union for the Conservation of Nature (IUCN) lists their status as High Concern. Additionally, these Roach are highly vulnerable to extinction in the next century from climate change effects on their small streams (Moyle *et al.* 2013).

***Hesperoleucus parvipinnis* Snyder, 1913**
Gualala Roach

Holotype: USNM 74466. Originally described from Gualala River, Sonoma Co., CA. *Paratypes*: CAS-SU 14903.

Gualala Roach were first collected by Snyder (1908) who recognized them as *Rutilus symmetricus* but noted they bore "a distinctive local stamp by which they can be recognized without difficulty (p 175)." He later (1913) described them as *H. parvipinnis.* Murphy (1948) suggested these individuals constituted a subspecies not a species. Aguilar & Jones (2009) found them to be strongly genetically different from any other Roach along the California coast, suggesting they were more than a subspecies. Baumsteiger *et al.* (2017) found individuals within the Gualala system to be distinctive at the species level in all analyses, with pairwise F_{ST} estimates between these individuals and Northern Roach to be the highest in the study (0.895). Thus the consensus reconfirms what Snyder (1913) proposed, that Gualala Roach are indeed a distinct species within *Hesperoleucus*.

Description. Adult Gualala Roach are small (typically 50–80 mm) and bronzy in color, similar in general appearance to California Roach (*H. symmetricus*). However, they differ from other Roach species by having smaller scales (54–65 along the lateral line), shorter, more rounded fins, a shorter snout (in relation to head length) and a more robust body (Table 1). Gualala Roach have 7–8 dorsal rays (average 8) and 6–8 (average 7) anal rays (Hopkirk 1973). Snyder (1913 p. 66) described Gualala Roach as having "a light lateral stripe two scales wide extending from upper edge of gill opening to base of caudal and entirely above the lateral line; below is a somewhat wider dark stripe, which in turn is followed by several narrower and very distinct dark stripes which grow lighter ventrally."

Distribution. Gualala Roach are confined to the Gualala River and its tributaries in Sonoma Co. They are the most abundant fish species in the South and Wheatfield forks and in most headwater streams (Entrix 1992; DeHaven 2008). Occurrence is greatly reduced in the colder North Fork (Parker and Pool 1964; CDFG 1991) and in the mainstem below its confluence with the North Fork (Kimsey 1953; DeHaven 2008).

Status. Historically, Gualala Roach were present throughout the Gualala River basin (Higgins 1997). Agency salmonid surveys indicate Roach may have increased in abundance due to habitat alterations favorable to warm water-tolerant species (Higgins 1997). Moyle *et al.* (2013) rate this species as "highly vulnerable" to extinction due to climate change. Statewide this is a species of Special Concern (IUCN status, Near-threatened) because of its limited distribution and increasing threats from vineyard and rural residential development, including introductions of non-native fishes (Moyle *et al.* 2015).

Clear Lake Roach, *Hesperoleucus venustus* x *H. symmetricus*

Because the Clear Lake Basin has had hydrological connections to both Sacramento and Russian Rivers in the past (Hopkirk 1973; Moyle 2002; Baumsteiger *et al.* 2016), it is no surprise that a genomic appraisal found Clear Lake Roach to be admixed between Coastal and CA Roach species (Baumsteiger *et al.* 2017). Such hybrid lineages are neither well defined nor distinctive at the genetic/genomic level, so much debate has ensued as to how to properly classify hybrid 'species' (Baack and Rieseberg 2007; Sangster 2014). With no clear rules in place, we focus instead on other factors. While originating as a hybrid, the Clear Lake Roach is now completely isolated from both parent species. There is no sign of either positive (e.g., hybrid vigor) or negative (reduced reproductive capacity) hybrid impacts because individuals occupy small stream habitats in large numbers in much the same way as populations of both parental species. All this suggests hybridization was not a recent event and Clear Lake Roach are behaving similar to Roach populations without mixed ancestry. Given indications that Northern Roach also potentially began as hybrids between Hitch and Roach (but in the more distant past), the Clear Lake Roach is presumably on a similar evolutionary pathway to species status. We therefore treat it as a species or distinct population segment (for the sake of its conservation) by its common name but as a hybrid by its scientific name (until better rules are in place for naming hybrid 'species').

Description. Clear Lake Roach are very similar to California Roach in appearance. Clear Lake Roach have 8–10 dorsal rays (average 9) and 7–9 anal rays (average 8) (Hopkirk 1973). The head is large and conical and the dorsal fin positioned behind the insertion point of the pelvic fin. Eyes are small to moderate in size, the snout is short, and the mouth is sub-terminal, slanting at a downward. The pharyngeal teeth (0,5–4,0) have curved tips, which overhang grinding surfaces. Clear Lake Roach are usually dark on the upper half of their bodies, ranging from a shadowy gray to a steel blue, while the lower half of the body is much lighter, usually a dull white. Scales are small, numbering 49–58 (average 53) along the lateral line.

Distribution. Clear Lake Roach are restricted today to tributaries of Clear Lake, where they are widely distributed and presumed native to the lake as well (Stone 1876). Individuals are now unable to occupy the lake due to abundant alien predators (Moyle 2002). Taylor *et al.* (1982) found these fish in all major tributary systems: Siegler, Cole, Kelsey, Adobe, Highland, Scotts and Middle Creeks. All streams except Cole Creek become intermittent by late fall in their lower reaches. Clear Lake Roach were not found above waterfalls or in high gradient stream sections in all tributaries (Taylor *et al.* 1982).

Status. Stone (1876) noted that Roach were present in Clear Lake in "vast abundance" in shallow water; this observation assumes they were identified correctly. Today, Clear Lake Roach are absent from the lake proper but presumably continue to maintain populations in the tributary systems, although systematic surveys have not been performed since Taylor *et al.* (1982). Clear Lake Roach are a state Species of Special Concern, with an IUCN rating of Near-threatened (Moyle *et al.* 2015). This status is given because of the increasing isolation of their populations in combination with removal of water from their streams and development of the watersheds for vineyards and rural housing. Moyle *et al.* (2013) rated them "highly vulnerable" to climate change.

Discussion

Our analysis shows that the genera *Hesperoleucus* and *Lavinia* represent distinct lineages and that *Hesperoleucus* is best treated as four species that can be further subdivided into subspecies and distinct population segments (Fig. 4).

The Roach–Hitch complex reflects the complex geology of California that provides many opportunities for isolation and speciation (Harrison 2013). Roach in particular show speciation in response to isolation and local adaptation. The diverse taxa are small stream specialists, capable of handling the physiological challenges of streams that experience multiple years of severe droughts on top of annual summer drought, brought on by the Mediterranean climate. This taxonomic investigation reveals the potential for speciation via hybridization (Northern Roach, Clear Lake Roach), the ability of Roach to adapt to some of most extreme habitats known for fishes (Red Hills Roach), and their ability to adapt readily to new habitats (Eel River, Hetch-Hetchy Reservoir) under the right conditions. Our study also reveals that Roach are more diverse than once thought which presents challenges for conservation. Most Roach taxa are threatened to some degree by climate change and by diversion of water from their streams, as well as by land use changes and introductions of alien species. Even the most widespread taxon, California Roach, is no longer present in over half its range and is separated into dozens of historically-connected populations that are now isolated from one another. We hope that our genomics-based recognition of species, subspecies, and distinct population segments will improve the chances of these inconspicuous but diverse endemic fish persisting for the indefinite future. The next step from here is to do the surveys needed to determine the status of each taxon and to find ways to alleviate threats to their existence.

Finally, we need to mention that we continue to be impressed by the perspicuity of John Otterbein Snyder and other 19th and early 20th century taxonomists. It took the latest genomic techniques to show convincingly that Snyder's taxonomic determinations were by and large correct, after years of demotion.

Acknowledgements

We are grateful for the logistical and financial support of the University of California Davis Center for Watershed Sciences: thanks especially to Cathryn Lawrence and Jay Lund. Fish used in this study were collected over decades by affiliates of the Moyle Laboratory too numerous to mention, although the efforts of Dr. Larry Brown are especially notable. Curator Irene Engilis was very helpful in working with us to use the fish collection of the

Museum of Wildlife, Fish and Conservation Biology at UC Davis. We appreciate the insights into developing Roach genomics provided by Michael Miller and Sean O'Rourke from the Department of Animal Sciences at UC Davis. The distribution map was created by Nick Santos, assisted by Amber Manfree.

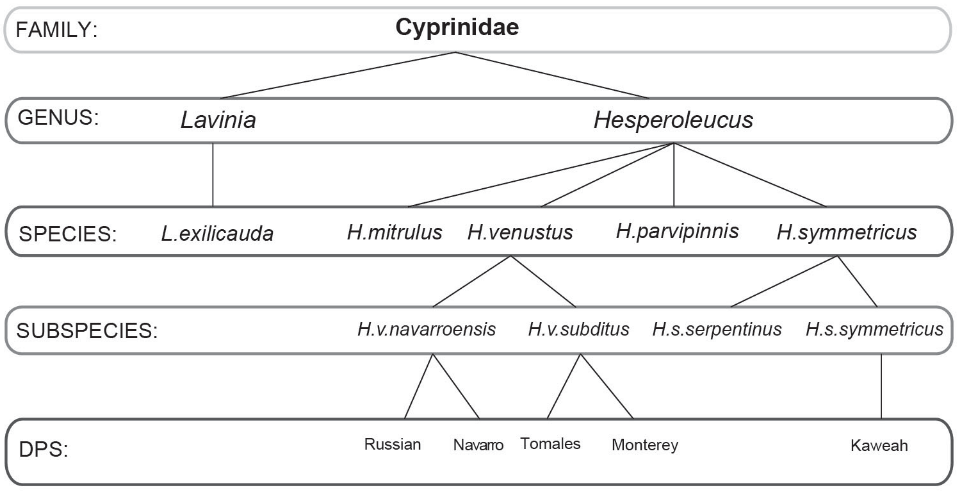

FIGURE 4. Complete taxonomic hierarchy for the California Roach/Hitch Species Complex

References

Abbott, R., Albach, D., Ansell, S., Arntzen, J.W., Baird, S.J., Bierne, N., Boughman, J., Brelsford, A., Buerkle, C.A., Buggs, R. & Butlin, R.K. (2013) Hybridization and speciation. *Journal of Evolutionary Biology*, 26, 229–246.

Aguilar, A. & Jones, W.J. (2009) Nuclear and mitochondrial diversification in two native California minnows: insights into taxonomic identity and regional phylogeography. *Molecular Phylogenetics and Evolution*, 51, 373–381.

Anacker, B.L. & Harrison, S.P. (2012) Climate and the evolution of serpentine endemism in California. *Evolutionary Ecology,* 26, 1011–1023.

Andrews, K.R., Good, J.M., Miller, M.R., Luikart, G. & Hohenlohe, P.A. (2016) Harnessing the power of RADseq for ecological and evolutionary genomics. *Nature Reviews Genetics*, 17, 81–92.

Avise, J.C. & Ayala, F.J. (1976) Genetic differentiation in speciose versus depauperate phylads: evidence from the California minnows. *Evolution*, 30, 46–58.

Avise, J.C., Smith, J.J. & Ayala, F.J. (1975) Adaptive differentiation with little genic change between two native California minnows. *Evolution*, 29, 411–426.

Ayres, W.O. (1854) Descriptions of new species of cyprinoids. Originally published in *Daily Placer Times and Transcript*, May 1854 and reprinted in 1855 in *Proceedings of California Academy of Sciences,* 1, 18–22.

Baack, E.J. & Rieseberg, L.H. (2007) A genomic view of introgression and hybrid speciation. *Current Opinion in Genetics & Development* 17(6), 513-518.

Baird, S.F. & Girard, C.F. (1854) Descriptions of new species of fishes collected in Texas, New Mexico and Sonora, by Mr. John H. Clark, on the US and Mexican boundary survey and in Texas by Capt. Stewart Van Vliet, *Proceedings, Academy of Natural Sciences of Philadelphia* ,7, 24–29.

Baumsteiger, J., Kinziger, A.P. & Aguilar, A. (2016) Novel concordance between geographic, environmental, and genetic structure in the ecological generalist prickly sculpin (*Cottus asper*) in California. *Journal of Heredity*, 107, 504–517.

Baumsteiger, J., Moyle, P.B., Aguilar, A., O'Rourke, S.M. & Miller, M.R. (2017) Genomics clarifies taxonomic boundaries in a difficult species complex. *PloS One*, 12(12), e0189417.

Brown, L.R. & Moyle, P.B. (1993) Distribution, ecology, and status of the fishes of the San Joaquin River drainage, California. *California Fish and Game*, 79, 96–114.

Brown, L.R. & Moyle, P.B. (1997). Invading species in the Eel River, California: successes, failures, and relationships with resident species. *Environmental Biology of Fishes*, 49, 271–291.

Brown, L.R., Moyle, P.B., Bennett, W.A. & Quelvog, B.D. (1992) Implications of morphological variation among populations of California roach *Lavinia symmetricus* (Cyprinidae) for conservation policy. *Biological Conservation*, 62, 1–10.

CDFG (California Department of Fish and Game) (1991) *Little North Fork Gualala River Electroshocking Summary, 1986-1991*. Unpublished Report, Yountville, CA. 20 pp.

Cook, D. (2005) *Chinook Salmon Spawning Study, Russian River, Fall 2002–2004*. File Report. Sonoma County Water Agency,

Santa Rosa, CA. 20 pp.
DeHaven, R.W. (2008) *Adult and Juvenile Steelhead Population Surveys, Gualala River, California, 2008.* Unpublished report, prepared by the author December 31, 2008, for use by agencies, groups and individuals involved in steelhead recovery efforts. 47 pp.
De Queiroz, K. (2007) Species concepts and species delimitation. *Systematic Biology,* 56 (6), 879–886.
Entrix Inc. (1992) *South Fork Gualala River Fishery Resource Study*. Prepared for the Sea Ranch Water Company. Walnut Creek, CA. 63 pp.
Evermann, B. & Clark, H.W. (1931) A distributional list of the species of freshwater fish known to occur in California. *California Division of Fish and Game Fish Bulletin*, 35, 1–67.
Feliciano, J.B. (2004) *A Study of the Salmonid Populations in the Navarro River Watershed: Tracking Declines and Tools for Monitoring*. Ph.D. Dissertation, University of California, Davis. 80 pp.
Fong, D. (1999) 1997 *California Freshwater Shrimp (Syncaris pacifica) Surveys within Point Reyes National Seashore and Golden Gate National Recreation Area (GGNRA)* Prepared for the GGNRA, Division of Resource Management and Planning, and the U.S. Fish and Wildlife Service, Endangered Species Permits, Ecological Services, Portland Regional Office. 30 pp.
Fricke, R. & Eschmeyer, W.N. (2018) A guide to the fish collections in the Catalog of Fishes. Electronic version. Available from: http://researcharchive.calacademy.org/research/ichthyology/ catalog/fishcatmain.asp (accessed 6 August 2018).
Gard, M. & Randall, P. (2004) Setting priorities for native fish conservation: An example from the South Yuba River watershed. *California Fish and Game*, 90, 1–12.
Goodwin, P., Cuffe, C.K., Nielsen, J.L. & Light, T. (1993) *Russian River Estuary Study, 1992–1993*. Department of Planning, Sonoma County, California, U.S.A. 186 pp.
Greenfield, D.W. & Deckert, G.D. (1973). Introgressive hybridization between *Gila orcutti* and *Hesperoleucus symmetricus* (Pisces: Cyprinidae) in the Cuyama River Basin, California: II. Ecological aspects. *Copeia,* 1973, 417–427.
Harrison, S. (2013) *Plant and Animal Endemism in California*. University of California Press, Berkeley. 189 pp.
Higgins, P. (1997) *Gualala River Watershed Literature Search and Assimilation*. Redwood Coast Land Conservancy, Gualala CA. 57 pp.
Hopkirk, J.D. (1973) Endemism in fishes of the Clear Lake region of central California. *University of California Publications in Zoology,* 96, 1–160.
Hubbs, C.L. Follett, W.I. & Dempster, L.J. (1979) List of the fishes of California. *Occasional Papers of the California Academy of Sciences,* 133, 1–51
Jones, W.J. (2001) *DNA Sequence Divergence and Speciation in Two California Minnows (Cyprinidae:* Lavinia exilicauda *and* L. symmetricus). PhD Dissertation, University of California, Santa Cruz. Ca. 150 pp.
Jones, W.J., Quelvog, B.D. & Bernardi, G. (2002) Morphological and genetic analysis of the Red Hills roach (Cyprinidae: *Lavinia symmetricus*). *Conservation Genetics*, 3, 261–276.
Jordan, D.S. & Evermann, B.W. (1896) *A Check-list of the Fishes and Fishlike Vertebrates of North and Middle America*. US Government Printing Office, Washington D.C. 584 pp.
Kimsey, J.B. (1953) *Population Sampling of Three North Coastal Streams Closed to Summer Trout Fishing -1952 Season. First Progress Report*. California Department of Fish and Game, Sacramento. 15 pp.
Kinziger, A.P., Hellmair, M., Fong, S.R., Goodman, D.H. & Kelsey, H. (2016) Evolution of rough sculpin (*Cottus asperrimus*) genetic divergence and late Quaternary displacement on the Hat Creek fault, California, USA. *Conservation Genetics*, 17, 1257–1267.
Leidy, R.A. (1984) Distribution and ecology of stream fishes in the San Francisco Bay drainage, *Hilgardia,* 52(8), 1–175.
Leidy, R.A. (2007) *Ecology, Assemblage Structure, Distribution, and Status of Fishes in Streams Tributary to the San Francisco Estuary, California.* San Francisco Estuary Institute, San Francisco. 194 pp.
Linnaeus, C. (1758) *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum chararteribus, differentiis, synonymis, locis (Holmiae: Laurentii Salvii)*. *Tomus 1: Regnum animale.* 10th Ed. Stockholm, 824 pp.
Mallet, J. (2007) Hybrid speciation. *Nature*, 446(7133), 279.
Miller, R.R. (1945) The status of *Lavinia ardesiaca*, a cyprinid fish from the Pajaro-Salinas River basin, California. *Copeia*, 1945, 197–204.
Miller, R.R. (1963) Synonymy, characters, and variation of *Gila crassicauda*, a rare Californian minnow, with an account of its hybridization with *Lavinia exilicauda*. *California Fish and Game*, 49, 20–29.
Moyle, P.B. (2002) *Inland Fishes of California*. University of California Press, Berkeley, California. 502 pp.
Moyle, P.B., Crain, P.K., Whitener, K. & Mount, J.F. (2003) Alien fishes in natural streams: fish distribution, assemblage structure, and conservation in the Cosumnes River, California, USA. *Environmental Biology of Fishes,* 68, 143–162.
Moyle, P.B. & Daniels, R.A. (1982) Fishes of the Pit River system, and Surprise Valley region. *University of California Publications in Zoology*, 115, 1–82.
Moyle, P.B., Hobbs, J. & O'Rear, T. (2012) Fishes. *In* A. Palaima, ed. *Ecology, Conservation and Restoration of Tidal Marshes: The San Francisco Estuary.* University of California Press. Berkeley. pp. 161–173.
Moyle, P.B., Katz, J.V.E. & Quiñones, R.M. (2011) Rapid decline of California's native inland fishes: a status assessment. *Biological Conservation,* 144, 2414-2423.
Moyle, P.B., Kiernan, J.D., Crain, P.K. & Quinones, R.M. (2013) Climate change vulnerability of native and alien freshwater

fishes of California: a systematic assessment approach. *PLoS One*, 8(5), e63883.
Moyle, P.B., Lusardi, R. Samuel, P. & Katz, J. (2017) *State of the Salmonids: Status of California's Emblematic Fishes 2017.* Center for Watershed Sciences, University of California, Davis and California Trout, San Francisco, CA., 579 pp.
Moyle, P.B. & Massingill, M. (1981) Hybridization between hitch, *Lavinia exilicauda*, and Sacramento blackfish, *Orthodon microlepidotus*, in San Luis Reservoir, California. *California Fish and Game,* 67, 196–198.
Moyle, P.B. & Nichols, R.D. (1973) Ecology of some native and introduced fishes of the Sierra Nevada foothills in central California. *Copeia*, 1973, 478–490.
Moyle, P.B., Quiñones, R.M., Katz, J.V.E. & Weaver, J. (2015) *Fish Species of Special Concern in California*. 3rd edition. California Department of Fish and Wildlife, Sacramento *Ca.* 300 pp. *https://www.wildlife.ca.gov/Conservation/Fishes/Special-Concern*
Moyle, P.B., Williams, J.E. & Wikramanayake, E.D (1989) *Fish Species of Special Concern of California*. California Department of Fish and Game. Sacramento. 272 pp.
Murphy, G. (1943) Sexual dimorphism in the minnows *Hesperoleucus* and *Rhinichthys*. *Copeia*, 1943, 187–188.
Murphy, G. (1948*) Distribution of Variation of the Roach* (Hesperoleucus) *in the Coastal Region of California*. M.A. Thesis, University of California, Berkeley. 55 pp.
Page, L.M., Espinosa-Pérez, H., Findley, L.T., Gilbert, C.R., Lea, R.N., Mandrak, N.E., Mayden, R.L. & Nelson, J.S. (2013) *Common and Scientific Names of Fishes from the United States, Canada, and Mexico,* American Fisheries Society, Bethesda, Maryland. 243 pp.
Parker, C. & Pool, R. (1964) *North Fork Gualala River Stream Survey, North Fork Gualala River surveyed by foot and automobile from the mouth to the headwaters, a total of 15 miles*. September 17–18, 1964. File report, California Department of Fish and Game, Region 3, Yountville, CA. 2 pp.
Pintler, H.E. & Johnson, W.C. (1958) Chemical control of rough fish in the Russian River drainage, California. *California Fish and Game*, *44*, 91–124.
Power, M.E., Bouma-Gregson, K., Higgins, P. & Carlson, S.M. (2015) The thirsty Eel: summer and winter flow thresholds that tilt the Eel River of northwestern California from salmon-supporting to cyanobacterially degraded states. *Copei*a, 2015, 200–211.
Reid, S.B., Cowan, W. & Byers, S. (2003) *Mainstem upper Pit River fish surveys including the North and South Fork Pit Rivers, September 2002*. File Report, U.S. Fish and Wildlife Service, Klamath Falls, Oregon. 53 pp
Rutter, C. (1908) The fishes of the Sacramento-San Joaquin basin: with a study of their distribution and variation. *Bulletin, U.S. Fish Commission,* 27, 103–152.
Sangster, G. (2014) The application of species criteria in avian taxonomy and its implications for the debate over species concepts. *Biological Reviews,* 89, 199–214.
Scheerer, P.D., Gunckel, S.L., Heck M.P. & Jacobs, S.E. (2010) Status and distribution of native fishes in the Goose Lake Basin. Northwestern Naturalist, 91, 271–287.
Schönhuth, S., Hillis, D.M., Neely, D.A., Lozano-Vilano, L., Perdices, A. & Mayden, R. L. (2012) Phylogeny, diversity, and species delimitation of the North American round-nosed minnows (Teleostei: *Dionda*), as inferred from mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution*, 62, 427–446.
Seehausen, O., Butlin, R.K., Keller, I., Wagner, C.E., Boughman, J.W., Hohenlohe, P.A., Peichel, C.L., Saetre, G.P., Bank, C., Brannstrom, A. & Brelsford, A. (2014) Genomics and the origin of species. *Nature Reviews Genetics*, 15, 176–192.
Shapovalov, L. & Dill, W.A. (1950) A check list of the fresh-water and anadromous fishes of California. *California Fish and Game,* 36, 382–391.
Shapovalov, L., Dill, W.A. & Cordone, A.J. (1959) A revised checklist of the freshwater and anadromous fishes of California. *California Fish and Game*, *45*, 159–180.
Smith, J.J. (1982) Fishes of the Pajaro River system. *University of California Publications in Zoology*, 115, 83–170.
Smith, J.J. (2007) *Steelhead Distribution and Ecology in the Upper Pajaro River System and Mainstem Pajaro River.* Unpublished Report 7, Department of Biology, San Jose State University. *Ca.* 40 pp.
Snyder, J.O. (1905) Notes on the fishes of the streams flowing into the San Francisco Bay. *Report for U.S. Bureau Fisheries for 1904*, 327–338.
Snyder, J.O. (1908) The fishes of the coastal streams of Oregon and northern California. *Bulletin, U.S. Bureau of Fisheries,* 27, 153–189.
Snyder, J.O. (1913) The fishes of the streams tributary to Monterey Bay, California*. Bulletin, U.S. Bureau of Fisheries,* 32, 49–72.
Stone, L. (1876) *Report of Operations in 1873: Clear Lake*. United States Commission of Fish and Fisheries, Report of the Commissioner for 1873–74 and 1874-75, Appendix B, 377–381.
Taylor, T.L., Moyle, P.B. & Price, D.G. (1982) Fishes of the Clear Lake basin. *University of California Publications in Zoology,* 115, 171–224.