Calif. Fish and Game 79(3):96-114 1993

DISTRIBUTION, ECOLOGY, AND STATUS OF THE FISHES OF THE SAN JOAQUIN RIVER DRAINAGE, CALIFORNIA

LARRY R. BROWN[1] AND PETER B. MOYLE
Department of Wildlife and Fisheries Biology
University of California
Davis, CA 95616

In 1985 and 1986 we sampled streams of the San Joaquin River drainage in south-central California. The purposes of the survey were: (i) to see if further declines in native fish populations had occurred since 1970 when they were last surveyed; (ii) to verify the species distributions and species-habitat relationships observed in previous studies; (iii) to verify the species assemblages observed in previous studies; and (iv) to determine the status of the recently described Kern brook lamprey (*Lampetra hubbsi*). We also reviewed the status of the native fish fauna as compared to pre-European times. Only 11 species of the original fauna of 19 species were found and only 6 of the 11 were common. Hardhead (*Mylopharodon conocephalus*) and hitch (*Lavinia exilicauda*) were found in fewer localities than in 1970. The decline in hardhead was associated with an expansion of smallmouth bass (*Micropterus dolomieu*) populations. Three assemblages of native species were identified, in agreement with earlier studies. A fourth assemblage identified in earlier studies, composed largely of introduced fishes, was divided into two subgroups on the basis of our analysis. Each assemblage of species was associated with a distinct set of habitat characteristics. Populations of Kern brook lamprey were found in the Kaweah, Kings, San Joaquin, and Merced rivers. Lampreys were absent from the lower reaches of the rivers and, except in the Kings River, were only found below major dams. In the Kings River lampreys were captured above and below Pine Flat Reservoir. Because the populations are restricted in range, effectively isolated from one another, and all but one can be affected by reservoir operations, special protection for them is warranted.

INTRODUCTION

About half of California's water flows through the Sacramento-San Joaquin drainage basin, which includes the Central Valley (Karhl et al. 1978). Despite the large size of the drainage, only 34 species of freshwater or anadromous fish are native to it, 17 of them endemic (Moyle 1976, Moyle and Williams 1990). The San Joaquin basin is the most southern and most arid portion of the Sacramento-San Joaquin drainage and historically contained 19 of the 34 species (Table 1), including 12 of the 17 endemic forms (Moyle 1976). The Kern brook lamprey (*Lampetra hubbsi*) is found only in the San Joaquin River drainage (Vladykov and Kott 1976), as are three subspecies of rainbow trout (*Oncorhynchus mykiss whitei*, *O.m. aquabonita*, and *O.*

[1]Present adress: U.S. Geological Survey, 2800 Cottage Way, Rm. W-2234, Sacramento, CA 95825

m. gilberti) (Moyle 1976, Berg 1987). In addition, the California roach (*Lavinia symmetricus*) appears to have a number of distinctive populations in the drainage although their taxonomic status has not been fully determined (Brown et al. 1992).

Because the San Joaquin Valley is intensively farmed, most of the water that once flowed into the San Joaquin River or into large lakes on the valley floor, has been diverted for irrigation (Karhl et al. 1978). The valley lakes have been drained and converted to farmland. All major streams entering the San Joaquin Valley have been dammed. Additional development of the limited water remaining is taking place in response to the rapid growth of human populations in the region, especially in the vicinity of the cities of Modesto, Fresno, and Bakersfield.

Not surprisingly, the native fish fauna of the region is in decline (Brown and Moyle 1992), as is the fauna of the entire state (Moyle and Williams 1990). In 1970 Moyle and Nichols (1973, 1974) surveyed the fish fauna of the foothill streams on the east side of the San Joaquin Valley between elevations of 90 and 1100 m and found evidence of considerable decline in the distribution and abundance of the native fishes. They only surveyed a relatively limited portion of the entire drainage because of time constraints and because preliminary surveys indicated that native fishes were

Table 1. Native fishes of San Joaquin River Drainage, California.

Species	Percentage[a] 1986	Percentage[a] 1970	Status[b]
Pacific lamprey, *Lampetra tridentata*	6	0	D?
Kern brook lamprey, *Lampetra hubbsi*	5	0	D
White sturgeon, *Acipenser transmontanus*	0	0	R
Delta smelt, *Hypomesus transpacificus*	0	0	R
Chinook salmon, *Oncorhynchus tshawytscha*	0	0	D
Rainbow trout, *Oncorhynchus mykiss*	32	20	C
Thicktail chub, *Gila crassicauda*	0	0	E
Splittail, *Pogonichthys macrolepidotus*	0	0	R
Sacramento blackfish, *Orthodon microlepidotus*	0	0	C
Hitch, *Lavinia exilicauda*	5	10	D
California roach, *Lavinia symmetricus*	27	32	D
Sacramento squawfish, *Ptychocheilus grandis*	31	38	C
Hardhead, *Mylopharodon conocephalus*	7	9	D
Sacramento sucker, *Catostomus occidentalis*	48	42	C
Prickly sculpin, *Cottus asper*	7	2	C
Riffle sculpin, *Cottus gulosus*	4	2	D
Threespine stickleback, *Gasterosteus aculeatus*	3	1	D
Sacramento perch, *Archoplites interruptus*	0	0	E
Tule perch, *Hysterocarpus traski*	0	0	R

[a]Percentage refers to the percentage of samples in which the species was collected during this study in 1986 (n = 186) and by Moyle and Nichols (1973, 1974) in 1970 (n = 130).
[b]Status within the drainage is abbreviated as follows: E = extinct; R = rare, probably no longer resident; D = depleted and declining, range and numbers substantially reduced; C = common, widely distributed.

largely absent from lower elevation sites, and rainbow trout, mainly from introductions, were the principal inhabitants of sites at higher elevations.

In 1985 and 1986, we resurveyed the fish fauna of the San Joaquin River drainage but expanded the survey to more sites, including sites at lower elevations, sites on the west side of the valley, and sites in the Kern River drainage (Fig. 1). The Kern River is the southernmost of the major San Joaquin Valley rivers and was not sampled by Moyle and Nichols (1974). However, we did not sample the intensively farmed valley floor because sampling by Saiki (1984) and Jennings and Saiki (1990) demonstrated the scarcity of native fishes there. The purpose of the survey was to answer the following questions:

1. Have further declines in the distribution and abundance of native fishes taken place since the 1970 surveys of Moyle and Nichols (1973, 1974)?
2. Would the species distributions and species-habitat relationships observed by Moyle and Nichols (1973, 1974) hold up under more extensive sampling and use of additional sampling gear (electrofishers)?
3. Would the species assemblages described by Moyle and Nichols (1973, 1974) hold up under more extensive sampling, use of additional sampling gear and application of more sophisticated statistical analyses?
4. What is the status of the Kern brook lamprey, a species described subsequent to the 1970 surveys and known from only two localities?

STUDY AREA

The San Joaquin River drainage consists of all the streams that flow into the San Joaquin Valley of south-central California, a drainage area of about 83,000 km². Most of the region receives an average of less than 25 cm of rain per year, and the main streams depend on run-off from the Sierra Nevada on the east side of the valley. The Coast Range on the west side of the valley is comparatively low and arid and supports only a few small streams. During this study, only three westside streams inspected contained water and fish: Warthan Creek, Los Gatos Creek, and Puerto Creek. The streams flow into two main basins, Tulare Basin and San Joaquin River Basin.

Historically, the Tulare Basin was dominated by four huge, interconnected terminal lakes occupying the low center of the southern half of the valley. The largest was Tulare Lake, with a surface area of over 2000 km². The lakes were created by water flowing in from the Kern, Kaweah, Tule, and Kings River drainages, as well as several smaller drainages. During wet years, these lakes overflowed into the San Joaquin River, which also received water from the upper San Joaquin drainage and from the Fresno, Chowchilla, Merced, Tuolumne, and Stanislaus rivers. Natural flows in these streams were highly seasonal, with high flows occurring in spring following snow-melt in the Sierra Nevada. By late summer, the flows in the main streams were very low and small tributaries were often intermittent. Presently, virtually all streams of any size are dammed and stream flows on the valley floor are almost completely controlled, except during the largest floods. As a consequence, Tulare Lake is dry (and farmed) and during the summer the San Joaquin River on the

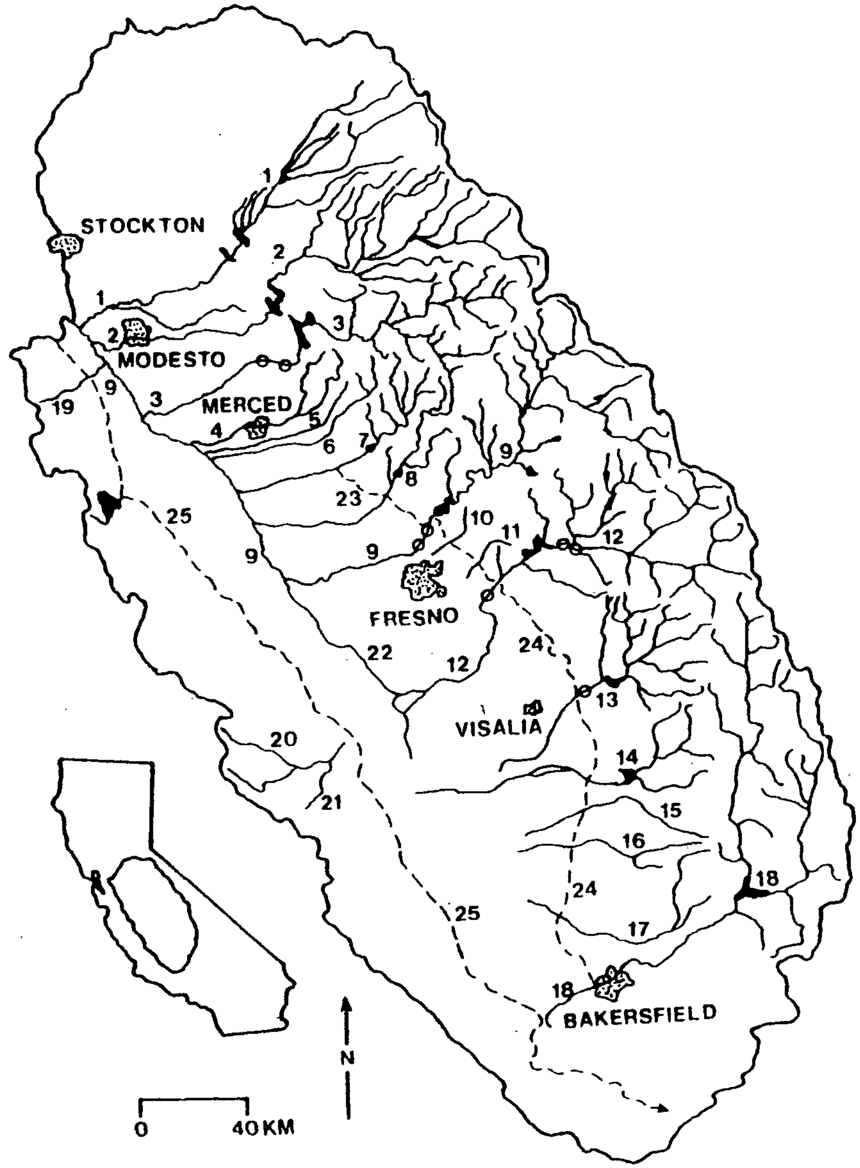

Figure 1. Drainages sampled during this study: (1) Stanislaus River, (2) Tuolumne River, (3) Merced River, (4) Bear Creek, (5) Miles Creek, (6) Mariposa Creek, (7) Chowchilla River, (8) Fresno River, (9) San Joaquin River, (10) Dry Creek, (11) Fancher Creek, (12) Kings River, (13) Kaweah River, (14) Tule River, (15) Deer Creek, (16) White River, (17) Poso Creek, (18) Kern River, (19) Puerto Creek, (20) Los Gatos Creek, and (21) Warthan Creek. Also shown are Fresno Slough (22) and the following major canals (dashed lines): (23) Madera Canal, (24) Friant-Kern Canal, and (25) California Aqueduct. Circles indicate locations where Kern brook lamprey were collected.

valley floor flows mainly with polluted irrigation return water. Stream flows in the Stanislaus, Tuolumne, and Merced Rivers are increased in the fall to attract and provide spawning habitat for chinook salmon (*Oncorhynchus tshawytscha*).

METHODS

A preliminary survey of 33 sites was conducted in September 1985. This survey was used for distributional studies but not for statistical analyses. The main survey was conducted from July through September 1986. Highest priority for sampling was given to the 130 sites sampled by Moyle and Nichols (1973, 1974). However, we were denied access to some sites on private land, others were inundated by new reservoirs, and others were dry so we were able to sample only 84 of the original sites.

Because we were interested in comparing the abundances of the fishes among sites and wanted to make sure that we recorded all species present at a site, three sampling methods were used: electrofishing, seining, and snorkeling. The methods chosen for each site were those that would sample it most thoroughly. At each site at least 50 m of stream was sampled, except for extremely small streams or for intermittent streams where only isolated pools were present. Sampling was halted if no additional species or habitat types were encountered after approximately 15 minutes.

Electrofishing was used primarily in shallow, rocky streams. A single pass was made through each reach using a Smith-Root Type VII or XI backpack electrofisher (battery powered). In most cases, there was one person shocking the fish and one person dipnetting them. Seines were used in habitats too large for effective electrofishing or in water with high conductivity. Depending on the habitat, seines used were 6.6 x 1.3 m or 10 x 1.3 m with 6-mm mesh. Snorkeling was used in deep pools and runs of the larger streams. One or two researchers swam in an upstream direction and counted fish of all species and estimated their standard lengths (SL). All fish captured by seining or electrofishing were measured (SL), unless more than 50 individuals of a species were caught, in which case a representative sample of 25-50 fish was measured.

At each site, the following environmental variables were measured: water and air temperature (°C); maximum depth (cm); pH (measured with an electronic pH meter); and conductivity (measured with a YSI S-C-T meter). We estimated: flow (estimated, m^3/min); water clarity (1-5 scale, where 1 = crystal clear and 5 = extremely muddy); percentage of bottom covered with rooted aquatic plants; percentage of water surface covered with floating aquatic plants or algae mats; percentage of habitat in pool, run, and riffle; percentage of water surface likely to be shaded most of the day; extent of human modification (1-5 scale, where 1 = unmodified and 5 = extremely modified, e.g. a cement-lined ditch); and percentage substrate as mud, sand, gravel, rubble, boulder, and bedrock (according to the Wentworth particle scale, Bovee and Milhous 1978). Mean depth (cm) was estimated by measuring the depth at a point determined by eye to represent the average depth in the study reach. Mean stream width (m) was estimated by measuring the width of the stream at a point determined by eye to represent the average width of the study reach. In addition, elevation, gradient, and

33
84
117

stream order (Strahler 1957) were determined from USGS 7.5' or 15' topographical maps.

All fish except lamprey were identified using keys in Moyle (1976). Because there is no taxonomic key to the ammocoetes of California lampreys, they could not be identified to species with certainty. Pacific lamprey (*Lampetra tridentata*) and Kern brook lamprey have different numbers of trunk myomeres (Vladykov and Kott 1976, Richards, Beamish, and Beamish 1982). All ammocoetes with trunk myomere counts of 63-69 were assumed to be Pacific lamprey and those with myomere counts of 51-57 were assumed to be Kern brook lamprey. This means it was possible we misidentified river lamprey (*L. ayersi*) ammocoetes as Pacific lamprey and Pacific brook lamprey (*L. richardsoni*) as Kern brook lamprey. However, river lamprey appear to be most abundant in the lower Sacramento-San Joaquin River system and have not been reported from the areas we sampled (Moyle 1976). Also, to verify our tentative identification of low myomere count ammocoetes as Kern brook lamprey, we returned in March and May 1987 to two of the sites from which we collected ammocoetes with low myomere counts and collected transforming individuals. Those with well developed tooth plates were identified as Kern brook lamprey.

We sampled 186 sites in 1986 (Table 2). After reviewing the data, we decided that data from 156 of the sites were appropriate for quantitative statistical analyses. The remaining 30 sites were big river sites where the edges were sampled for lampreys. Most other fishes were not adequately sampled because of great depth, high flows, or low visibility. Because of the variety of sampling methods used, rank abundance of each species in each sample was used for analyses rather than actual numbers collected or observed. Only species occurring in at least 5% of the samples were included in quantitative analyses.

For each common species, we calculated Pearson product moment correlations between species rank abundances and each of the environmental variables measured. Correlations were also calculated between species rank abundances and percentage of native fish at each site and total number of species at each site. Strictly speaking, these latter correlations were not statistically valid because the variables were not independent. However, as shown in Moyle and Nichols (1973), the comparisons do have descriptive value. Correlations were considered significant at $P < 0.05$. For each species, the mean and standard deviation of each of the environmental variables was calculated based on data from the stations at which the species was found.

A principal components analysis was conducted on the rank abundance data to determine patterns of co-occurrence among species. Principal components with eigenvalues greater than or equal to one were rotated using a varimax rotation (SAS 1982). Principal components analysis is a multivariate method for reducing a large number of intercorrelated variables to a reduced number of orthogonal (independent) variables. The loadings of the original variables on a principal component indicate the correlations of the variables to the principal component. The varimax rotation makes a final adjustment to maximize the amount of variation explained by the first few principal components. Pearson product moment correlations were also calculated among species, using rank abundances.

Table 2. Total number of sites sampled and number of sites included in quantitative analyses for each drainage sampled during this study.

Drainage	Total Sites	Quantitative Sites
Stanislaus River	19	12
Tuolumne River	21	16
Merced River	7	3
Bear Creek	2	2
Miles Creek	2	2
Mariposa Creek	2	2
Chowchilla River	13	13
Fresno River	9	9
San Joaquin River	21	19
Dry Creek	1	1
Fancher Creek	1	1
Kings River	27	20
Kaweah River	18	18
Tule River	16	15
Deer Creek	6	6
White River	1	1
Poso Creek	1	1
Kern River	16	12
Puerto Creek	1	1
Los Gatos Creek	1	1
Warthan Creek	1	1
Total	186	156

RESULTS

General Distributional Patterns

Eleven of the 19 original native species were collected in this study (Table 1), in addition to 19 introduced species (Table 3). Only six species of native fish (rainbow trout, hitch, hardhead, Sacramento squawfish, California roach, Sacramento sucker) were collected frequently enough to use in the quantitative analyses, as were six introduced species (brown trout, mosquitofish, green sunfish, bluegill, largemouth bass, smallmouth bass). Distributions of native species were similar to those shown in Moyle and Nichols (1974), with exceptions noted in the species accounts below. Native fishes were largely confined to a narrow band of habitat in the foothills, usually above the major Sierra Nevada foothill dams or in tributary streams below them. We review the results of other studies in the following species accounts to give the most accurate depiction possible of the distribution and abundance of each species.

Table 3. Introduced fishes collected from streams of the San Joaquin River Drainage during thi study in 1986 and by Moyle and Nichols (1973, 1974) in 1970.

Species	Percentage[a] 1986	Percentage[a] 1970
Largemouth bass, *Micropterus salmoides*	19	31
Smallmouth bass, *Micropterus dolomieu*	7	7
Redeye bass, *Micropterus coosae*	1	0
Green sunfish, *Lepomis cyanellus*	25	46
Bluegill, *Lepomis macrochirus*	12	23
Redear sunfish, *Lepomis microlophus*	4	1
Black crappie, *Pomoxis nigromaculatus*	<1	0
White crappie, *Pomoxis annularis*	2	0
Bigscale logperch, *Percina macrolepida*	<1	0
Western mosquitofish, *Gambusia affinis*	23	26
Carp, *Cyprinus carpio*	2	2
Goldfish, *Carassius auratus*	<1	1
Golden shiner, *Notemigonus chrysoleucas*	3	1
Fathead minnow, *Pimephales promelus*	<1	0
White catfish, *Ameiurus catus*	3	9
Black bullhead, *Ameiurus melas*	4	0
Brown bullhead, *Ameiurus nebulosus*	0	7
Brown trout, *Salmo trutta*	9	1
Threadfin shad, *Dorosoma petenense*	<1	0

[a] Percentage refers to the percentage of samples in which the species was collected in 1986 (n = 156) an in 1970 (n = 130).

Native Fishes

Rainbow trout. Rainbow trout occurred at 59 (38%) of the 156 sites in 1986. Thei abundance was positively correlated with stream order, depth, gradient, elevation percentage riffle, and percentage boulders and was negatively correlated wit temperature, water clarity, pH, conductivity, percentage rooted and floating vegetation percentage pools, human modification, and total number of species (Table 4). These correlations indicate that rainbow trout were characteristic of clear, cold hig elevation, high gradient streams, the same pattern found by Moyle and Nichol (1973).

Hitch. These native cyprinids were found at only 8 (5%) of the 156 sites. Moyl and Nichols (1973) found them at 13 (10%) sites, despite sampling a more limite geographic area. In 1986, hitch were absent from the Tule River, Bear Creek an Fresno River drainages where they were collected in 1970. We did capture hitch i the Fresno River in 1985. Hitch abundance was correlated with percentage run an percentage shade and negatively correlated with stream order, water temperature, an percentage pool (Table 4). The typical hitch stream was a sandy bottomed, lo gradient stream at moderately low elevations, containing a mixture of native an introduced species. The mean elevation of sites with hitch was 418 m, the lowest fo any native species (Table 4). The habitat where we found hitch was similar to tha

Table 4. Means (SD) of selected environmental variables for six native species of fishes.

	Rainbow trout	Hitch	Hardhead	Sacramento squawfish	California roach	Sacramento sucker
Number of sites	59	8	10	46	47	75
Order[a]	2.5 (1.1)$^{++}$	1.1 (1.7)$^{-}$	2.4 (1.8)	2.4 (1.7)$^{+}$	1.5 (1.4)$^{-}$	2.4 (1.5)$^{++}$
Water temperature (°C)	18 (15)$^{--}$	21 (4)$^{-}$	20 (6)$^{-}$	22 (5)	21 (4)	21 (5)
Maximum depth (cm)	130 (99)$^{++}$	100 (36)	132 (74)	125 (77)$^{+}$	94 (71)	127 (85)$^{++}$
Flow (cfs)	26 (61)	8 (12)	34 (42)	25 (61)	5 (10)	24 (55)$^{++}$
Turbidity (1-5)	2.0 (0.5)$^{--}$	2.6 (0.7)	2.5 (0.4)	2.4 (0.5)	2.3 (0.6)$^{-}$	2.4 (0.6)
Gradient (m/km)	41 (27)$^{++}$	13 (12)	14 (13)	21 (20)	28 (19)	24 (21)
Elevation (m)	807 (282)$^{++}$	418 (325)	590 (324)	423 (246)$^{--}$	480 (203)	494 (267)
Rooted vegetation (%)	0.03 (0.3)$^{--}$	13.0 (20.2)	0.4 (0.8)	0.9 (2.0)$^{+}$	3.3 (11.4)	1.5 (7.1)$^{--}$
Floating vegetation (%)	0.6 (3.5)$^{--}$	7.1 (17.4)	2.4 (3.7)	5.9 (18.9)	9.7 (21.7)	5.7 (18.1)
Pool (%)	51 (31)$^{--}$	51 (46)$^{-}$	57 (43)	56 (35)	60 (32)	53 (34)$^{--}$
Riffle (%)	34 (22)$^{++}$	8 (11)	24 (32)	23 (21)	27 (23)	26 (23)$^{+}$
Mud (%)	0.3 (1.4)	1.5 (3.5)	0.2 (0.6)	0.3 (1.5)	0.5 (2.9)	0.2 (1.2)
Sand (%)	25 (24)$^{--}$	59 (37)	39 (34)	34 (28)	27 (25)$^{--}$	35 (29)
Gravel (%)	10 (13)	8 (13)	6 (5)	10 (17)	13 (14)	9 (12)
Rubble (%)	21 (13)	8 (13)	22 (24)	21 (17)	23 (17)$^{+}$	19 (17)
Boulder (%)	32 (20)$^{++}$	17 (21)	31 (32)	27 (24)	25 (19)	26 (22)
Bedrock (%)	12 (16)	7 (18)	2 (4)	8 (16)	11 (15)	11 (19)$^{+}$
Number of species	2.4 (1.1)$^{--}$	2.7 (1.3)	4.3 (1.1)	3.5 (1.0)	2.7 (1.3)$^{--}$	3.1 (1.1)$^{--}$
% native fish	88 (25)	67 (36)	83 (35)$^{+}$	79 (34)$^{++}$	89 (25)$^{++}$	80 (33)$^{++}$

[a] Superscripts indicate significant positive (+, $P < 0.05$ and ++, $P < 0.01$) and negative (-, $P < 0.05$ and --, $P < 0.01$) correlations of species rank abundance with the physical variables.

described by Moyle and Nichols (1973).

Hardhead. Hardhead were found only at 10 (6%) sites. Moyle and Nichols (1973) found them at 12 (9%) sites. Five of the sites in this study were on the Kern River, which was not sampled by Moyle and Nichols (1973, 1974). We failed to collect hardhead from three streams where they were found by Moyle and Nichols (1973, 1974), Horse Creek in the Kaweah River drainage and Big Creek and Dinky Creek in the Kings River drainage. In 1986, we did not find hardhead at three sites where we found them in 1985. We also did not collect hardhead from the Tuolumne River, where intensive sampling indicated they have been present in small numbers (EA Engineering, Science, and Technology, 1990, unpublished data). The small number of sites containing hardhead limited the correlations to a negative correlation of abundance with temperature and a positive correlation with percentage of native fish (Table 4). The positive correlation is consistent with the results from other studies that indicate hardhead are found in the least disturbed sections of the larger streams dominated by native species (Moyle 1976). The absence or scarcity of hardhead in otherwise seemingly suitable habitats that contain smallmouth bass, especially in the upper Kings River, suggests that predation by bass may be limiting hardhead numbers. Overall, hardhead were uncommon in the San Joaquin River drainage and appear to be declining.

Sacramento squawfish. These predatory cyprinids were abundant and widely distributed in both the 1970 and 1986 studies. In 1986, they were present at 46 (29%) sites and were collected at most sites where they were found in 1970. Squawfish abundance was positively correlated with stream order, maximum depth, pH, percentage of rooted vegetation, percentage of shade, and percentage of native fish but negatively correlated only with elevation (Table 4). This pattern indicates that squawfish were most common in the larger streams at lower elevations at sites with well developed riparian vegetation and native fish communities.

California roach. Roach were found at 47 (30%) of the sample sites in 1986 and 42 (32%) in 1970. They were not collected from the Kern River drainage but were the dominant species in the three streams sampled on the west side of the San Joaquin Valley. Their abundance was positively correlated with conductivity, percentage of rubble, and percentage of native fish. Roach were negatively correlated with stream order, stream width, turbidity, percentage of sand, and number of species (Table 4). These fish were most common in small, clear intermittent streams where they were often the only species present, although they were found in habitats ranging from cool trout streams to warm isolated pools. In the latter habitats, they were often found at extremely high densities. Taxonomic analyses of the roach collected in this study indicated that the population in each tributary drainage exhibits minor morphological and meristic differences from populations in the other drainages (Brown et al. 1992).

Sacramento sucker. Sacramento suckers were the most commonly collected native fish in both the 1970 (42% of sites) and the 1986 (48% of sites) surveys. They were found in a wide variety of habitats. Their abundance was positively correlated with stream order, maximum depth, flow, percentage bedrock, and percentage native fish (Table 4). Sucker abundance was negatively correlated with percentage of rooted vegetation, percentage of pool, percentage of shade, and total number of species. Suckers were most abundant in the larger, clear, cool streams that also contained either rainbow trout or California roach. Even though suckers were commonly collected with introduced species in disturbed habitats, they were rarely abundant in such situations.

Kern brook lamprey. Presumptive Kern brook lamprey were collected in 1985, 1986, and 1987 from lower Merced River, the San Joaquin River below Friant Dam, the Kings River above and below Pine Flat Dam, and the lower Kaweah River (Fig. 1). Wang (1986) described ammocoetes that probably belonged to this species from a site above Friant Dam (Millerton Reservoir) but below Kerckoff Reservoir. With the exception of the upper Kings River site, all collection localities were below major dams. Typical collection localities for the ammocoetes were sandy-bottomed backwaters or shallow river edges. Brook lampreys were not collected from similar habitats in the lower Kern, Tule, Tuolumne and Stanislaus rivers, although considerable effort was made to find them. When encountered, ammocoetes were usually locally abundant. Previous records of Kern brook lamprey were from the Merced River and the Friant-Kern Canal (Vladykov and Kott 1976, 1984). This canal delivers water from Millerton Reservoir to farmlands to the south. In 1988, ammocoetes and adults of Kern brook lamprey were collected by California Department of Fish and Game personnel from the silty-bottomed siphons of the Friant-Kern canal when the siphons were treated with rotenone to rid the canal of white bass (*Morone chrysops*) (Moyle et al. 1989).

Pacific lamprey. Presumptive Pacific lamprey ammocoetes were found in the lower Stanislaus, Tuolumne, Merced, and Kings rivers, as well as the San Joaquin River below Friant dam (in 1985 only). Lampreys were not collected in 1970 because electroshockers were not used and ammocoetes are not vulnerable to seines, the main method of collection in 1970. We expected to find Pacific lampreys in the Stanislaus, Tuolumne, and Merced rivers because they are anadromous and these rivers are accessible from the sea as indicated by small runs of chinook salmon (*Oncorhynchus tshawytscha*). However, the San Joaquin and Kings river sites are likely to be accessible only during wet years, when water spills from the dams. During wet years, lampreys and salmon (Moyle 1970) may occasionally gain access to these rivers and spawn. Because Pacific lampreys may persist as larvae for 5-7 years in streams (Moyle 1976) the progeny of such spawnings will persist in the system for a number of years. It is likely that the ammocoetes we captured were the result of such an event.

Uncommon native fishes. Prickly sculpins (*Cottus asper*) riffle sculpins (*Cottus gulosus*) and threespine sticklebacks (*Gasterosteus aculeatus*) were collected at only a small number of sites in the 1970 and 1986 studies. Prickly sculpins were found in the lower Stanislaus, Merced, Fresno, Kings, and Kaweah rivers and in the San Joaquin River below Friant Dam. This sculpin disperses readily because of its planktonic larval stage and tolerance of a wide variety of environmental conditions. They are common in many of the reservoirs in the drainage. The reservoirs probably act as a source of larvae to downstream areas, so small numbers were expected below the dams (Moyle 1976). Riffle sculpins, in contrast, require small, cold, permanent streams and disperse very slowly because they have benthic larvae (Smith 1982). We found them mainly in a few isolated populations above dams in the upper San Joaquin River, the Kings River, and the Kaweah River, although a substantial population also exists in a 4-km reach of the Tuolumne River below LaGrange Dam, with small numbers occurring as far as 36 km downstream from the dam (EA Engineering, Science, and Technology, unpublished data, 1990). Sculpins of undetermined species have also been observed in the Middle Fork Stanislaus River, which we did not sample (Brian Quelvog, Calif. Dept. Fish and Game, pers. comm.). Threespine sticklebacks were found only in the San Joaquin River immediately below Friant Dam, in a small tributary to the San Joaquin River above Kerckoff Reservoir and in a 30-km reach of the Kings River below Pine Flat Dam.

Introduced Fishes

Brown trout and smallmouth bass. These two species have scattered but complementary distribution patterns throughout the drainage that probably more reflect their planting history by humans than their ecological requirements. Brown trout were captured at 16 (10%) sites and their abundance was correlated with the same environmental factors as rainbow trout (Table 5). Smallmouth bass were captured at nine sites in both 1970 and 1986 and showed few correlations with environmental variables (Table 5). The main difference between the 2 years is that bass were more abundant and widely distributed in the upper Kings River drainage in 1986 than they were in 1970, an expansion associated with decline of hardhead in the same area. Sites from which smallmouth bass were collected in 1970 but not in 1986 were either dry in 1986 or inundated by new reservoirs.

Largemouth bass. Largemouth bass were captured at 28 sites (18%). Their abundance was positively correlated with water temperature, turbidity, percentage of rooted and floating vegetation, percentage of pool, percentage of sand, and human modification. They were negatively correlated with gradient, elevation, percentage of riffle, and percentage of rubble (Table 5). As found by Moyle and Nichols (1973), we found largemouth bass in warm, pond-like habitats in highly disturbed areas. They were often particularly abundant below impoundments, which not only reduce flows downstream (resulting in more pools and warmer water) but act as sources of immigrants. Where largemouth bass were common, native fishes were uncommon or absent.

Green sunfish and mosquitofish. These two species were abundant, widely distributed, and often co-occurring. Green sunfish were present at 43 (28%) sites, and mosquitofish were present at 30 (19%) sites. The abundance of both species had positive correlations with water temperature, turbidity, percentage of rooted vegetation, percentage of pool, percentage of sand, and human modification (Table 5). They were negatively correlated with stream order, maximum depth, gradient, elevation, percentage of riffle, and percentage of rubble, boulder, and bedrock. These results support Moyle and Nichols' (1973) characterization of their habitat as warm, intermittent streams in areas highly disturbed by livestock grazing and human activity

Table 5. Means (SD) of selected environmental variables for six introduced species of fishes.

	Brown trout	Smallmouth bass	Largemouth bass	Green sunfish	Bluegill	Mosquitofish
Number of sites	16	9	28	43	18	30
Order[a]	2.2 (1.0)	3.0 (1.9)	1.7 (1.8)	1.3 (1.8)$^{--}$	1.7 (1.6)	1.4 (2.0)$^{-}$
Water temperature (°C)	17 (4.2)$^{--}$	26 (3)	26 (3)$^{++}$	24 (4)$^{++}$	25 (3)$^{++}$	24 (3)$^{++}$
Maximum depth (cm)	102 (77)	110 (40)	92 (58)	91 (46)$^{-}$	93 (61)	82 (32)$^{-}$
Flow (cfs)	10.6 (24.8)	17.1 (32.2)	11.1 (42.9)	5.0 (16.2)$^{-}$	1.6 (3.7)	10.4 (25.7)
Turbidity (1-5)	2.1 (0.7)$^{--}$	2.7 (0.7)	2.9 (0.6)$^{++}$	2.9 (0.6)$^{++}$	3.0 (0.5)$^{++}$	3.0 (0.5)$^{++}$
Gradient (m/km)	30 (14)$^{+}$	16 (14)	13 (9)$^{-}$	13 (10)$^{-}$	13 (9)	10 (9)$^{--}$
Elevation (m)	960 (245)$^{++}$	249 (124)	330 (166)$^{--}$	387 (232)$^{--}$	398 (248)	271 (146)$^{--}$
Rooted vegetation (%)	0.2 (0.5)	2.2 (2.6)	10.6 (22.0)$^{++}$	9.5 (19.6)$^{++}$	8.8 (17.6)	11.5 (17.5)$^{++}$
Pool (%)	50 (26)	62 (42)	78 (31)$^{+}$	82 (33)$^{++}$	84 (25)$^{+}$	77 (38)$^{++}$
Riffle (%)	33 (22)$^{++}$	11 (18)	12 (19)$^{-}$	5 (9)$^{--}$	9 (16)	6 (14)$^{--}$
Mud (%)	0.0	2.2 (6.7)$^{+}$	0.0	1.1 (4.8)	0.0	1.9 (5.9)$^{++}$
Sand (%)	30 (28)	44 (34)	53 (34)$^{++}$	55 (33)$^{++}$	46 (30)	54 (34)$^{++}$
Gravel (%)	11 (19)	8 (12)	7 (16)	8 (15)	9 (20)	11 (18)
Rubble (%)	19 (15)	14 (14)	12 (13)$^{-}$	14 (17)$^{-}$	15 (17)	13 (15)$^{-}$
Boulder (%)	27 (18)	27 (25)	22 (23)	18 (19)$^{--}$	23 (22)	19 (24)$^{-}$
Bedrock (%)	12 (14)	5 (13)	6 (17)	4 (8)$^{-}$	6 (9)	1 (4)$^{-}$
Number of species	2.2 (1.3)$^{--}$	4.1 (0.6)	3.5 (1.2)	3.6 (1.2)$^{--}$	3.8 (1.1)$^{--}$	3.3 (1.4)
% native fish	41 (39)$^{--}$	35 (45)	20 (33)	29 (35)$^{-}$	14 (25)	12 (24)

[a] Superscripts indicate significant positive (+, $P < 0.05$ and ++, $P < 0.01$) and negative (-, $P < 0.05$ and --, $P < 0.01$) correlations of species rank abundance with the physical variables.

where other species of fish are uncommon. Green sunfish are widely distributed because of their natural dispersal abilities (Smith 1982). They frequently are found in low numbers in relatively undisturbed streams with native fishes. They are able to invade these streams in low numbers but do not become abundant until physical conditions favor them.

Bluegill and other species. Bluegill were found at 18 (12%) sites but were usually not abundant. It is likely that most of the fish represent escapees from farm ponds or reservoirs. Their abundance was positively correlated with water temperature, turbidity, and percentage of pools, indicating their presence in pond-like habitats with other introduced warmwater fishes (Table 5). Twelve other introduced warmwater fishes had only sporadic occurrences, mainly in river reaches below reservoirs (Table 3). These and at least five other introduced species are common in waters of the valley floor (Saiki 1984, Jennings and Saiki 1990). The only species of note is redeye bass (*Micropterus coosae*) from a single site on the South Fork of the Stanislaus River, where they were common. Redeye bass were introduced there in 1962 (Moyle 1976) and have recently been collected from New Melones Reservoir on the Stanislaus River (Randy Kelly, Calif. Dept. Fish and Game, pers. comm.), indicating that they are slowly dispersing downstream.

Species Assemblages

Moyle and Nichols (1973) used correlation analysis to identify four assemblages of species: (i) the Rainbow Trout Association (mainly rainbow trout alone); (ii) the California Roach Association (California roach plus juvenile Sacramento suckers); (iii) the Native Cyprinid-Catostomid Association (mainly Sacramento squawfish, hardhead, and Sacramento sucker); and (iv) the Introduced Fish Association (mainly largemouth bass, bluegill, green sunfish, and mosquitofish). A similar pattern was evident in our own correlation analyses but the principal components analysis (PCA) indicated that the Introduced Fishes Association could be divided into two subgroups. The PCA yielded five components with eigenvalues greater than one. The five rotated principal components (varimax rotation) explained 69% of the variance in rank abundance of the 12 most abundant species (Table 6).

The first principal component defined the Native Cyprinid-Catostomid Association, but without hardhead. Squawfish and suckers showed high positive loadings on this component indicating a high degree of association of the two species. Hitch and brown trout showed low negative loadings indicating they were present at sites where squawfish and suckers were absent. Green sunfish and mosquitofish loaded positively on the second principal component 2; rainbow trout and brown trout load negatively on it. The second principal component thus identified the Rainbow Trout Association and a subset of the Introduced Species Association. It separated fishes associated with undisturbed, clear, high gradient streams from those associated with highly disturbed, turbid, low gradient, small streams. The third principal component represented the remainder of the Introduced Species Association that occurred in larger streams and was loaded heavily by largemouth bass and bluegill. The negative loading of hitch

Table 6. Principal component loadings (after Varimax rotation) of species rank abundances for common fishes of the San Joaquin River Drainage. Loadings of less than 0.4 are not shown.

Species	Principal Component 1	2	3	4	5
Sacramento squawfish	0.80				
Sacramento sucker	0.78				
Brown trout	-0.56	-0.50			
Rainbow trout		-0.75			
Green sunfish		0.75			
Mosquitofish		0.66			
Hitch	-0.42		-0.41		
Largemouth bass			0.79		
Bluegill			0.81		
Smallmouth bass				0.86	
Hardhead				-0.59	
Calif. roach					0.85
Variance explained (%)	17	17	15	10	10
Cumulative variance explained (%)	17	34	49	59	69

showed that hitch were negatively correlated with the abundance of the other two species. The fourth principal component separated smallmouth bass from hardhead. Neither of these species showed many correlations with environmental factors measured, in part due to the small sample sizes for both. However, both species were commonly found in deep pools of large, cool streams, suggesting that the two species were not found together because of interactions between them, presumably smallmouth bass predation on juvenile hardhead. The fifth principal component identified the California Roach Association that dominated the small, warm intermittent streams.

DISCUSSION

It is clear that native fishes have been greatly reduced in numbers and distribution since the arrival of Europeans in California. Only 11 of the 19 native species were collected in this study and only six of the eleven were found at more than a few sites. Except for Pacific lamprey, the five uncommon species occurred in scattered, isolated populations, where localized extinction was possible, with no possibility of natural recolonization because of dams. This situation was also characteristic of the distributions of two of the more widely distributed species, hitch and hardhead. Introduced species now dominate many streams, especially those altered by human activity, and native fishes are largely gone from the valley floor (Saiki 1984, Jennings and Saiki 1990).

Two of the eight species not collected in this study (delta smelt, federally listed as threatened, and white sturgeon) are estuarine species that formerly ascended further up the San Joaquin River than they do today. Neither was collected by Saiki (1984); however, white sturgeon were collected by Jennings and Saiki (1990). Four of the eight species were once abundant on the valley floor but are now either extinct (thicktail chub, Sacramento perch) or very rare there (tule perch, Sacramento splittail) (Moyle 1976, Saiki 1984, Jennings and Saiki 1990, Moyle and Williams 1990). Tule perch and splittail still persist in the estuary (Moyle et al. 1982) and are occasionally collected from valley floor rivers (Jennings and Saiki 1990). The only native species that is still abundant on the valley floor is Sacramento blackfish (Saiki 1984), a species that is remarkably tolerant of poor water quality. Chinook salmon were not found at our sampling sites because their presence is seasonal and they are not present in the summer. Salmon spawn in the lower Stanislaus, Tuolumne, and Merced rivers but the juveniles usually emigrate during March through May (Sasaki 1966). Prior to the construction of the dams on the rivers we sampled, it is likely that chinook salmon were present at many of our sample sites; runs of adult salmon were once 300,000-500,000 or more per year in the drainage (Lufkin 1990). In 1990-91, less than 1,000 adult salmon were present in the drainage (Calif. Dept. Fish and Game 1992).

Have further declines of the native fishes taken place since 1970? Fifteen years is a short time to detect differences in fish distribution over a wide area, especially between two surveys that did not overlap completely in their sampling sites. However, in 1986 hitch were not found in the Tule River, Bear Creek, or Fresno River where they were found in 1970 and hardhead were absent from the Kaweah River drainage and two streams in the Kings River drainage where they were found in 1970. The decline of hardhead may be associated with the expansion of smallmouth bass populations. Further declines may have taken place since this survey was completed as the period from 1986 to 1992 was one of severe drought in the drainage, which would exacerbate the already precarious position of many of the native fish populations.

Are the species distributions, species-habitat relationships and species assemblages observed consistent with those of Moyle and Nichols (1973, 1974)? The species distributions and species-habitat patterns observed in 1970 were very similar to the results of our 1986 survey, except for the differences already noted for hitch and hardhead. The species assemblages identified in 1986 differed slightly from those identified by Moyle and Nichols (1973, 1974). Similar to Moyle and Nichols (1973, 1974), three assemblages of native fishes were found, each occupying a narrow elevational band in the Sierra foothills. They were the Rainbow Trout Association, Native Cyprinid-Catostomid Association, and the California Roach Association. The California Roach Association was absent, apparently naturally, from the Kern River drainage, but was the only assemblage found in the few permanent streams on the arid west side of the valley. The Introduced Fishes Association was not distinctly defined in 1986 compared to 1970. Moyle and Nichols (1973) characterized the Introduced Fishes Association by the presence of largemouth bass, green sunfish, bluegill, and mosquitofish. The principal components analysis indicated that the Introduced Fishes Association can be divided into two subgroups. The first group included green sunfish and mosquitofish that characterized the smaller streams and the second group included largemouth bass and bluegill that were generally found in larger streams. The values of the Pearson product moment correlations among these species were similar in both studies; therefore, the division of the Introduced Fishes Association into subgroups is most likely the result of the greater sensitivity of principal components analysis to species relationships compared to simpler techniques.

What is the status of the Kern brook lamprey? The Kern brook lamprey was of special interest in this study because it is a recently described taxon and the only species identified as endemic to the San Joaquin Valley. The five or six known Kern brook lamprey populations probably need special protection, because they are isolated from one another and with one exception, occur below dams, so are subject to the vagaries of water releases from the dams. Moyle et al. (1989) regard them as a Species of Special Concern, a status which seems appropriate.

CONCLUSIONS

Based on our results and other studies (Saiki 1984, Jennings and Saiki 1990), only five of the original 19 species of the San Joaquin drainage are reasonably abundant and widely distributed (rainbow trout, Sacramento squawfish, California roach, Sacramento blackfish, Sacramento sucker). Once abundant anadromous fishes are now a tiny fraction of their original numbers. Most aquatic habitats on the valley floor are probably degraded beyond hope of recovery to the point where they can support native fish assemblages. Most foothill streams, even those containing native fishes, are in a degraded condition (Brown and Moyle 1992). It is clear that the fish fauna has declined in distribution and abundance since Europeans came to California, a decline that appears to be continuing and seems unlikely to be halted soon. The best hope for protecting some remnants of the fauna and their aquatic habitats (and the attendant native plants, invertebrates, and amphibians) is to establish a series of preserves or Aquatic Diversity Management Areas, along the lines suggested by Moyle and Yoshiyama (1992).

ACKNOWLEDGMENTS

Preliminary surveys in 1985 were funded by the Water Resources Center, University of California (W-659). The 1986 survey was sponsored by the Endangered Species Tax Checkoff Fund, California Department of Fish and Game (Contract C-260607), supervised by D. McGriff. D. White, E. Wikramanayake, and G. Sato helped to collect the field data. C. Chadwick, D. Christensen, W. Loudermilk, and N. Villa of the California Department of Fish and Game suggested sampling sites, especially for lamprey. B. Quelvog and an anonymous reviewer significantly improved the paper.

LITERATURE CITED

Bovee, K. D., and R.T. Milhous. 1978. Hydraulic simulation in instream flow studies: theory and technique. Instream flow information paper 5. *United States Fish and Wildlife Service*, Biological Services Program FWS-OBS 78-33.

Brown, L.R., and P.B. Moyle. 1992. Native fishes of the San Joaquin drainage: status c remnant fauna and its habitats. Pages 89-98 *in* D. F. Williams, T. A. Rado, and S. Byr eds. Proceedings of the Conference on Endangered and Sensitive Species of the San Joaq Valley, California. California Energy Commission, Sacramento, CA.

_____, _____, W. A. Bennett, and B. Quelvog. 1992. Morphological variation amc populations of California roach (Cyprinidae: *Lavinia symmetricus*): implications conservation strategies. Biol. Cons. 62:1-10.

California Department of Fish and Game. 1992. San Joaquin River chinook salmon enhancem project annual report fiscal year 1990-1991. Calif. Dep. Fish and Game, Fresno, CA. 8

Jennings, M.R., and M.K. Saiki. 1990. Establishment of red shiner, *Notropis lutrensis*, in San Joaquin Valley, California. Calif. Fish and Game 76:46-57.

Kahrl, W.L., W.A. Bowen, S. Brand, M.L. Shelton, D.L. Fuller, D.A. Ryan. 1978. T California water atlas. The Governor's Office of Planning and Research, Sacramento, C 118 p.

Lufkin, A., ed. 1990. Salmon and steelhead in California. University of Calif. Press, Berkel CA. 305 p.

Moyle, P.B. 1970. Occurrence of king (chinook) salmon in the Kings River, Fresno Cour Calif. Fish and Game 56:314-315.

_____. 1976. Inland fishes of California. University of Calif. Press, Berkeley, CA. 405 p.

_____, and R.D. Nichols. 1973. Ecology of some native and introduced fishes of the Sie Nevada foothills in Central California. Copeia 1973:473-490.

_____, _____. 1974. Decline of the native fish fauna of the Sierra Nevada foothills, Cen California. American Midl. Nat. 92:72-83.

_____, and J.E. Williams. 1990. Biodiversity loss in the temperate zone: decline of the nat fish fauna of California. Cons. Biol. 4:275-284.

_____, _____, and E.D. Wikramanayake. 1989. Fish species of special concern of Califor Calif. Dept. Fish and Game, Sacramento, CA. 222 p.

_____, and R.M. Yoshiyama. 1992. Fishes, aquatic diversity management areas, and endange species: a plan to protect California's native aquatic biota. The California Policy Semi University of California, Berkeley, CA. 222 p.

Richards, J.E., R.J. Beamish, and F.W.H. Beamish. 1982. Descriptions and keys for ammococ of lampreys from British Columbia, Canada. Can. J. Fish. Aquat. Sci. 39:1484-1495.

Saiki, M.K. 1984. Environmental conditions and fish faunas in low elevation rivers on irrigated San Joaquin Valley floor. Calif. Fish and Game 70:145-157.

Sasaki, S. 1966. Distribution and food habits of King salmon, *Oncorhynchus tshawytscha*, steelhead rainbow trout, *Salmo gairdneri*, in the Sacramento-San Joaquin Delta. Pages 1 114 *in* J.L. Turner and D.W. Kelley (compilers). Ecological Studies of the Sacramento-S Joaquin Delta, Part II, Fishes of the Delta. Calif. Dept. Fish and Game, Fish Bull. 136 168.

SAS Institute Inc. 1982. SAS user's guide: statistics. SAS Institute Inc., Cary, North Caroli 584 p.

Smith, J.J. 1982. Distribution and ecology of stream fishes of the Sacramento-San Joaq drainage system, California. II. Fishes of the Pajaro River system. Univ. Calif. Publ. Zo 115:83-170.

Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. Trans. An Geophysical Union 38:913-920.

Vladykov, V.D. and E. Kott. 1976. A new nonparasitic species of lamprey of the ge *Entosphenus* Gill, 1862, (Petromyzonidae) from south central California. *Bull. So. Ca Acad. Sci.* 75:60-67.

Vladykov, V.D. and E. Kott. 1984. A second record for California and additional information on *Entosphenus hubbsi* Vladykov and Kott 1976 (Petromyzontidae). Calif. Fish and Game 70:121-127.

Wang, J.C.S. 1986. Fishes of the Sacramento-San Joaquin estuary and adjacent waters, California. Interagency Ecol. Stud. Prog. for the Sacramento-San Joaquin Estuary, Tech. Rept. 9, Sacramento, CA.

Received: 9 July 1991
Accepted: 3 September 1993

Calif. Fish and Game (79)3:115-125 1993

FIRE EFFECTS ON A MONTANE SIERRA NEVADA MEADOW

ROBERT S. BOYD
Department of Botany and Microbiology
and Alabama Agricultural Experiment Station
Auburn University, AL 36849-5407

ROY A. WOODWARD
Bechtel Corporation
50 Beale Street
San Francisco, CA 94119-3965

GARY WALTER
California Department of Parks and Recreation
P.O. Drawer D
Tahoma, CA 95733

The effects of a late fall burn on a mountain meadow at Grover Hol Springs State Park, California, were evaluated. Both wet (*Carex* sp. dominated) and dry (*Poa* sp. dominated) meadow plots were burned by a low to moderate intensity fire in mid-November 1987. Fire resulted in few detectable changes in species composition 10.5 months later. Postfire decreases in *Poa* sp. and *Juncus* sp., and increases in *Carex* sp. and *Muhlenbergia* sp. were observed. Burning increased bare ground area by more than three fold in both wet and dry plots, but there was no significant invasion of burned areas by exotic species after the fire. Under high soil moisture conditions, burning resulted in relatively little change in meadow vegetation.

INTRODUCTION

Fire is a natural process in most grassland ecosystems (Vogl 1974). Desp widespread acceptance of the natural role of fire in grasslands and many ot vegetation types, little is known about fire effects in North American mount meadows (Ratliff 1985). Rundel et al. (1977) pointed out the lack of informat about fire effects on high elevation Sierra Nevada communities in general. Ther but one published account of a wildfire burning a meadow in the Sierra Nev (DeBenedetti and Parsons 1979).

Meadow fire may be a positive factor essential to maintaining meadows agai invasion by woody species (Gibbens and Heady 1964). Fire may also hav destructive effect by consuming the organic matter forming the bulk of many meadow soils (Bennett 1965, Vogl 1974). There are few data available from wh to draw any conclusions. DeBenedetti and Parsons (1979, 1984) documented ra recovery of the vegetation despite apparently extensive destruction of soil orga matter and root biomass due to the occurrence of fire during drought conditions