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AQUATIC INVERTEBRATES OF THE GRAND STAIRCASE–ESCALANTE NATIONAL MONUMENT, UTAH

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ABSTRACT—We use multiple years of collections in rivers, perennial wetlands, and ephemeral tinajas to report on overall biodiversity of aquatic invertebrates in the Grand Staircase–Escalante National Monument, Utah. A total of 570 samples of aquatic invertebrates was collected at 166 locations. Over the study period, invertebrates were identified from 31 orders, 104 families, and 192 genera. Major habitat types (rivers, perennial wetlands, and ephemeral tinajas) supported unique and taxonomically rich assemblages of invertebrates; taxonomic richness was greatest in rivers. Among rivers, richness of genera of aquatic invertebrates was greatest in groundwater-fed streams and perennial, snowmelt-runoff, rivers and least in flood-prone rivers. Future studies should focus on identifying and collecting invertebrates from unique habitats, especially the numerous wetland-like habitats that occur across the Grand Staircase–Escalante National Monument, such as hanging gardens and alcove pools, as well as ephemeral streams.

RESUMEN—Utilizamos colecciones de años múltiples en ríos, pantanos perennes y tinajas efímeras para hacer un informe sobre la biodiversidad total de los invertebrados acuáticos en el Monumento Nacional de Grand Staircase Escalante en el estado de Utah. Un total de 570 muestras de invertebrados acuáticos fue recogido en 166 sitios. Durante el período del estudio, invertebrados de 31 órdenes, 104 familias y 192 géneros fueron identificados. Todos los tipos principales de hábitat (ríos, pantanos perennes, y tinajas efímeras) abarcaron ensamblajes únicos y taxonómicamente ricos de invertebrados. La riqueza taxonómica de invertebrados acuáticos fue más alta en los ríos. Entre los ríos, la riqueza de géneros de invertebrados acuáticos fue más alta en los arroyos alimentados por agua subterránea y en los ríos perennes de nieve derretida, y más baja en los ríos propensos a inundaciones. Los estudios futuros deben centrarse en identificar y recoger invertebrados de hábitats únicos, especialmente en los numerosos hábitats como pantanales que se presenten en todo el Monumento Nacional de Grand Staircase Escalante, como en los jardines colgantes y en las pozas, así como en los arroyos efímeros.

Number of species occupying a habitat is a common measure of biodiversity used by scientists and managers (Hayek and Buzas, 1997). Thienemann (1954) concluded that richness of aquatic invertebrates conformed to three ecological principles: it is proportional to habitat diversity within a locality; it is inversely proportional to amount of extreme habitat conditions; and it is proportional to habitat stability and age of locality. The first principle predicts that richness of taxa increases with increasing spatial heterogeneity. This has been observed for many taxa and is predicted by niche theory (e.g., Abele, 1974; MacArthur, 1975). Application of the first principle in streams generally has shown that richness of invertebrate taxa increases with increasing physical complexity at all spatial scales (Vinson and Hawkins, 1998).

Hydrology (e.g., flow in rivers and permanence of standing water) is a major source of habitat variability that encompasses Thienemann's principles as hydrology controls both structural complexity and disturbance regimes of habitat (e.g., frequency and magnitude of floods). In constructing a conceptual model of streamflow for the continental United States, Poff and Ward (1989) argued that stream communities were influenced by several hydrologic factors; intermittency of flow, predictability of flow, frequency of floods, and predictability of floods. Richness of aquatic invertebrate taxa was predicted to be greatest in streams with predictable stable-flow regimes, to be intermediate in streams with predictable flood regimes, and be least in streams with unpredictable floods or intermittency.

Temperature also exerts tremendous control over richness of aquatic invertebrates. Temperature regimes vary widely in aquatic habitats, but usually in predictable patterns for habitats in the same region (Sweeney, 1984). The annual water-temperature regime has several components, including minimum-maximum, annual, and diel variation, timing of minimum and maximum, rate of seasonal change, and number of annual degree days that influence stream insects (Ward and Stanford, 1982). Water temperature affects growth, feeding, and metabolic functions, but also controls physiochemical parameters such as amount of available dissolved oxygen. Most research on effects of water temperature on aquatic insects has evaluated physiological and behavioral responses to natural and altered thermal regimes (Ward and Stanford, 1982) or in relation to distribution of species latitudinally (Vannote and Sweeney, 1980) and up elevational (Ward, 1986) gradients. Authors who explored relationships between richness of taxa and thermal variation have focused on annual temperature range and generally have found richness of invertebrate taxa to increase with annual variation in water temperature (Vinson and Hawkins, 1998) and decrease with variation in diel temperature (Brussock and Brown, 1991).

Here we make use of multiple years of collections of aquatic invertebrates to report on biodiversity of aquatic invertebrates in an arid region with highly variable hydrologic and thermal regimes, the Grand Staircase–Escalante National Monument, Utah. Our objectives were to describe differences in biodiversity of aquatic invertebrates among major types of aquatic habitats and to describe how overall biodiversity is related to diversity of aquatic habitats.

Materials and Methods—*Study Area*—Grand Staircase–Escalante National Monument comprises 7,689 km^2 in southern Utah. Elevations range from 1,100 to 3,000 m. At Escalante, Utah (1,616 m), mean annual air temperatures vary from -10°C in winter to 33°C in summer (National Oceanic and Atmospheric Administration, 2002). Mean annual precipitation is ca. 30 cm. Winters are cold and windy and summers are characterized by hot days and cool nights. Moisture falls predominantly as snow in January–May. Early summer usually is dry, whereas intense localized thunderstorms are common in late summer, caused by the North American Monsoon (hereafter, monsoon) when moisture is advected from the Pacific Ocean and Gulf of California (Adams and Comrie, 1997).

Aquatic habitats include perennial and ephemeral streams, springs, wetland ponds, tinajas (ephemeral rock pools), and alcove pools (permanent rock pools located below large cliff pour offs). Streamflows are influenced by groundwater, spring snowmelt, and monsoons. Short-lived monsoonal storm flows can be 50 times greater than mean annual flows and 10 times greater than spring peak flows. Water-temperature regimes also vary widely both within and among systems. Temperatures in some streams can range from zero in winter to $>30^{\circ}$C during summer; whereas groundwater-derived systems vary no more than a few degrees throughout the year. Systems also vary widely in width, depth, gradient, shading, allochthonous inputs, and composition of benthic substrate.

Physical Parameters—Streamflow data for major perennial streams in Grand Staircase–Escalante National Monument were obtained from gages maintained by the United States Geological Survey (Table 1). Discharge-regime patterns were then fit into the classification scheme of Poff and Ward (1989). In lentic habitats, dimensions (length, width, depth), and amount and type of shading (either vegetative or topographic) were noted. Water temperatures were collected continuously every 2–4 h using recording thermographs (HOBO Temp logger, Onset Inc., Bourne, Massachusetts) at several lotic and lentic locations (Table 1).

Collections of Aquatic Invertebrates—At 166 locations, 570 samples of aquatic invertebrates were collected. The majority of these sites were streams (103), but samples also were collected in 63 lentic habitats including 7 alcove pools, 1 hanging garden, 8 wetland ponds, 5 springs, and 42 tinajas. Samples of aquatic invertebrates were collected during 1998–2004. A list of sampled sites and coordinates is available from the authors and Grand Staircase–Escalante National Monument, Kanab, Utah. Our sampling strategy was twofold; qualitatively sample as many locations as possible and repeatedly sample across seasons and years a subset of perennial habitats collecting both quantitative and qualitative samples. Lotic aquatic invertebrates were collected both qualitatively and quantitatively. Lentic invertebrates were collected qualitatively. Qualitative samples were collected with a rectangular kicknet (457 by 229 mm) with a 500-μm-mesh net and by hand-picking invertebrates from woody debris and large boulders. All major habitat types (e.g., riffles, pools, backwaters, macrophyte beds) were sampled and composited to form a single sample from each site for each sampling date. Quantitative samples were collected using a Surber net (0.093 m^2) or a rectangular kicknet with 500-μm-mesh nets. For kicknet samples, the area of each sample was ca. 0.18 m^2 (455 by 400 mm). Kicknets (n = 4) or Surber samples (n = 8) were collected in four different riffles and composited to make a sample of ca. 0.74 m^2.

Laboratory Methods—Qualitative samples of invertebrates were processed in their entirety, i.e., all organisms were removed and identified. Quantitative

TABLE 1—Summary of mean daily stream discharge and instantaneous water temperatures collected at ca. 4-h intervals within Grand Staircase–Escalante National Monument, Utah; NA indicates not applicable.

			Discharge ($m^3 s^{-1}$) or water temperature (°C)			
Type	Locality	Dates	Maximum	Minimum	Mean	Maximum diel range
Discharge	Deer Creek, USGS Station 09338900	2001–2007	0.2	0.1	0.2	NA
Discharge	Boulder Creek, USGS Station 09339000	1950–2007[a]	7.1	0.1	0.8	NA
Discharge	Escalante River, USGS Station 09337500	1911–2007[a]	24.1	0	0.5	NA
Discharge	Pine Creek, USGS Station 09337000	1950–2007[a]	5.8	0	0.2	NA
Temperature	East Fork Boulder Creek, near Highway 12	January 2000–October 2001	23.6	−0.2	9.2	19.7
Temperature	Calf Creek, near Highway 12	May 2000–June 2001	25.6	3.7	15.4	15.8
Temperature	Calf Creek, near source	April 2000–June 2001	15.2	8.6	13.7	4.7
Temperature	Deer Creek, at Burr Trail Bridge	January 2000–September 2001	22.4	0.2	10.2	11.5
Temperature	Escalante River, near Escalante	January 2000–September 2001	31.1	−1.0	8.8	18.6
Temperature	Escalante River, at Highway 12 bridge	May 2000–September 2001	29.1	−0.6	13.5	11.9
Temperature	Pine Creek, at lower Box Canyon trailhead	January 2000–June 2001	22.1	−0.6	8.0	11.5
Temperature	Pine Creek, at upper Box Canyon trailhead	January 2000–September 2001	18.2	−0.6	8.8	10.9
Temperature	Tinaja near Highway 12	June 2000–June 2003	27.5	4.1	16.2	9.6
Temperature	Tinaja near Boulder Creek	May 2001–October 2001	23.2	0.2	18.1	3.4
Temperature	Tinaja near Boulder Creek	May 2001–October 2001	38.3	0.2	19.4	28.3

[a] Indicates data record was not continuous; data are available from the United States Geological Survey.

samples of invertebrates were subsampled if the sample appeared to contain >500 organisms following the methods of Vinson and Hawkins (1996).

Analysis of Invertebrate Biodiversity—Due to difficulty in assigning species names to many immature aquatic insects, most individuals were identified to genus and all data reported herein are at the genus level. Filtering data in this way improved our capacity to make comparisons among habitat types and habitats with different sampling efforts. Samples were then standardized to presence-absence, so that quantitative samples could be compared to qualitative samples.

Differences in biodiversity of aquatic invertebrates among major habitats were evaluated using accumulation curves, which measure how many new taxa are found as sampling effort increases either by sampling more locations, dates, or identifying more individuals (Ugland et al., 2003). We calculated smoothed-taxa accumulation using EstimateS, version 8.0 (http://purl.oclc.org/estimates). Taxa-accumulation curves were constructed for: 1) actual observations and a Chao-2 estimated based on presence-absence data from all sites (Chao, 1987); 2) three major habitat types (tinajas, wetlands, and streams); and 3) three major hydrologic classes of perennial streams (perennial flood prone, perennial runoff, and mesic groundwater).

Non-metric Multidimensional Scaling—Non-metric multidimensional scaling was used to examine differences among assemblages of invertebrates among habitats (Primer-E, version 5.2.8, Primer-E Ltd., Ivybridge, United Kingdom). We used ordinations based on Sorenson/Bray-Curtis distance measurements to provide graphical representations of assemblage patterns. In two-dimensional ordination, samples that group in proximity indicate similar assemblages, whereas samples far apart indicate relatively dissimilar assemblages. Significance of a priori grouping of habitat (streams, tinajas, and wetlands) was tested with analysis of similarity. Analysis of similarity has the advantage over discriminate analyses of not requiring assumptions about normality or homogeneity of the community data. In this test, the statistic R is a measure of effect size, where $R = 1$ indicates that samples within a group are more similar to each other than members from other groups, and an $R = 0$ indicates that within-group similarity is equal to among-group similarity. An R near 1 indicates strong grouping, whereas an R near 0 indicates weak grouping. Genera influencing these patterns were determined using indicator-species analysis (Dufrene and Legendre, 1997) in the computer program PC-ORD (version 4.41, MJM Software, Gleneden Beach, Oregon). We focused our interpretation of indicator-species analysis to genera unique within a single habitat type. Statistical significance of indicator-species analysis was determined through Monte-Carlo randomization to determine applicability as indicator taxa.

Results—*Aquatic Invertebrates*—Invertebrates were identified from 31 orders, 104 families, and 192 genera (Table 2). Diversity was greatest among insects. We collected the following number of genera: 39 Coleoptera, 35 Diptera (excluding Chironomidae), 18 Ephemeroptera, 10 Heteroptera (aquatic Hemiptera), 16 Odonata, 16 Plecoptera, 29 Trichoptera, 13 Crustacea, and 8 Mollusca.

The Chao-2 estimator, which uses rarity as a correction factor (http://purl.oclc.org/estimates), suggested the true number of genera at these sites was 245 (Fig. 1a), 22% more than the 192 genera we collected. Rarity in our samples was high; 23% of all genera collected (45 genera) were at only one location and 52% of all genera collected (100 genera) were at ≤5 locations.

Each of the primary habitats evaluated supported diverse assemblages of aquatic invertebrates (Table 2). Perennial wetlands were characterized by genera of Coleoptera, Diptera, Heteroptera, and Odonata. Ephemeral tinajas had high richness of Coleoptera, Diptera, Heteroptera, Odonata, and Crustaceans. Invertebrate assemblages in streams varied depending on stream, but overall they were characterized by having high richness within Diptera, Plecoptera, Trichoptera, and Mollusca. Streams had the greatest richness of genera, followed by perennial wetlands, and then seasonal tinajas (Fig. 1b). No genera-accumulation curve reached an apparent asymptote suggesting each of these habitats likely harbors numerous additional taxa.

Richness of aquatic-invertebrate genera in Calf Creek (a mesic groundwater stream) was 1.2 times greater than the Escalante River (a flood-prone perennial stream) and similar to Boulder Creek (a perennial runoff stream) after 30 samples (Fig. 1c). Calf Creek supported the most genera of Odonata, Trichoptera, and Crustacea. Boulder Creek supported the most Ephemeroptera and Plecoptera. Escalante River supported the most genera of Coleoptera and Diptera. Richness of Heteroptera was similar among all three streams.

Using ordination by non-metric multidimensional scaling, assemblages of invertebrates at Grand Staircase–Escalante National Monument appeared to group by habitat type; streams, perennial wetlands, or tinajas (Fig. 2a). Overall grouping by analysis of similarity was significant with a global $R = 0.45$ ($P < 0.001$). Lentic habitats (wetlands and tinajas) formed distinct groups separate from lotic habitats (streams versus wetlands, $R = 0.354$; streams versus tinajas, $R = 0.522$; $P < 0.001$ for both). Different lentic

TABLE 2—Summary of aquatic macroinvertebrates collected during 1998–2004 by habitat type in Grand Staircase–Escalante National Monument, Utah.

			Lentic habitats				
Measure	All locations	Rivers	Alcove pools	Hanging gardens	Wetlands, ponds, lakes, reservoirs	Springs and seeps	Tinajas
Number of locations	166	103	7	1	8	5	42
Number of samples	570	420	14	1	14	5	118
Total genera of invertebrates	192	168	39	8	42	13	58
Total genera of insects	165	151	34	8	32	11	48
Genera of Coleoptera	39	32	14	6	14	5	18
Genera of Diptera (non-Chironomidae)	35	33	7	2	4	1	10
Genera of Ephemeroptera	18	18	2	1	2	1	2
Genera of Heteroptera	10	9	4	1	3	2	7
Genera of Megaloptera	1	1	0	0	0	0	0
Genera of Odonata	16	14	6	0	5	1	6
Genera of Plecoptera	16	16	0	0	0	0	0
Genera of Trichoptera	29	27	1	0	4	1	5
Genera of Crustacea	13	7	2	0	4	1	7
Genera of Mollusca	8	7	2	0	5	1	1

and lotic habitats also appeared to have distinct faunas ($R = 0.207$, $P < 0.001$), with the largest differences occurring among stream classes.

Boulder Creek, Escalante River, and Calf Creek exhibited distinct differences in assemblages of invertebrates using non-metric multidimensional scaling (Fig. 2b). Groupings were statistically significant (analysis of similarity, overall $R = 0.290$, $P < 0.001$). Pairwise analysis of similarity showed that each of these streams were significantly different ($P < 0.001$) from each other and that the effect size (R) was large (Calf Creek versus Boulder Creek, $R = 0.355$; Calf Creek versus Escalante River, $R = 0.288$; Boulder Creek versus Escalante River, $R = 0.252$). Indicator-species analysis showed a large number of genera of insects unique to each stream (Table 4). Boulder Creek had assemblages of invertebrates common to clear lotic waters; namely high numbers of genera of Ephemer-

TABLE 3—Summary of aquatic macroinvertebrates collected during 1998–2004 in three streams in Grand Staircase–Escalante National Monument, Utah.

Measure	Boulder Creek (perennial runoff)	Calf Creek (mesic groundwater)	Escalante River (perennial flood prone)
Number of samples	33	55	78
Total genera of invertebrates	67	83	82
Total genera of insects	65	76	78
Genera of Coleoptera	10	18	21
Genera of Diptera (non-Chironomidae)	13	16	18
Genera of Ephemeroptera	14	8	12
Genera of Heteroptera	4	4	3
Genera of Megaloptera	0	0	0
Genera of Odonata	2	9	5
Genera of Plecoptera	9	2	5
Genera of Trichoptera	13	18	13
Genera of Crustacea	1	4	2
Genera of Mollusca	1	2	2

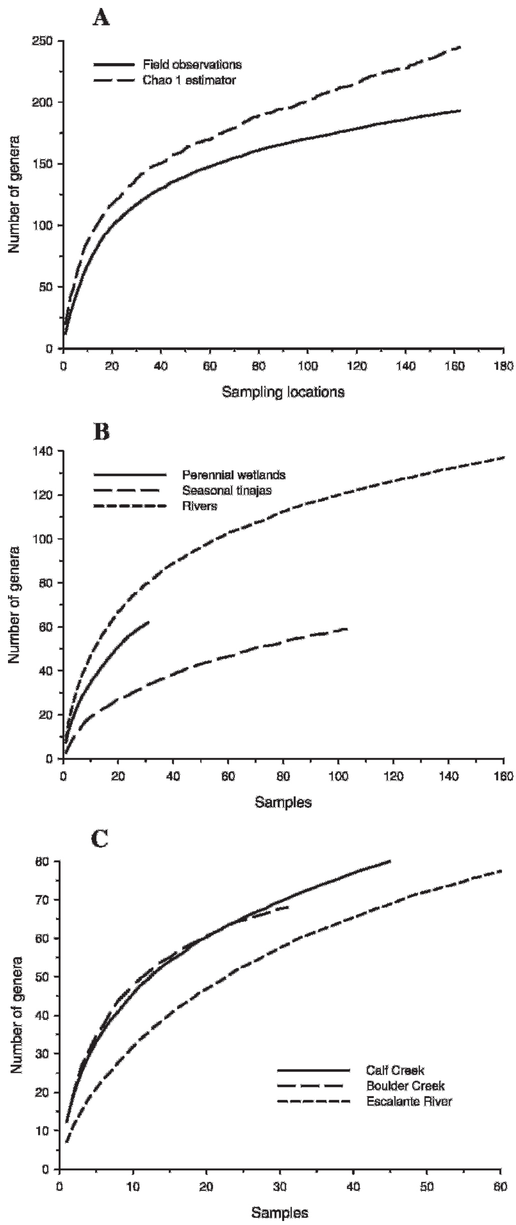

FIG. 1—Accumulation curves for genera of aquatic invertebrates based on field collections and the Chao-2 estimate: A) for all sites sampled; B) for three primary aquatic habitats (perennial wetlands, ephemeral tinajas, and rivers); and C) for three major types of rivers in Grand Staircase–Escalante National Monument, Utah.

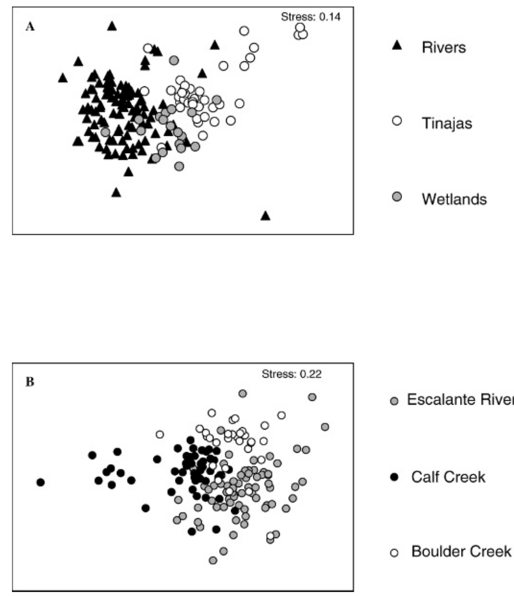

FIG. 2—Ordination of genera of invertebrates with non-metric multidimensional scaling using presence-absence data to compare: A) three dominant habitat types (perennial wetlands, ephemeral tinajas, and rivers; and B) three rivers with different hydrologic regimes in Grand Staircase–Escalante National Monument, Utah. Each point represents invertebrates collected at a single site on a single date. Points in proximity represent similar assemblages of invertebrates and points more distant indicate differing assemblages.

optera, Plecoptera, Elmidae (Coleoptera), and several genera of Trichoptera typical of mountain streams. Calf Creek was typified by organisms common in rivers with constant discharge and temperature regimes; namely several genera of Dytiscidae (Coleoptera), Limnephilidae (Trichoptera), and numerous Odonata. Escalante River was characterized by fewer unique organisms. Taxa that only occurred in the Escalante River were typical of desert streams, including the mayfly *Cameleobaetidius* (Ephemeroptera: Baetidae), the burrowing crane fly *Rhabdomastix* (Diptera: Tipulidae), and two dragonflies (Odonata: Gomphidae).

Streamflow and Longevity of Water—Streamflow regimes within Grand Staircase–Escalante National Monument varied widely among streams (Table 1). Escalante River was characterized as a perennial flood-prone stream (Poff and Ward, 1989), and exhibits both a large sustained runoff each spring due to snowmelt (typically ca. 4 $m^3 s^{-1}$) and frequent unpredictable floods caused by late-summer monsoon storms that can exceed 10 $m^3 s^{-1}$. Pine Creek and Boulder Creek were classified as perennial runoff streams

TABLE 4—Genera of aquatic invertebrates that are unique to three streams in Grand Staircase–Escalante National Monument, Utah, with differing streamflow regimes (sensu Poff and Ward 1989).

Order	Family	Genus	Boulder Creek (perennial runoff)	Calf Creek (mesic groundwater)	Escalante River (perennial flood prone)
Amphipoda					
	Gammaridae	*Gammarus*		X	
Arhynchobdellida					
	Erpobdellidae	*Nephelopsis*		X	
Branchiopoda					
	Daphniidae	*Daphnia*		X	
Coleoptera					
	Elmidae	*Cleptelmis*[a]	X		
		Stenelmis			X
	Scirtidae	*Elodes*		X	
	Hydrophilidae	*Enochrus*			X
	Dytiscidae	*Stictotarsus*		X	
		Hygrotus			X
		Laccophilus			X
Decapoda					
	Cambaridae	*Orconectes*		X	
Diptera					
	Athericidae	*Atherix*[a]	X		
	Ceratopogonidae	*Culicoides*			X
		Dasyhelea			X
	Culicidae	*Culex*		X	
	Stratiomyidae	*Caloparyphus*[a]		X	
		Euparyphus[a]		X	
	Tipulidae	*Rhabdomastix*			X
Ephemeroptera					
	Ameletidae	*Ameletus*[a]	X		
	Baetidae	*Camelobaetidius*			X
	Heptageniidae	*Epeorus*[a]	X		
	Siphlonuridae	*Siphlonurus*[a]	X		
Gastropoda					
	Lymnaeidae	*Radix*		X	
Heteroptera					
	Corixidae	*Corisella*		X	
	Notonectidae	*Notonecta*[a]		X	
Isopoda					
	Asellidae	*Caecidotea*		X	
Odonata					
	Aeschnidae	*Anax*		X	
	Coenagrionidae	*Enallagma*[a]		X	
		Ischnura		X	
	Cordulegastridae	*Cordulegaster*		X	
	Gomphidae	*Gomphus*			X
		Erpetogomphus			X
	Lestidae	*Archilestes*		X	
Plecoptera					
	Chloroperlidae	*Suwallia*[a]	X		
		Sweltsa	X		
	Nemouridae	*Amphinemura*[a]	X		
		Malenka[a]	X		
		Zapada			X
	Perlidae	*Hesperoperla*	X		

Table 4—Continued.

Order	Family	Genus	Boulder Creek (perennial runoff)	Calf Creek (mesic groundwater)	Escalante River (perennial flood prone)
	Perlodidae	*Skwala*		X	
Trichoptera					
	Glossosomatidae	*Glossosoma*		X	
	Hydropsychidae	*Arctopsyche*	X		
	Lepidostomatidae	*Lepidostoma*[a]	X		
	Leptoceridae	*Oecetis*			X
		Ylodes			X
	Limnephilidae	*Amphicosmoecus*			X
		Limnephilus		X	
	Philopotamidae	*Wormaldia*		X	
	Seriocostomatidae	*Gumaga*[a]		X	
	Uenoidae	*Oligophlebodes*		X	

[a] Indicates statistically significant difference ($P < 0.05$) using indicator-species analysis.

(Poff and Ward, 1989). These streams have annual, snowmelt, peak flows of ca. 2–3 $m^3 s^{-1}$ and few high flows occur in response to monsoon storms. Calf Creek and Deer Creek were classified as mesic groundwater streams. These streams are characterized by steady low flows ca. 0.15 $m^3 s^{-1}$ and little seasonal fluctuation in flow throughout the year either in response to snowmelt or monsoon storms.

Although we were unable to quantify longevity of lentic habitats, habitats suspected to be perennial based on occurrence of obligate wetland plants generally were located within drainages (e.g., steep-walled canyons) or directly below high, rock-wall, pour-offs in topographically shaded areas. Tinajas were the most prevalent ephemeral lentic habitat. Tinajas occurred both within and outside of defined drainages. These habitats filled quickly following storms. Field observations suggested that duration of water in tinajas was highly variable and depended on surface area and volume, shading, and air temperatures.

Water Temperatures—Water temperatures in rivers exhibited strong seasonal patterns, with temperatures ≤31.1°C occurring in summer in the Escalante River, although other streams typically were cooler (Table 1). Minimum water temperatures occurred in winter and were near 0°C for most locations. One exception was near the headwaters of Calf Creek, where temperature varied little year around. Deer Creek and Calf Creek, both mesic groundwater streams, exhibited warmer winter temperatures than other rivers. Maximum diel variations varied from ca. 5°C in headwaters of Calf Creek to near 20°C in Escalante River and Boulder Creek. Annual ranges of water temperature varied from ca. 7°C at headwaters of Calf Creek to >30°C in the Escalante River.

In general, water temperatures in tinajas were similar in winter and warmer in summer than river temperatures (Table 1). The maximum temperature of a tinaja recorded in summer was 38°C. Tinajas shaded from direct sunlight had lower maximum temperatures and narrower daily ranges in summer than those exposed to the sun. We also observed an ameliorating effect of precipitation in summer on water temperatures in tinajas (Fig. 3). Shortly after storms, the diel range in water temperature decreased only to increase as water evaporated over successive days. New storms would increase water volumes and restore thermal stability until evaporation again reduced water volume.

Discussion—Grand Staircase–Escalante National Monument appears to have a diverse assemblage of aquatic invertebrates compared to other southwestern regions that have been surveyed. In a survey of tributaries from Grand Canyon National Park, Arizona, Oberlin et al. (1999) collected 42 genera, compared to the 151 genera we found in streams of Grand Staircase–Escalante National Monument. Likewise, Haden et al. (2003) collected 49 taxa in a survey of 92 river miles of the Green and Colorado rivers in Canyonlands National Park, Utah. We found 109

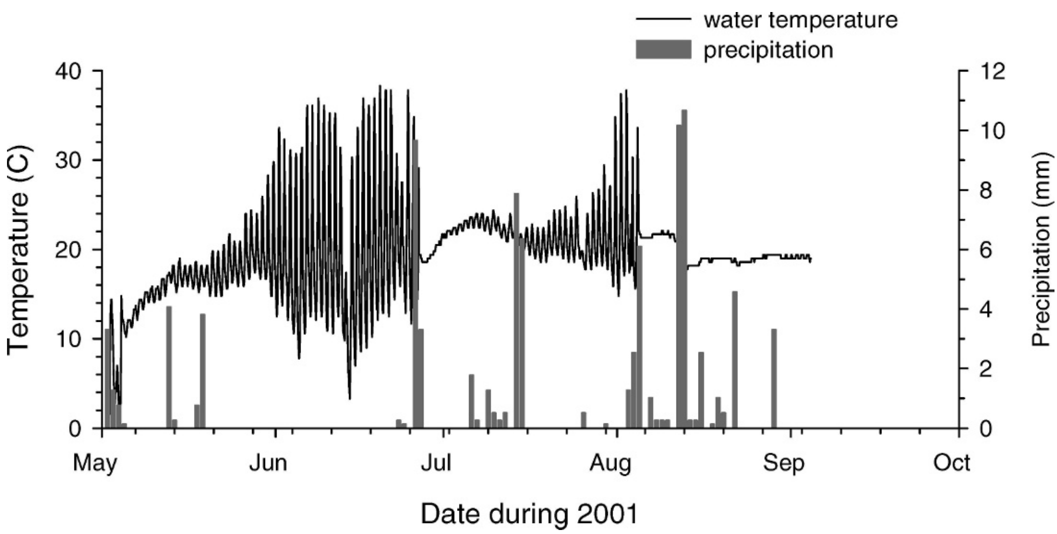

FIG. 3—Continuous water temperature recorded at ca. 4-h intervals on an exposed tinaja near Boulder Creek, Grand Staircase–Escalante National Monument, Utah, and precipitation recorded at Escalante, Utah, May-September 2001.

taxa of invertebrates in 42 tinajas, whereas Anderson et al. (1999) collected 44 taxa of aquatic invertebrates from 460 tinajas in and adjacent to Capitol Reef National Park, Utah. In other studies of southwestern tinajas and wetlands, researchers consistently have found fewer taxa. For example, Baron et al. (1998) collected 64 taxa of aquatic invertebrates from 76 intermittent stream pools and Kubly (1992) collected 95 taxa of aquatic invertebrates from 12 tinajas in the White Tank Mountains, Arizona.

We suggest two reasons for the high number of taxa in Grand Staircase–Escalante National Monument. First, habitat diversity appears high. This diversity is expressed among major habitat types, e.g. streams, perennial wetlands, tinajas, alcove pools, and spring-seeps, but also is expressed within habitat types, especially streams and tinajas. Streams within Grand Staircase–Escalante National Monument varied widely with respect to their flow and thermal regimes. Although located in proximity to one another, all major streams had distinct differences in predictability, frequency, and timing of high flow events. Poff and Ward (1989) hypothesized that differences in these hydrologic variables result in changing contributions of biotic and abiotic processes that act to determine assemblages of invertebrates. Our data support this idea, as each class of stream we evaluated appeared to support a different assemblage of aquatic invertebrates (Fig. 2b), which led to high overall taxonomic richness (Fig. 1). Diversity in habitat conditions among lentic habitats was similarly high, particularly among tinajas. Tinajas varied widely with respect to their solar exposure, permanence of water, assemblages of wetland plants, water temperatures, and amount of organic matter. This variability influenced assemblages of aquatic invertebrates and added to overall diversity of organisms collected in these habitats (Fig. 1). Secondly, we suggest high diversity of invertebrates in Grand Staircase–Escalante National Monument also is promoted by its geographic position, which provides a large regional pool of available colonizers. Grand Staircase–Escalante National Monument is located at the juxtaposition of two ecoregions, the Western Cordillera to the north and the Cold Desert to the south (Omernik, 1987). This region is also at the location of three intersecting biotic provinces of Dice (1943); Artemisian (the Great Basin), Navahonian (Colorado Plateau), and Mohavian (Mojave Desert). Likewise, we collected several taxa associated with more Neotropical assemblages that are likely relict taxa from more temperate times in the arid Southwest (e.g., *Telebasis*, Odonata, Coenagrionidae; *Smicridea*, Trichoptera, Hydropsychidae; *Leucotrichia*, Trichoptera, Hydroptilidae).

To our knowledge, aquatic habitats in Grand Staircase–Escalante National Monument and the broader Colorado Plateau have not been quantified with respect to diversity. The work presented here provides a strong empirical foundation for the need to inventory habitats and habitat characteristics and for monitoring changes in assemblages of invertebrates over time. Future studies should focus on identifying and sampling new habitats, especially the numerous wetland-like habitats that occur across the Colorado Plateau, such as hanging gardens and alcove pools, as well as ephemeral streams, because these are poorly sampled and may be first affected by future changes in climate.

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