Ecology of Some Native and Introduced Fishes of the Sierra Nevada Foothills in Central California

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Collections were made of fishes occurring in the streams of the Sierra Nevada foothills in Central California. Environmental factors associated with each collection were recorded. Correlation analyses indicated which environmental factors affected the distribution of 11 of the 21 species collected: *Micropterus salmoides, Lepomis cyanellus, L. macrochirus, Gambusia affinis, Notemigonus crysoleucas, Lavinia exilicauda, Ptychocheilus grandis, Mylopharodon conocephalus, Hesperoleucus symmetricus, Catostomus occidentalis* and *Salmo gairdneri*. The fishes were found to belong to four distinct fish associations, each found in a distinctive set of environmental conditions. The Rainbow Trout Association was found in the cold, clear permanent streams of the higher elevations. The California Roach Association was found in the small, warm intermittent tributaries to the larger streams. The Native Cyprinid–Catostomid Association was found in the larger low elevation streams. The Introduced Fishes Association was found in low elevation intermittent streams that had been highly modified by man's activities.

CALIFORNIA'S great Sacramento-San Joaquin River complex has long been isolated from other drainage systems. This isolation has produced a varied and interesting fish fauna that is over 75 percent endemic (Miller, 1958). Since the late nineteenth century, intensive agriculture, mining, industry and the development of large population centers in the Sacramento-San Joaquin Valley and contiguous areas has drastically changed the quality and distribution of the water, particularly on the Valley floor. These changes, combined with wide-spread introduction of fish of many species from the eastern United States, have had serious repercussions on the native fish fauna. At least one species, the thicktailed chub, *Gila crassicauda* (Baird and Girard), is now either extinct or extremely rare (Miller, 1963). Other species such as the tule perch, *Hysterocarpus traskii* Gibbons, the tidewater goby, *Eucyclogobius newberryi* (Girard), and the Sacramento perch, *Archoplites interruptus* (Girard), are becoming increasingly uncommon within their original range. A few species, such as the hitch, *Lavinia exilicauda* Baird and Girard, the Sacramento blackfish, *Orthodon microlepidotus* (Ayres), and the Sacramento sucker, *Catostomus occidentalis* Ayres, still maintain populations and occasionally even become "pest" fish in reservoirs, where large numbers may severely limit the abundance of game fish (Calhoun, 1966).

Whatever the status of the individual native species, the original associations of native fish species have been disrupted completely on the Valley floor and to a lesser extent at higher altitudes. Fortunately, there are still relatively undisturbed associations of native fishes in many of the intermittent streams of the foothills of the Sierra Nevada mountains. Four such associations have been described by Murphy (1941) and Hopkirk (1967) for the Sacramento River system and named according to their most characteristic native species: hitch, sucker, roach and trout. The future of the foothill fish associations is precarious at best. Development of the foothills, including changes in land and water use, has been proceeding at an accelerated pace in recent years. Dams are now planned for most of the larger streams that do not already have them. The purpose of this paper, therefore, is to describe the foothill fish associations as they are today in the San Joaquin River system and to analyze statistically the ecological factors that affect the distribution of the more abundant species as well as the associations themselves.

The Study Area

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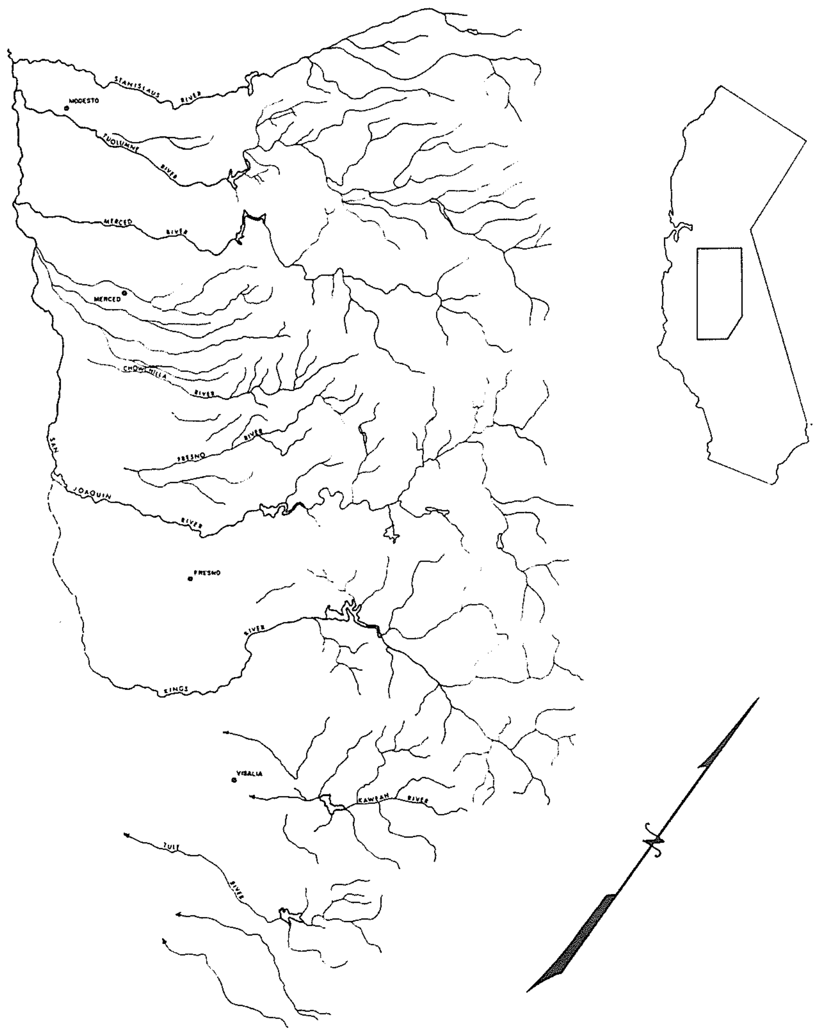

Fig. 1. Central California drainage systems sampled for foothill fishes, 27 July–4 September, 1970. The foothill region includes about the middle third of each of the main river systems.

elevations of 90 and 1100 m. Mean elevation for the collections was 401 m. At least one collection of fish was made from most of the streams accessible by road in Tulare, Fresno, Madera, Mariposa, and Tuolumne counties, California. A few collections were also made in Stanislaus County (Fig. 1). Most of the streams that were sampled are seasonally intermittent and flow over their entire course only when there is water from winter rains or runoff from the spring melt of snow in the mountains. During the study period (July 27–September 4, 1970), most streams sampled were not flowing, particularly at lower elevations, except where exposed bedrock brought the small underground flow to the surface. At this time, the fish were confined to and concentrated in isolated pools. The hillsides along the streams are rocky, heavily grazed, dry grasslands with a scattering of oaks (*Quercus* spp.) and, at the higher elevations, digger pine (*Pinus sabiniana*).

METHODS

Three major considerations determined the methods used: (1) the study area was large and the streams few and far between; (2) to assure seasonal consistency, all sampling had to be done in as short a time as possible, during the period when stream flows were

TABLE 1. NATIVE (N) AND INTRODUCED (I) FISHES COLLECTED AT 130 SAMPLING SITES IN STREAMS OF THE SIERRA NEVADA FOOTHILLS, CALIFORNIA, JULY 27–SEPTEMBER 4, 1970.

Name	Origin	%*
Family Centrarchidae		
Largemouth bass, *Micropterus salmoides*	I	31
Smallmouth bass, *Micropterus dolomieui*	I	7
Green sunfish, *Lepomis cyanellus*	I	46
Bluegill, *Lepomis macrochirus*	I	23
Redear sunfish, *Lepomis microlophus*	I	1
Family Cottidae		
Prickly sculpin, *Cottus asper*	N	2
Riffle sculpin, *Cottus gulosus*	N	2
Family Gasterosteidae		
Threespine stickleback, *Gasterosteus aculeatus*	N	1
Family Poecilidae		
Mosquitofish, *Gambusia affinis*	I	26
Family Cyprinidae		
Carp, *Cyprinus carpio*	I	2
Goldfish, *Carassius auratus*	I	1
Golden shiner, *Notemigonus crysoleucas*	I	8
Hitch, *Lavinia exilicauda*	N	10
Sacramento squawfish, *Ptychocheilus grandis*	N	38
Hardhead, *Mylopharodon conocephalus*	N	9
California roach, *Hesperoleucus symmetricus*	N	32
Family Catostomidae		
Sacramento sucker, *Catostomus occidentalis*	N	42
Family Ictaluridae		
White catfish, *Ictalurus catus*	I	9
Brown bullhead, *Ictalurus nebulosus*	I	7
Family Salmonidae		
Rainbow trout, *Salmo gairdneri*	N	20
Brown trout, *Salmo trutta*	I	1

* Percent samples in which fish occurred.

lowest; and (3) the available collecting and water sampling gear was limited. At each of the 130 sampling sites as many fish as possible were collected using minnow seines of several sizes. The number of fish of each species caught was then recorded and the fish returned to the water. Visual checks at the sample sites, by snorkeling when necessary, indicated that the seining provided a good estimate of the relative numbers of fish of each species present. Using the information from both seine hauls and visual checks, each fish species was assigned an abundance rating, on a *0–5* scale. On this scale a rating of *0* meant that no fish of that species was present; *1* meant that only one or two individuals were observed; *2* that 3–10 individuals were observed; *3* that the species was common; *4* that the species was abundant; and *5* meant that the area was swarming with the fish, a large number being brought up with every seine haul. A similar rating was also made for abundance of all the fish combined. Using the seining counts, the percentage of fish of each species in the entire sample was calculated.

At each site data were gathered on 20 easily measured or estimated environmental variables that were judged likely to affect the distribution of fishes. Those selected are: 1) elevation, in meters; 2) air and water temperature. Since air temperatures fluctuated 11–17 C during the day and the water temperatures tended to fluctuate with the air temperatures, the data analysis was based on the difference between the air and water temperatures. The data differences were coded: *1*, a difference of 0–2.8 C; *2*, 2.9–5.7 C; *3*, 5.8–8.6 C; *4*, 8.7–11.5 C; *5*, 11.6–14.4 C; 3) mean depth of water of the area sampled, measured in meters; 4) maximum depth, in meters; 5) width of water surface in meters; 6) water flow in liters per second as estimated with a velocity head rod; 7) turbidity rated on a *0–5* scale, where *0* is extremely clear and *5* is extremely turbid; 8) percentage of the bottom covered with rooted aquatic plants; 9) percentage of the water surface covered with floating mats of algae, water fern (*Azolla* spp.) or duckweed (*Lemna* spp.); 10) percentage of sampling area made up of pools, which are defined as wide areas of water with little or no noticeable flow; 11) the percentage of the sampling area made up of riffles where the water flowed over rocks and gravel and there were distinct breaks in the water surface; 12) percentage of stream bottom composed of silt; 13) percentage of bottom composed of sand, defined as rock particles less than 2 mm in diameter; 14) percentage of the bottom composed of gravel defined as pieces of rock, mostly 2–75 mm in diameter; 15) percentage of bottom covered with cobbles, mostly 75–300 mm in diameter; 16) percentage of bottom covered with bedrock or boulders larger than 300 mm in diameter; 17) the quality and amount of cover available to the fish, rated on a *0–5* scale, where *0* indicated no cover and *5* that the cover was plentiful and varied; 18) percentage of the water surface that was apparently shaded most of the day; 19) the extent to which human activities had visibly altered the stream channel and water quality as rated on a *0–5* scale, where *0* indicates no apparent alterations and *5* indicates that both the channel and water had been markedly altered; 20) stream type, which was rated as follows: *1*, small, with intermittent flow; *2*, medium sized, with intermittent flow; *3*, large, with intermittent flow; *4*, small (1–15 l/sec) with permanent flow; *5*, medium (15–30 l/sec) permanent flow; and *6*, large (30+ l/sec) with permanent flow. Each stream was classified by observing the flow at the time of sampling and by information from hydrological maps.

For each of the 130 collection localities, the following information was placed on punch cards: 1) the data from the foregoing 20 environmental variables, 2) the abundance rating and the catch percentage for each of the eleven most abundant fish species, 3) the abundance rating and the catch percentage for all other species captured combined, 4) the total number of species captured, and 5) the percentage of fish captured that belonged to endemic species. All 130 cards were then run through a computer programmed to obtain a Pearson correlation matrix for the 46 variables, as well as the means and standard deviations of the variables. The 130 cards were then sorted eleven separate times, each sort separating out all the cards for samples that contained one of the eleven most abundant fish species. The means and standard deviations for all the variables in these samples were then calculated. The means and standard deviations of the variables were also obtained for the four fish associations defined later in this paper. In the analysis of the abundance relationships between species, only the correlations between the abundance ratings are used in this paper since the abundance ratings and the sample percentages for each species were highly correlated.

Species Ecology

In all, twenty species of fish were collected from the foothill streams during the study. Only eleven of these species were collected in large enough numbers to warrant a detailed statistical analysis of their ecology (Table 1). Nine of the twenty species (45%) are native, the remaining eleven species are introduced.

In the following sections the ecological relationships of the eleven most abundant fish species are discussed. The means of the habitat variables, and their relationships to each other, are presented in Tables 2, 3, 4 and 5. Abbreviations for fish species in these tables are: LMB—largemouth bass; GSF—green sunfish; BG—bluegill; GAM—mosquitofish; GSH—golden shiner; HCH—hitch; SQ—Sacramento squawfish; HH—hardhead; RCH—California roach; SKR—Sacramento sucker; and RB—rainbow trout.

Largemouth bass.—This introduced predatory centrarchid occurred in 31% of the 130 collections and made up, on the average, only 8% of the fish in collections in which it occurred (Tables 1, 2). It was most abundant in warm turbid pools of intermittent streams at lower elevations (Table 3). These pools usually had sand or mud bottoms and were not well shaded. They often had extensive growths of rooted and floating aquatic vegetation (Table 3). Sites where largemouth bass were taken showed signs of heavy use by man, such as small dams, rip-rapping and cattle trampled banks. As might be expected of a largely piscivorous carnivore, at the top of the food chain, the largemouth bass was found where fish species diversity was high compared to that in other foothill areas. On the average four other species occurred with it. Those which were found most frequently are mosquitofish, green sunfish and bluegill (Tables 2, 4). Hitch and golden shiner were also often found where bass were most abundant, as were the less common introduced species, especially redear sunfish, white catfish, brown bullhead and carp (Tables 2, 4).

TABLE 2. PATTERNS OF FISH SPECIES CO-OCCURRENCE IN THE SIERRA NEVADA FOOTHILLS, CALIFORNIA, AS SHOWN BY MEANS OF ABUNDANCE RATINGS (0–5 SCALE) AND MEANS OF THE PERCENTAGES OF FISHES OCCURRING IN SAMPLES CONTAINING AT LEAST ONE MEMBER OF A SPECIES SELECTED FROM THE ELEVEN MOST ABUNDANT FOOTHILL FISH SPECIES. Species abbreviations are listed in the text.

	Species Selected										
	LMB	GSF	BG	GAM	GSH	HCH	SQ	HH	RCH	SKR	RB
N	40	60	30	34	11	13	49	12	42	54	26
LMB	1.9	0.9	1.4	1.3	1.4	1.6	0.6	0.6	0.2	0.5	0.0
%	8	3	7	4	7	5	2	2	1	2	0
GSF	1.5	2.1	1.2	1.5	1.5	1.9	0.7	1.1	0.6	0.6	< 0.1
%	14	25	10	10	9	12	5	3	4	2	< 1
BG	1.1	0.5	1.9	0.8	0.8	0.3	0.5	0.5	0.2	0.4	0.0
%	8	4	17	6	6	4	4	1	1	3	0
GAM	1.5	1.0	0.9	2.4	1.8	1.5	0.4	0.4	0.2	0.6	0.0
%	25	16	16	44	27	27	8	3	1	7	0
GSH	0.4	0.3	0.3	0.4	2.0	0.2	0.1	0.2	0.0	0.1	0.0
%	2	2	2	2	11	< 1	< 1	< 1	0	< 1	0
HCH	0.7	0.5	0.1	0.5	0.5	2.5	0.3	0.3	0.1	0.3	0.0
%	5	4	< 1	2	< 1	2	2	3	< 1	2	0
SQ	0.9	0.7	1.0	0.7	0.9	1.1	2.4	2.6	0.9	1.6	0.5
%	10	8	16	7	8	13	32	32	9	23	6
HH	0.2	0.3	0.4	0.3	0.3	0.2	0.7	2.8	0.1	0.4	0.2
%	3	6	5	5	5	1	9	40	< 1	5	1
RCH	0.3	0.6	0.5	0.4	0.0	0.3	0.9	0.3	2.7	1.0	0.7
%	6	15	8	9	0	6	14	3	65	18	13
SKR	0.7	0.7	0.9	0.8	1.1	0.9	1.5	1.4	1.0	2.2	0.8
%	6	8	11	9	9	4	16	11	13	27	17
RB	0.0	0.1	0.0	0.0	0.0	0.0	0.2	0.3	0.4	0.4	1.9
%	0	< 1	0	0	0	0	1	< 1	4	3	60
Other Spp.	1.0	0.8	0.9	0.7	1.2	0.7	0.5	0.3	0.2	0.4	0.1
%	15	9	10	3	18	7	7	2	2	8	2

Green sunfish.—The green sunfish was the most widely distributed introduced fish in the study area, ranging from the valley floor to an elevation of 690 m. It occurred in 46% of the samples. This is not too surprising because it is small, very aggressive and is native to warm intermittent and sluggish streams of the Midwest (Cross, 1967; Hubbs and Lagler, 1958). Green sunfish were abundant in small intermittent streams at lower elevations, especially in warm, turbid, muddy-bottomed pools that had large amounts of aquatic vegetation and where there were sizable populations of largemouth bass and mosquitofish (Tables 2, 3, 4). Although the abundance of green sunfish was negatively correlated with the abundance of most of the native fishes, it frequently was found in the streams with them, but in low numbers (Tables 2, 4). It was not unusual to find green sunfish the sole or numerically dominant species in smaller streams at low elevations, especially in those streams that had been considerably modified by human activities (Table 3).

Bluegill.—Bluegill were present in 23% of the samples but seldom in large numbers. They were most abundant at low elevations in the deeper, more heavily vegetated pools where fish diversity was relatively high (Table 3). Largemouth bass and mosquitofish were usually present here also. Many of the fish in these pools may have gotten there

TABLE 3. MEANS OF ENVIRONMENTAL VARIABLES ASSOCIATED WITH FIVE INTRODUCED SPECIES OF FISHES IN STREAMS OF THE SIERRA NEVADA FOOTHILLS, CALIFORNIA. Explanations of species abbreviations and the variables are given in the text.

	Species				
Variable	LMB	GSF	BG	GAM	GSH
Number samples	40	60	30	34	11
Temp. (1–5)	2.8*	2.7*	2.9	2.8*	3.2
Elev. (m)	254 *	331 *	288 *	245 *	277
Depth (m)	0.5	0.5	0.5	0.4	0.5
Max. Depth (m)	1.5	1.4	1.7**	1.3	1.1
Width (m)	5.0	4.0	5.6	4.8	4.5
Flow (l/sec)	8.9	4.6*	11.2	7.6	4.1
Turbidity (1–5)	2.4**	2.4**	2.1	2.5**	1.8
Rooted veg. (%)	35 **	36 **	31 **	39 **	35
Floating veg. (%)	23 **	26 **	20	27 **	35 **
Pools (%)	67 **	73 **	65 **	56	57
Riffles (%)	19 **	17 **	24 *	24 *	25
Bottom types (%):					
Silt	14	15 **	14	19 **	8
Sand	36	40	39	37	44
Gravel	12	9	6	15	14
Cobbles	23	18	18	19	21
Boulders	16	18 *	22	11 *	12
Cover (1–5)	2.6	2.7	2.8	2.7	2.1*
Shade	25 *	36	26 *	27 *	11 *
Man mod. (1–5)	2.9**	3.0**	2.7	2.8	3.2**
Stream type (1–6)	2.7	2.0*	2.9	2.7*	2.5
Total fish abund. (1–5)	2.9	3.0**	2.7	2.9**	3.3**
Number species	4.9**	3.9**	4.5**	4.5**	4.9**
Native fish (%)	31 *	40	40 *	32 *	22 *

** Significant positive correlation ($P < .05$) between the variable and the fish species abundance ratings, in the matrix for all localities (N–130).
* Significant negative correlation, as above.

TABLE 4. CORRELATIONS BETWEEN ABUNDANCE RATINGS OF THE ELEVEN MOST ABUNDANT FISHES IN 130 SAMPLES OF FISHES FROM STREAMS OF THE SIERRA NEVADA FOOTHILLS, CALIFORNIA. Boldface coefficients are significant ($P < .05$).

	LMB	GSF	BG	GAM	GSH	HCH	SQ	HH	SKR	RCH	RB
LMB	1.00										
BSF	**.29**	1.00									
BG	**.60**	.10	1.00								
GAM	**.48**	**.40**	**.19**	1.00							
GSH	**.23**	**.20**	**.23**	**.30**	1.00						
HCH	**.37**	**.29**	–.09	**.17**	–.01	1.00					
SQ	–.01	–.16	.02	–.12	–.03	.01	1.00				
HH	–.01	.05	.03	–.05	.01	–.00	**.44**	1.00			
SKR	–.10	**–.30**	–.06	–.07	–.00	.01	**.43**	.14	1.00		
RCH	**–.29**	**–.22**	**–.18**	**–.23**	**–.18**	–.12	–.07	–.15	.07	1.00	
RB	**–.30**	**–.39**	**–.25**	**–.27**	–.13	–.15	–.18	–.07	–.07	–.02	1.00

from farm ponds which occasionally overflow in the spring. Bluegill and largemouth bass are commonly stocked in such ponds.

Mosquitofish.—Schools of this small (10–40 mm TL) introduced larvivorous species were taken most frequently from warm turbid pools of intermittent streams at low elevations (Table 3). In such pools it was usually found in aquatic vegetation or in shallow water along the edges of pools where water temperatures approached daytime air temperatures (33–38 C). Centrarchids were usually abundant in the deeper waters of these pools but native cyprinids, except the hitch, were uncommon (Tables 2, 4). Streams with mosquitofish usually showed signs of having been extensively changed by human activity, particularly cattle raising (Table 3).

Golden shiner.—The golden shiner, although widely used as a bait fish in California, occurred in only 8% of the samples, and then usually in low numbers. It was found most often in the large warm pools or slow moving stretches of low-altitude streams where other introduced fishes were abundant (Tables 2, 3, 4).

Hitch.—This native cyprinid is more characteristic of the sloughs and large sluggish rivers of the Valley floor than of the intermittent foothill streams (Calhoun, 1966; Murphy, 1948). Nevertheless, it occurred in 10% of the collections. Hitch dominated numerically in four of the samples. It was most abundant in warm, sandy-bottomed streams with large pools where other introduced species, usually green sunfish, largemouth bass and mosquitofish were common (Tables 4, 5). Most of the hitch taken were less than 150 mm long, although in large bodies of water they frequently exceed 300 mm (Calhoun, 1966).

Sacramento squawfish.—The squawfish, a large predaceous minnow, is widely distributed in foothill streams and reservoirs. It occurred in 38% of the samples and was most abundant in the larger intermittent and permanent streams at about the 300 m elevation level (Table 5). These streams contained deep sandy- or rock-bottomed pools that are fairly well shaded and show few signs of modification by man (Table 5). Squawfish were seldom abundant where introduced centrarchids were common. However, they tended to predominate both in size and numbers, where other native cyprinids and the Sacramento sucker were common (Tables 2, 4). Although squawfish were often found with rainbow trout and California roach, they were seldom abundant where either was common.

Hardhead.—This large omnivorous native cyprinid was represented in only 9% of the samples but where it occurred it was abundant (Table 2). It was found primarily in clear, deep, sand- and rock-bottomed pools of the larger streams at elevations between 270 and 420 m (Table 5). These streams showed little evidence of man-caused changes, and, on the average, only 10% of the fish taken with the hardhead were introduced species. The hardhead was always found with the Sacramento squawfish and usually with the Sacramento sucker (Tables 2, 4).

California roach.—The California roach is a small (usually less than 100 mm TL) native minnow that was most abundant in well-shaded, clear and rock-bottomed pools of small intermittent tributaries to larger streams (Table 5). It was widely distributed in the foothills at moderate elevations (average, 458 m). Where it was taken it tended to be numerically dominant, averaging 65% of the fish in 42 collections containing it. In 38% of these collections 90% or more of the fish were roach. Fishes that were collected most commonly with the roach were Sacramento sucker, Sacramento squawfish and green sunfish (Tables 2, 4). For the most part, the roach was most abundant where introduced species were rare or absent. The fact that roach were found most often crowded in large numbers in warm (30–35 C) isolated pools indicates that it is able to survive for extended periods in the summer at low dissolved oxygen levels. Low oxygen levels presumably keep other native fish species from permanently occupying the roach's habitat. However, during the study dead and dying roach were observed in several of the shallower and more exposed pools.

Sacramento sucker.—This bottom feeder was the most widely distributed fish encountered. It occurred in 42% of the samples and was taken at elevations ranging from the Valley floor to 880 m. Although it was found in

TABLE 5. MEANS OF ENVIRONMENTAL VARIABLES ASSOCIATED WITH SIX SPECIES OF FISHES ENDEMIC TO THE STREAMS OF THE SIERRA NEVADA FOOTHILLS, CALIFORNIA. Explanations of the species abbreviations and the variables are given in the text.

Variable	Species					
	HCH	SQ	HH	RCH	SKR	RB
Number samples	13	49	12	42	54	26
Temperature (1–5)	2.5*	3.0	3.5	3.3	3.2	4.7**
Elevation (m)	276	312 *	294	458	371	748 **
Depth (m)	0.4	0.5	0.5	0.4	0.4	0.4
Max. Depth (m)	1.4	1.7**	1.8*	1.3	1.4	1.6
Width (m)	3.7	5.8	4.6	3.3	6.2**	4.3
Flow (l/sec)	7.4	10.2	5.1	6.1	10.2	11.7
Turbidity (1–5)	2.1	1.8	1.8	1.7*	1.7*	1.2*
Rooted veg. (%)	31	20	28	24	22	6 *
Floating veg. (%)	25	15	19	17	16	2 *
Pools (%)	69	53	53	55	47	34 *
Riffles (%)	13 *	38	34	37	39 **	57 **
Bottom types (%)						
Silt	5	4 *	3	6	6 **	9
Sand	50	36	47	27 *	39	31
Gravel	15	9	6	10	10	4
Cobbles	24	26	14	26	20	15
Boulders	6 *	26	28	30	25	40 **
Cover (1–5)	2.5	2.8	3.0	3.1**	2.7	3
Shade (%)	30	29 *	33	53 **	33	61 **
Man mod. (1–5)	3.1	2.3*	1.7*	2.5	2.6	1.9*
Stream type (1–5)	2.5	3.2	2.7	2.6	3.4**	4.1**
Total fish abund. (1–5)	2.9	2.8**	3.2**	2.8**	2.9**	2.1*
Number species	5.2**	4.1	4.6**	3.0*	4.1**	2.0*
Native fish (%)	45	75 **	90 **	91 **	79 **	96 **

** Significant positive correlation ($P < .05$) between the variable and the fish species abundance ratings in the matrix for all localities.
* Significant negative correlation, as above.

all types of streams, it was most abundant in the larger, clear, permanent streams at intermediate elevations (Table 3). Its most usual fish associates were native minnows, especially squawfish and roach (Tables 2, 4). Where the sucker was abundant, other fish also tended to be abundant, both in species and in numbers (Table 2). Most of the suckers taken were shorter than 75 mm total length, and were presumably young of the year. Larger specimens were observed only occasionally and these in larger pools and flowing streams. This is not surprising since typically the adults live in the large rivers, lakes and reservoirs, and make extensive migrations up tributaries to spawn in spring (Calhoun, 1966).

Rainbow trout.—Although the rainbow trout has been widely planted for sport fishing in streams throughout California, it is probably native to most of the streams where it was taken in this study (Calhoun, 1966). However, trout populations in some of these streams may now be artificially maintained by stocking. As is indicated in the extensive literature on rainbow trout in California (which is summarized in Calhoun, 1966), rainbows frequent the cool, clear, fast-flowing permanent streams at the higher elevations. In the foothill region these are streams that have been comparatively little modified by man (Table 5). Overall abundance of fishes and species diversity in such streams was found to be low, probably in part because of low natural productivity and in part because of the occasional use of piscicides by the California Department of Fish and Game to eliminate possible trout competitors, especially Sacramento squawfish

TABLE 6. AVERAGE ABUNDANCE RATINGS (AR) AND AVERAGE PERCENTAGES (%) IN SAMPLES OF FISHES IN THE FOUR FOOTHILL FISH ASSOCIATIONS.

	Associations							
N	Introduced Fish 41		Native Cyprinid-Catostomid 24		California Roach 24		Rainbow Trout 13	
Species	AR	%	AR	%	AR	%	AR	%
LMB	1.2	6	0.3	< 1	0.1	1	0.0	0
GSF	1.9	31	0.5	2	0.6	2	0.0	0
BG	0.8	9	0.4	1	0.1	1	0.0	0
GAM	1.4	32	0.2	< 1	0.2	1	0.0	0
GSH	0.4	3	0.1	< 1	0.0	0	0.0	0
HCH	0.3	1	0.1	< 1	0.1	1	0.0	0
SQ	0.4	2	2.6	49	0.3	1	0.0	0
HH	0.0	0	1.2	18	0.0	0	0.0	0
RCH	0.1	1	0.5	5	3.1	90	0.0	0
SKR	0.4	1	1.9	24	0.7	3	0.2	2
RB	0.0	0	0.2	< 1	0.3	1	1.9	98
Other Spp.	1.2	14	0.3	< 1	0.0	0	0.0	0
Native fish	—	4	—	96	—	97	—	100

and Sacramento sucker. The last two, along with California roach, were the only species ever collected in any numbers with the trout. It is likely, however, that sculpins may have been missed in the sampling of many of the trout streams.

FISH ASSOCIATIONS

When the correlation matrix for the entire set of data was examined, it became evident that there were four distinct associations of fish species. Abundance ratings of fishes in these associations were positively correlated with each other and showed negative correlations or no correlations with species in other associations (Table 4). The associations thus indicated are: 1) the Introduced Fishes Association, consisting of largemouth bass, bluegill, green sunfish and mosquitofish, along with other less-common introduced species and the native hitch; 2) the Native Cyprinid-Catostomid Association, predominately Sacramento squawfish, Sacramento sucker and/or hardhead, along with

TABLE 7. PERCENTAGES OF SAMPLES ASSIGNED TO EACH OF THE FOUR FISH ASSOCIATIONS THAT WERE FOUND IN THE SIX TYPES OF STREAMS OF THE SIERRA NEVADA FOOTHILLS, CALIFORNIA.

	Fish Associations				
Stream Type	Introduced Fish	Native Cyprinid-Catostomid	California Roach	Rainbow Trout	All Samples
1	73	29	67	0	44
2	3	12	0	0	5
3	0	4	0	0	1
4	7	25	29	0	28
5	3	21	4	78	15
6	14	8	0	22	7
Intermittent (1–3)	76	45	67	0	50
Permanent (4–6)	24	55	33	100	50
N	41	24	24	13	130

TAGES (%) IN SAMPLES OF FISHES
IONS.

ifornia oach 24	Rainbow Trout 13	
%	AR	%
1	0.0	0
2	0.0	0
1	0.0	0
1	0.0	0
0	0.0	0
1	0.0	0
1	0.0	0
0	0.0	0
90	0.0	0
3	0.2	2
1	1.9	98
0	0.0	0
97	—	10(

ns were positively correlated
er and showed negative cor-
correlations with species in
ons (Table 4). The associa-
cated are: 1) the Introduced
ion, consisting of largemouth
green sunfish and mosquito-
th other less-common int
and the native hitch; 2) the
l-Catostomid Association, pre-
cramento squawfish, Sacra-
and/or hardhead, along with

FISH ASSOCIATIONS THAT WERE
FOOTHILLS, CALIFORNIA.

Rainbow Trout	All Samples
0	44
0	5
0	1
0	28
78	15
22	7
0	50
100	50
13	130

small numbers of California roach in some localities; 3) the California Roach Association, made-up almost completely of roach; and 4) the Rainbow Trout Association, made-up mostly of rainbow trout.

To obtain means and standard deviations for each of the 46 variables for each association, so that the environment where each association was found could be characterized more exactly, each sample was assigned to one of the four associations if 70% or more of the fish in that sample belonged to the dominant species of the association. The 70% level was chosen because when the punch cards were sorted for rainbow trout and for California roach, both of which belong to associations dominated by single species, it was found that in most of the samples containing these species, they either made-up more than 70% or less than 30% of the catch. On this basis, 78% of the samples could be assigned to one or another of the four associations (Table 6). Twenty-two of the 28 remaining samples could be described as representing transition populations since they contained about an equal mixture of fish from two different associations. Eleven of these 22 were transition collections between the Native Cyprinid-Catostomid Association and the Introduced Fishes Association. Of the remaining six collections, four were samples from small streams dominated by hitch, one was from a site dominated by threespine stickleback and riffle sculpin, and one was from a site containing a mixture of species from all four associations. In all, only 57% of the collections contained 70% or more of native fishes.

Introduced Fishes Association.—This was the most common association encountered (32% of the samples) and, because it occurred at the lowest elevations in the foothills, it contained the greatest variety of fishes. In addition to the four dominant introduced species, there were frequently a few native fishes in samples from sites containing this association. These fish were usually large and had evidently come from higher elevations during the high-water flows of winter. Frequently present also in the samples were a few representatives of the other introduced species. These fish had presumably moved upstream to the foothill pools during high water, from the large rivers and reservoirs where they are more abundant. This association is similar to the hitch association of Murphy (1948) and Hopkirk (1967).

The Introduced Fishes Association was most often found in the warm turbid pools of the smaller intermittent streams (Tables 7, 8). Such pools lacked shade, had large amounts of aquatic vegetation and had muddy-sandy bottoms (Table 8). The streams and the areas around them were usually extensively modified by human activities.

Native Cyprinid-Catostomid Association.—The Sacramento squawfish is usually the numerically dominant fish of this association, although sometimes the Sacramento sucker or the hardhead play this role (Table 6). This association occurred in several types of streams (Table 7) at intermediate elevations and often included some fish from other associations, most commonly green sunfish and California roach (Table 6). Although the Native Cyprinid-Catostomid Association occurred in all of the six stream types, the habitats in which the association was found had much in common. They tended to be clear and warm, bottoms were of sand or bedrock, and the stream stretches usually had pools (Table 8). Even the intermittent streams were usually flowing, if only a trickle, in the sections where this association was found. These stream stretches were largely unshaded, contained little aquatic vegetation, and showed few signs of having been altered by man.

California Roach Association.—Since California roach made up 90% of the fish of this association, the characteristics of the small, clear, mostly intermittent, streams where it was found are much like those already described for the roach as a species (Tables 6, 7, 8). However, the streams where the roach made up 70% or more of the fish population were even smaller than those associated with the overall range of the fish and contained a greater percentage of pools (Table 8).

Rainbow Trout Association.—This association is also dominated by a single species of fish, the rainbow trout, and is found in the cool permanent streams at higher elevations in the foothills (Tables 6, 7, 8).

These associations of the San Joaquin River system are approximately equivalent to the four associations of the Sacramento

TABLE 8. MEANS OF ENVIRONMENTAL VARIABLES ASSOCIATED WITH THE FOUR FISH ASSOCIATIONS IN STREAMS OF THE SIERRA NEVADA FOOTHILLS, CALIFORNIA.

	Fish Associations			
	Introduced Fish	Native Cyprinid-Catostomid	California Roach	Rainbow Trout
Temperature (1–5)	2.6[c]	33.0[c]	3.6[c]	4.8[a]
Elevation (m)	286 [c]	334 [c]	446 [b]	846 [a]
Depth (m)	0.5	0.4	0.4	0.5
Max. Depth (m)	1.3	1.8	1.0[c]	1.4
Width (m)	4.5	5.7	1.6[c]	2.1[b]
Flow (l/sec)	7.1	11.7	2.5	11.9
Turbidity (1–5)	2.8[a]	1.6[c]	1.6[c]	1.2[c]
Rooted veg. (%)	36 [c]	16	24	7 [c]
Floating veg. (%)	25	11	17	4 [c]
Pools (%)	68 [c]	41 [c]	60	33 [b]
Riffles (%)	20 [b]	47 [c]	31 [b]	58 [c]
Bottom types (%):				
Silt	21	1 [a]	9	15
Sand	33	43	26	31
Gravel	11	6	15	4 [c]
Cobbles	24	22	24	15
Boulders	11 [c]	29	27	36
Cover (1–5)	2.7	2	3	3.2
Shade (%)	32	30 [b]	61 [b]	68 [b]
Man mod. (1–5)	3.2[c]	1.7[b]	3.0[b]	1.5[b]
Stream type (1–6)	2.3[c]	3.6	2.0[b]	4.2[a]
Total fish abund. (1–5)	2.7[c]	2.9[c]	3.0[c]	1.9[a]
Number species	3.7[c]	3.8[b]	2.3[c]	1.1[a]
N	41	24	24	13

[a] Mean ± one standard deviation does not overlap the mean of any other association.
[b] Mean ± one standard deviation overlaps the mean of one other association.
[c] Mean ± one standard deviation overlaps the mean of two other associations. Means not footnoted ± one standard deviation overlap all other three means.

River system of Murphy (1948) and Hopkirk (1967). However, they seem to have less species diversity, presumably because the foothill streams of the San Joaquin River system are generally smaller and less permanent than those of the Sacramento River system.

DISCUSSION

As is shown in the tables, especially Tables 6, 7 and 8, there is considerable overlap in the characteristics of the four fish associations, both in environmental characteristics and in fish species present. The overlap of environmental characteristics is especially apparent when means and standard deviations are examined (Table 8). For most of the variables considered, the mean, plus or minus one standard deviation, for one association overlaps the mean of the same variable for two or three other associations. The Rainbow Trout Association has the least amount of overlap of variables, followed by the California Roach Association. However, each association, at least those of the native fishes, has its own set of means and ranges around those means for the environmental variables and these can be considered to intersect to form a hypervolume, much as Hutchinson (1965) described for the niches of individual species.

The Introduced Fishes Association, however, does not fit this conceptual pattern very well, because it is recent in origin and less consistent in its species composition. Presumably, it has not had time to develop and become established *in situ*. The similarities of its associated environmental charac-

TABLE 9. CORRELATIONS BETWEEN SELECTED ENVIRONMENTAL VARIABLES RECORDED AT THE 30 FISH SAMPLING STATIONS IN THE STREAMS OF THE SIERRA NEVADA FOOTHILLS, CALIFORNIA. Boldface coefficients are significant (P > .05).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. Temp. (1–5)	1.00														
2. Elev. (m)	.37	1.00													
3. Max. depth (m)	.14	.03	1.00												
4. Flow (l/sec)	.20	.01	–.45	1.00											
5. Turbidity (1–5)	–.39	–.40	–.11	–.26	1.00										
6. Rooted veg. (%)	–.27	–.33	–.17	–.31	.29	1.00									
7. Floating veg. (%)	–.27	–.31	–.21	–.38	.25	.86	1.00								
8. Pools (%)	–.30	–.19	.06	–.48	.45	.21	.25	1.00							
9. Riffles (%)	.26	.34	.06	.40	–.51	–.20	–.24	–.74	1.00						
10. Mud (%)	–.19	–.05	–.11	–.21	.27	.26	.27	.12	–.21	1.00					
11. Sand (%)	.05	.06	.08	–.20	.03	–.17	–.09	.11	–.20	–.34	1.00				
12. Boulder (%)	.28	.35	.27	.15	–.36	–.12	–.15	–.15	.42	–.25	–.19	1.00			
13. Shade (%)	.30	.45	–.20	–.26	–.13	–.24	–.20	.06	–.06	.12	–.07	.09	1.00		
14. Man mod. (%)	–.30	–.25	–.22	–.21	.20	.25	.23	.24	–.37	.31	–.06	–.45	–.05	1.00	
15. Stream type	.40	.13	.26	.76	–.35	–.30	–.36	–.69	.55	–.22	–.10	.18	–.09	–.33	1.00

teristics to those of the Native Cyprinid-Catostomid Association indicates that it may well be still expanding its dominance into waters now occupied by the native fishes or will do so as the waters become more altered by human activities (Table 8). In the study area, the introduced fishes were most often found where there were: 1) impoundments that decreased stream flow and increased the pool-type habitat; 2) organic pollution from livestock, and, to a lesser extent, from sewage that promoted algal growths and increased turbidity and 3) siltation, mostly from roadways and construction, that increased turbidity and made the pools shallower by deposition of mud and silt.

It should be emphasized that the individual environmental factors considered are not necessarily independent variables (Table 9). For example, two factors strongly associated with fish distribution, elevation and water temperature, were highly correlated with each other. As the elevation increased there was a greater divergence between water temperatures and air temperatures. Most of the other variables that seemed to be important in determining the distribution of the foothill fishes were either positively or negatively correlated with elevation and temperature (Table 9).

Not surprisingly, the variables which have a positive or negative correlation with these two variables also had a similar correlation with rainbow trout abundance and, to a lesser extent, with the California roach abundance and with their respective associations. Conversely, correlations of these variables with member species of the Introduced Fishes Association, and also of the Native Cyprinid-Catostomid Association, tended to have the opposite sign.

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LITERATURE CITED

CALHOUN, A. C., ED. 1966. Inland Fisheries Management, Calif. Dept. of Fish and Game.

CROSS, F. B. 1967. Handbook of the Fishes of Kansas. Univ. Kansas Mus. Nat. Hist. Spec. Pub. No. 45.

HOPKIRK, J. D. 1967. Endemism in fishes of the Clear Lake Region. Ph.D. thesis. Univ. Calif. Berkeley.

HUBBS, C. L., AND K. F. LAGLER. 1958. Fishes of the Great Lakes Region. Univ. Mich. Press, Ann Arbor.

HUTCHINSON, G. E. 1965. The Ecological Theater and the Evolutionary Play. Yale Univ. Press, New Haven.

MILLER, R. R. 1958. Origin and affinities of the freshwater fish fauna of western North America, p. 187–222. *In*: Zoogeography, C. L. Hubbs, ed., AAAS.

————. 1963. Synonymy, characters, and variation of *Gila crassicauda*, a rare California minnow, with an account of its hybridization with *Lavinia exilicauda*. Calif. Fish and Game 99:20–29.

MURPHY, G. I. 1948. Distribution and variation of the roach (*Hesperolevcus*) in the coastal region of California. M.A. thesis, Univ. Calif. Berkeley.

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Olfactory Orientation in Breeding Mexican Toads, *Bufo valliceps*

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Breeding male toads, *Bufo valliceps*, were collected from or en route to breeding sites and tested in an olfactometer for the ability to discriminate and respond to the odor of water from their home breeding habitats. Six of seven populations tested demonstrated a preference for this odor. Alternatives discriminated against included slightly humidified air and the odors of distant and adjacent bodies of water, either temporary or permanent, all of which were used for breeding by conspecifics. The response diminished through time but could be revived by injection of gonadotropins. Toads in breeding condition which had not been exposed to their breeding habitat for at least one month responded positively to its odor. Tests for celestial orientation yielded no evidence of either a nocturnal or diurnal celestial-compass mechanism.

HOMING by anurans to breeding sites is well documented (Heusser, 1969; Jameson, 1957; Oldham, 1966, 1967; Tracy and Dole, 1969b). Several types of orientation mechanisms may function during these breeding movements. Individuals are sometimes attracted to conspecific mating calls (Bogert, 1947, 1960). However, breeding choruses do not seem to be of primary importance since animals returning to their home ponds after displacement often ignore choruses in foreign ponds and recorded choruses (Jameson, 1957; Oldham, 1966, 1967). Field studies involving sensory ablation have implicated both visual and olfactory mechanisms (Oldham, 1966, 1967). Several species respond positively to the odors of their breeding habitats in the laboratory (Grubb, in press; Jungfer, 1943; Martof, 1962). Celestial cues can guide some species along a particular compass course (Y-axis) relative to the shoreline of a breeding pond (Ferguson, 1967; Gorman and Ferguson, 1970; Tracy and Dole, 1969a). Other mechanisms, such as reference to local landmarks and kinesthesia, are possible but have not been satisfactorily investigated in anurans. A species may use more than one orientation mechanism. Both *Bufo woodhousei fowleri* and *Pseudacris triseriata* respond to mating calls, celestial cues and pond odors (Grubb, in press; Ferguson and Landreth, 1966; Landreth and Ferguson, 1966; Martof, 1962).

Some of the same mechanisms probably function in nonbreeding homing movements in anurans although these have been less extensively studied. Y-axis orientation is used by some species (Ferguson, Landreth and Turnipseed, 1965; Ferguson et al., 1968; Taylor and Ferguson, 1970). Local visual and olfactory cues have also been implicated by sensory ablation studies (Dole, 1968, 1972; Grubb, 1970).

In central Texas, the Mexican toad, *Bufo valliceps*, breeds from March through September, usually after rains (Blair, 1960). Individuals show fidelity to particular breeding sites (Blair, 1960) and may move up to 300