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National Park, Utah, USA
Author(s): G. Allen Haden, Joseph P. Shannon, Kevin P. Wilson, W. Blinn
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BENTHIC COMMUNITY STRUCTURE OF THE GREEN AND COLORADO RIVERS THROUGH CANYONLANDS NATIONAL PARK, UTAH, USA

G. ALLEN HADEN,* JOSEPH P. SHANNON, KEVIN P. WILSON, AND DEAN W. BLINN

Department of Biological Sciences, P.O. Box 5640, Northern Arizona University, Flagstaff, AZ 86011
*Correspondent: Allen.Haden@nau.edu

ABSTRACT—We sampled the aquatic benthos at 6 remote sites on the Colorado and Green rivers through Canyonlands National Park, Utah, USA. This study provides the first published description of benthic standing mass, invertebrate community composition, and primary carbon source for this portion of the Colorado River system. High suspended sediment concentrations prohibited growth of primary producers. The primary carbon source for benthic invertebrates was terrestrial organic matter. The invertebrate community was composed of 49 taxa, mostly mayflies, caddisflies, and diptera, which were dominated by filterer/collector species. A smaller portion of the community was made up of predatory stoneflies and odonates. Standing mass of invertebrates on cobble substrates within a given site was stable over the multiyear sample period (1993 through 1996) and was comparable with other southwestern streams (overall mean = 0.41 g/m² ash-free dry mass ± 0.01 SE). Invertebrate standing mass at each site was controlled by the availability of primary carbon. Primary carbon availability was controlled by supply to the site and retention within the site. Both aspects might be influenced by anthropogenic alteration of the river basin and discharge patterns upstream of the study site.

RESUMEN—Muestreamos bentos acuáticos en 6 sitios remotos en los Ríos Colorado y Green en el Parque Nacional de Canyonlands, Utah, USA. Este estudio presenta la primera descripción de biomasa actual de bentos, composición de la comunidad de invertebrados, y fuentes de carbón primario para esta parte del sistema del Rió Colorado. La concentración alta de sedimentos suspendidos impidió el crecimiento de productores primaries. La fuente de carbón para los invertebrados bentónicos fue materia orgánica terrestre. La comunidad invertebrada consistió de 49 taxa, de los cuales la mayoría fueron de ephemeróptera, tricóptera, y díptera, que fueron dominados por filtradores/colectores. Una porción más pequeña de la comunidad estuvo compuesta de los depredadores plecóptera y odonata. La biomasa actual de invertebrados en sustrato de piedras en un sitio fue estable entre la época de muestro multi-anual (1993–1996) y fue comparable a otros riachuelos en el suroeste de USA (promedio general = 0.41 g/m² masa seca sin cenizas ± 0.01 EE). La biomasa de invertebrados en cada sitio estuvo controlada por la disponibilidad de carbón primario. El carbón primario disponible estuvo controlado por el abastecimiento al sitio y retención en el sitio. Los dos aspectos pueden ser influidos por cambios antropogénicos en la cuenca y los patrones de descargas río arriba del sitio de estudio.

The Colorado River of the southwestern United States is highly regulated and segmented by impoundments throughout much of its course (Stanford and Ward, 1986; Richter et al., 1998). Regulation started soon after settlement of the area in the 1800s, and there is little information on the pre-settlement benthic flora and fauna of the main stem of the Colorado River in this arid region (Ward et al., 1986; Blinn and Cole, 1991). Ecological information from this period would have provided insight on the benthic ecology of a large desert river, as well as provided ground work to man-

agers concerned with the state of the present-day lotic ecosystem.

Stanford and Ward (1986) proposed that the lower Green River and Colorado River in Canyonlands National Park might provide the best example of the pre-regulated Colorado River because these reaches retain similar hydrographs to the pre-dam condition and are the farthest downstream from large impoundments on any portion of the present day Colorado River system. The serial discontinuity concept predicts that the effects of impoundment decrease with increasing distance down-

stream and many ecological parameters will return to a pre-impoundment state (Ward and Stanford, 1983).

The Green and Colorado rivers in Canyonlands National Park (CNP) provide important habitat for populations of endangered native fish as well as many introduced species, which depend on the benthic community as a food resource (Holden and Stalnaker, 1975; Valdez and Williams, 1993). The availability and form of food to support native fish populations in this generally turbid river has been the subject of much speculation. Ward et al. (1986) considered the pre-dam river to provide poor habitat for benthic organisms due to high suspended sediment loads and severe floods that hindered development of an invertebrate assemblage. Accordingly, invertebrate standing mass should be low and vary in response to flooding. In contrast, Cummins (1973) suggested that there should be little temporal variation in standing mass of macroinvertebrates in temperate streams even though the taxonomic composition of the community changes in response to environmental conditions. We predict that aquatic macroinvertebrate assemblages in these rivers should exhibit stable standing mass even as community composition changes seasonally. We base this prediction on the hypothesis of Poff (1992) that aquatic communities will persist through predictable changes in environmental conditions that have previously exerted selective pressures on the community. Flooding and suspended sediment concentrations exhibit predictable variations in the Colorado River. The aquatic community should be adjusted to theses extremes and remain relatively stable throughout the year.

Our study examines these concepts of community development at sites that have high suspended sediment concentrations, have high annual variability in discharge, and are located in an arid biome. We provide the first description of the abundance, standing mass, taxa, feeding guilds, and primary carbon sources for benthic macroinvertebrate communities at 6 sites on the Green and Colorado rivers within CNP. We discuss measurements of abiotic factors governing the distribution and abundance of benthos such as discharge, water temperature, and suspended sediment concentrations, as well as anthropogenic effects that could affect composition and standing mass of the ben-

thos in these sites. Previously published studies on the type and abundance of aquatic macroinvertebrates near our study area are limited to 1 site near the Colorado-Utah border (Ward et al., 1986) and at the Ouray National Wildlife Refuge, Utah (Wolz and Shiozawa, 1995). Neither of these study sites is within 100 km of our study sites.

METHODS AND MATERIALS—*Study Area*—The Colorado River drains approximately 600,000 km² west of the Rocky Mountains and is the largest lotic system of the American Southwest (Stanford and Ward, 1986; Fig. 1). Much of the water is supplied by mountainous headwaters (Andrews, 1991). The study area is located in the arid Colorado Plateau, which represents over 37% of the drainage area but provides only 15% of the total runoff for the basin (Andrews, 1991). The sparsely vegetated plateau region supplies large quantities of sediment, which keeps the river turbid for all but short periods of the year (Woodbury, 1959; Andrews, 1991).

Distances from the study sites to the nearest major upstream dams are longer than anywhere else in the drainage (Flaming Gorge Dam, Wyoming, 654 km; Blue Mesa Reservoir, Colorado, 395 km). However, large portions of the drainage upstream of the study sites are disconnected from the rest of the river by impoundments on the main-stem rivers and their tributaries (Fig. 1). Of the 115,000-km² Green River drainage, 35% (39,847 km²) is above Flaming Gorge Dam. Likewise, on the Colorado River above its confluence with the Green River, more than 50% (35,207 km²) of the 67,000-km² drainage is above major impoundments. Granby Reservoir on the Colorado River, Blue Mesa Reservoir on the Gunnison River, Williams Fork Reservoir on the Williams Fork, and McPhee Reservoir on the Dolores River are the major impoundments that act as discontinuities.

Collections were made at 6 study sites on the Colorado and Green rivers within CNP. There were 2 sites on the Green River (Millard Canyon and Jasper Canyon; 53.6 and 15.2 km above the confluence, respectively). The Colorado River above the confluence with the Green River was represented by 2 sites (Shafer Canyon and Salt Canyon; 59.2 and 5.8 km above the confluence, respectively). The Colorado River below the confluence in Cataract Canyon also contained 2 sites (Rapid 3 and Rapid 11; 8.0 and 14.0 km below the confluence, respectively; Fig. 1). The Green and Colorado rivers above their confluence are characterized by low-gradient, alluvial channels. The Colorado River below the confluence in Cataract Canyon is a canyon-bound reach with steep gradients, rapids, and coarser substrates.

Physicochemical Data—Discharge estimates for the study sites above Lake Powell were collected by Unit-
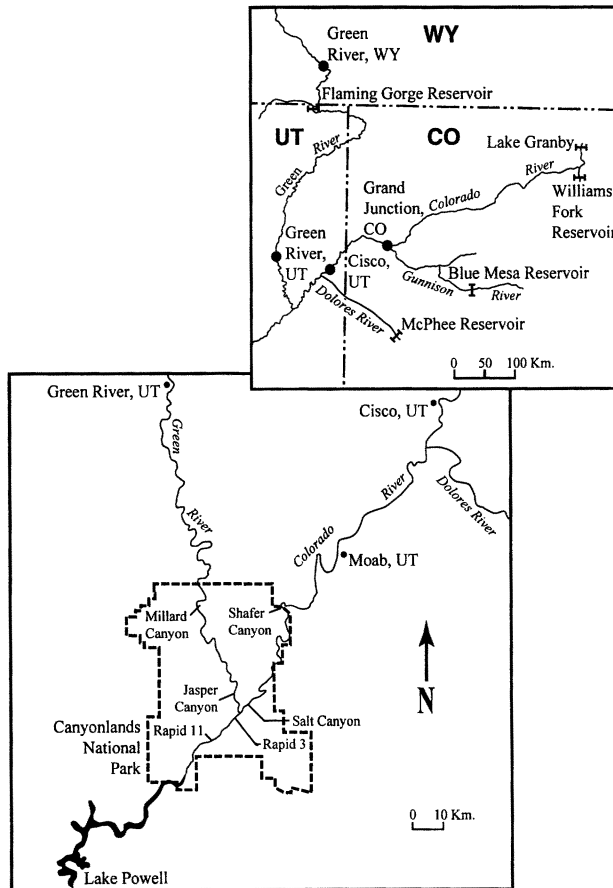
FIG. 1—Study area with major impoundments and benthic sampling site locations on Green and Colorado rivers, Canyonlands National Park, Utah.

ed States Geological Survey gauges at Cisco, Colorado and Green River, Utah (Fig. 1). Hydrographs for each station were constructed to illustrate the timing and magnitude of flows over base flow from 1993 through 1996.

Water temperature (°C) was continually monitored at 30-min intervals in each of the 3 reaches above Lake Powell from July 1995 to October 1996 using Hobo Temp temperature data loggers (Onset Computers, Inc., Pocasset, Massachusetts). Various parameters of temperature were calculated from the continuous data sets, including average temperature, maximum temperature, minimum temperature, and total annual degree-day accumulation (Σ mean daily water temperature).

Water quality variables including temperature, conductivity (mS), dissolved oxygen (DO; mg/L), and pH were measured with a Hydrolab Scout II at each sample site concurrent with benthic sampling. Water clarity was estimated using a Secchi disc. Light availability ($\mu E/m^2/s$) within the water column was

estimated using a LiCor spherical photometer. Suspended particulate concentrations were estimated by collecting a 1-L grab sample ($n = 3$) from the top 0.5 m of the water column. The sample was filtered through a pre-weighed Whatman 934 AH glass filter, dried to a constant weight at 60°C, and weighed for dry weight of particulates. The filters were then burned for 1 h at 500°C for ash-free dry mass determinations of the organic portion of particulates. Time of day and general site conditions were also recorded at the time of collection.

Nutrient samples ($n = 3$ per site, per sample period) were collected from above the confluence for both the Green and Colorado rivers and below the confluence on the Colorado River in Cataract Canyon during July 1996 and May 1997. These samples were analyzed for nitrate-nitrogen (NO_3-N), ammonia (NH_3), and ortho-phosphate (O-PO_4). Samples were analyzed on a Technicon Auto Analyzer II.

Benthic Collections—Collections of aquatic benthos on cobble substrates, soft sediment substrates in

pools, and drift were made during October 1993, October 1994, October 1995, March 1996, July 1996, and October 1996. Cobble bars were sampled using a modified Hess substrate sampler for randomly spaced collections on each cobble bar ($n = 6$). Sampling was standardized by stirring the benthos for 30 s with a metal trowel for each sample. Depth and water velocity (m/s) were collected for each sample.

Pool habitats were sampled with a Petit Ponar dredge. Four collections along 3 evenly spaced transects were made from shoreline to thalweg ($n = 12$) at each site. Depth was recorded for each sample. Samples were rinsed through a 0.60-mm sieve to separate sediments from organic material. All samples were preserved in 70% ethanol and sorted in the laboratory by eye without magnification.

Each benthic sample was sorted into 3 categories: phytobenthos (all algae and aquatic macrophytes), detritus, and invertebrates. Invertebrates were identified to genera when possible and enumerated at the family level. All categories were dried at 60°C to a constant mass, weighed, burned for 1 h at 500°C, and weighed again to estimate ash-free dry mass. Preservation in ethanol has been shown to alter the AFDM of benthic invertebrates (Stanford, 1973). To allow conversion of AFDM to calories using estimates from Cummins and Wuycheck (1971), we made comparison collections of each benthic category. Regressions of AFDM of preserved material to AFDM of fresh material were used to correct for the effects of preservation. Regression results are given in Haden (1997). Ash-free dry mass estimates presented in the results have been converted to unpreserved equivalents.

Organic drift was estimated from samples ($n = 3$ per sample period) taken from the Green River and Colorado River above the confluence, as well as the Colorado River in Cataract Canyon, on trips from October 1995 through October 1996. Samples were taken from the surface of the river with a circular tow net (48-cm opening and 500-μm mesh). Current velocity (m/s) was measured with a Marsh-McBirney electronic flow meter to allow volumetric calculations. Samples were dried, and AFDM for the unsorted samples was estimated in the same manner as the benthic samples.

Statistical Analyses—All biomass comparisons were made using AFDM per unit area (g/m²). Patterns in physical parameters and benthic standing mass were analyzed using multivariate analysis of variance (MANOVA). Predictor variables of trip date, site, and habitat (pool or cobble) were tested against response variables of biomass from each benthic category. Post-hoc Tukey tests (Bonferroni adjusted $P \leq 0.05$) on univariate models that showed significant patterns ($P \leq 0.05$) were used to further define patterns in benthic biomass. We examined the relationship of phytobenthic and detrital standing mass to

invertebrate standing mass and depth using regression analysis. Benthic data were transformed by ln + 1 transformations to increase homoscedascity of variance. Drift data were analyzed using non-parametric Mann-Whitney U tests because of smaller sample size and non-normal distributions. All calculations and analyses were performed using SYSTAT (version 5.1) computer software (SYSTAT, 1992).

RESULTS—*Physicochemical Parameters*—The hydrographs for the Green and Colorado rivers are characterized by fairly constant minimum discharges for most of the year (Fig. 2). Minimum discharge on the Green and Colorado rivers was approximately 85 m³/s. Discharges in Cataract Canyon below the confluence are a combination of the 2 discharge estimates. Maximum discharge was lower on the Green River compared to the Colorado River above the confluence. Maximum discharge ranged from 1,416 to 413 m³/s in the Colorado above the confluence, and the Green River maximum discharge ranged from 850 to 330 m³/s. Although there was considerable variation in the amount of peak discharge from year to year, the timing of peak discharge was fairly consistent. Maximum discharge occurred in June for the 5 years examined in this study (Fig. 2). Discharge above base flow in both rivers generally occurred between March and July annually for the years examined.

Water temperature for the Green and Colorado rivers is similar (Fig. 3). Temperatures ranged from freezing during the winter months to maximum temperatures >25°C in the summer months (Table 1). The 16 months of continuous temperature data showed that the timing of peak high temperatures occurred in late August in 2 consecutive years, suggesting that, like the hydrograph, water temperature patterns are temporally predictable from year to year in response to climate conditions. Annual accumulations of water temperature degree-days were similar for both the Green and Colorado rivers. Annual degree-day sums are 4,792 for the Green River and 4,810 for the Colorado River above the confluence. Water temperatures in Cataract Canyon were intermediate between the Green and Colorado river above the confluence.

The Green and Colorado rivers through Canyonlands National Park are generally turbid. Secchi depths were <0.4 m during any
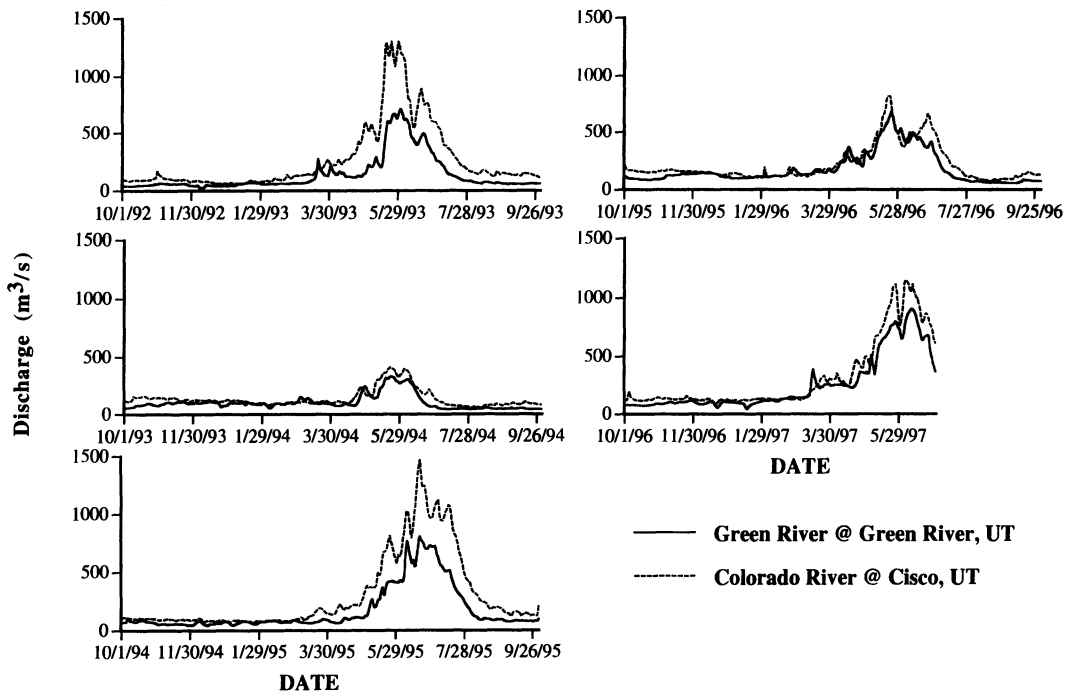
FIG. 2—Mean daily discharge (m³/s) for Green River at Green River, Utah and Colorado River at Cisco, Utah (October 1992 through May 1997). Discharge recorded at United States Geological Survey gauging stations. Discharge at Cataract Canyon estimated by combining flows from Green and Colorado river gauges.
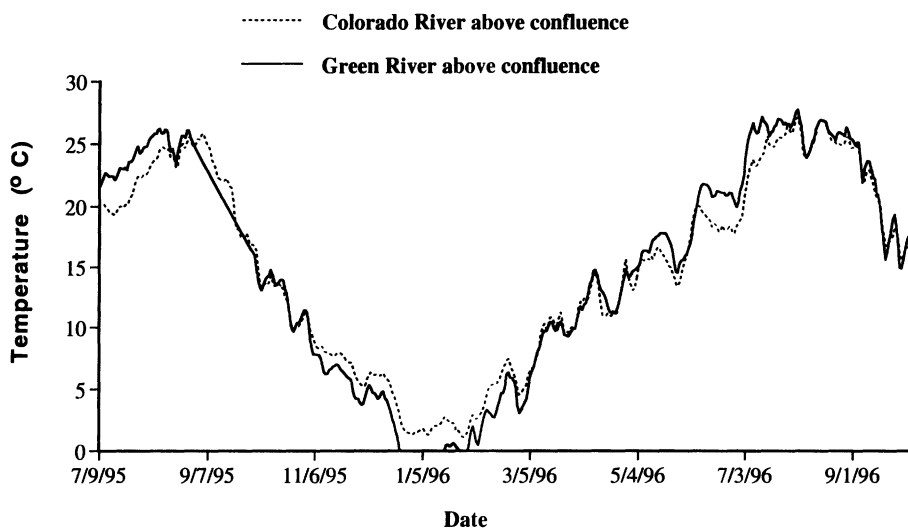

FIG. 3—Continuous water temperature record (°C) for Colorado River and Green River above their confluence from July 1995 through October 1996. Thermal record for Cataract Canyon is incomplete but temperatures are intermediate between Green River and Colorado River above confluence.

TABLE 1—Selected physicochemical parameters from Green River and Colorado River, above their confluence, and Cataract Canyon, Utah. Data collected from October 1993 through October 1996. Mean ± SE, (range), and number of samples (n) given for each parameter. * = samples taken during October 1996 and May 1997 only.

	Green River (above confluence)	Colorado River (above confluence)	Colorado River Cataract Canyon
Dissolved oxygen (mg/L), n = 7	9.3 ± 0.1, (7.4–10.8)	9.9 ± 0.1, (8.5–11.1)	9.6 ± 0.1, (8.3–10.6)
pH, n = 7	8.2 ± 0.01 (8.0–8.6)	8.1 ± 0.01 (8.0–8.3)	8.1 ± 0.01 (7.8–8.4)
Conductivity (mS), n = 7	0.854 ± 0.013 (0.409–1.035)	1.088 ± 0.018 (0.363–1.357)	0.958 ± 0.018 (0.369–1.270)
Temperature (°C), n = 365	12.1 ± 8.65 (0.0–26.6)	12.8 ± 2.24 (1.1–25.9)	insufficient data
Secchi depth (m), n = 7	0.11 ± 0.01 (0.04–0.25)	0.16 ± 0.01 (0.08–0.40)	0.09 ± 0.01 (0.03–0.20)
*NH_4 (mg/L), n = 6	(<0.020–0.057)	(0.023–0.025)	(0.030–0.040)
*NO_3^- (mg/L), n = 6	(0.020–0.247)	(0.337–0.510)	(0.263–0.453)
*$O-PO_4$ (mg/L), n = 6	(0.0500–0.303)	(0.123–0.307)	(0.133–0.127)

sampling trip and generally <0.2 m (Table 1). Suspended sediment loads in the top 0.5 m of the water column were as high as 2.5 g/L, which reduced light availability to the substrate. Light extinction coefficients showed that compensation depth (available light energy <20 $\mu E/m^2/s$) ranged from 1.06 m on the Colorado River above the confluence in March 1996 to 0.12 m in Cataract Canyon during October 1995. Although low turbidity conditions never occurred during our sample periods, we have observed that the Green and the Colorado rivers above the confluence became less turbid after long periods of base flow in the winter of 1996 just before ice formation in the channel (A. Haden, pers. observ.).

Other water quality parameters (DO, conductivity, and pH) were also similar between the Green and Colorado rivers. The ranges of these parameters overlapped for both rivers, but the Colorado River tended to have slightly higher conductivities than the Green River (Table 1). Nutrient levels (NH_3, NO_3-N, and O-PO_4) increased >50% during the rising limb of the hydrograph or when local ephemeral tributaries were in spate compared to base flow conditions. Nutrient levels were generally within the bounds of unpolluted waters (Reid and Wood, 1976; Table 1).

Standing Mass Estimates—Cobble versus Pool Habitat—Detrital, macroinvertebrate, and phytobenthic AFDM showed significant differences between grouping variables of habitat type (cobbles or pools), sampling date, and study site (Table 2). Because cobbles contained 8 times more standing mass of macroinvertebrates (0.41 ± 0.008 *SE* versus 0.05 ± 0.01 g/m^2 AFDM) and 18 times more standing mass of phytobenthos than pools (1.27 ± 0.49 and 0.07 ± 0.03, respectively), subsequent analyses for differences between trip date and study site were conducted on pool and cobble habitats separately. Overall, detrital biomass in pools (35.46 ± 4.47) was not significantly different than detrital biomass in cobbles (17.06 ± 2.35).

Pool Habitats—Pools varied in their capacity to hold detritus by sample site (ANOVA, $F = 6.3515$, $df = 488$, $P = 0.01$) and exhibited no significant change by trip date. Morphology of pools determined the capacity to hold detritus. Regression analysis showed detrital standing mass was higher in shallow near-shore areas

TABLE 2—Results of multivariate analysis of variance (MANOVA) comparing benthic categories among sites, trip dates, and habitat (pool or cobble) at 6 sampling sites in Canyonlands National Park, Utah. Data collected during 7 sampling trips from October 1993 through October 1996. Response variables of macroinvertebrate (I), phytobenthic (P), and detrital (D) standing mass (AFDM g/m^2) analyzed against grouping variables of trip date, sample site, and substrate (cobble or pool). Only significant ($P \leq 0.05$) response variables shown. Overall Wilks' Lambda was significant ($P \leq 0.0001$).

Source	Wilkes' Lambda	Approximate F-statistic	df	P	Response variable
Trip date	0.961	9.783	3, 726	<0.0001	I, P
Site	0.945	4.010	3, 726	<0.0001	I, D
Habitat	0.849	42.988	3, 726	<0.0001	I, P

with low velocity ($R^2 = 0.05$, $n = 489$, $P < 0.001$). Deeper pools located in constricted sites that showed signs of scouring contained less detritus as a whole. However, when analysis of detritus standing mass was constrained to samples <2 m in depth, there was no significant difference between sites. Invertebrate and phytobenthic standing mass was generally low and did not vary by either trip date or sample site.

Cobble Habitats—Cobble substrates showed significant overall variation in invertebrate and phytobenthic standing mass by trip date, and invertebrate and detrital standing mass varied by sample site (Table 3). However, variation by sample site was more pronounced and biologically meaningful than variation by trip date. Five of 6 sites (Millard, Shafer, Salt, Rapid 3, and Rapid 11) showed no significant variation in invertebrate standing mass by sample date. Only 1 site (Jasper) showed significant variation of invertebrate standing mass among trips ($F = 2.41$, $df = 6$, $P = 0.046$). However, post-hoc Bonferroni adjusted, pairwise, Tukey comparisons showed no significant differences among dates. The greatest difference between

mean values of any 2 trips was at Jasper with 1.9 ± 1.3 SE g/m^2 AFDM in July 1996 compared to 0.004 ± 0.004 in October 1994. Estimates of caloric standing mass ranged from approximately 436 to 13,294 (cal/m^2) over all sites.

Although invertebrate standing mass was generally stable over time within a given site, there were differences in standing mass between sites. Cobble habitat at Millard on the Green River supported significantly more invertebrate standing mass than all other sites (Fig. 4).

Phytobenthic standing mass on cobble habitats was generally low (1.27 ± 0.49 SE g/m^2 AFDM) and peaked during October 1994 at 7.1 ± 3.12. This increase was caused by an increase in the standing mass of the crust-forming cyanophyte, *Oscillatoria*, which comprised over 95% of the phytobenthic standing mass. During other sample periods, the filamentous green alga *Cladophora* was the dominant alga, even though standing mass was low (0.11 ± 0.034).

Although phytobenthic biomass was low, there was a high standing mass of allochtho-

TABLE 3—Results of multivariate analysis of variance (MANOVA) comparing benthic categories among sites and trip dates on cobble substrates at 6 sampling sites in Canyonlands National Park, Utah. Data collected during 7 sampling trips from October 1993 through October 1996. Response variables of macroinvertebrate (I), phytobenthic (P), and detrital (D) standing mass (AFDM g/m^2) analyzed against grouping variables of trip date and sample site. Only significant ($P \leq 0.05$) response variables shown. Overall Wilks' Lambda was significant ($P \leq 0.0001$).

Source	Wilkes' Lambda	Approximate F-statistic	df	P	Response variable
Trip date	0.885	10.23	3, 235	<0.0001	I, P
Site	0.821	17.083	3, 235	<0.0001	I, D

TABLE 4—Seasonal and site occurrence of invertebrate taxa collected from cobbles and pools in Green and Colorado rivers in Canyonlands National Park, Utah. Collections made during 7 seasonal trips from October 1993 through October 1996. O = October, M = March, J = July. * = isolated pool habitat only.

	Green River		Colorado River		Cataract Canyon	
	Millard	Jasper	Shafer	Salt	Rapid 3	Rapid 11
ODONATA						
Coenagrionidae						
Argia sp.	O	O, M	O	O, M, J	O, J	O
Gomphidae						
Ophiogomphus sp.	J	J		J		
Stylurus sp.	M		O		O	M
Erpetogomphus sp.	O					
Gomphus sp.						O
EPHEMEROPTERA						
Heptageniidae						
Heptagenia sp.	O, M	O, J	O, J	O, J	O, J	O, J
Rithrogena hageni	O, M	M				M
Trichorthidae						
Tricorthodes sp.	O, J	J	O	O	J	
Polymitarcyidae						
Ephoron sp.	J	J	J	J	J	J
Leptophlebiidae						
Traverella sp.	O, J	J	O	O, J	O, J	O, J
Baetidae						
Baetis sp.	O	O, J	O		J	J
Acentrella sp.	O		O	O		O, J
Camelobatidius sp.	O				O, J	J
Paracloedes sp.	J		J	M	M	M
Oligoneuriidae						
Lachlania sp.	J	J				
Homoeoneuria sp.	O		O			
Isonychiidae						
Isonychia sp.				O, J		
PLECOPTERA						
Perlodidae						
Isogenoides sp.			O			
Isoperla sp.	O		O			
Frisonla sp.		M				M
Perlidae						
Doroneuria sp.	J		O		J	
Acroneuria sp.	O, M			O		
Taeniopterygidae						
Taenionema sp.	M					
Oemoteryx sp.		M				
TRICOPTERA						
Hydropsychidae						
Hydropsyche sp.	O			O, J	O, J	
Smicridea sp.	O, J	O, J		J		O, J
Ceratopsyche sp.	J		O, J		J	
Cheumatopsyche sp.	O, M	M				J
Hydroptilidae						
Hydroptila sp.	O		J			
Brachycentridae						
Brachycentrus sp.		J				
Leptoceridae						
Nectopsyche sp.		J				

TABLE 4—Continued.

	Green River		Colorado River		Cataract Canyon	
	Millard	Jasper	Shafer	Salt	Rapid 3	Rapid 11
HEMIPTERA						
Corixidae						
Sigara sp.	O*					
Trichocorixa sp.			O			O
Hesperocorixa sp.					O*	
Notonectidae						
Notonecta sp.					O	O*
DIPTERA						
Chironomidae	O, M	O, J	O, J	O, M, J	O, M, J	O, M, J
Tabanidae						
Silvius sp.						M
Empididae						
Chelifera sp.	M	O	M	M		M
Hemerodromia sp.			J	O, M		
Ceratopogonidae	O					
Tipulidae						
Tipula sp.		O				
Simuliidae	O	M, J		J	O, J	O, M, J
LEPIDOPTERA						
Pyralidae						
Petrophila sp.	O					
COLEOPTERA						
Elmidae						
Huleechius sp.	O, M	M		M		
Neoelmis sp.	O			O, J	J	J
Microcylloepus sp.	O, M	J		O, M, J	J	J
Atractelmis sp.		O				
MEGALOPTERA						
Corydalidae						
Corydalus sp.	O, J	O, J			O	
NEMATOMORPHA				M	J	O, M
HYDROCARINA		J	M			

nous detritus available as a carbon source for higher trophic levels (17.06 ± 2.35 SE g/m² AFDM). Detrital standing mass was significantly higher at sites on the Green River (Millard and Jasper) than sites in Cataract Canyon (Rapid 3 and Rapid 11; Fig. 5). Detrital standing mass at sites on the Colorado River was not significantly different from either Green River or Cataract Canyon sites. In general, detrital standing mass on cobble bars was a significant predictor of invertebrate standing mass (R^2 adjusted = 0.14, $P < 0.001$, $n = 240$).

Community Composition—The invertebrate community was composed primarily of aquatic insects associated with cobble habitats. Forty-nine taxa representing 13 orders of aquatic macroinvertebrates were found in CNP (Table 4). Mayflies were the most diverse with 12 taxa. Plecopterans and trichopterans were the second most diverse groups with 6 taxa each. Most taxa were either filter/collectors or predators, reflecting the primary food resource available in CNP. Grazer and shredder taxa were low in abundance and diversity.

Drift—Organic drift was significantly higher on the Green River than the Colorado River above the confluence or in Cataract Canyon (Fig. 6). Within each drift sample site there was little temporal variation in organic drift with 2 exceptions. In October 1996, the Green River had significantly less organic drift than any of the 3 previous sampling periods, decreasing from previous levels by an order of magnitude to 0.007 ± 0.004 SE g/m³ AFDM. During the
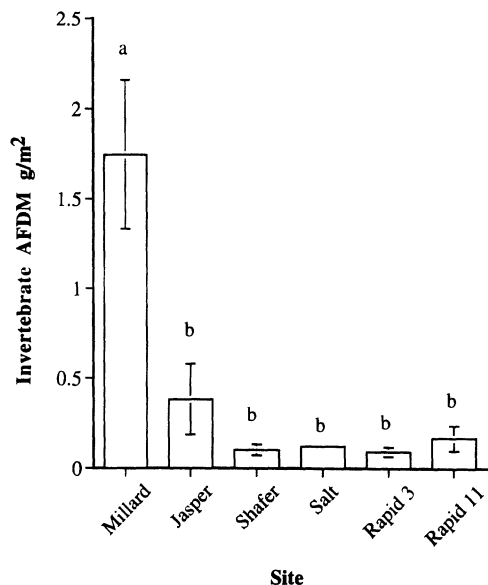
FIG. 4—Mean invertebrate biomass estimates (AFDM g/m² ± SE) from cobble substrates at 6 sampling sites in Canyonlands National Park, Utah. Invertebrate biomass generally constant over time within a site but varied significantly between sites (Bonfferoni adjusted $P < 0.05$). Significant differences between sample sites denoted by dissimilar letters. For all sites $n = 42$, except Millard and Shafer, $n = 36$.

FIG. 5—Mean detritus biomass estimates (AFDM g/m² ± SE) across all sample dates from cobble substrates at 6 sampling sites in Canyonlands National Park, Utah. Detrital biomass constant over time within a site but varied significantly between sites (Bonfferoni adjusted $P < 0.05$). Significant differences between sample sites denoted by dissimilar letters. For all sites $n = 42$, except Millard and Shafer, $n = 36$.

same sample period, organic drift in the Colorado River above the confluence increased 5-fold to 0.52 ± 0.038 in response to local ungauged runoff events.

DISCUSSION—The primary carbon source driving the aquatic ecosystem of the Colorado and Green rivers in Canyonlands National Park is terrestrially derived (allochthonous) organic material. High sediment loads, which persist for most of the year, block light penetration into the water column and severely limit photosynthetic (autotrophic) production of primary carbon. Suspended sediment has been shown to limit light penetration through the water column and decrease primary production and standing mass of algae (Lloyd et al., 1987). High suspended sediment concentrations also limit the growth of algae through abrasion (Fisher et al., 1982; Duncan and Blinn, 1989). The source of allochthonous materials in CNP might not be totally terrestrial. Some materials might be derived from within
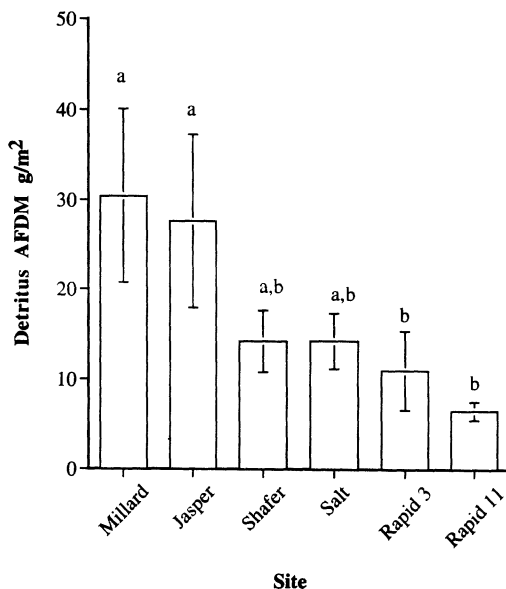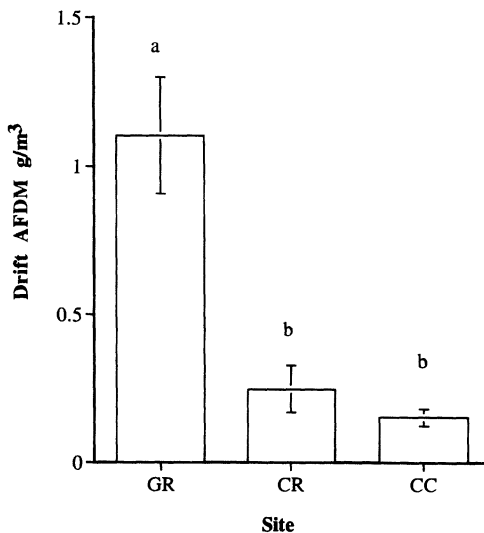

FIG. 6—Organic drift biomass (AFDM g/m³ ± SE) averaged over 4 sampling trips for Green River above confluence (GR), Colorado River above confluence (CR), and Cataract Canyon (CC). Analyses did not include drift above 0.5 m in size. Significant differences ($P < 0.05$) between sample sites denoted by dissimilar letters.

stream processes that take place upstream from the study area. Subsequently, this material is imported into the study area. Additionally, the energy used by higher trophic levels might be produced by bacterial and fungal production (sensu Cummins, 1974). This microbial production is dependent on the larger allochthonous particles for substrate and carbon source.

The feeding guilds of the invertebrate assemblage reflect the reliance on allochthonous detritus as a primary carbon source. The aquatic invertebrates in CNP are dominated by filter/collector organisms (simuliids and filtering mayflies). The feeding guilds of aquatic invertebrates have been shown to be good indicators of stream function (Cummins, 1974; Wallace and Webster, 1996; Covich et al., 1999).

Although there were spatial differences caused by site conditions, standing mass within a site was generally constant, supporting the hypothesis of Cummins (1973), which predicts that standing mass is relatively stable for temperate streams. The biological stability of this invertebrate assemblage, even when under the influence of highly variable physical parameters, is an important aspect of the ecology of this system. Poff (1992) predicted that assemblages could persist through short-term environmental changes if they have life history strategies that allow them to avoid or endure the change. This strategy is only successful when the timing and magnitude of environmental variability is predictable.

Standing mass of invertebrates at each site is a function of food availability at each site. Food resource limitation has been shown to have negative effects on the standing mass of invertebrates in a detrital-based ecosystem (Wallace et al., 1999). Our study showed similar results, in that invertebrate standing mass at each site was well correlated with detrital standing mass. The factors that regulate detrital standing mass defined most of the differences in invertebrate biomass between sites.

The organic matter dynamics of these rivers are crucial to the understanding of the benthic ecology. Other studies have shown that standing mass of detritus is regulated by both the supply of allochthonous materials and the capacity for a specific site to retain those materials for processing by invertebrates (Bilby and

Likens, 1980; Winterbourn et al., 1981; Wallace et al., 1999). Our results were not clear as to the exact mechanisms that governed detrital standing mass. However, 2 hypotheses were indicated. Our data showed that the amount of drift (as an indicator of supply) was generally higher on the Green River than on the Colorado River. The supply of organic material for the Green River should be greater than the Colorado River because the land area below large dams available to contribute particulate organic materials was greater. This implies that in arid land rivers, drainage area, as well as distance downstream from a dam, can be an important factor contributing to recovery from impoundment. As an alternative hypothesis, variation in the hydrograph might play an important role in detrital retention. Stream power has been shown to play an important role in retention of organic matter (Speaker et al., 1984). Richter et al. (1998) showed that the hydrology of the Colorado River might be more affected by dams with respect to timing and duration of flows than the Green River. These variations might negatively affect retention of detritus on the Colorado River. Likewise, stream power (Speaker et al., 1984) might play an important role in the supply of organic matter to the Cataract Canyon sites. Drift and standing mass of detritus was lower than expected for these sites, given the combined supply from the Colorado and Green rivers. Higher stream power in this steeper, canyon-bound reach might flush organic matter through this portion of the river. Our temporally limited sampling regimen might not have captured the flux through this reach. Underlying the supply and hydrologic factors are specific site conditions that influence the retention of detrital matter and the food source for invertebrates. Depth and morphology of the stream bottom have been shown to affect organic matter retention, albeit in much smaller streams (Webster et al., 1994). Synoptic studies that look at import and export through the various reaches in a temporally discrete manner should be beneficial to understanding the ecology of the CNP aquatic resources.

Standing mass on cobble bars was comparable to studies from other rivers and streams in the Southwest (Stevens et al., 1997; Oberlin et al., 1999). However, cobble substrate was relatively rare in the Green and Colorado rivers

above the confluence (Haden et al., 1999), with sandy substrate being predominant. Our study found that invertebrate mass on sand substrates (pools) was low compared to cobbles. Wolz and Shiozawa (1995) found that soft substrates in the main channel of the Green River near Ouray, Utah had lower densities of invertebrates than other soft sediment habitats (side channel, backwaters, and flooded wetlands). Lack of stable substrate might be a factor limiting the overall standing mass of invertebrates in CNP. However, use of alternative habitats might mitigate the loss of cobble substrate and add to the total standing mass of invertebrates. Other studies of rivers with predominantly soft sediments suggested that wood substrates were important invertebrate habitat (Benke et al., 1984; Haden et al., 1999). The relative contribution of flood plain and other non-cobble habitats might be important to the entire river ecosystem (Bayley, 1995) and warrants further investigation.

The Green and Colorado rivers through CNP might provide an example of how the pre-dam Colorado River ecosystem functioned. The pre-dam carbon source and invertebrate assemblage were probably regulated by high sediment concentrations, as is the present ecosystem. Many of the findings of this study can be applied to other reaches of the Colorado River, which experienced high suspended sediment concentrations for much of the time prior to impoundment. The caveat to the application of these data to other areas is that primary carbon retention within a site might be influenced by channel morphology and hydrology. These aspects should be considered on a case-by-case basis when trying to assess potential pre-impoundment invertebrate community standing mass.

In summary, we found that the aquatic ecosystem of the Green and Colorado rivers through CNP is productive and complex. Although food resources were limited to allochthonous sources due to high suspended sediment concentrations, there was an invertebrate assemblage that processed this form of primary carbon and provided a food resource for higher trophic levels. Importantly, the generally stable biomass of this assemblage indicated that variability of environmental parameters in CNP was not enough to disrupt biological processes. Although hard substrate habitats might

be limited for benthic invertebrates, the complexity of habitats available in large rivers might mitigate the loss of channel habitat and augment the standing mass and species richness of the invertebrate assemblage (Haden et al., 1999). Further research is warranted and should provide insight into the function of the pre-dam era Colorado River and arid biome rivers in general.

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