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WATERSHED INFLUENCE ON THE MACROINVERTEBRATE FAUNA OF TEN MAJOR TRIBUTARIES OF THE COLORADO RIVER THROUGH GRAND CANYON, ARIZONA

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ABSTRACT—The biota of ten major tributaries of the Colorado River through Grand Canyon, Arizona, were examined bimonthly in 1991 and annually in 1993, 1994, and 1996. Identification, distribution and phenology of 42 insect genera are reported. We found significant variability in macroinvertebrate biomass between tributaries and seasonal differences within tributaries. Some of these differences can be explained in terms of stream source and watershed characteristics. Spring-fed tributaries originating within the Grand Canyon had higher macroinvertebrate biomass than tributaries draining large watersheds from outside the Grand Canyon. Tributaries that receive a substantial amount of their water from terrestrial runoff typically are less stable, have higher turbidity, and fewer food resources so that fewer species and/or individuals can be sustained. Irrigation, grazing, and other land use practices that reduce flow and increase sedimentation within these watersheds may have repercussions far downstream of where they occur.

RESUMEN—La biota de diez tributarios mayores del Río Colorado a través del Gran Cañón, Arizona, fueron examinados bimestralmente en 1991 y anualmente en 1993, 1994, y 1996. La identificación, distribución, y fenología de 42 géneros de insectos son registrados. Encontramos una variedad significativa en biomasa de macroinvertebrados entre tributarios tanto como diferencias estacionales dentro de tributarios. Algunas de estas diferencias pueden ser explicadas en términos de las características del nacimiento de los tributarios y de las cuencas. Los tributarios de origen manantial dentro del Gran Cañón tenían mayor biomasa de macroinvertebrados que los tributarios alimentados por cuencas grandes de fuera del Gran Cañón. Los tributarios que reciben gran cantidad de agua proveniente de terrenos de desagües son típicamente más inestables, tienen mayor turbiedad, y menos recursos de comida por lo que menos especies y/o individuos pueden ser sostenidos. Regar, pastar, y otras prácticas de uso de la tierra que reducen el flujo e incrementan la sedimentación dentro de estas cuencas pueden tener repercusiones mucho más río abajo que de donde ocurren.

There is relatively little information available on macroinvertebrates in the remote tributary habitats of the Colorado River through Grand Canyon National Park, Arizona. Even less is known about abiotic factors that regulate the distribution and phenology of these organisms. Polhemus and Polhemus (1976) reported 14 species of aquatic heteropterans in assorted tributaries and Hofknecht (1981) reported 52 insect families from 30 tributaries and springs, in contrast to only five insect families from the main river channel.

This study was initiated to provide additional information on the macroinvertebrate communities of 10 major tributaries of the Colorado River through Grand Canyon National Park. These tributaries vary widely in physicochemical characteristics and are home to a variety of different biotic communities, all of which may invade the Colorado River under certain conditions. The invasion of species may be enhanced with the proposed changes in operation of Glen Canyon Dam to alter water temperature and discharge regimes in the Colorado River, subsequently providing proper conditions for colonization by macroinvertebrates. Comparison of these widely disparate tributaries will provide distributional information on aquatic macroinvertebrates within the Grand Canyon and offer valuable information on the extent to which watershed characteristics influence macroinvertebrate communities.

MATERIALS AND METHODS—The study area includes 10 major tributaries along 361 km of the Colorado River downstream from Glen Canyon Dam

(Fig. 1). Five tributaries (Vasey's Paradise, Nankoweap Creek, Bright Angel Creek, Tapeats Creek, and Spring Canyon) originate from spring sources within the Grand Canyon and are not as heavily influenced by watershed runoff as the other five tributaries. The Paria River, Little Colorado River (LCR), and Kanab Creek drain large watersheds and carry large quantities of sediment into the Colorado River (Hofknecht, 1981; Andrews, 1991; Webb et al., 1991). These three tributaries also exhibit significant periods of reduced or no flow within many reaches. Although Havasu and Diamond creeks derive the majority of their water from springs a short distance upstream (24 and 16 km, respectively) from their confluence with the Colorado River, they are still highly susceptible to flooding from intermittent streams above the spring source (Hofknecht, 1981; Melis et al., 1996). Therefore, they are grouped with the Paria River, LCR, and Kanab Creek as tributaries that are influenced by watershed runoff from outside the Canyon.

Aquatic macroinvertebrates, phytobenthos, and detritus were collected bimonthly during 1991 and annually (June) during 1993, 1994, and 1996 at each site. Duplicate samples were taken along three transects, 30 m apart, with a Hess sampler (1 mm mesh size, 0.11 m^2 sample area). One sample from each transect was used for macroinvertebrate taxonomy and the other was used to determine macroinvertebrate biomass. All six samples were used for biomass estimates of detritus and the phytobenthos. Transects were located above the influence of the mainstem, starting at least 10 m above the mesquite tree line which indicates the old high water zone (>2,265 m^3/s mainstem discharge). We tested the validity of using three samples by comparing the standard deviations for 1991 macroinvertebrate biomass data ($n = 3$) with that of annual data ($n = 6$). No significant difference was detected between these comparisons (Paired Student t-test; $n = 360$; $df = 1{,}079$; $P = 0.14$).

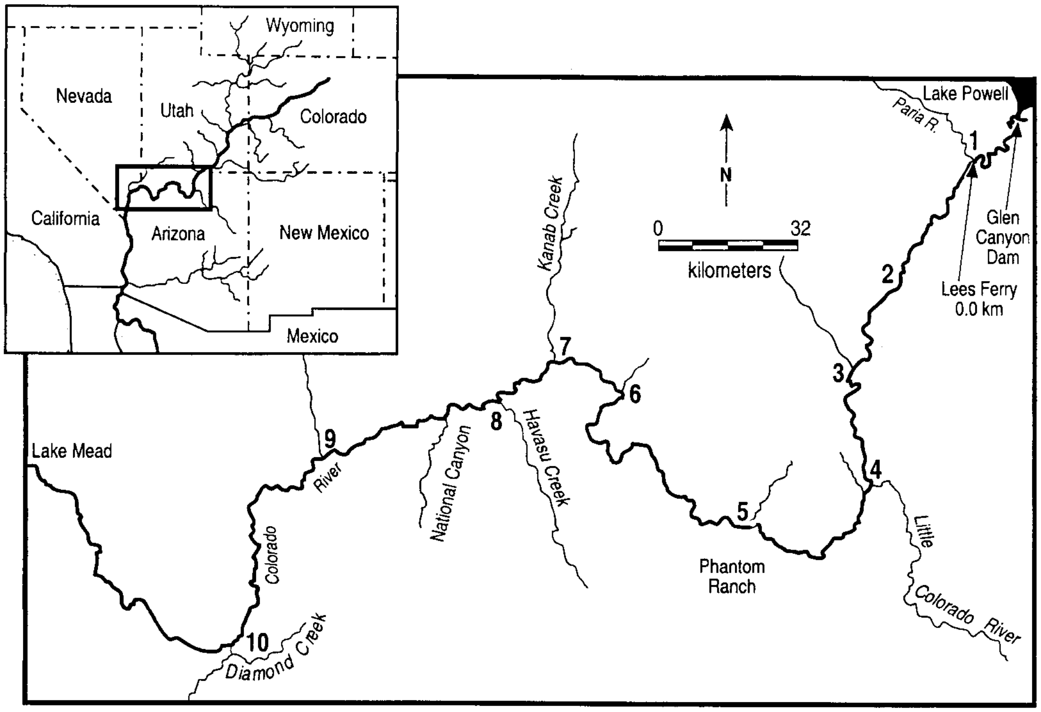
Biomass samples were sorted into the following ten biotic categories used in previous studies of the mainstem Colorado River (Blinn et al., 1995; Stevens et al., 1997): miscellaneous primary producers, cyanobacterian crust (*Oscillatoria* sp.), chironomids (Diptera), *Gammarus lacustris* (Amphipoda), gastropods, oligochaetes, simuliids (Diptera), lumbriculids, miscellaneous macroinvertebrates, and detritus. Miscellaneous macroinvertebrates included taxa that were found occasionally in the Colorado River, but not in large enough numbers to be included as individual categories. Although this was not necessarily the case in the tributaries, these samples were processed according to this established protocol. Miscellaneous primary producers, *Oscillatoria*, and detritus were oven-dried at 60°C, weighed, ashed at 500°C for 1 h, and reweighed for ash-free dry mass determinations (g AFDM/m^2). Each invertebrate category was oven-dried at 60°C, weighed, and dry weights were converted to ash-free dry mass (g AFDM/m^2) from regression equations (Shannon et al., 1994, 1996).

Taxonomic samples were sorted into the following four biotic categories: miscellaneous primary producers, *Oscillatoria*, detritus, and macroinvertebrates. Miscellaneous primary producers, *Oscillatoria*, and detritus were dried and ashed as previously described for biomass samples. Miscellaneous primary producers included bryophytes, macrophytes, diatom mats, filamentous green algae, and *Nostoc* sp. Macroinvertebrates were sorted into the same categories used in biomass determinations, but only miscellaneous macroinvertebrates were identified to lower taxonomic levels (genera) with keys from Merritt and Cummins (1996). Species identifications for Trichoptera and Ephemeroptera larvae were provided by E. Ruiter and C. R. Lugo-Ortiz, respectively.

Water temperature (°C), dissolved oxygen (mg/l), pH, and specific conductance (mS) were measured at each sampling site with a Hydro-Lab Scout II®. Current velocity (m/s) and water depth (m) were measured at each Hess location with a Marsh-McBirney electronic flow meter.

Multivariate analysis of variance (MANOVA) was used to analyze ln+1 transformed data for the influence of month, tributary, and origin of tributary on 1991 water quality parameters (temperature, dissolved oxygen, pH, specific conductance, water velocity, and water depth), biomasses, and effect of year on biomasses within each tributary. In all statistical analyses, origin of each tributary was designated as outside or inside the Grand Canyon in order to determine influence of drainage characteristics on macroinvertebrate populations. All analyses were performed using SYSTAT computer software (Version 5.1, Wilkinson, 1989).

RESULTS—Water quality parameters for 1991 were diverse, but only specific conductance varied significantly with origin of tributaries (MANOVA Wilks' Lambda; $F_{6,280} = 6$; $P < 0.001$). Tributaries originating outside of Grand Canyon had higher conductivities (1.29 mS ± 0.09) than those originating from within Grand Canyon (0.48 mS ± 0.01). The warmest water temperature occurred during July (Paria River, 35.5°C) and the coldest in January (Nankoweap Creek, 1°C). Paria River and Nankoweap Creek had the largest annual temperature ranges (7.1–35.5°C and 1.0–28.4°C, respectively, Table 1). Havasu Creek and Spring Canyon had much smaller annual ranges (10.9–21.5°C and 20.2–28.0°C, respectively). Spring Canyon



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TRIBUTARY	MAP KEY	Rkm	ORIGIN	DRAINAGE AREA (km^2)	DRAINAGE LENGTH (km)	BASE DISCHARGE (m^3/s)
Paria River	1	1.0	A	3,652	125.8	0.08
Vasey's Paradise	2	50.8	B	0.5[1]	1.3	0.05
Nankoweap Creek	3	83.2	B	85	14.8	0.01
Little Colorado River	4	98.6	A	69,790	536.3	0.80
Bright Angel Creek	5	140.8	B	260	29.6	0.42
Tapeats Creek	6	214.8	B	216	34.3	1.94
Kanab Creek	7	231.2	A	6,076	164.7	0.02
Havasu Creek	8	249.6	A	7,822	213.7	1.35
Spring Canyon	9	327.2	B	50	8.2	<0.01
Diamond Creek	10	361.6	A	717	34.8	0.07

FIG. 1—Site map of selected tributaries in the Colorado River corridor, Grand Canyon National Park, including geographic information. The origin of each tributary is designated as A for originating outside the Grand Canyon or B for originating inside the Grand Canyon. Drainage area (km^2) and drainage length (km) are from the United States Geological Survey (pers. comm.) and Melis et al. (1995). [1] Area of Vasey's Paradise around spring near river at the collection site, springs are ca. 50 m from river.

TABLE 1—Annual mean values (±*SE*) and ranges for water temperature (°C), pH, dissolved oxygen (mg/l), and specific conductance (mS) from bimonthly measurements for 10 major tributaries of the Colorado River through Grand Canyon during 1991. n = 6 months except for Vasey's Paradise and Diamond Creek where n = 5 months.

Tributary	Temperature	pH	Dissolved oxygen	Specific conductance
Paria River	16.5 (4.6)	8.1 (0.1)	8.9 (1.0)	0.78 (0.08)
	7.1–35.5	7.8–8.5	6.7–12.2	0.53–0.99
Vasey's Paradise	14.4 (1.9)	8.3 (0.1)	8.0 (1.4)	0.34 (0.02)
	7.4–18.2	8.1–8.5	8.3–10.4	0.28–0.36
Nankoweap Creek	15.5 (4.2)	8.5 (0.1)	9.6 (0.9)	0.61 (0.02)
	1.0–28.4	8.2–8.9	7.6–12.4	0.55–0.69
Little Colorado River	16.4 (2.6)	7.8 (0.1)	9.1 (0.4)	2.5 (0.72)
	9.4–24.2	7.3–8.1	7.5–10.3	0.33–4.49
Bright Angel Creek	13.3 (2.8)	8.4 (0.1)	10.0 (0.5)	0.33 (0.03)
	6.2–25.4	8.0–8.6	8.2–11.4	0.22–0.40
Tapeats Creek	14.6 (2.3)	8.3 (0.1)	10.4 (0.2)	0.31 (0.02)
	9.7–15.6	7.9–8.6	9.8–10.9	0.23–0.33
Kanab Creek	13.9 (2.6)	8.1 (0.1)	10.6 (0.5)	1.27 (0.11)
	7.8–22.8	7.7–8.3	9.2–12.0	0.9–1.80
Havasu Creek	15.4 (1.8)	8.2 (0.1)	9.9 (0.2)	0.73 (0.01)
	10.9–21.5	8.0–8.4	9.2–10.3	0.70–0.75
Spring Canyon	23.9 (1.3)	7.3 (0.3)	7.2 (0.5)	0.62 (0.03)
	20.2–28.0	6.3–7.9	5.6–8.8	0.48–0.68
Diamond Creek	15.8 (4.1)	8.3 (0.1)	9.1 (1.1)	0.74 (0.05)
	11.2–24.2	8.0–8.6	8.4–11.0	0.63–0.89

had the warmest winter temperature (21.3°C) and Vasey's Paradise had the coolest summer temperature (16.4°C). Dissolved oxygen concentrations varied between summer lows of 6.7 mg/l and winter highs of 12.4 mg/l. The highest pH for each tributary occurred during winter months (January or November) and 8.9 was the highest pH recorded (Nankoweap Creek in January). Spring Canyon had the lowest pH recorded (6.3 in May and November). Water depth at the point of collection ranged from 1 cm to 90 cm, and water velocity ranged from 0.01 m/s to 3.6 m/s.

Multivariate analyses (MANOVA) showed that collection month, tributary, and origin of tributary significantly influenced biomass (g AFDM/m^2) in tributaries of the Colorado River through Grand Canyon in 1991 (Table 2). The interaction between origin of tributary and month was not significant indicating that differences between biotic communities originating from inside and outside the Canyon were not a seasonal phenomenon. The exotic amphipod, *Gammarus lacustris,* which contributes a large proportion of the macroinvertebrate biomass above the Paria River in the mainstem of the Colorado River (Shannon et al., 1994; Blinn et al., 1995), was not found in the tributaries and was eliminated from analyses.

Total macroinvertebrate biomass (g AFDM/m^2) for all tributaries combined was highest during January and lowest in May during 1991 (Fig. 2). Simuliids, chironomids, and miscellaneous macroinvertebrates showed significant seasonal changes in standing stock (Table 2), with highest annual biomass in January for all three groups. In categories representing the macroinvertebrate food base, only detritus was significantly affected by month (Table 2). Detrital biomass was also highest in January.

In all months, miscellaneous macroinvertebrates made up the largest percentage (41–72%) of total macroinvertebrate biomass (Fig. 3). They were especially prevalent in autumn communities. Dipterans (chironomids and simuliids) were an important component of the winter macroinvertebrate community, although gastropods increased in summer and fall. Annelid biomass remained constant during the collection period although in May semi-aquatic lumbriculids reached their high-

TABLE 2—MANOVA results on the effect of month, tributary, and origin of tributary on biotic communities in 10 major tributaries of the Colorado River through Grand Canyon. Samples were collected bimonthly during 1991. Univariates include lumbriculids (1), oligochaetes (3), simuliids (4), chironomids (5), miscellaneous macroinvertebrates (6), miscellaneous primary producers (7), detritus (8), gastropods (9), and *Oscillatoria* (10). All categories were analyzed as ash-free dry mass (g AFDM/m^2) on ln+1 transformed data. Only significant univariates are indicated.

Source	Wilks' lambda	Approximate *F*-statistic	*df*	*P*	Significant univariates
Month	0.564	2.23	45,736	0.000	4*, 5***, 6**, 8*
Tributary	0.305	2.47	90,1163	0.000	1***, 3**, 6***, 7***, 8*, 9**, 10*
Origin	0.781	5.23	9,168	0.000	1***, 3*, 6***, 7**, 8*, 10*
Origin·month	0.742	1.09	45,709	0.322	

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

est relative abundance while the smaller oligochaete was absent.

Mean annual biomass (g AFDM/m^2) for all macroinvertebrates combined was highest in Bright Angel Creek and lowest in Paria River (Fig. 4). Macroinvertebrate standing stock was also high in Spring Canyon, Vasey's Paradise, and Tapeats Creek, but Nankoweap Creek, LCR, Diamond Creek, and Havasu Creek had comparatively low macroinvertebrate biomass.

Annual biomass of lumbriculids, oligochaetes, gastropods, miscellaneous macroinvertebrates, miscellaneous primary producers, detritus, and *Oscillatoria* varied significantly among tributaries (Table 2). Lumbriculids were found only at Vasey's Paradise, Bright Angel Creek, Tapeats Creek, and Spring Canyon (Fig. 5). They contributed the greatest amount of biomass to Bright Angel Creek where they made up 34% of total macroinvertebrate biomass. Oligochaete worms occurred only in Vasey's Paradise, Nankoweap Creek, Bright Angel Creek, and Spring Canyon (Fig. 5). They may have been numerically abundant at several sites, including Vasey's Paradise and Bright Angel Creek, but because of their small size they contributed only 14% and 9%, respectively, to total biomass at these two tributaries. Gastropods were found in only 4 of the 10 tributaries examined: Vasey's Paradise, Nankoweap Creek, LCR, and Bright Angel Creek (Fig. 5). In LCR, gastropods made up the largest percentage of total macroinvertebrate mass (58%). Numerically, snails were not common in LCR, but because so few macroinvertebrates were found there, the few snails that did occur made up a large percentage of total macroinvertebrate mass. Snails were actually far more abundant in Vasey's Paradise and Nankoweap Creek where they made up 33% and 21% of total macroinvertebrate biomass, respectively. The distribution of gastropods and simuliids was al-

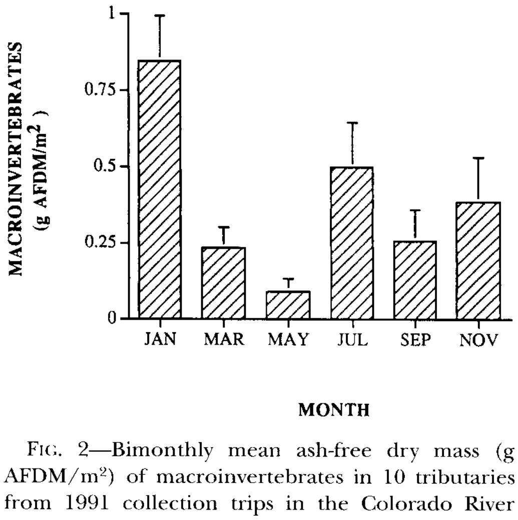

FIG. 2—Bimonthly mean ash-free dry mass (g AFDM/m^2) of macroinvertebrates in 10 tributaries from 1991 collection trips in the Colorado River through Grand Canyon. Error bars represent ±1 *SE*.

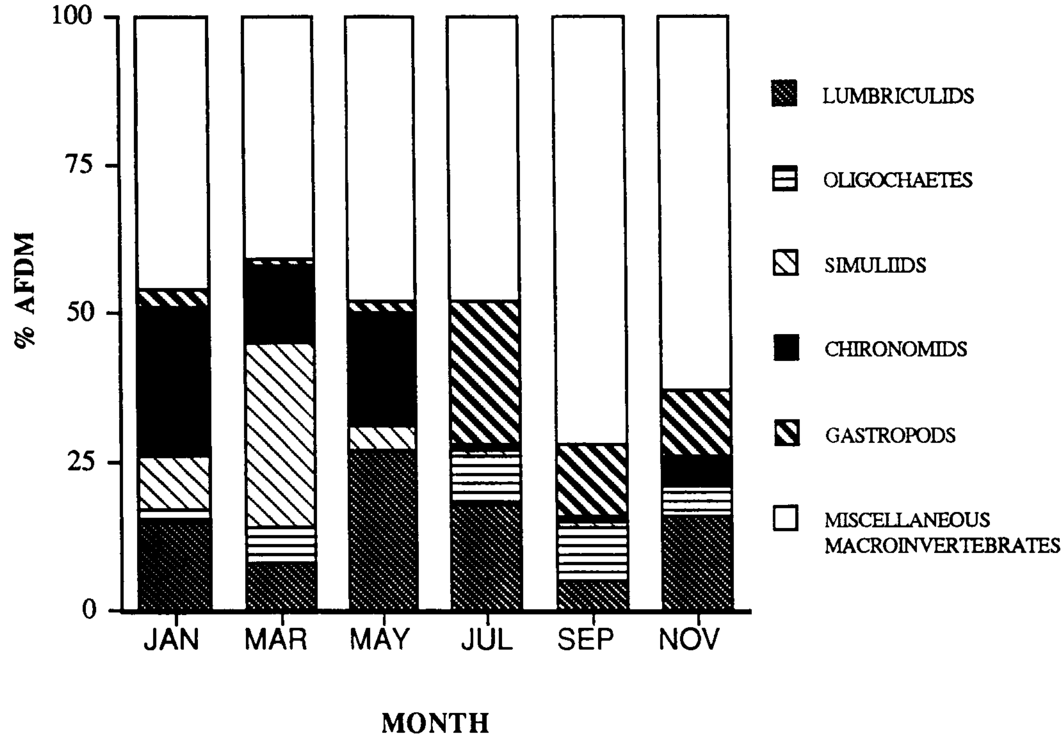

FIG. 3—Bimonthly percent ash-free dry mass (% AFDM) of six macroinvertebrate categories in 10 tributaries from 1991 collection trips in the Colorado River through Grand Canyon.

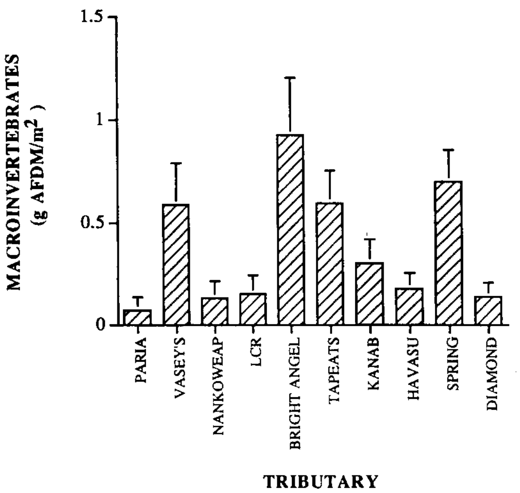

FIG. 4—Mean annual ash-free dry mass (g AFDM/m^2) for macroinvertebrates in 10 tributaries from 1991 bimonthly collection trips in the Colorado River through Grand Canyon. Error bars represent ±1 *SE*.

most dichotomous in the tributaries of the Colorado River; gastropods were found only in the upper tributaries (Bright Angel Creek and above), whereas simuliids were far more abundant in lower tributaries (Bright Angel and below; Fig. 5).

Miscellaneous macroinvertebrates made up the largest percentage of total macroinvertebrate mass in Vasey's Paradise, Nankoweap Creek, Bright Angel Creek, Tapeats Creek, Havasu Creek, Spring Canyon, and Diamond Creek (Fig. 5). The biotic community in Paria River was composed of 50% chironomids and 50% miscellaneous macroinvertebrates. Mean annual biomass of miscellaneous macroinvertebrates was highest in Spring Canyon and lowest in Paria River (Fig. 6). A total of 42 insect genera in 29 families were identified in this category. The distribution and phenology of these aquatic insects are shown in Table 3.

With 9 families and 12 genera represented, the Trichoptera were the most diverse insect group found in tributaries of the Colorado River, although most genera were restricted to

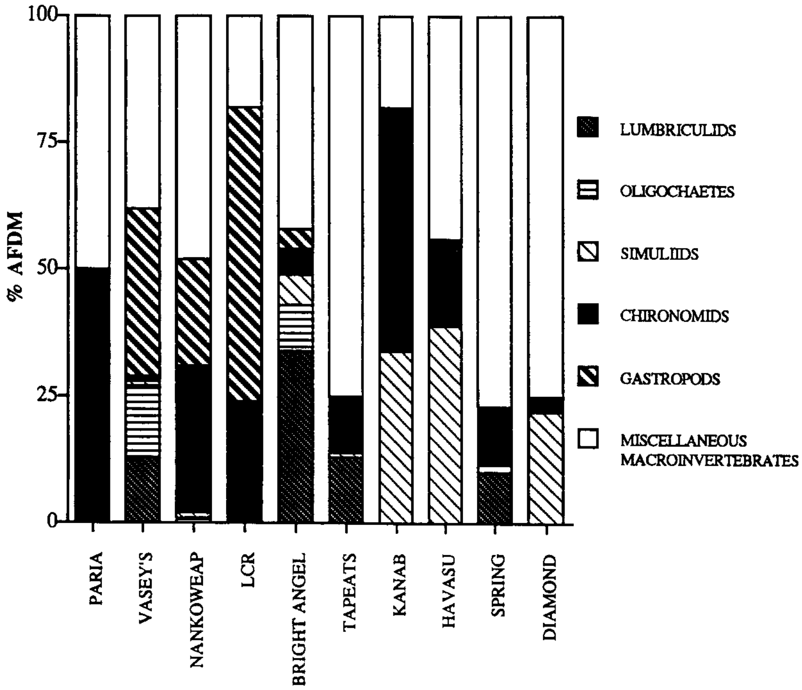

FIG. 5—Annual percent ash-free dry mass (%AFDM) of 6 macroinvertebrate categories in 10 major tributaries from 1991 bimonthly collections in the Colorado River through Grand Canyon.

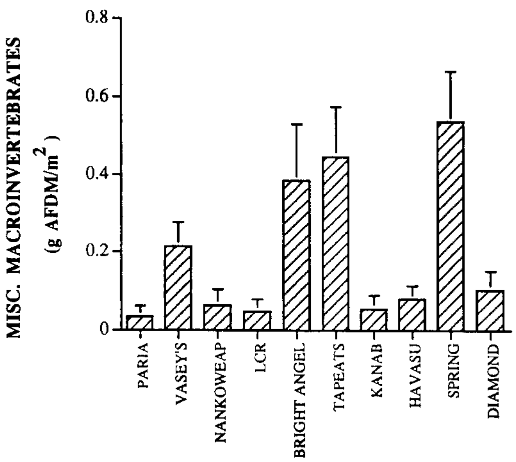

FIG. 6—Mean annual ash-free dry mass (g AFDM/m^2) for miscellaneous macroinvertebrates in 10 tributaries from 1991 bimonthly collections in the Colorado River through Grand Canyon. Error bars represent ±1 *SE*.

only one or two locations (Table 3). *Hydropsyche oslari* Banks was the most widespread caddisfly and the only miscellaneous macroinvertebrate found in Paria River and LCR. *Cheumatopsyche arizonensis* (Ling) was found only in Spring Canyon.

With only three families and four genera, the Ephemeroptera were not well represented in tributaries of the Colorado River (Table 3). *Baetis magnus* was found at Vasey's Paradise and *B. tricaudatis* was common in Bright Angel, Tapeats, and Havasu creeks. *Acentrella turbida* was found only in Bright Angel Creek.

The macroinvertebrate food base varied significantly by tributary (Table 2). Vasey's Paradise had the highest mean annual biomass of miscellaneous primary producers, detritus, and *Oscillatoria* (Fig. 7). Miscellaneous primary producer biomass also was high in Spring Canyon, but Paria River, Nankoweap Creek, LCR, and Havasu Creek had low biomasses of miscellaneous primary producers. High detrital biomass was found in Tapeats Creek and Spring Canyon, but Kanab Creek and Dia-

TABLE 3—Distribution (sites) and phenology (month) of 42 aquatic insect genera in 10 major tributaries of Colorado River through Grand Canyon collected bimonthly in 1991. Site designates are provided in Fig. 1.

Order	Family	Genus	Jan	Mar	May	Jul	Sep	Nov
Trichoptera	Hydropsychidae	*Hydropsyche*	1, 4, 5, 6, 8	1, 5, 6, 8,	1, 5, 6, 8	1, 6, 8	6	6
		Cheumatopsyche	9	9	9	9	9	9
	Philopotamidae	*Chimarra*	5			9	5	
	Helicopsychidae	*Helicopsyche*	5	5, 6	5	5	5	5
	Hydroptilidae	*Leucotrichia*	2	2			9	2
		Hydroptila			9	9	9	
		Ochrotichia		10			2	
	Rhyacophilidae	*Rhyacophila*	7		6			
	Brachycentridae	*Micrasema*				6		
	Lepidostomatidae	*Lepidostoma*				6		
	Polycentropodidae	*Polyplectropus*				6		
	Psychomyiidae	*Tinodes*		6				6
Ephemoroptera	Baetidae	*Baetis*	2, 5, 6, 8, 9	2, 5, 6, 8, 9, 10	2, 3, 5, 6, 10	2, 5, 6, 8, 9	5, 6, 9, 10	2, 3, 5, 6, 9
		Acentrella	5	5	5	5	5	5
	Heptageniidae	*Epeorus*		6		6	6	6
	Tricorythidae	*Tricorythodes*		10				
Lepidoptera	Pyralidae	*Petrophila*	2, 5	2, 5	2	2, 5	2, 5	2, 5, 6
Diptera	Tipulidae	*Antocha*	6	6	6	6, 7	6	6
		Limonia		2		2	2	
		Tipula		2				
	Empididae	*Clinocera*		2	2	2	2	
		Hemerodromia						6
	Tabanidae	*Tabanus*		5		5	10	3
		Silivus	9	2, 5				
	Stratiomyidae	*Calparyphus*				9	9	3
		Euparyphus	9	10	9			
Megaloptera	Corydalidae	*Corydalus*	9	5		5, 8, 9	5, 7, 8, 9, 10	9
Coleoptera	Elmidae	*Optioservus*	6	6	6	6		6
		Microcylloepus	5	5	5	5, 8		5
	Dytiscidae	*Hydaticus*			8			
	Dryopidae	*Helichus*						9
	Gyrinidae	*Gyrinus*				9		
Plecoptera	Perlodidae	*Isoperla*	6		6	6	6	6

TABLE 3—Continued.

Order	Family	Genus	Jan	Mar	May	Jul	Sep	Nov
Odonata	Coenagrionidae	*Argia*	2, 3	2, 5, 9	2, 5, 8, 9	2, 9	2, 5, 9, 10	2, 3, 9
	Libellulidae	*Perithemis*		10		10	10	
		Paltothemis						9
		Brechmorhoga					9	9
	Gomphidae	*Erpetogomphus*						9
Hemiptera	Veliidae	*Rhagovelia*	9		9	9	9	9
		Microvelia					9	
	Naucoridae	*Ambrysus*				9	9	7
	Gelastocoridae	*Gelastocoris*					9	

mond Creek had very little detritus. *Oscillatoria* biomass was low throughout all tributaries.

In general, tributaries originating inside the Grand Canyon had greater mean annual biomasses of macroinvertebrates, primary producers (miscellaneous and *Oscillatoria* combined), and detritus than those originating from outside (Fig. 8). Lumbriculids and oligochaetes occurred only in tributaries that originated from springs inside the Grand Canyon (Fig. 5). With the exception of Nankoweap Creek, mean annual miscellaneous macroinvertebrate biomass was highest in creeks originating within the Canyon (Fig. 6).

MANOVA results showed that summer biomass varied significantly between years in Nankoweap Creek, LCR, Kanab Creek, Havasu Creek, Spring Canyon and Diamond Creek (Table 4). The summer communities in Paria River, Vasey's Paradise, Bright Angel Creek, and Tapeats Creek were more consistent over time, showing no difference in biomass between years.

DISCUSSION—Differences between tributaries of the Colorado River through Grand Canyon can be explained in terms of several abiotic parameters, including the stream's source and watershed characteristics. Five of the 10 tributaries examined in this study originate from spring sources within the Grand Canyon and the remaining five are fed primarily from large watersheds. Spring-fed streams often vary in physicochemical and biological characteristics from other types of streams (Covich, 1988). Most importantly, they tend to maintain a more constant aquatic environment than nearby streams supplied by runoff (Thorp and Covich, 1991). Temperatures in spring-fed streams usually are more constant and their discharge and velocities are usually more consistent over time because of connection to underground rivers. Streams that receive a large proportion of their water from watershed runoff tend to have a far less stable regime. These streams are subject to seasonal or periodic disturbances in the form of flash floods and desiccation. Tremendous amounts of suspended sediments are carried by these streams, especially in the arid southwest (Bane and Lind, 1978; Lewis and Harrel, 1978; Grimm and Fisher, 1989, 1991; Blinn et al., 1995; Shannon et al., 1996). Therefore, it is not surprising that tributaries

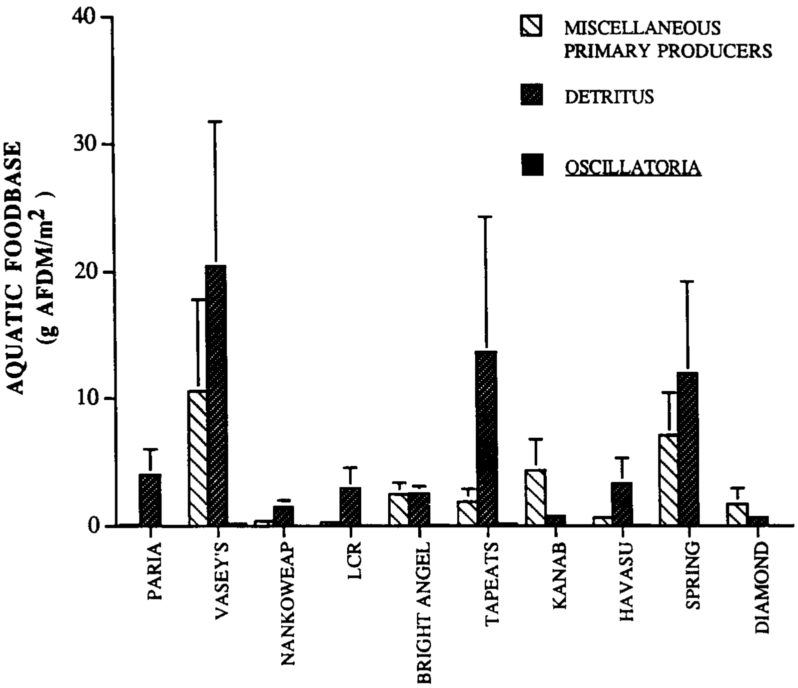

FIG. 7—Mean annual ash-free dry mass (g AFDM/m^2) of aquatic food base in 10 tributaries from 1991 bimonthly collections in the Colorado River through Grand Canyon. Error bars represent ±1 *SE*.

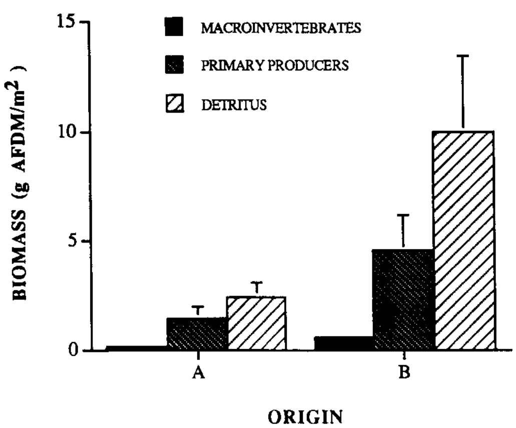

FIG. 8—Mean annual ash-free dry mass (g AFDM/m^2) of macroinvertebrates, primary producers, and detritus in tributaries of the Colorado River originating from outside (A) and inside (B) the Grand Canyon. Error bars represent ±1 *SE*.

originating from these different sources vary significantly in biotic composition and macroinvertebrate community structure.

Tributaries originating outside the Grand Canyon had higher conductivities with greater variation between months. LCR had the highest average annual conductivity (2.4 mS) and the greatest annual range (0.33–4.49 mS). This is an indication that at certain times of the year the LCR is carrying large amounts of total dissolved solids (TDS). Calcium carbonate, in particular, may pose problems when it precipitates out as travertine, and encrusts algae and invertebrates with calcareous deposits that may interfere with gas exchange, feeding, and reproduction.

Low macroinvertebrate diversity and biomass characterized Paria River, LCR, and Kanab Creek, all tributaries that originate from outside the Grand Canyon and drain large watersheds. Chironomids and *Hydropsyche oslari* were the only invertebrates found in Paria River collections during 1991. Hofknecht (1981)

TABLE 4—MANOVA results comparing 1991, 1993, 1994, and 1996 summer biotic communities in 10 major tributaries of the Colorado River through Grand Canyon. Univariates include lumbriculids (1), oligochaetes (3), simuliids (4), chironomids (5), miscellaneous macroinvertebrates (6), miscellaneous primary producers (7), detritus (8), and *Oscillatoria* (10). All categories were analyzed as ash-free dry mass (g AFMD/m^2) on ln+1 transformed data. Only significant univariates are indicated.

Tributary	Wilks' lambda	Approximate *F*-statistic	*df*	*P*	Significant univariates
Paria River	0.530	0.84	12,37	0.608	
Vasey's Paradise	0.150	1.25	24,32	0.272	1*, 4*
Nankoweap Creek	0.128	2.68	15,36	0.008	7***
Little Colorado River	0.047	6.76	12,37	0.000	4*
Bright Angel Creek	0.078	1.73	24,29	0.078	4**, 7*
Tapeats Creek	0.104	1.83	21,32	0.059	
Kanab Creek	0.027	3.82	21,32	0.000	7***
Havasu Creek	0.116	2.18	18,34	0.024	6**, 8***
Spring Canyon	0.035	2.67	24,29	0.006	1**, 5***, 7**
Diamond Creek	0.084	2.45	16,16	0.041	7***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

reported that a hydropsychid caddisfly was also the dominant invertebrate in Paria collections in 1977 and 1978. *Hydropsyche* larvae are widespread in erosional habitats where they construct silken nets to filter particles (diatoms, detritus, and animals) from the current (Merritt and Cummins, 1996). *Hydropsyche oslari*, chironomids, and gastropods were the only macroinvertebrate groups found in LCR, and *H. oslari* was found only in January collections, the only month when specific conductance was low (0.33 mS) compared to other months (0.92–4.49 mS). Gastropods, found only in January and July, increased the annual macroinvertebrate biomass of LCR, but their contribution to the community as a whole may be deceiving. Hofknecht (1981) did not report any gastropods from LCR, and gastropods are generally not thought to be common at this location. Kanab Creek had a slightly more diverse fauna, but macroinvertebrate biomass remained low.

Hofknecht (1981) also reported consistently low values for macroinvertebrate biomass and density in Paria River and Kanab Creek; only distributional data were reported for LCR. There are several possible explanations why these tributaries are inhospitable to many lotic invertebrates. They often undergo periods of reduced, or no flow in some reaches which can limit habitation by certain aquatic invertebrates. Some invertebrates are capable of inhabiting intermittent streams by adjusting their life cycles or by moving to hyporheic zones during periods of drought. These zones also may be a source of colonizers following desiccation. However, hyporheic zones usually are limited in xeric regions because of large amounts of suspended sediment carried in stream channels during flash floods. It is estimated that Paria River and LCR contribute a combined mean load of 1.12×10^7 metric tons of suspended sediment to the Colorado River every year (Andrews, 1991). Kanab, Havasu, and Diamond creeks also contribute sediment during flash floods and debris flows (Webb et al., 1991; Melis et al., 1995, 1996). These fine sediments tend to infiltrate cobble substrata, filling in interstitial spaces and reducing the amount of oxygen available to organisms (Wagner et al., 1993; Govedich et al., 1996). Sampling of the hyporheic zone of Colorado River tributaries in June 1992 and September 1993 yielded no invertebrates (J. Stanford and B. Ellis, pers. comm.). Deposits of travertine found below the wetted perimeter of some tributaries may also seal off the stream bed from interstitial spaces below, preventing any exchange between the two habitats.

Flash floods also contribute a high degree of instability to tributaries originating outside the Grand Canyon. High discharges cause significant mortality to individuals and eliminate important food resources (Grimm and Fisher, 1989; Blinn et al., 1995; Oberlin, 1995). Suspended sediments carried by these floods adversely affect aquatic invertebrates by reducing algal food, clogging feeding structures, damaging gas exchange structures, and dislodging organisms making them more susceptible to predation (Newcombe and MacDonald, 1991). Therefore, the timing of floods may cause significant variations in biotic communities between years in southwestern streams. With the exception of Paria River, all tributaries originating from outside the Grand Canyon showed differences in biomass between years, but three of the spring-fed tributaries were consistent over time.

Havasu Creek and Diamond Creek were also among the tributaries with the lowest macroinvertebrate biomass. These two tributaries differ from Paria River, LCR, and Kanab Creek because they receive most of their water from spring sources within the Grand Canyon, but were designated as originating from outside the Grand Canyon because they are influenced by intermittent streams above the spring heads. Therefore, flows in these creeks are regulated to a large extent by seasonal precipitation and flash floods (Hofknecht, 1981; Melis et al., 1996). These tributaries are heavily impacted by human use, as well. Havasu Springs is located on the Havasupai Indian Reservation and is used for recreational purposes. Above the spring, Havasu Creek is used for irrigation. Diamond Springs is located on the Hualapai Reservation and also is used for irrigation. Furthermore, Diamond Creek is the major take-out site for most commercial river trips and the heavily used road that provides the only access to this remote location follows and crosses the stream channel for 2 km near the confluence.

With the exception of Nankoweap Creek, spring-fed streams originating in the Grand Canyon had greater macroinvertebrate biomass and biodiversity than streams originating outside the Canyon. Discharge in Nankoweap Creek is the lowest relative to drainage area, therefore the watershed effect is likely more pronounced than for other tributaries. Greatest annual macroinvertebrate biomasses occurred in Bright Angel Creek and Spring Canyon. Hofknecht (1981) found the highest numbers of benthic invertebrates and highest mean annual biomass in Bright Angel and Tapeats creeks, but only compositional data were reported from Vasey's Paradise, Nankoweap Creek, or Spring Canyon. Because all of these tributaries are perennial, they provide a more stable and consistent habitat for aquatic organisms. For example, water temperatures are less variable, flooding is less intense, and sediment loads are much lower. These tributaries also are unregulated and human impact is minimal. Finally, mean annual biomass of primary producers and detritus are greater in tributaries originating inside the Grand Canyon. These are a major food resource for macroinvertebrates and provide substratum for growth of periphyton, another important food source.

The annual thermal regime in these tributaries is also an important structuring component governing biodiversity. Tapeats Creek and Spring Canyon have annual thermal ranges of ca. 7.6°C that support 14 and 18 genera of hemimetabolous aquatic insects, respectively. However, their annual ranges do not overlap with Tapeats Creek which is colder ($\bar{X}$ = 14.6°C *SE* ± 2.3) than Spring Canyon ($\bar{X}$ = 23.9°C ± 1.3). These thermal ranges are apparently optimum for aquatic insect development for both growth and fecundity (Vannote and Sweeny, 1980). The mainstem Colorado River supports virtually no Ephemeroptera, Plecoptera or Trichoptera (Stevens et al., 1997) and is cold stenothermic (ca. 10°C), therefore not allowing successful recruitment from tributaries.

Macroinvertebrate biomass in Nankoweap Creek was more similar to those tributaries originating outside the Grand Canyon than to the other spring-fed tributaries. The relatively long drainage (14.8 km) and low discharge of Nankoweap Creek (0.1 m^3/s), which also lacks riparian vegetation, result in a small exposed creek where negative watershed characteristics override positive attributes of this spring system. Also, Nankoweap Creek has heavy calcium carbonate deposition and a wide annual temperature range of 27.4°C, which may limit macroinvertebrate fauna in this tributary. Total plant biomass was also low in Nankoweap Creek, suggesting that food may be a limited resource.

A stream's source and watershed characteristics may have a significant impact on macroinvertebrate communities. Within the Grand Canyon, tributaries that receive a substantial amount of their water from terrestrial run-off have low macroinvertebrate diversity and biomass compared to tributaries that are fed from spring sources within the Canyon. These tributaries typically are less stable, have higher turbidity, and fewer food resources. As a result, few species or individuals can be sustained in these habitats. Although these tributaries are relatively remote and minimally impacted within the Grand Canyon itself, it is apparent that irrigation, grazing, and other land use practices that reduce flow and increase sedimentation within these watersheds have repercussions far downstream of where they occur. Given the importance of these tributaries to the native fish community of Grand Canyon (Carothers and Brown, 1991) continual monitoring of all aspects of their ecology is a prerequisite to understanding dynamics of native fish populations.

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