TRICHOPTERA AND OTHER MACROINVERTEBRATES IN SPRINGS OF THE GREAT BASIN: SPECIES COMPOSITION, RICHNESS, AND DISTRIBUTION

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ABSTRACT.—Detailed surveys of aquatic invertebrates in 28 springs along the western border of the Great Basin were made using pan traps, emergence traps, black lights, and benthic sampling devices from 1994 to 1998. Although all macroinvertebrate groups were collected, caddisflies (Insecta: Trichoptera) were sampled most intensively. Fifty-eight species of caddisflies were collected from the 28 springs, with up to 18 species from a single spring. Although several springs had very similar physicochemical characteristics, none had identical trichopteran species composition. Using Ward's minimum variance clustering technique, and with all macroinvertebrates identified to the lowest possible level, we found 3 taxa assemblages. These assemblages occurred in springs with the following physical conditions: (1) warm water (15.9°C), low elevation (1794 m); (2) cold water (8.5°C), mid-elevation (2334 m); and (3) cold water (6.6°C), high elevation (1794 m). Although the warm water group had a distinct assemblage of invertebrates (amphipods, gastropods, Trichoptera), distinct assemblages did not separate the 2 cold water groups. Discriminant analysis indicated that temperature, conductivity, alkalinity, and elevation were most responsible for discriminating group 1 from groups 2 and 3; temperature and elevation distinguished the latter 2 groups. Spring permanence, lack of disturbance, and cold water temperatures were the factors most responsible for explaining higher species richness of Trichoptera.

Key words: desert springs, endemic species, caddisflies, amphipods, Plecoptera.

From both evolutionary and ecological perspectives, springs are noteworthy habitats for study (Hynes 1970, Odum 1971, Glazier 1998, Williams and Williams 1998). Desert springs in particular are especially important scientifically because they form a specialized subset of springs characterized by the following properties: (1) they are often the only source of water available, which makes them critical habitat not only for aquatic fauna but also for amphibians, birds, and mammals; (2) the aquatic habitat is an isolated patch and is not interconnected in a network to downstream aquatic habitats as are most temperate headwater streams; and (3) many springs and spring streams were connected during the Pleistocene so that the effect of natural habitat fragmentation on population distributions, population genetics, and speciation that occurred over time can be observed.

Studies on desert springs in North America began with the research of Brues (1928, 1932) on invertebrates of hot springs, La Rivers (1948, 1950, 1953) on Hemiptera of the Great Basin, and Noel (1954) on the ecology of a New Mexico spring brook. For the next 4 decades, few articles on aquatic invertebrates in desert springs

were published (e.g., Bruns and Minckley 1980, Meffe and Marsh 1983). Not until the last decade has research interest on desert springs been renewed (e.g., Cushing and Gaines 1989, Gaines et al. 1989, Shepard 1992, Hovingh 1993, Cushing 1996, Larsen and Olson 1997, Shepard and Threloff 1997, Thomas et al. 1997).

Little research has been directed specifically at Trichoptera in desert springs with the exception of the work by Colburn (1984), who examined the life history of *Limnephilus assimilis* in Death Valley. Erman and Erman (1990) did extensive work on Trichoptera in springs of the Sierra Nevada, many of which are located on the east side of the range and are on the western border of the Great Basin. Faunal surveys of springs in the Great Basin conducted for land management agencies (Herbst 1992, 1996, Sada and Nachlinger 1996, 1998) have included Trichoptera in their collections. However, these surveys usually consisted of one visit to a site and were limited to benthic collections. So, while useful, they usually provide only generic level identifications and are incomplete inventories of the caddisflies. Trichoptera also were collected in

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the work of Gaines et al. (1989) and Anderson and Anderson (1995) in desert springs of Washington and Oregon, respectively, but these studies also relied on benthic collections.

This research examined the aquatic invertebrate communities of desert springs on the western border of the Great Basin. The objectives were (1) to document the trichopteran species composition of the springs in this area; (2) to determine if distinct Trichoptera assemblages were present in relation to physical habitat conditions; (3) to determine if other selected invertebrates showed the same pattern as Trichoptera; and (4) to determine what physical factors are important in determining species richness at a site.

METHODS

Study Area

Located in the rain shadow of the Sierra Nevada range, the Great Basin receives limited precipitation and is the largest desert region in the United States (Rumney 1987). Estimated annual precipitation over the entire region averages about 27.9 cm (Eakin et al. 1976), with about 10–15 cm of rain occurring in the basins and 40–150 cm of snow in the mountain ranges. Most precipitation falls from November through March and is associated with cyclonic fronts. However, thunderstorms in the summer can produce intense downpours in localized areas. Evaporation greatly exceeds precipitation in the Great Basin. For example, in Reno, Nevada, annual precipitation averages 17.8 cm, but the evaporation rate equals 61 cm, creating a 44-cm deficit (Planert and Williams 1995). Streams within the Great Basin are endorheic; i.e., they terminate by infiltrating back into the groundwater through evaporation or by flowing into an inland (often saline) lake.

We visited and sampled 170 springs over a 5-year period. Of these, we used the results from 28 (Table 1) in the analysis of spring assemblages and Trichoptera species richness. These 28 springs were visited repeatedly, and multiple collection techniques were used to assure as complete a sampling effort as possible. These springs were selected because they were reasonably accessible, equipment could be left at the site, and the habitat appeared to be undisturbed. Springs that were not used were too inaccessible to sample regularly, were

dry or clearly temporary, were so disturbed from grazing activities that few invertebrates remained, had been impacted severely by water diversion or recreational activities, or were hot springs (temperatures >40°C).

Physical-Chemical Measurements

All physical and chemical measurements were taken at the spring source unless the riparian vegetation was so impenetrable that access to the source was impossible. This situation occurred at 3 springs (Marble Canyon hillside, Graham Ranch, Barrel), and measurements for these springs were made at access points some distance (50–200 m) below the source. Water temperature and conductivity were measured using a Hach portable meter (model 44600), pH with an Oakton pHTestr2, dissolved oxygen using a YSI portable meter (model 55), and alkalinity and hardness with digital titration using a Hach DREL/2000 portable laboratory. Water temperature, conductivity, and dissolved oxygen were measured each time we visited the spring. Alkalinity and hardness, which are highly correlated with conductivity, were measured less frequently.

Using a tape measure, we measured width (±5 cm) approximately every 10 m from the source downstream 50–200 m. At the location of the width measurement, depth was measured to the nearest cm either 3 or 4 times at equidistant points across the stream using a metal meter stick. Length of the spring was measured directly with a hip chain. Discharge was measured using one of several methods: direct capture of flow into a container of known volume (for springs that exited from a pipe source); capture of the flow into a large, heavy-duty plastic bag that was then emptied into a calibrated bucket (for flows between 0.5 and 7 L · s^{-1}); a portable flume (useful when substrate was soft and channel was not filled with riparian vegetation); or a pygmy flow meter and the velocity-area method for the largest springs. Discharge was measured several times at each spring.

Biological Sampling

Benthic sampling was accomplished through a variety of methods, depending on the site and conditions. A primary consideration was to minimize disturbance to the habitat, especially in the case of small springs. Samplers

TABLE 1. Physical-chemical characteristics of 28 springs from eastern Inyo and Mono counties, California.

Spring code	Spring full name	#[a]	Conductivity (µS · cm⁻¹)	Temp (C)	Dissolved oxygen (mg · L⁻¹)	pH	Alkalinity (mg · L⁻¹)	Hardness (mg · L⁻¹)	Q (L · s⁻¹)	Elev (m)	Mean width (cm)	Mean depth (cm)	Max depth (cm)	Length (m)	Veg[b]	Con[c]	Latitude
AlC	Alpers Canyon	13	103	8.7	4.8	7.1	46	45	2.5	2226	82	6.8	11	1600	3	2	37°46′ 17″
AnS4	Antelope Spring (DS)	6	490	16.5	4.4	7.8	140	238	2.3	1707	108	2.4	7	765	3	2	37°20′ 05″
BaC1	Baxter Canyon	10	129	11.5	2.1	8.5	38	38	6	2341	92	4.3	10	40	2	1	37°52′ 56″
BaS1	Barrel Spring	10	401	14.2	6.8	8.4	156	198	6.9	1402	61	1.9	4	800	3	2	36°53′ 20″
BlC1	Black Canyon	6	284	10.1	5.7	7.8	102	135	6.1	2561	125	3.4	7	2200	2	2	37°21′ 50″
BoS1	Boulder Spring	5	96	6.3	3.3	7	32	33	0.3	3049	32	2.2	9	180	1	1	37°29′ 08″
CaF	Cave Fork	5	128	6.3	3.2	8	38	43	4.7	3049	48	6.0	16	105	1	1	37°30′ 06″
Cor	Corral	9	384	18.2	2	8.4	124	82	5.2	1512	391	3.4	9	800	1	2	37°16′ 30″
DCE	Dry Creek (east source)	17	57	6	7.4	7	19	7	1.5	2366	97	6.7	11	85	3	1	37°50′ 37″
EaF	East Fork (west source)	14	103	9.3	4.1	7.6	29	30	3.5	2439	136	3.9	8	185	3	1	37°51′ 06″
GM1	Glass Mountain 1	14	67	5.1	7.5	7.7	26	15	12	2732	52	7.9	15	300	1	1	37°46′ 17″
GM2	Glass Mountain 2	14	83	5	7.5	7.4	31	25	1.5	2732	58	3.8	7	165	1	1	37°46′ 17″
Gra	Graham Ranch	10	547	17	7.5	8.6	125	211	6	1402	117	3.9	11	2500	3	2	37°11′ 25″
GrM1	Green Monster (1)	19	207	5.8	6.4	7.5	44	79	12	2439	103	5.3	10	150	3	2	37°44′ 54″
JoS	Joe's Spring	6	470	15.3	3.4	7.7	134	216	7	1830	62	4.5	11	260	3	2	37°21′ 24″
LS1	Layton Spring	9	311	21.3	2.5	8.4	95	39	80	2073	123	16.9	28	500	1	1	37°38′ 08″
MaC	Marble Canyon 1	7	570	12	4.8	7.6	162	253	0.7	2050	29	1.7	6	50	1	2	37°17′ 40″
MaChil	Marble Canyon hillside	6	526	12.8	6.4	7.5	165	221	2	2040	300	5.5	10	250	2	2	37°17′ 40″
Mon1	Montenegro	6	385	12.8	5.8	7.7	124	187	1.2	2165	220	4.4	17	140	2	2	37°17′ 40″
MTN1	Middle Trib to North Cyn	10	104	9.3	3.5	7.6	30	32	2	2439	107	2.5	7	75	3	1	37°51′ 38″
NFC3	N Fork Crooked Cr 3	5	217	5.8	4.3	7.7	70	90	5	3018	50	17.0	25	135	1	1	37°30′ 00″
OwG1	Owen's Gorge	6	275	15	4.6	7.5	74	76	30	1829	228	10.8	19	170	2	1	37°33′ 06″
RivS	River Springs	4	171	16.2	2.8	8.4	60	29	4	1976	100	12.0	17	1500	3	2	37°56′ 21″
SaM	Sawmill Meadow	6	51	5	4.6	6.7	16	5	0.1	2805	31	1.4	2.5	40	3	2	37°46′ 36″
SoF	South Fork Cottonwood	9	315	9.5	5.7	7.1	103	145	60	2878	142	19.3	30	325	1	1	37°31′ 56″
TaC1	Taylor Canyon 1st source	15	71	7.6	7.2	8.2	26	15	11	2268	82	8.8	20	300	3	1	37°49′ 55″
TaC2	Taylor Canyon 2nd source	11	71	7.6	7.2	7.9	27	16	9	2268	183	4.6	10	130	3	1	37°49′ 55″
TaC4	Taylor Canyon 4th source	10	72	7.9	7.2	8.1	26	16	5	2256	99	3.5	8	10	3	1	37°50′ 00″

[a]# = species richness of Trichoptera.
[b]1 = open meadow, 2 = mid-story present, 3 = mid- and overstory riparian vegetation present.
[c]1 = spring flows into another stream, 2 = spring flows into ground.

typically used to collect aquatic invertebrates (Surber sampler, Hess sampler, D-frame net) were used infrequently and only in the largest of the spring systems. The overall small size of the springs, insufficient flow over the lip of the sampling device to carry the invertebrates into the collecting bag, or a thick growth of macrophytes (*Nasturtium* or *Mimulus*) all limited the use of conventional sampling devices.

Because no single quantitative benthic sampling technique could be applied evenly across all spring types, we used a combination of techniques to document the benthic invertebrates: (1) hand-picking invertebrates from leaf packs, off rocks, or from aquatic vegetation; (2) inserting a 4-inch- (10.2-cm-) diameter PVC pipe into the substrate to a depth of 3–5 cm, from which we scooped out the substrate into a D-frame net; (3) using an aquarium net (25 × 18-cm frame) to take a miniature kick sample; and (4) scooping substrate directly into a D-frame net, rinsing it, and bagging it. Samples were usually taken within 20 m of the source except where the source was inaccessible (as noted above), when the total length of the spring was <200 m, or when the flow was so great (i.e., Layton Spring, South Fork Cottonwood) that the temperature was constant for a greater distance downstream. All samples were preserved in 70% ethanol. Invertebrates were picked from the substrate in the laboratory using a dissecting microscope.

To catch adult insects, we used black lights, pan traps, and emergence traps (Myers and Resh 1999). In addition, we used a D-frame net to capture adult insects from beneath undercut banks (Myers and Resh 2000), used a sweep net, and caught them by hand. Larvae and pupae of caddisflies were brought back to the lab alive, to rear out adults when needed for species-level identification.

All invertebrates were identified to the lowest taxonomic level possible. Most specimens are deposited in the Essig Museum of Entomology, UC Berkeley, but specimens of some Plecoptera are at the Monte L. Bean Museum at Provo, Utah.

Data Analysis

Physical characteristics of the springs were summarized and the correlation among the variables was calculated. Presence/absence of 141 taxa at 28 sites was used in a Ward's minimum variance clustering technique (Euclidian distance) to determine if there were distinct assemblages of invertebrates. The same technique was applied to caddisflies alone to determine if the same assemblage patterns were present in this group. To determine which physical factors were important in distinguishing among the groups, discriminant analysis was used. Multiple regression was used to determine which physical factors were most responsible for caddisfly species richness at the springs. When multiple spring sources joined downstream (i.e., Taylor Canyon), data from only one source were used in the regression analysis. For the discriminant analysis and multiple regression, physical factors were transformed (log10) to normalize the variables.

RESULTS

Physical-Chemical Characteristics

Among the physical and chemical characteristics of the springs (Table 1), conductivity, alkalinity, and hardness were highly, positively

TABLE 2. Correlation of physical and chemical characteristics at 28 springs. Q = discharge, DO = dissolved oxygen.

	Cond	Temp	DO	pH	Alkalinity	Hard	Q	Elev	Width	Depth	Max	Length
Conductivity	—											
Water temp	0.74	—										
DO	–0.10	–0.42	—									
pH	0.29	0.56	–0.12	—								
Alkalinity	0.96	0.72	–0.10	0.28	—							
Hardness	0.93	0.53	0.04	0.14	0.92	—						
Discharge	0.15	0.37	–0.14	0.10	0.15	–0.01	—					
Elevation	–0.64	–0.79	–0.01	–0.55	–0.62	–0.51	0.00	—				
Mean width	0.44	0.48	–0.10	0.19	0.45	0.27	0.09	–0.47	—			
Mean depth	0.02	0.13	–0.12	0.02	0.03	–0.08	0.73	0.21	0.00	—		
Max depth	0.04	0.14	–0.08	0.13	0.03	–0.06	0.71	0.19	0.05	0.91	—	
Length	0.39	0.42	0.04	0.33	0.38	0.35	–0.05	–0.42	0.05	–0.04	–0.10	—

correlated (Table 2), and temperature and elevation were inversely correlated. Springs at lower elevations had higher temperatures and higher conductivities. The pH was circumneutral and varied within a relatively narrow range (6.7–8.6). Discharge was highly variable among springs and ranged from <1 L $\cdot$ s^{-1} to about 80 L $\cdot$ s^{-1}. Alkalinity at a site varied more than hardness, but this was probably more a reflection of the test (i.e, judging a tritation endpoint) than true variability. A comparison of alkalinity and conductivity between the springs of this study and those of Erman and Erman (1990) and Glazier and Gooch (1987) indicates 3 distinct regression lines (Fig. 1).

Biological Characteristics

INVERTEBRATE ASSEMBLAGES AND DISTRIBUTIONS.—We collected, counted, and identified 76,683 invertebrates. Of these, 29,019 (38%) were caddisflies. Approximately 90 taxa (excluding Trichoptera) were identified from the springs (Table 3). Because only Plecoptera and elmid beetles were identified to species level, the actual number of species present in the springs is much higher. In addition, because we focused our collection efforts on Trichoptera, no other groups were collected as intensively, and therefore collections for taxa other than Trichoptera are most certainly incomplete.

Using Ward's minimum variance clustering technique and identifying all macroinvertebrates to the lowest possible level, we found 3 taxa assemblages. These can be distinguished as warm, low elevation (group 1); cold, mid-elevation (group 2); and cold, high elevation (group 3; Fig. 2). Discriminant analysis indicated that water temperature, conductivity, alkalinity, and elevation were the physical factors most responsible for group discrimination. All 4 factors were significantly different between group 1 and groups 2 and 3 (Table 4). Groups 2 and 3 were significantly different from each other only in water temperature and elevation (Table 4).

Group 1 (warm, low elevation) springs were distinguished from the cold springs (groups 2 and 3) by several invertebrate groups. Amphipods (*Gammarus* or *Hyallela)* and gastropods (hydrobiid and physid snails) were 2 of the most dominant groups in warm springs but were usually absent from cold springs. Warm
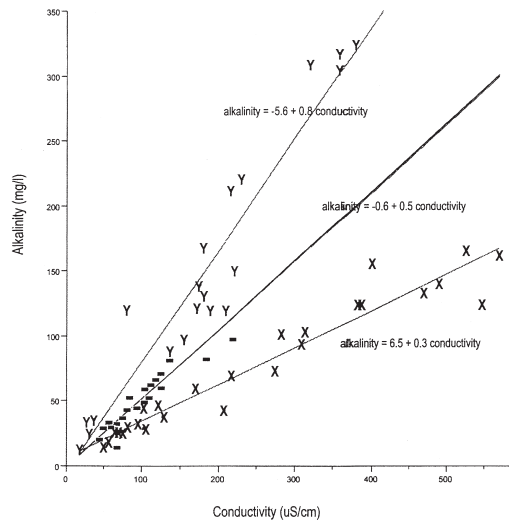

Fig. 1. Comparison of alkalinity and conductivity measurements for springs from 3 locations: X = eastern Inyo and Mono counties, California (this study); ■ = eastern Sierra (Erman and Erman 1990); **Y =** Pennsylvania (Glazier and Gooch 1987).

springs were also characterized by several commonly occurring caddisflies (next section), while *Rhyacophila* occurred only in cold springs. Other groups of insects that had representatives in either group 1 or groups 2 and 3 were Coleoptera and Plecoptera. The elmid *Heterlimnius* occurred in cold springs, whereas *Optioservus divergens* was found in several warm springs. *Microcylloepus* was only in the warmest spring surveyed, Layton Spring (21°C). While the majority of Plecoptera were found in springs of groups 2 and 3, two species, *Isoperla mormona* and *Malenka biloba,* were found in group 1 springs.

No distinct faunal assemblage distinguished the various groups of the cold springs. Neighboring springs (that had a fluvial connection) were more closely related to each other than to other springs (i.e., the 3 sources in Taylor Canyon; Fig. 2). Physical characteristics between the groups of cold springs were also very similar. While warm springs were significantly different from cold springs for several characteristics (Table 4), the 2 groups of cold springs were significantly different from each other in only 2 categories, elevation (2800 m vs. 2335 m) and temperature (6.6°C vs. 8.5°C). Because of the lack of faunal distinction, it appears that these physical differences between

TABLE 3. Invertebrates collected from springs in the western Great Basin, excluding Trichoptera.

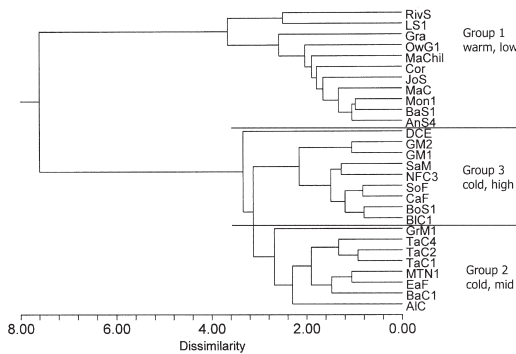| **Amphipoda**	**Hemiptera**	**Coleoptera**	**Diptera**
Hyalella sp.	Gerridae	*Agabetes* sp.	*Antocha* sp.
Stygobromus n. sp.	Saldidae	*Agabinus* sp.	*Atrichopogon* sp.
Gammarus sp.	**Lepidoptera**	*Agabus* sp.	Ceratopogonidae
Gastropoda	*Petrophila* sp.	*Ametor* sp.	*Chelifera* sp.
Helisoma sp.	**Odonata**	*Crenitis* sp.	Chironomidae
Hydrobiidae	*Cordulegaster* sp.	Dytiscidae	Culicidae
Lymnaeidae	*Aeshna* sp.	*Helophorus* sp.	*Dicranota* sp.
Physella sp.	*Anax* sp.	*Heterlimnius corpulentus*	Dixidae
Valvata sp.	*Argia* sp.	*Hydrophilus* sp.	Empididae
Hirudinea	Libellulidae	*Lara* sp.	Ephydridae
Hydracarina	*Libellula* sp.	*Microcylloepus similis*	*Forcipomyia* sp.
Nematoda	**Plecoptera**	*Narpus concolor*	*Hexatoma* sp.
Nematomorph	*Capnia mono*	*Narpus* sp.	*Holorusia* sp.
Oligochaeta	*Doroneuria baumanni*	*Optioservus divergens*	*Limnophora* sp.
Pelecypoda	*Haploperla chilnualna*	*Peltodytes* sp.	*Meringodixa* sp.
Turbellaria	*Hesperoperla pacifica*	Scirtidae	Muscidae
	Isoperla sp.	*Tropisternus* sp.	*Odontomyia* sp.
Insecta	*Isoperla mormona*		*Oreogeton* sp.
Ephemeroptera	*Isoperla sordida*		Pelecorhynchidae
Ameletus sp.	*Kogotus nonus*		*Pericoma* sp.
Baetis sp.	*Malenka biloba*		*Prinocera* sp.
Baetidae	*Malenka californica*		Psychodidae
Caudatella sp.	*Moselia infuscata*		Ptycopteridae
Cinygma sp.	*Paraleuctra vershina*		Simuliidae
Cinygmula sp.	*Suwallia* sp.		Stratiomyidae
Drunella sp.	*Sweltsa resima*		Tabanidae
Ephemerellidae	*Yoraperla brevis*		Thaumaleidae
Heptageniidae	*Zapada cinctipes*		Tipulidae
Ironodes sp.	*Zapada oregonensis*		*Tipula* sp.
Paraleptophlebia			
Rhithrogena sp.			
Serratella sp.			
Tricorythodes sp.			

Fig. 2. Cluster analysis of springs based on presence/absence data for 141 taxa of benthic macroinvertebrates using Ward's minimum variance. Group 1: water temperature = 15.9°C, elevation = 1794 m; group 2: water temperature = 8.5°C, elevation = 2334 m; group 3: water temperature = 6.6°C, elevation = 2799 m. Spring codes given in Table 1.

group 2 and group 3 springs do not translate into meaningful biological differences.

Trichoptera

We collected a total of 58 different species in 14 different families of caddisflies (Table 5). Four to 18 species were found in a spring. Several springs had very similar physicochemical characteristics; however, none had identical trichopteran composition. Although *Lepidostoma cascadense* and *Rhyacophila brunnea* were restricted to cold springs, they were collected from the most springs (12 each). *Lepidostoma rayneri, L. roafi,* and *L. unicolor* were also frequently collected (10, 8, and 7 springs, respectively). Across the region (including all 170 springs surveyed), *Hesperophylax designatus* was the most commonly encountered caddisfly. It was found in temporary springs, springs impacted by grazing, very cold springs at high elevations, and a few of the warmer (14°C), low-elevation springs. Of the 28 springs intensively studied, it was present in 11.

TABLE 4. Mean and (standard deviation) of physical factors most responsible for distinguishing among the 3 invertebrate assemblages, based on discriminant analysis. Asterisk (*) shows that there were significant differences ($P < 0.001$) between the group marked and the other groups.

	Group 1	Group 2	Group 3
Conductivity ($\mu S \cdot cm^{-1}$)	396* (118)	107 (45)	144 (101)
Temperature (°C)	15.9* (2.5)	8.5* (1.7)	6.6* (1.9)
Alkalinity ($mg \cdot L^{-1}$)	119.7* (33.8)	33 (8.2)	48 (34)
Elevation (m)	1793.6* (280)	2334.5* (92)	2798.9* (232)

TABLE 5. Trichoptera collected from springs in the western portion of the Great Basin.

TRICHOPTERA

Glossosomatidae
  Anagapetus chandleri Ross
  Glossosma califica Denning
Rhyacophilidae
  Rhyacophila brunnea Banks
  R. harmstoni Ross
  R. oreta Ross
  R. pellisa Ross
  R. tucula Ross
  R. vaccua Milne
  R. vao Milne
  R. verrula Milne
Hydroptilidae
  Hydroptila arctia Ross
  H. rono Ross
  H. xera Ross
  Hydroptila sp.
  Ochrotrichia argentea Flint & Blickle
  O. arizonica Denning & Blickle
  O. lometa (Ross)
  Ochrotrichia new species
  Oxyethira dualis Morton
  Neotrichia okapa Ross
Hydropsychidae
  Hydropsyche californica Banks
  H. cockerelli Banks
  H. occidentalis Banks
  H. oslari Banks
  Parapsyche almota Ross
  P. elsis Milne
Philopotamidae
  Wormaldia gabriella (Banks)
  Dolophilodes novusamericanus (Ling)
Psychomyiidae
  Tinodes provo Ross and Merkley
Apataniidae
  Aptania sorex (Ross)
  Pedomoecus sierra Ross

Brachycentridae
  Micrasema bactro Ross
Helicopsychidae
  Helicopsyche borealis (Hagen)
Lepidostomatidae
  Lepidostoma cascadense (Milne)
  L. castalianum Weaver and Myers
  L. cinereum (Banks)
  L. ojanum Weaver and Myers
  L. rayneri Ross
  L. roafi (Milne)
  L. unicolor (Banks)
Leptoceridae
  Ylodes frontalis (Banks)
Limnephilidae
  Chyranda centralis (Banks)
  Dicosmoecus pallicornis Banks
  Desmona bethula Denning
  Ecclisomyia sp.
  Ecclisomyia maculosa Banks
  Hesperophylax designatus (Walker)
  Homophylax adriana Denning
  H. nevadensis Banks
  Limnephilus acula Ross & Merkley
  L. bucketti Denning
  L. morrisoni Banks
  L. peltus Denning
  L. spinatus Banks
  Onocosmoecus unicolor Banks
  Psychoglypha sp.
Sericostomatidae
  Gumaga griseola (McLachlan)
Uenoidae
  Neophylax splendens Denning
  Oligophlebodes sierra Ross

Using Ward's minimum variance clustering technique and only Trichoptera individuals, we found the springs of one assemblage (group 1, warm springs) were identical to the warm springs group that was formed when all invertebrates were used (Fig. 3). However, the cold springs did not clearly break into 2 groups for the Trichoptera as they did for all invertebrates; and the groups that formed appeared to be more closely associated with geographic location (Fig. 3). One consistent characteristic was that *Lepidostoma castalianum* was found only in the mid-elevation cold springs and not in the higher, colder springs. *Gumaga griseola, Helicopsyche borealis, Tinodes provo, Lepidostoma ojanum,*
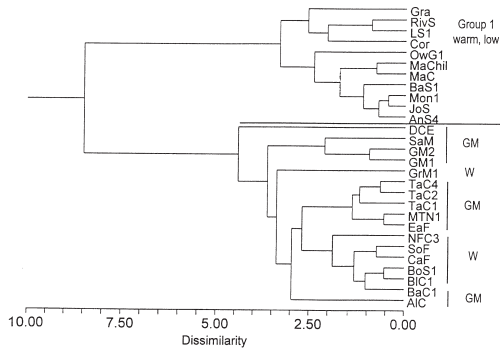
Fig. 3. Cluster analysis of springs based on Trichoptera alone. Geographic associations among the cold springs are shown. GM = Glass Mountains, W = White Mountains. Spring codes given in Table 1.

TABLE 6. Results of the multiple regression model that best explained species richness of Trichoptera at 24 springs. $R^2 = 0.62$, R^2 adjusted = 0.54.

	F ratio	Prob > F	Relationship
Log alkalinity	18.4	0.0004	negative
Log discharge	8.0	0.011	positive
Log dissolved O_2	8.1	0.010	positive
Elevation	6.2	0.022	negative

Ochrotrichia arizonica, and *Wormaldia gabriella* formed a core group that commonly occurred in the warm springs. Within the family Hydropsychidae, 1 or more of 4 species of *Hydropsyche* occurred in the warm springs while 1 of 2 species of *Parapsyche* occurred in the cold springs.

In the 28 springs examined in this study, multiple regression showed that species richness of Trichoptera was inversely related to alkalinity and elevation and positively related to discharge and dissolved oxygen ($R^2 = 0.62$; Table 6). However, when discharge and species richness alone were used in the regression, there was not a significant relationship between them (F ratio = 1.6, P = 0.21).

DISCUSSION

Physical-Chemical

Results of the physical-chemical analysis of the Great Basin springs can be compared with 2 other regional studies of springs: Erman and Erman (1990) in the Sierra Nevada of California and Glazier and Gooch (1987) in Pennsylvania. Unlike the results of Erman and Erman (1990), who found spring source water to be fully saturated, dissolved oxygen in the springs studied in this research varied from as low as 2.0 mg · L^{-1} to fully saturated. The dissolved oxygen in the 20 springs that Glazier and Gooch studied ranged from a low of 5.3 mg · L^{-1} to fully saturated. The 3 studies produced 3 distinct regression lines for the relationship between alkalinity and conductivity (Fig. 1). The Sierra Nevada, which is dominated by

granitic rocks, has springs and streams that typically have low dissolved solids, which is reflected in the conductivities (all <185 µS · cm^{-1}) found by Erman and Erman (1990). In contrast, the springs Glazier and Gooch (1987) studied were primarily limestone in origin, and the conductivities of their springs ranged much higher (18–380 µS · cm^{-1}). Springs in this research had their origins in a variety of parent materials including granite (Glass Mountains), metamorphics (Black Canyon, White Mountains), and limestone (Marble Canyon, White Mountains). The variability in parent material is reflected in the range of conductivities (51–570 µS · cm^{-1}) and alkalinities (16–165 mg · L^{-1}) recorded.

The pH of the 3 groups of springs also showed distinct differences; those in Pennsylvania had the lowest mean pH (6.8) and included individual springs with relatively low pH values (5.2–5.5). The average pH in the Sierra Nevada study was 6.9, but no springs had a pH of less than 6.1. In this research the average pH of the springs was 7.8, and only one spring had a pH of less than 7.0. Also the water temperature of the Sierra Nevada springs was very cold (mean = 6.3°C; Erman and Erman 1990), whereas that in Pennsylvania was several degrees warmer (mean = 10.8°C; Glazier and Gooch 1987). In this research the mean temperature of all springs was 10.5°C, but mean water temperatures for the 3 assemblage groups (based on all invertebrates) were 6.6°, 8.5°, and 15.9°C.

Biological Characteristics

INVERTEBRATE ASSEMBLAGES AND DISTRIBUTIONS.—This research focused on caddisflies; if an equal effort had been made for any other group, species richness likely would have been much higher. For example, in a study of 7 springs in Illinois, oligochaetes were found to be the most diverse taxon (24 species; Webb et al. 1995). In a recent study at Montezuma

Well, Arizona, 10 species of oligochaetes were found (Wetzel et al. 1999). Diptera were found to be the most diverse group collected from springs in semiarid rangeland in Oregon (Anderson and Anderson 1995), and chironomids are often particularly diverse in springs (Blackwood et al. 1995, Lindegaard 1995).

As has been observed elsewhere (Hynes 1976), many Plecoptera collected from spring sources were brachypterous. This was true for *Sweltsa resima* (South Fork Cottonwood) and for *Hesperoperla pacifica* (Black Canyon). As reduction in dispersal ability has been related to permanence of habitats (Hynes 1970, Travis and Dytham 1999), presence of brachypterous forms may be an indication that these springs have been present for a long period of time. Although some Plecoptera were widespread and commonly encountered (e.g., *Malenka* sp., *S. resima, Yoraperla brevis, Hesperoperla pacifica*), many occurred only at one spring and often only one or a few individuals were collected (e.g., *Suwallia* sp., *Doroneuria baumanni, Moselia infuscata, Paraleuctra vershina, Isoperla sordida, I. mormona*). Plecoptera were found primarily in the cold springs (groups 2 and 3), but 2 species, *Isoperla mormona* and *Malenka biloba,* were found in the warmer springs (group 1).

Three different genera of amphipods were found in the 28 springs: *Hyallela, Gammarus,* and *Stygobromus.* Of the 3 genera, *Hyallela* occurred in the most springs and was the only amphipod found in the Glass Mountains (3 springs). *Gammarus* was found only in Owens Valley Gorge spring. It is unknown what factors determine whether *Gammarus* or *Hyallela* will occupy a spring. An undescribed species of *Stygobromus* was discovered at 3 sites: Marble Canyon hillside spring, Black Canyon, and Log Spring in the Sylvania Mountains, Nevada. At Marble Canyon and Black Canyon, *Stygobromus* was found in samples taken at or near the source. At Log Spring they were found in a patch of watercress directly below a pipe that was tapping the groundwater. While Marble Canyon and Black Canyon are in reasonably close proximity, and both are on the western slope of the White Mountains, Log Spring is 45 km to the east. The wide separation between populations indicates either that there is a viable underground connection between the populations (e.g., via groundwater) or that perhaps the species was once more widespread

and has become isolated as aquatic habitats have become fragmented. Genetic analysis could determine the degree of isolation between these populations.

Glazier (1991) argued that peracardians (amphipods and asselids), molluscs, and triclads dominate in hardwater limestone springs whereas insects dominate in acidic softwater springs. If 25 mg · L^{-1} CaCO$_3$ is used to represent hardwater (Glazier did not specify a cutoff point), 27 of 28 springs in the present survey would be considered hardwater. Twenty-seven springs also had a pH of 7.0 or higher, and so they would not be considered "acidic." According to Glazier's hypothesis, all of these springs should be dominated by non-insects. However, only 10 of the springs had amphipods, only 9 had gastropods, asselids were not found at any of the 28 springs examined, and turbellarians were ubiquitous. The latter group is not a good assemblage indicator because of its widespread distribution. Of the 16 springs that did not have either amphipods or gastropods, their absence in at least 2 springs can be explained by disturbance (Joe's Spring, Marble Canyon 1). However, in the remaining springs there is no obvious explanation for their absence. It may be that prior disturbance eliminated populations; however, the presence of turbellarians, nematodes, and other poorly dispersing invertebrates in these springs suggests these springs have been permanent and undisturbed for reasonably long periods of time. A 2nd explanation is that perhaps the springs were never colonized by these invertebrates. At any rate, it appears that a generalization about the dominance of non-insects in hardwater springs is not appropriate for Great Basin springs, nor was it for those surveyed by Erman (1998) in the Sierra Nevada or Williams and Williams (1998) in Canada.

TRICHOPTERA.—The regional trichopteran fauna of springs has been studied intensively in 4 locations: Italy (Cianficconi et al. 1998), Canada (Williams 1991), the Sierra Nevada of California (Erman and Erman 1990), and now the western Great Basin (Table 7). In all these studies the genus *Rhyacophila* was represented by the most species (14 in Italy, 8 in each California study, 6 in Canada). In the same studies the genus *Lepidostoma* was the next richest. In the current research 7 species of *Lepidostoma* were found; however, 5 species (*L. cascadense, L. roafi, L. cinereum, L. unicolor,*

TABLE 7. Number of trichopteran species found in springs of diverse locations.

Location	# of springs surveyed	# of species found	Author
Italy	397	136	Cianficconi et al. 1998
Canada	25	46	Williams 1991
USA			
Sierra Nevada	21	36	Erman and Erman 1990
Great Basin	28	58	Myers and Resh

and *L. rayneri*) are widespread and not restricted to springs. Only 2 species appear to be endemic to springs of this area (*L. ojanum* and *L. castalianum*).

Sixteen species of Trichoptera collected in this research project were also found by Erman and Erman (1990). Of these 16, they considered 5 species to be spring specialists (*Hesperophylax designatus, Homophylax nevadensis, Limnephilus peltus, Rhyacophila oreta,* and *R. verrula*). *Hesperophylax designatus, Chyranda centralis, Rhyacophila brunnea, R. verrula,* and *R. vaccua* were common to springs studied in Canada, the Sierra Nevada, and the Great Basin. Although many of the trichopteran species present in springs can be considered habitat generalists and are found in other lotic habitats as well, the 4 studies have all discovered undescribed species of caddisflies (e.g., Weaver and Myers 1998) that are apparently endemic to springs.

In the 28 springs examined in this study, species richness of Trichoptera was inversely related to alkalinity and elevation and positively related to discharge and dissolved oxygen. This result is biologically intuitive because the springs that were at lower elevations had higher water temperatures and lower dissolved oxygen levels. Because the source water was quickly oxygenated by turbulence, it is more likely that warm temperatures limited species richness. Springs within the warm group assemblage (group 1) had a lower mean species richness of caddisflies (7.2) than the cold springs (10.8).

Discharge can be considered an indicator of "island" size; one nearly universal biological trait is that larger islands have greater species richness (MacArthur and Wilson 1967). However, the relationship between species richness and discharge was weak, and many of the smaller springs were very species rich. Erman and Erman (1995) found a positive relationship between species richness and alkalinity

and concluded that alkalinity is a proxy for spring permanence. In the springs examined here, the opposite relationship with alkalinity was found. It is clear that habitat permanence is very important to species richness. However, permanence must be evaluated by some other means in this region.

The mean number of caddisfly species per spring in the Sierra Nevada (8.7) was similar to that in the current study (9.1), but much higher than that reported by Williams (1991) in Canada (3.9). However, this is most likely a reflection of the intensity of sampling effort in the California studies rather than the result of true differences in species number. Williams (1991) made one visit to a site and took only benthic samples. Sampling in the California studies involved a variety of methods and included the collection of adults.

Cluster analysis grouped the Trichoptera into 3 assemblages (Fig. 3). Group 1, the warm water group, had several members that occurred repeatedly in these springs: *Gumaga griseola, Helicopsyche borealis, Tinodes provo, Lepidostoma ojanum, Ochrotrichia arizonica,* and *Wormaldia gabriella.* Several different species of *Hydropsyche* (*H. occidentalis, H. oslari, H. cockerelli, H. californica*) also occurred in group 1. At some springs 2 different *Hydropsyche* species coexisted. There was no clear pattern to the occurrence of *Hydropsyche* species in the various springs of group 1, although *H. occidentalis* tended to be in the warmest springs of the group. The genus *Hydropsyche* is widespread across California; the species that occur(s) in a spring may depend on which species initially colonized the spring.

Cold springs were characterized by the presence of *Rhyacophila* spp. and by the substitution of *Parapsyche almota* or *P. elsis* for *Hydropsyche* spp. *Lepidostoma castalianum* was found only in the mid-elevation cold springs, but that was one of the few patterns

discernible. Using different methods, Erman and Erman (1990) concluded that species assemblages could not be detected among the cold springs they surveyed. While warm springs had a core of species that occurred repeatedly, cold springs did not have a consistent core group and fauna of the springs tended to be very individualistic. Whether the unique species assemblages are caused by the stochastic nature of colonization, past disturbances, or biotic factors such as competition is unknown.

Conclusion

Although all macroinvertebrates clustered into 3 groups, functionally it appears that there were 2 primary categories: warm and cold springs. Warm springs were characterized by a core group of caddisflies, hydrobiid snails, and amphipods. In contrast, cold springs did not have a consistent core group of species; one of the most remarkable characteristics of the fauna was the uniqueness of assemblages at each spring. Springs that share a common fluvial connection have more similar faunas (e.g., GM1/GM2 and the 3 sources at Taylor Canyon), and, perhaps with an even longer and more intensive sampling effort, the species composition would be found to be the same in these neighboring springs. However, each spring clearly has its own history, its own physical and chemical characteristics, and its own pattern of colonization that creates a unique assemblage. Unique assemblages of aquatic invertebrates have been found in other stable aquatic systems in which the physical and chemical characteristics among sites are similar (e.g., Erman and Erman 1990, Death 1995, Death and Winterbourn 1995).

Although there was a positive relationship between species richness and discharge (a surrogate for "island" size), this relationship was weak, and some of the smallest springs (e.g., Dry Creek and GM2, discharge = 1.5 L · s^{-1}) had the most species of caddisflies (17 and 14 species, respectively). This points to the importance of protecting these small islands of biodiversity. For example, Montenegro Spring, which is quite small (Q = 1.2 L · s^{-1}, length = 140 m), has only 6 species of caddisflies. However, one of these is an endemic species of *Lepidostoma* (Weaver and Myers 1998).

Two factors important in species richness are habitat permanence and stability (Death 1995, Death and Winterbourn 1995, Erman and Erman 1995). Although desert springs are assumed to be stable, constant environments, they are subjected to both natural (i.e., flooding, drying) and anthropogenic (i.e., water extraction, mining, livestock grazing) disturbance. It is clear that permanence and stability are critical for species richness in these springs as well. Disturbed springs have fewer species (Myers 2000). While it is possible to detect evidence of past disturbance at some sites, at others the physical habitat has recovered to the extent that past disturbances are difficult to discern visually. Past land use can have long-term effects on invertebrate biodiversity (Harding et al 1998). Unfortunately, tracking the history of these isolated springs is not an easy task.

Erman and Erman (1995) found that species richness is strongly linked with spring permanence and that alkalinity levels are a proxy for permanence. This relationship between alkalinity and richness (permanence) did not hold true for this group of springs in the Great Basin. Presence of nonvagile invertebrates (e.g., snails, amphipods, flatworms) and species richness may be better indicators of stable, nondisturbed springs. Even though springs that appeared to be in the least disturbed condition were selected for this research, current and past disturbances (e.g., livestock grazing) are known to have occurred in these study sites. This problem is analogous to the difficulties in finding "reference" streams for impact assessments (Reynoldson et al. 1997). In the desert it is difficult to find springs that have not been impacted by mining, water diversion, water extraction, homesteads, or grazing from nonnative ungulates (livestock, burros, wild horses). The magnitude of these past impacts on current biodiversity of aquatic invertebrates is unknown. This research provides baseline information on the current species composition of aquatic invertebrates of selected springs. The effects of future disturbances, recoveries, and additional spring faunal inventories can be compared with the results of this survey.

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