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FOOD HABITS OF THE BROWN SMOOTHHOUND SHARK (*MUSTELUS HENLEI*) FROM TWO SITES IN TOMALES BAY

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Brown smoothhound sharks were non-destructively sampled for stomach contents at two locations in Tomales Bay. Sharks near Hog Island consumed more slender crabs and fish, but fewer yellow shore crabs and polychaete worms than those near Indian Beach. Thus, brown smoothhound shark food habits are not homogeneous throughout the Bay, as was implied from previous studies using shark derby-caught fish. Survival of sharks from stomach eversion was > 85%.

INTRODUCTION

The brown smoothhound (*Mustelus henlei*) is a common, bottom-oriented shark in shallow waters off California. Although it has been found from the Gulf of California to Humboldt Bay (Miller and Lea 1972), it is most common inside the bays and estuaries of Northern California such as San Francisco and Tomales bays (Love 1991). This shark has a subterminal mouth and small, coarse teeth, and its main food items are crabs, shrimp, polychaete worms, and fish (Karl 1979, Russo 1975). Previous diet studies in Tomales Bay used specimens obtained from shark fishing derbies, which were not site-specific within the bay.

Numerous methods have been developed for removal of stomach contents without harming fish. The simplest of these is merely removing the contents with a forceps (Wales 1962). Another method uses water to flush contents out of the stomach (Seaburg 1957). The stomach flushing technique is efficient with high survival of fish after treatment, but efficiency is negatively correlated with size (Meehan and Miller 1978). The ability of sharks to evert their stomachs under stress and survive is well known (Russo 1975, Springer and Gold 1989). Researchers have used this ability to develop a stomach eversion technique for examining the diet and feeding habits of lemon sharks (*Negaprion brevirostris*) (Cortes and Gruber 1990) and grey smoothhound sharks (*Mustelus californicus*) (SanFilippo 1992). With this technique, the stomach and its contents are manually pulled out through the esophagus and mouth.

The purpose of this study was to examine the food habits of the brown smoothhound sharks captured with short duration gill-net sets at two different locations in Tomales Bay, using a stomach eversion technique. This method is non-destructive to the sharks but allows for complete sampling of the stomach contents, as has been shown for gray

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smoothhound sharks (SanFilippo 1992). In addition, gill-net placement allows investigation of site-specific food habits.

METHODS

Fish Collection

Fish were collected during 7-16 July 1992 at two locations in Tomales Bay. The first was in the outer bay region (Smith et al. 1991) near Hog Island at a depth of 4-6 m, and the second was in the inner bay region near Indian Beach at a depth of 3-6 m (Fig. 1). Two gill-nets, 3 m high x 100 m long with 6 cm mesh were deployed at each site by boat and allowed to set for 30 min. Captured fish were removed from the net and placed into a seawater-filled, insulated cooler where they were immediately anesthetized using dissolved CO_2 (Summerfelt and Smith 1990).

Stomach Eversion

After approximately 10 min in the CO_2-seawater bath, the fish were removed, sexed, measured to the nearest cm, and held caudal end up. Stomach tongs (20 or 45 cm length) were gently inserted through the esophagus and closed onto a portion of the stomach near the duodenum. The tongs were then slowly withdrawn, everting the stomach and releasing the stomach contents onto a 1-mm stiff plastic mesh situated over a bucket. After collection of the stomach contents, the shark was then held snout end up which allowed the stomach to slide down the esophagus and be swallowed back to normal position. The food items were sealed in a plastic bag. The shark was then marked by punching a small hole in the posterior region of the dorsal fin, revived with a fresh seawater flow over the gills, and released. Sharks were marked to prevent multiple sampling of the same fish.

Prey Analysis

Stomach contents were analyzed at Bodega Marine Laboratory (BML) using a dissecting microscope and taxonomic keys (Morris et al. 1980, Smith and Carlton 1975, Miller and Lea 1972). Frequency of the items within the stomach (Hyslop 1980) and the carapace width (mm) for crabs were recorded. Shark length and prey data were compared using regression and *t*-test analyses (Sokal and Rohlf 1981).

Survivorship

For survivorship studies, 7 sharks were transported to BML in oxygenated, seawater-filled coolers. After 12-30 h acclimation in seawater tanks, shark stomachs were everted. Contents of this eversion with those from field-sampled sharks were used in the study. Following a 36 h recovery, stomachs were everted again. After 24-48 h subsequent recovery, surviving sharks were released into the wild. No control group was used because of time and space constraints.

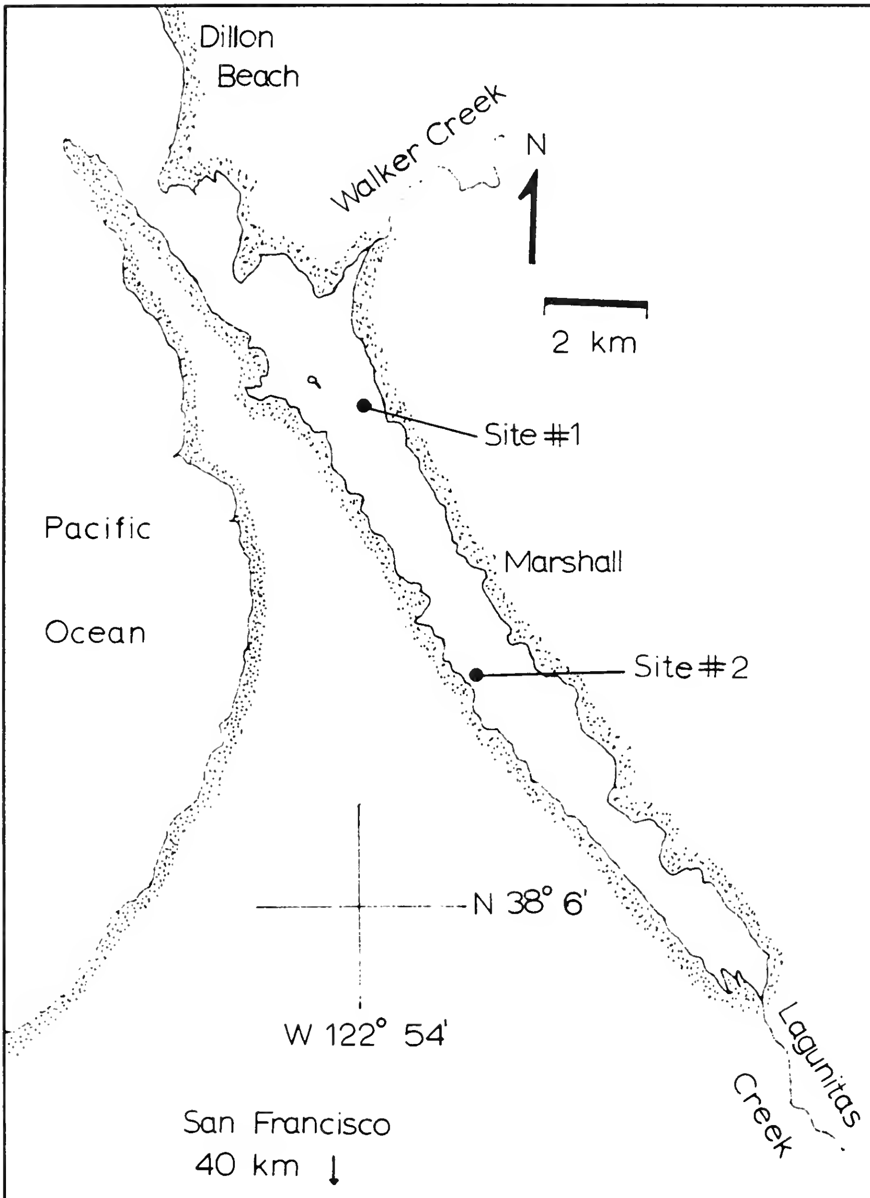

Figure 1. Map of Tomales Bay, on the northern California coast, showing sampling sites #1 (Hog Island) and #2 (Indian Beach).

RESULTS

Fifty-four brown smoothhound sharks were captured and stomach contents collected by stomach eversion. The sharks ranged from 67 to 92 cm total length, and there was no difference in mean fish length between sampling sites (t-test, $P > 0.05$). Only three sharks had empty stomachs. Stomach contents analysis indicated some dietary differences between the collection sites. At the Hog Island site, 75% of the sharks contained slender crabs (*Cancer gracilis*) while 25% contained yellow shore crabs (*Hemigrapsus oregonensis*). However at the Indian Beach site, 91% contained *H. oregonensis* and only 12% contained *Cancer gracilis* (Table 1). Sharks sampled from the Hog Island site contained a higher (t-test, $P < 0.05$) number of *C. gracilis* while the number of ingested *H. oregonensis* was higher (t-test, $P < 0.05$) at Indian Beach. Pea crabs (*Scleroplax granulata*) and kelp crabs (*Pugettia producta*) were only rarely found in the stomach contents.

Bay shrimp (*Crangon stylirostris*) also constituted an important part of the smoothhound diet. No significant difference (t-test, $P > 0.05$) in the mean number of *C. stylirostris* existed between the two sampling sites. However, the mean was somewhat greater at the Indian Beach location. Other shrimp such as the bay ghost shrimp (*Callianassa californiensis*) and the blue mud shrimp (*Upogebia pugettensis*) were rarely found and did not show significant differences (t-test, $P > 0.05$) between sites.

Of the sharks captured, 27% of the stomachs contained fish. Highly digested remains made species determination difficult, and thus a large proportion of fish are recorded under the "Unidentified" category. However the brown smoothhounds captured at Hog Island contained a significantly higher mean number of total fish than the Indian Beach individuals. In addition, the mean number of staghorn sculpins (*Leptocottus armatus*) was higher (t-test, $P < 0.05$) at Hog Island.

Marine worms were also highly digested and could only be classified under the title "Polychaeta." The mean number of polychaetes differed between the two sampling locations with Indian Beach showing a higher (t-test, $P < 0.05$) mean. The mean number of eelgrass (*Zostera marina*) blades ingested was higher (t-test, $P < 0.05$) at Hog Island than at the Indian Beach site.

Although the prey item proportions differed between sampled sites, the sharks maintained a similar diversity of prey and feeding level. The mean number of identified species between locations as well as the mean number of items between locations showed no significant (t-test, $P > 0.05$) differences. Regressions comparing shark length with food item size, number of food items, and the number of different species present in the stomach indicated no significant ($P > 0.05$) relationships.

The stomach eversion technique for sampling stomach contents resulted in little mortality, with 6 of 7 brown smoothhound sharks surviving two stomach eversions within 36 hours. Although reviving the sharks after the procedure typically took 2-5 min, the sharks demonstrated no ill-effects afterward. The one mortality that occurred took place within the first 24 hours after arrival at the laboratory, quite possibly from transportation-related stress.

Table 1. Food items of brown smoothhound sharks from two locations at Tomales Bay, California, 1992.

	Hog Island			Indian Beach			Total		
	items/shark	%Freq	Freq	items/shark	%Freq	Freq	items/shark	%Freq	Freq
Crabs									
*Hemigrapsus oregonensis**	0.50	25%	5	3.18	91%	31	2.18	72%	39
*Cancer gracilis**	1.90	75%	15	0.21	12%	4	0.83	35%	19
Scleroplax granulata	0.05	5%	1	0.06	6%	2	0.06	6%	3
Pugettia producta	0.00	0%	0	0.03	3%	1	0.02	2%	1
Shrimp									
Crangon stylirostris	0.30	20%	4	0.82	41%	14	0.63	33%	18
Callianassa californiensis	0.05	5%	1	0.00	0%	0	0.02	2%	1
Upogebia pugettensis	0.05	5%	1	0.03	3%	1	0.04	4%	2
Marine Worms									
Polychaeta*	0.10	10%	2	0.47	35%	12	0.33	26%	14
Fish									
Engraulis mordax	0.00	0%	0	0.06	6%	2	0.04	4%	2
*Leptocottus armatus**	0.15	15%	3	0.00	0%	0	0.06	6%	3
Syngnathus leptohynchus	0.05	5%	1	0.00	0%	0	0.02	2%	1
Unidentified	0.30	25%	5	0.09	9%	3	0.17	15%	8
Eelgrass									
*Zostera marina**	0.35	30%	6	0.00	0%	0	0.13	11%	6
Tunicata	0.00	0%	0	0.06	6%	2	0.04	4%	2
Squid	0.05	5%	1	0.00	0%	0	0.02	2%	1
Empty	N/A	15%	3	N/A	0%	0	N/A	6%	3
Mean Number of Items	3.85			5.00			4.57		
Mean Number of Species	2.35			2.18			2.24		

* = Significant difference in mean number of items between locations.

DISCUSSION

Past food habit studies on Tomales Bay brown smoothhound sharks relied upon shark derbies for specimens for stomach content analysis (Russo 1975, Karl 1979). Although many individuals can be captured per day, collecting sites are frequently not well documented. Dietary sampling biases may also be expected from angled specimens which may be hungry and willing to consume bait or artificial lures. Our fish were sampled at two known sites by gill-nets and should better represent the food habits of the population at these locations. We found that food habits of the brown smoothhound shark were not homogeneous within Tomales Bay, contrary to previous studies (Russo 1975, Karl 1979).

We found similar diet items, but some significant differences in brown smoothhound sharks' species selection between sampling locations in Tomales Bay (Table 1). Because of the similar temperature conditions throughout the bay during summer, the sharks would be expected to have similar metabolic demands. The differences in prey species composition between sites may result from different salinities and/or habitats found in Tomales Bay.

The outer bay containing the Hog Island site is basically oceanic habitat with oceanic salinities, while the inner bay containing the Indian Beach site is a bay habitat demonstrating bay salinities (Smith et al. 1991). *Cancer gracilis* is intolerant of brackish waters and its distribution would be restricted to the oceanic conditions of the Hog Island site (Morris et al. 1980). *Hemigrapsus oregonensis* is more euryhaline, tolerating both hypersaline and brackish waters (Morris et al. 1980) and would expectedly be abundant at the Indian Beach site. The observed differences in brown smoothhound shark diet may result from a differential abundance in prey species between locations. Our regression analysis showed that the sampled sharks demonstrated no prey size selectivity with regard to shark length ($P > 0.05$), possibly a function of the relatively small size range sampled with the gill-nets.

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

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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.*

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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 Moyle1992), 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 km^2. 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 km^2. 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

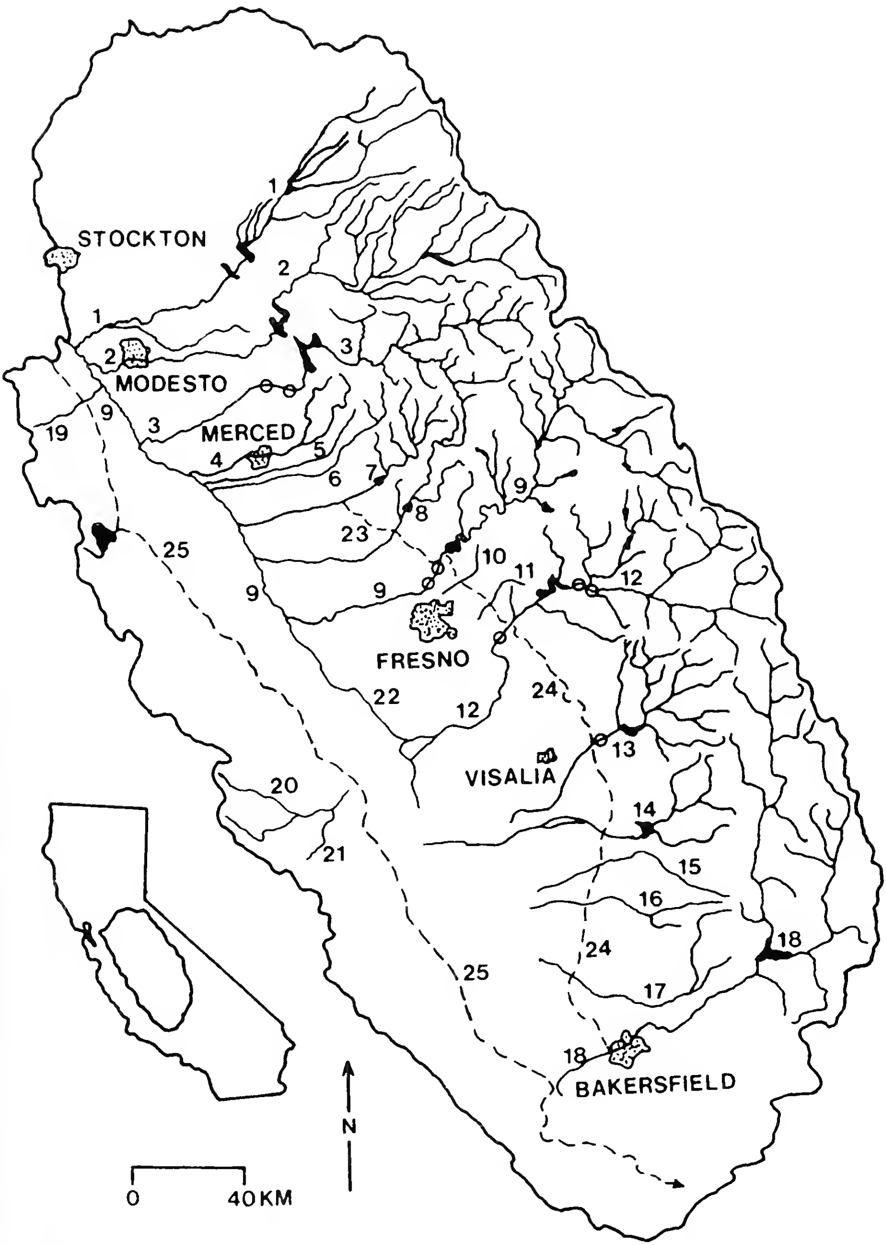

Figure 1. Drainages sampled during this study: (1) Stanislaus River, (2) Tuolumne River, (3) Merced River, (4) Bear Creek, (5) Miles Creek, (6) Mariposa Creek, (7) Chowchilla River, (8) Fresno River, (9) San Joaquin River, (10) Dry Creek, (11) Fancher Creek, (12) Kings River, (13) Kaweah River, (14) 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 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 this study in 1986 and by Moyle and Nichols (1973, 1974) in 1970.

Species	Percentage[a] 1986	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 ($n = 156$) and in 1970 ($n = 130$).

Native Fishes

Rainbow trout. Rainbow trout occurred at 59 (38%) of the 156 sites in 1986. Their abundance was positively correlated with stream order, depth, gradient, elevation, percentage riffle, and percentage boulders and was negatively correlated with 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 high elevation, high gradient streams, the same pattern found by Moyle and Nichols (1973).

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

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.

	Principal Component				
Species	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).

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FIRE EFFECTS ON A MONTANE SIERRA NEVADA MEADOW

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The effects of a late fall burn on a mountain meadow at Grover Hot 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). Despite widespread acceptance of the natural role of fire in grasslands and many other vegetation types, little is known about fire effects in North American mountain meadows (Ratliff 1985). Rundel et al. (1977) pointed out the lack of information about fire effects on high elevation Sierra Nevada communities in general. There is but one published account of a wildfire burning a meadow in the Sierra Nevada (DeBenedetti and Parsons 1979).

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

Managers of most public wildlands are charged with maintaining them in a 'natural' condition (Parsons et al. 1986). The California Department of Parks and Recreation (DPR) has been exploring the utility of fire in managing many vegetation types. Fire has not been used in mountain meadows due to a lack of information on its historical role in such communities and reports of negative impacts (Bennett 1965, Vogl 1974). As with fire in other communities, timing of a fire relative to soil and vegetation moisture conditions in a meadow can be the deciding factor in determining a fire's overall effect (Wright and Bailey 1982). A properly timed prescribed burn can prevent destruction of soil organic matter while decreasing litter buildup and returning nutrients to the soil in plant-available form (Wright and Bailey 1982). Resource ecologists at DPR had observed the effects of a 1985 wildfire occurring on a small portion of the mountain meadow in Grover Hot Springs State Park, Alpine County, California. They noted an apparent increase in abundance of the native perennial grass *Elymus triticoides* in the drier areas of the meadow and increased vigor of the vegetation in the burned area.

The meadow at Grover Hot Springs State Park is currently little-impacted by human disturbances and is relatively free of weedy non-native species. Livestock grazing and fire have been excluded for over 25 years and litter levels in some portions of the meadow are high. Managers recognized that fire may improve vigor of meadow species by increasing nutrient release from litter (Wright and Bailey 1982), but desired to avoid drastic changes in species composition or invasion by alien species. The objective of this study was to determine temperature extremes following burning of wet and dry meadow types at a montane meadow at Grover Hot Springs State Park. We also observed short-term changes in species composition of meadow vegetation due to prescribed fire in order to determine the acceptability of prescribed burning as a management tool.

METHODS

Grover Hot Springs State Park (lat 38.7°N, long 119.8° W) is located on the east side of the Sierra Nevada mountains 28 km south of Lake Tahoe at an elevation of 1,830 m. Annual precipitation, based on a 30-year average from a United States Geological Survey weather station at nearby Woodfords, California, is 50 cm. Most precipitation (87%) falls between October and April, with more than 25 cm of snow falling each month between December and February. The meadow area used for this study is north of Hot Springs Creek and east of Buck Creek, covering approximately 21 ha (Figure 1). The southern boundary of the meadow is a thin band of riparian trees (*Salix* sp. and *Alnus* sp.) along Hot Springs Creek, which is eroded as much as 2 m below the level of the meadow. The eastern and northern edges are bounded by coniferous forest, dominated by *Pinus jeffreyi* Grev. & Balf. in A. Murr. There are two small 'islands' of forest within this meadow area growing on slightly higher, rocky outcrops. Wet meadow areas had a dense cover of *Carex* sp. and *Juncus* sp., whereas the dry areas (bordering the forest) were much more open and supported a more diverse assemblage of species.

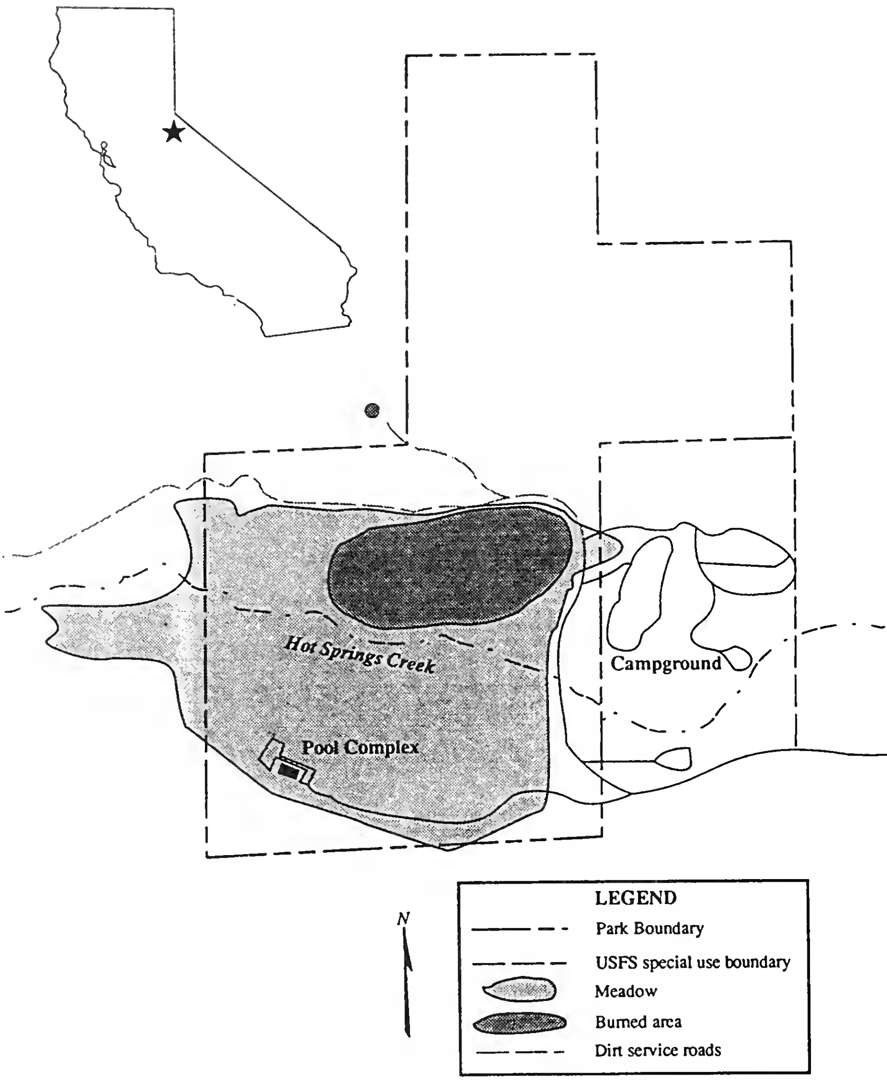

Figure 1. Map of Grover Hot Springs State Park, California. The meadow bordering Hot Springs Creek is shown, along with the portion of the meadow burned in the escaped fire. Solid lines not delimiting the meadow, or burned meadow portion, are paved roads.

We stratified our samples by hydrologic meadow type based on plant species composition and cover. We employed a paired plot approach; pairs of circular plots, 20 m diameter, were placed in each meadow type, one member of each pair was to be burned and one unburned. Plots were subjectively selected in pairs, and we tried to match the vegetation of members of each pair in order to make detection of the effects of fire easier. Members of pairs were usually within 20 m of each other in order to keep other site characteristics constant. It was impossible to have the same number of plots in both wet and dry meadow types because most of the meadow was composed of the wet type and many of the dry areas had such large percentages of bare soil that a prescribed fire under high-moisture conditions would not carry through the plots.

Five pairs of dry area plots and 10 pairs of wet area plots were established in early August 1987. The center of each plot was marked with a numbered metal stake and the vegetation of each plot was characterized by five tosses of a 0.25 m^2 sampling hoop in which the species present were recorded and the cover of each species was visually estimated. Species cover included all standing, live or dead, material. Litter was defined as dead plant material lying on the soil surface. Voucher specimens of plant species identified in this study were deposited with DPR. Plant species names follow Munz and Keck (1968).

Maximum fire temperature was estimated with temperature-indicator crayons (Omega Engineering, Stamford, CT). Crayons with 39 melting points were used, ranging from 66-621°C. Crayons from 66-260°C had melting points separated by ca 7°C (28 crayons), from 260-343°C differed by ca 14°C (7 crayons), and from 343-621°C by 50°C (4 crayons). Temperature indicators were made by stapling a piece of each crayon into an envelope of 1 mm mesh steel window screen. One indicator, containing all 39 pieces of crayon, was placed near the undisturbed center of each plot at the mineral soil surface. Litter removed during placement was replaced over the indicator. After burning, the indicator was retrieved and the maximum temperature determined by identifying which crayon pieces remained unmelted in the envelope.

Statistical comparisons of temperature data were made with the Mann-Whitney *U* test (Zar 1984). This is a nonparametric rank-sum technique. Vegetation data was compared using the Wilcoxon paired sample nonparametric procedure or the Mann-Whitney *U*-test (Zar 1984).

Fuel quantity, fuel moisture, and soil moisture were measured prior to burning each plot by tossing a 0.25 m^2 sampling hoop into the plot. All above-ground plant material within the hoop was clipped and a surface soil sample (0-3 cm depth) collected, weighed, dried at 60°C for 3 days and re-weighed to determine moisture levels at the time of burning.

The burn prescription, based on recommendations from State Park Resource Ecologists and complying with local fire and air pollution ordinances, required air temperatures of 4-16°C, 20-40% relative humidity, wind speed 0-8 kph, and fuel moisture (1 hr) ranging from 5-10%. Burning of the plots was begun 11 November 1987 after the meadow had been moistened by several storms. Conditions during burning were: 2-14°C, 21% relative humidity, wind 2 kph from the west, and fuel moisture (1 hr) 5-7%. Most of the plots were burned the first day and the fires were of low intensity. On the second day, increased winds and lower humidity forced cancellation of further burning. Conditions that day were: 4-20°C, relative humidity 16%, wind 8-16 kph from the west, and fuel moisture (1 hr) 4-6%. However, a smoldering spot in one of the previous day's burned plots crossed its firebreak. The resulting escaped fire, of low to moderate intensity, burned most of the meadow north of Hot Springs Creek and east of Buck Creek (21 ha total), including a number of control plots (Fig. 1); of the 10 dry plots 9 were burned, of the 20 wet plots 8 burned, 11 were unburned, and 1 was partially burned - the partially burned plot was not included in the analysis. The escaped fire was extinguished by fire fighters using fire breaks and water.

The following summer, data on number of species and amount of live cover by each species were collected from plots selected by tossing a 0.25 m^2 sampling hoop five times into each plot. The area of bare soil and amount of litter were also recorded, with litter being defined as all dead plant material. Because litter was defined differently in each of the two sampling years, species cover data were not directly comparable. To circumvent this problem we subtracted 1988 live cover from 1987 cover for each species, classified each plot as burned or unburned, and tested for a fire effect on species covers by the Mann-Whitney *U* test. In this way relative changes due to fire could be detected by comparing the differences of burned and unburned areas. A similar procedure was performed to detect fire effects on bare soil area and species richness/plot.

After the escaped fire, we supplemented our original experimental design by including another sampling area which contained both dry and wet meadow areas. When it had been extinguished, the western edge of the escaped fire was oriented north-south, along the main moisture gradient from dry to wet meadow types. This border area was little disturbed by fire-fighting activities, the fire having stopped due to a change in wind direction combined with water applied from a pumper truck. The major disturbance were tracks left by vehicles at the border of the burned and unburned areas. We marked this fire border in 1987 and returned in 1988 to sample burned and unburned meadow areas. At each of 20 sites spaced every 5 m along the border, we tossed a 0.25 m^2 sampling hoop at least 5 m into the burned and unburned parts of the meadow. The 5 m distance was sufficient to avoid the areas disturbed by vehicle tracks and also decreased the influence of edge effects. We recorded the species present and estimated their living covers, and clipped the unburned and burned plots at every other site (for a total of 10 samples of each type). Dry biomass was determined by weighing after drying at 60°C for 3 days.

One of the presumed benefits of fire is an increase in nutrient input to the soil. We checked nutrient status of the plants in the biomass samples by measuring total nitrogen in a ground sub-sample from each biomass sample (10 burned and 10 unburned samples) using a Leco CHN-600 nitrogen analyzer.

RESULTS

Prior to the fire, species richness (Table 1) was greater on the dry plots (24 species) than on the wet plots (9 species). Large differences existed in the cover of species present in both areas. *Carex* species covered 64% of wet plots but only 9% of dry plots. The native perennial grasses *Poa* and *Elymus* were more abundant on dry plots, with a twelve-fold difference in *Poa* and no *Elymus* at all on wet plots. Dry meadow plots had more litter and bare soil than wet meadow plots.

Most of the species listed in Table 1 are native. Only *Senecio vulgaris*, *Rumex acetosella*, *Taraxacum officinale*, and *Bromus tectorum* are exotic, and of these, only *Bromus tectorum* averaged more than 1% cover (and this only on dry meadow plots).

Table 1. Species covers (expressed as mean percent cover, standard error in parentheses) in the wet and dry area experimental plots prior to burning.

Species	Wet plots (n=20)		Dry plots (n=10)	
Carex spp.	64.00	(5.80)	8.90	(2.40)
Juncus spp.	14.00	(3.40)	13.00	(1.90)
Achillea lanulosa Nutt.	0.31	(0.26)	0.80	(0.59)
Potentilla gracilis Doug. ex Hook.	0.52	(0.23)	1.50	(0.66)
Poa spp.	1.60	(0.68)	19.00	(3.40)
Senecio vulgaris L.	0.30	(0.15)	0.25	(0.25)
Muhlenbergia richardsonis (Trin.) Rydb.	1.20	(0.50)	1.40	(0.43)
Taraxacum officinale Wiggers.	0.01	(0.10)	0	
Elymus glaucus Buckl.	0		7.70	(2.30)
Trifolium wormskioldii Lehm.	0		0.10	(0.10)
Equisetum laevigatum A.Br.	0		0.02	(0.02)
Polygonum douglasii Greene.	0		0.22	(0.13)
Stipa columbiana Macoun.	0		0.12	(0.12)
Penstemon oreocharis Greene.	0		0.17	(0.11)
Rumex acetosella L.	0		0.02	(0.02)
Vicia americana Muhl. ssp. *oregana* (Nutt.) Abrams.	0		0.17	(0.14)
Bromus tectorum L.	0		1.30	(0.84)
Epilobium paniculatum Nutt. ex T. & G.	0		0.02	(0.02)
Sysyrinchium idahoense Bick.	0		0.01	(0.01)
Erigeron spp.	0		0.05	(0.04)
Others	0.16	(0.51)	0.30	(0.22)
Litter	17.00	(16.00)	34.00	(3.00)
Bare Ground	0.71	(2.30)	11.00	(2.80)
At time of fire:				
Soil moisture (%)	76.0	(14.0)	23.0	(4.2)
Above-ground dry weight (g/m^2)	1,260.0	(148.0)	440.0	(100.0)

Wet and dry meadow plots varied at the time of the burn. Almost three times as much fuel was present on wet meadow plots (Table 1, $P < 0.001$). Soil moisture was also 3.3 times higher in wet meadow plots at the time of the burn (Table 1, $P < 0.005$). Temperatures at the soil surface during the fires ranged from 79 to 302°C. Wet and dry meadow plots did not differ in mean maximum burn temperature: 153 (±61.2)°C and 185 (± 83.8)°C, respectively, P = 0.51 (note: ± value is one standard error). Failure of fire temperatures to reflect the difference in fuel was probably due to drier conditions in dry meadow plots at the time of burning. Two of the temperature indicators were in wet meadow plots burned by the escaped fire. They had a higher mean temperature when compared to the five prescribed-burned plots in wet meadow areas, 222 (±54)°C versus 169 (±94)°C. Flame lengths during the prescribed fire were under 0.5 m (considered a low intensity fire) but exceeded 1 m for the escaped fire (moderate intensity).

Burned wet meadow plots showed an increase in bare ground compared to unburned plots 10.5 mo later. Percent bare ground/plot was 1.7 (± 1.2) prior to the fire and 8.3 (± 2.0) after the fire, whereas unburned plots averaged 0.091 (± 0.091) in 1987 and 0.018 (± 0.018) in 1988. There was no significant change in species richness between burned and unburned wet meadow plots. Burned plots averaged 4.1 (± 0.44) species prior to the fire and 4.9 (± 0.58) after, whereas unburned plots contained 2.7 (± 0.27) species in 1987 and 3.1 (± 0.46) in 1988.

Individual species exhibited few differences in cover due to fire. Of five taxa examined (Table 2), only *Poa* had less cover on burned plots one year after the fire (Table 2). *Poa* species were not reliably distinguishable in a vegetative condition in the field and hence several species are included in this result. Weedy species not included in Table 2 were *Senecio vulgaris* and *Taraxacum officinale*. *Senecio* was not observed in 1988 on any plots. *Taraxacum* was only recorded on one plot prior to the fire and occurred on two others (both burned) after the fire. Cover by *Taraxacum* on these plots in 1988 was low (<2%).

Examination of the fire border plots also showed few significant differences between burned and unburned areas. Fire increased living *Carex* cover almost threefold (Table 3), and increased *Muhlenbergia richardsonis* (Trin.) Rydb. while decreasing cover by *Juncus*. Species richness was not affected by fire, but the amount of bare ground increased almost threefold. Biomass was lower on burned plots, but tissue moisture levels were significantly higher. We found no significant difference in nitrogen content of plant material clipped from burned and unburned plots (Table 3).

Almost all control (unburned) dry meadow plots burned in the escaped fire, leaving only one pair unburned. The remaining unburned pair of plots was not enough to allow statistical analysis; however, the fire border plots cover the gradient from wet to dry areas and include some plots equivalent to the dry meadow plots we selected before the fire. These selected dry meadow plots averaged 9% cover by *Carex* (Table

Table 2. Comparison of 1987 prefire and 1988 post fire data for wet meadow plots. Species and bare ground data are mean changes in estimated percent cover (1988 data subtracted from 1987 data, S.E. in parentheses). Statistical significance refers to results of the Mann-Whitney *U* -test.

Species/Characteristic Compared	Burned plots (n = 8)		Unburned plots (n = 11)		P
Carex spp.	38.00	(8.40)	54.00	(6.80)	0.23
Juncus spp.	11.00	(4.60)	11.00	(4.50)	0.98
Poa spp.	-2.90	(0.88)	0.35	(0.49)	0.003
Muhlenbergia richardsonis	0.28	(0.56)	1.00	(0.71)	0.44
Achillea lanulosa	-0.25	(0.17)	-0.09	(0.09)	0.38
Bare ground	-6.60	(2.70)	0.07	(0.09)	0.004
Species richness/plot	-0.75	(0.31)	-0.36	(0.47)	0.30

Table 3. Cover by species for burned and unburned border plots. Statistical comparisons were made by the Wilcoxon paired-sample test. Species, bare ground, and litter data are mean estimated percent covers (standard errors in parentheses).

Species/trait examined	Burned Plots		Unburned Plots		*P*
Carex spp.	18.00	(3.70)	6.20	(1.50)	0.001
Juncus spp.	4.60	(0.61)	6.60	(1.00)	0.05
Poa spp.	2.10	(0.84)	5.50	(1.40)	0.05
Muhlenbergia richardsonis	3.80	(2.0)	0.25	(0.25)	0.05
Achillea lanulosa	0.25	(0.25)	3.50	(2.10)	0.20
All others	13.00	(1.20)	15.0 0	(1.60)	0.20
Bare ground	21.00	(4.50)	7.60	(2.10)	0.002
Litter	49.00	(4.30)	62.00	(5.30)	0.05
Species richness	3.10	(0.30)	3.80	(0.33)	0.30
Fresh biomass (gm/m^2)	332.00	(81.00)	572.00	(137.00)	0.02
Dry biomass (gm/m^2)	184.00	(58.00)	416.00	(114.00)	0.01
Percent water	48.00	(2.00)	31.00	(2.80)	0.01
Percent nitrogen	2.10	(0.05)	1.90	(0.12)	0.11

1). Therefore, those plots with 5% or less *Carex* along the fire border probably were equivalent to our original dry meadow plots. Assuming these plots were properly paired before the fire, these plots (five pairs) were analyzed separately to determine the effect of fire on bare soil area of dry meadow plots. Bare soil area was almost three-fold higher in burned plots than unburned plots: 34% (± 33) versus 13% (± 12) ($P <$ 0.05).

Vehicles were driven across the meadow during efforts to control the escaped fire and left ruts due to soil compaction. A year later these access routes were still visible in wet meadow areas. In 1988, the amount of live *Carex* in vehicle-compacted areas was noticeably less than in the surrounding site. We also noted that some areas had large amounts of soil disturbance due to maneuvering of vehicles, smolders that had destroyed plant material and litter down to bare mineral soil, and excavation of smoldering areas by fire crews in an effort to fully extinguish the fire. These disturbed areas were still relatively bare in 1988. During the summer of 1989, the vehicle-compacted areas were still visible and were the only noticeable difference between burned and unburned areas.

DISCUSSION

Neither the wet nor dry meadow sites at Grover Hot Springs fit easily into the Sierra Nevada meadow classification system proposed by Ratliff (1982). Wet meadow areas contained 4 identifiable *Carex* species (*Carex aquatilis* Wahl., *Carex bolanderi* Olney, *Carex douglasii* Boott., and *Carex praegracilis* W. Boott.), none of which were used in his system. His Nebraska sedge class (being less wet than the beaked sedge class) seems the closest fit, although *Juncus* was more abundant on our plots.

Dry meadow areas were dominated by *Poa* species, including *Poa pratensis* L., *Poa nevadensis* Vasey ex Scribn., and *Poa scabrella* (Thurb.) Benth. ex Vasey. Dominance by *Poa* suggests the Kentucky bluegrass meadow class, which is found on relatively well-drained soils and may have significant cover by *Carex*, *Juncus*, and bare ground (Ratliff 1982). *Elymus* is an important component of these plots but was not mentioned by Ratliff (1982). Our search for dry meadow plots containing *Elymus* undoubtedly inflated its importance.

Fire left the species composition of the meadow relatively unchanged. There was no marked increase in exotic species or major shifts in native species composition. Species richness in both the fire border and wet meadow plots did not change greatly as a result of the fire. In the fire border plots, cover of some native species increased while others decreased. Decreased biomass on the burned plots was primarily due to reduction of litter volume, as reflected in the decreased cover by litter and the increase in bare ground. This was also indicated by the higher moisture level of material clipped from burned area plots, reflecting the greater amount of green plant material present relative to litter. We should note that this study was conducted during a drought. For example, data from a weather station maintained at the park from June 1987 until May 1988 totaled only 33% of the 30 year precipitation average from the nearby weather station at Woodfords, California.

Fires in grasslands generally release nutrients from burned litter (Vogl 1974). In our study, burning did not result in increased nitrogen levels in plant tissues even though post fire growth appeared more vigorous. This may have been due to dilution of the green plant portion of each plot by a larger amount of dead material (litter). In a study of spring burning in Rocky Mountain meadows, Nimir and Payne (1978) found fire increased soil pH, potassium, and nitrate levels but they did not monitor plant nutrient levels. However, since fertilization has been shown to increase Sierra Nevada meadow productivity (Evans and Neal 1982, Ratliff 1985), release of nutrients by fire in our study should have had a positive effect. This positive effect would only have occurred if released nutrients were not flushed from the soil during the winter, because we burned when plants were dormant and therefore unable to immediately take up any released nutrients. Because this fire was not hot enough to destroy soil organic matter, retention of released nutrients is likely. The increase in *Carex* cover (Table 3) may reflect improved growth in response to an increase in nutrients.

The increase in bare soil after the fire appeared to be the only undesirable impact of fire on the meadow. Dry meadow plots had such high amounts of bare soil in their unburned state (see Table 1) that we believe they were not made more vulnerable to invasion by exotic species due to creation of openings by fire. Some weedy exotic species (e.g., *Bromus tectorum*) were present in both burned and unburned dry meadow plots of the fire border study and showed no dramatic response to fire. In contrast, unburned wet meadow plots had very little bare area and this was significantly increased by fire. We did not detect substantial invasion of these bare areas by 1988, but did note more *Taraxacum* in some areas outside of the burned plots. If open areas are rapidly closed by the recovering native plants, increase in *Taraxacum* will be limited. Overall, given the rapid recovery of the meadow one year after burning, it does not appear that there will be an invasion problem in the wet meadow areas. The limited evidence available (Ratliff 1985) points to natural fires occurring in meadows at intervals of several hundred years. We therefore do not recommend a repeat of the burn for a fairly long period of time to allow complete reinvasion of bare areas by native species.

Wright and Bailey (1982) and Ratliff (1985) predicted that burning under relatively wet conditions would probably not result in long-term vegetation changes in mountain meadows. Our study supports their prediction. The drastic change in meadow vegetation of a subalpine Sierran meadow (DeBenedetti and Parsons 1979, DeBenedetti 1980, DeBenedetti and Parsons 1984) was primarily due to the fire occurring during drought conditions. Our results show that burning when plants are dormant and soil moisture is high enough to prevent organic matter in the soil from burning prevents change in meadow vegetation and allows rapid post fire recovery.

Ratliff (1985) concluded that not enough was known about fire in mountain meadows to prescribe its use as a management tool. We have shown that, under the prescription used here, fire does not change meadow vegetation greatly or make meadows significantly more susceptible to invasion by exotic species after one year. Thus, it can be used without these effects on the vegetation. However, neither have we demonstrated a benefit of prescribed burning sufficient to justify the costs of conducting prescription burns. Prescribed fire may be beneficial in ways not detected or not pertinent to the meadow at Grover Hot Springs: by accelerating nutrient cycling, making meadows less likely to suffer from catastrophic fire during drought years, or discouraging invasion by woody species. We hope that our work will encourage further experimentation with fire in montane meadows.

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A SAMPLER FOR QUANTIFYING THE VERTICAL DISTRIBUTION OF MACROINVERTEBRATES IN SHALLOW WETLANDS

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A sampler for quantifying the vertical distribution of aquatic macroinvertebrates in wetlands is described. This device will facilitate quantitative sampling of macroinvertebrates in waterfowl ecology and related studies. Because it simultaneously collects benthic and pelagic invertebrates, the sampler reduces bias associated with sampling macroinvertebrates that occupy the benthic-pelagic interface of wetlands. The sampling device also separates benthic and pelagic macro-invertebrates into separate vertical profiles to facilitate studies of distribution patterns or the influence of chemical and physical gradients on invertebrate vertical distribution.

INTRODUCTION

Interest in quantifying aquatic macroinvertebrates in wetlands is increasing because they are consumed by waterfowl (Drobney and Fredrickson 1979, Swanson et al. 1979, Euliss and Harris 1987) and shorebirds (Hicklin and Smith 1979, Baldassarre and Fischer 1984, Boates and Smith 1989). They are also important in the epizootiology of avian botulism (Bell et al. 1955, Jensen and Allen 1960, Duncan and Jensen 1976) and are valuable as biological indicators of pesticide residues in wetlands (Grue et al. 1989). Consequently, there is a need to develop a variety of quantitative sampling gear for aquatic invertebrates to address broad ecological questions. In this paper, we describe a tube sampler that separates the water column and benthos of shallow wetlands into distinct vertical profiles. We developed the device to describe vertical distribution patterns of invertebrates in wetlands for research on avian botulism epizootiology and microhabitat selection by wetland macroinvertebrates in relation to vertical abiotic gradients.

The described sampler (Fig. 1) is similar to the multiple tube sampler described by Euliss et al. (1992) in that benthic and pelagic invertebrates are quantified

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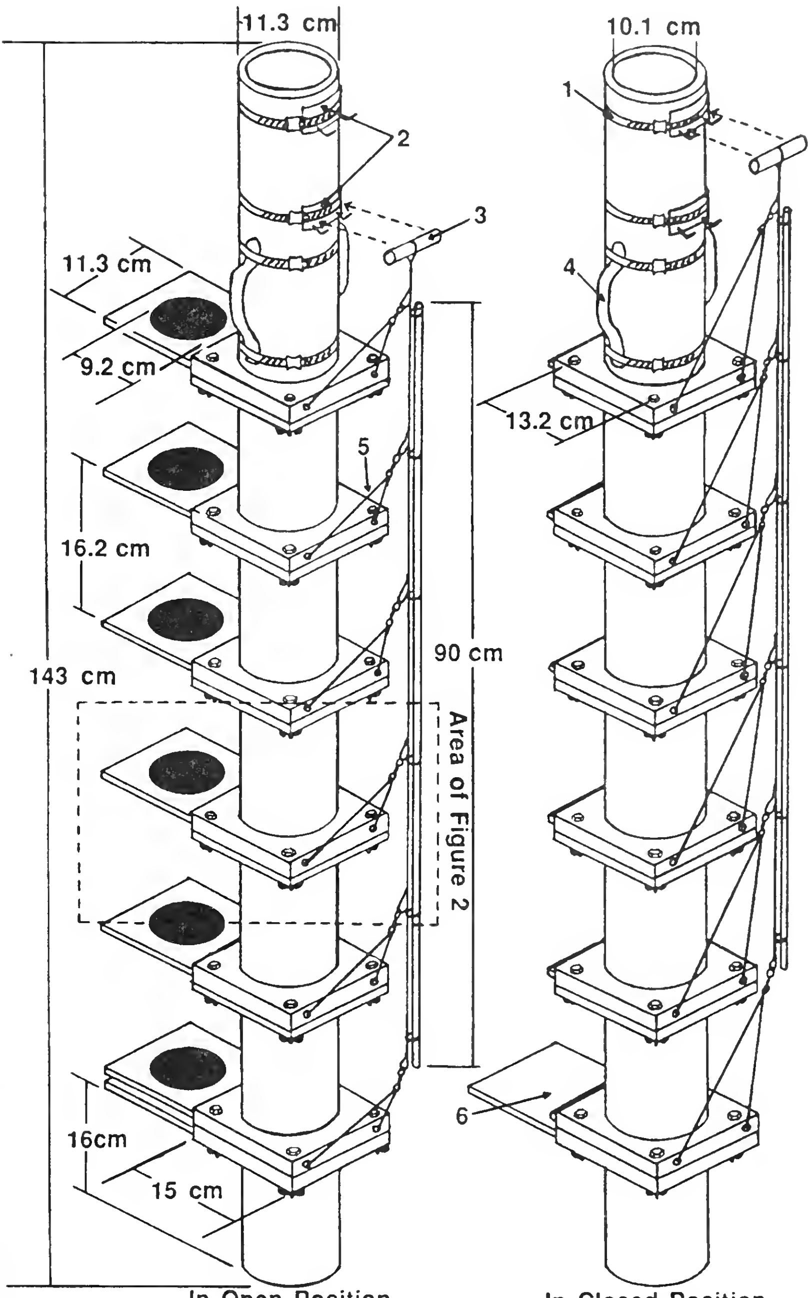

Figure 1. Schematic view of sampler in open and closed position. Numbered parts are: 1) Radiator-type hose clamps; 2) Closure cable handle storage hooks; 3) Closure cable handle; 4) Sampler handle; 5) Braided nylon line; and 6) Sediment tube section door (in open position).

simultaneously. Thus, bias from double sampling does not occur because separate devices are not required to sample benthic and pelagic organisms (Euliss et al. 1992). The portion of the tube that samples the water-column is partitioned into individual compartments to facilitate sampling of specific profiles in the water-column.

The sampler is constructed by stacking several interconnected 10.1-cm ID (11.3-cm OD) clear acrylic-tube water-column samplers on a bottom tube that samples benthos (Fig. 1). We used 15.2-cm long tubes, but tube length may be modified for individual needs. Several acrylic doors isolate water-column samples into separate vertical profiles. The leading edges of the doors are sharpened to cut minor vegetation as they are closed. The bottom of the tube is also sharpened to facilitate penetration of sediments. Acrylic doors (flat 6-cm-thick acrylic) are integrated into the base of each compartment (Fig. 2) to physically block the movement of invertebrates among profiles. A 9-cm-diameter 0.5-mm-mesh stainless steel screen is attached with clear silicone adhesive to the center of each door. The doors are sanded to reduce their thickness and to facilitate rapid closure. A laminated acrylic sheet is attached flush with the top of each compartment to form a firm attachment plate with the adjacent compartment. Acrylic cement was used to bond door housing units and joint plates.

The top tube section of the sampler must be long enough to facilitate placement of sampler handles and brackets used to lock sampler doors. Sampler handles and the door closure handle brackets are attached with standard hose clamps to the top tube. Handles may be obtained from hardware stores and the two brackets were constructed from 16 mm x 7 mm (0.25 inch) rods welded to a metal plate.

The water-column compartments and the sediment tube are stacked vertically and coupled together at the corners with 7 mm bolts. Wing nuts are used to facilitate breakdown and assembly of the sampler in the field.

Compartment doors are secured to the closure cable with a loop of small-diameter braided nylon line. Nylon line is inserted through two holes in the rear of each door housing and then into two holes drilled in the leading edge of the door. A knot in the nylon line prevents the line from pulling out of the doors when they are closed. A snap swivel attaches the loop of nylon line to the closure cable. The closure cable is constructed with 1.5 mm plastic-coated braided wire cable, a 7 mm OD wooden dowel, and a handle of 25 mm OD wooden dowel. The 90 cm wooden dowel is attached to the wire cable to prevent tangling.

A sample is collected by lowering the sampling device into the water with doors in the open position. The bottom tube section is forced into the sediment to the joint plate of the sediment compartment. Immediately after the sampling device is seated into the sediments, the closure cable is raised to simultaneously close all doors. The sampler is then rocked back and forth to break the sediment seal and lifted to the surface. Individual water-column compartments are disassembled and the samples washed into specimen jars. Re-assembly of the sampler averages 2 minutes per individual water-column sample.

Benthic samples are removed from the sampling device by hand. The core is forced through the top of the tube by hand until the protruding core is the desired depth from the benthic-pelagic interface. The door is then closed to sever the sample from

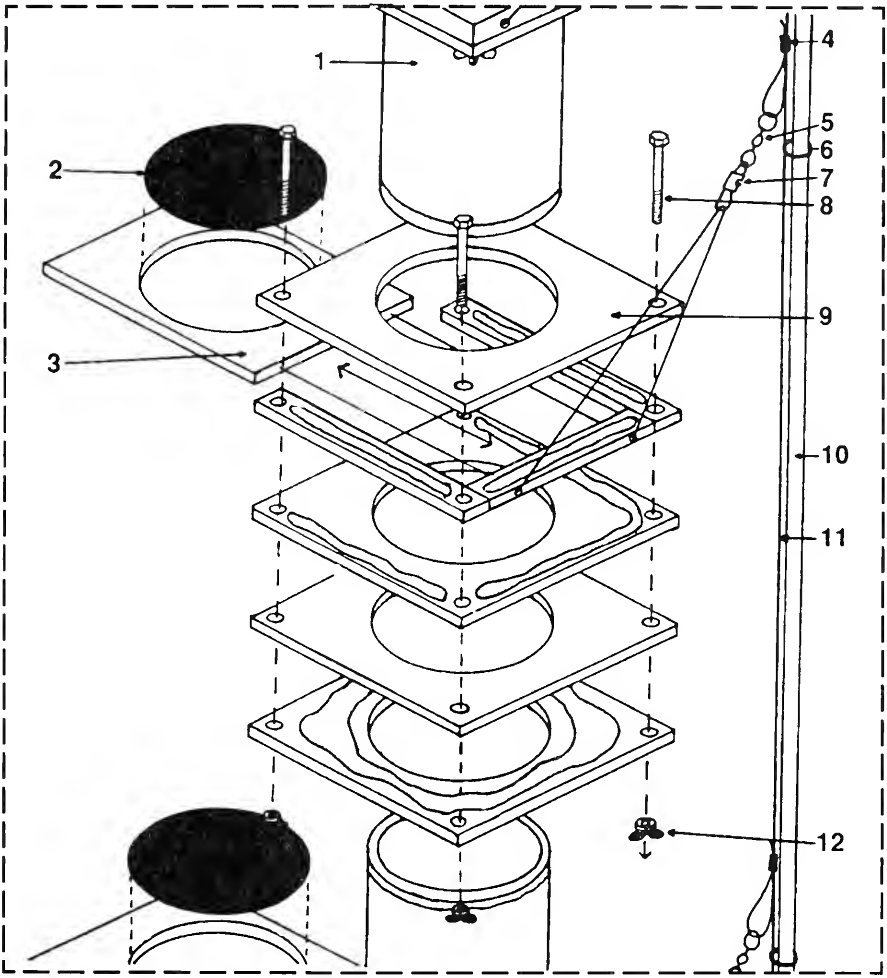

Figure 2. Expanded view of water-column compartment and door closure unit. Numbered parts are: 1) Tube compartment; 2) Screen; 3) Sliding door; 4) Cable line clamp; 5) Barrel swivel; 6) Nylon tie; 7) Snap; 8) Bolt; 9) Joint plate (top section); 10) Wood dowel; 11) Plastic coated wire cable; and 12) Wing nut.

the remaining core. Individual sediment cores are then placed in a modified self-cleaning screen (Euliss and Swanson 1989) to concentrate sample residues and placed in specimen jars.

We used the described sampling device for two field seasons to collect macroinvertebrates in shallow wetlands. Our study sites contained minimal submergent and emergent vegetation that would interfere with the operation of this device. The sampler withstood rigorous use and required only occasional minor maintenance of the cable used to close the doors. Materials for the sampling device cost about $175.00. Total construction time was about 8 hours.

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TULE ELK RELOCATED TO BRUSHY MOUNTAIN, MENDOCINO COUNTY, CALIFORNIA

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Nineteen tule elk (*Cervus elaphus nannodes*) from Grizzly Island Wildlife Area, Solano County, California and 11 tule elk from Tupman Tule Elk Reserve, Kern County, California were relocated to Brushy Mountain, Mendocino County, California on 30 July and 18 September 1986, respectively, as part of the California Department of Fish and Game tule elk management program (Koch 1987, Livezey et al. 1988). The elk from Grizzly Island were captured by a helicopter/corral system (Koch 1987), and the elk from Tupman were immobilized with the drug carfentanil (Mueleman et al. 1984). Ten of the 30 elk were fitted with radio-telemetry collars and all 30 elk were eartagged.

A total of 221 radio-locations (57%) or observations (43%) of radio-collared elk and more than 130 observations of non-collared elk were collected from July 1986 through October 1988 (Livezey 1987, 1988, and 1991). The two groups of released elk fragmented into at least 12 smaller groups or individuals that travelled as far as 28 km from the release site. There were eight confirmed elk mortalities during the study period. Renarcotization of the carfentanil (Stanley et al. 1988) caused the death of two cows and a male yearling. Four cows and one bull died of unknown causes. One of these, a cow, was killed and eaten or scavenged by a black bear (*Ursus americanus*), and another, a bull, was scavenged by coyotes (*Canis latrans*). Two cows examined within 10 hours and two days of death, respectively, showed no apparent cause of death and had not been scavenged.

The relocation efforts were a success; two small subherds of elk were established. The main group, which settled in the Brushy Mountain/Eden Valley area 0-6 km from the release site, was comprised of at least five cows, three bulls, two female yearlings and three male yearlings. The other group, which established itself in the Laytonville area 18-20 km west of the release site, was comprised of one cow and one bull that joined with two cows, a female yearling, and a calf that were individuals or their decendents from a 1979 or 1980 tule elk relocation (BLM 1983). No elk calves were observed during the 1987 calving season, but at least five 1988 calves were born from cows released in 1986.

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locations of elk from June through October 1988.

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