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NATIONAL WATER-QUALITY ASSESSMENT PROGRAM

Water-Resources Investigations Report 00-4125

U.S. Department of the Interior
U.S. Geological Survey

USGS
science for a changing world

Benthic Macroinvertebrate Assemblages and Their Relations with Environmental Variables in the Sacramento and San Joaquin River Drainages, California, 1993–1997

By Larry R. Brown *and* Jason T. May[1]

U.S. GEOLOGICAL SURVEY

Water-Resources Investigations Report 00-4125

National Water-Quality Assessment Program

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[1]California State University Sacramento Foundation, Placer Hall, 6000 J Street, Sacramento, California 95619

Sacramento, California
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U.S. DEPARTMENT OF THE INTERIOR
BRUCE BABBITT, Secretary

U.S. GEOLOGICAL SURVEY
Charles G. Groat, Director

For additional information write to:

District Chief
U.S. Geological Survey
Water Resources Division
Placer Hall
6000 J Street
Sacramento, California 95819-6129

Copies of this report can be purchased from:

U.S. Geological Survey
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FOREWORD

The mission of the U.S. Geological Survey (USGS) is to assess the quantity and quality of the earth resources of the Nation and to provide information that will assist resource managers and policymakers at Federal, State, and local levels in making sound decisions. Assessment of water-quality conditions and trends is an important part of this overall mission.

One of the greatest challenges faced by water-resources scientists is acquiring reliable information that will guide the use and protection of the Nation's water resources. That challenge is being addressed by Federal, State, interstate, and local water-resource agencies and by many academic institutions. These organizations are collecting water-quality data for a host of purposes that include: compliance with permits and water-supply standards; development of remediation plans for specific contamination problems; operational decisions on industrial, wastewater, or water-supply facilities; and research on factors that affect water quality. An additional need for water-quality information is to provide a basis on which regional- and national-level policy decisions can be based. Wise decisions must be based on sound information. As a society we need to know whether certain types of water-quality problems are isolated or ubiquitous, whether there are significant differences in conditions among regions, whether the conditions are changing over time, and why these conditions change from place to place and over time. The information can be used to help determine the efficacy of existing water-quality policies and to help analysts determine the need for and likely consequences of new policies.

To address these needs, the U.S. Congress appropriated funds in 1986 for the USGS to begin a pilot program in seven project areas to develop and refine the National Water-Quality Assessment (NAWQA) Program. In 1991, the USGS began full implementation of the program. The NAWQA Program builds upon an existing base of water-quality studies of the USGS, as well as those of other Federal, State, and local agencies. The objectives of the NAWQA Program are to:

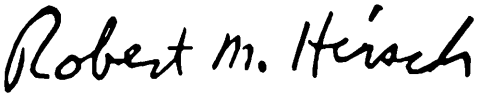
- Describe current water-quality conditions for a large part of the Nation's freshwater streams, rivers, and aquifers.
- Describe how water quality is changing over time.
- Improve understanding of the primary natural and human factors that affect water-quality conditions.

This information will help support the development and evaluation of management, regulatory, and monitoring decisions by other Federal, State, and local agencies to protect, use, and enhance water resources.

The goals of the NAWQA Program are being achieved through ongoing and proposed investigations of 60 of the Nation's most important river basins and aquifer systems, which are referred to as study units. These study units are distributed throughout the Nation and cover a diversity of hydrogeologic settings. More than two-thirds of the Nation's freshwater use occurs within the 60 study units and more than two-thirds of the people served by public water-supply systems live within their boundaries.

National synthesis of data analysis, based on aggregation of comparable information obtained from the study units, is a major component of the program. This effort focuses on selected water-quality topics using nationally consistent information. Comparative studies will explain differences and similarities in observed water-quality conditions among study areas and will identify changes and trends and their causes. The first topics addressed by the national synthesis are pesticides, nutrients, volatile organic compounds, and aquatic biology. Discussions on these and other water-quality topics will be published in periodic summaries of the quality of the Nation's ground and surface water as the information becomes available.

This report is an element of the comprehensive body of information developed as part of the NAWQA Program. The program depends heavily on the advice, cooperation, and information from many Federal, State, interstate, Tribal, and local agencies and the public. The assistance and suggestions of all are greatly appreciated.



Robert M. Hirsch
Chief Hydrologist

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Conversion Factors

Multiply	By	To obtain
cm (centimeter)	0.3937	inch
km (kilometer)	0.6214	mile
km^2 (square kilometer)	0.3861	square mile
m (meter)	3.281	foot
m^2 (square meter)	1.196	square yard
m^3/s (cubic meter per second)	35.31	cubic foot per second
mg (milligram)	0.00003527	ounce avoirdupois
mg/L (milligram per liter)	8.345	pound per million gallon (U.S.)
mL (milliliter)	0.06103	cubic inch
mm (millimeter)	0.03937	inch
m/s (meter per second)	3.281	foot per second

Temperature is given in degrees Celsius (°C), which can be converted to degrees Fahrenheit (°F) by the following equation:

$$°F=1.8(°C)+32.$$

Vertical Datum

Sea level: In this paper, "sea level" refers to the National Geodetic Vertical Datum of 1929—a geodetic datum derived from a general adjustment of the first-order level nets of the United States and Canada, formerly called Sea Level Datum of 1929.

Abbreviations and Acronyms

µS/cm, microsiemens per centimeter at 25 degrees Celsius

ANOVA, one-way analysis of variance
CCA, canonical correspondence analysis
EPT, Ephemeroptera, Plecoptera, and Trichoptera
PC, principal components
PCA, principal components analysis
TWINSPAN, two-way indicator species analysis
NAWQA, National Water-Quality Assessment (Program)
USGS, U.S. Geological Survey

Benthic Macroinvertebrate Assemblages and Their Relations with Environmental Variables in the Sacramento and San Joaquin River Drainages, California, 1993–1997

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ABSTRACT

Data were collected in the San Joaquin and Sacramento river drainages to evaluate associations between macroinvertebrate assemblages and environmental variables as part of the National Water-Quality Assessment Program of the U.S. Geological Survey. Samples were collected at 53 sites from 1993 to 1995 in the San Joaquin River drainage and in 1996 and 1997 in the Sacramento River drainage. Macroinvertebrates were collected from riffles or from large woody debris (snags) when riffles were absent. Macroinvertebrate taxa were aggregated to the family (or higher) level of taxonomic organization, resulting in 81 taxa for analyses. Only the 50 most common taxa were used for two-way indicator species analysis (TWINSPAN) and canonical correspondence analysis. TWINSPAN analysis defined four groups of riffle samples and four groups of snag samples based on macroinvertebrate assemblages. Analysis of variance identified differences in environmental and biotic characteristics of the groups. These results combined with the results of canonical correspondence analysis indicated that patterns in riffle sample assemblage structure were highly correlated with a gradient in physical and chemical conditions associated with elevation. The results also suggested that flow regulation associated with large storage reservoirs has negative effects on the total number of taxa and density of macroinvertebrates below foothill dams. Analysis of the snag samples showed that, although elevation remained a significant variable, mean dominant substrate size, gradient, specific conductance, water temperature, percentage of the basin in agricultural land use, and percentage of the basin in combined agricultural and urban land uses were more important factors in explaining assemblage structure. Macroinvertebrate assemblages on snags may be useful in family level bioassessments of environmental conditions in valley floor habitats. In the Sierra Nevada and its foothills, the strong influence of elevation made it difficult to attribute differences in macroinvertebrate assemblage structure among sites to specific environmental conditions. Additional work is needed in the foothills and Sierra Nevada to better define macroinvertebrate assemblages and their relations to environmental variables.

INTRODUCTION

The use of benthic macroinvertebrate assemblages for bioassessments of water-quality conditions is a commonly used technique (Lenat, 1988; Ohio Environmental Protection Agency, 1987a,b,c; Plafkin and others, 1989; Fore and others, 1996). Development of bioassessment techniques and implementation of biocriteria has been an ongoing effort in California since 1993. In 1996, standardized procedures for using benthic macroinvertebrates in assessing water quality conditions (California Stream Bioassessment Procedure) were introduced by the California Department of Fish and Game (Harrington, 1996). Current efforts have focused on developing biocritera on a watershed basis and in wadeable streams where riffles are available for sampling. Development of methods for

nonwadeable streams or streams without riffle habitat is exploratory at this time.

Published information on the taxonomy, distribution, and responses to environmental variables of macroinvertebrates in the Sacramento and San Joaquin river drainages is limited. Hawkins and others (1997) sampled higher elevation streams in the Sierra Nevada, but did not sample lower elevation streams. Leland and Fend (1998) studied macroinvertebrate communities in the lower San Joaquin River and some tributaries using artificial substrates, but did not include the Sacramento River system or higher elevations in the San Joaquin River system. Bottorf and Knight (1989) sampled all elevations in the Cosumnes River system, but limited their analyses to stoneflies (Plecoptera). Two literature reviews failed to identify any additional published studies at the geographic scale of drainage or larger (Brown, 1996; Erman, 1997).

The National Water-Quality Assessment (NAWQA) Program of the U.S. Geological Survey (USGS) includes collections of fishes, benthic macroinvertebrates, and benthic algae as part of the assessment of water quality conditions of the nation's surface waters. The three NAWQA study areas in California are in the San Joaquin, Sacramento, and Santa Ana river systems. Data collection has been completed in the San Joaquin (1993–1995) and Sacramento (1996–1998) river study areas and is ongoing in the Santa Ana River (1999–2001) study area. Analysis of the data from the San Joaquin and Sacramento river drainages provides an excellent opportunity to assess the relations of benthic macroinvertebrate communities to water quality and habitat conditions in a large river system of critical importance as a water supply to central and southern California.

Purpose and Scope

The purpose of this report is to assess the practicality of developing regional biocriteria for the combined Sacramento–San Joaquin river system by determining whether samples can be categorized on the basis of benthic macroinvertebrate assemblage structure, and to evaluate the relations of the sample categories to a variety of environmental variables. The use of macroinvertebrate assemblages on snags (woody debris) for bioassessments in lower elevation streams without riffle habitat also was evaluated. Water quality of such streams is a major concern to water managers, but the development of bioassessment techniques in California has been limited to wadeable streams with riffle habitat.

Description of the Study Area

The Sacramento and San Joaquin rivers drain a combined area of about 137,000 km^2 (fig. 1) (Domagalski and others, 1998; Gronberg and others, 1998). The climate in the Sacramento and San Joaquin valleys varies from semiarid in the north to arid in the south. Winters are mild and summers are hot. Mean annual precipitation on the valley floor varies from about 36 to 63 cm in the Sacramento Valley and from about 13 to 30 cm in the San Joaquin Valley. Precipitation declines from a high in the northern Sacramento Valley to a low in the southern San Joaquin Valley.

The range of elevation in the combined Sacramento–San Joaquin river drainage is considerable. The Sierra Nevada reaches elevations exceeding 4,000 m in contrast to the lowest parts of the valley floor, which are near sea level. Most of the precipitation in the drainage falls in the Sierra Nevada as snow, with more than 200 cm/yr falling in some areas.

The study area includes a total of 10 ecoregions (fig. 1) (Omernik, 1987). The Sacramento and San Joaquin river drainages are both dominated by the Central California Valley, Southern and Central California chaparral and woodlands, and Sierra Nevada ecoregions. All but two sites in this study were within these three ecoregions. The Sacramento River drainage includes small parts of the Klamath Mountains, which contains one site (fig. 1), Snake River High Desert, Eastern Cascades Slopes and Foothills, Northern Basin and Range, and Coast Ranges ecoregions. The San Joaquin River drainage includes small parts of the Southern Basin and Range ecoregion and the Southern California Mountains ecoregion, which contains one site (fig. 1).

The natural flow regime of Central Valley streams has been significantly modified by water development activities (Domagalski and others, 1998; Gronberg and others, 1998). All of the large rivers, and many of the smaller streams, have been dammed for flood control and storage of runoff. Most of the large storage reservoirs are located in the Sierra Nevada foothills. The stored water is transported through natural channels or constructed canals for a variety of purposes, including irrigation of agricultural land, fulfillment of

environmental requirements, and municipal and industrial uses for downstream communities (Domagalski and others, 1998; Gronberg and others, 1998). Water is routinely transported out of the drainage to southern California. Water- quality concerns include agricultural return flows, urban runoff, mine drainage, and others that result from human activities (Domagalski and others, 1998; Gronberg and others, 1998).

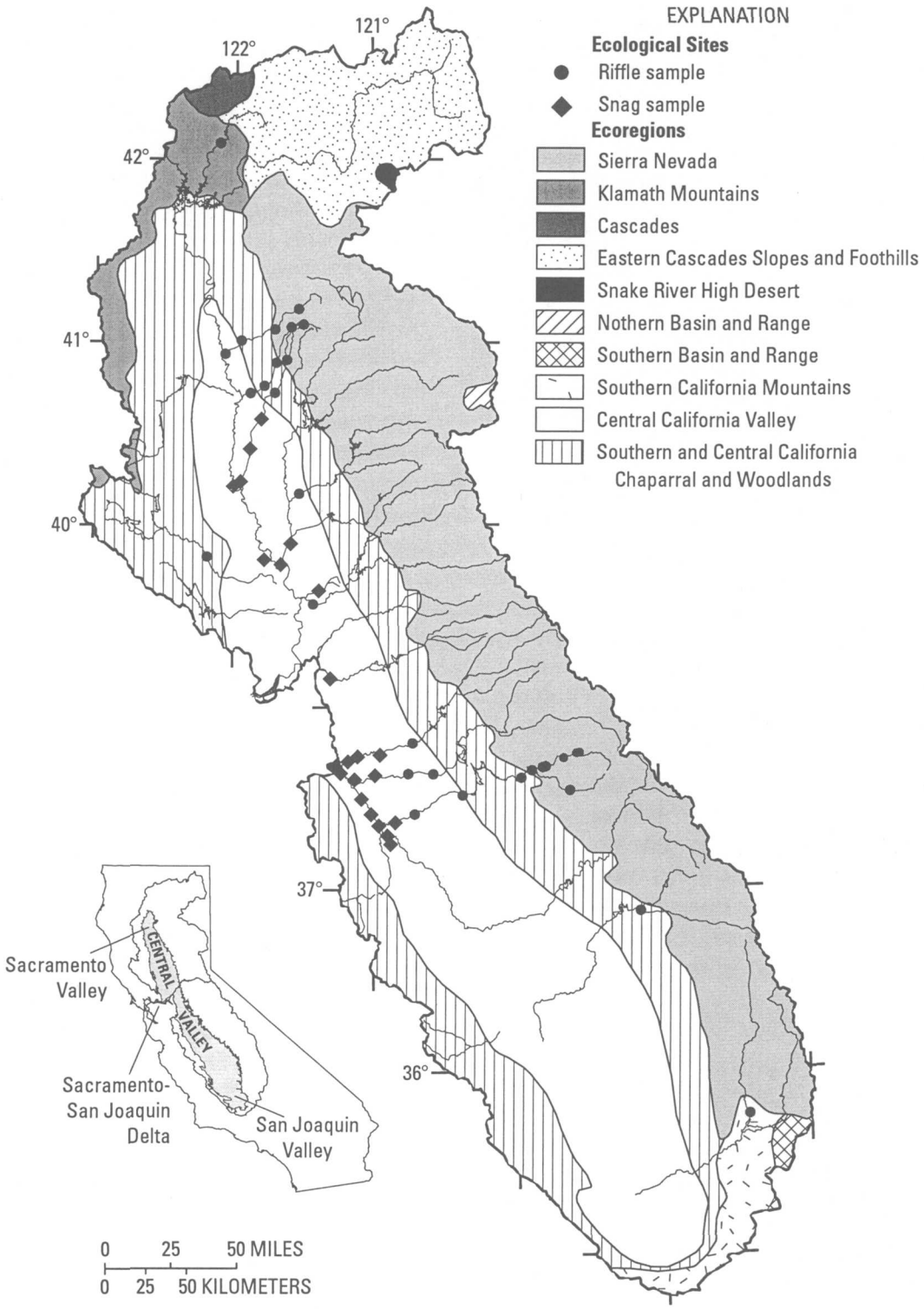

Figure 1. Locations of sampling sites and ecoregions in the Sacramento and San Joaquin river drainages, California.

METHODS

Sampling Design

Twenty-three sites were sampled in the Sacramento River system and 30 sites were sampled in the San Joaquin River system (fig. 2). The primary focus of sampling activities was to document water-quality conditions at lower elevations where human disturbances are prevalent. The secondary purpose was to document gradients in macroinvertebrate assemblages and environmental conditions from the valley floor to

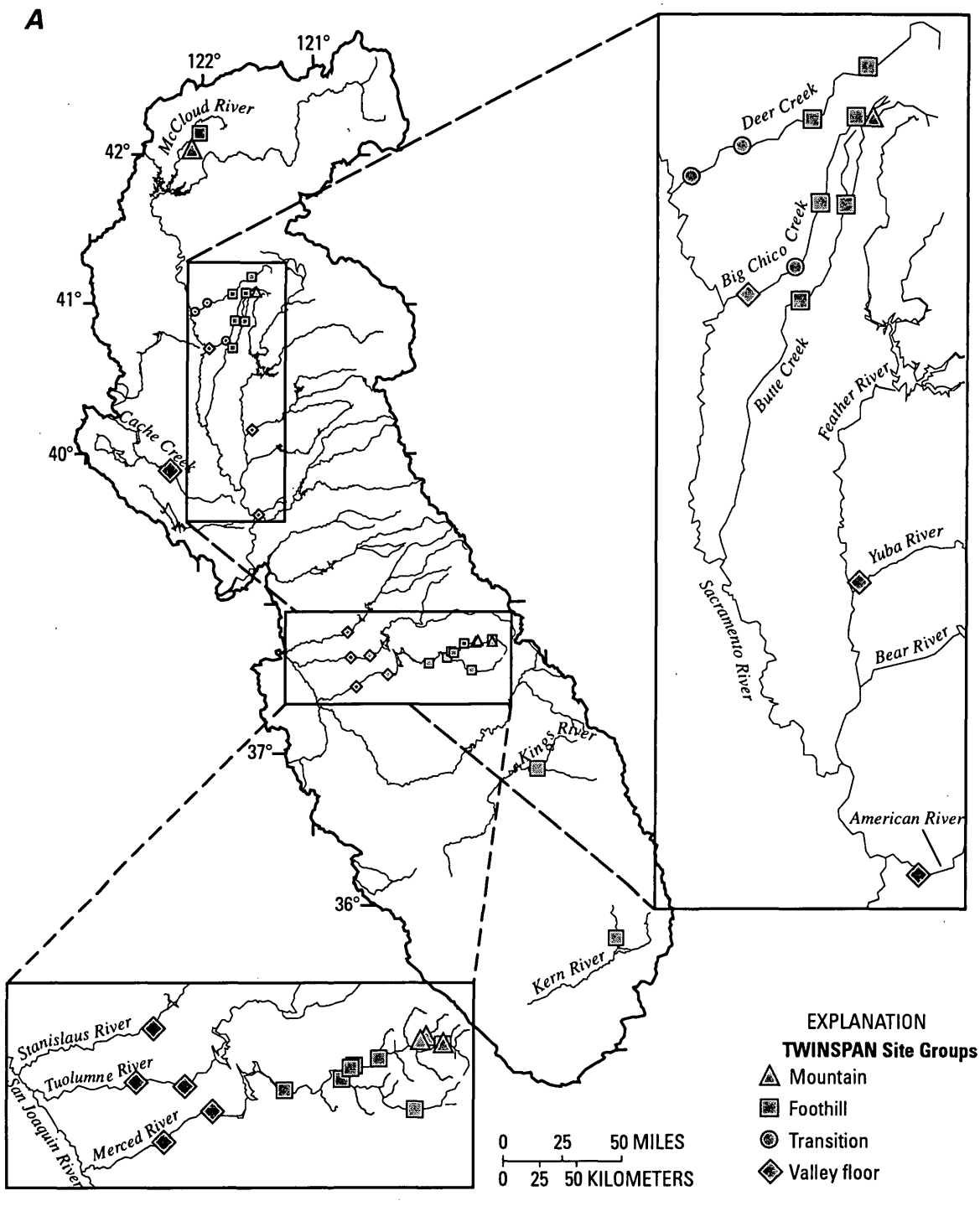

Figure 2. Classification of sampling sites into TWINSPAN sample groups for both riffle (*A*) and snag (*B*) samples in the Sacramento and San Joaquin river drainages, California. Sampling sites with more than one code were sampled in more than one year and samples from different years were placed in the groups indicated.

higher elevations in the Sierra Nevada. All sites were sampled at least once during low-flow conditions during the late summer or early autumn.

Data from multiyear sampling of selected sites provide a measure of annual variability in macroinvertebrate assemblages. All sites could not be sampled in all years and multiple-reach sampling was not done at all sites because of economic and logistic constraints. In the Sacramento River drainage, 10 sites were sampled during both 1996 and 1997. In the San Joaquin River drainage, two sites were sampled in 1993 and 1994, one site was sampled in 1994 and 1995, and four sites were sampled during all 3 years. In addition, three adjacent stream reaches were sampled at each of

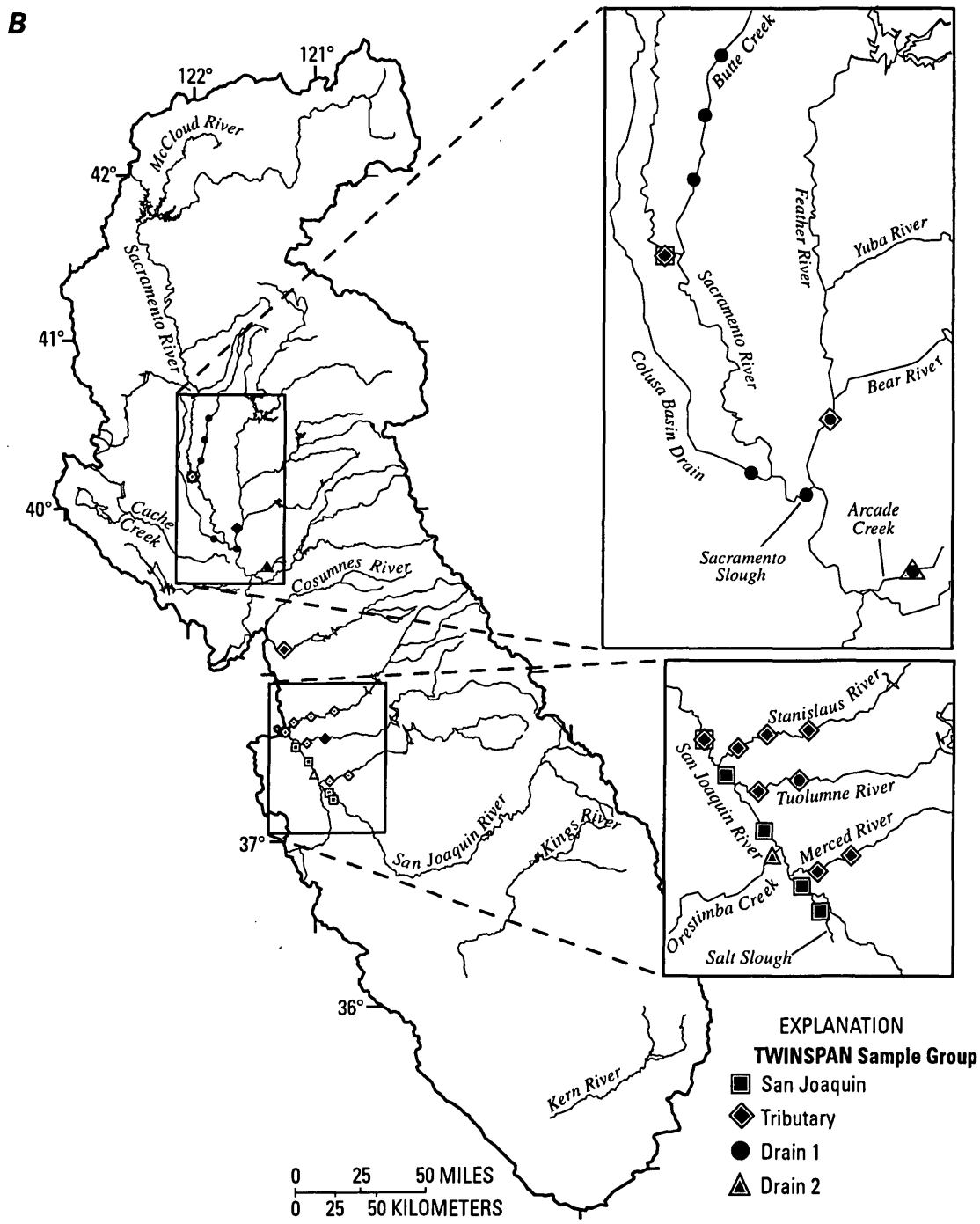

Figure 2.—Continued

two sites in the Sacramento River system (fig. 2*A*, McCloud River site and second-most downstream site on Deer Creek) and at each of three sites in the San Joaquin River system (fig. 2*B*, most downstream site on Merced River and second-most downstream site on the Tuolumne and Stanislaus rivers) to provide a measure of reach-scale variability. In addition to macroinvertebrate sampling, a variety of water quality and habitat variables was measured at each site.

Sampling was done within selected stream reaches (Meador and others, 1993). At sites where two or more types of geomorphic channel units (riffles, runs, and pools) were present, reach length was defined as the length of stream, including at least two repetitions of each type of geomorphic channel unit present at the site. At sites without two or more types of geomorphic channel unit, reach length was defined as 20 times the mean channel width. Reach lengths in this study varied from 150 m at small wadeable streams to 1,200 m at large rivers. Within each stream reach, macroinvertebrates were collected from a habitat expected to have a high diversity of taxa (Cuffney and others, 1993). Riffles were the preferred sampling habitat. Large woody debris (snags) was the preferred sampling habitat when riffles were absent.

Collection of Data

Macroinvertebrate Data

Sampling was done using a large kick net with a rectangular 0.5-m-wide by 0.25-m-tall opening fitted with a 425-μm mesh net and removable sample bottle. At sites where riffles were present, a sample was collected at each of five locations within the riffle habitats available. Samples were collected by placing the opening of the net firmly on the substrate and collecting the organisms within a 0.5 m by 0.5 m (0.25 m^2) area in front of the net. Rocks (large gravel and larger) were scrubbed with a vegetable brush or by hand, and then examined for closely adhering organisms. Any organisms present were removed by hand or with forceps. The remaining smaller substrate particles were disturbed to a depth of 10 cm using a metal rod or by kicking for 30 seconds. Organisms from all five locations were composited into a single sample.

Snag sampling was done with the same kick net used for riffle sampling. Snags were sampled at five locations within the sampling reach. The snags were visually examined, and only those that had clearly been in the stream for an extended period and were well colonized by aquatic biota were selected; however, there was no objective way to assess the colonization period for each snag sampled. The net was held downstream of the snag selected. When feasible, snags were sampled in place by brushing organisms into the net; otherwise, the snags were carefully removed using a pruning saw or pruning shears and the organisms brushed into a bucket. Loose bark was removed, and any concealed organisms were brushed into the net or bucket. Snags were then carefully examined for boring organisms, and any organisms present were removed with forceps. Aquatic vegetation that had become entangled around the snag was considered part of the habitat and also was examined for organisms. The length and diameter of the sampled area were measured and a sample area was calculated. Depending on the size of the snags available, one or more snags were sampled at each of the five locations within the reach. Organisms from all five locations were composited into a single sample.

Composited samples were sieved through a 425-μm mesh screen. Large debris was removed by hand. If the volume of the remaining sample was 750 mL or less, the entire sample was preserved in 10-percent formalin. If the volume of the remaining sample was greater than 750 mL, the sample was split into equal-sized components prior to adding the preservative (see Cuffney and others [1993] for additional details). Large or rare taxa that might be missed in a random split were extracted from the sample by hand and included with the split to be analyzed to ensure that all taxa present at a site were included.

Samples were shipped to the Biological Quality Assurance Unit of the USGS National Water Quality Laboratory, Arvada, Colo., for identification of organisms. Organisms were identified to the lowest possible taxon. Outside experts in various taxonomic groups were consulted for difficult organisms. San Joaquin data were based on complete counts of the sample or subsample analyzed. Sacramento data were based on counts of 500 organisms from the sample or subsample. To ensure comparability of samples, taxonomic data were aggregated to family level or higher.

Habitat and Water Quality Data

Habitat variables were measured at each of six transects within each sampling reach (Meador and

others, 1993). At sites with distinct geomorphic channel units (riffle, run, or pool), transects were placed to reflect the availability of each habitat; otherwise, transects were placed at equally spaced intervals. Stream width (wetted channel) was measured with a fiberglass tape or rangefinder. Open canopy (number of degrees of sky above the transect not obscured by objects) was measured at midstream with a clinometer. Percent canopy was measured with a spherical densiometer.

Depth, velocity, and substrate were measured at a minimum of three points at each transect, including points at about one-quarter, one-half, and three-quarters of the stream width. Depth was measured with a wading rod. Velocity was measured with a Marsh–McBirney electronic flow meter. Substrate was measured as the dominant substrate at each transect point and was classified as (1) organic detritus, (2) silt, (3) mud, (4) sand (0.02–2 mm), (5) gravel (2–64 mm), (6) cobble (64–256 mm), (7) boulder, or (8) bedrock or hardpan (solid rock or clay forming a continuous surface). Additional measurements were made as needed to account for morphological features, such as channel bars and islands.

Stream gradient, stream sinuosity, and elevation were determined from USGS 1:24,000 topographic maps. Stream sinuosity was calculated as river distance divided by the straightline distance between the upstream and downstream ends of a segment of stream (minimum length of 2 km) containing the sample site. Basin area and percentages of agricultural and urban land use within a basin were determined using geographic information system databases.

Water quality measurements taken at each site included specific conductance, pH, and alkalinity. Specific conductance and pH were measured with electronic meters. Alkalinity was determined by titration. Water temperature and dissolved oxygen were measured directly in the river with electronic meters. Discharge measurements were daily mean values for gaged sites and instantaneous measurements at ungaged sites.

Data Analysis

A total of 85 macroinvertebrate samples was included in the analysis. Taxa were aggregated at the family level or higher taxonomic levels as appropriate. For the multivariate analyses described below, macroinvertebrate data were analyzed as the natural logarithm of relative abundance. Only taxa present in 5 percent or more of the 85 samples were included in two-way indicator species analysis (TWINSPAN) and canonical correspondence analysis (CCA). Taxa that were not sampled efficiently by our methods were excluded from all analyses. These taxa included crayfish, semiaquatic hemipterans (except Naucoridae), and clams.

Water quality and habitat variables were examined for normality with normal probability plots. Values were $\log_{10}(x+1)$ transformed to improve normality when appropriate. Statistical analyses were done on all samples, riffle samples only, and snag samples only.

Relations among the habitat and water quality variables were examined using principal components analysis (PCA). Only principal components (PC) with eigenvalues greater than one were retained for interpretation. Loadings were arbitrarily designated as high for absolute values greater than 0.70, moderate for absolute values from 0.5 to 0.69, and low for absolute values less than 0.5.

TWINSPAN (Hill, 1979) was used to determine groupings of samples on the basis of macroinvertebrate assemblages. TWINSPAN is a divisive classification technique that produces an ordered matrix of samples and species. The analysis was limited to two sequential divisions that could potentially produce four groups. The four TWINSPAN sample groups produced by the second division were used for comparison of environmental variables using one-way analysis of variance (ANOVA). Differences were considered statistically significant at $p < 0.05$. The Tukey method (Wilkinson and Coward, 1998) was used for pairwise comparisons when the ANOVA was statistically significant. Comparisons of basic biological metrics between sample types (riffle and snag) and among TWINSPAN sample groups also were done. Sample types were compared using a t-test. Sample groups were compared using ANOVA, similar to the environmental variables. The metrics analyzed include total number of taxa, total density, total number of EPT (Ephemeroptera, Plecoptera, and Trichoptera) taxa, EPT taxa density, and dominance (percentage of total density comprised by the most abundant taxon). Metrics were examined for normality with normal probability plots. Values were $\ln(x+1)$ transformed to improve normality when appropriate. Metric analysis was based on all taxa collected.

Associations of benthic macroinvertebrate assemblages with environmental variables were explored using CCA (ter Braak, 1986, 1987; Jongman and others, 1995). The forward selection mode of CCA was used. This method tests the statistical significance of each environmental variable using a Monte Carlo simulation before adding it to the final model. All variables significant at $p < 0.05$ were included in the final model.

Spatial and annual variabilities were assessed by calculating Jaccard and Bray–Curtis similarities (Wilkinson and others, 1998) among samples collected at each reach for each multiple-reach site and among samples from each year for each site sampled in more than 1 year. Jaccard similarities are calculated on the basis of the presence or absence of taxa, making it a somewhat qualitative measure of assemblage similarity. Bray–Curtis similarities are calculated on the basis of percentage abundances of taxa, giving a more quantitative measure of similarity compared to Jaccard similarities. Separate analyses were done for riffle and snag samples.

A total of 81 taxa were collected during the study. The majority of the taxa (67) were insects. Of the 81 taxa collected, 31 were excluded from multivariate analyses. The 50 taxa retained for multivariate analyses included 41 insect families; 3 amphipod families—water mites (order Acari), snails (order Limnophila), and leeches (class Hirudinea); nematodes (class Nematoda); oligochaetes (class Oligochaeta); and flatworms (Class Turbellaria) (table 1).

PRINCIPAL COMPONENTS ANALYSIS OF ENVIRONMENTAL VARIABLES

Examination of the factor loadings of the original variables on the first two PCs of the three data sets revealed the major environmental gradients potentially affecting benthic macroinvertebrates (table 2). Principal components analysis of the environmental data from all samples resulted in four PCs with eigenvalues greater than 1, which explained 75 percent of the variance in the data. The first two PCs explained 39 and 19 percent of the variance, respectively. The first principal component represents a gradient in elevation and correlated variables, including gradient, basin area, open canopy, land use, discharge, and mean dominant substrate. None of the water quality variables had high loadings on PC1. No variable loaded highly on PC2, but the moderate loadings of six variables indicate that this component represents a stream-size and water-quality gradient.

Riffle Samples

Analysis of data from the riffle sites resulted in six PCs with eigenvalues greater than 1, which explained 86 percent of the variance in the environmental data. The first two PCs explained 30 and 21 percent of the variance, respectively.

Similar to the analysis of all samples, the first principal component of the riffle sample analysis represents a gradient in elevation and correlated variables, including gradient, basin area, and open canopy (table 2). Mean velocity and mean width also had high loadings on PC1 for the riffle samples. None of the water quality variables had high loadings on PC1. Alkalinity and specific conductance loaded highly on PC2 and described a gradient in water quality independent of the gradient in elevation described by PC1.

Snag Samples

Analysis of the data from the snag samples resulted in five PCs with eigenvalues greater than 1, which explained 79 percent of the variance in the snag sample environmental data. The first two PCs explained 33 and 21 percent of the variance, respectively.

Results for the snag samples were very different from the results of the analysis of all the samples or the riffle samples (table 2). The first PC represents a stream-size gradient, relatively independent of elevation. The stream-size gradient included a moderate association with combined agricultural and urban land use in the basin. The second PC represents a gradient in water quality associated with agricultural land use.

Overall, the results of the three analyses suggest that environmental gradients on the valley floor, where the snag samples were collected, were very different than the environmental gradients associated with the riffle samples. Also, the strong elevational gradient evident in the riffle samples seems to dominate the combined analysis. Thus, separate analyses of riffle and snag samples are probably most appropriate for assessing the relations of benthic macroinvertebrate assemblages with environmental variables in these very different environmental settings.

Table 1. TWINSPAN taxa groups and occurrence of taxa in samples in TWINSPAN sample groups for riffle and snag samples, Sacramento–San Joaquin river drainages, California

[Taxa are indented in the order class, order, and family. Taxa groups refer to the TWINSPAN taxa groups for riffle (R) and snag (S) samples. The numbers (1–4) indicate groups after two TWINSPAN divisions of the riffle and snag samples. Taxa code refers to codes used in figures 2*B* and 3*B*. TWINSPAN, two-way indicator species analysis; —, taxon was not present in the sample group]

Taxon	Taxa groups		Taxa code	Riffle Sample Groups				Snag Sample Groups			
	R	S		Valley (N = 13)	Transition (N = 7)	Foothills (N = 19)	Mountain (N = 6)	San Joaquin (N = 7)	Tributary (N = 24)	Drain group 1 (N = 7)	Drain group 2 (N = 2)
Arachnoidea											
Acari	2	1	ACARI	12	7	18	6	4	24	4	0
Gastropoda											
Limnophila	4	4	GASTRO	7	1	2	1	1	11	3	2
Hirudinae	—	4	HIRU	0	0	0	0	0	3	2	1
Insecta											
Coleoptera											
Elmidae	2	3	C1	7	7	18	6	0	7	3	1
Psephenidae	2	4	C2	0	6	8	0	0	0	0	1
Ptilodactylidae	1	—	C3	0	2	6	0	0	0	0	0
Diptera											
Athericidae	3	—	D1	0	5	4	1	0	0	0	0
Blephariceridae	2	—	D2	1	3	11	2	0	0	0	0
Ceratopogonidae	2	4	D3	1	4	9	2	1	0	3	1
Chironomidae	2	3	D4	12	7	19	6	7	24	7	1
Empididae	2	1	D5	5	6	14	2	5	23	0	0
Simuliidae	1	1	D6	7	5	15	6	4	18	1	1
Tipulidae	1	2	D7	2	4	17	5	2	3	1	0
Ephemeroptera											
Ameletidae	1	1	E1	0	0	4	3	0	1	0	0
Baetidae	3	2	E2	13	7	19	6	2	23	3	2
Caenidae	4	4	E3	0	1	0	0	1	2	3	1
Ephemerellidae	2	1	E4	10	7	19	6	0	14	0	0
Heptageniidae	2	2	E5	10	7	19	6	2	19	3	0
Leptohyphidae	4	1	E6	13	6	1	0	2	24	1	0
Leptophlebiidae	1	—	E7	2	0	9	5	0	0	0	0
Hemiptera											
Naucoridae	4	1	H1	1	2	0	0	0	5	0	0
Lepidoptera											
Pyralidae	4	1	L1	8	6	7	0	0	6	0	0
Megaloptera											
Corydalidae	1	—	M1	2	1	10	5	0	0	0	0

Table 1. TWINSPAN taxa groups and occurrence of taxa in samples in TWINSPAN sample groups for riffle and snag samples, Sacramento–San Joaquin river drainages, California—Continued

Taxon	Taxa groups		Taxa code	Riffle Sample Groups				Snag Sample Groups			
	R	S		Valley (N = 13)	Transition (N = 7)	Foothills (N = 19)	Mountain (N = 6)	San Joaquin (N = 7)	Tributary (N = 24)	Drain group 1 (N = 7)	Drain group 2 (N = 2)
Odonata											
Calopterygidae	4	2	O1	4	2	1	0	0	8	1	0
Coenagrionidae	3	4	O2	5	2	3	0	2	6	6	1
Gomphidae	4	1	O3	1	4	3	0	0	2	0	0
Libellulidae	4	—	O4	3	2	3	0	0	0	0	0
Plecoptera											
Capniidae	1	—	P1	0	0	3	1	0	0	0	0
Chloroperlidae	1	—	P2	0	0	14	3	0	0	0	0
Nemouridae	1	—	P3	0	0	10	6	0	0	0	0
Perlidae	1	—	P4	4	5	19	6	0	0	0	0
Perlodidae	1	—	P5	2	5	19	5	0	0	0	0
Pteronarcyidae	3	—	P6	2	7	10	0	0	0	0	0
Trichoptera											
Brachycentridae	1	1	T1	1	6	9	3	0	1	0	0
Glossosomatidae	3	—	T2	8	6	14	5	0	0	0	0
Helicopsychidae	2	—	T3	1	5	4	0	0	0	0	0
Hydropsychidae	3	1	T4	13	7	19	5	7	24	2	0
Hydroptilidae	4	2	T5	6	6	12	3	1	20	3	1
Lepidostomatidae	1	—	T6	1	0	3	4	0	0	0	0
Leptoceridae	4	1	T7	5	7	2	0	1	15	1	0
Limnephilidae	1	—	T8	0	0	6	1	0	0	0	0
Philipotomatidae	1	—	T9	1	3	14	1	0	0	0	0
Rhyacophilidae	1	—	T10	0	5	17	6	0	0	0	0
Uenoidea	1	—	T11	0	0	1	3	0	0	0	
Malacostraca											
Amphipoda											
Corophiidae	—	1	A1	0	0	0	0	7	0	0	0
Crangonyctidae	4	4	A2	3	0	0	0	0	0	2	0
Talitridae	4	4	A3	1	0	0	0	1	6	2	0
Nematoda	2	2	NEMA	3	5	8	3	3	3	1	0
Oligochaeta	4	4	OLIGO	13	7	17	7	7	21	7	2
Turbellaria	4	4	TURB	8	2	5	0	0	2	1	0

Table 2. Loadings of environmental variables on the first two principal components (PC) derived from principal components analyses of environmental data from all samples, only riffle samples, and only snag samples , Sacramento–San Joaquin river drainages, California

[Boldfaced values, absolute value of loading was greater than 0.70 and was considered high. mg $CaCO_3$/L, milligrams of calcium carbonate per liter; mg/L, milligram per liter; µS/cm, microsiemens per centimeter; km^2, square kilometer; m^3/s, cubic meter per second; m/s, meter per second; —, absolute value of loading was less than 0.30; NA, not included in analysis]

	All Samples		Riffle Samples		Snag Samples	
Variable	PC1	PC2	PC1	PC2	PC1	PC2
Water quality						
Alkalinity (mg CaCO3/L)[1]	0.44	–0.68	—	**–0.88**	–0.37	**0.87**
Dissolved oxygen (mg/L)	–0.31	0.54	—	—	0.58	—
Oxygen saturation (percent)	—	—	—	—	0.36	—
pH	—	–0.40	—	0.65	—	**0.70**
Specific conductance (µS/cm)[1]	0.53	–0.65	—	**–0.89**	—	**0.87**
Habitat variables						
Agricultural land use (percent)[1]	**0.85**	—	NA	NA	—	0.79
Agricultural and urban land use (percent)[1]	**0.80**	–0.42	0.65	–0.32	–0.64	0.55
Basin area (km^2)[1]	**0.77**	0.48	**0.83**	—	**0.91**	—
Discharge (m^3/s)[1]	**0.72**	0.51	0.61	0.43	**0.85**	—
Elevation (m)[1]	**–0.90**	—	**–0.79**	—	–0.55	—
Gradient (percent)	**–0.77**	—	**–0.73**	0.31	–0.69	–0.31
Mean depth (m)	0.47	0.40	0.44	—	0.56	—
Mean dominant substrate	**–0.72**	0.37	–0.38	0.57	0.37	–0.37
Mean velocity (m/s)	0.47	0.50	**0.70**	—	0.59	—
Mean width (m)[1]	0.63	0.65	**0.76**	–0.51	**0.89**	—
Open canopy (degrees)	**0.77**	0.34	**0.87**	—	**0.74**	0.40
Percent canopy (percent)	–0.57	–0.34	–0.63	—	–0.53	–0.48
Sinuosity[1]	0.47	—	—	—	0.51	—
Water temperature (°C)	0.59	–0.49	0.42	–0.62	–0.35	0.56

[1]Variable was $\log_{10}(x+1)$ transformed for analysis.

TWINSPAN GROUPINGS

TWINSPAN analysis of all samples largely separated the riffle samples from the snag samples. The first TWINSPAN division resulted in one group composed entirely of riffle samples. The second group, resulting from the first TWINSPAN division, included 12 riffle samples and all of the snag samples. Riffle samples included in this second group were all samples from low elevation sites. Because the TWINSPAN analysis of the combined samples largely separated riffle and snag samples, the remainder of this report presents the results of the separate analyses, with a few exceptions. The results of the PCA analyses are consistent with this decision because they suggest that the macroinvertebrate assemblages of the riffle and snag samples are responding to a different suite of environmental variables.

Sample Groups

Riffle Samples

The first two TWINSPAN divisions of the riffle samples resulted in four groups that represent elevational strata (fig. 2*A*). The valley floor group includes samples from the lowest elevations sampled. Most samples are from larger streams below major storage reservoirs. The sample from the most downstream site on Big Chico Creek is an exception because of the relatively small size of the creek. The transition group includes samples from sites located at the transition from foothill to valley-floor habitat on Deer Creek and Big Chico Creek, both unregulated streams. The foothill group includes samples from sites located at a wide range of elevations in the Sierra Nevada foothills and mountains (286–1,268 m). The mountain group includes samples from the sites at higher elevations (682–1,426 m), including sites that overlap with the

foothill group. Samples for different years or reaches were split between the foothill and mountain groups for the most upstream site on the Merced River and the McCloud River site.

Snag Samples

The first two TWINSPAN divisions of the snag samples resulted in four groups (fig. 2*B*) that represent different habitat types. The tributary group includes samples from sites on the tributary rivers and samples from the Sacramento River in 1997 and the most downstream site on the San Joaquin River in 1994. The San Joaquin group includes samples from the mainstem San Joaquin River and Salt Slough, except for the sample from the most downstream San Joaquin River site in 1994. The San Joaquin group also includes the sample from the Sacramento River in 1996. Drain group 1 includes samples from sites on agricultural drains and natural creeks affected by agricultural return flows, urban runoff, or water diversions. Two exceptions, because of the larger size of the streams, are the 1994 sample from the second-most downstream site on the Tuolumne River and the 1997 sample from the Feather River. Drain group 2 includes the 1996 sample from Arcade Creek and the sample from Orestimba Creek.

Taxa Groups

Riffle Samples

The riffle samples included 48 of the 50 common taxa analyzed (table 1). Leeches (Hirudinae) and corophiid amphipods were absent. The first two TWINSPAN divisions of the riffle samples resulted in four groups of taxa (table 1). The first group (riffle group 1 in table 1) comprised 17 taxa, including 2 dipteran families, 2 ephemeropteran families, 1 megalopteran family, 5 plecopteran families, 6 trichopteran families, and 1 coleopteran family. These taxa generally were most abundant in mountain and foothill samples and were generally absent from the valley samples. All but two of these taxa are considered intolerant of environmental degradation on the basis of tolerance values developed for benthic macroinvertebrates (Bob Wisseman, Aquatic Biology Associates, written commun., 1996). One ephemeropteran family (Ameletidae), three plecopteran families (Capniidae, Chloroperlidae, and Nemouridae) and two trichopteran families (Lepidostomidae and Uenoidae) were found only in foothill and mountain samples.

The second group (riffle group 2 in table 1) comprised 11 taxa, including the water mites (order Acari), nematodes, 2 coleopteran families, 4 dipteran families, 2 ephemeropteran families, and 1 trichopteran family. These taxa were broadly distributed among the samples, but tended to be less abundant or absent from valley samples. Eight of these taxa are considered moderately tolerant of environmental degradation, and the remaining three taxa are considered intolerant (Bob Wisseman, Aquatic Biology Associates, written commun., 1996).

The third group (riffle group 3 in table 1) comprised 6 taxa, including 1 dipteran family, 1 ephemeropteran family, 1 plecopteran family, 2 trichopteran families, and 1 odonate family. These taxa tended to be most abundant or occurred most frequently in samples from the foothill and transition groups. There is no clear pattern in tolerance.

The fourth group (riffle group 4 in table 1) comprised 14 taxa, including the gastropods, oligochaetes, turbellarians, 2 ephemeropteran families, the only hemipteran family, the only lepidopteran family, 3 odonate families, 2 trichopteran families, and the only 2 amphipod families. These taxa were most abundant or occurred most frequently in samples from valley or transition group sites. All but one of the taxa are considered moderately tolerant or tolerant of environmental degradation (Bob Wisseman, Aquatic Biology Associates, written commun., 1996).

Snag Samples

Only 31 of the 50 common taxa occurred in snag samples (table 1). Megalopterans and plecopterans were completely absent and only 4 of 11 trichopteran families were present. The first group (snag group 1 in table 1) resulting from the first two TWINSPAN divisions of the snag samples comprised 13 taxa, including 3 ephemeropteran families; 3 trichopteran families; 2 dipteran families; one each of hemipteran, lepidopteran, odonate, and amphipod families; and the water mites. These taxa occurred most frequently in San Joaquin or tributary group samples, with few occurrences in drain samples. Seven of these taxa are considered moderately tolerant of environmental degradation and the remaining four are considered intolerant (Bob Wisseman, Aquatic Biology Associates, written commun., 1996).

The second group (snag group 2 in table 1) comprised 6 taxa, including the nematodes; 2 ephemeropteran families; and one each of the dipteran, odonate, and trichopteran families. These taxa were most abundant or frequent in tributary samples but also occurred in some samples from all of the other site groups. Five of these taxa are considered moderately tolerant of environmental degradation (Bob Wisseman, Aquatic Biology Associates, written commun., 1996).

The third group (snag group 3 in table 1) comprised only two broadly distributed taxa. Chironomids were found in all but one sample and were abundant in some samples from all sample groups. The elmids (Coleoptera) occurred sporadically in samples from all site groups, except the San Joaquin group. Both of these taxa are considered moderately tolerant of environmental degradation (Bob Wisseman, Aquatic Biology Associates, written commun., 1996).

The fourth group (snag group 4 in table 1) comprised 10 taxa, including the leeches, gastropods, oligochaetes, turbellarians, 1 coleopteran family, 1 dipteran family, 1 ephemeropteran family, 1 odonate family, and 2 amphipod families. This group included taxa that occurred sporadically, but most frequently and most abundantly in samples from the two drain groups. These taxa are considered tolerant or moderately tolerant of environmental degradation (Bob Wisseman, Aquatic Biology Associates, written commun., 1996).

Overall, the riffle taxa groups were dominated by intolerant and moderately tolerant taxa, and the snag taxa groups were dominated by moderately tolerant and tolerant taxa. These results suggest that the snag samples represent macroinvertebrate assemblages responding to environmental conditions harsher than those associated with the riffle samples.

COMPARISONS OF BIOTIC AND ENVIRONMENTAL VARIABLES AMONG SAMPLE GROUPS

In addition to the differences in environmental gradients between riffle and snag samples revealed by PCA, there were statistically significant differences between riffle and snag samples for several biological variables (table 3). Snag samples had fewer taxa than riffle samples, but total densities of organisms were not statistically different. The number of EPT taxa and the EPT density were statistically different with snag samples having fewer EPT taxa and lower densities of EPT taxa. Snag samples also tended to be more dominated by a single taxon with mean dominance of snag samples averaging over 50 percent.

Riffle Samples

The valley group had fewer taxa and fewer EPT taxa than the other groups (table 3). The highest number of taxa occurred in the transition and foothill groups. Total density was highly variable with wide ranges in values for all groups. The transition group had the highest mean total density but was not statistically different from the mountain group. EPT density was significantly higher in the transition sample group than in any other of the groups. The valley group had the highest dominance value but was significantly different only from the foothill group, which had the lowest value.

The dominant taxa in the valley group samples were baetids (6 samples), hydropsychids (3 samples), chironomids (2 samples), and pyralids (1 sample). The dominant taxa in the transition group samples were chironomids (3 samples), oligochaetes (1 sample), hydropsychids (1 sample), acari (1 sample), and hydroptilids (1 sample). The dominant taxa in the foothill group samples were baetids (6 samples), hydropsychids (3 samples), chironomids (2 samples), elmids (2 samples), simuliids (1 sample), heptageniids (1 sample), brachycentrids (1 sample), and acari (1 sample). Mountain samples were dominated by either chironomids (4 samples) or heptageniids (2 samples). The dominant taxa are all moderately tolerant of environmental degradation, except for the intolerant brachycentrid trichopterans and the tolerant oligochaetes (Bob Wisseman, Aquatic Biology Associates, written commun., 1996).

There were statistically significant differences in environmental conditions among riffle sample groups for 8 of the 18 variables compared (table 4). In six cases, the valley group and mountain group had the most extreme values and were significantly different from each other. The foothill and transition groups were generally intermediate and grouped with either the valley group or the mountain group. In the remaining two cases, the mountain or valley group represented one extreme and the transition group the other extreme.

Table 3. Mean or geometric mean (for transformed variables) values of biological variables for sample types and TWINSPAN sample groups, Sacramento–San Joaquin river drainages, California. Differences among means were tested with a t-test for sample types and one-way analysis of variance within TWINSPAN sample groups

[TWINSPAN, two-way indicator species analysis. Densities are organisms per square meter. EPT, families in the orders Ephemeroptera, Plecoptera, and Trichoptera. Dominance is the percentage of total density represented by the most abundant taxa. Similar superscripts (A–C) indicate means that were not significantly different (t-test, or Tukey method after analysis of variance)]

	Sample Size	Total number of taxa		Total density [1] (×1,000)		Number of EPT taxa		EPT density [1] (×1,000)		Dominance [1]	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Sample types											
Riffles	45	25 ^{A}	15–34	6.3	1.3–98.2	11 ^{A}	5–16	3.1 ^{A}	0.6–49.7	36 ^{A}	15–88
Snags	40	15 ^{B}	7–22	4.5	0.4–45.3	4 ^{B}	0–8	0.7 ^{B}	0–23.4	54 ^{B}	24–79
Riffle sample groups											
Valley	13	19 ^{A}	15–24	5.5 ^{A}	1.6–90.7	7 ^{A}	5–10	2.9 ^{A}	0.6–11.4	46 ^{A}	24–88
Transition	7	30 ^{B}	27–34	23.7 ^{B}	4.8–98.2	13 ^{B}	11–16	10.5 ^{B}	1.8–49.7	34 ^{A,B}	24–46
Foothill	19	27 ^{B,C}	23–33	4.4 ^{A}	1.3–32.6	13 ^{B}	8–16	2.4 ^{A}	0.8–13.3	30 ^{B}	15–50
Mountain	6	25 ^{C}	21–28	5.6 ^{A,B}	2.6–24.4	13 ^{B}	7–16	2.1 ^{A}	0.7–3.9	41 ^{A,B}	24–59
Snag sample groups											
San Joaquin	7	12 ^{A}	9–17	4.7	1.2–19.3	2 ^{A}	1–5	1.3 ^{A}	0.3–5.9	52	32–77
Tributary	24	17 ^{B}	13–22	4.6	0.4–45.3	6 ^{B}	4–8	1.2 ^{A}	0.1–23.4	53	24–79
Drain group 1	7	14 ^{A}	11–18	4.2	1.3–12.1	2 ^{A}	0–5	0.1 ^{B}	0–2.0	60	41–78
Drain group 2	2	11 ^{A}	7–15	3.7	0.7–20.8	2 ^{A}	1–3	0.4 ^{A,B}	0.2–0.9	62	50–75

[1]Data were ln(x+1) transformed for analysis.

Table 4. Mean or geometric mean (for transformed variables) values of environmental variables for TWINSPAN sample groups and the results of one-way analysis of variance comparisons of group means , Sacramento–San Joaquin river drainages, California

[Similar superscripts (A–C) indicate means values that were not significantly different (Tukey method, $p < 0.05$). TWINSPAN, two-way indicator species analysis; mg $CaCO_3$/L, milligrams of calcium carbonate per liter; mg/L, milligram per liter; µS/cm, microsiemens per centimeter; km^2, square kilometer; m^3/s, cubic meter per second; m/s, meter per second. —, data not available]

Variable	Riffle Sample Groups				Snag Sample Groups			
	Valley (N = 13)	Transition (N = 7)	Foothills (N = 19)	Mountain (N = 6)	San Joaquin (N = 7)	Tributary (N = 24)	Drain group 1 (N = 7)	Drain group 2 (N = 2)
Water quality								
Alkalinity (mg CaCO3/L)[1]	40	65	30	24	124^{A}	39^{B}	106^{A}	105^{A}
Dissolved oxygen (mg/L)	9.1	9.0	9.3	9.7	7.8	8.6	8.0	7.3
Oxygen saturation (percent)	99	103	102	98	88	94	95	85
pH	7.5^{A}	8.2^{B}	$8.0^{A,B}$	$7.7^{A,B}$	7.9	7.5	7.8	7.5
Specific conductance (µS/cm)[1]	102	143	73	61	831^{A}	114^{B}	281^{C}	$352^{A,C}$
Habitat variables								
Agricultural land use (percent)[1]	—	—	—	—	28.9^{A}	8.4^{B}	$11.8^{A,B}$	$13.6^{A,B}$
Agricultural and urban land use (percent)[1]	3.6^{A}	0.2^{B}	0.2^{B}	0.1^{B}	30.3^{A}	10.4^{B}	26.8^{A}	98.0^{A}
Basin area (km^2)[1]	$2{,}228^{A}$	402^{B}	565^{B}	298^{B}	$8{,}689^{A}$	$4{,}216^{A,B}$	$1{,}827^{B}$	48^{C}
Discharge (m^3/s)[1]	3.6	1.7	2.2	1.3	21.2^{A}	12.8^{A}	$7.0^{A,B}$	0.4^{B}
Elevation (m)[1]	35^{A}	109^{B}	630^{C}	$1{,}034^{C}$	10	12	12	17
Gradient (percent)	0.160^{A}	$0.741^{A,B}$	2.008^{B}	2.176^{B}	0.019^{A}	0.036^{A}	0.053^{A}	0.168^{B}
Mean depth (m)	0.87	1.01	0.84	0.83	1.51	1.10	1.45	0.55
Mean dominant substrate	5.1^{A}	4.9^{A}	5.9^{B}	$5.7^{A,B}$	3.7^{A}	3.8^{A}	2.4^{B}	$3.3^{A,B}$
Mean velocity (m/s)	0.42	0.22	0.27	0.18	0.48^{A}	0.40^{A}	0.15^{B}	$0.29^{A,B}$
Mean width (m)[1]	$32.6^{A,2}$	16.3^{B}	$20.0^{A,B}$	15.9^{B}	46.8^{A}	37.8^{A}	35.6^{A}	5.1^{B}
Open canopy (degrees)	132^{A}	$117^{A,B}$	$80^{B,C}$	51^{C}	158^{A}	127^{A}	$123^{A,B}$	65^{B}
Percent canopy	24	22	25	50	$2^{A,2}$	$17^{A,B}$	$24^{A,B}$	31^{B}
Sinuosity[1]	1.21	1.22	1.24	1.21	1.71^{A}	1.63^{A}	1.16^{B}	1.05^{B}
Water temperature (°C)	$19.3^{A,B}$	21.4^{A}	$15.4^{B,C}$	10.6^{C}	21.0	20.7	23.0	23.0

[1]Variable was $\log_{10}(x+1)$ transformed for analysis.

[2]Although the one-way analysis of variance was significant ($p < 0.05$), none of the pairwise tests were significant at $p < 0.05$. Pairwise tests significant at $p < 0.10$ are shown.

Snag Samples

The snag sample groups showed fewer differences in biological variables than the riffle samples (table 3). The tributary group had more taxa than the San Joaquin group and drain groups; however, total density did not vary among groups. The tributary group had the highest number of EPT taxa, but the differences in EPT density were not as definitive. EPT density of drain group 1 was significantly lower than the San Joaquin and tributary groups. Mean dominance exceeded 50 percent for all groups.

The tributary group samples were dominated by chironomids (15 samples); hydropsychids (5 samples); and oligochaetes, baetids, simuliids, and lepidostomatids (1 sample each). The dominant taxa in the San Joaquin group samples were oligochaetes (2 samples), hydropsychids (2 samples), corophiid ampipods (2 samples), and chironomids (1 sample). The dominant taxa in drain group 1 samples were chironomids (4 samples), oligochaetes (2 samples), and caenids (1 sample). The dominant taxa in the two drain group 2 samples were chironomids (1 sample) and gastropods (1 sample). The dominant taxa are all moderately tolerant of environmental degradation, except for the intolerant lepidostomatid trichopterans and the tolerant gastropods and oligochaetes (Bob Wisseman, Aquatic Biology Associates, written commun., 1996).

The snag sample groups tended to have broadly overlapping means for most environmental variables with no obvious common pattern even though 13 of 19 comparisons were significant (table 4). There were a few obvious differences. Tributary samples had the lowest values of alkalinity and specific conductance and also the lowest percentages of human land use. For most comparisons, the two drain groups were similar, except for basin area, gradient, and mean width.

MACROINVERTEBRATE ASSEMBLAGES

Associations with Environmental Variables

Riffle samples

The forward selection procedure in CCA resulted in retention of seven variables in the CCA model for the riffle samples (table 5). The first axis of the riffle analysis was dominated by the association of elevation with macroinvertebrate assemblages. The remaining axes were less dominated by any one variable but appeared to stress the correlations of variables reflective of stream size, including basin area, discharge, and open canopy with macroinvertebrate assemblages. In general, the environmental gradients identified as important to organisms in the CCA were similar to the environmental gradients identified by PCA of the physical variables alone (tables 2 and 5). However, some variables with only low to moderate loadings on one of the first two PCs had significant explanatory value in CCA. These variables included agricultural and urban land use, discharge, dissolved oxygen, and pH.

The CCA plot of the riffle sample scores indicates relatively good separation of the valley group and transition group from the other groups and each other, but a great deal of overlap between the foothill and mountain groups (fig. 3*A*). The good separation of the valley sample group from the other three groups appears to represent a response of the benthic macroinvertebrate assemblage to the strong elevation and land-use gradient. High percentages of snails, flatworms, libellulid and coenagrionid odonates, leptohyphid ephemeroptera, and amphipods, particularly in the family Crangonyctidae, characterized the valley samples (fig. 3*B*). These taxa are considered tolerant or moderately tolerant of environmental degradation.

The elevation land-use gradient also was important for separating the transition sample group from the foothill and mountain sample groups, but stream discharge, dissolved oxygen, pH, and open canopy also were important. The transition sample group is well separated from the foothill group, except for three foothill samples, and is well separated from the mountain samples. The separation of the mountain and transition groups is reflected by the associated taxa (fig. 3*B*). The mountain samples are characterized by megalopterans and a variety of EPT taxa. Most of these taxa are considered intolerant of environmental degradation (Bob Wisseman, Aquatic Biology Associates, written commun., 1996). Lepidopterans, leptocerid trichopterans, caenid ephemeroptera, gomphid odonates, and naucorid hemipterans characterized the transition group samples. These taxa are considered moderately tolerant to environmental degradation (Bob Wisseman, Aquatic Biology Associates, written commun., 1996). The foothill sample group was so diffuse that it was not characterized by any particular group of taxa.

The extensive overlap of foothill and mountain sample groups argues against using the TWINSPAN groupings. The CCA plot (fig. 3*A*) suggests that the samples in the upper left quadrant of the plot form a more legitimate mountain group especially because it puts all of the McCloud River samples and the two samples from the most upstream site on the Merced River together. The importance of gradients in elevation and correlated environmental variables has been noted in other studies, and the classification of sites into montane and nonmontane groups is a common result (Carter and others, 1996; Cuffney and others, 1997; Whittier and others, 1998). Defining subgroups within these categories appears to be more difficult and may be dependent on geographic scale and sampling intensity. Two studies of the moderately sized Yakima River drainage (15,540 km^2) in Washington successfully defined subgroups within larger montane groups (Carter and others, 1996; Cuffney and others, 1997). In addition, Cuffney and others (1997) were able to distinguish among different sites in a group of lower elevation small stream sites and among different sites in a group of large river sites on the basis of the effects of agricultural activities on algae, macroinvertebrate, and fish communities. In contrast, Whittier and others (1998) were unable to distinguish among groups of montane sites from five different ecoregions.

The overlapping results for the foothill and mountain groups of the riffle samples could be due to several factors. TWINSPAN and CCA are very different types of analyses. The most basic difference is that TWINSPAN is based on a conversion of continuous data into categories whereas CCA is based on direct analyses of continuous data. This suggests that CCA is more sensitive to small differences in the data, and the groups suggested by that technique should be accepted especially because the CCA sample scores group in a more intuitively appealing manner. However, further

Table 5. Results of canonical correspondence analyses relating benthic macroinvertebrate density to environmental variables for riffle and snag samples from the Sacramento and San Joaquin river drainages, California

[Boldfaced coefficients had t-values greater than 2.1, indicating a significant contribution to the axis]

Environmental Variable	Eigenvalue	Canonical Coefficient			
		Axis 1	Axis 2	Axis 3	Axis 4
Riffle samples					
Agricultural and urban land use	0.03	**–0.15**	**0.38**	–0.22	0.41
Basin area	0.04	**0.23**	0.39	**–0.67**	**–0.65**
Discharge	0.05	**–0.32**	–0.01	**0.70**	**–0.39**
Dissolved oxygen	0.03	**–0.11**	**0.32**	–0.15	**–0.43**
Elevation	0.19	**–1.03**	–0.18	0.25	0.40
Open canopy	0.05	–0.01	**–0.68**	**1.02**	0.55
pH	0.07	**0.16**	**–0.69**	**–0.36**	**–0.53**
Percentage of species variance explained		18.4	6.7	4.9	3.4
Percentage of species environment relation explained		46.3	16.8	12.3	8.6
Snag samples					
Agricultural land use	0.08	**–0.54**	**0.62**	**1.25**	–0.41
Agricultural and urban land use	0.09	**0.75**	–0.35	**–0.66**	**0.87**
Elevation	0.06	–0.06	0.06	–0.13	**0.79**
Gradient	0.14	0.08	–0.22	**1.49**	**–0.72**
Mean dominant substrate	0.08	**–0.29**	0.20	**0.72**	0.22
Specific conductance	0.15	**0.37**	**0.73**	–0.12	0.14
Water temperature	0.06	0.03	–0.22	0.16	**–1.00**
Percentage of species variance explained		10.4	8.0	7.9	5.3
Percentage of species environment relation explained		26.7	20.4	20.2	13.8

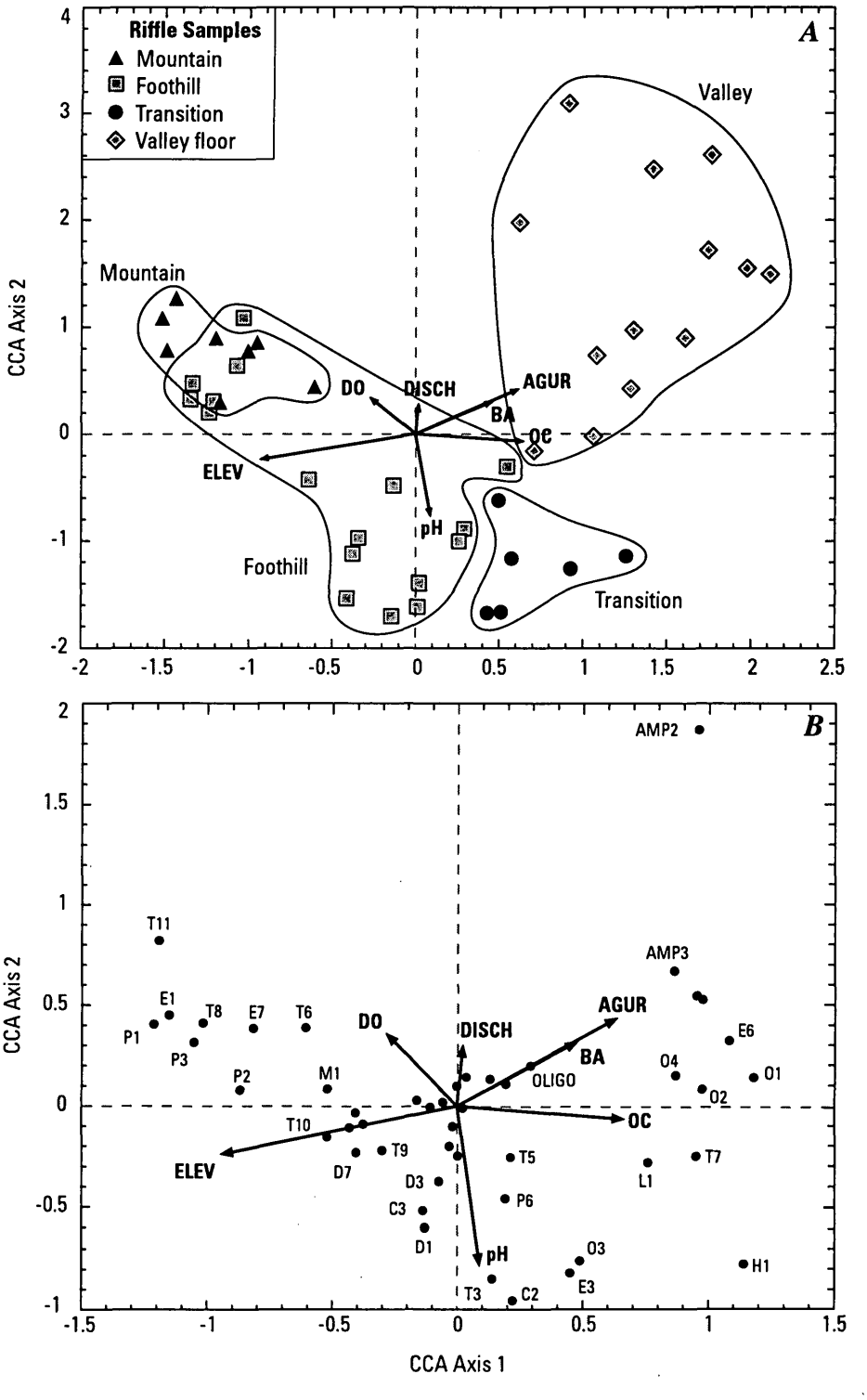

Figure 3. Scores on the first two canonical correspondence analysis axes for riffle samples (*A*) and riffle taxa (*B*), Sacramento–San Joaquin river drainages, California. See table 1 for taxa codes. Level-2 TWINSPAN groups are enclosed by lines. For both plots, the arrows represent the correlation of physical variables with the axes (AGUR = agricultural + urban land use, BA = basin area, DISCH = discharge, DO = dissolved oxygen, ELEV = elevation, and OC = open canopy). Arrows parallel to an axis indicate a high correlation and perpendicular to an axis indicate a low correlation. TWINSPAN, two-way indicator species analysis.

study is needed to identify the sources of variation causing the different results.

Two sources may be particularly important. First, the foothill and mountain sample sites may have had very different temperature regimes associated with the steep elevation gradient and different channel morphologies. In addition, the relatively prolonged period of sample collection of a month or more in any particular year could result in samples collected at different times in the seasonal progression of the macroinvertebrate community. Hawkins and others (1997) found that stream temperature and sampling date were the most important factors in explaining insect assemblage structure in samples from many of the same geographic areas within the same range in elevation that were sampled at foothill and mountain sites in this study.

Second, the family level of identification may be insufficient to understand the response of the macroinvertebrate assemblage to the environment in the Sierra Nevada, especially on a regional level. Erman (1997) compiled various species lists for the Sierra Nevada and found records for 122 species of Plecoptera, of which 32 were endemic to the Sierra Nevada, and 199 species of Trichoptera, including 37 endemic species. Diversity in particular drainages also can be high. Bottorff and Knight (1989) documented 69 species of Plecoptera in 36 genera in the Cosumnes River drainage, one of the smaller Sierra Nevada rivers. Bottorff and Knight (1989) also noted the highest species richness at elevations between about 500 and 1,500 m, which encompasses most of the mountain and foothill sites in this study. Thus, the highest elevation sites in this study actually may have been at a transition zone between areas of higher and lower species richness. A greater monitoring effort at the species level is needed in the Sierra Nevada to fully describe the diversity and long-term trends in the macroinvertebrate fauna (Erman, 1997).

The sites in the transition group represent areas of transition between foothill and valley habitat. The number of total taxa and number of EPT taxa were comparable to the foothill and mountain groups and greater than the valley group (table 3). Total macroinvertebrate density in the transition group was greater than for any other, although it was not significantly different from the mountain sites because of high variability (table 3). EPT density in the transition samples was the highest of any of the groups (table 3). The valley sites had the lowest taxa richness, primarily because of the loss of EPT taxa. The absence of Plecoptera from valley floor habitats has been noted previously (Bottorff, 1989). Transition group sites occurred only on relatively small, unregulated streams in the Sacramento River drainage (fig. 2*A*). This type of habitat either has been submerged under reservoirs or occurs downstream of large dams that alter the hydrologic regime for most of the medium to large-sized streams of the Central Valley.

The absence of transition zone sites in the regulated reaches of streams with large storage reservoirs is important for two reasons. First, the data suggest that the reservoirs have negatively affected biodiversity and assemblage structure of aquatic macroinvertebrates in Central Valley stream systems. Unfortunately, the historical species-level data needed to assess the importance of such effects do not exist for Central Valley streams (Brown, 1996; Erman, 1997). The effects of dams, diversions, and flow regulation on benthic macroinvertebrates can be significant and complex (Brittain and Saltveit, 1989; Ward and Stanford, 1995). Second, reductions in the diversity and productivity of the benthic macroinvertebrate assemblages in regulated stream reaches may be an important consideration in management of anadromous salmonids in the Central Valley. Regulated stream reaches represent the only remaining habitat for anadromous salmonids in many Central Valley streams (Yoshiyama and others, 1996, 1998). Adult and larval aquatic macroinvertebrates are the major food resource for juvenile anadromous salmonids in freshwater habitats (Groot and Margolis, 1991). A loss of production of food for young chinook salmon (*Oncorhynchus tchawytscha*) and steelhead (*Oncorhynchus mykiss*) could be a contributing factor to their declines in the Central Valley. These declines would represent an indirect effect of dams on these fish species in addition to the direct effects of flow regulation, water diversion, temperature regime alterations, loss of upstream spawning habitat, and degradation of existing spawning habitat. Additional studies addressing food habits of juvenile salmonids and biomass of benthic macroinvertebrates, as well as density, are needed to assess this hypothesis more fully. If food production for fish has been reduced by human activities, then restoration of such production might be an important factor to consider as part of ongoing stream restoration activities in the Central Valley.

Snag Samples

The forward selection procedure in CCA resulted in retention of seven variables in the CCA model for the snag samples (table 5). The first two axes of the model stressed the association of macroinvertebrate assemblages with land use and associated water quality conditions as represented by specific conductance. The third and fourth axes were more complex. Agricultural land use was important on the first three axes, highlighting the important association of this activity on the valley floor with macroinvertebrate assemblages. As for the riffle samples, the environmental gradients identified as important to macroinvertebrates on snags in the CCA were similar to the environmental gradients identified by PCA of the environmental variables alone (tables 2 and 5). Similar to the riffle samples, some variables with only low to moderate loadings on one of the first two PCs, including agricultural and urban land use, elevation, gradient, mean dominant substrate, and water temperature, had significant explanatory value in CCA.

The snag sample groups (fig. 4*A*) were better separated than the riffle groups (fig. 3*A*) in the CCA plot. The San Joaquin group was isolated from the other snag sample groups. The tributary sample group was isolated near and to the left of the origin. The two drain groups overlapped and formed a diffuse group to the right of the origin. Agricultural land use and specific conductance were the most important variables separating the San Joaquin and tributary groups. Sites in the tributary group were characterized by low concentrations of total dissolved solids (as measured by specific conductance) and low levels of human land use (table 4). Gradient and combined agricultural and urban land use were the most important factors in separating out the drain sites.

The San Joaquin group separated from the tributary group along the gradients of agricultural land use and specific conductance (fig. 4*A*). The separation was largely due to high percentage abundances of corophiid amphipods associated with high values of agricultural land use and specific conductance (fig. 4*B*). The tributary group was characterized by a variety of ephemeropterans, trichopterans, odonates, and the naucorid hemipterans. The taxa present are considered intolerant or moderately tolerant of degraded environmental conditions (Bob Wisseman, Aquatic Biology Associates, written commun., 1996). Leland and Fend (1998) also noted the major difference between San Joaquin River and tributary sites and identified the dominant amphipod as *Corophium spinicornae*, an estuarine amphipod common in the Sacramento–San Joaquin Delta (Hazel and Kelley, 1966). Leland and Fend (1998) identified the major environmental gradient as total dissolved solids, which is closely correlated to specific conductance. The classification of the samples from the most downstream site on the San Joaquin River in 1994 is also consistent with Leland and Fend's (1998) results. They noted that summertime water quality actually improves from upstream to downstream because of dilution of agricultural return flows by high quality water from the tributary rivers. Thus, total dissolved solids concentrations at the most downstream San Joaquin River site most resembled the tributary sites, and the macroinvertebrate community reflected that difference. Examination of the raw data for the 1994 San Joaquin sample revealed low densities of corophiid amphipods and hydropsychid caddisflies, the two dominant taxa in samples in the San Joaquin group, and the presence of taxa more abundant in tributary group samples. The inclusion of the Sacramento River 1996 sample in the San Joaquin group was based on the occurrence of corophiid amphipods at low density.

Corophium spinicornae was absent from the 1997 Sacramento River sample. *C. spinicornae* is most abundant in the Sacramento–San Joaquin Delta (Hazel and Kelley 1966), and the area we sampled may be near its upstream distribution limit. This species shows large fluctuations in abundance in response to environmental conditions even in the Sacramento–San Joaquin Delta, where it is most abundant (Hymanson and others, 1994). It seems likely that the absence (or extreme rarity) of the taxon was indicative of environmental conditions, perhaps related to a large flood in January 1997.

The two drain groups were separated from the other groups primarily on the basis of gradient, mean dominant substrate, and combined agricultural and urban land use. The drain groups were characterized by crangonyctid amphipods, ceratopogonid dipterans, leeches, snails, flatworms, coenagrionid odonates, and elmid coleopterans. These taxa are considered tolerant or moderately tolerant of environmental degradation (Bob Wisseman, Aquatic Biology Associates, written

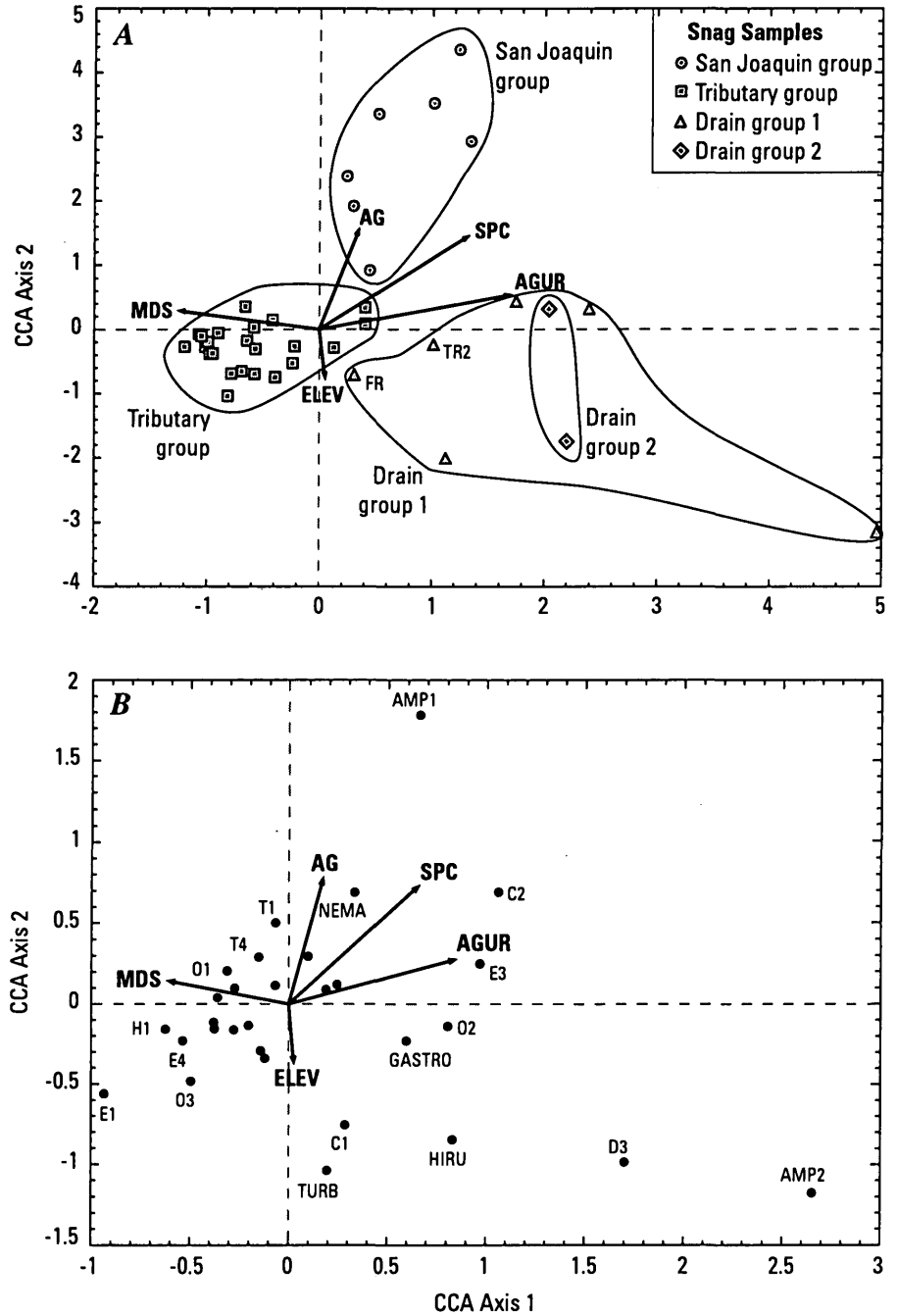

Figure 4. Scores on the first two canonical correspondence analysis axes for snag samples (*A*) and snag taxa scores (*B*). See table 1 for taxa codes. Level-2 TWINSPAN groups are encircled. For both plots, the arrows represent the correlation of physical variables with the axes (AG = agricultural land use, AGUR = agricultural + urban land use, ELEV = elevation, GRAD = gradient, MDS = mean dominant substrate, SPC = specific conductance, and WT = water temperature). Arrows parallel to an axis indicate a high correlation and perpendicular to an axis indicate a low correlation. TWINSPAN, two-way indicator species analysis.

commun., 1996). The two sites in drain group 2 (fig. 4*A*) were separated on the basis of high percentage abundances of gastropods and baetid mayflies compared with the other samples; however, these differences were relatively minor compared to the separation of the drain groups from the San Joaquin and tributary groups. The differences in gradient among groups were caused mainly by Orestimba Creek and Arcade Creek (fig. 2*B*). These creeks are natural streams with relatively high gradients (0.16 and 0.17 percent, respectively) compared with the other snag sites (<0.06 percent), but carry primarily agricultural return flows and urban runoff, respectively. The finer substrate at drain sites is likely due to sedimentation of silt and mud from agricultural and urban erosion. The substrate at San Joaquin and tributary sites was dominated by sand.

In general, the sites in the drain groups are stressful to aquatic organisms in ways not captured by the environmental variables included in the analysis. Discharge in these waterways can be highly variable on even hourly periods, depending on agricultural and urban water sources. In addition, both the larger drains and the smaller creeks can carry high levels of dissolved pesticides, at times (Domagalski, 1996; Panshin and others, 1998) reaching levels toxic to *Ceriodaphnia dubia* in bioassays (Valerie Connor, Central Valley Regional Water Quality Control Board, written commun., 1999).

The two unusual samples in the group are located to the far left of the others in figure 4*A* (points labeled FR and TR2). In 1997, the snags at the Feather River site (FR in fig. 4*A*) were covered with a thick layer of fine sediment during sampling, probably deposited during the January 1997 flood when large quantities of sediment were transported into the stream. Most EPT taxa present in 1996 were absent in 1997. This resulted in a macroinvertebrate assemblage dominated by chironomids and oligochaetes, similar to that found in the drain groups. The Tuolumne River site near Modesto (TR2 in fig. 4*A*) was dominated by talitrid amphipods and oligochaetes in 1994. This assemblage was unusual compared to all the other sites, but most resembled samples in the drain groups.

Annual and Spatial Variability

Similarity among reaches was higher than similarity among years for all comparisons, but the differences were not statistically significant (t-tests, all $p > 0.05$). Jaccard similarities were (mean ± 1 standard deviation) 0.73 ± 0.08 (n = 6) for multiple-reach riffle comparisons, 0.66 ± 0.10 (n = 11) for multiple-year riffle comparisons, 0.65 ± 0.10 (n = 9) for multiple-reach snag comparisons, and 0.57 ± 0.11 (n = 14) for multiple-year snag comparisons. Bray–Curtis similarities were 0.54 ± 0.16 (n = 6) for multiple-reach riffle comparisons, 0.49 ± 0.15 (n = 11) for multiple-year riffle comparisons, 0.55 ± 0.17 (n = 9) for multiple-reach snag comparisons, and 0.47 ± 0.22 (n = 14) for multiple-year snag comparisons. Bray–Curtis similarities always had higher standard deviations compared with Jaccard similarities, indicating greater variability. These results indicate that presence and absence of taxa were more similar and less variable than percentage abundances of taxa.

The variability in reach similarity was not associated with any changes in TWINSPAN sample group membership for any of the three reaches sampled at any of the snag multiple-reach sites. All of the samples from snag multiple-reach sites were in the tributary sample group and included 1995 samples from the most downstream site on the Merced River and the second-most downstream sites on the Tuolumne and Merced rivers. This was not the case for riffle samples. All three reaches sampled in 1996 at the second-most downstream site on Deer Creek were in the transition group, but reaches sampled at the McCloud River in 1996 were split between the mountain (2 reaches) and foothill (1 reach) sample groups.

The multiple-reach samples suggest that our results are robust with regard to reach-scale variability at a site. The multiple-reach snag sample results are consistent with results from artificial substrate samples from the lower San Joaquin river system. Based on results from replicate substrates, within-reach variability was low (Leland and Fend, 1998). Leland and Fend (1998) found annual variability to be greater than within-reach variability, but our results showed no statistical difference between annual and reach variability. This difference between studies is likely due to differences in sampling. Leland and Fend (1998) sampled all of their sites in 2 consecutive years (1985 and 1986), one much wetter than the other, resulting in large annual differences. Our comparisons included a mixture of comparisons from similar and different water years, resulting in a lower mean annual variability.

IMPLICATIONS FOR BIOASSESSMENTS

Our results have several implications for development of regional bioassessments in the combined Sacramento–San Joaquin river drainage. The concepts of ecoregions and watersheds are complementary, and both levels of organization must be considered when designing and interpreting bioassessments (Omernik and Bailey, 1997). Clearly, the sites in the Central Valley ecoregion are different from the foothills and mountains, although the differences between the latter two ecoregions remain unclear. As suggested earlier, differences between these ecoregions may become clearer at lower levels of taxonomic resolution. If so, these ecoregions probably should be subdivided to account for zonation by elevation or other factors. From a bioassessment perspective, the ecoregion must be suitably homogenous so that the response of the macroinvertebrate assemblage to human activities can be distinguished from the response to natural variation. This appears to be the case for Central Valley snag samples, but not for foothill and mountain riffle samples. As our understanding of the California macroinvertebrate fauna improves, it seems likely that the concept of watershed may be needed to account for patterns of endemism and differences in seasonal development of macroinvertebrate assemblages in response to differing temperature regimes associated with canyon morphologies or other factors. The concept of watershed is obviously critical in understanding the effects of human and natural processes on the biota of any particular stream.

There has also been recent discussion of the degree of taxonomic resolution necessary to assess variation in benthic macroinvertebrate assemblage structure. Bowman and Bailey (1997) reviewed eight data sets from the literature and concluded that results at the genus level of identification remained consistent when aggregated to higher levels (up to and including Class). One caveat was that there was a significant negative correlation between the level of consistency and the diversity of the community, as defined by the lowest level of taxonomy used. Similarly, Bournad and others (1996) concluded that the family level was sufficient to detect environmental disturbances in the Rhone River, France, but indicated that the species level of identification would be necessary to elucidate finer scale processes associated with the effects of tributary streams. Our data suggest that, for Central Valley snag samples, the family level is sufficient for evaluating the effects of the environment on macroinvertebrate assemblages, but for the Sierra Nevada and foothill riffle samples, genus or species level data may be needed.

SUMMARY

Except for foothill and mountain riffle samples, the macroinvertebrate assemblages of the combined Sacramento–San Joaquin River drainage could be grouped using multivariate statistical techniques (figs. 2, 3*A*, 4*A*). There were differences in biological (table 3) and environmental (table 4) characteristics of the sample groups suggesting that the differences in benthic macroinvertebrate assemblages were related to environmental conditions. The CCA analyses emphasized these differences and highlighted the correlation of benthic macroinvertebrate assemblages with environmental gradients (table 5, figs. 3 and 4). For the riffle samples, elevation was the most important factor (table 5). For the snag samples, land use, specific conductance, and mean dominant substrate were important (table 5). Results from the riffle samples indicate that stream regulation may be associated with declines in the number of taxa and density of macroinvertebrates in the transition area between the valley floor and Sierra Nevada foothills. Our results suggest that natural environmental conditions in the Central Valley ecoregion are sufficiently homogenous for detection of the effects of human land use on macroinvertebrate assemblages. Additional work, probably at lower levels of taxonomy, is needed in the foothill and Sierra Nevada ecoregions.

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