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INTERIM FLOW EFFECTS FROM GLEN CANYON DAM ON THE AQUATIC FOOD BASE IN THE COLORADO RIVER IN GRAND CANYON NATIONAL PARK, ARIZONA

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ABSTRACT

The purpose of this study was to provide seasonal baseline data during Interim Flows (140 $m^3 s^{-1}$ to 565 $m^3 s^{-1}$ or 5,000 to 20,000 cfs) on the aquatic food base in the Colorado River ecosystem in Grand Canyon downstream from Glen Canyon Dam (GCD). We examined the distribution, mass, and drift for aquatic algal and macroinvertebrate benthos. This study provides an initial evaluation of Interim Flow (IF) effects on Colorado River benthic ecology, and can be used as baseline data for the preferred EIS alternative.

We found high variability between three consecutive March collections due to the erratic annual precipitation patterns. Also, riffle habitats were more susceptible to the high precipitation events than pools. This is an important finding because >80% of the system-wide benthic mass occurred in riffle habitats. Consistent baseflows have led to a strict zonation of the two dominant primary producers, Cladophora glomerata near or below the baseflow, and Oscillatoria spp. in the upper varial zone. An increase in species richness continued to occur for both primary and secondary producers, with emergent aquatic macrophytes creating a new diverse benthic habitat. The overall decrease in benthic mass with distance below the Glen Canyon Dam tailwaters still occurred due the input of suspended sediments (Blinn et al. 1992, 1994). However, higher benthic mass was found at the Tanner Cobble bar site, with C. glomerata mass estimates higher than at Lees Ferry. This suggests that the scale at which we make decisions on ecological and management questions needs further examination.

In-situ experiments showed that Cladophora glomerata and associated invertebrates entered stream drift in significant amounts after two consecutive night exposures in the Colorado River below Glen Canyon Dam. C. glomerata demonstrated diurnal drift during steady flows, while invertebrates did not exhibit this pattern. Coarse particulate organic material is negatively correlated with stream gradient in the Colorado River: drift packets of C. glomerata and associated epiphytic diatoms and invertebrates quickly disintegrated down river due to hydraulics and/or suspended sediments. Drift was pulverized by rapids which subsequently increased the fine particulate organic matter throughout the river corridor in Grand Canyon National Park. Due to river hydraulics and suspended sediment, organic drift mass throughout the river corridor is reach specific. Terrestrial insects represented <0.001% of the total invertebrate mass to mainstem drift due to the limited riparian zone in an arid biome, while tributaries contributed <0.1%. Origin of tributary flow, spring groundwater versus surface derived-flow, significantly altered amount and composition of drift.

INTRODUCTION

Glen Canyon Dam operations strongly affect the lower trophic levels of the aquatic ecosystem in Grand Canyon National Park (Blinn et al. 1992, 1994). Algae and macroinvertebrates provide an important food base for native and game fish and terrestrial fauna, and link the aquatic and terrestrial components of the ecosystem. The aquatic food base is affected by the duration and timing of low releases from Glen Canyon Dam, as well as the range in daily fluctuations and localized reach-based geomorphic parameters downstream. This study of the aquatic food base in the Colorado River was designed to monitor Interim Flow (IF) effects on the standing mass and distribution of benthos between Lees Ferry and Diamond Creek, Arizona.

Growing concern over the impacts of river regulation on environmental resources in the Colorado River corridor downstream from Glen Canyon Dam prompted the Department of the Interior to conduct environmental impact studies in lower Glen Canyon and in the Grand Canyon. Phase I of the Glen Canyon Environmental Studies (GCES) Program concluded that the dam exerted significant impacts on the downstream fluvial ecosystem, but higher than normal flows precluded assessment of the effects of low and normal dam operations. GCES Phase II was an integrated effort to assess the effects of low and normal fluctuations on processes and resources at the ecosystem level. These studies demonstrated significant effects of normal operations on riverine resources. Interim Flows were implemented on 1 August, 1991 to prevent further degradation of resources during the development of the Glen Canyon Dam Environmental Impact Statement. Interim Flows consist of restricted minimum (140 $m^3 s^{-1}$) and maximum (566 $m^3 s^{-1}$) flows, and reduced ramping rates.

A primary objective of the GCES IF discharge criteria is to maintain the aquatic food base in the Colorado River. The IF criteria were designed to stabilize the area available for colonization by benthic algae, thereby decreasing loss through desiccation or freezing of the benthos and increasing primary and secondary production. Our monitoring project is specifically designed to test these hypotheses and management concerns.

OBJECTIVES

Objective One: Monitor the effects of Interim Flows from Glen Canyon Dam on the standing mass of the benthic community in the Colorado River between Lees Ferry and Diamond Creek.

Objective Two: Monitor the effects of Interim Flows on organic drift in the Colorado River corridor in Grand Canyon.

Objective Three: Prepare monitoring data for inclusion into the GCES/NPS GIS database.

CHAPTER ONE: STANDING STOCK OF LOWER TROPHIC LEVELS

INTRODUCTION

Discharge, suspended sediments, solar insolation and water temperature are the primary factors influencing benthic community structure in the Colorado River through Grand Canyon. Variability in river discharge can affect the structure and function of benthic communities by altering the stability and availability of substrates (Power et al. 1988, Cobb et al. 1992), water velocity (Peterson and Stevenson 1992), aerial exposure (Blinn et al. 1995), light quantity (Duncan & Blinn 1989) and water quality (Scullion & Sinton 1983). Regulated rivers eliminate seasonal hydrographic changes and remove important life history cues for some aquatic insects thereby reducing diversity (Power et al. 1988).

Periphyton mass is adversely affected by suspended sediments through a decrease in photosynthetic efficiency from light attenuation (Duncan & Blinn 1989, Davies-Colley et al. 1992), scouring and through increases in nutrients and toxic compounds absorbed onto sediments (Newcombe & MacDonald 1992). Suspended sediments can reduce benthic invertebrate density through scouring (Culp et al. 1985), clogging filter feeders, and reducing feeding efficiency (Newcombe & MacDonald 1991, Quinn et al. 1992). Ross and Pieterse (1994) reported a significant positive relationship between discharge and suspended sediment loads in the Vaal River, South Africa.

Seasonal fluctuations in water temperature provide critical cues for life history development of aquatic invertebrates (Vannote & Sweeney 1980). Ward and Stanford (1982) reviewed the thermal equilibrium hypothesis of Vannote and Sweeney and determined that a reduction in body size limits aquatic insect survival in constantly cold water. Steady thermal regimes may reduce diversity of aquatic insects to taxa adapted only to confined temperatures (Ward & Stanford 1983). Epiphyton mass and diversity respond similarly to aquatic insects in constantly cold water (Blinn et al. 1989, Blinn & Cole 1991).

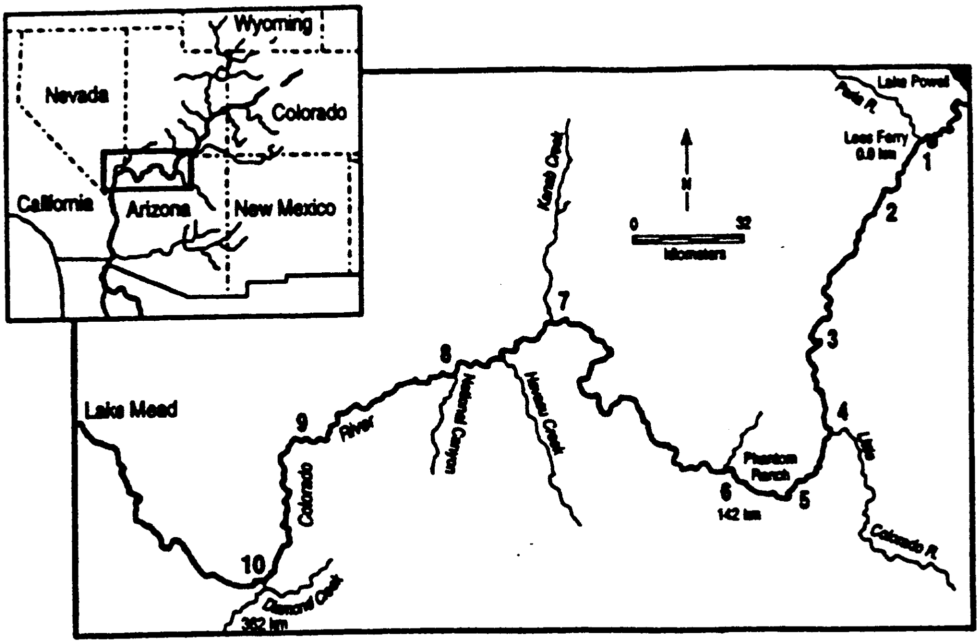
The structure of the benthic community in the Colorado River through Grand Canyon has been altered by the construction of Glen Canyon Dam through changes in river discharge, suspended sediments and water temperature. Interim Flow (IF) criteria has increased the baseflow while reducing peak flow and hourly ramping rates from Glen Canyon Dam. A similar change in flow regime implemented on the Patuxent River, MD, caused a doubling in benthic macroinvertebrate density and improved community condition (Morgan et al. 1991).

Standing mass and habitat requirements of the benthos in the Colorado River through Glen and Grand Canyons were assessed seasonally from September, 1992 through October, 1994 and March, 1995. Monitoring the lower aquatic trophic levels in this large river in an arid biome contributes to a better understanding of linkages between benthos and higher trophic levels, a prerequisite for resource management. Our seasonal sampling frequency was employed to compare high and low volume discharge months prior to collection trips. Sampling sites ($n = 11$) were the same as those established during GCES Phase II research flows and include low velocity pools/eddies and high velocity cobble bars in both wide ($n = 5$) and narrow ($n = 5$) reaches (Schmidt & Graf 1990, Blinn et al. 1992, 1994). We added a pool site at RKM 3.2L, which is adjacent to the Paria Cobble site, for better resolution immediately below the confluence of the first major tributary.

METHODS

Sampling was conducted from March 3 to 21, 1995 at three transects 30 m apart in each habitat type (Fig. 1). Peterson or Petit Ponar dredges were used in the pool habitats and Hess substrate samplers were utilized in tributaries and on cobble bars. Pool habitats were sampled at five locations along three transects: thalweg (<28 $m^3 s^{-1}$), lower-littoral (approximately 140 $m^3 m^{-1}$), mid-littoral, submerged or within the varial zone (approximately 280 $m^3 s^{-1}$), and upper littoral (566 $m^3 s^{-1}$). Six cobble and 12 pool samples were taken for abundance and mass determinations. Cobble bar collections were taken at the lowest water flow possible with three paired samples in the lower and mid-littoral zones. Single samples were collected in the zone of fluctuation (varial zone), at waters edge and the upper littoral zone. All samples were placed on ice and processed within 24 h. At the time of collection the following data were recorded: general habitat conditions, depth, current velocity, transect, relative distance to shore, time of day, discharge estimated on site and verified from U.S.G.S. gauging station data.

Interim flow (IF) criteria includes a minimum flow of 227 $m^3 s^{-1}$ from 0700 to 1900 h and 142 $m^3 s^{-1}$ at night with a maximum flow of 566 $m^3 s^{-1}$. January and June collections were preceded by low to moderate volume discharge regimes, while March and September collections were preceded by moderate to high volume discharges. Low flow months (<600,000 af released) had a daily



Name	Site	Pool	Habitat Riffle (km*)	Tributary Habitat	Geomorphic Reach Width	Elevation (msl)	Reach Orientation
Lees Ferry / Paria	1	0.0	0.8/3.1	1.0	Wide	947	Southwest
South Canyon	2	50.4	50.8	50.8	Narrow	871	South
Nankoweap	3	84.8	83.2	83.2	Wide	842	Southeast
Little Colorado	4	98.4	98.7	98.6	Wide	821	Southwest
Tanner	5	108.8	109.6	104	Wide	810	Southwest
Phantom Ranch	6	140.0	142.4	140.8	Narrow	734	West
Tapeats / Kanab	7	230.4	232.0	214.8/231.2	Narrow	568	West
National	8	265.5	240	249.6	Narrow	540	Southwest
Spring Canyon	9	326.4	328.9	327.2	Wide	450	South
Diamond	10	360.0	352.0	361.6	Narrow	409	Southwest

* Glen Canyon Dam is 25.3 km up-river from Lees Ferry (RK 0.0)

Figure 1. Map of benthic and drift collection sites in the Colorado River corridor through Grand Canyon National Park including habitat, geomorphic reach width, elevation and reach orientation. Drift collections were taken within 15 km downstream from benthic collection sites.

fluctuation limit of 142 m^3 s^{-1} and a mean daily flow of <286 m^3 s^{-1}. Moderate flow months (600,000 to 800,000 af released) had a daily fluctuation limit of 170 m^3 s^{-1} and mean daily flow of 286 to 380 m^3 s^{-1}. High flow months (600,000 to 800,000 af released) had a daily fluctuation limit of 227 m^3 s^{-1} and a mean daily flow of >380 m^3 s^{-1}. Ramping rates were the same for all discharge months; i.e., 71 m^3 s^{-1} up and 42 m^3 s^{-1} down (U.S.B.R. 1994).

Water quality collections for temperature (°C), specific conductance (mS), dissolved oxygen (mg/L), and pH were taken with a Hydro-Lab Scout II® at the time of each sampling. Water transparency was estimated with a Secchi disk.

Taxonomic samples were selectively collected in high density areas in each habitat. Adult and pharate specimens were collected with sweep nets, white and UV lights, spot samples, and Thienemann (water surface) collections.

Biotic samples were sorted into the following 11 categories: Cladophora glomerata, cyanobacteria algal crust (Oscillatoria spp.), miscellaneous algae, detritus, chironomids, Gammarus lacustris, gastropods, lumbriculids and tubificids (Oligochaeta), simuliids, and miscellaneous macroinvertebrates. Each category was oven-dried at 60°C to a constant mass. Ash-free dry mass (AFDM) conversions were estimated from dry weight to AFDM regression equations.

Monitoring Elevated Baseflows: Due to high water releases (360 - 570 $m \cdot s^{-1}$) from Glen Canyon Dam starting in June 1995 and expected to continue through August we anticipated some change in benthic mass and production from below the previous baseflow and up through the varial zone. We estimated primary production and primary and secondary producer mass at three channel stages at Lees Ferry cobble bar (RKM 0.1). The collection stages were; channel (>142 $m \cdot s^{-1}$), lower varial (~350 $m \cdot s^{-1}$) and upper varial (>450 $m \cdot s^{-1}$). Triplicate Hess samples were taken from the channel and lower varial zone and processed in accordance with the down river protocol. Epiphyte mass was collected with 20 cm^2 scrapings from each stage elevation (n=9). Algae were placed in a Whirl-Pak with 100 ml of filtered (0.45 μm) river water and shaken for 60 s and filtered onto glass fiber filters (GF/A), oven dried and ashed at 500° C for one h to obtain ash-free dry mass. We also measured C. glomerata filament length from the channel. Primary production followed that as described in Blinn et al. (1994).

Quality Control: Every tenth sample processed in the laboratory was accessed for accuracy of identification, density and weighing by another technician (n = 150). We calculated three identification errors per 100 organisms and a density error of ±6 per 100 organisms and a weighing error of ±0.00001 g. Field processing quality control data was collected for each site, where all water used in processing was collected, filtered and preserved. All organic material was placed in an oven for 1 h at 500°C for AFDM estimates. We calculated an error of ±0.14 g AFDM per 100 samples composed primarily of very fine particulate organic matter (detritus). All initial and reduced data entry is subject to 100% hard copy evaluation by another technician. All field data sheets are photo-copied and stored outside of the Department of Biological Sciences at Northern Arizona University. Data sets are backed-up in duplicate on disketts and for long term storage on a Macintosh 3.5.1 Bernoulii Box ® on Iomega Shareware/Data® software.

Statistical Analyses: Multivariate analyses of variance (MANOVA) were used to analyze categorical predictor variables (mass estimates) and multiple response variables (physical parameters) for significant temporal and spatial trends. Seasonal calculations were based on pooled values for similar collection months. Elevated base flow data was analyzedwith the Independent T-Test with seperate variances, using date, channel zone and biotic categories as variables. All calculations were performed with SYSTAT computer software on ln+1 transformed data (Version 5.1, Wilkinson 1989).

RESULTS AND DISCUSSION

Our data indicated that winter storms elevate suspended sediment loads and may produce within season variability. We analyzed March collections from 1993, 1994 and 1995 to determine if there were any within season variablility for primary and secondary mass, water quality or habitat characteristics. March 1993 and 1995 were both extraordinarily wet winters and we sampled after the largest storms had passed. MANOVA analyses detected a significant overall difference between March collections and between sites for both riffle and pool habitats (Table 1). Pool communities were more resilient to annual and site variability than riffle communities. Water quality and habitat characteristics also varied significantly between collection trips and sites (Table 2).

Detritus and tubificid mass estimates varied significantly between March collections (Fig. 2). Overall detrital loads were greater in the high precipitation years of 1993 and 1995 compared to collections in 1994 during a dry year. This was probably due to the input of allochthonous materials from tributary spates particularly in 1995 when many large side canyons such as Nankoweap Creek, Bright Angel Creek, Crystal Creek and Prospect Canyon flooded. Tubificid mass estimates followed a similar pattern with 1994 the lowest estimate for the three

Table 1. Results of MANOVA analyses for March benthic collections from 1993, 1994, and 1995 in the Colorado River through Grand Canyon for both pool and riffle habitats. Predictor variables of each March trip and site were analyzed against biotic categories as response variables (AFDM·m^{-2} ln+1 transformed data). Taxonomic categories include: Cladophora (C), Oscillatoria (O), miscellaneous algae/macrophytes (A), detritus (D), chironomids (M), Gammarus (G), gastropods (S), simuliids (B), lumbriculids (L), tubificids (T), and miscellaneous macroinvertebrates (I). These analyses indicate a within season variability for selected taxa with pools more resilient to change than riffles. Only significant univariate response variables are listed ($p<0.03$). Overall Wilks' Lambda, site x year x habitat, was significant ($p < 0.0001$).

Source	Wilks' Lambda	Approximate F Statistic	df	p	Significant Response Variable
POOL					
Year	0.9	2.5	22,662	<0.001	T, D
Site	0.9	3.7	11,331	<0.0001	G,T,C,S,A
RIFFLE					
Year	0.7	3.0	22,344	<0.0001	M,C,D,S
Site	0.6	11.5	11,172	<0.0001	L,G,M,C,D, S,A

Table 2. Results of MANOVA analyses for March water quality and habitat factors from 1993, 1994, and 1995 in the Colorado River through Grand Canyon at riffle sites. Predictor variables of each March trip and site were analyzed against response variables of: water velocity (V), depth (D), dissolved oxygen (DO), conductivity (C), temperature (T), pH (PH), discharge (DS) and Secchi depth (S). Only significant univariate response variables are listed ($p<0.01$). Overall Wilks' Lambda, site x year, was significant ($p < 0.0001$)

Source	Wilks' Lambda	Approximate F Statistic	df	p	Significant Response Variable
Year	0.04	105.2	14,352	<0.0001	V,D,DO,C,T, PH
Site	0.05	493.5	7,176	<0.0001	D,DO,C,T,PH, S

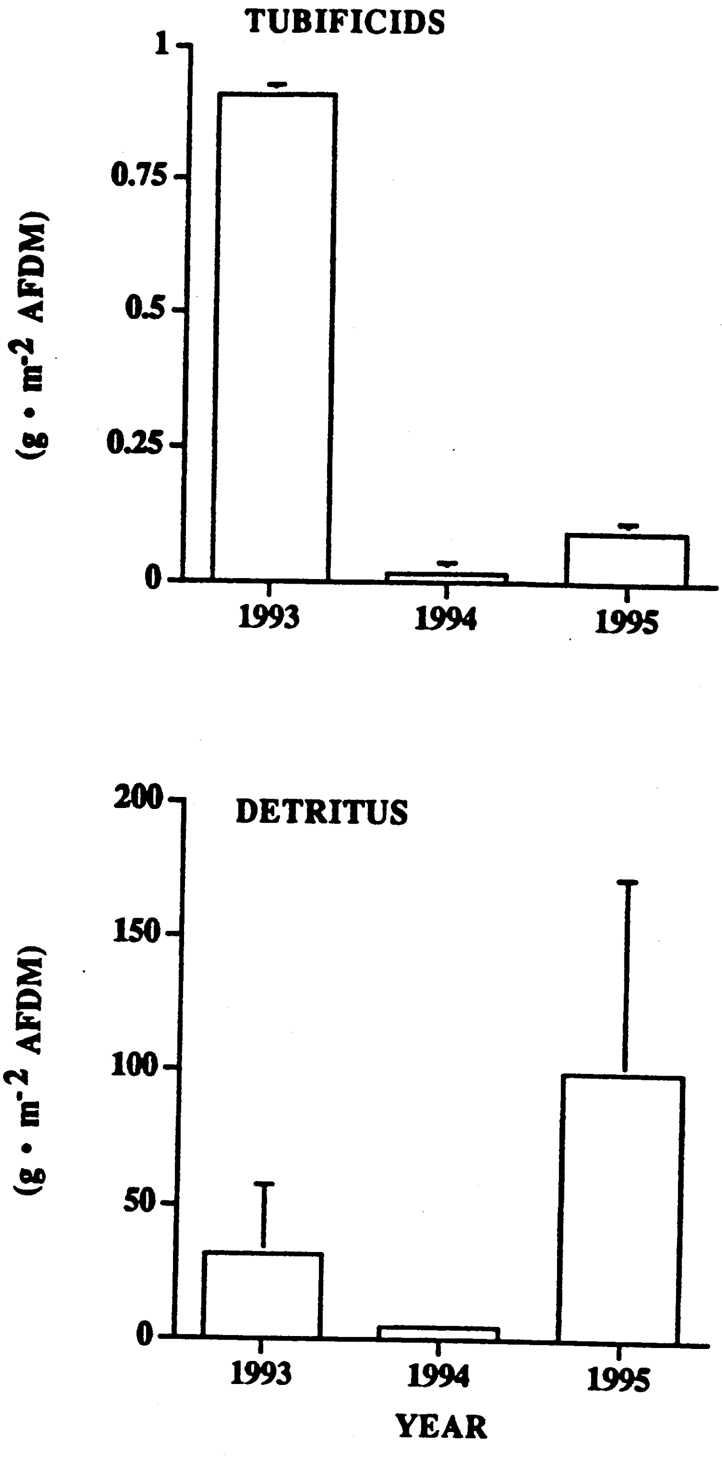


Figure 2. System-wide average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for tubificids and detritus in pools from three consecutive March collection trips in the Colorado River through Grand Canyon. Error bars represent ± 1 S.E.

consecutive March collections. The increase in tubificid mass may be correlated with increases in detrital loads which provide food for these decomposers. An alternative explanation may be that Interim Flows (IF) had negatively altered the habitat of these bottom dwelling worms by compacting the sand within eddie/pools and reducing available habitat as pools filled with sand (Blinn et al. 1994).

Pool mass estimates also changed significantly by site within the three consecutive March collections for Cladophora glomerata, miscellaneous algae/macrophytes, Gammarus lacustris, gastropods and tubificids (Figs. 3, 4 & 5). Although detectable patterns are difficult to discern, the majority of the mass within pools is found at Lees Ferry and throughout Marble Canyon (RKM 1-99), with the exception of an increase in miscellaneous algae/macrophyte mass in the lower Canyon during 1995. The miscellaneous algae/macrophyte collections were composed primarily of horsetails (Equisetum spp.) found emergent along the varial zone.

Water quality parameters varied significantly between year and sites during the three consecutive March collections (Table 2). Temperature, dissolved oxygen (DO), conductivity and pH all varied significantly between trips, however, the variability for these parameters may not be of biological significance. System-wide water temperature during March averaged 8.9°C (SE ±0.12) in 1993, 10.2°C (SE ±0.17) in 1994, and 10.1°C (SE ± 0.19) in 1995. Average system-wide DO increased each year from 9.0 mg/L (SE ±0.1) to 10.2 mg/L (SE ±0.1) to 11.7 mg/L (SE ±0.1) for the three consecutive March collections, respectively. Mean conductivity throughout the mainstem decreased through time from 1.05 mS (SE ±0.003) to 0.95 mS (SE ±0.006) to 0.93 mS (SE ±0.005) for the three consecutive March collections. Average hydrogen-ion concentration also decreased through time within the mainstem during March collections with a pH of 7.8 (SE ±0.02) measured in 1993, 8.1 (SE ±0.02) in 1994, and 8.11 (SE ±0.03) recorded in 1995. These water quality data are typical and do not reveal any major within season variability. Longitudinal changes during these three consecutive March collections followed similar patterns encountered throughout our sampling program. Secchi depth was not significantly different between March collections and averaged 0.89 m (SE ±0.23) and ranged from over 7 m at Lees Ferry to 0.02 m in the lower reaches.

Habitat parameters varied significantly between March collection trips and between years (Table 2). Average water velocity and depth changed significantly between collections: 0.5 $m \cdot s^{-1}$ (SE ±0.05)/0.38 m (SE ±0.01) in 1993, 0.35 $m \cdot s^{-1}$ (SE ± 0.03)/0.39 m (SE ±0.02) in 1994, and 0.67 $m \cdot s^{-1}$(SE ±0.04)/0.51 m (SE

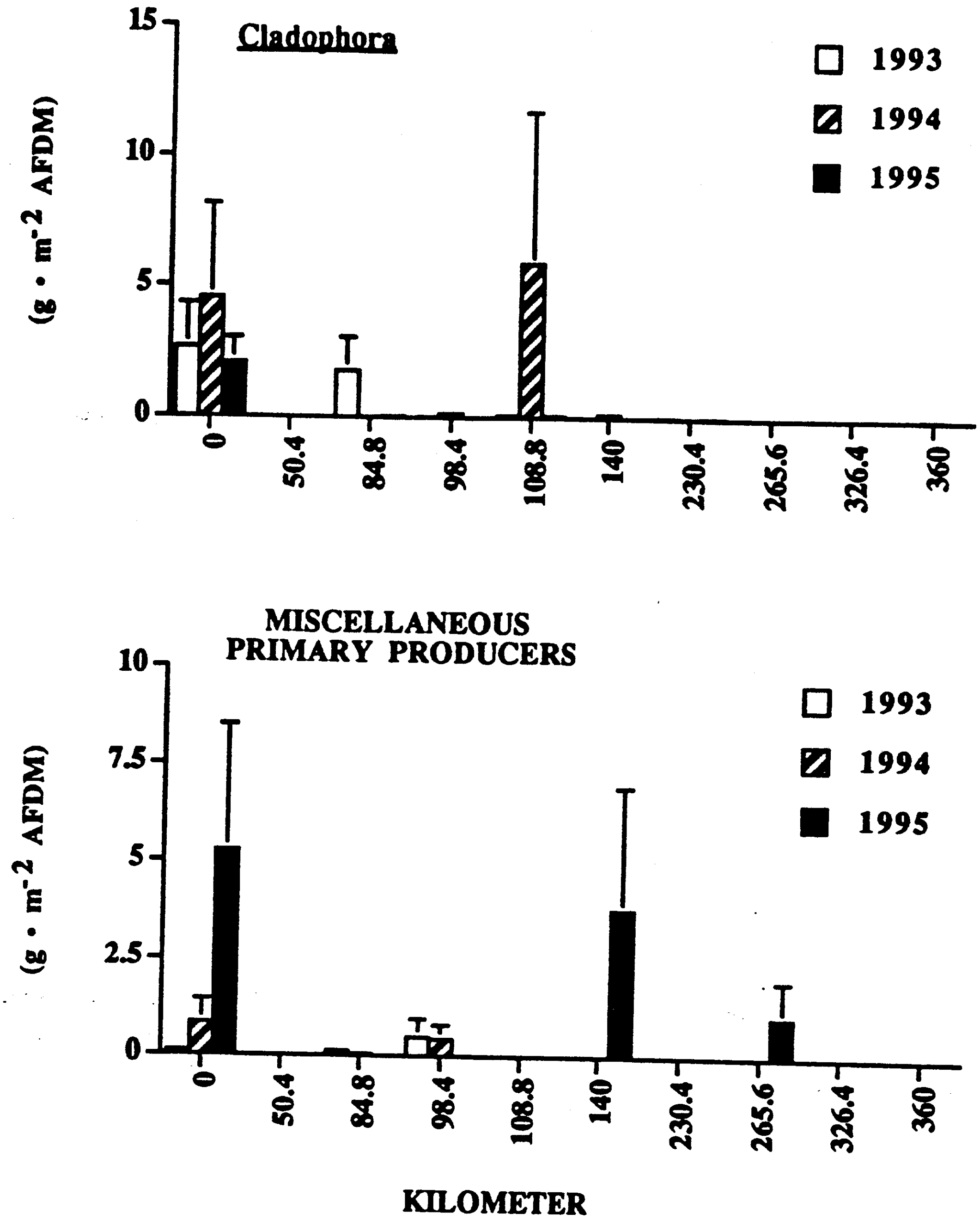


Figure 3. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for Cladophora glomerata and miscellaneous primary producers in pools from March collection trips in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 360). Error bars represent ± 1 S.E.

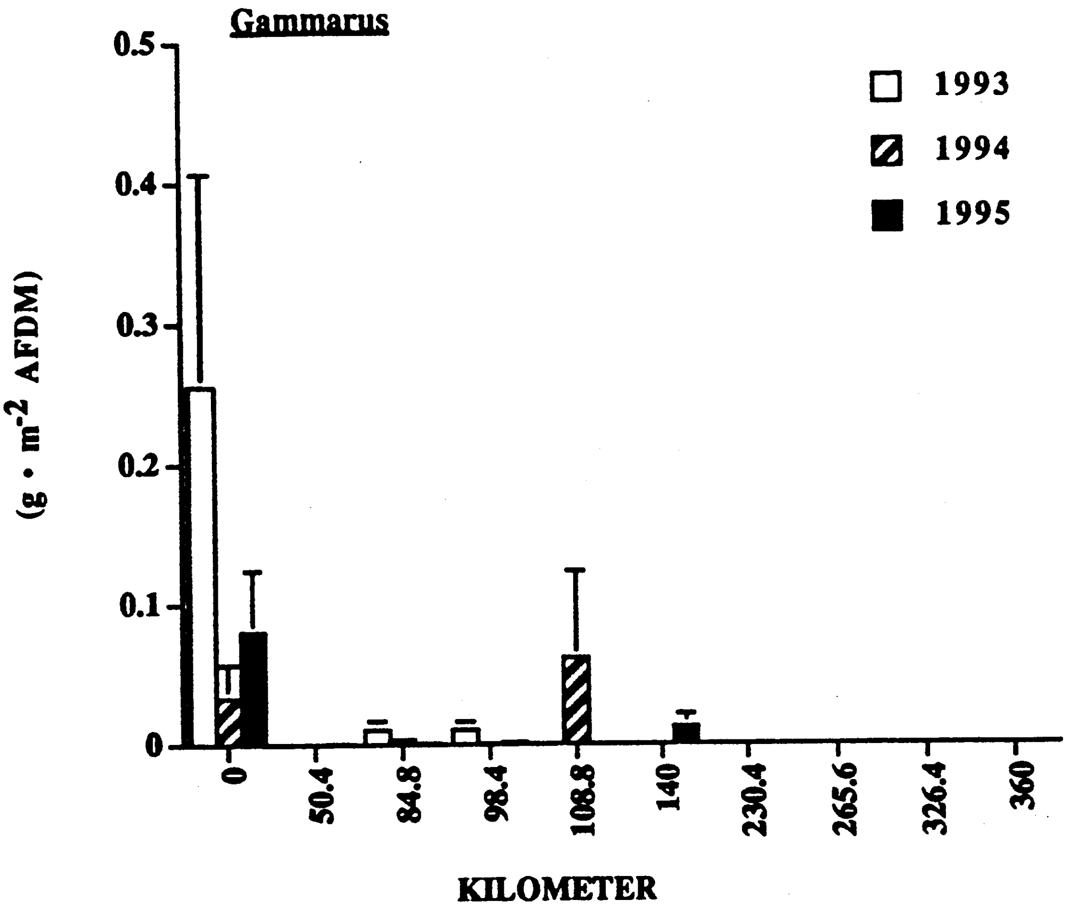


Figure 4. Average ash-free dry mass (g • m^{-2} AFDM) for Gammarus lacustris in pools from March collection trips in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 360). Error bars represent ± 1 S.E.

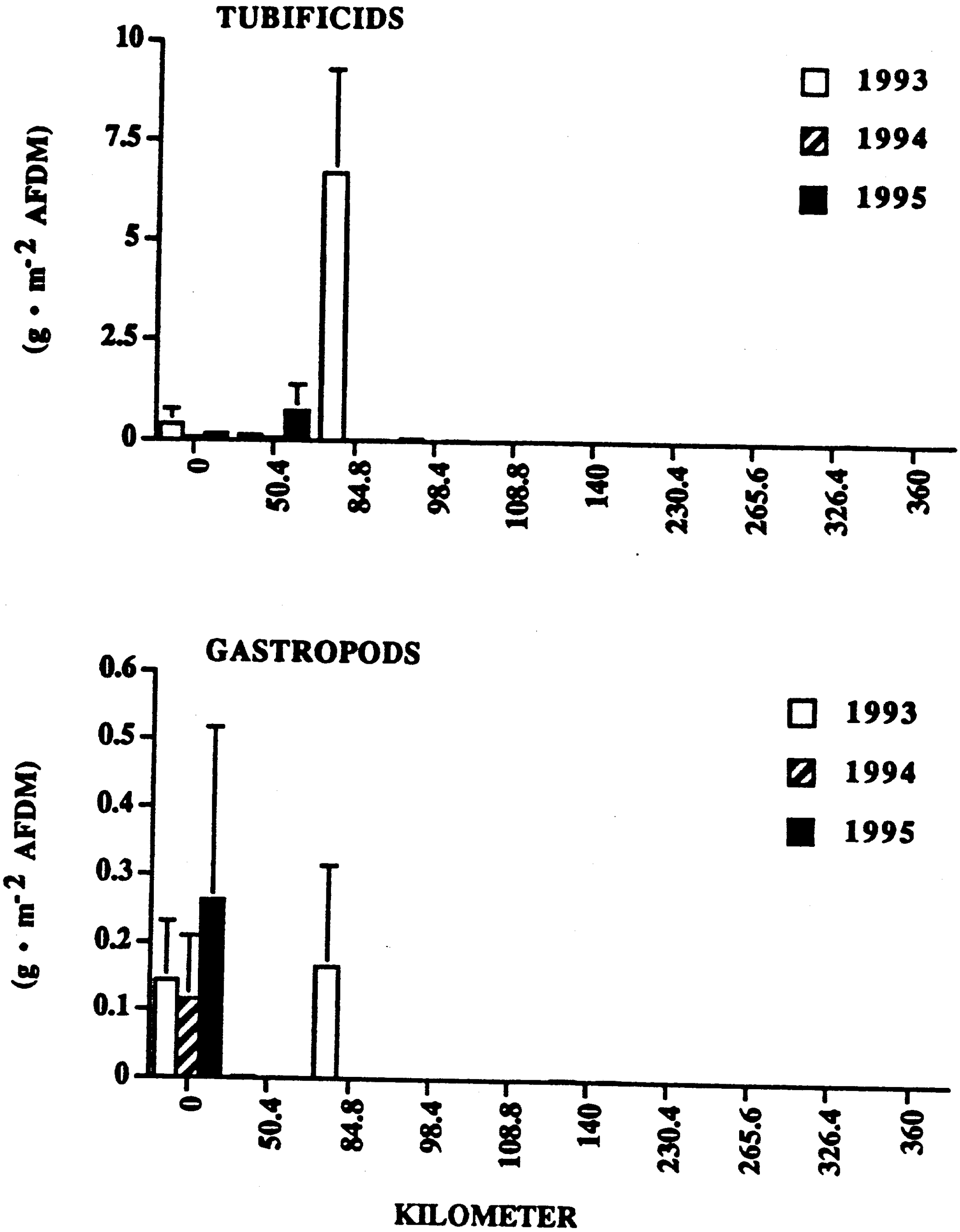


Figure 5. Average ash-free dry mass (g • m^{-2} AFDM) for tubificids and gastropods in pools from March collection trips in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 360). Error bars represent ± 1 S.E.

±0.08) in 1995. However, these values may not vary enough to be of biological significance. Discharge did not change between collections (average 245 $m^3 \cdot s^{-1}$) or between sites, and current velocity did not change between sites. Overall it appears that the abiotic factors during three consecutive March collections are biologically consistent even during contrasting wet and dry periods.

Riffle communities varied significantly between March collections for Cladophora, Oscillatoria, detritus and chironomid system-wide mass estimates (Fig. 6). Overall, Cladophora mass decreased about 40% during years with major storm events (1993 and 1995) compared to the dry year of 1994. This decrease may be attributed to increases in suspended sediments from tributary spates which reduce light and subsequent biotic production (Blinn et al. 1994). These spates also increase scouring. Oscillatoria mass increased dramatically in 1995 (0.23 $g \cdot m^{-2}$) from trace amounts (<0.01 $g \cdot m^{-2}$) collected in 1993 and 1994. Detritus in riffles followed a similar pattern as the pools, but the mass estimates were an order of magnitude lower in riffles. Chironomid mass also increased by about 100% during the dry year of 1994 over the two wet years.

Longitudinal variability was also significant for selected biota between March collection trips (Figs. 7-10). At Lees Ferry, Cladophora mass estimates showed a positive correlation with storm events, however, sites below the Paria River (RKM 3.1) showed a negative relationship with years that had major storm events. These patterns revealed the overriding influence of high sediment loads from the Paria River on the benthic community structure in the Colorado River below Lees Ferry. Increases in available nutrients from run-off, coupled with limited sediment input due to the lack of tributaries in the Lees Ferry reach, may explain the higher Cladophora mass during storm years at Lees Ferry. Miscellaneous algae/macrophytes are apparently not negatively impacted by storms as a general increase in mass is observed for Cladophora in riffles from Nankoweap Cobble (RKM 83.2) to Tanner Cobble (RKM 109.6). The bryophyte, Fontinalis spp., is the primary colonizer at these riffle sites. Although detrital loads in riffles were an order of magnitude less than pools, they did follow the same pattern of increasing mass during the wet years of 1993 and 1995 as a result of tributary influence. Lumbricid, Gammarus, and chironomid mass estimates were higher in the dry year (1994) than the stormy years (1993 and 1995; Figs. 9 & 10). Highest macroinvertebrate mass estimates were collected in the tailwaters at Lees Ferry down to Tanner Cobble, with the exception of an increase in chironomid mass at 205 Mile Rapid (RKM 328.9) in 1995. Gastropod mass dropped during the consecutive three-year March collections at Lees Ferry with a slight increase at Nankoweap Cobble in 1995.

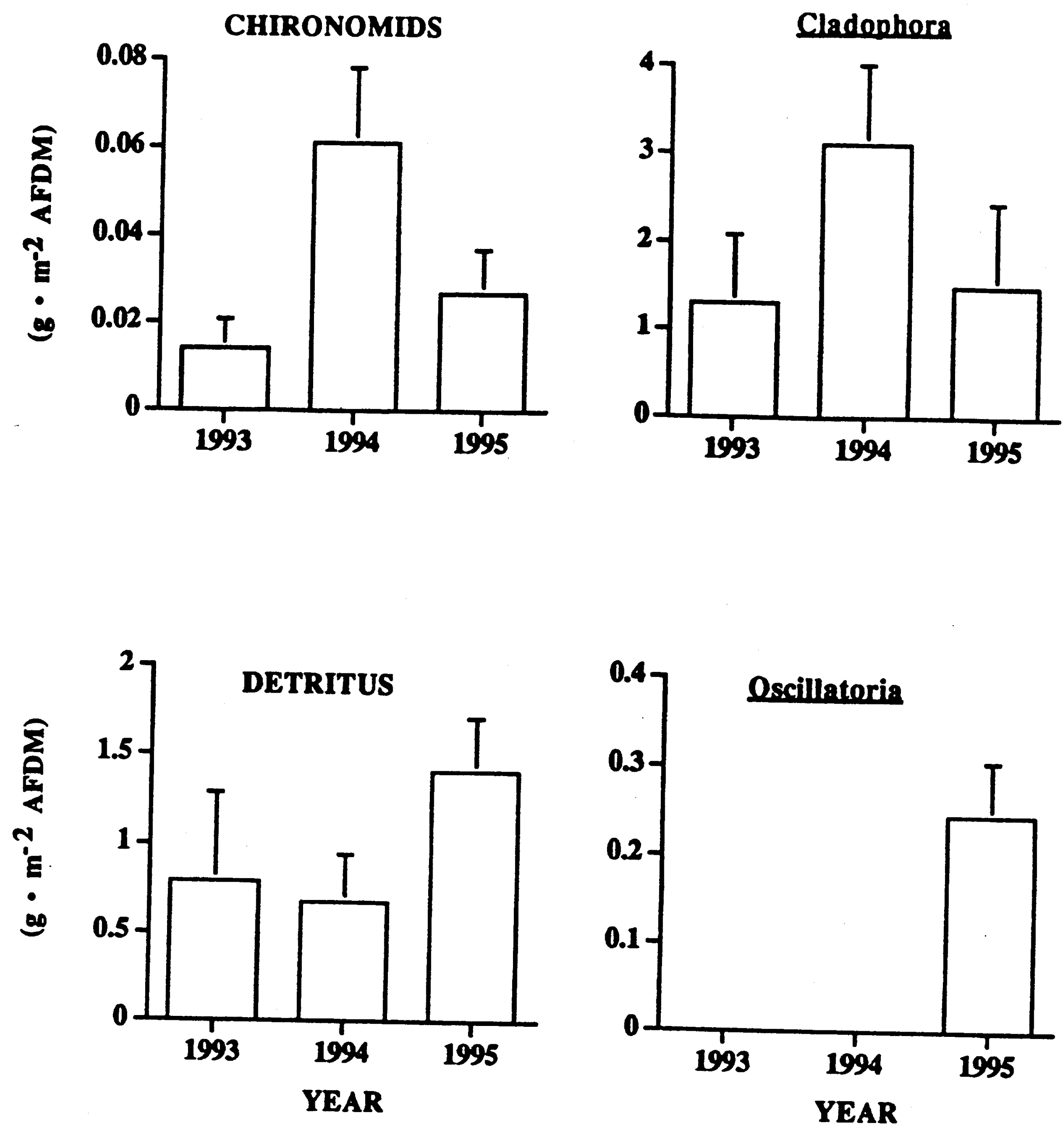


Figure 6. System-wide average ash-free dry mass (g • m^{-2} AFDM) for chironomids, Cladophora glomerata, detritus and Oscillatoria spp. in riffles from three consecutive March collection trips in the Colorado River through Grand Canyon. Error bars represent ± 1 S.E.

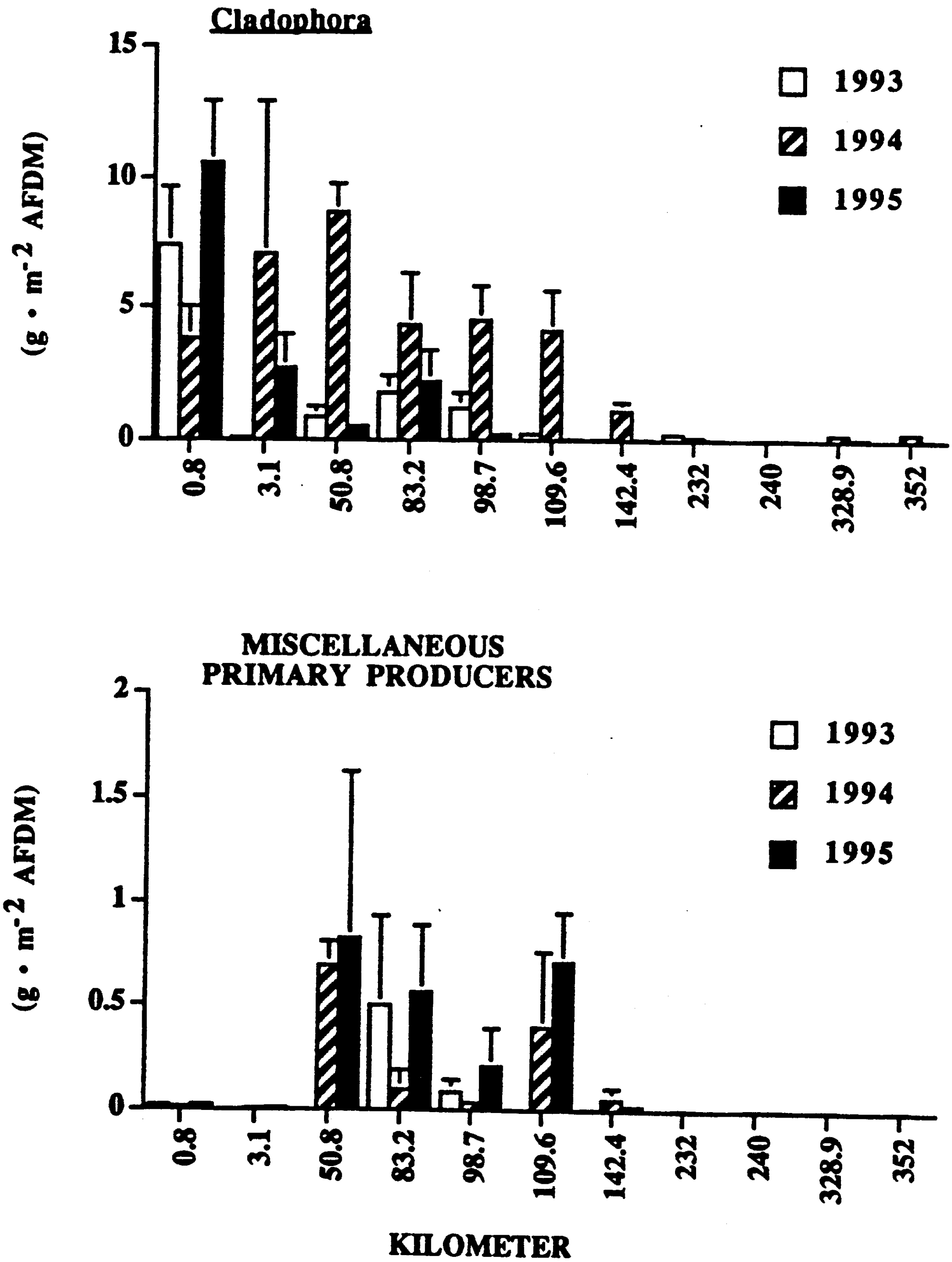


Figure 7. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for Cladophora glomerata and miscellaneous primary producers in riffles from March collection trips in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 360). Error bars represent ± 1 S.E.

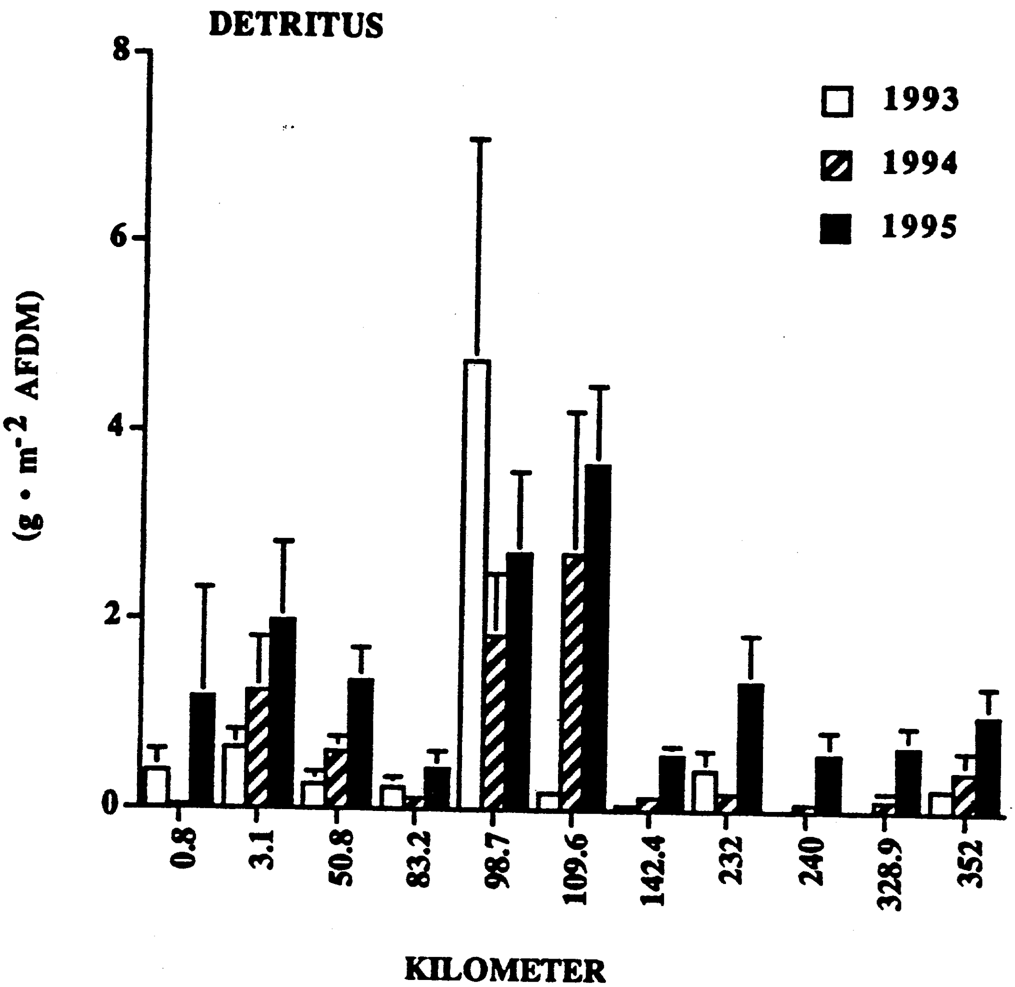


Figure 8. Average ash-free dry mass (g • m^{-2} AFDM) for detritus in riffles from March collection trips in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 360). Error bars represent ± 1 S.E.

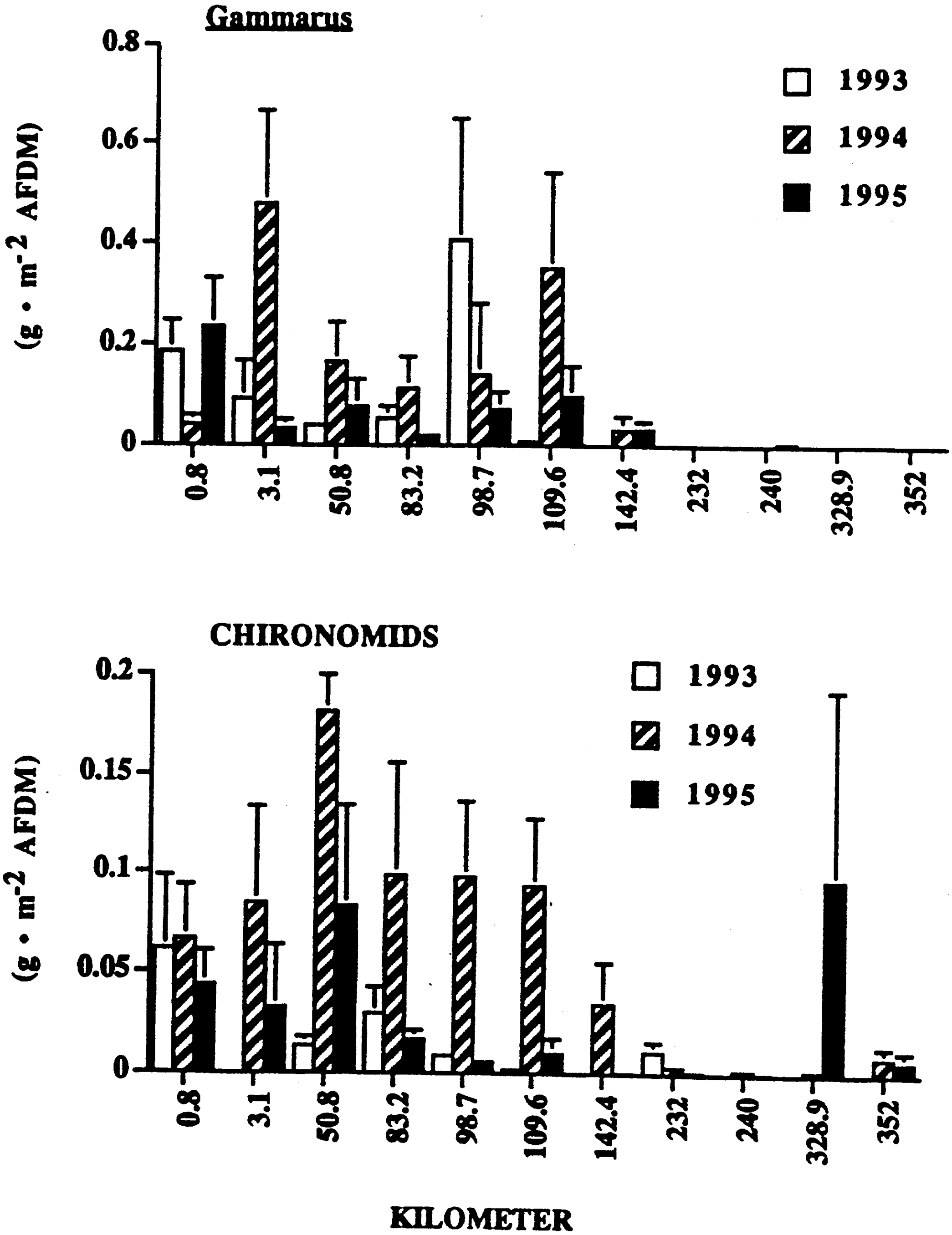


Figure 9. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for Gammarus lacustris and chironomids in riffles from March collection trips in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 360). Error bars represent ± 1 S.E.

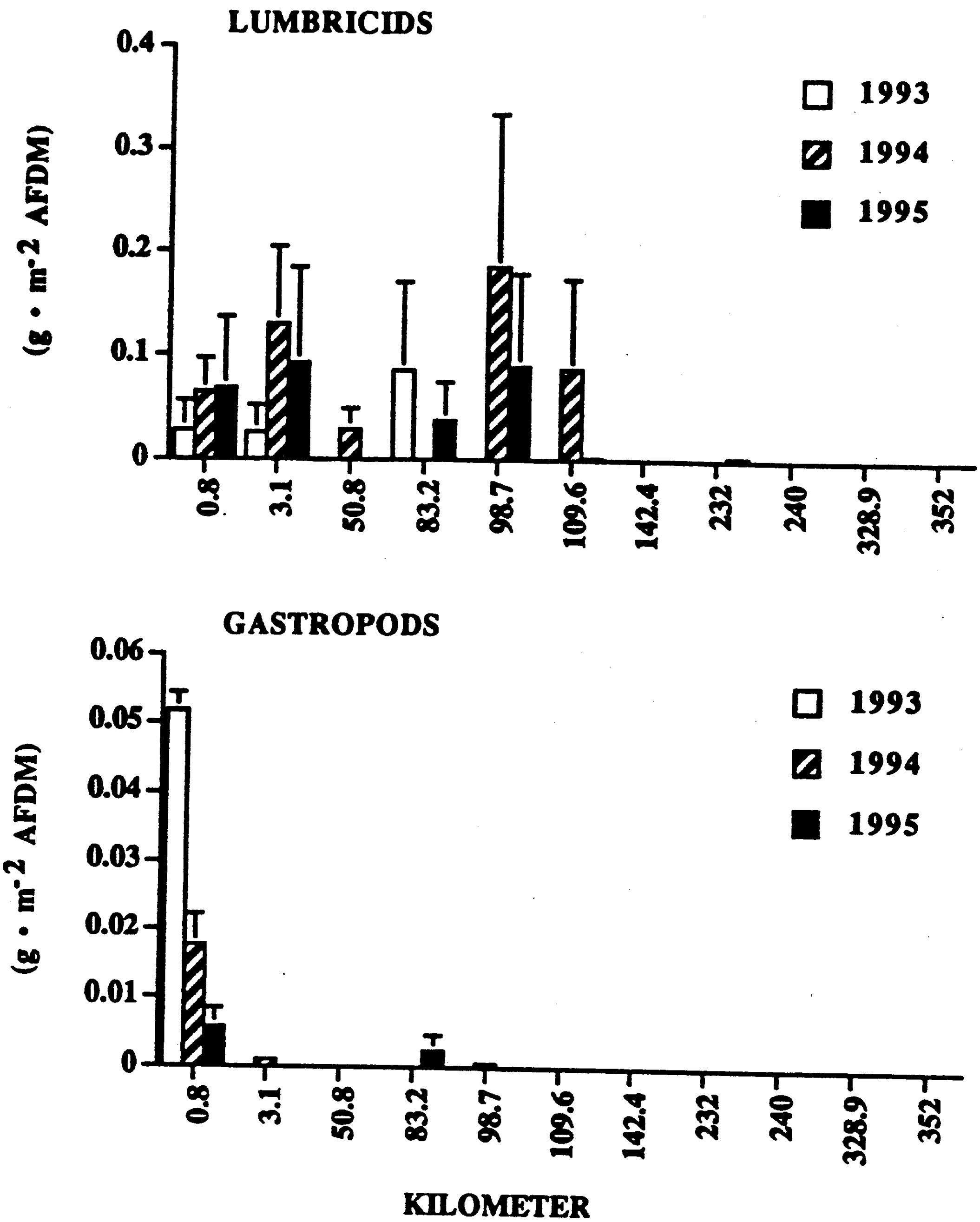


Figure 10. Average ash-free dry mass (g • m^{-2} AFDM) for gastropods and lumbricids in riffles from March collection trips in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 360). Error bars represent ± 1 S.E.

The results for the three consecutive March collection trips indicate that within season variability for mass estimates are high for selected biotic categories and that pool habitats are more resilient to change than riffles. Storm periods generally reduce primary and secondary mass, but increase detrital loads. Although winter storms may reduce mass in March, our June collections in 1993 had the greatest macroinvertebrate standing mass recorded in our study. This collection also followed a low discharge spring release pattern from Glen Canyon Dam, indicating that natural high water floods followed by low discharge can increase mass of the benthic community, probably through nutrient input. There has been considerable discussion on the peak and duration of habitat maintenance flows, but limited or no discussion on post-flows, which may be more critical.

Primary Producer Zonation

During the March 1995 collection trip we sampled primary producer mass in the varial zone just above the waterline and at the 566 $m \cdot s^{-1}$ stage. Normally we were only interested in the macroinvertebrate assemblage in this area of the channel, but our experimental work with C. glomerata and Oscillatoria at Lees Ferry and Cathedral Island (RKM 5) suggested that we needed to improve our resolution on the distribution of these two algal components throughout the river corridor. Analyses of data indicated that C. glomerata is the dominant primary producer below 283 $m \cdot s^{-1}$ (submerged during the collection period), while Oscillatoria is dominant in the varial zone (dry during collection; Wilks' Lambda, $F_{(3,325)}=14.4$, $p<0.0001$; Fig. 11). The bryophyte, Fontinalis spp. was collected in the varial zone at Phantom Cobble (RKM 142.4) and through Marble Canyon below 283 $m \cdot s^{-1}$. During March 1995, 82% of C. glomerata mass was located in the submerged zone below the current baseflow of 142 $m \cdot s^{-1}$. Conversely, 98% of Oscillatoria mass was found above 283 $m \cdot s^{-1}$. Samples from the upper varial zone were dry at the time of collection, but this zone becomes inundated during the high flow months of January, July and August. The low varial zone, which was submerged at the time of collection, may be dewatered on a daily or seasonal basis during low or moderate flow months. This would include about 60 of the 66 samples collected from this zone if baseflow was achieved. Although we estimate that all of these samples were collected near a baseflow of 142 $m \cdot s^{-1}$, we can not be certain of their exact stage location. However, the 283 $m \cdot s^{-1}$ flow is only realized during periods of sustained baseflow throughout the study site; i.e., during the 1991 Research Flows. Weekend flows during low volume months can reach baseflow for several hours daily under IF in Glen Canyon. Blinn et al.

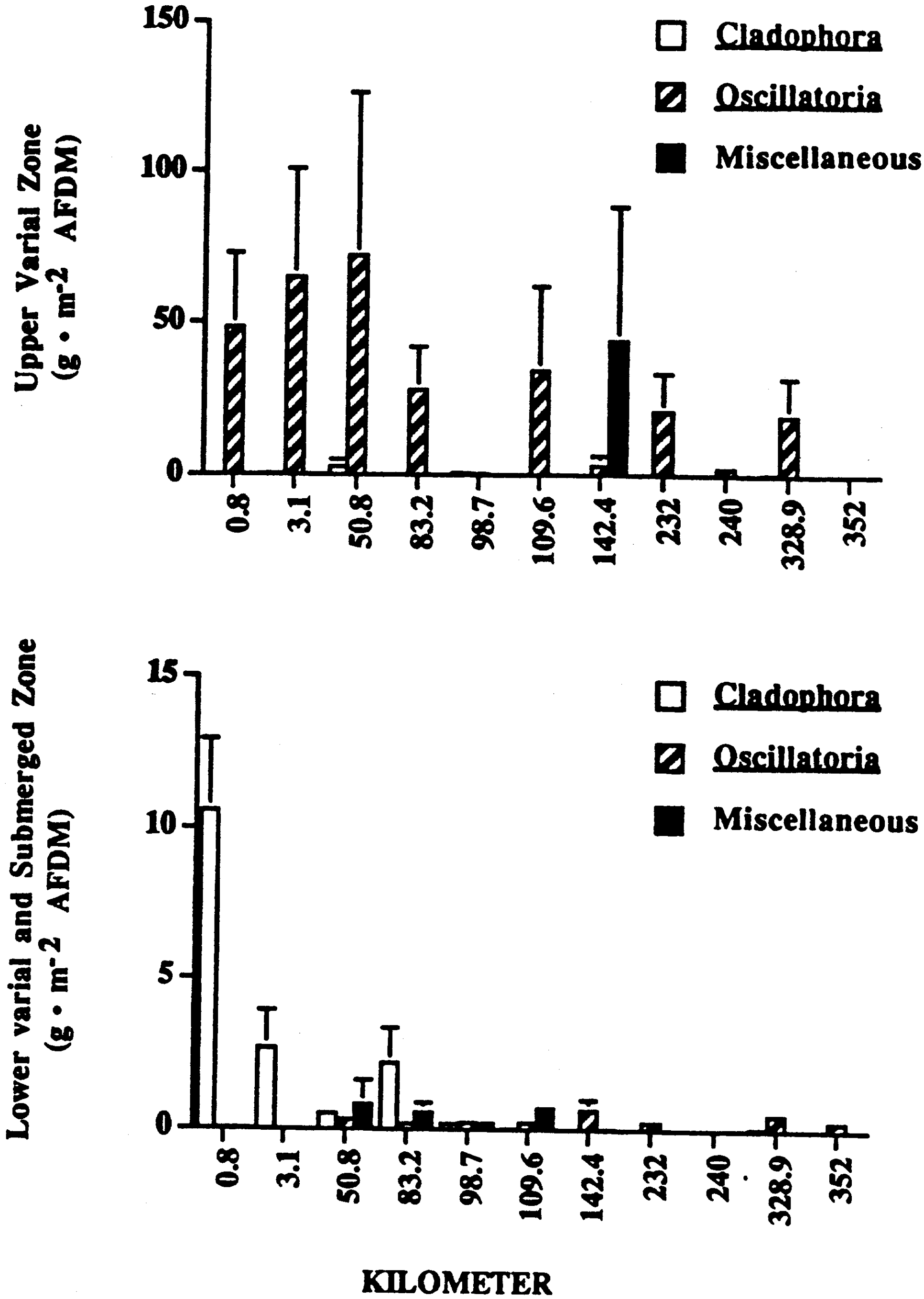


Figure 11. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for Cladophora glomerata, Oscillatoria spp. and miscellaneous primary producers in riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 352). Collections were taken in March 1995 for comparison of the upper varial zone ($\geq 283\ m^3 \cdot s^{-1}$) and the lower varial and submerged zone ($< 283\ m^3 \cdot s^{-1}$). Error bars represent ± 1 S.E.

(1995) documented the severe impact of short term desiccation on the energy budget within the highly productive tailwaters of Glen Canyon Dam.

The strong habitat partitioning of Cladophora and Oscillatoria revealed the importance of baseflows in defining the distribution of benthic communities in the regulated Colorado River. This is especially important because Oscillatoria is a poor substrate for macroinvertebrate colonization in comparison to Cladophora (Blinn et al. 1994). Our results supported the study by Shaver (1995) that suggested a complex interaction for colonization space occur between C. glomerata and Oscillatoria in the Colorado River ecosystem below Glen Canyon Dam.

Interim Flow Benthic Patterns

The ten collection trips conducted between September 1992 and March 1995, during Interim Flows (IF) have provided an important data base that describes patterns in the ecology of benthic communities in the Colorado River through Grand Canyon. Cladophora glomerata mass increased in riffle habitats through IF until this past March, after which time elevated suspended sediments reduced Cladophora mass to those of the March and January 1993 collections (Fig. 12). Both of these latter collections followed winters that were well above average in precipitation. Therefore, monitoring C. glomerata mass is highly informative because of the positive correlation between this keystone species and the macroinvertebrate benthic community throughout the study site (Blinn et al. 1994).

We divided the study site into three main reaches: Glen Canyon tailwaters (Glen Canyon Dam to the Paria River; RKM -25-1.0), Marble Canyon (Paria to Little Colorado Rivers; RKM 1.0-99) and Grand Canyon (LCR to Diamond Creek; RKM 99-362). We analyzed each biotic category in these reaches for changes in mass during IF collections. We further analyzed pool and riffle habitats independently.

MANOVA analyses of Glen Canyon riffles showed an overall significant difference between collection trips (Table 3; Figs. 13-17). Miscellaneous primary producers (MPP) and C. glomerata showed a variable but general increase in mass estimates during IF (Fig. 13). Detritus was also variable and remained between 0.1 and 1.8 $g \cdot m^{-2}$ (Fig. 14). Miscellaneous macroinvertebrate mass estimates were highly variable and an order of magnitude lower in comparison to down river reaches (Fig. 15). This is probably due the lack of

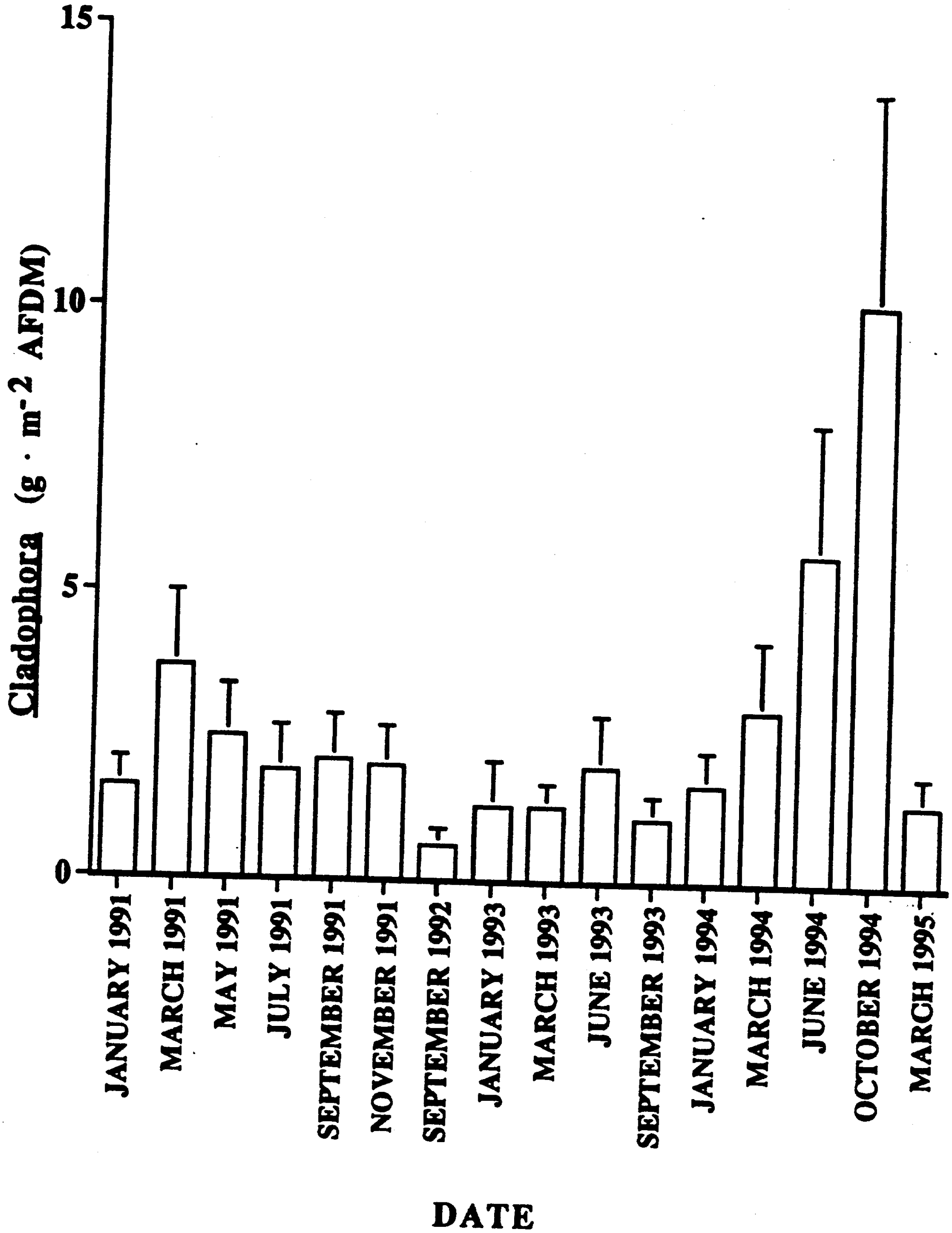


Figure 12. System-wide Cladophora glomerata ash-free dry mass (g • m^{-2} AFDM) collected with a Hess from riffle habitats in the Colorado River through Grand Canyon National Park. Biomass was averaged from 11 stations for each collection trip. Error bars represent ± 1 S.E.

Table 3. Results of MANOVA analyses for benthic collections during Interim Flow from 1992 through 1995 (n=10) in the Colorado River through Grand Canyon for both pool and riffle habitats within the three major reaches: Glen Canyon, Marble Canyon and Grand Canyon. Predictor variables of each collection trip were analyzed against biotic categories as response variables (AFDM·m^{-2} ln+1 transformed data). Taxonomic categories include: Cladophora (C), Oscillatoria (O), miscellaneous algae/macrophytes (A), detritus (D), chironomids (M), Gammarus (G), gastropods (S), simuliids (B), lumbriculids (L), tubificids (T), and miscellaneous macroinvertebrates (I). These analyses indicate high variability for selected taxa under Interim Flows with pools more resilient to change than riffles. Only significant univariate response variables are listed (p<0.03). Overall Wilks' Lambda, reach x habitat, was significant (p < 0.0001)

Source	Wilks' Lambda	Approximate F Statistic	df	p	Significant Respons Variable
		RIFFLE HABITATS			
Glen Canyon	0.1	2.5	99,505	<0.00001	L,G,M,I,C,S,A
Marble Canyon	0.3	5.0	99,2402	<0.00001	L,G,B,M,I,C,D O,A
Grand Canyon	0.4	5.0	99,3339	<0.00001	G,B,M,I,C,D O,A
		POOL HABITATS			
Glen Canyon	0.5	1.1	9,1007	0.18	M
Marble Canyon	0.3	0.7	99,4616	<0.00001	T,D,O
Grand Canyon	0.4	5.0	99,8368	<0.00001	B,M,C,D,O,A

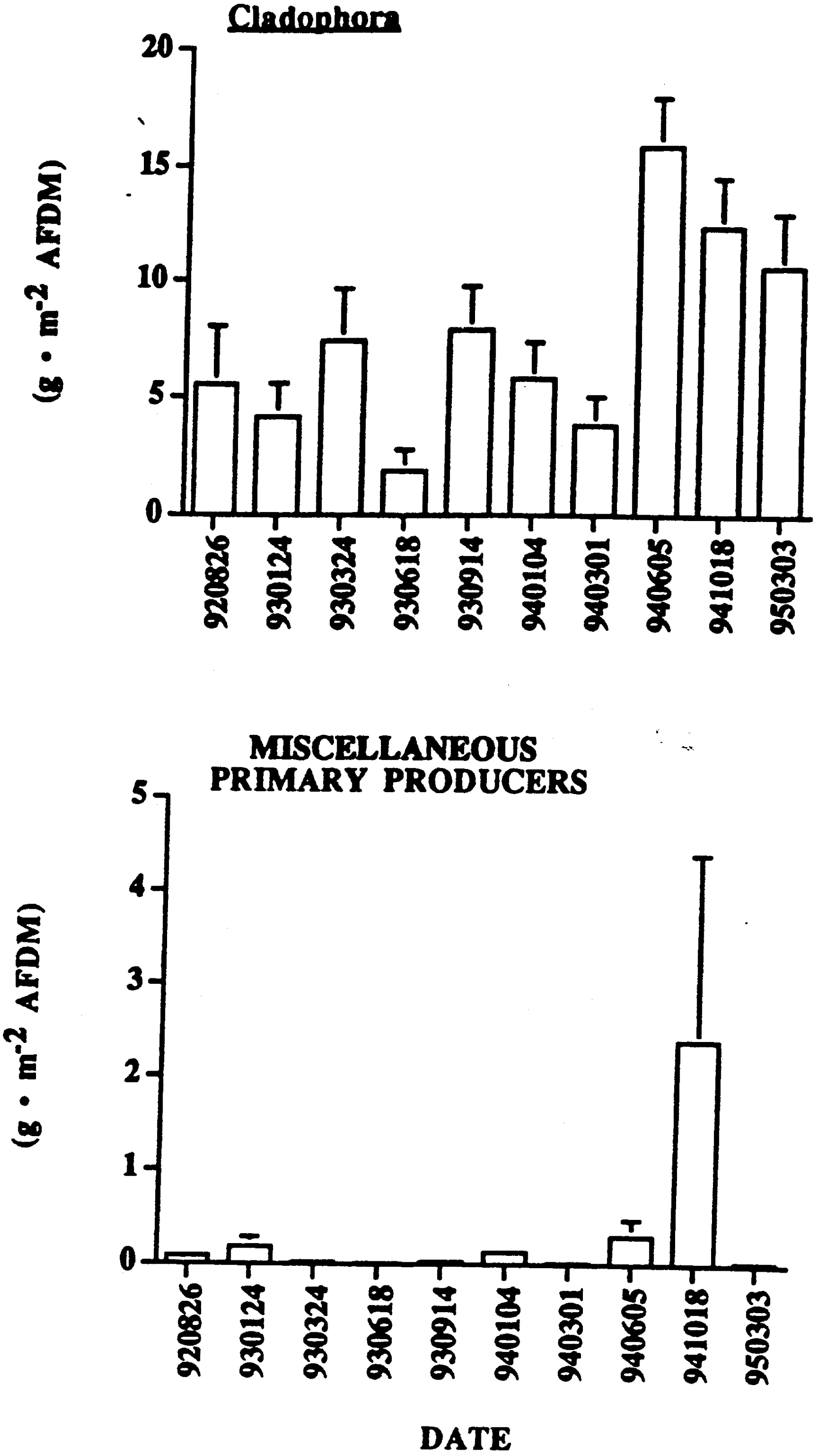


Figure 13. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for Cladophora glomerata and miscellaneous primary producers in riffles through Glen Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

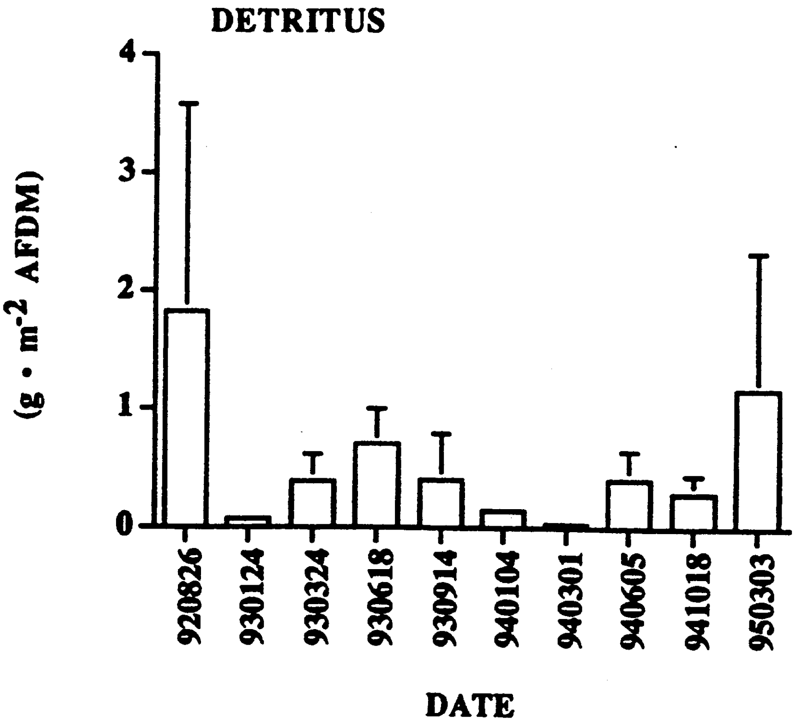


Figure 14. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for detritus in riffles through Glen Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

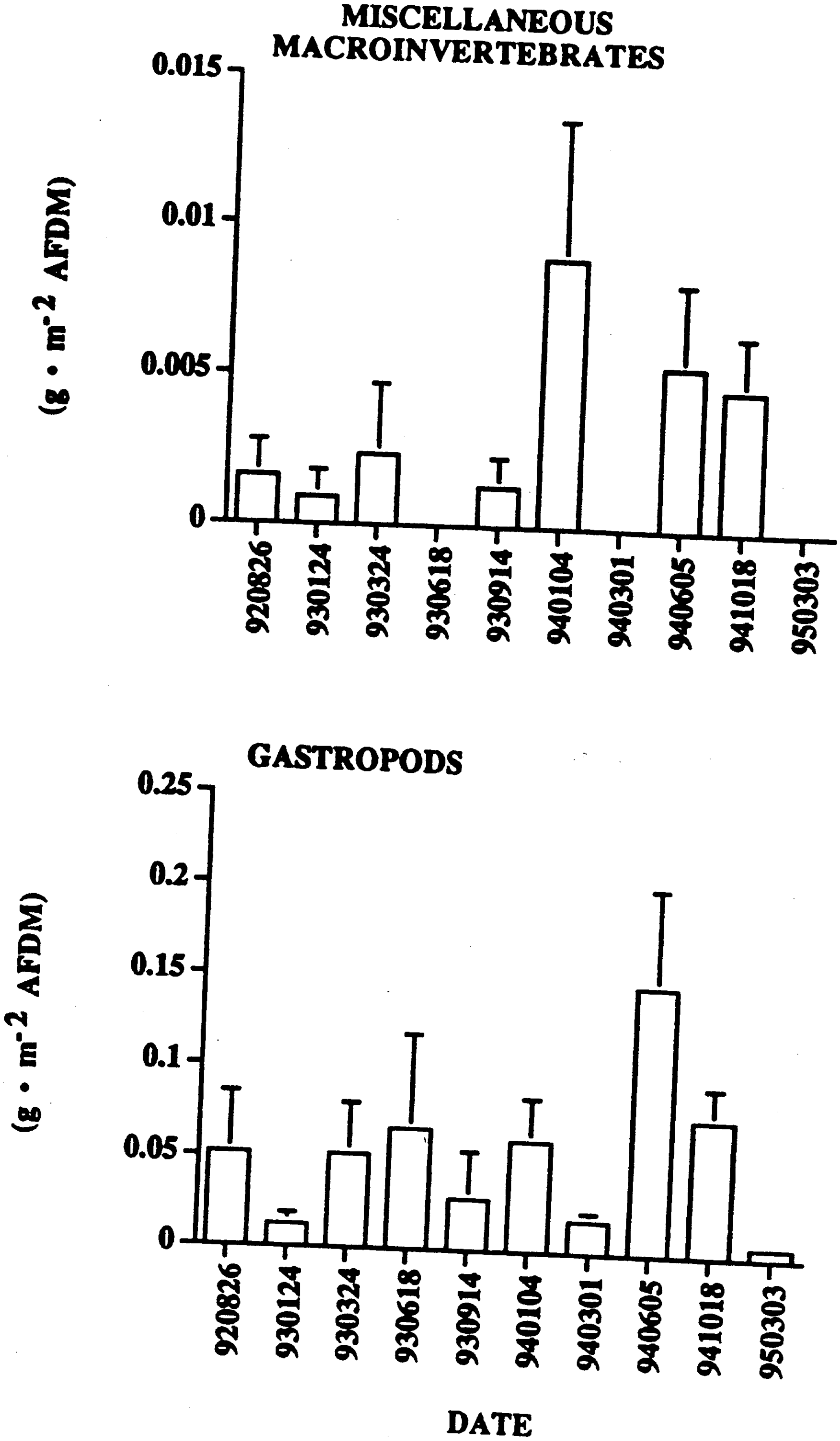


Figure 15. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for miscellaneous macroinvertebrates and gastropods in riffles through Glen Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

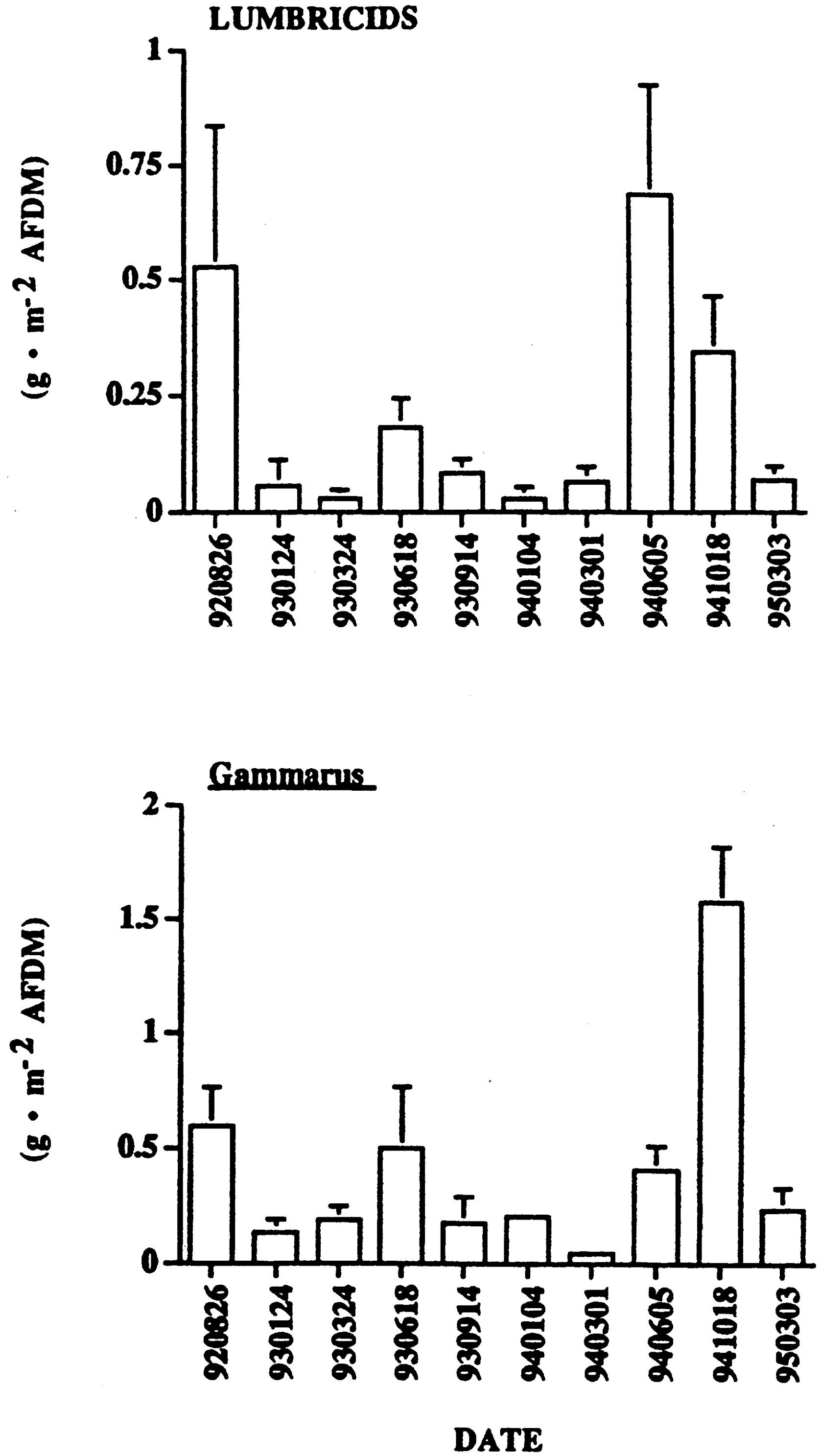


Figure 16. Average ash-free dry mass (g • m^{-2} AFDM) for lumbricids and Gammarus lacustris in riffles through Glen Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

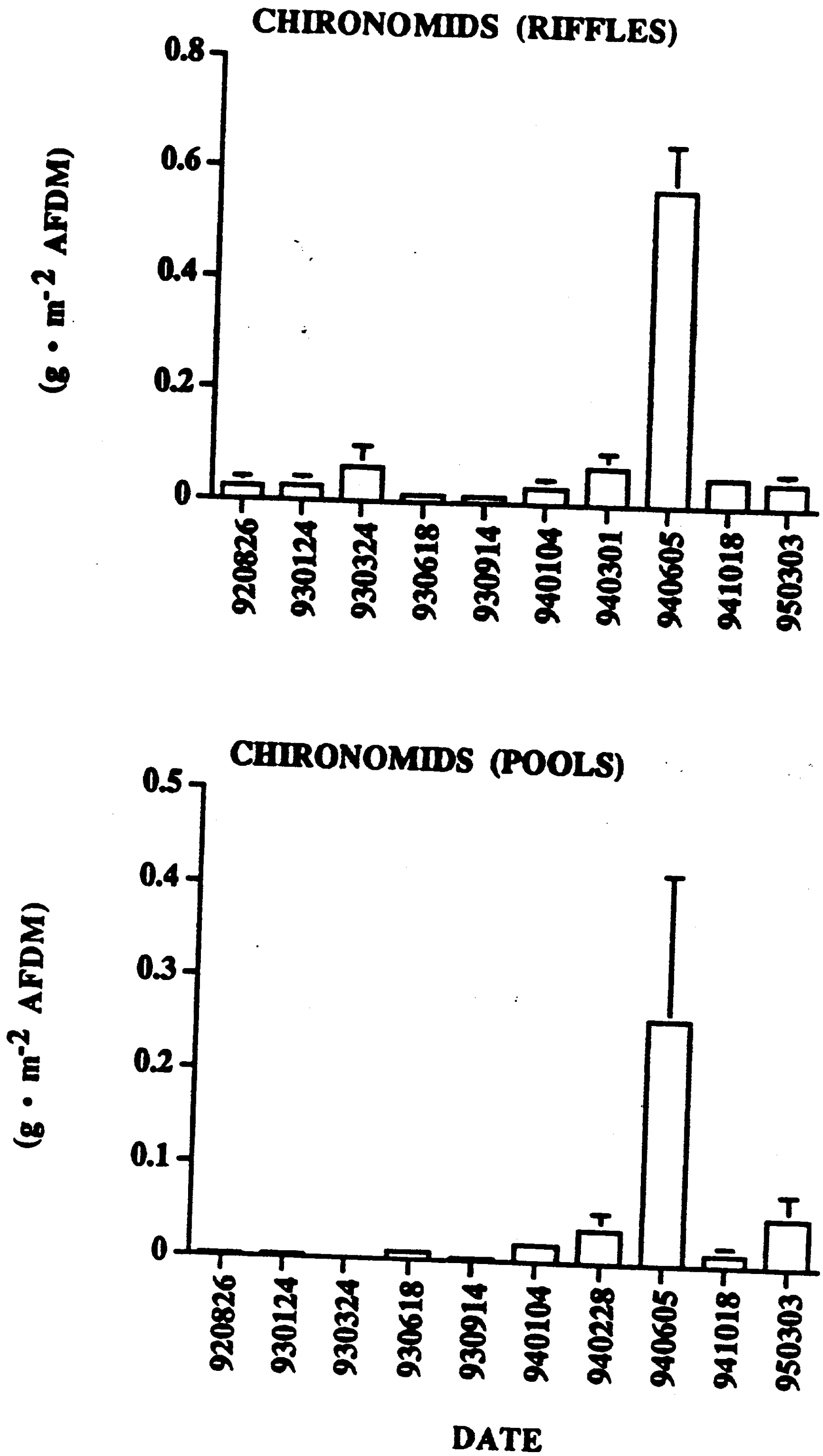


Figure 17. Average ash-free dry mass (g • m^{-2} AFDM) for chironomids in riffles and pools through Glen Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

tributaries as a source of aquatic insects and the consistently cold water reducing biodiversity. Gastropod mass peaked in June collections. The tailwater reach had the highest mass of gastropods of all sites averaging 0.051 $g \cdot m^{-2}$, with Nankoweap Cobble (RKM 83.2) the next most abundant site for gastropods (Fig. 15). Lumbricids, Gammarus, and chironomids showed similar patterns of seasonal peaks in June and were also much higher in mass than down river sites (Blinn et al 1994; Figs. 16 & 17). Glen Canyon pools did not show a significant overall change in mass during IF (Table 3). However, univariate analyses indicated that chironomid larval mass changed significantly, with an overall increase through time and a peak in June 1994 (Fig. 17). Again, riffles were considerably more sensitive to change than pools, especially in the cold, clear tailwaters at Lees Ferry.

MANOVA analyses of Marble Canyon riffles and pools revealed a significant overall difference in mass estimates between collection trips during IF (Table 3). Cladophora glomerata mass showed a general increase over time and was even higher than that at Glen Canyon in October 1994 (Figs. 13 & 18). Oscillatoria also varied significantly between collection trips in riffles and was found in trace amounts in Marble Canyon in October 1994 and March 1995 (Fig. 18). Miscellaneous primary producers (composed primarily of Fontinalis) were also significantly different between trips and showed a general increase in mass over time in riffles (Fig. 19). Detritus, in both riffles and pools, varied significantly between collection trips with pools accumulating detritus over time (Fig. 20). Tubificids in pools changed significantly during IF reaching a peak in January 1993 and declining during June 1994 (Fig. 21). Lumbricid, Gammarus, miscellaneous macroinvertebrate, chironomid and simuliid mass all varied significantly in riffle habitats between collection trips and showed a general increase in mass through time (Figs. 21-23). In March 1995, we collected two new taxa from the mainstem in Marble and Grand Canyons: a stonefly (Taenionema pacificum) and a caddisfly (Rhycophila coloradensis). Taenionema pacificum is common along the upper Colorado, San Juan, Yampa and South Platte Rivers (Ward & Kondratieff 1992). Members in the order Taeniopterygidae prefer lotic-erosional habitats, usually as sprawlers and clingers that are generally shredders, but can be detritivores, collectors-gathers or scrapers (Merritt and Cummins 1984). Rhycophila coloradensis is common in all drainages of the Colorado River basin (Ward & Kondratieff 1992). The genus Rhycophila also prefers lotic-erosional habitats and are free ranging clingers and engulfing predators (Merritt & Cummins 1984). Both of these aquatic insect taxa were observed mating and ovipositing directly in the mainstem of the Colorado River. Future collection trips will potentially determine fecundity success. We

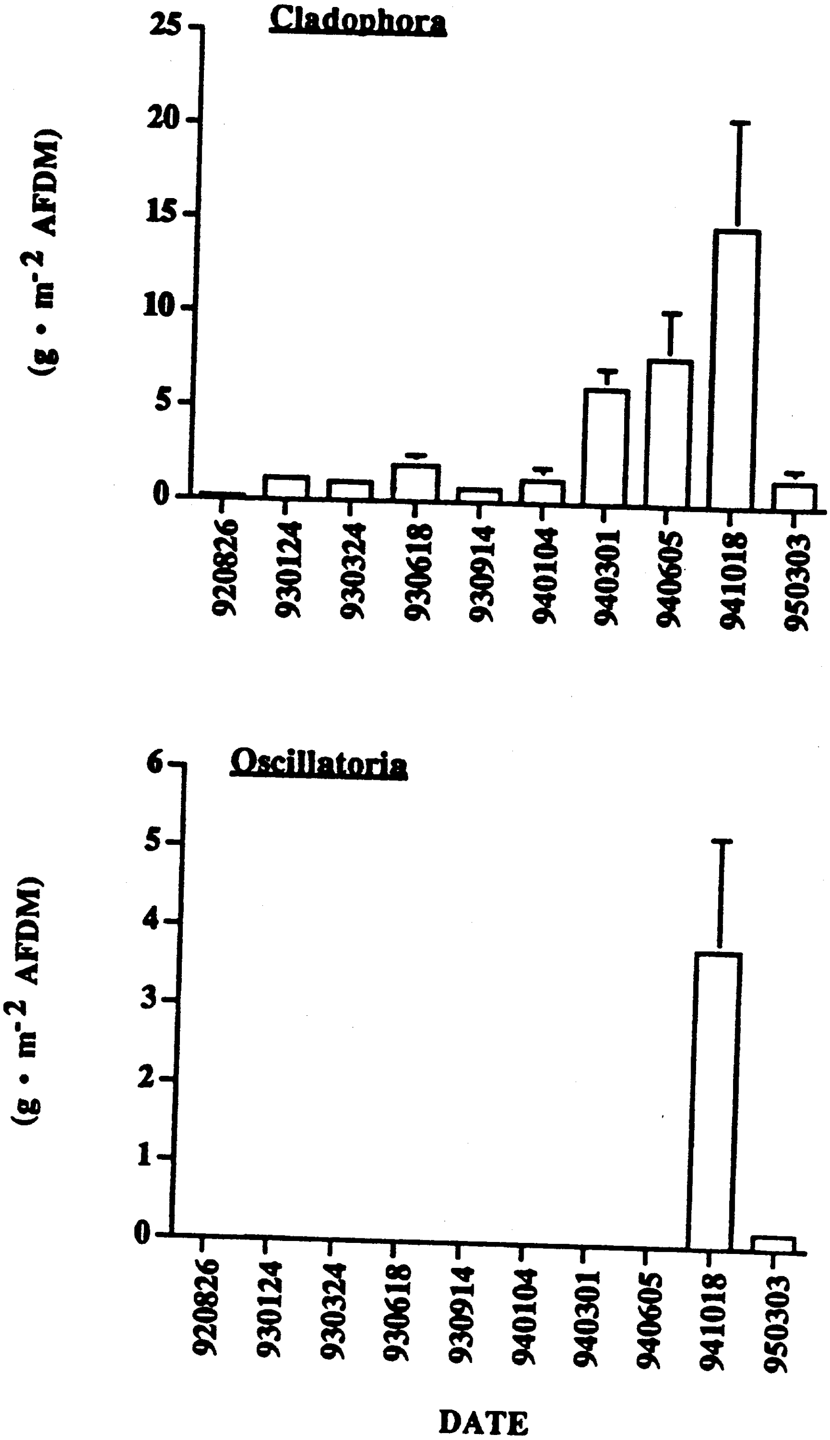


Figure 18. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for Cladophora glomerata and Oscillatoria spp. in riffles through Marble Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

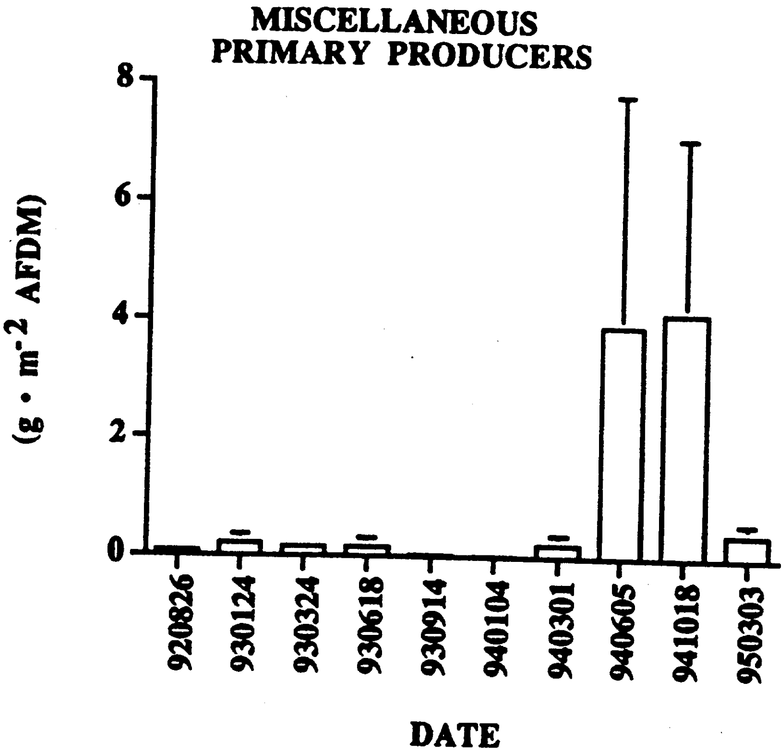


Figure 19. Average ash-free dry mass ($g \cdot m^{-2}$AFDM) for miscellaneous primary producers in riffles through Marble Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

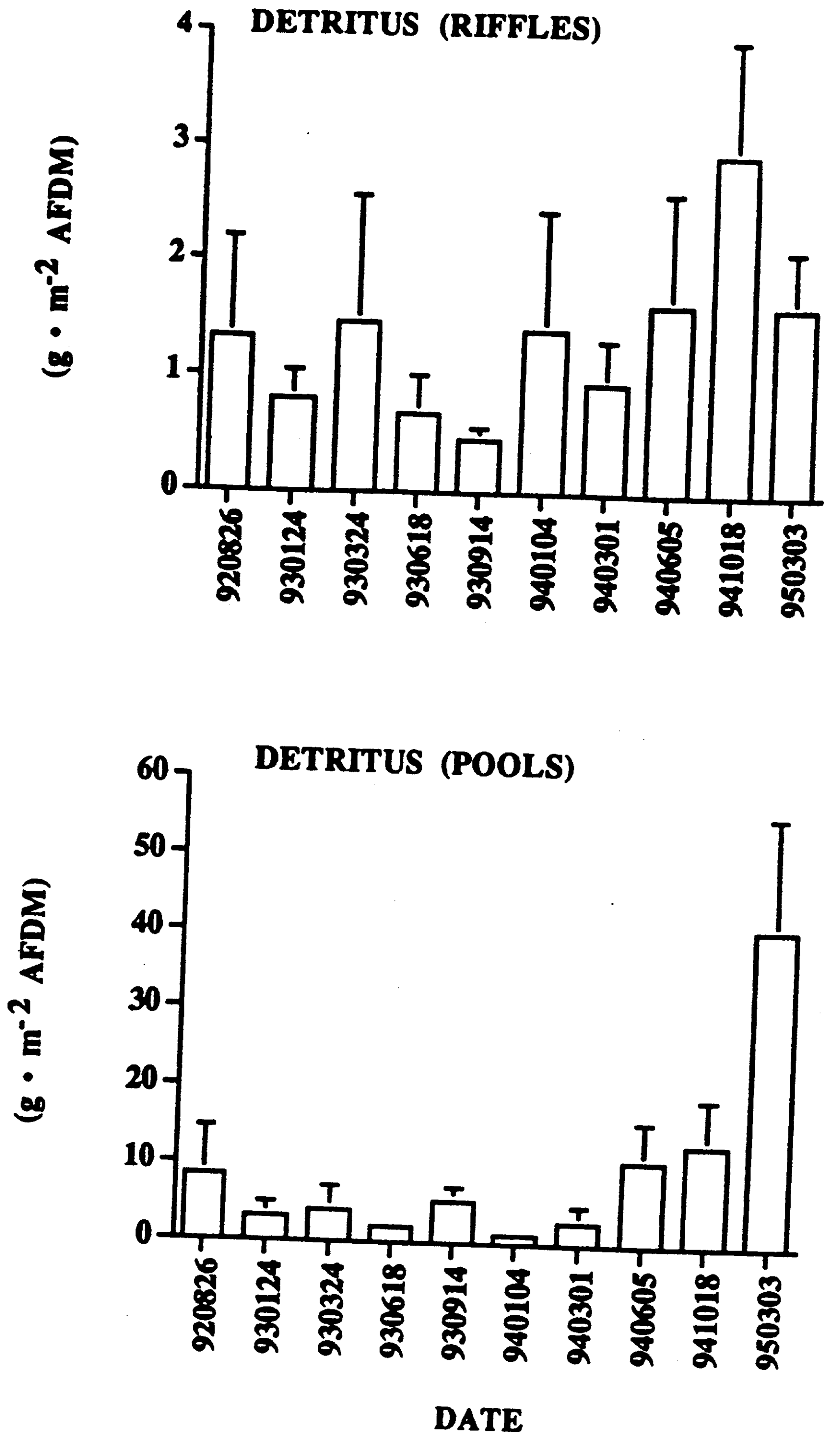


Figure 20. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for detritus in riffles and pools through Marble Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

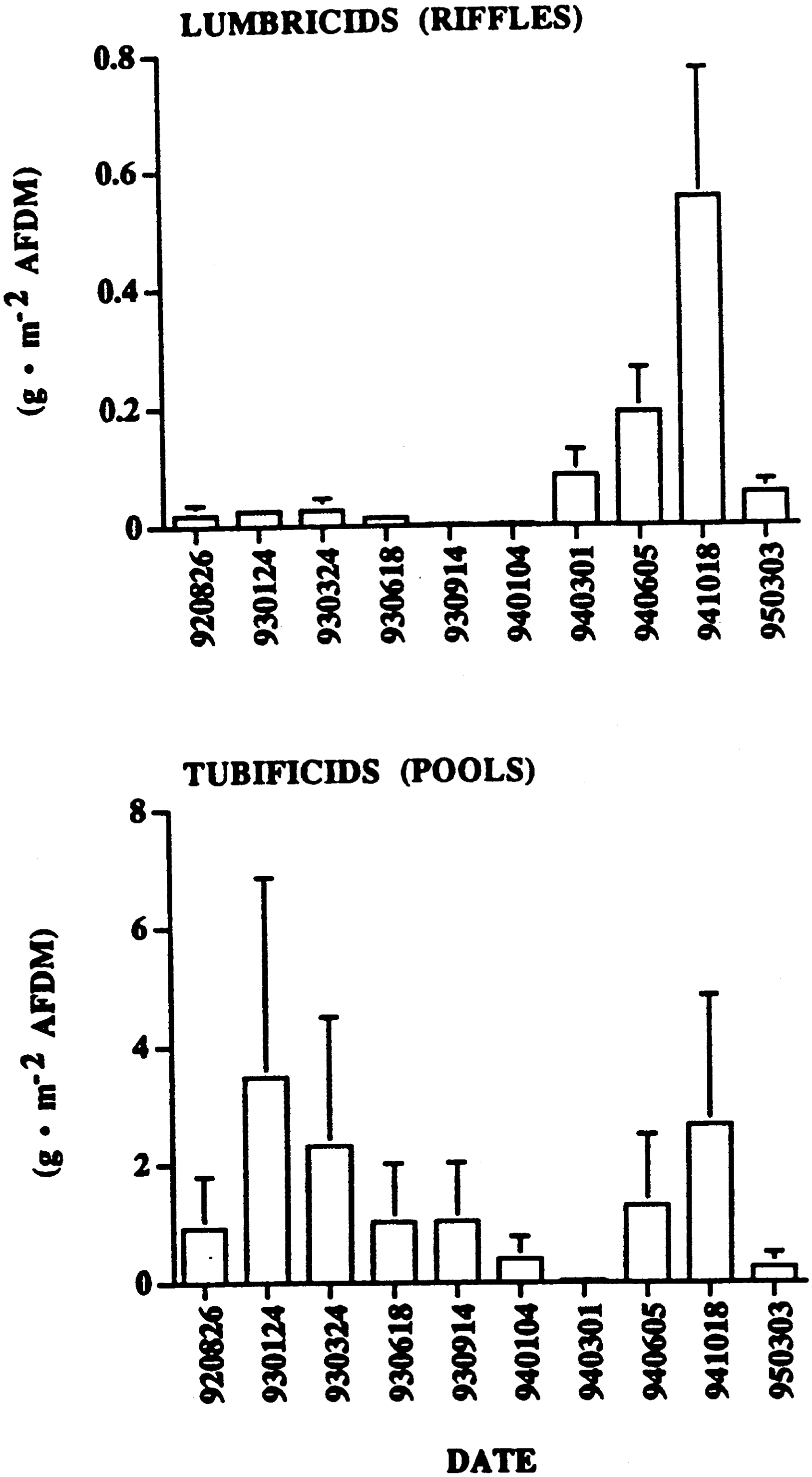


Figure 21. Average ash-free dry mass (g • m^{-2} AFDM) for lumbricids in riffles and tubificids in pools through Marble Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

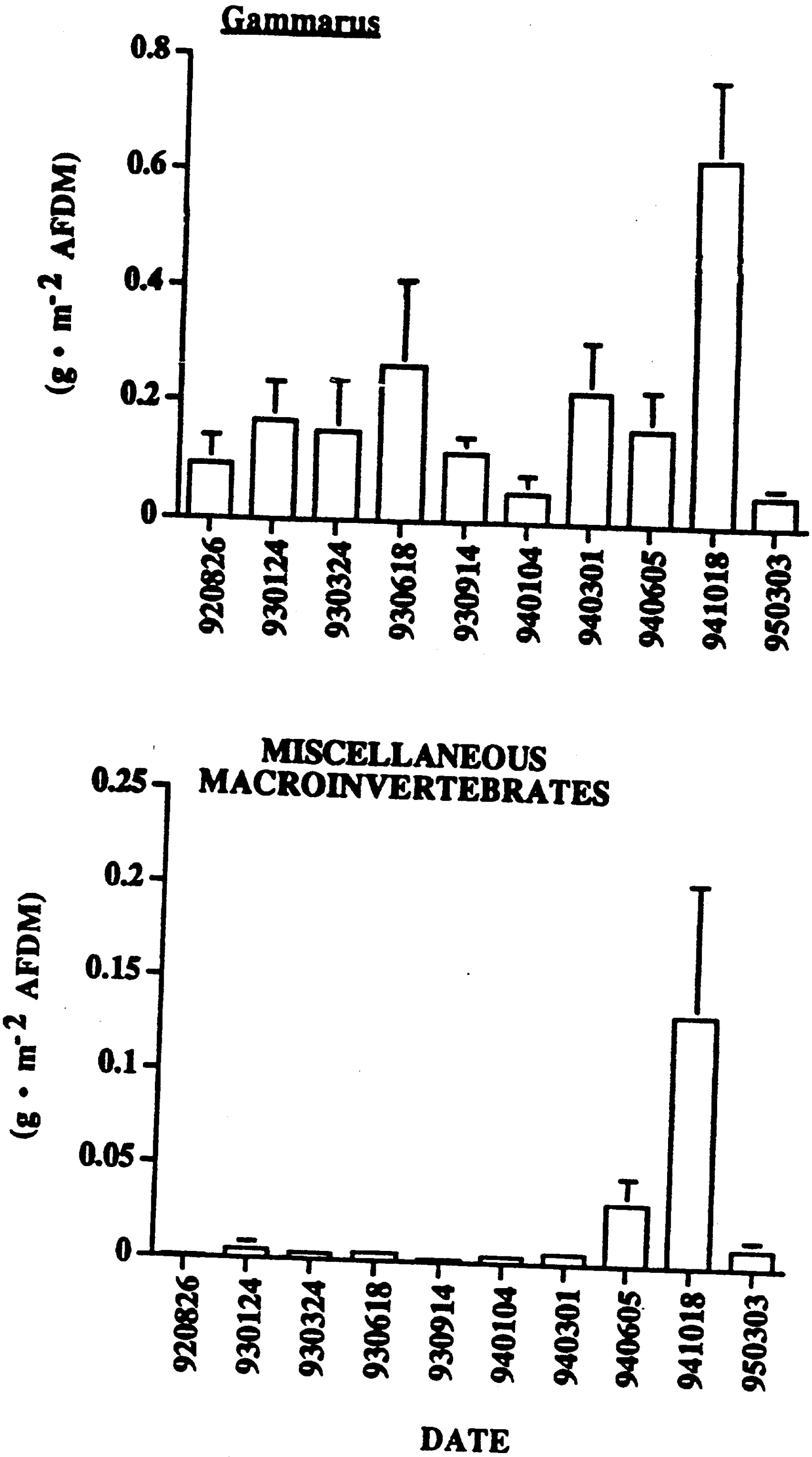


Figure 22. Average ash-free dry mass (g • m-2 AFDM) for Gammarus lacustris and miscellaneous macroinvertebrates in riffles through Marble Canyon in the Colorado River . Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

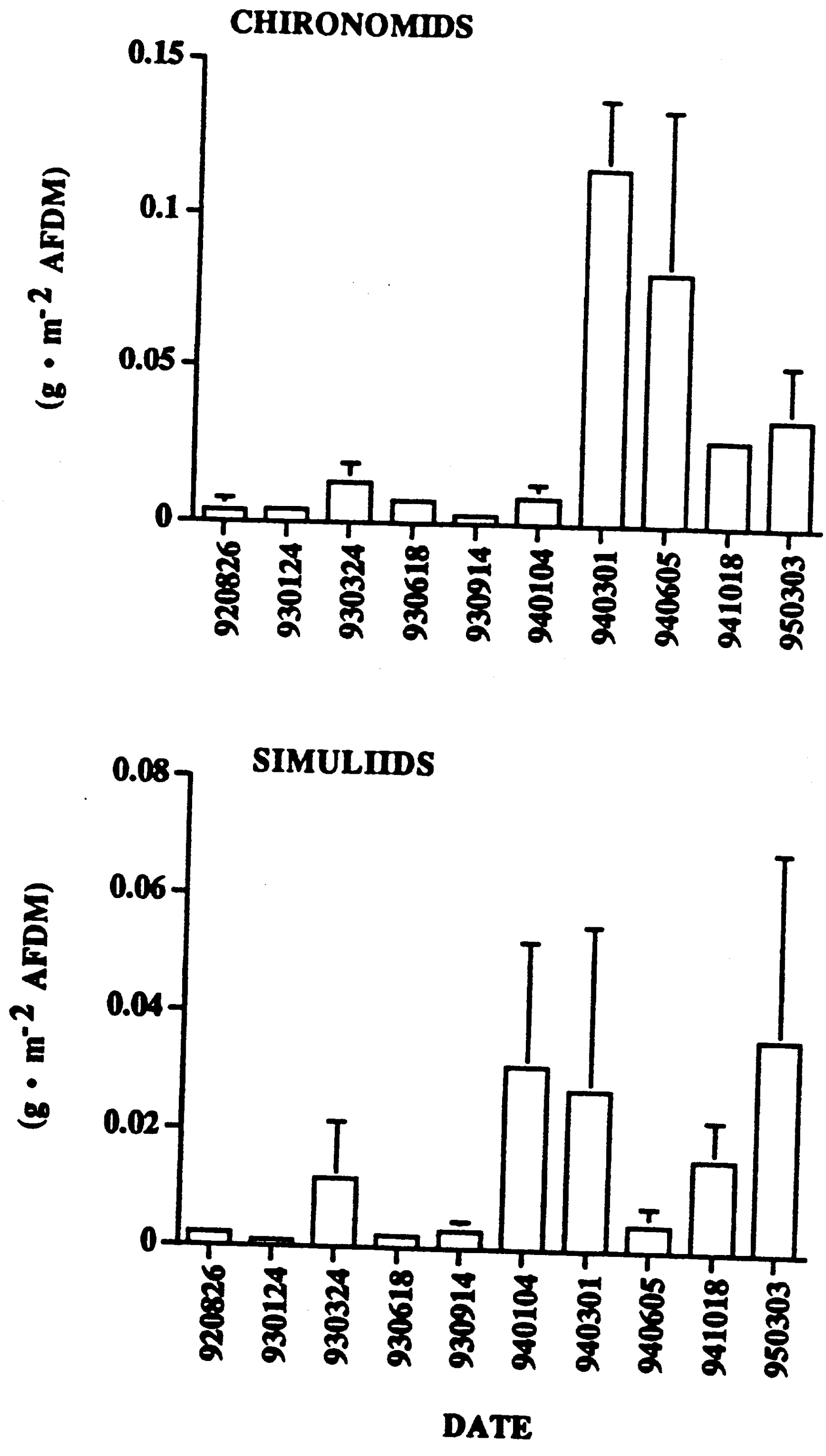


Figure 23. Average ash-free dry mass (g • m^{-2} AFDM) for chironomids and simuliids in riffles through Marble Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

also collected Gerridae and Naucoridae from the margins of pools within emergent vegetation in Marble and Grand Canyons. It is noteworthy that these collections were made from random drops of the Petersen dredge, suggesting that densities of these insects are increasing within marsh habitats.

MANOVA analyses also indicated that pools and riffles in the Grand Canyon reach varied between collection trips (Table 3, Figs. 24-30). Generally, both primary and secondary producer mass increased during IF in both habitats. We also had an increase in the number of biotic categories in pools that changed significantly between trips, suggesting changes in the stability of pool habitats in Grand Canyon. Even though there is a general increase in bed-load sand down-river and river regulation adds to the instability of pool habitats, the increase in the benthic mass in pools may be attributed to the consistency of IF. These Grand Canyon sites are not as impacted by the daily hydrograph as upper sites and therefore trends are more readily apparent downriver. The increase in seasonal water temperature in the lower Grand Canyon may also have led to higher variability within pools.

MONITORING ELEVATED BASEFLOWS

Record spring precipitation in the upper Colorado River basin resulted in an increase in discharge from Glen Canyon Dam, starting in June and continuing through August 1995. Benthic collections at three stage elevations on 12 June were compared to those taken on 28 August at the Lees Ferry cobble bar site (RKM 1.0). Overall we found colonization of the lower varial zone comparable to the continuously submerged channel (<227 $m^3 \cdot s^{-1}$) after 76 d, along with limited colonization of the upper varial zone and an increase in algal and macrophyte composition. Cladophora glomerata AFDM decreased by 70% in the channel between June and August ($p = 0.006$), but increased in the lower varial zone (~300 $m^3 \cdot s^{-1}$) by 94% (Table 4). The decrease in C. glomerata AFDM in the channel may be from a reduction in filament length which ranged from an average of 58 cm in June to 20 cm in August ($n = 30$). Epiphyton AFDM in the channel increased significantly ($p = 0.006$) by 40% from June to August and there was no significant difference between the channel and lower varial zone in August (Table 4). Macrophyte and filamentous algal AFDM increased during the sampling period by 99% in the channel and varial zone. Chara spp., Potamogeton pectinatus and Draparnaldia spp. made up the major increase in species richness for primary producers. Oscillatoria spp. moved from the lower varial zone in June to the upper varial zone (>450 $m^3 \cdot s^{-1}$) in August (Table 4). This shift by Oscillatoria is related to the inundation of the lower varial zone and further supports the primary producer zonation pattern previously stated.

Table 4. Comparsion of mean benthic biomass and primary productivity at Lees Ferry cobble bar (RKM 1.0) at three stage levels from June 12 through August 28, 1995 at a mininum disharge of ~360 $m^{-3} \cdot s^{-1}$ with a daily average of ~480 $m^{-3} \cdot s^{-1}$.

Biotic Paramter	Channel (<227 $m^3 \cdot s^{-1}$)		Lower Varial (-300 $m^3 \cdot s^{-1}$)		Upper Varial (>450 $m^3 \cdot s^{-1}$)	
	June	August	June	August	June	August
Primary Production						
GROSS						
($g \cdot O_2 \cdot m^{-2} \cdot h^{-1}$)	0.55	0.52	0.23	0.52		0.09
(±SE)	0.06	0.05	0.10	0.05		0.003
NET						
($g \cdot O_2 \cdot m^{-2} \cdot h^{-1}$)	0.27	0.17	0.17	0.40		0.008
(±SE)	0.07	0.01	0.14	0.11		0.004
Epiphyton						
AFDM ($g \cdot m^2$)	0.019	0.032		0.023		
(±SE)	0.002	0.003		0.004		
Cladophora glomerata						
AFDM ($g \cdot m^2$)	15.1	6.8	0.6	8.6		
(±SE)	1.6	1.6	0.5	4.2		
Miscellaneous Primary Producers						
AFDM ($g \cdot m^2$)	0.03	9.7	0.04	3.3		
(±SE)	0.02	7.8	0.03	2.6		
Oscillatoria spp.						
AFDM ($g \cdot m^2$)	0.0	0.0	9.1	0.0		12.5
(±SE)			8.9			3.8
Macroinvertebrates						
AFDM ($g \cdot m^2$)	3.83	0.88	2.17	2.54		
(±SE)	0.52	0.32	1.08	0.77		
Macroinvertebrates						
($\# \cdot m^2$)	11436	7256	855	4397		
(±SE)	6257	1727	538	2640		

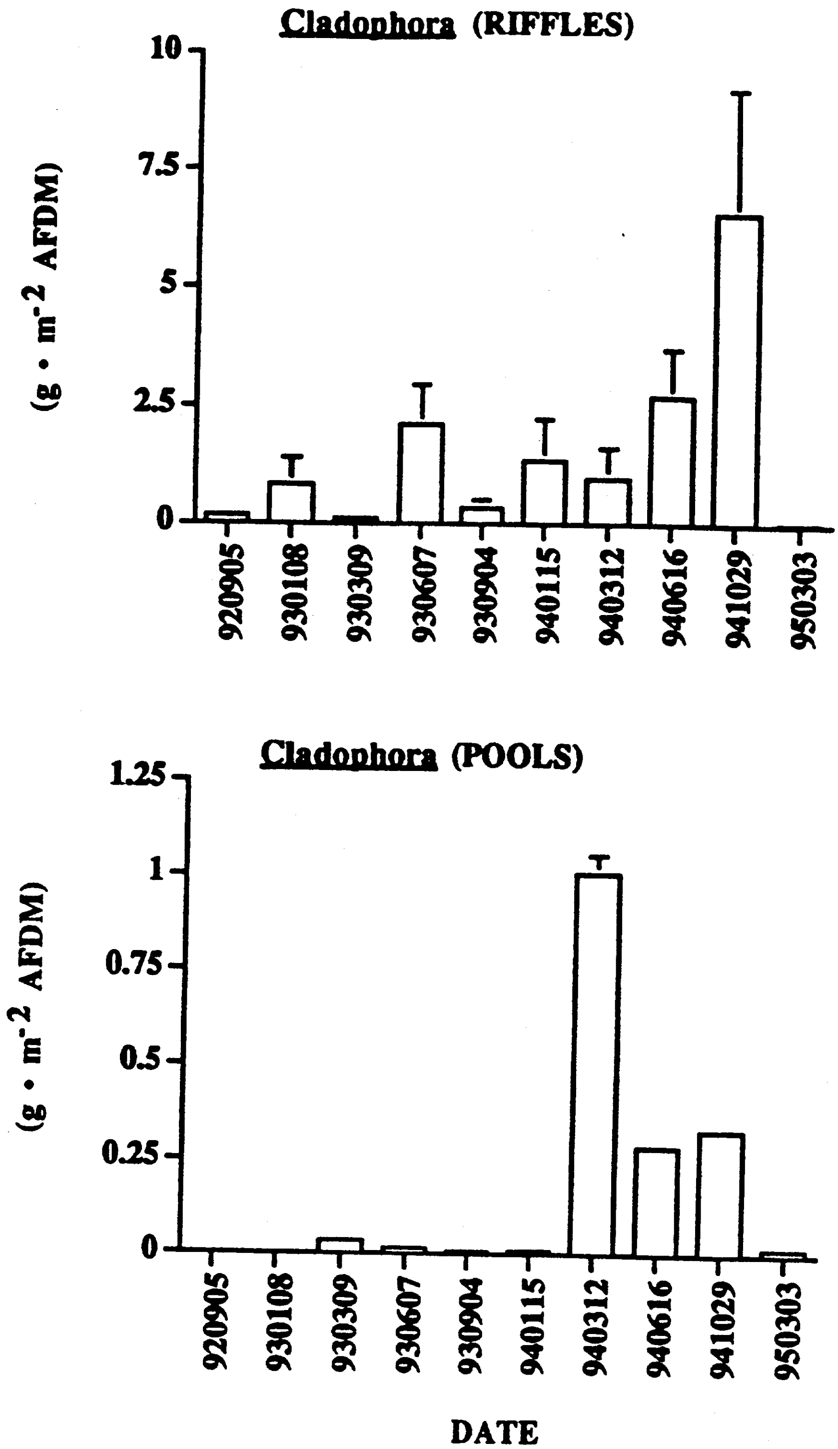
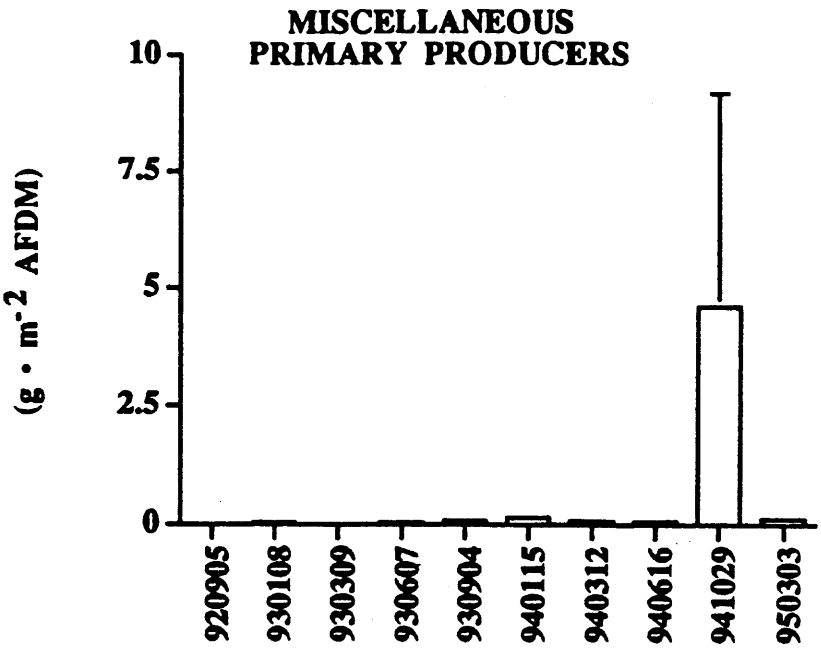


Figure 24. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for Cladophora glomerata in riffles and pools through Grand Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.



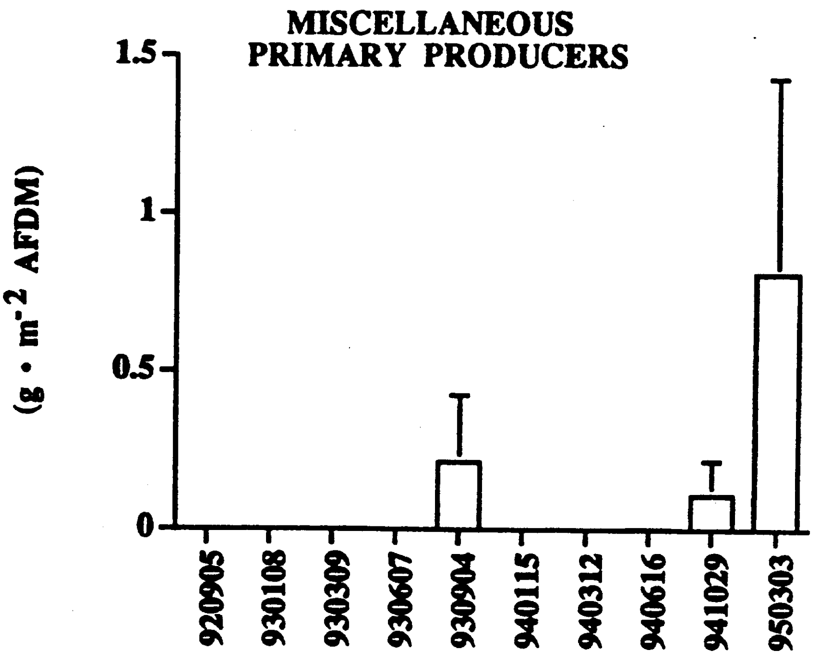


Figure 25. Average ash-free dry mass (g • m^{-2} AFDM) for miscellaneous primary producers in riffles and pools through Grand Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

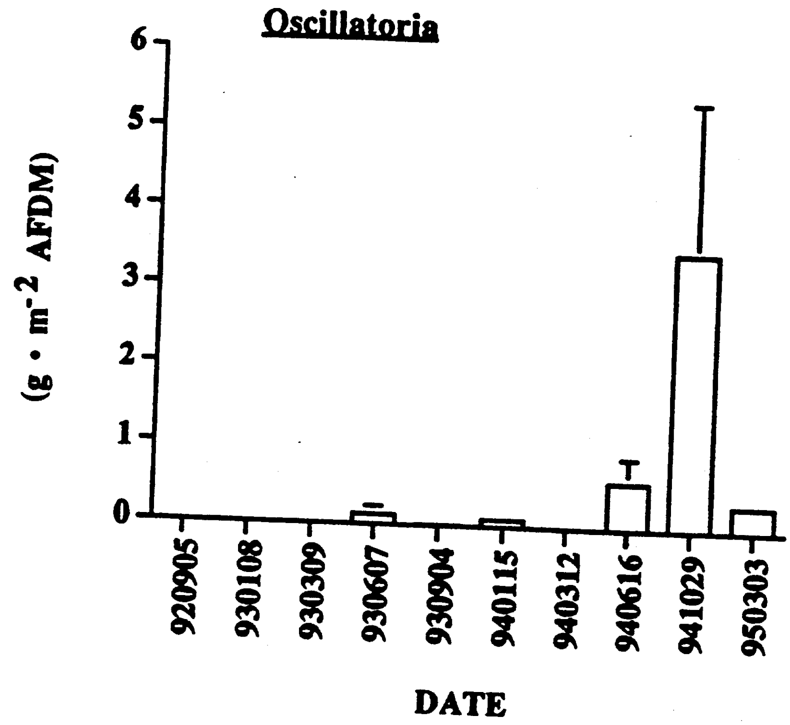


Figure 26. Average ash-free dry mass (g • m^{-2} AFDM) for Oscillatoria spp. in riffles through Grand Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

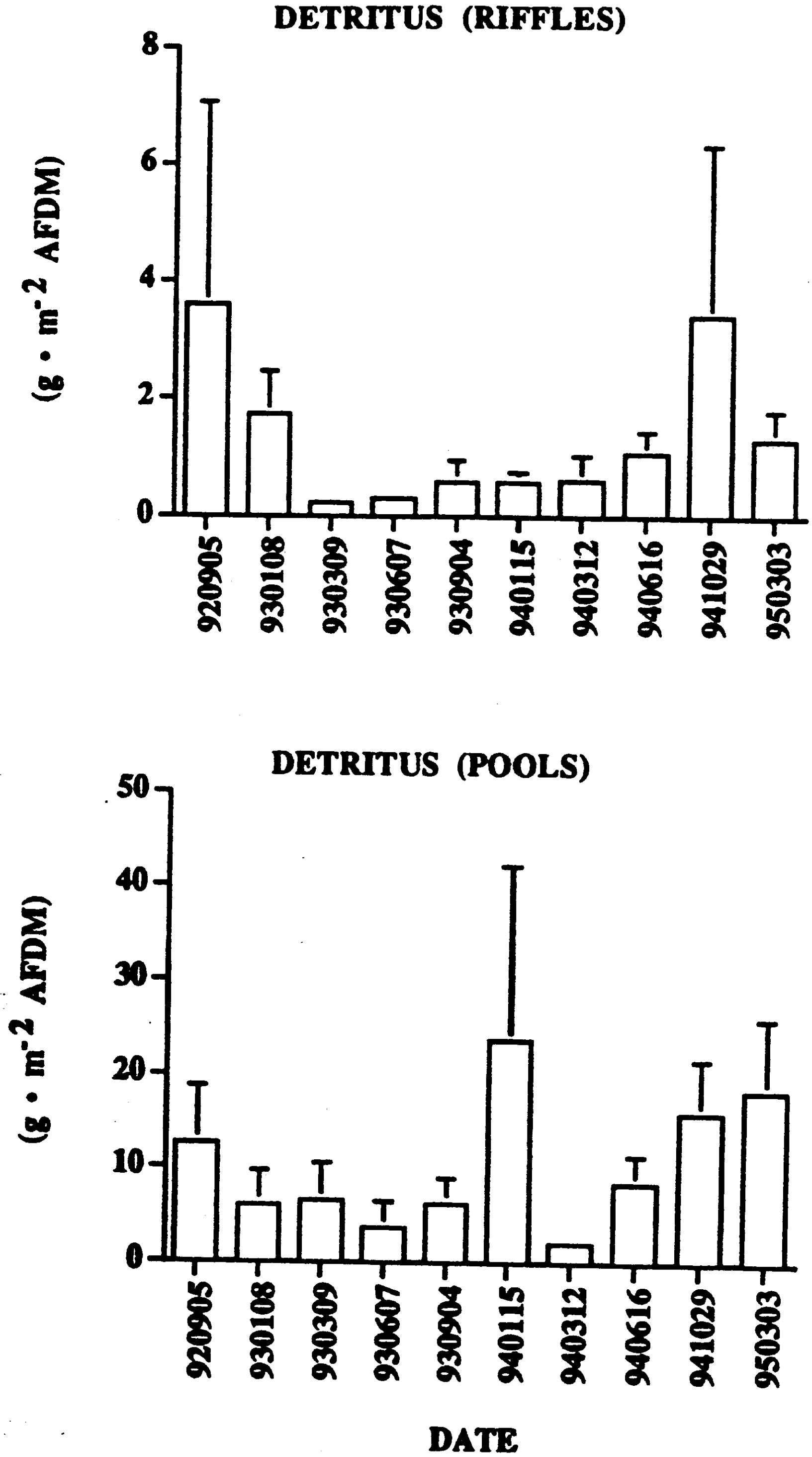


Figure 27. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for detritus in riffles and pools through Grand Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.

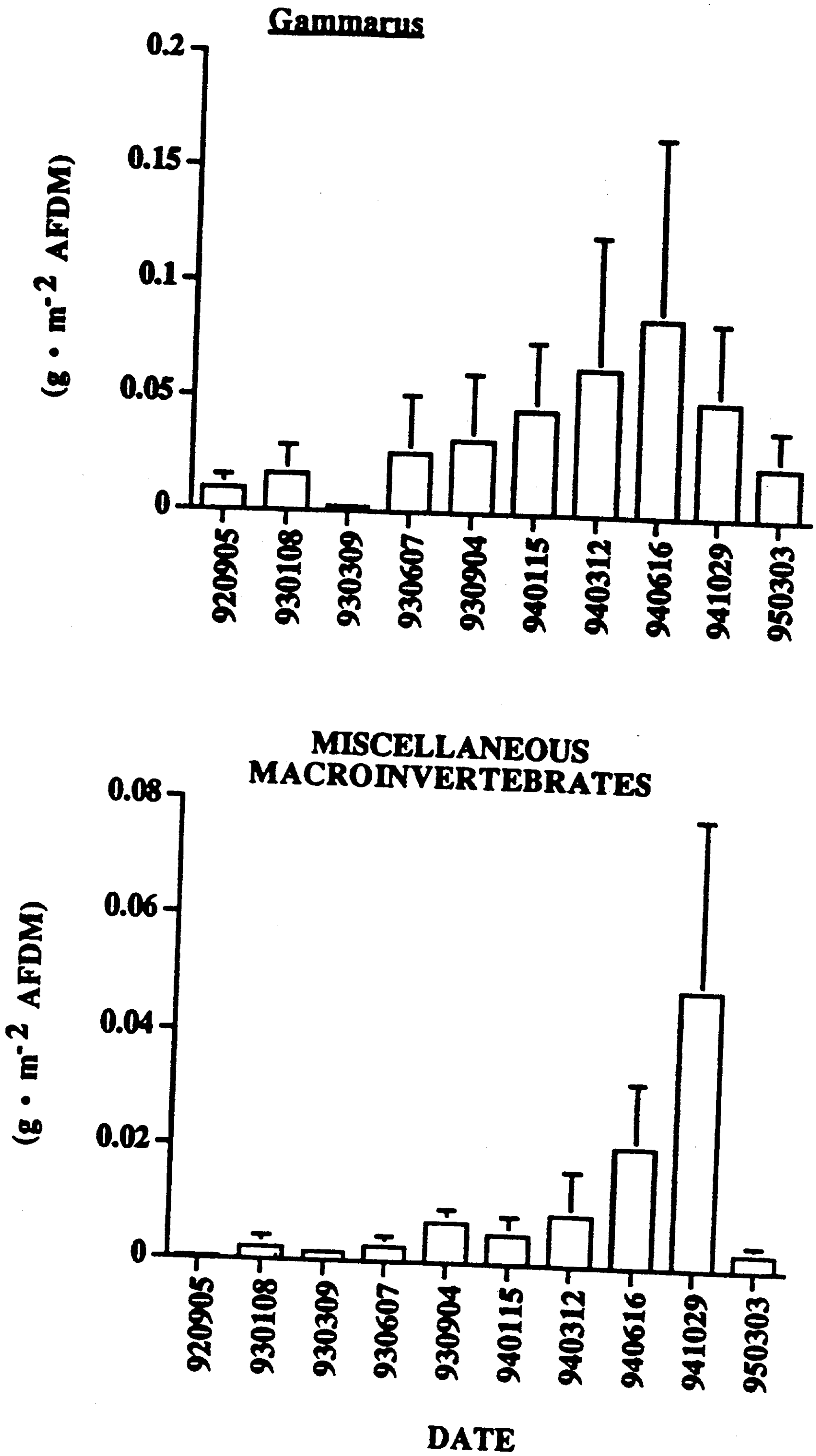
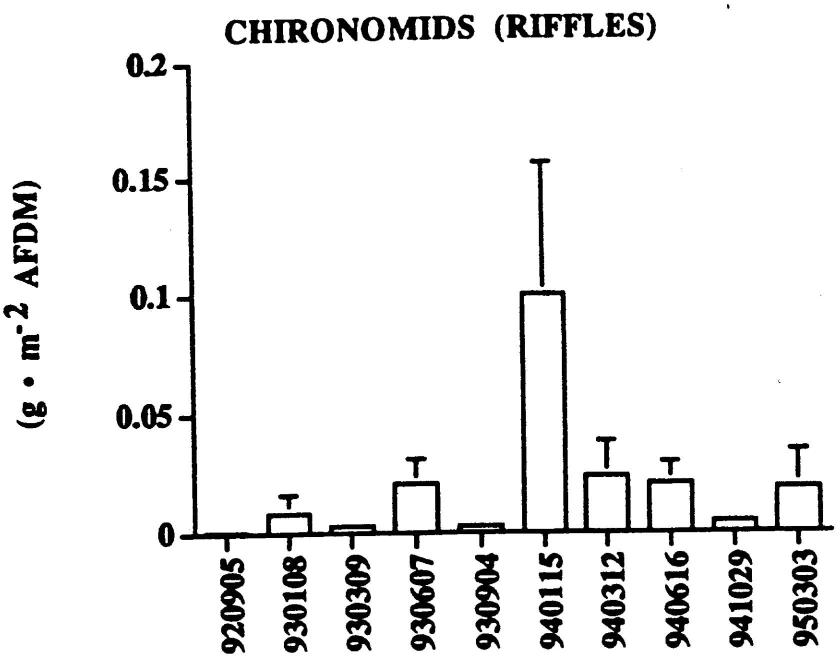


Figure 28. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for Gammarus lacustris and miscellaneous macroinvertebrates in riffles through Grand Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent ± 1 S.E.



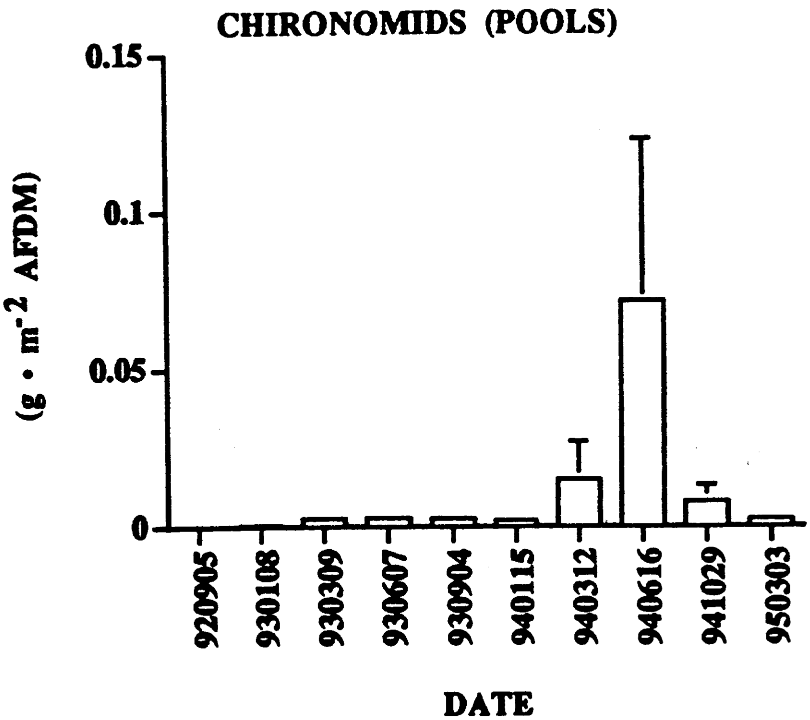


Figure 29. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for chironomids in riffles and pools through Grand Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent $\pm$ 1 S.E.

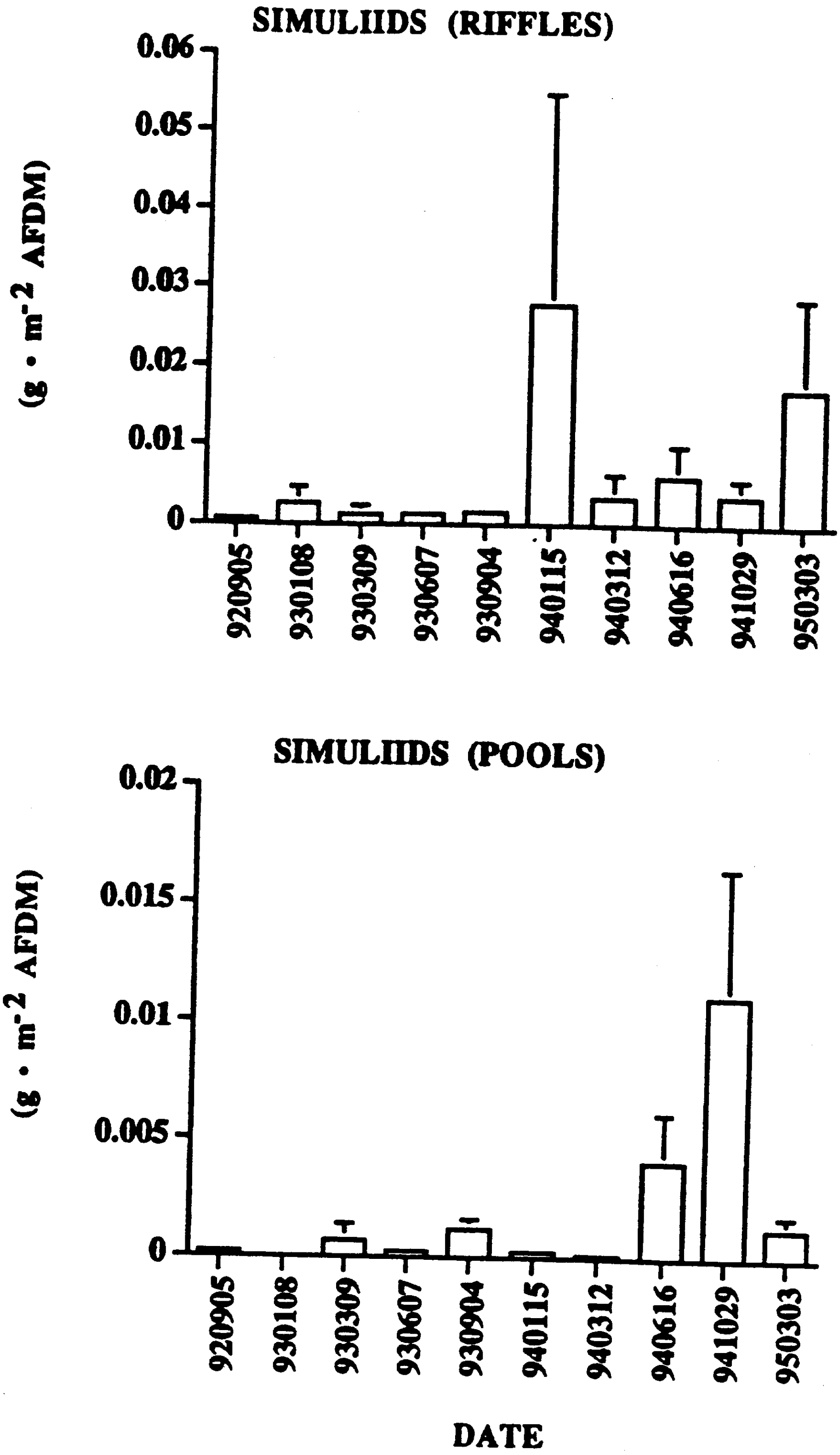


Figure 30. Average ash-free dry mass ($g \cdot m^{-2}$ AFDM) for simuliids in riffles and pools through Grand Canyon in the Colorado River. Seasonal collections were taken between September 1992 and March 1995. Error bars represent $\pm$ 1 S.E.

The colonization rates during this sampling period were faster than that reported by Blinn et al. (1994, 1995), and may have resulted from changes in the nutrient regime of Lake Powell due to the spring/summer high in-flow, and/or because cobbles were already colonized with a biofilm while experimental cobbles were desiccated for several months.

Primary production estimates remained consistent in the channel, i.e., increased in the lower and upper varial zones (Table 4). A 70% increase in both net and gross primary production was detected in the lower varial zone. The upper varial zone was not examined for primary production in June because cobbles were barren, but two months later in August we estimated 0.008 $g \cdot O_2 \cdot m^{-2} \cdot h^{-1}$ net primary production in this zone.

Macroinvertebrate AFDM was significantly higher ($p = 0.01$) in the channel in June than in the lower varial zone (Table 4). However, in August there was no significant difference between the channel and lower varial zone. This vertical shift in macroinvertebrate AFDM corresponds with the increase in algal and macrophyte cover within the lower varial zone. Organic drift estimates did not significantly change between June and August sampling periods, with macroinvertebrate density averaging $2.2 \cdot m^{-3} \cdot s^{-1}$ (SE ± 1.4) and primary producer AFDM averaging 0.035 $g \cdot m^{-3} \cdot s^{-1}$ (SE ± 0.009).

This data set on elevated base flows indicates how rapidly changes in dam operations, within IF criteria, can alter the structure of the benthic community. Techniques and protocols used to detect patterns in elevated base flows on the benthos can also be applied to the spike flow currently proposed for spring 1996. However, more samples will be required to reduce variance and improve statistical accuracy.

CONCLUSIONS

Reduced discharge energy from Interim Flows (IF) has produced detectable patterns in the benthic community structure of the Colorado River through Grand Canyon. We found within season variability to be high due erratic precipitation patterns. Also, riffle habitats are more susceptible to these high precipitation events than pools. This is an important because >80% of the system-wide benthic mass occurs within riffle habitats. Consistent base flows have led to a strict zonation of the two dominant primary producers, Cladophora glomerata near or below the baseflow, and Oscillatoria spp. in the upper varial zone. An increase in species richness in primary and secondary producers continues to occur with emergent aquatic macrophytes creating a new diverse habitat.

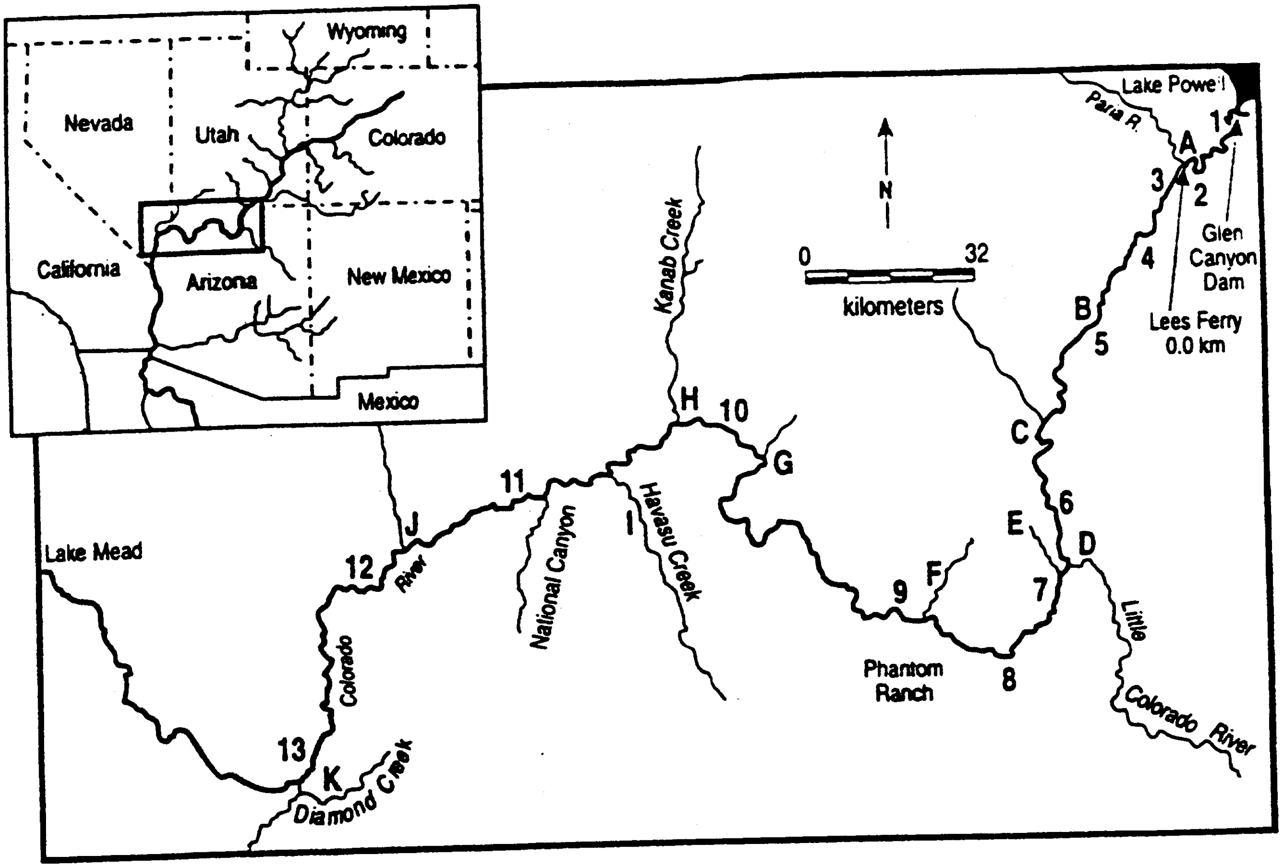
CHAPTER TWO: ORGANIC STREAM DRIFT

INTRODUCTION

The importance of drift to stream ecology has received considerable attention over the past several decades (Waters 1972, 1981; Allan & Russek 1985; Brittain & Eikeland 1988; Wilzbach et al. 1988; Wooster & Sih 1995), however, few studies have focused on similar behaviour in regulated running waters, especially in arid biomes. In general, a positive correlation exists between invertebrate drift mass and discharge (Brooker & Hemsworth 1978; Blinn & Cole 1991), with a change in flow after long periods of stable discharge yielding greatest organic transport (Irvine 1985; Perry & Perry 1986). Elevated discharge increases scouring and exerts selective pressures on benthic organisms (Brittain & Eikeland 1988; Poff & Ward 1991). Reduced flow can increase stream drift through behavioural factors such as crowding, reduced dissolved oxygen, and avoidance of desiccation (Minshall & Winger 1968; MacPhee & Brusven 1973; Corrarino & Brusven 1983; Perry & Perry 1986; Blinn et al. 1995).

Macro-algal drift in regulated streams has received less attention than invertebrate (Lowe 1979) or phytoplankton drift (Barnese & Lowe 1992). Armitage (1977) reported that filamentous algae and moss dominated the non-faunal drift in the regulated River Tees below Cow Green Dam, Great Britain. Leibfried and Blinn (1986) reported increased algal drift during the rising arm of the hydrograph from Glen Canyon Dam (GCD) in the Colorado River, Arizona, and Lieberman and Burke (1993) found that the bulk of the plant mass transported in the lower Colorado River was from autochthonous production.

Over 60% of the algal standing stock (primarily Cladophora glomerata) and invertebrate mass in the Colorado River corridor (386 km) through Glen and Grand Canyon is produced in the upper 26 km between Glen Canyon Dam (GCD) and the Paria River (Blinn et al. 1994, Fig. 31). The clear, cold tailwaters and abundant armoured substrata immediately below GCD provide excellent habitat for C. glomerata. This highly branched filamentous green alga is a refugia as well as a substrate that supports epiphytic algal assemblages in the tailwaters of GCD (Blinn et al. 1989; Hardwick et al. 1992; Shannon et al. 1994; Blinn et al. 1995). The dramatic decrease in down river standing crop of C. glomerata results from high loads of suspended sediments at major perennial tributaries, particularly the Paria River (RKM 1) and Little Colorado River (RKM 98.7). Both tributaries drain extensive arid landscapes in Arizona, Utah, and New Mexico, USA.



MAINSTEM

Site Number	Kilometer	Name
1	-24	Glen Canyon
2	0	Lees Ferry
3	3	2 Mile Wash
4	31	House Rock
5	67	40 Mile
6	88	54 Mile
7	104	Morning Star Mine
8	116	Tanner
9	150	Horn Creek
10	228	Ponchos Kitchen
11	272	Tuckup
12	339	Granite Park
13	358	224.5 Camp

TRIBUTARY

Site Number	Kilometer	Name
A	1	Paria River
B	51	Vasey's Paradise
C	83	Nankoweap Creek
D	98	Little Colorado River
E	104	Lava Chuar
F	141	Bright Angel Creek
G	214	Tapeats Creek
H	231	Kanab Creek
I	250	Havasu Creek
J	327	Spring Canyon
K	362	Diamond Creek

Figure 31. Map of drift collection stations in the Colorado River (1-13) and major tributaries (A-K) through Grand Canyon National Park. Glen Canyon Dam is located 25.3 km up river from Lees Ferry, Arizona, which is designated as 0.0 km.

Although C. glomerata is hydrodynamically adapted to lotic environments (Usher & Blinn 1990; Dodds & Gudder 1992), filamentous streamers frequently detach from cobble in the tailwaters of GCD and become part of downstream drift, especially during flows associated with hydroelectric power production (Angradi & Kubly 1993; Blinn et al. 1995). Due to the cessation of normal allochthonous riverine drift caused by GCD and the overall limited downstream production in the Grand Canyon reach (Blinn et al. 1994), it has been proposed that stream drift, and especially C. glomerata drift packets with associated epiphyton and invertebrate communities, provide coarse particulate organic matter (CPOM) to downstream biota in the Colorado River.

We examined several aspects of organic drift in this large regulated river located in an arid biome. Specifically, we 1) examined the quantity and composition of stream drift in the Colorado River along a 386 km corridor below GCD, 2) examined the contribution of stream drift from tributaries to the Colorado River corridor, 3) compared the quantity and composition of stream drift and total organic carbon (DTOC) during variable and steady flows, 4) determined the effects of river hydraulics (rapids) on the mass, invertebrate composition, and food energy of C. glomerata drift packets throughout the Colorado River corridor, and 5) examined organic retention processes within the Colorado River.

STUDY AREA

We investigated the quantity and composition of stream drift below Glen Canyon Dam (GCD) in the Colorado River through Grand Canyon National Park between Lees Ferry and Diamond Creek (386 km; Fig. 31). Lees Ferry, located 25.3 km below GCD, is designated as river kilometer (0.0 RKM).

Glen Canyon Dam releases hypolimnial water from Lake Powell and has a maximum power plant discharge of 934 $m^3 \cdot s^{-1}$ (Stanford & Ward 1991). Flows below GCD have a peak discharge of 566 $m^3 \cdot s^{-1}$ and a minimum of 141 $m^3 \cdot s^{-1}$ with a maximum up-ramp of 71 $m^3 \cdot s^{-1}$ and a maximum down-ramp of 42 $m^3 \cdot s^{-1}$. Maximum ranges of daily fluctuations vary from 170 $m^3 \cdot s^{-1}$ to 226 $m^3 \cdot s^{-1}$ based on projected monthly water allotments.

The biota throughout the canyon are affected by discharge regulation, channel morphology, and biome effects via tributary inputs of suspended sediments (Blinn et al. 1994). The river upstream from the Paria River (1.0 RKM) support high standing crops of Cladophora glomerata and an invertebrate assemblage of Gammarus lacustris, chironomid larvae, oligochaetes and gastropods (Blinn et al. 1995). The consistently clear, cold tailwaters (8-10°C) below GCD are dramatically altered at the Paria River confluence where a mean of 3.0 x 10^6 tons of suspended sediments enter the Colorado River annually (Andrews 1991). Due to rapid light extinction, mean annual standing mass of C. glomerata and associated invertebrates are dramatically reduced throughout the remainder of the river corridor (Blinn et al. 1994). The Colorado River within Grand Canyon is a run-pool-drop river with a gradient of 1.5 $m \cdot km^{-1}$. Pools and rapids are formed by channel constrictions created by tributary debris flows during summer monsoon and winter storms. Summer air temperatures exceed 35°C, while winter air temperatures drop below 0°C at night.

METHODS

Down River Drift Collections

Near-shore surface drift samples (0-0.5 m deep) were collected on September 1993, and January, March, and June 1994 at the 13 down river sites (Fig. 31). Collections were made with a circular tow net (48 cm diameter opening, 0.5 mm mesh) held in place behind a moored pontoon raft or secured to the river bank. Collections were taken in triplicate at approximately 0600 h and 1800 h, 12 h hydrograph cycle, at each site to establish the affects of discharge on drift. September samples were preserved with AFA (alcohol, formalin, and acetic acid) whereas all other collections were processed live within 48 h and sorted into seven categories including: G. lacustris, chironomid larvae, simuliid larvae, miscellaneous invertebrates, C. glomerata, miscellaneous algae/macrophytes and detritus. Miscellaneous invertebates included; lumbriculids, tubificids, physids, trichopterans, terrestrial insects and unidentifiable animals. Detritus is composed of organic flotsam derived from both autochthonous (algal/bryophyte/macrophyte fragments) and allochthonous (tributary up-land and riparian vegetation) sources (Angradi 1995). Invertebrates were numerated while sorting and all categories were oven-dried at 60°C and weighed. Ash-free dry mass (AFDM) estimates were determined for each biotic category by ashing at 500°C for one h and re-weighing to a constant weight. All collection and sorting techniques followed this protocol unless otherwise noted.

Current velocity was measured for volumetric calculations using a Marsh-McBirney electronic flow meter (Model # 201). River discharge was determined in reference to United States Geological Survey gauge data by time of day at the nearest stream gauge for each collection (Glen Canyon Environmental Studies, Flagstaff, AZ; personnel communication). The duration of all collections (n = 276) averaged 4 min (SE ± 0.16) with an average of 24.4 m^3 (SE ± 1.4) of water sampled through nets. The standard sampling error was within ±10% of the mean total drifting mass (0.054 g m^{-3} s^{-1}, S.E. ± 0.005; Culp et al. 1994).

In order to understand organic retention processes within the Colorado River we collected channel drift, eddy/pool drift and benthic samples in eddies and pools and compared mass estimates of each in March 1995. Collections were made at sites 2-6, 10-12, and 13 along the Colorado River corridor; sites 1 and 7-9 were excluded because they lacked eddy/pool habitats (Fig. 1). Channel drift (n =3; 0.5 mm net mesh) was collected from behind an eight m pontoon motorboat held steady in mid-channel. Eddy/pool drift was collected perpendicular to the channel on three transects set 30 m apart. The drift net was pulled into shore from the channel/eddy interface along each transect three times. This sampling design accounted for drift patchiness due to variable surface currents. Total distance pulled (~56 m) was recorded for each transect for volumetric determinations. An inflatable kayak was used to deploy the drift net to minimize disturbance to surface waters. Eddy/pool habitats were further separated into two geomorphic categories for comparison; true eddies or backwaters that had counter flow below rapids (sites: 2-6 and 12; Fig. 1) and pools above rapids with unidirectional flow (sites: 10,11,13). Four benthic collections were made with either a Petite Ponar or Peterson dredge along the same three transects used in the eddy drift sampling (n=12). Current velocity was measured at a depth of 50 cm for each dredge drop while the boat was held steady in an effort to define the flow patterns within the habitat. The average flow speed per transect was used in volumetric calculations for the eddy/pool drift samples. Collections were analyzed for size fractions after dry mass was obtained. Benthic samples were sieved through a 0.6 mm screen. Material from each habitat (channel drift, eddy drift and benthos) were combined and dry sieved into <1 mm, 1-9 mm and ≥10 mm size fractions at each site. Each sample was shaken for 30 s which allowed the separation of size fractions without particulate degradation.

Cladophora glomerata Drift Packets

Twelve to 20 packets of drifting C. glomerata were randomly collected in January, March, June, and September 1992 with a hand dip net (30 x 25 cm, 0.5 mm mesh) from surface to 1 m deep at Lees Ferry (RKM 0.0), below the confluence of the Paria River (RKM 1.0), Nankoweap Creek (RKM 83.2), Tanner Creek (RKM 108.8) and Diamond Creek (RKM 361.6). Twenty samples were also collected above and below Badger Creek Rapid (RKM 12.8) to ascertain the effect of a single large rapid on the integrity of C. glomerata packets. Samples were sorted in the field into 10 biotic categories: C. glomerata, detritus, miscellaneous algae and macrophytes, G. lacustris, chironomid larvae, simuliid larvae, tubificids, lumbriculids, gastropods, and miscellaneous invertebrates. Tubificid densities were established through regression analyses of mass because of fragmentation while sorting. The resulting equation was:

$$\text{Tubificid density} = 2418.57\ (\text{g dry mass}) + 14.93\ (\text{g dry mass})$$
$$(\underline{R}^2 = 0.887;\ \underline{F}_{1,138} = 1066;\ \underline{p} < 0.0001).$$

Epiphyton was removed from C. glomerata by agitating filaments in WhirlPacs® containing 200 ml of filtered river water for 1 min (Blinn et al. 1995). Hyrax® mounts were made to determine diatom density and composition of a minimum of 200 frustules at 1000x magnification for each sample.

Steady Versus Fluctuating Flows

We examined the influence of steady versus repeated fluctuating flows on stream drift at Lees Ferry by collecting drift with a circular net (48 cm diameter opening, 1 mm nylon mesh). The net was held at the surface by a float and deployed from a navigational buoy so each set would be in the same position in the channel. Collections were taken at 6-h intervals starting at 0600 h for 5 d. Discharges from Glen Canyon Dam were held steady (226 $m^3 \cdot s^{-1}$) the first 3 d (29-31 May 1993) followed by 2 d of fluctuating flows (discharges from 141 to 283 $m^3 \cdot s^{-1}$). Water velocity was measured with a Marsh-McBirney electronic flow meter before and after each collection period for volumetric calculations. Samples were sorted using the above protocol.

Drift and total dissolved organic carbon (TOC) samples were collected at 0600 h and 1800 h (low and high water) on May 1994 at Lees Ferry, at the confluence of the Paria River (RKM 3.2) during steady flows and on the first day of fluctuating flows. Triplicate 100 ml samples of river water were taken at each site and filtered through a sterile 0.2 µm Millipore membrane and stored on ice and analyzed within 48 h. Two hundred fifty µml aliquots were injected into a Rosemount/Dohrmann DC-180 Total Organic Carbon Analyzer and TOC ($mg \cdot L^{-1}$) was measured for each sample.

Tributary Drift Collections

The contribution of organic drift to the Colorado River from 11 tributaries was measured between Lees Ferry and Diamond Creek in January, March, and June, 1994 (Fig. 31). A rectangular drift net (0.135 m^2; 0.363 mm mesh) was positioned for 10 min ($\underline{n} = 3$) at each tributary. Volumetric data were collected in the same manner as mainstem collections. Discharge estimates were made for all tributaries except the Little Colorado River (RKM 98.6) which was obtained from United States Geological Survey (Glen Canyon Environmental Studies, Flagstaff, AZ, personal communication).

We compared drift mass from tributaries within two distinct drainage types; large basins originating outside of Grand Canyon National Park (>500 km^2; mean discharge 1.67 $m^3 \cdot s^{-1}$) and small basins, primarily spring fed, originating within Grand Canyon National Park (<260 km^2; mean discharge 0.43 $m^3 \cdot s^{-1}$). The Paria River, Little Colorado River, Kanab Creek, Havasu Creek, and Diamond Creek are large basin drainages characterized by seasonally variable and erratic discharges (Fig. 31). Vasey's Paradise, Nankoweap Creek, Bright Angel Creek, Tapeats Creek and Spring Canyon are springs that originate within the canyon and have consistent discharges, while Lava Chuar may dry during the summer.

In-situ Desiccation Experiments

We conducted an experiment designed to determine the effect of repeated 12-h night exposure periods on C. glomerata and invertebrate drift. A raft constructed from a rectangular frame of 2 x 12 dimensional lumber strapped down on two mini-snout tubes, 4.3 m in length, was stationed at Lees Ferry. Sixteen wooden sluiceways (15 x 60 cm) with a removable nylon mesh net (0.5 mm) on the downstream side were suspended from five 2 x 4 rail-frames, 61 cm off the deck of the frame and 81 cm apart. Tops and upstream ends of each sluiceway were covered with nylon mesh (0.5 mm) net to eliminate recruitment, and each sluice was hung in the water at a depth of 50 cm. An aluminum keel, 15 cm long and 2 cm high, was fastened to the bottom of each sluice to keep them parallel to the current.

Sluiceways were divided into two treatments, eight continuously submerged controls and eight that were gently pulled out of the water nightly for 12 h (1800-0600 h) for three consecutive days. The latter treatment was designed to simulate dam operations. Four cobbles (each 30 cm in diameter) with C. glomerata and associated invertebrates were placed into each sluice. These cobbles were gathered from below the permanently wetted 141 $m^3 \cdot s^{-1}$ discharge stage at Lees Ferry (RKM 0.8). Sluiceway nets were sampled immediately after being pulled from the water at the start of each desiccation period in order to collect the organisms that were flushed from the cobbles from the previous exposure period. Samples were placed on ice and sorted live within 24 h. Samples were also taken from the cobbles within each sluice at the end of the experiment for control and treatment quantification. Plastic circular templates (20 cm^2) were randomly placed on cobbles and the area within scraped clean.

Percent cloud cover, % humidity, water temperature, daily minimum and maximum air temperatures, Secchi depth, and river discharge were taken at 0600 h, 1200 h and 1800 h. Discharge was obtained from the United States Geological Survey staging gauge at Lees Ferry (Glen Canyon Environmental Studies, Flagstaff, AZ). Current velocities were taken in each sluice with a Marsh-McBirney electronic flow meter.

Statistical Analyses

Multivariate analyses of variance (MANOVA) were used to analyze categorical predictor variables (mass estimates) and multiple response variables (physical parameters/treatment) for drift and sluiceway experiments. Multivariate repeated measures analyses were also performed on sluiceway data. Hydraulic impact on C. glomerata drift packets were analyzed with a Student t-test. Multiple regression analyses were used to analyze drift habitat types versus benthic collections. All calculations were performed with SYSTAT computer software on ln+1 transformed data (Version 5.1, Wilkinson, 1989).

RESULTS

Downriver Drift

There was a significant positive correlation between stream drift mass, discharge ($p < 0.001$) and distance from Glen Canyon Dam (GCD) ($p < 0.001$). Discharge (226 to 566 $m^3 \cdot s^{-1}$) had a selective effect on drift components. Univariate analysis showed that detritus was positively influenced by discharge ($p < 0.0001$), whereas other categories (Gammarus lacustris, Cladophora glomerata, chironomids, simuliids, tubificids, and gastropods) showed a significant negative relationship to discharge ($p < 0.001$). The relationship between drift and discharge, however, is not linear due to the dramatic drop in mass between 340 and 452 $m^3 \cdot s^{-1}$ (Fig. 32). Discharges between 266 and 340 $m^3 \cdot s^{-1}$ increased drift by 55%, with an 80% increase above 452 $m^3 \cdot s^{-1}$.

There were no significant ($p = 0.25$) differences in overall drift mass or any biotic category ($p > 0.06$) during the rising and falling arm of the hydrograph over a 24 h period. Ramping rates ≤ 71 $m^3 \cdot s^{-1} \cdot h$ lacked adequate energy to consistently carry drift on the rising arm of the hydrograph.

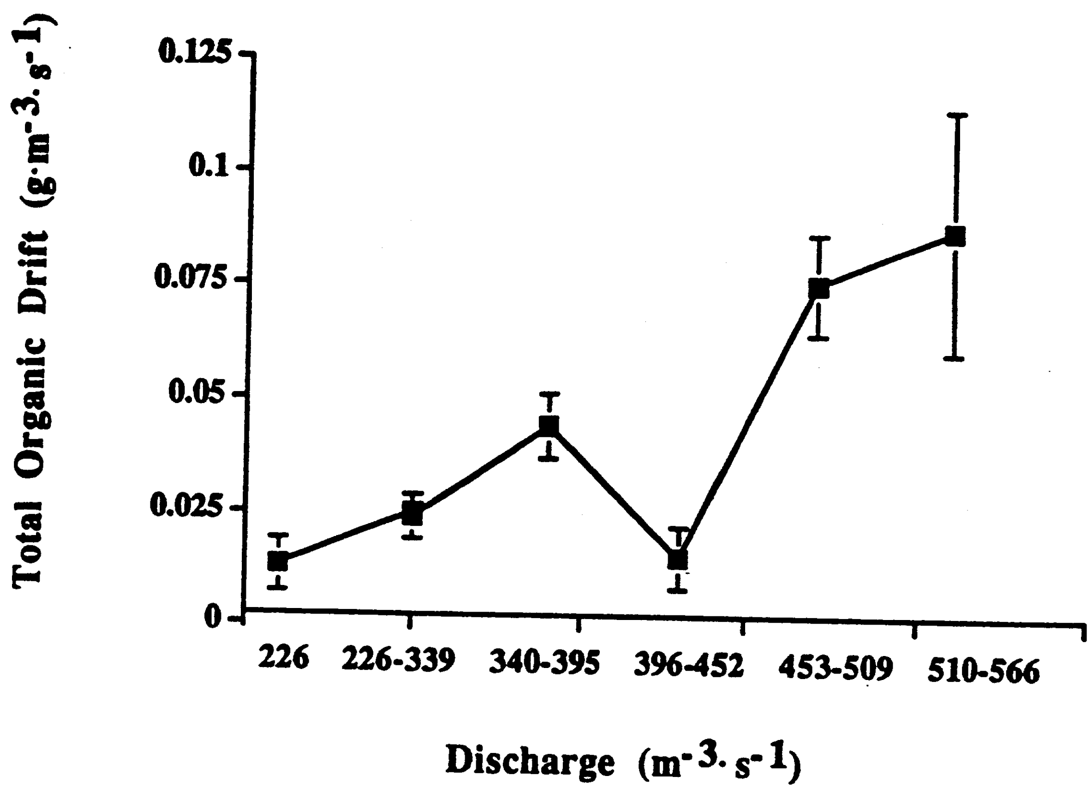


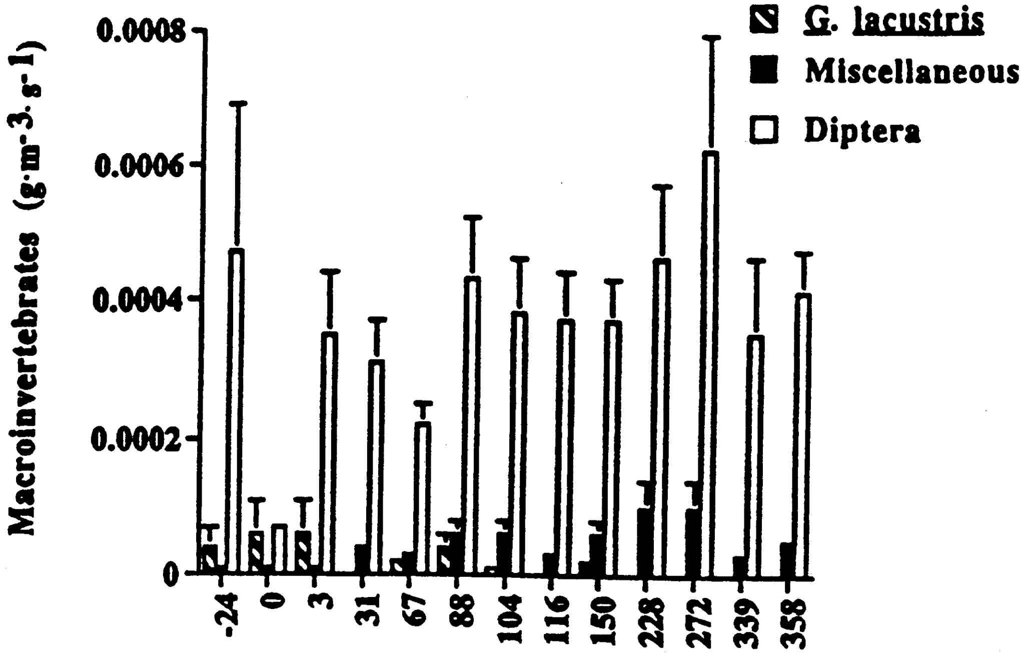
Figure 32. Comparison of near-shore stream drift collections (g AFDM $m^{-3} \cdot s^{-1}$) and discharge ($m^{-3} \cdot s^{-1}$) in the Colorado River corridor through Glen and Grand Canyons, Arizona. Error bars represent ± 1 S.E.

Drift composition changed with distance from GCD. There was a significant increase in detrital drift through Grand Canyon ($p < 0.01$), however, G. lacustris and miscellaneous algae/macrophytes did not show a significant difference between sites and decreased down river ($p = 0.99$; $p = 0.09$; respectively; Fig. 33). Aquatic diptera and miscellaneous invertebrate drift mass varied significantly between sites ($p < 0.001$), and increased with distance, while C. glomerata drift remained constant (Fig. 33). Chironomid larvae made up 72% of the dipteran drift through Marble Canyon (RKM 0-99), while simuliid larvae comprised 81% of the dipteran drift below RKM 99. Terrestrial insects comprised <0.001% of the total number of animals in drift samples.

Univariate analyses showed all drift categories except G. lacustris and miscellaneous algae/macrophytes ($p = 0.82$; $p = 0.28$, respectively) varied seasonally. Collections during September 1993 had the highest mean total organic drift mass (0.08 $g \cdot m^{-3} \cdot s^{-1}$ AFDM) and were composed primarily of detritus. Cladophora glomerata drift reached a seasonal maximum of 0.015 $g \cdot m^{-3} \cdot s^{-1}$ AFDM in June. Invertebrate drift mass was 2.3 g $m^{-3} \cdot s^{1}$ (S.E. ±0.3) in March compared to 5.9 g $m^{-3} \cdot s^{-1}$ (S.E. ±0.8) in June which included a 55% increase in dipterans and a 66% increase in miscellaneous invertebrates.

Multiple regression analyses determined that detritus was the only category to show a significant positive relationship between drift in the channel and eddy/pools and benthic collections (Table 4). A significant positive relationship was found between the two drift types for C. glomerata and diptera mass ($p < 0.05$), but no significant relationship was found between eddy/pool drift and benthic samples for C. glomerata or diptera, suggesting that these biotic components are not readily deposited in pools (Table 4). Detritus (1.0 g $m^{-3} \cdot s^{-1}$) was dominant in channel drift and made up 0.5 g $m^{-3} \cdot s^{-1}$ in eddy/pool drift. Therefore, 50% of channel drift is entrained in eddy pools. Detritus is the only category that showed a significant relationship between eddy/pool types ($p = 0.01$) with an average of 50% more detritus moving through both channel and eddy/pool collections in pools above rapids than in the backwaters below rapids, indicating little retention of organic matter.

There were no significant differences ($p=0.8$) in size fractions of coarse particulate organic matter between channel drift, eddy/pool drift and benthos at each site, indicating a reach-based origin of drift. However, there was a significant increase in <1 mm and 1-9 mm size fractions and a significant decrease in fractions ≥10 mm in size with distance down river ($p < 0.01$; Fig. 34). Fractions ≥10 mm were composed primarily of C. glomerata packets, with occasional fragments of the aquatic moss, Fontinalis spp., and Equisetum spp. The 1-9 mm size fraction was made up of near equal proportions of detritus and



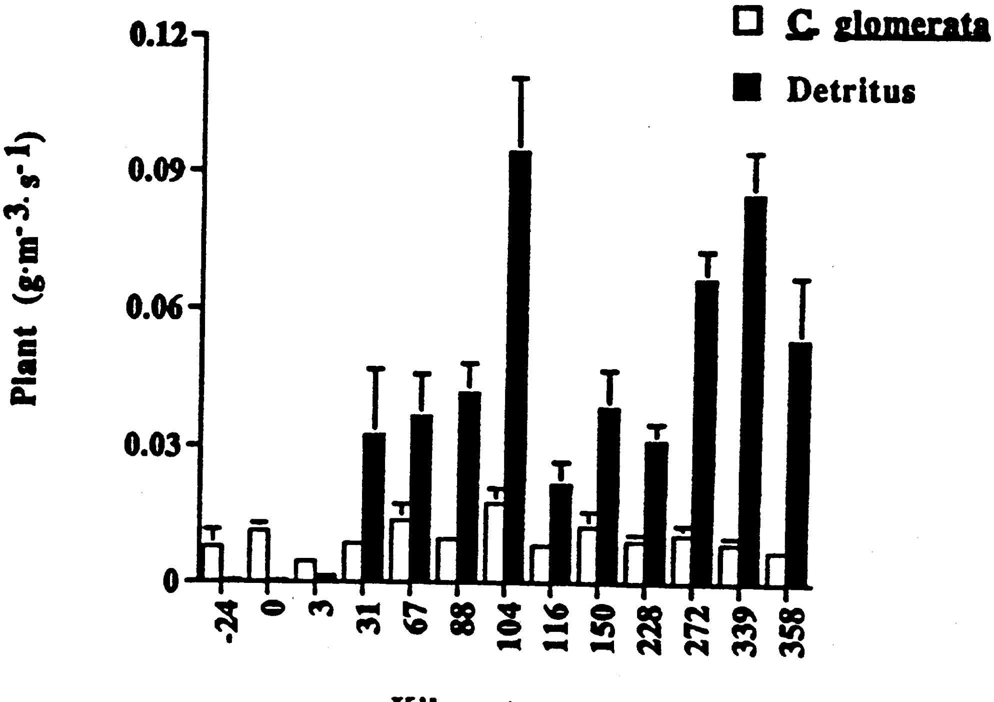


Figure 33. Average mass (g AFDM $m^{-3} \cdot s^{-1}$) of plant and macroinvertebrate river drift at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362) during September 1993, January 1994, March 1994 and June 1994. Only trace amounts of miscellaneous algae/bryophytes/macrophytes were collected (<0.001 $g \cdot m^{-3} \cdot s^{-1}$). Error bars represent ± 1 S.E.

Table 5. Multiple regression analyses of drift mass between three habitats in the Colorado River through Grand Canyon; channel drift, eddy/pool drift and eddy/pool benthos. Detritus was the only drift component from the channel that was entrained in eddy/pools and accumulated in the benthos. Cladophora glomerata and aquatic diptera channel drift became entrained in the eddy/pools but did not accumulate in the benthos. These results indicate that this constrained fluvial ecosystem retains little organic material. Only significant biotic categories are listed ($p<0.05$).

Source	Variable	Coefficient	Probability	Standard Error of Estimate
Channel Drift x Eddy/Pool Drift	C. glomerata	-99.3	<0.0001	0.38
	Detritus	-1.7	0.003	
	Aquatic diptera	-654.7	0.04	
	Constant	1.9		

ANOVA	df	f	p	Multiple R^2
	4,56	12.5	<0.001	0.47

Source	Variable	Coefficient	Probability	Standard Error of Estimate
Benthic X Eddy/Pool Drift	Detritus	0.004	0.03	0.47
	Constant	2.4		

ANOVA	df	f	p	Multiple R^2
	6,54	2.4	0.04	0.21

Source	Variable	Coefficient	Probability	Standard Error of Estimate
Channel Drift X Benthic	Detritus	0.009	0.02	0.93
	Constant	4.2		

ANOVA	df	f	p	Multiple R^2
	6,59	2.8	0.02	0.22

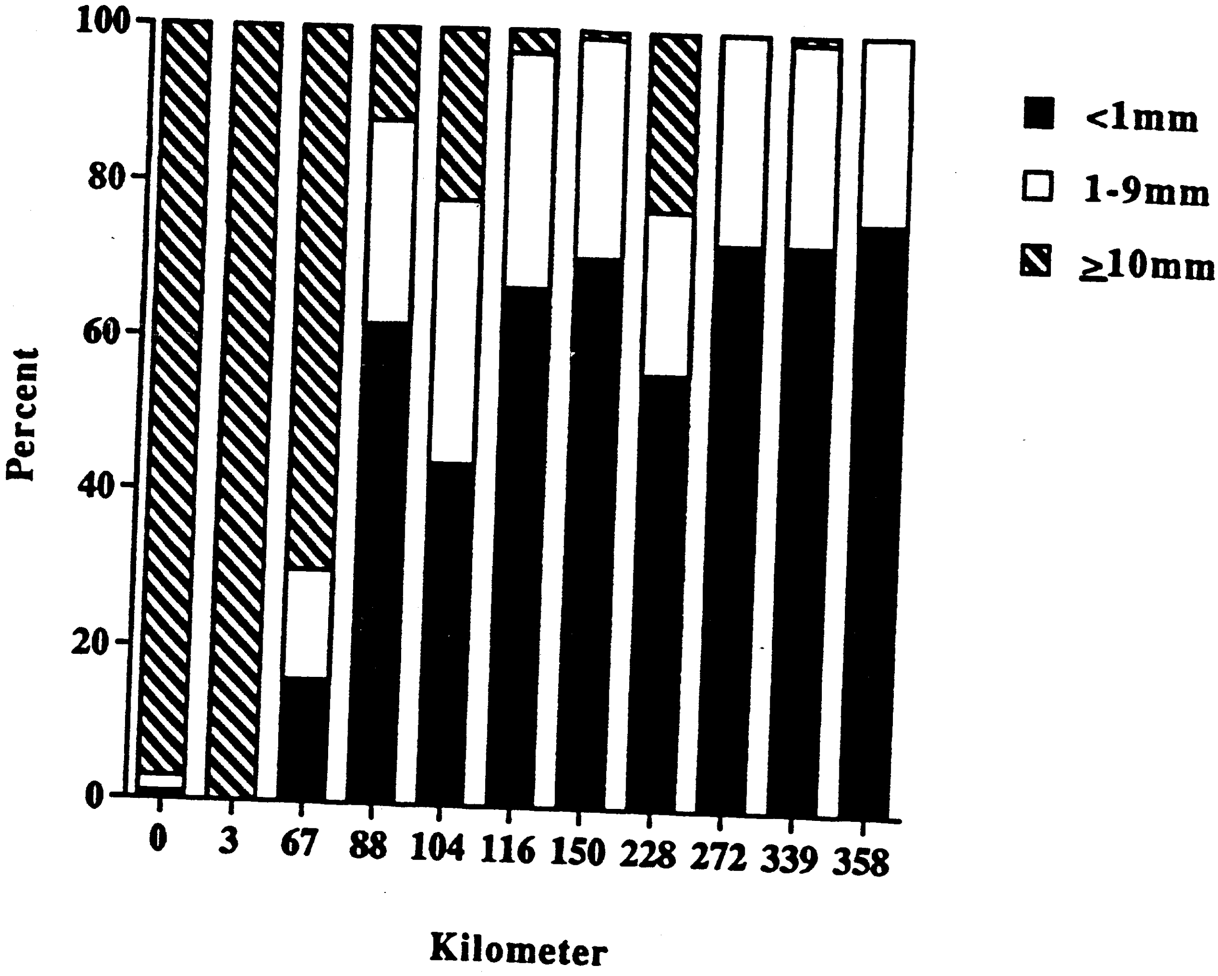


Figure 34. Percent size fraction composition for channel drift from the Colorado River through Grand Canyon during March 1995. MANOVA univariate results defined a significant size fraction difference by site for the 1-9 mm and <1 mm fractions ($p < 0.01$ for both)

C. glomerata filaments, while fractions <1mm were exclusively pulverized detrital material.

Cladophora glomerata Drift Packets

The mass of C. glomerata in drift packets changed significantly both spatially ($p < 0.0001$) and temporally ($p = 0.013$) in the Colorado River through Grand Canyon. Maximum AFDM of C. glomerata in drift packets occurred at Lees Ferry (0.16 g, S.E. ±0.06), but dropped 4-fold below the confluence of the Paria River and 10-fold (<0.01 g AFDM, S.E. ±0.01) below RKM 85. Drift packets of C. glomerata had the highest mass during September (0.6 g AFDM, S.E. ±0.2) and the lowest mass during March (0.01 g, S.E. ±0.002).

We noted a significant ($p = 0.015$) reduction in AFDM mass for C. glomerata drift packets above (0.046 g, S.E. ±0.01) and below (0.012 g, S.E. ±0.004) the rapid at Badger Creek (RKM 12.8). No invertebrates were found in the Badger Creek Rapid collections; they were apparently lost while passing through the smaller upstream Paria River rapid. Badger Creek is the first major rapid below Lees Ferry and has a 2.0 m vertical drop (Kieffer 1985).

Epiphytic diatom densities on C. glomerata drift packets changed significantly with distance from GCD ($p < 0.01$, Fig. 35). Epiphyton density was highest at Lees Ferry (450 x 10^3 cells mg^{-1} AFDM C. glomerata) and decreased by 40% below the Paria confluence (RKM 3.2) and by 64% at Tanner (RKM 109). The proportion of upright and prostrate diatom taxa remained consistent with distance downstream, although the composition changed (Fig. 35). The more prostrate taxa included Cocconeis pediculus, Gomphonema spp., and Achnanthes spp., while up-right taxa included Rhoicosphenia curvata, Diatoma tenue, and D. vulgare. The greatest difference in composition by site was between GCD tailwaters (GCD/Lees Ferry) and Marble Canyon (Two Mile/Tanner Washes) where D. vulgare was replaced by D. tenue and C. pediculus. There was no significant difference in diatom composition ($p > 0.05$) between GCD and Lees Ferry or Two-Mile Wash and Tanner Wash (RKM 108).

Chironomid larvae associated with C. glomerata drift packets showed a significant difference in AFDM spatially ($p < 0.000$) and seasonally ($p = 0.015$). Maximum standing mass of chironomid larvae occurred in packets at Lees Ferry ($\bar{x} = 0.00014$ g AFDM), but decreased 10-fold at RKM 5 (0.00002 g AFDM). Other invertebrates were absent from drift packets by RKM 5. Average chironomid larvae standing mass in C. glomerata drift was highest during the summer ($\bar{x} = 0.00602$ g AFDM, S.E. ±0.002) and substantially reduced during

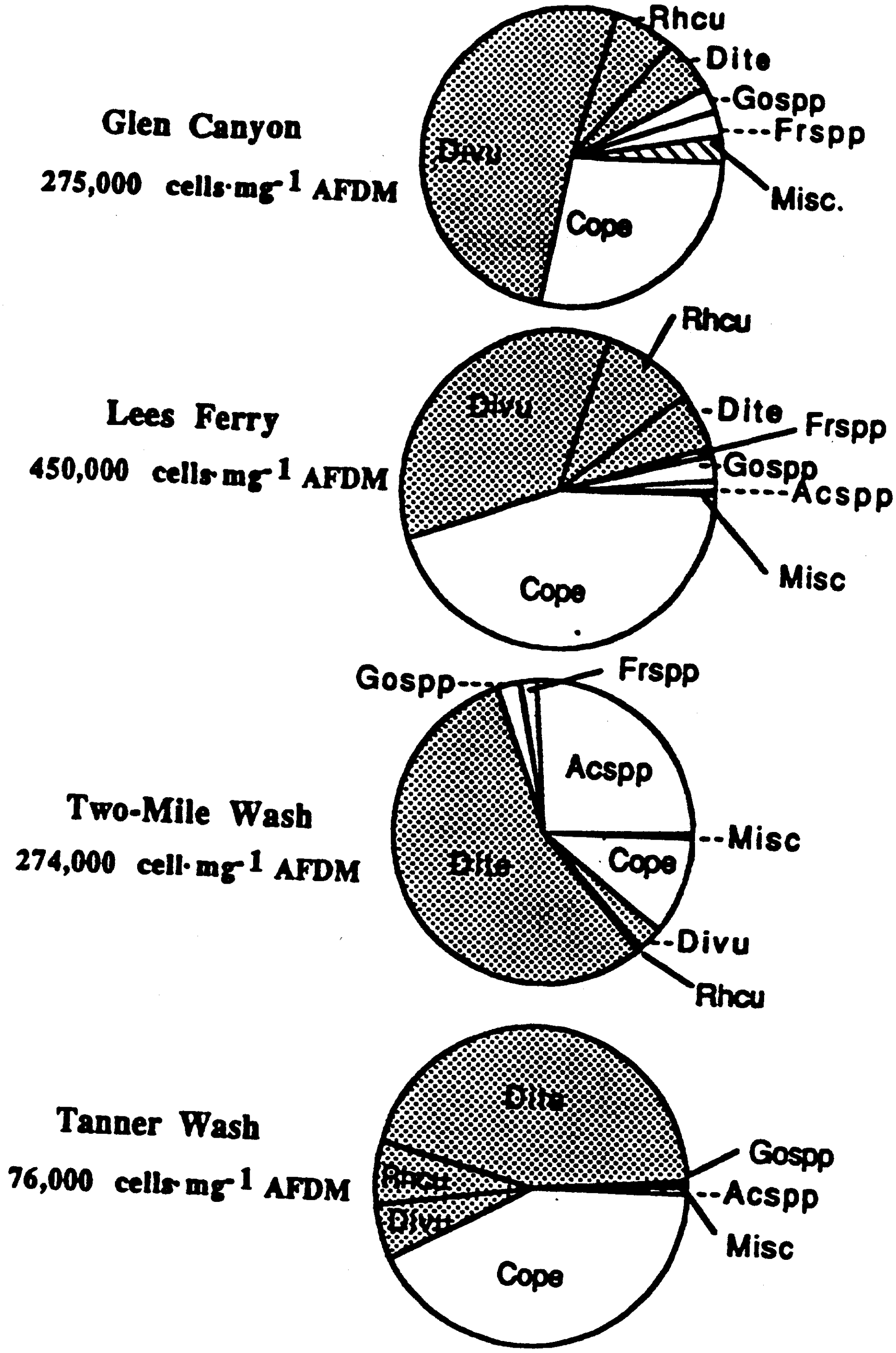


Figure 35. Density and composition of epiphytic diatoms on Cladophora glomerata drift packets at Glen Canyon (RKM -24), Lees Ferry (RKM 0), Two-Mile Wash (RKM 3.1), and Tanner Wash (RKM 109) in the Colorado River, Arizona. Stippled sections represent upright diatom taxa, while clear sections represent more prostrate taxa. Divu = Diatoma vulgare, Cope = Cocconeis pediculus, Rhcu = Rhoicosphenia curvata, Dite = Diatoma tenue, Gospp = Gomphonema spp., Frspp = Fragilaria spp., Ascpp = Achnanthes spp., Misc. = miscellaneous diatom taxa.

other seasons; fall = 0.0009 g (S.E. ±0.00001), winter = ±0.00012 g (S.E. ±0.00006), and spring = 0.00010 g (S.E. ±0.00004).

Energy contained in drift packets of C. glomerata was negatively correlated with distance from GCD. Drift packets in the tailwaters contained an estimated seasonal average of 5700 J·mg DW, while the Marble Canyon reach (RKM 0.0 - 99) carried 1800 J·mg DW and drift packets in the Grand Canyon (RKM 99 - 360) contained only 2 J·mg DW. These values were calculated from energy equivalents taken from Blinn et al. (1995).

Tributary Drift

The contribution of tributary drift to the Colorado River was minimal. Mean organic drift (AFDM) from tributaries was 0.13 g $m^{-3} \cdot s^{-1}$ (S.E. ±0.04), compared with 0.5 g $m^{-3} \cdot s^{-1}$ (SE ±0.004) in the mainstem of the Colorado River. Based on mean discharges for tributaries (1.1 $m^{-3} \cdot s^{-1}$) and the mainstem (374 $m^{-3} \cdot s^{-1}$), we estimated that <0.1% (~0.14 g $m^{-3} \cdot s^{-1}$) of organic drift in the Colorado River (total drift = 167 g $m^{-3} \cdot s^{-1}$) is contributed by tributaries. We calculated tributaries released an average of 2.8 animals $m^{-3} \cdot s^{-1}$ (3 animals at 1.1 $m^{-3} \cdot s^{-1}$), while the mainstem transported 3.2 animals $m^{-3} \cdot s^{-1}$ (1,200 animals at 374 $m^{-3} \cdot s^{-1}$). Drift varied significantly between tributaries ($p < 0.0001$; Fig. 36), however, no significant seasonal patterns were detected under baseflow conditions within tributaries during January, March, June, and September ($p = 0.4$). The Paria River (RKM 1.0), Little Colorado River (RKM 98.6), and Diamond Creek (RKM 361.6) contributed the highest average stream drift to the Colorado River; i.e., 0.78, 0.35, and 0.12 g $m^{-3} \cdot s^{-1}$, respectively. Drift from the Paria and Little Colorado Rivers was primarily detritus, while C. glomerata was the dominant drift component at Diamond Creek.

Aquatic dipterans, C. glomerata and detritus varied significantly by tributary ($p < 0.0001$), while other biotic categories did not vary significantly between tributaries ($p > 0.06$; Fig. 31). Diamond Creek released the most aquatic dipteran larvae (0.001 g $m^{-3} \cdot s^{-1}$; 0.05 simuliids $m^{-3} \cdot s^{-1}$ and 7 chironomids $m^{-3} \cdot s^{-1}$), compared with 0.02 g $m^{-3} \cdot s^{-1}$ (4.8 animals $m^{-3} \cdot s^{-1}$) for other invertebrates. Aquatic invertebrates in other tributaries consisted of Plecoptera, Trichoptera, Ephemeroptera, Odonata, gastropods, lumbriculids and assorted terrestrial insects. These were the dominant invertebrate groups in tributary drift (0.002 g $m^{-3} \cdot s^{-1}$; 1.2 animals $m^{-3} \cdot s^{-1}$), but contributed little to the overall drift mass in the mainstem (0.0007 g $m^{-3} \cdot s^{-1}$; 0.38 animals $m^{-3} \cdot s^{-1}$).

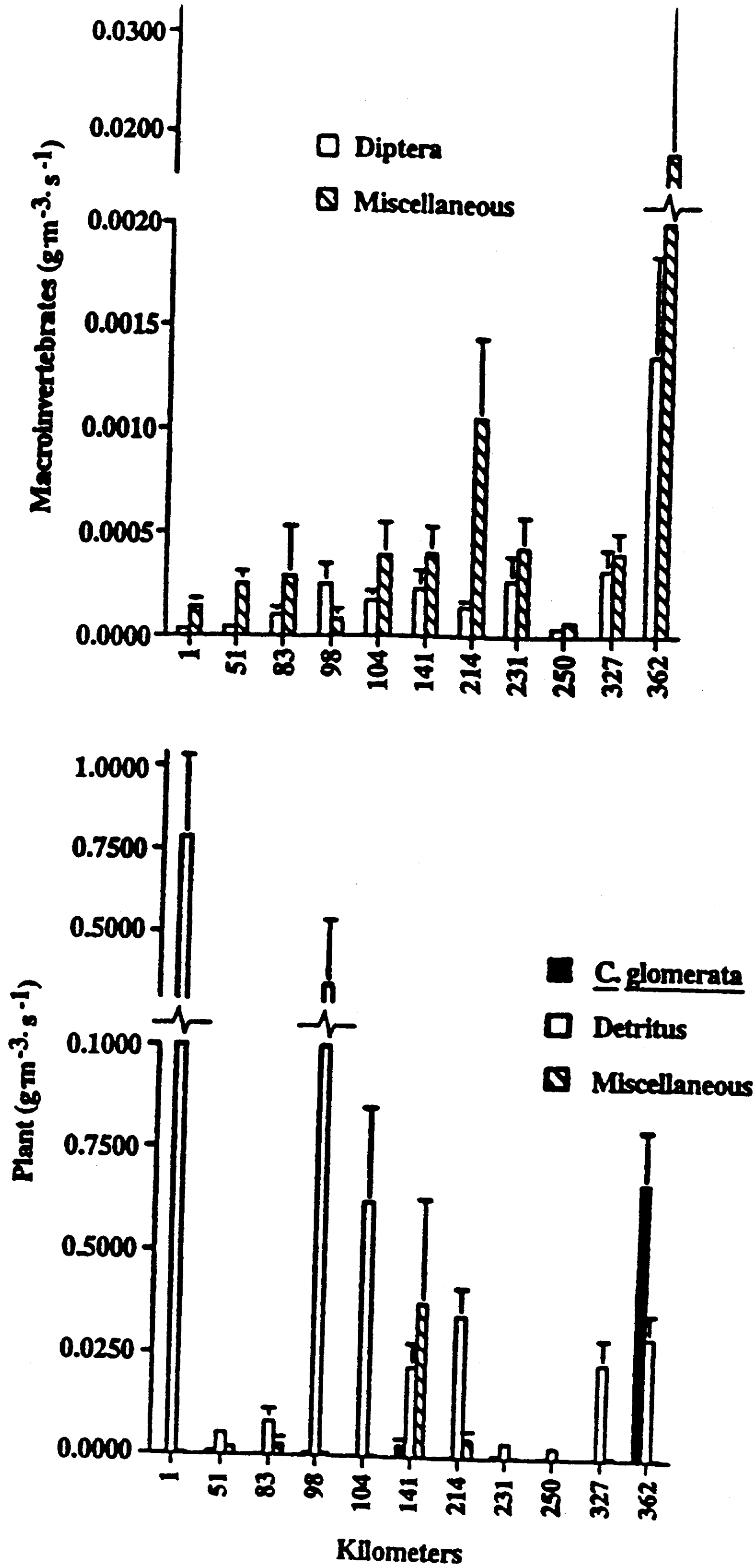


Figure 36. Average mass (g AFDM m-3·s-1) of plant and macroinvertebrate stream drift at selected tributaries in the Colorado River between Lees Ferry and Diamond Creek (RKM 362). Values represent means for samples collected during January, March and June 1994.

Multivariate comparisons showed a significant ($p = 0.002$) overall difference between tributary drift between large drainages that extend outside Grand Canyon National Park and small spring-fed tributaries that orginate within the Canyon, with larger drainages releasing 90% more organic matter. Cladophora glomerata and detrital drift were significantly greater in larger drainages than that for spring-fed tributaries ($p < 0.01$). Large drainages contributed an average of 0.01 g $m^3 \cdot s^{-1}$ C. glomerata and 0.204 g $m^3 \cdot s^{-1}$ detrital drift to the Colorado River, while small spring-fed drainages released an average of 0.0008 g $m^3 \cdot s^{-1}$ of C. glomerata and 0.019 g $m^3 \cdot s^{-1}$ of detritus. Diamond Creek is primarily responsible for the high AFDM of C. glomerata drift from the large drainage tributaries (Fig. 36).

Organic Drift in Steady Versus Fluctuating Flows

Multivariate comparisons between 3 d of steady (227 $m^3 \cdot s^{-1}$) and 2 d of fluctuating flows (141-283 $m^3 \cdot s^{-1}$) at Lees Ferry showed a significant difference between treatments for algal and invertebrate mass and density ($p < 0.0001$, Table 2). There was an overall significant increase in algal and invertebrate drift mass and density ($p < 0.001$; Table 5) during fluctuating flows, while univariate analysis showed macrophytes, C. glomerata, detritus, tubificids, and gastropods had a significant positive correlation with discharge ($p < 0.001$).

Cladophora glomerata made up 98.5% of the primary producer drift mass for both steady and fluctuating flows (Table 5). The aquatic macrophyte, Potamogeton, the red algae, Rhodochorton and Batrachospermum, and the macroalga, Chara, comprised the remaining 1.5%. A channel-wide calculation for total living plant material in stream drift at Lees Ferry was estimated at ~428 $g \cdot s^{-1}$ AFDM at a mean annual discharge of 283 $m^3 \cdot s^{-1}$.

Cladophora glomerata and macrophyte AFDM changed significantly on a diurnal basis ($p = 0.01$; $p = 0.04$, respectively). Mean AFDM of drifting plants from 0600 and 1200 h was 1.3 $g \cdot m^{-3} \cdot s^{-1}$ (S.E. ±0.3), while drifting mass from 1800 and 2400 h was 1.0 $g \cdot m^{-3} \cdot s^{-1}$ (S.E. ±0.2). Neither invertebrate AFDM or abundance changed diurnally through the collection period.

Mean drifting mass and abundance of invertebrates were 0.015 $g \cdot m^3 \cdot s^{-1}$ (S.E. ±0.008) and 49.5 animals $m^{-3} \cdot s^{-1}$ (S.E. ±9.0) during fluctuating flows (Table 5). We calculated a channel-wide mass of 4.5 $g \cdot s^{-1}$ for invertebrate drift at a discharge of 283 $m^3 \cdot s^{-1}$. Gammarus lacustris and chironomids comprised 33% and 62%, respectively, of the drifting invertebrate mass.

Table 6. Comparison of ash-free dry mass ($g \cdot m^{-3}$) and abundance ($animals \cdot m^{-3}$) in stream drift during steady and fluctuating flows in the Colorado River at Lees Ferry, Arizona. Multivariate analyses revealed a significant overall difference between steady and fluctuating flows (Wilks' Lambda; $F_{3,85} = 44.1$, $p < 0.0001$).

DRIFT CATEGORIES	STEADY FLOWS ($227\ m^3 \cdot s^{-1}$)		FLUCTUATING FLOWS ($158\text{-}354\ m^3 \cdot s^{-1}$)	
	MASS ($g \cdot m^{-3} \cdot s^{-1}$)	DENSITY ($Animals \cdot m^{-3} \cdot s^{-1}$)	MASS ($g \cdot m^{-3} \cdot s^{-1}$)	DENSITY ($Animals \cdot m^{-3} \cdot s^{-1}$)
Cladophora glomerata	0.58314		2.28272	
Oscillatoria spp.	0		0	
Other algae	0.01084		0.033574	
Detritus	0.02491		0.03294	
Chironomids	0.00449	31.7	0.00889	58.0
Gammarus lacustris	0.00149	1.7	0.00638	4.8
Simuliids	0.00012	0.1	0.0	0.0
Lumbriculids	0.0	0.0	0.00048	0.1
Tubificids	0.00009	2.4	0.00039	6.6
Gastropods	0.00017	0.08	0.00016	0.01
Miscellaneous macroinvertebrates	0.00048	0.2	0.00047	0.7

During a similar discharge regime on May 1994, organic drift followed the same pattern as stated above, while TOC averaged 39.5 $mg \cdot L^{-1}$ (S.D. ±0.6, n = 12) during steady flows and 32.6 $mg \cdot L^{-1}$ (S.D. ±0.6, n = 12) under fluctuating flows for both sites. The Paria River was running clear at base flow during the collection period.

Sluiceway Experiments

Three days of repeated night exposure of C. glomerata and associated invertebrates resulted in a significant loss in mass to stream drift ($p < 0.0001$, Figs.3 7 & 38). Average daily AFDM loss of C. glomerata in exposed treatments was 0.13 g (S.D. ±0.09) compared to 0.03 g (S.D. ±0.01) for controls. Detritus, Oscillatoria and miscellaneous aquatic plants did not show a significant loss due to exposure ($p > 0.2$) and were found in trace amounts, i.e, cumulative average for all controls was 0.008 $g \cdot m^{-2}$ AFDM.

Continuously submerged control sluiceways did not show a significant loss in algal or macroinvertebrate AFDM ($p = 0.24$, Fig. 37). There were no significant differences between initial and final controls for algae and invertebrates ($p = 0.38$, Fig. 37). All univariate analyses of compositional categories within controls were insignificant ($p > 0.09$). Repeated measures analyses indicated that control AFDM did not vary significantly during the experimental period ($p = 0.6$), but showed a significant difference between controls and exposed sluiceways by each consecutive day ($p < 0.0001$), supporting the MANOVA analyses.

Daily loss of invertebrates from exposed treatment sluiceways averaged 0.008 g AFDM (S.E. ±0.002) or 17 animals (S.E. ±4.1) and a 3 d total loss of 0.023 g AFDM (S.E. ±0.008) or 520 animals (S.E. ±31.4; Fig. 38) with ~75% of the animal mass lost the first exposure period. Univariate analyses of invertebrate composition showed a significant loss of lumbriculids ($p < 0.05$, 0.0004 g AFDM) and G. lacustris ($p < 0.2$, 0.028 g AFDM) after a 1-d exposure, and a significant loss of gastropods ($p < 0.001$, 0.0008 g AFDM) after two successive days of exposure.

Air temperatures during the sluiceway experiment ranged from 13 to 36° C with a mean of 25.5°C. Humidity ranged from 19 to 62% with a mean of 35.8%. Cloud cover increased significantly ($p < 0.01$, $n = 9$) over the 3-d experimental period from 0 to 100% overcast with light showers on day three. Water clarity was high and constant with Secchi depths >7 m. Discharge ran 41 to 566 $m^3 \cdot s^{-1}$ ($\bar{x}$ = 387 $m^3 \cdot s^{-1}$), and changed by as much as 424 $m^3 \cdot s^{-1}$ in 12 h. However, current velocity at the up-stream end of each sluiceway averaged 0.38 $m \cdot s^{-1}$ and did not vary significantly during the experiment ($p = 1.0$, $n = 16$).

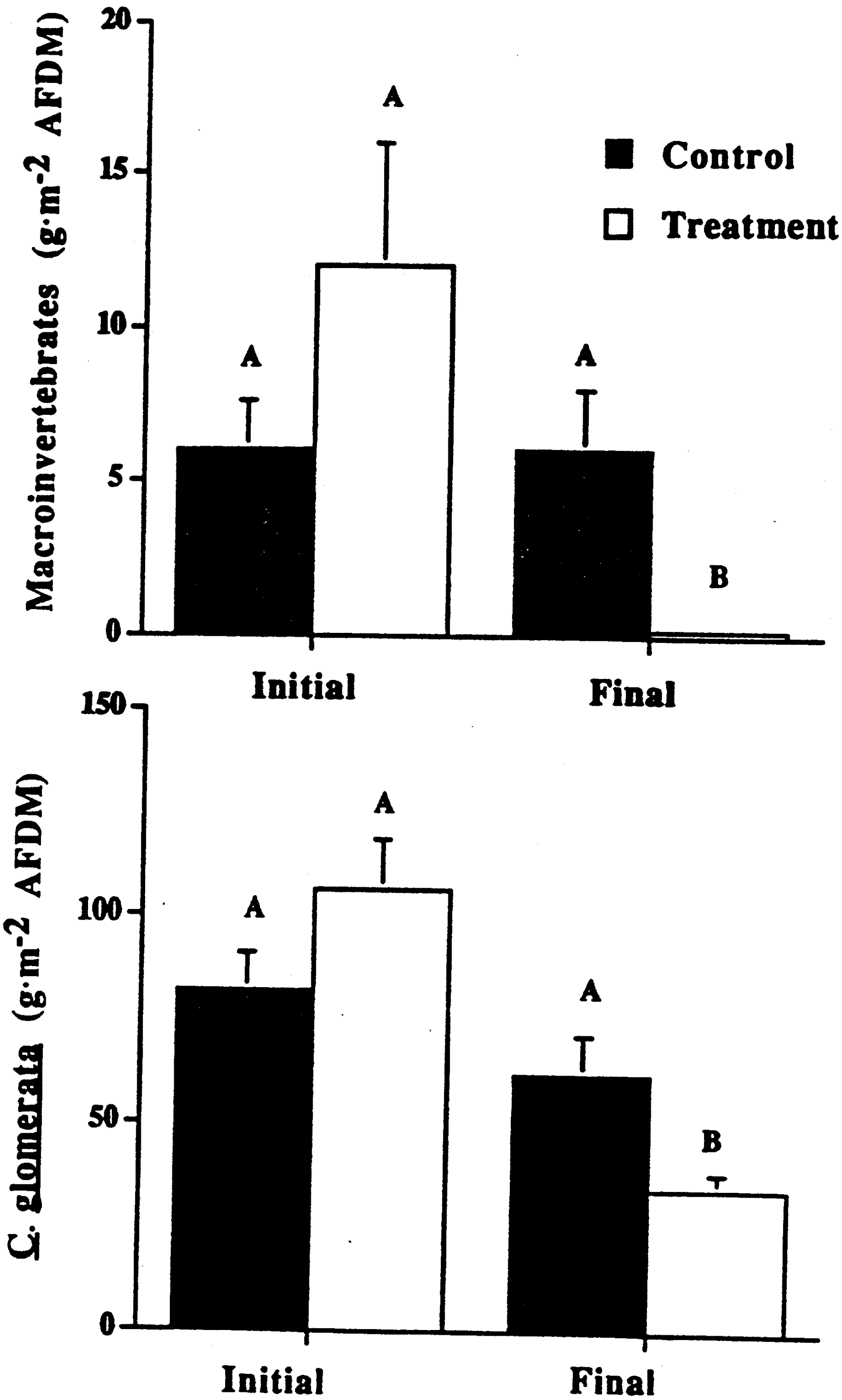


Figure 37. Ash-free dry mass (AFDM) values for Cladophora glomerata and macroinvertebrate benthos lost to stream drift in sluiceway experiments. Treatments were subjected to 3 consecutive nights of exposure compared to continuously submerged controls. Control AFDM was collected at the start (initial) and end (final) of the experiment. Letters designate significant differences in AFDM ($p < 0.01$). Error bars represent ± 1 S.E.

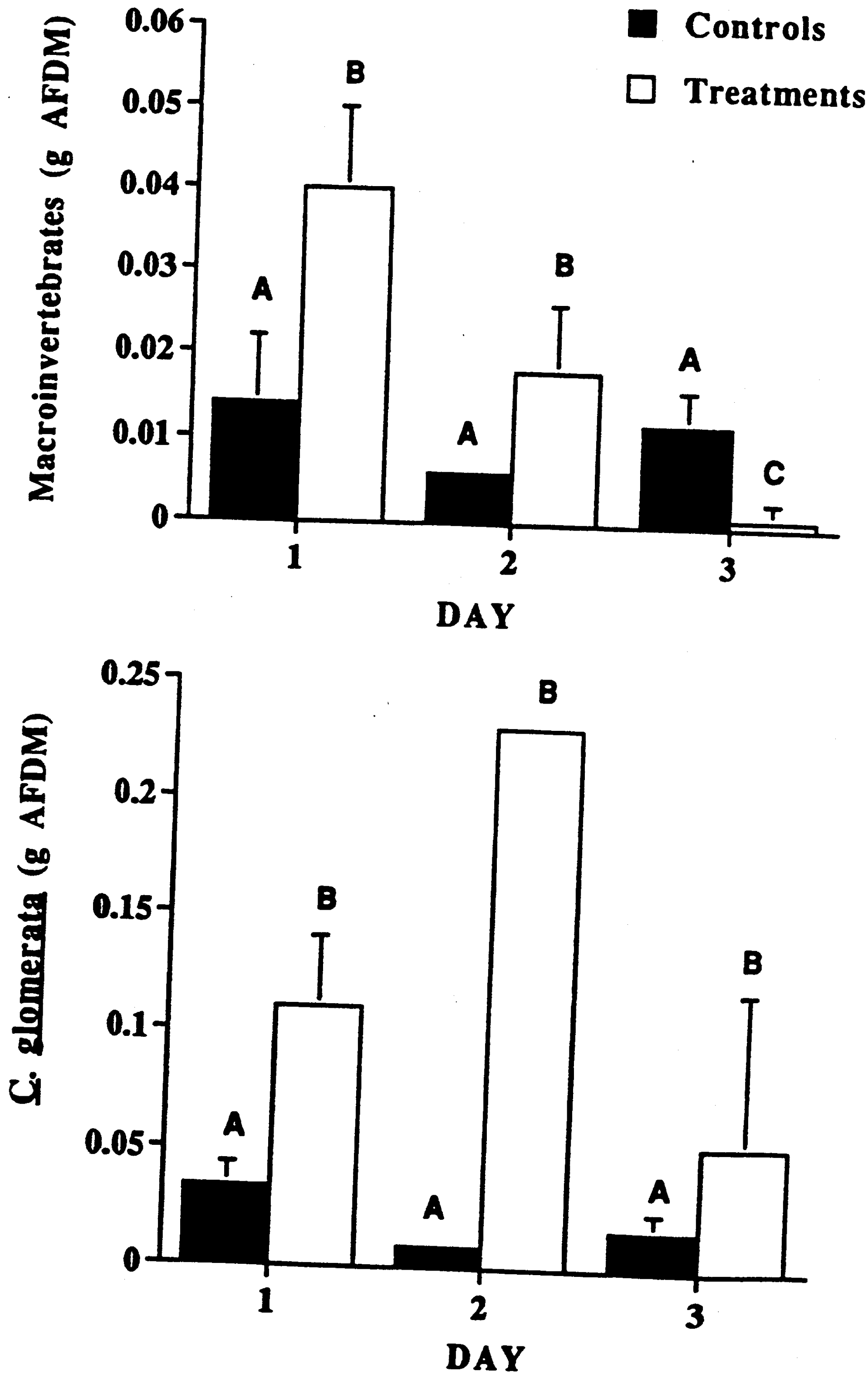


Figure 38. Daily losses of ash-free dry mass (AFDM) for Cladophora glomerata and macroinvertebrates collected in experimental sluiceway drift nets. Treatments were subjected to 3 consecutive nights of exposure (12h) compared to continuously submerged controls. Letters designate significant differences in AFDM ($p < 0.03$). Error bars represent ± 1 S.E.

DISCUSSION

The high benthic standing mass in the tailwaters immediately below Glen Canyon Dam (GCD) contributes negligible coarse particulate organic carbon (CPOM) to downstream aquatic communities in the Colorado River corridor through Grand Canyon. Although operations of GCD dislodge large packets of C. glomerata and associated invertebrates from cobbles through variable discharge and intervals of desiccation (Angradi & Kubly 1993, Blinn et al. 1995; Angradi 1995), rapids along the river corridor quickly pulverize packets and limit transport of CPOM to down stream biotic communities. The rapids are caused by debris fans from tributary inputs and cause hydraulic stress to organic drift; i.e, water velocity can increase by more than 10-fold through rapids (Kieffer 1985, 1990).

Cladophora mass yielded an average of 5700 joules per drift packet at Lees Ferry, based on energy equivalents derived by Blinn et al. (1995), but was reduced by 22% below the confluence of the Paria River, just 1.0 km down stream. There was an additional 26% reduction in energy in drift packets below Badger Rapid (RKM 12.8). This suggests that CPOM is negatively correlated with stream gradient in the river corridor through Grand Canyon National Park. The Paria riffle is a minor rapid with a vertical drop of less than 1 m, while Badger Rapid is the first major rapid with a vertical drop of 2 m (Keiffer 1990).

Invertebrates in C. glomerata packets displayed an even greater distance-related reduction in AFDM than algal components through the first two rapids. Invertebrates in C. glomerata drift packets had an annual mean mass of 0.015 g AFDM (~1,550 joules) at Lees Ferry, but were reduced by >80% below the Paria River and by 99% below Badger Rapid (RKM 12.8). In contrast, Power (1990) reported high densities of insect larvae in floating mats of C. glomerata in the unregulated pool-riffle reach of the Eel River, CA. Floating mats with larval chironomids were consumed 15-16 times more frequently by fish than submerged mats of C. glomerata in the Eel River, with up to 6 times higher emergence rates by larvae compared with submerged mats. These comparisons indicate that drifting CPOM can provide important links in the trophic ecology for small rivers, but large lotic ecosystems with hydraulic turbulence greatly reduce downstream transport of CPOM.

Pulverization of CPOM by rapids through the river corridor does not result in the expected overall increase in TOC with distance from GCD. Samples (n = 12 sites) collected throughout the river corridor during steady flows (May 1993) showed no significant differences in TOC concentrations (33 $mg \cdot L^{-1}$) between Lees Ferry (RKM 0.0) and Diamond Creek (RKM 362) (W.S. Vernieu, personal communication, Glen Canyon Environmental Studies, Flagstaff, AZ). Cellot and Rostan (1993) also reported no significant variation in dissolved organic carbon with distance down the regulated Upper Rhone River. Based on these data, it appears that microbial processing is minimal in cold regulated rivers like the Colorado River. Perhaps, low water temperatures (≤12°C) in the river limit bacterial processing. Further studies on the role of bacteria and fungi in the Colorado River food web need to be investigated.

Zooplankton drift density in the Colorado River through Grand Canyon remains relatively constant (100 animals $m^{-3} \cdot s^{-1}$), but decreased in condition downstream (parasites, body structures missing, etc.) between GCD and Diamond Creek (Haury 1988). Ward (1975) also reported that hypolimnial released zooplankton do not contribute appreciable amounts of organic matter to the downstream communities in a Colorado mountain reservoir. In contrast, Sabri et al. (1993) reported a positive relationship between zooplankton density and discharge in the regulated River Tigris due largely to the occurrence of numerous islands within the channel creating backwaters that flushed with rising hydrographs. The Colorado River in Grand Canyon has a highly constricted channel and for the most part lacks backwaters of any significant size which may contribute to the limited importance of zooplankton drift in this river.

Our data indicate that terrestrial insects comprise a small portion of the stream drift in the river corridor through Grand Canyon National Park, yet Minckley (1991) reports terrestrial insects are commonly found in stomachs of the endemic humpback chub (Gila cypha). Perhaps terrestrial invertebrate drift is highly punctuated during and immediately after rainstorms and is therefore a rare but locally important resource for the fisheries in the Colorado River through Grand Canyon. The narrow band of riparian vegetation along the shores of the Colorado River in the arid Southwest provides limited habitat for terrestrial insects (Stevens 1989). In the regulated Caney Fork River, Tennessee, Layzer et al. (1989) indicated that terrestrial insects made up a significant amount of stream drift mass (9.2%) in June while river fluctuations were highest, but contributed little during the remaining months of the year. In contrast, Armitage (1977) reported that terrestrial insects contributed ~10% of the annual drift mass in the mesic watershed of the River Tees, Great Britain.

Experimental sluiceway experiments at Lees Ferry indicated exposures of C. glomerata under fluctuating flows significantly increase organic drift. Fifty-five percent of the C. glomerata mass entered drift after 3 nights of repeated exposure. Other investigators (Blinn et al. 1995; Angradi & Kubly 1993; Usher & Blinn 1990) reported comparable losses in C. glomerata mass after successive exposures in the tailwaters of GCD and laboratory stream tanks. Furthermore, in-situ drift experiments demonstrated significant differences between steady and fluctuating flows. Fluctuating flows (141-283 $m^3 \cdot s^{-1}$) showed a 20% increase in C. glomerata drift at 1600 and 2400 h compared to steady flows (226 $m^3 \cdot s^{-1}$). The peak hydrostatic wave from GCD reaches Lees Ferry at 1600 h which accounts for the evening increase in C. glomerata drift. In contrast, invertebrates did not exhibit behavioural drift in the tailwaters of GCD. Tailwater conditions, with dramatic daily changes in velocity, may have selected for organisms that do not change their behaviour on a diurnal basis (Waters 1972). Furthermore, Shannon and coworkers (1994) found no significant differences in feeding behaviour between in-situ day and night feeding experiments for G. lacustris in the tailwaters of GCD. Armitage (1977) also reported that chironomids and baetids lacked a diurnal drift behavior in the regulated River Tees, Great Britain.

The close relationship between composition of C. glomerata drift packets and the benthic community within each corresponding reach throughout the Colorado River suggests that composition and quantity of drift is reach specific and not cumulative throughout the study site. Thorp and Delong (1994) found similar patterns of reach-based CPOM production from shallow benthic hard substratum and riparian zones in rivers with large photic zones. Tailwater benthic communities (RKM 26 below GCD) have high standing crops of C. glomerata and associated G. lacustris and chironomid larvae (e.g. Cricotopus annulator), as does the tailwaters drift. Shannon and coworkers (1994) reported a reduction in C. glomerata and invertebrate standing stock in downstream reaches due to elevated suspended sediments from tributaries draining arid landscapes, drift mass follows the same pattern.

Elevated suspended sediments reduce photosynthetic available radiation (PAR) in the water column with distance downstream and cause a negative bottom-up trophic response in the Colorado River (Blinn et al. 1994). Reductions in light energy result in an overall reduced mass and a change in composition in benthic algae from C. glomerata to Oscillatoria spp. The compositional change in primary producers causes a reduction in grazers (chironomid larvae and G. lacustris) and an increase in filter-feeders (Simulium arcticum, Blinn et al. 1994). Compositional changes in benthic primary consumers correlate with changes in composition of steam drift throughout the 387 km study area in Glen Canyon and Grand Canyon National Park.

Suspended sediments dislodged from bed load material during fluctuations in discharge coupled with tributary input may be important factors contributing to invertebrate drift in the Colorado River. Doeg and Milledge (1991) increased the level of suspended sediments in experimental channels in the Acheron River, Australia, to mimic natural flood events. They reported a 7-fold increase in the number of drifting invertebrates after 45 min of sediment additions in comparison to control channels. Composition of drifting taxa was also variable with amphipods and some species of Chironomidae very susceptible to suspended sediment loads. This corroborates the reduction in drifting G. lacustris below the Little Colorado River and the relatively high numerical level of dipteran drift dominated by simuliids. Rosenberg and Weins (1978) along with Culp et al. (1985) also stated that sediment saltation during high discharge events create an increase in invertebrate drift.

Down river compositional shifts in the fishery can also be linked to the increase in suspended sediments and resulting changes in drift and benthic composition. Rainbow trout have been introduced into the clear tailwaters of GCD, but decrease in number through Marble Canyon and are restricted to tributary mouths below the Little Colorado River confluence (Carothers & Brown 1991). Trout are replaced in down river sections by bottom feeding carp, channel catfish and several native fish species; humpback chub, flannelmouth sucker, and bluehead sucker. Minckley (1991) stated that while these endemic fish are opportunistic feeders they are primarily detritivores.

Total volume of stream drift increased with distance down river from GCD, and changed in composition from C. glomerata to detritus, particularly when the Paria and Little Colorado Rivers were in spate. Detrital drift collected near cobble bars was not correlated with benthic mass of invertebrates in the Colorado River, but instead showed a positive correlation with slow velocity depositional pools (Blinn et al. 1994). Corkum (1992) reported a similar relationship between velocity, detritus and invertebrate abundance in accordance with drainage biome effects. Tributaries contribute negligible amounts of detritus to mainstem drift, however, riparian vegetation can be an important source of detrital loads during periods of low precipitation as was reported in a reach which lacks tributaries below Lake Mead in the lower Colorado River (Lieberman & Burke 1993). However, the lower Colorado River lacks the hydraulic variability of the Grand Canyon and while size fractioning within CPOM samples showed that particulate material decreased down river, Lieberman and Burke (1993) found an increase in larger size particles.

Down river detritus, which represents a large portion of the total drift mass, was the only component to show a positive correlation with discharge. The low flows and erratic ramping rates of the past decade below GCD may have resulted in detritus being the only component directly affected, perhaps due to buoyancy.

The non-linear relationship of total drift and discharge (Fig. 2) may be a function of eddie/pools emptying during discharges above 450 $m^{-3} \cdot s^{-1}$ and below 400 $m^{-3} \cdot s^{-1}$, and filling between 400 and 450 $m^{-3} s^{-1}$. Our data also indicate a threshold of about 480 $m^{-3} \cdot s^{-1}$ at which point total drift mass dramatically increases. As water stage increases, mostly the base littoral zone is swept, reducing the ratio of drift to flow volume. A threshold of ~480 probably begins to entrain pool-stored drift. Leibfried and Blinn (1986) reported a similar pattern at Lees Ferry.

Entrapment and decomposition of drifting material in the eddie dominated Colorado River through Grand Canyon National Park occurs in recirculation zones (eddies) and pools, rather than in debris dams. The Colorado River through the Grand Canyon has an average width/mean depth ratio of 12.1 at 680 $m^3 \cdot s^{-1}$ and an average channel width of 67 m (United States Department of Interior 1994). Therefore, the magnitude of annual discharges (283 $m^3 \cdot s^{-1}$) are great enough to eliminate debris dams which play an important role in resource processing in many lower order lotic ecosystems (Bilby & Ward 1991). Debris packets up to 40 cm^2 travel through the Colorado River corridor in a sinal wave pattern generally within the top two meters of the water column (Shannon, personal observations). Comparison of channel and eddie/pool drift and benthic samples within eddie/pools revealed the limited retention capabilities of eddies and pools in this arid geomorphically constrained river. Only 50% of drifting detritus and C. glomerata is captured in backwaters and only detritus is positively correlated between benthic and drift samples.

Detritus either breaks apart and/or is transported through the deeply incised Grand Canyon. The Little Colorado River (RKM 99), the single largest tributary in the study, flooded several times during the winter of 1993. At that time large rafts of organic flotsam, largely composed of sticks and logs, at times covered the surface of 500 m^2 eddies. Benthic sampling during the subsequent year recovered minor percentages of the flotsam.

Fluorescent dye dispersion studies between GCD and Diamond Creek by Graf (1995) support our paradigm of swift transport of organic material, with little retention in pools or eddies through the river corridor. Discharge variability did not significantly affect water velocity in the Colorado River, as the dye did not disperse faster under variable discharges compared to steady flows (Graf, 1995). These data also correlate with the insignificant change in drift mass with ramping state.

Our data reveal how a constricted, large volume desert river with fluvial tributary effects, can act as a conduit for organic matter produced in the upper tailwaters. Tributary input of suspended sediments molds the benthic community structure, while debris flows create large hydraulic gradients pulverizing drift resulting in reach based drift patterns. Fluctuating and reduced discharge regimes exposing colonized cobbles for 12 h at night contributes significantly to drift mass. Continued research on retention time, microbial processing and TOC is essential to better understand the organic budget of the Colorado River through Grand Canyon National Park.

CHAPTER THREE: MANAGEMENT CONSIDERATIONS

1) Data complied from Blinn at al. (1995) indicates that increasing the baseflow from 142 $m^3 \cdot s^{-1}$ to 227 $m^3 \cdot s^{-1}$ in the tailwaters reach may increase the amount of energy available for fish by 1.6 fold. The occasional weekend discharges at the current baseflow (142 $m^3 \cdot s^{-1}$), even at night, can take over 6 months for complete recovery in this reach. Therefore, subtle changes in dam operations can have important positive trophic implications in the Lees Ferry tailwaters and potentially down river.

2) Long-term monitoring and adaptive management plans should include flexible funding schedules so that in the event of a change in dam operations, such as that experienced during the summer of 1995, adequate funds are available to study changes and determine what, if any, impacts have been made on the aquatic food base.

3) The shape of the hydrograph for Habitat Maintenance Flows has been the topic of much discussion. In order to enhance the benefits of the aquatic food base, our data suggest that the discharge regime after peak flows is ultimately more important than the peak flow itself. The more stable the discharge pattern after high flows the greater the benthic production. For example, if typical summer flows during July and August were implemented after the spike flow, our data suggests little benefit would be derived in terms of increasing benthic biomass because we commonly see a reduction in September biomass throughout the river, even during dry summers.

Future Monitoring and Research

Ecologically appropriate management of water quality and the lower aquatic trophic levels of this river system would best be served by adopting a four-fold plan for future monitoring and research.

1. Continue system-wide and seasonal monitoring, and research on key resource components to improve our understanding of ecological linkages between lower aquatic and higher trophic levels. Mainstem monitoring should be continued at least on a seasonal basis, as well as before and after planned and unplanned high or low flow events. Annual reports and preparation of results for peer-reviewed publications should be encouraged. Monitoring should continue to take place on a system-wide, seasonal basis, and should include benthos, drift and backwater production, with summer low flow comparisons of benthos and drift in selected tributaries. Protocol, including data archival, for seasonal, system-wide monitoring should be reviewed in the next year, and any changes to existing protocol should be implemented in a fashion that maximizes continuity of interpretation for a long-term monitoring program.

2. Development of comprehensive analyses of flood impacts, including flood effects on drift, benthic standing mass and production, and backwater development. River regulation reduces flooding, the dominant form of natural disturbance in river systems, and produces ecologically novel conditions in tailwaters (Ward & Stanford 1983, Blinn & Cole 1990, Blinn et al. 1992, 1994, 1995). Restoration of sediment deposits and aquatic habitats is planned in the Grand Canyon by implementing a program of occasional high flows. The impacts of high flows in drift and benthic ecology are likely to be large, with undetermined impacts on higher trophic levels, particularly native and non-native fish. Improved understanding of how flooding affects the fluvial food and trophic interactions will greatly improve long-term management of this system.

3. Plan and initiate studies of thermal modification of the river. The National Park Service is engaged in long-term sustainable ecosystem management of this system under conditions of partially to largely clearwater, cold-stenothermic flow with little annual variation and rare floods. These are unique limnological conditions, for which few natural analogies exist except in cold-water springs. For the aquatic components of this ecosystem we recommend examination of temperature effects on interactions between C. glomerata and Oscillatoria, aquatic macrophytes, algal epiphytes, and dominant macroinvertebrate taxa presently in the mainstem. These studies should be initially conducted in a laboratory setting, and subsequently in field experiments. A thermal modification studies plan should be initiated as soon as possible so that an adequate database can be developed, and so that issues surrounding changes in biotic assemblages can be thoroughly reviewed and studied.

4. Initiate development of a comprehensive river ecosystem model relating physical conditions to benthic, planktonic and backwater production. Development of this model should progressively incorporate existing physical and biological monitoring data, as well as flood-related and thermal modification data. The model should be developed in a fashion that intergrates water quality with benthic and planktonic components, and should be extended to the fisheries and, potentially, to riparian trophic levels.

CHAPTER FOUR: LITERATURE CITED

ALLAN, J.D., AND E. RUSSEK. 1985. The quantification of stream drift. Can. J. Fish. Aquat. Sci. 42: 210-215.

ANDREWS, E.D. 1991. Sediment transport in the Colorado River basin, p. 54-74. In Committee on Glen Canyon Environmental Studies [eds.] Colorado River Ecology and Dam Management. National Academy Press, Washington D.C.

ANGRADI, T.R. 1995. Trophic linkages in the lower Colorado River: multiple isotope evidence. J. N. Am. Benthol. Soc. 4: 479-510.

ANGRADI, T.R., AND D.M. KUBLY. 1993. Effects of atmospheric exposures on chlorophyll a, biomass, and productivity of the epilithon of a tailwater river. Regulated Rivers 8: 345-358.

ARMITAGE, P.D. 1977. Invertebrate drift in the regulated River Tees, and an unregulated tributary Maize Beck, below Cow Green Dam. Freshwat. Biol. 7: 167-183.

BARNESE, L.E., AND R.J. LOWE. 1992. Effects of substrate, light, and benthic invertebrates on algal drift in small streams. J. N. Am. Benthol. Soc. 11: 49-59.

BILBY, R.E., AND J.W. WARD. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forest in southwestern Washington. Can. J. Fish. Aquat. Sci. 48: 2499-2508.

BLINN, D.W., AND G.A. COLE. 1991. Algal and invertebrate biota in the Colorado River: Comparison of pre-and post-dam conditions. p. 102-123. In Committee on Glen Canyon Environmental Studies [eds.] Colorado River Ecology and Dam Management. National Academy Press, Washington, D.C.

BLINN, D.W., R. TRUITT, AND A. PICKART. 1989. Response of epiphytic diatom communities from the tailwaters of Glen Canyon Dam, Arizona, to elevated water temperature. Regulated Rivers 4: 91-96.

BLINN, D.W., L.E. STEVENS, AND J.P. SHANNON. 1992. The effects of Glen Canyon Dam on the aquatic food base in the Colorado River Corridor in Grand Canyon, Arizona. Report submitted to Bureau of Reclamation, Glen Canyon Environmental Studies. Flagstaff, AZ.

BLINN, D.W., L.E. STEVENS, AND J.P. SHANNON. 1994. Interim flow effects of Glen Canyon Dam on the aquatic food base in the Colorado River corridor in Grand Canyon, Arizona. Report submitted to Bureau of Reclamation, Glen Canyon Environmental Studies. Flagstaff, AZ.

BLINN, D.W., J.P. SHANNON, L.E. STEVENS AND J.P. CARDER. 1995. Consequences of fluctutating discharge for lotic communities. J. N. Am. Benthol. Soc. 14:233-248.

BRITTAIN, J.E., AND T.J. EIKELAND. 1988. Invertebrate drift- a review. Hydrobiologia 166: 77-93.

BROOKER, M.P., AND R.J. HEMSWORTH. 1978. The effect of the release of an artificial discharge of water on invertebrate drift in the River Wye, Wales. Hydrobiologia 59:155-164.

CAROTHERS S.W., AND B.T. BROWN. 1991. The Colorado River through Grand Canyon, Natural History and Human Change. The University of Arizona Press, Tucson, AZ. 325 p.

CELLOT, B., AND J.C. ROSTAN. 1993. Dissolved organic carbon dynamics in the Upper Rhone: The influence of side-arms? Regulated Rivers 8: 391-397.

COBB, D.G., T.D. GALLOWAY, AND J.F. FLANNAGAN. 1992. Effects of discharge and substrate stability on density and species composition of stream insects. Can. J. Fish. Aq. Sci. 49:1788-1795

CORKUM, L.D. 1992. Relationships between density of macroinvertebrates and detritus in rivers. Arch. Hydrobiol. 2:149-166.

CORRARINO, C.A., AND M.A. BRUSVEN. 1983. The effects of reduced stream discharge on insect drift and stranding of near shore insects. Freshwat. Invert. Biol. 2: 88-98.

CULP, J.M., F.J. WRONA, AND R.W. DAVIES. 1985. Response of stream benthos and drift to fine sediment deposition versus transport. Can. J. Fish. Aquat. Sci. 64: 1345-1351.

CULP, J.M., G.J. GARRY, AND J. SCRIMGEOUR. 1994. The effect of sample duration on the quantification of stream drift. Freshwat. Biol. 31: 165-173.

DAVIES-COLLEY, R.J., C.W. HICKEY, J.M. QUINN, AND P.A. RYAN. 1992. Effects of clay discharges on streams. I. Optical properties and epilithon. Hydrobiologia 248:215-134.

DODDS, W., AND D.A. GUDDER. 1992. The ecology of Cladophora. J. Phycol. 28: 415-427.

DOEG T.J., AND G.A. MILLEDGE. 1991. Effect of experimentally increasing concentrations of suspended sediments in macroinvertebrate drift. Aust. J. Mar. Freshwat. Res. 42: 519-526.

DUNCAN, S.W. AND D.W. BLINN. 1989. Importance of physical variables on the seasonal dynamics of epilithic algae in a highly shaded canyon stream. J. Phycol. 25:455-461.

GRAF, J. B. 1995. Measured and predicted velocity and longitudinal dispersion at steady and unsteady flow, Colorado River, Glen Canyon Dam to Lake Mead. Water Res. Bull. AWRA. 31:265-281.

HARDWICK, G., D.W. BLINN, AND H.D. USHER. 1992. Epiphytic diatoms on Cladophora glomerata in the Colorado River, Arizona: longitudinal and vertical distribution in a regulated river. Southwest. Nat. 37: 148-156.

HAURY, L.R. 1988. Zooplankton of the Colorado River: Glen Canyon Dam to Diamond Creek. Report to Glen Canyon Environmental Studies. NTIS# PB88-183462/AS.

IRVINE, J.R. 1985. Effects of successive flow perturbations on stream invertebrates. Can. J. Fish. Aquat. Sci. 42: 1922-1927.

KIEFFER, S.W. 1985. The 1983 hydraulic jump in Crystal Rapid: implications for river-running and geomorphic evolution in the Grand Canyon. J. Geo. 93: 385-406.

KIEFFER, S.W. 1990. Hydraulics and geomorphology of the Colorado River in the Grand Canyon, p. 333. In S.S. Beus and M. Morales [eds.]. Grand Canyon Geology. Oxford University Press, New York.

LAYZER, J. B., T.J. NEHUS, W. PENNINGTON, J.A. GORE AND J.M. NESTLER. 1989. Seasonal variation in the composition of the drift below a peaking hydroelectric project. Regulated Rivers 3:29-34.

LEIBFRIED, W.C., AND D.W. BLINN. 1986. The effects of steady versus fluctuating flows on aquatic macroinvertebrates in the Colorado River below Glen Canyon Dam, Arizona. Glen Canyon Environmental Studies Report No. 15, National Technical Information Service PB88-206362/AS. U.S. Department of Commerce, Springfield, Virginia.

LIEBERMAN, D.M., AND T.A. BURKE. 1993. Particulate organic matter transport in the lower Colorado River, South-western USA. Regulated Rivers 8: 323-334.

LOWE, R. 1979. Phytobenthic ecology and regulated streams, p. 25-34. In J.V. Ward and J.A. Stanford [eds.] The Ecology of Regulated Streams. Plenum Press, New York.

MACPHEE C. AND M.A. BRUSVEN. 1973. The effects of river regulation resulting from hydroelectric peaking on selected invertebrates. Tech. Compl. Rep. Project A-035-IDA, Idaho Water Resources Research Institute, 26 p.

MERRITT, R.W., AND K.W. CUMMINS (eds.). 1984. An Introduction to the Aquatic Insects of North America. 2nd Ed. Kendell/Hunt, Dubuque, IA.

MINCKLEY, W.L. 1991. Native fishes of the Grand Canyon region: An obituary? p. 124-177. In Committee on Glen Canyon Environmental Studies [eds.] Colorado River Ecology and Dam Management. National Academy Press, Washington, D.C.

MINSHALL, G.W., AND P.V. WINGER. 1968. The effect of reduction in stream flow on invertebrate drift. Ecology 49: 580-582.

MORGAN, R.P., R.E. JACOBSEN, S.B. WEISBERT, L.A. McDOWELL AND H.T. WILSON. 1991. Effects of flow alteration on benthic macroinvertebrate communities below Brighton hydroelectric dam. Freshwat. Biol. 4:419-429.

NEWCOMBE, C.P. AND D.D. MacDONALD. 1991. Effects of suspended sediments on aquatic ecosystems. N. Am. J. Fish. Manag. 11:72-82.

PERRY, S.A., AND W.B. PERRY. 1986. Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA. Hydrobiologia 134: 171-182.

PETERSON, C.G. AND R.J. STEVENSON. 1992. Resistance and resilience of lotic algal communities: Importance of disturbance timing and current. Ecology 73:1445-1461.

POFF, N.L., AND J.V. WARD. 1991. Drift responses of benthic invertebrates to experimental stream flow variations in a hydrologically stable stream. Can. J. Fish. Aquat. Sci. 48: 1926-1936.

POWER, M.E., 1990. Benthic turfs vs floating mats of algae in river food webs. Oikos 58: 67-79.

POWER, M.E., R.J. STOUT, C.E. CUSHING, P.P. HARPER, F.R. HAUER, W.J. MATTHEWS, P.B. MOYLE, B. STATZNER, AND I.R. WAIS De BADGEN. 1988. Biotic and abiotic controls in river and stream communities. J. N. Am. Benthol. Soc. 7:456-479.

QUINN, J.M., R.J. DAVIES-COLLEY, C.W. HICKEY, M.L. VICKERS AND P.A. RYAN. 1992. Effects of clay discharges on streams. Hydrobiologia 248:235-247.

ROSENBERG, D. M., AND A.P. WEINS. 1978. Effects of sediment addition on macrobenthic invertebrates in a northern Canadian river. Water Res. 12: 753-763.

ROSS, J.C. AND A.J.H. PIETERSE. 1994. Light, temperature and flow regimes of the Vaal River at Balkfontein, South Africa. Hydrobiologia 277:1-15.

SABRI, A. W., H. ZAINAB, S.F. SHAWKAT, L. A. THEJAR, T.I. KASSIM AND K.A. RASHEED. 1993. Zooplankton population in the River Tigris: Effects of Samarra impoundment. Regulated Rivers 8: 237-250.

SCHMIDT, J.C. AND J.B. GRAF. 1990. Aggradation and degradation of alluvial sand deposits, 1965 to 1986, Colorado River, Grand Canyon National Park, Arizona. U.S. Geological Survey Profession Paper 1493. Washington, D.C.

SCULLION, J. AND A. SINTON. 1983. Effects of artifical freshets on substratum, composition, benthic invertebrate, fauna and invertebrate drift on two impounded rivers in mid-Wales. Hydrobiologia. 107:261-269.

SHANNON, J.P., D.W. BLINN, AND L.E. STEVENS. 1994. Trophic interactions and benthic animal community structure in the Colorado River, Arizona, USA. Freshwat. Biol. 31: 213-220.

SHAVER, M. 1995. The role of turbidity and desiccation in structuring benthic communities in the Colorado River, Arizona. MSc. Thesis, Northern Arizona, Flagstaff, AZ.

STANFORD, J.A., AND J.V. WARD. 1991. Limnology of Lake Powell and the chemistry of the Colorado River. p. 73-123. *In* Committee on Glen Canyon Environmental Studies [eds.] Colorado River Ecology and Dam Management. National Academy Press, Washington D.C.

STEVENS, L.E. 1989. Mechanisms of riparian plant community organization and succession in the Grand Canyon, AZ. Ph.D. thesis, Northern Arizona University, Flagstaff, AZ.

THORP, J.H., AND M.D. DELONG. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos 70: 305-308.

UNITED STATES DEPARTMENT OF INTERIOR. 1994. Operation of Glen Canyon Dam. Draft environmental impact statement. USDI Bureau of Reclamation, Salt Lake City, Utah.

USHER, H.D., AND D.W. BLINN. 1990. Influence of various exposure periods on the biomass and chlorophyll *a* on *Cladophora glomerata* (Chlorophyta). J. Phycol. 26: 244-249.

VANNOTE, R.L. AND B.W. SWEENEY. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. Am. Nat. 115:667-6695.

WARD, J.V. 1975. Downstream fate of zooplankton from a hypolimnial release mountain reservoir. Verh. Internat. Ver. Limnol. 19: 1798-1804.

WARD, J.V. AND B.C. KONDRATIEFF. 1992. An Illustrated Guide to the Mountain Stream Insects of Colorado. University of Colorado Press.

WARD, J.V. AND STANFORD. 1982. Thermal responses in the evolutionary ecology of aquatic insects. Ann. Rev. Entomol. 27:97-117.

WARD, J.V. AND J.A. STANFORD. 1983. The serial discontinuity concept of lotic ecosystem. Pp. 29-42. In: T. D. Fontaine and S.M. Bartell (Eds.). Dynamics of Lotic Ecosystems. Ann Arbor Scientific Publications, Ann Arbor, Mich.

WATERS, T.F. 1972. The drift of stream insects. Ann. Rev. Entomol. 17: 253-272.

WATERS, T.F. 1981. Seasonal patterns in production and drift of Gammarus pseudolimnaeus in Valley Creek, Minnesota. Ecology 62: 1458-1466.

WILKINSON, L. 1989. SYSTAT: The System for Statistics. Systat, Evanston, IL.

WILZBACH, M.A., K.W. CUMMINS, AND R. A. KNAPP. 1988. Toward a functional classification of stream invertebrate drift. Verh. Internat. Ver. Limnol. 23:1244-1254.

WOOSTER, D. AND A. SIH. 1995. A review of the drift and activity responses of stream prey to predator presence. Oikos 73: 3-8.

CHAPTER FIVE: PRESENTATIONS AND PUBLISHED ARTICLES RELATED TO THIS STUDY

Blinn, D.W., J.P. Shannon, L.E. Stevens, & J.P. Carder. 1995. Consequences of fluctuating discharge for lotic communities. Journal of the North American Benthological Society. 14:233-248.

Shaver, M.L. 1995. The role of turbidity and desiccation in structuring benthic communities in the Colorado River, Arizona. MSc. Thesis, Northern Arizona University, Flagstaff, AZ.

Shannon, J.P., D.W. Blinn, P.L. Benenati, K. Wilson, & M. Shaver. 1995. Mechanisms affecting the drift of Cladophora glomerata associated epiphytes, and macroinvertebrates in the Colorado River through Grand Canyon National Park, Arizona. 43rd Annual Meeting of the North American Benthological Society. Keystone, Colorado.

Shannon, J.P., D.W. Blinn, P.L. Benenati, & K.P. Wilson. 1995. Organic drift in a large regulated river in an arid biome: Colorado River through Grand Canyon National Park, USA. Submitted to Canadian Journal of Fisheries and Aquatic Sciences.

Shannon, J.P., K.P. Wilson, P.L. Benenati, D.W. Blinn, G. A. Haden, & L.E. Stevens. 1995. Benthic Community structure in the Colorado River drainage above and below Lake Powell in the autumn of 1993 and 1994. Biennial Conference of Research on the Colorado Plateau, Colorado Plateau Research Station. Flagstaff, Arizona. (submitted)

Melis, T.S., R.H. Webb, M. Kaplinski, J.E. Hazel, J.P. Shannon, D.W. Blinn, R.A. Valdez, & R.J. Ryel. 1995. Impacts of the 1993 Tanner Canyon debris flow on physical and aquatic resources of the Colorado River in Grand Canyon National Park, Arizona. Fall 1995 Meeting, American Geophysical Union. San Francisco, California. (submitted)