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, phenology, biomass, colonization rates, secondary production, winter desiccation, and stream 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 experimental flooding under consideration in 1995.

Our results indicate the following:

Benthic primary and secondary producer standing mass was assessed seasonally from September 1992 through June 1994 betweeen Lees Ferry and Diamond Creek. IF, and seasonal and climatic variation altered benthic community structure. In general algal and macroinvertebrate AFDM and species richness increased through time in downstream reaches. We attribute these changes to reduced daily discharge fluctuation and ramping rates, and exceptionally clear water flows. Aquatic habitats have also been altered during this period by both the operation of GCD and variability in tributary inflow.

Pool and riffle habitats have accumulated fine sediments reducing the area of hard substrates for colonization. Pool habitats have also accumulated fine sediments that have created a productive littoral zone along the length of the pool/eddie complexes sampled and decreased the total volume of water circulating within pools thereby reducing the accumulation of detritus during low flow months. Macrophyte biomass has also increased in depositional areas within Glen and Marble Canyons. Bryophyte biomass increased in eroisonal zones throughout the study site.

The winter of 1993 had large spates from watersheds extending beyond the Grand Canyon rim, while a summer monsoon in 1993 produced a debris flow in Tanner Wash, which restructured the pool and riffle habitats at that site. Both events were followed by an overall increase in benthic AFDM, perhaps a result of nutrient increase from tributary flows.

IF have allowed natural patterns in primary and secondary producer distribution to be recognized which were previously diluted by normal dam operations. This flow regime has also allowed sporadic colonization into the previously

depauperate varial zone. Pools of water in the varial zone left after high flow months have provided spawning habitats for mosquitos, particularly in the lower Canyon, which were previously rare along the mainstem.

Benthic primary production decreased downstream as turbidity increased, due to tributary input, and phytobenthos decreased. In general, higher production was measured during the summer compared to winter months. Higher downstream water temperature may offset this spatial pattern and should be considered when planning for a multiple level intake system. No significant difference occurred in production between C. glomerata with versus without epiphytes, suggesting that C. glomerata NPP may increase if epiphyte density decreases. Optimum light conditions for C. glomerata growth in this system requires further study.

Both G. lacustris and the chironomid community have high production rates in the submerged zone (≤ 140 m^3 s^{-1}) at Lees Ferry. However, both invertebrates are strongly affected by regulated flows from Glen Canyon Dam and suspended sediment input from tributaries. Gammarus lacustris and chironomid production was reduced by over 80% in the tailwater varial zone at Lees Ferry. Further reductions ($\geq 80\%$) in downstream production at the somewhat turbid habitat of Two Mile Wash were caused by suspended sediments entering from the Paria River. Considerable mass of both invertebrates enter stream drift on a daily basis. Inclusion of stream drift in production estimates increases overall production values for each invertebrate. Both G. lacustris and chironomid larvae play an important role as intermediate links in the Colorado River food web.

A strong positive correlation exists between detrital drift and discharge in the Colorado River corridor, while biotic components show a strong negative correlation to discharge. Drift components vary seasonally; e.g., September collections show highest drift mass. The high autochthonous production between GCD and Lees Ferry supply little coarse particulate organic matter (CPOM) to downstream reaches. Turbulence by rapids quickly pulverize packets of drifting C. glomerata into fine particulate organic matter (FPOM). Packets of C. glomerata and associated communites are reduced by 4-fold below the Paria confluence (RKM 1.0) and 10-fold by RKM 85. The function of downstream microbial loops on FPOM and the role these microbes serve in the Colorado River food web require further study. Tributaries provide $\leq 25\%$ of the total organic stream drift in the Colorado River through Grand Canyon National Park. Regulated flows significantly increase stream drift of aquatic benthos in the tailwaters of GCD.

Our in situ experiments indicated both variable water levels and elevated suspended sediment are less suitable conditions for C. glomerata colonization than for Oscillatoria phytobenthic communities. These observations are generally supported by patterns displayed by phytobenthic communities located downstream from Glen Canyon Dam. Chironomid AFDM increased more quickly than G. lacustris AFDM on translocated cobbles at Lees Ferry, and chironomid recruitment appeared to be less dependent on C. glomerata than recruitment by G. lacustris. Macroinvertebrates showed faster recolonization of desiccated cobbles in the continuously submerged zone than did benthic algae. In general, cobbles in the varial zone showed limited recruitment by macroinvertebrates compared to submerged and control cobbles.

We estimate the energy derived from animal mass associated with C. glomerata communities to be nearly an order of magnitude higher than energy derived from macroinvertebrate mass in Oscillatoria communities. Therefore, loss of C. glomerata habitat and the replacement by habitat more suitable for Oscillatoria reduces the overall food value of the phytobenthic community in the Colorado River through Grand Canyon National Park.

Winter nighttime desiccation exerts similar effects on the mass of C. glomerata as does summer desiccation. Three hours of nighttime freezing reduced AFDM by 50%, which is comparable to summer losses (48%) after a 12-h exposure. Treatment cobbles also showed a significant decrease in chlorophyll a compared to controls. Data for macroinvertebrate densities were not conclusive due the patchiness of the benthic community in the Colorado River. However, there was a strong pattern for loss of macroinvertebrate mass (93%) following one winter night exposure. Repeated desiccation and increasing sample size may resolve this discrepency.

INTRODUCTION

Glen Canyon Dam operations strongly affect the lower trophic levels of the aquatic ecosystem in Grand Canyon National Park (Blinn et al. 1992). Aquatic 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 of 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 effects on benthic distribution and production 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 consisted of reduced flow fluctuations with restricted minimum (140 $m^3 s^{-1}$) and limited maximum (566 $m^3 s^{-1}$) flows, and reduced ramping rates.

A primary objective of the GCES Interim Flows discharge criteria is to maintain the aquatic food base in the Colorado River. The Interim Flow 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.

OBJECTIVES

The objectives of this study were to determine whether and how Interim Flows are limiting the impacts of Glen Canyon Dam operations on benthic resources in the Grand Canyon.

Objective 1: Monitor the effects of Interim Flows from Glen Canyon Dam on the standing mass of the lower trophic level components in the Colorado River between Lees Ferry and Diamond Creek.

Objective 2: Monitor the effects of low, medium and high-volume monthly Interim Flows on primary and secondary production in the Colorado River corridor in the Grand Canyon

Objective 3: Monitor the effects of Interim Flows on organic drift in the Colorado River corridor in the Grand Canyon.

Objective 4: Monitor the effects of Interim Flows on the re-colonization of substrata by primary producers and secondary consumers and test the impact of freezing/desiccation on the aquatic benthos community in the Colorado River ecosystem.

Objective 5: Prepare monitoring data for inclusion into the GCES/NPS geographic information systems database.

In addition, we discuss considerations relating to improvement of management of this river system and its aquatic trophic levels.

CHAPTER ONE: STANDING MASS OF LOWER TROPHIC LEVELS

INTRODUCTION

Standing mass and habitat requirements of the aquatic benthos in the Colorado River through Glen and Grand Canyons were measured seasonally from September, 1992 through June, 1994. A seasonal sampling frequency was employed to compare high and low volume discharge months preceeding collection trips. Sampling sites (n = 10) were the same as those established during GCES Phase II research flows (Blinn et al. 1992) and include low velocity pool/eddies and high velocity cobble bars in both wide (n = 5) and narrow (n = 5) reaches (Schmidt & Graf 1990). Tributaries (n = 11) were sampled in June of each year, after winter run-off and prior to summer monsoons.

The benthic community in the Colorado River through Grand Canyon has been altered by the construction of Glen Canyon dam largely through changes in river discharge, suspended sediment concentration (turbidity) and water temperature. Interim flow criteria have increased the base flow while reducing peak flow and hourly ramping rates from Glen Canyon Dam. A similar change in flow regime was implemented on the Patuxent River, MD which resulted in a two-fold increase in benthic macroinvertebrate abundance (Morgan et al. 1991).

Variable discharges influence benthic communities by altering substrate stability (Power et al. 1988, Cobb et al. 1992), increasing hydraulic stress (Statzner et al. 1988, Peterson & Stevenson 1992), and modifying water quality (Scullion & Sinton 1983). Regulation of rivers also eliminates seasonal discharge and can remove critical life history cues for aquatic invertebrates (Power et al. 1988).

Suspended sediments primarily reduce photosynthetic efficiency in phytobenthic communities (Davies-Colley et al. 1992), and may also remove standing stock by scouring (Alabaster & Lloyd 1982, Duncan & Blinn 1989). Standing mass and biodiversity of benthic macroinvertebrate communities are reduced by suspended sediments through scouring, reductions in feeding efficiency, and interference with gas exchange (Culp et al. 1986, Newcombe & MacDonald 1991, Quinn et al. 1992). Ross and Pieterse (1994) reported a significant relationship between discharge and suspended sediment loads in the Vaal River, South Africa.

Steady thermal regimes in low order, heavily canopied streams commonly reduces the biodiversity of aquatic insects (Vannote et al. 1980). Likewise, the lack of seasonally variable temperatures in the tailwaters of dams restricts the biodiversity of macroinvertebrate communities because aquatic insects commonly

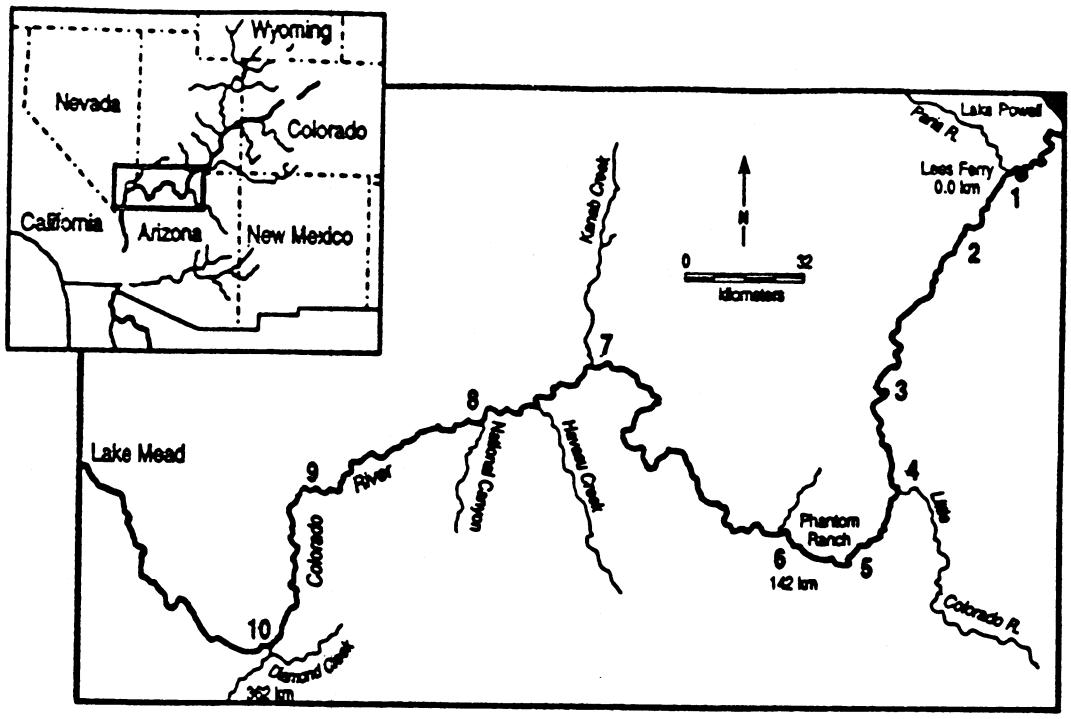
use thermal cues to initiate critical stages in their life history (Vannote & Sweeney 1980, Ward and Stanford 1983). The biodiversity of tailwater periphyton communities is also influenced by thermal regimes (Blinn et al. 1989)

METHODS

Sampling was conducted at three transects 30 m apart in each habitat type (Fig. 1). Peterson or Petit Ponar dredges were used in the fine sediment pools 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 zone of fluctuation (approximately 280 $m^3 s^{-1}$), and upper littoral (566 $m^3 s^{-1}$). Six cobble and twelve pool samples were taken for abundance and biomass determinations. Cobble bar collections were taken at the lowest water flow with three paired samples in the lower and mid-littoral zones. Single samples were collected in the varial zone (zone of fluctuation); at waters edge and the upper littoral zone. Tributary collections were made with a modified Hess (0.049 m^2), because of high aquatic insect densities. 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.

January and June collections were preceded by low to medium volume discharge regimes, while March and September were preceded by medium to high volume discharge regimes. Interim flow (IF) criteria includes a minium 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 $m^3 s^{-1}$. Low flow months (<600,000 af released) had a daily fluctuation limit of 142 $m^3 s^{-1}$ and mean daily flow of < 286 $m^3 s^{-1}$. Moderate flow months (600,000 - 800,000 af released) had a daily fluctuation limit of 170 $m^3 s^{-1}$ and mean daily flow of 286-380 $m^3 s^{-1}$. High flow months (>800,000 af released) had a daily fluctuation limit of 227 $m^3 s^{-1}$ and mean daily flow of >380 $m^3 s^{-1}$. Ramping rates were the same for all discharge months; 71 $m^3 s^{-1}$ up and 42 $m^3 s^{-1}$ down (U.S.B.R. 1994). Research flows (RF) from June, 1990 to August 1991, ranged from 142-930 $m^3 s^{-1}$ with variable ramping rates and constant flows (Patten 1991).

The following water quality measurements were made with a Hydro-Lab Scout II® at the time of each benthic sampling: water temperature (°C), specific conductance (mS), dissolved oxygen (mg L^{-1}), pH and total suspended solids (ppt). Water transparency was measured with a Secchi disk. Water from a spate



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

that occurred on 20 August, 1994, at approximately one km below Glen Canyon Dam was analyzed on a Technicron Auto Analyzer for nitrate, nitrite, ammonia, ortho-phosphate and total phosphorus (mg L^{-1}).

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.

Sediment samples (ca. 500 g) were taken along a cross section of each site using a Peterson and/or Petite Ponar dredge. These samples were oven-dried (60°C) to constant weight and sieved for % particle size using the Wentworth scale: gravel, very coarse sand, coarse sand, very fine sand, and silt.

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 constant mass. Ash-free dry mass (AFDM) conversions were estimated from dry weight to AFDM regression equations (Table 1). Tributary collections of macroinvertebrates were processed as outlined above and sorted into the following taxonomic categories: Coleoptera, Ephemeroptera, Heteroptera, Megaloptera, Odonata, Plecoptera, Trichoptera, and miscellaneous macroinvertebrates.

We studied the ecology of the biting black-fly, Simulium arcticum, by assessing population density and life stages at nine cobble stations; the Lees Ferry and Paria cobble sites rarely support black-fly larvae and were therefore omitted. Thirty cobbles were sampled for larvae and viable pupal cases. Cobble measurements were taken for approximate volumetric calculations.

Quality Control and Data Recovery: Every tenth sample processed in the laboratory was accessed for accuracy by a technician (n = 150). All initial and reduced data are subject to 100% hard copy evaluation by technicians. 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 (AFDM estimates) and multiple response variables (physical parameters) for significant temporal and spatial trends. Pearsons correlation analyses with Bonferroni probability adjustment were used to analyze the relationships among biotic categories and between abiotic variables. Seasonal calculations were based on pooled values for similar collection months.

Table 1. Regression equations used to convert taxonomic categories from dry mass (DM) to ash-free dry mass (AFDM).

Lumbriculids AFDM= 0.73525(DM)-0.00123	F=2015.8	p<0.0001	R^2=0.959	N= 89
Gammarus lacustris AFDM= 0.69989(DM)-0.00053	F=21621.8	p<0.0001	R^2=0.999	N=300
Oligochaeta AFDM= 0.76251(DM)-0.00002	F=53800	p<0.0001	R^2=0.997	N=163
Simuliid AFDM= 0.59603(DM)+0.00011	F=2681.3	p<0.0001	R^2=0.986	N=41
Chironomid AFDM= 0.59603(DM)-0.00005	F=6781.9	p<0.0001	R^2=0.967	N=230
Gastropods AFDM= 0.23328(DM)+0.00015	F=4941.6	p<0.0001	R^2=0.963	N=191
Misc. Macroinvertebrates AFDM= 0.60774(DM)+0.00044	F=2681.3	p<0.0001	R^2=0.989	N=53
Cladophora glomerata AFDM= 0.35606(DM)+0.00048	F=8336.6	p<0.0001	R^2=0.934	N=593
Detritus AFDM= 0.45363(DM)+0.02130	F=2045.9	p<0.0001	R^2=0.874	N=298
Oscillatoria spp. AFDM= 0.14839(DM)-0.08257	F=366.6	p<0.0001	R^2=0.514	N=348
Misc. Algae/Macrophytes AFDM= 0.37312(DM)+0.00179	F=478.5	p<0.0001	R^2=0.875	N=109

All calculations were performed with SYSTAT computer software on ln+1 transformed data (Version 5.1, Wilkinson 1989).

RESULTS AND DISCUSSION

WATER QUALITY VARIABLES

Water quality variables (temperature, specific conductance, dissolved oxygen (DO), pH and Secchi depth) varied significantly by collection site, trip, and season, (Table 2, Figs. 2-4).

Constant water temperatures in the Colorado River through Grand Canyon are a function of the hypolimnetic release of water from Lake Powell at Glen Canyon Dam (GCD) and the incised channel creating a river with reduced surface area and limited exposure to solar radiation. Water temperature increased with distance downriver regardless of season, with seasonal variability increasing downstream (Fig. 2A). Lees Ferry (RKM 0.0) has the coldest and most constant water temperature (9°C, SE ±0.35), while Spring Canyon (RKM 327.2) is the warmest (14.3°C, SE ±1.3) and most variable (Fig. 2A). The annual average river temperature of the Colorado River through Glen and Grand Canyons is 11°C (SE ±0.1). Highest benthic species richness coincides with peak June water temperatures in the lower Canyon. The thermal constancy of the water in the Colorado River likely reduces species richness by eliminating developmental cues (Vannote and Sweeney 1980).

Specific conductance remained relatively constant throughout most of the river during our study period, but increased below the confluence of the Little Colorado River (LCR, RKM 99) during low flows (Fig. 2B). Conductivity averaged 0.89 mS (SE ±0.02) at Lees Ferry (RKM 0.0), and increased to 0.99 mS, (SE ±0.03) below LCR and remained in that range throughout the remainder of the river. Dissolved ion concentrations at Granite Park (RKM 334) were only 0.75 mS (SE ±0.01) during the January, 1993 LCR flood (~950 m^3 s^{-1}) due to the pulse of meteoric water.

Dissolved oxygen (DO) concentrations increased downstream, but decreased slightly in the summer below National Canyon (RKM 166; Fig. 3A). Water released from GCD averaged 8.2 mg L^{-1} (SE ±0.45) DO at Lees Ferry and 9.3 mg L^{-1} (SE ±0.23) DO downstream at Diamond Creek (RKM 360). Downstream increases in DO are likely related to aeration in rapids, and are probably sufficiently near saturation to have miminal influence on the benthos.

Hydrogen-ion concentrations (pH) increased slightly downstream and varied seasonally. Although some variability was noted, pH values increased slightly

Table 2. MANOVA table of water quality parameters collected quarterly during interim flows from the Colorado River through Grand Canyon from September 1992 through June 1994. Predictor variables include collection site (Fig. 1), trip (n = 8) and season (2 trips/season). Response variables include: water temperature (°C), specific conductance (mS), pH, dissolved oxygen (mg L^{-1}), and Secchi depth (m).

Source	Wilks' Lambda	Approximate F Statistic	df	p	Univariate Significance
Site	0.02	51.9	126,7186	0.000	All 0.000
Trip	0.30	204.4	5,446	0.000	All 0.000
Season	0.57	154.4	6,1238	0.000	All 0.000

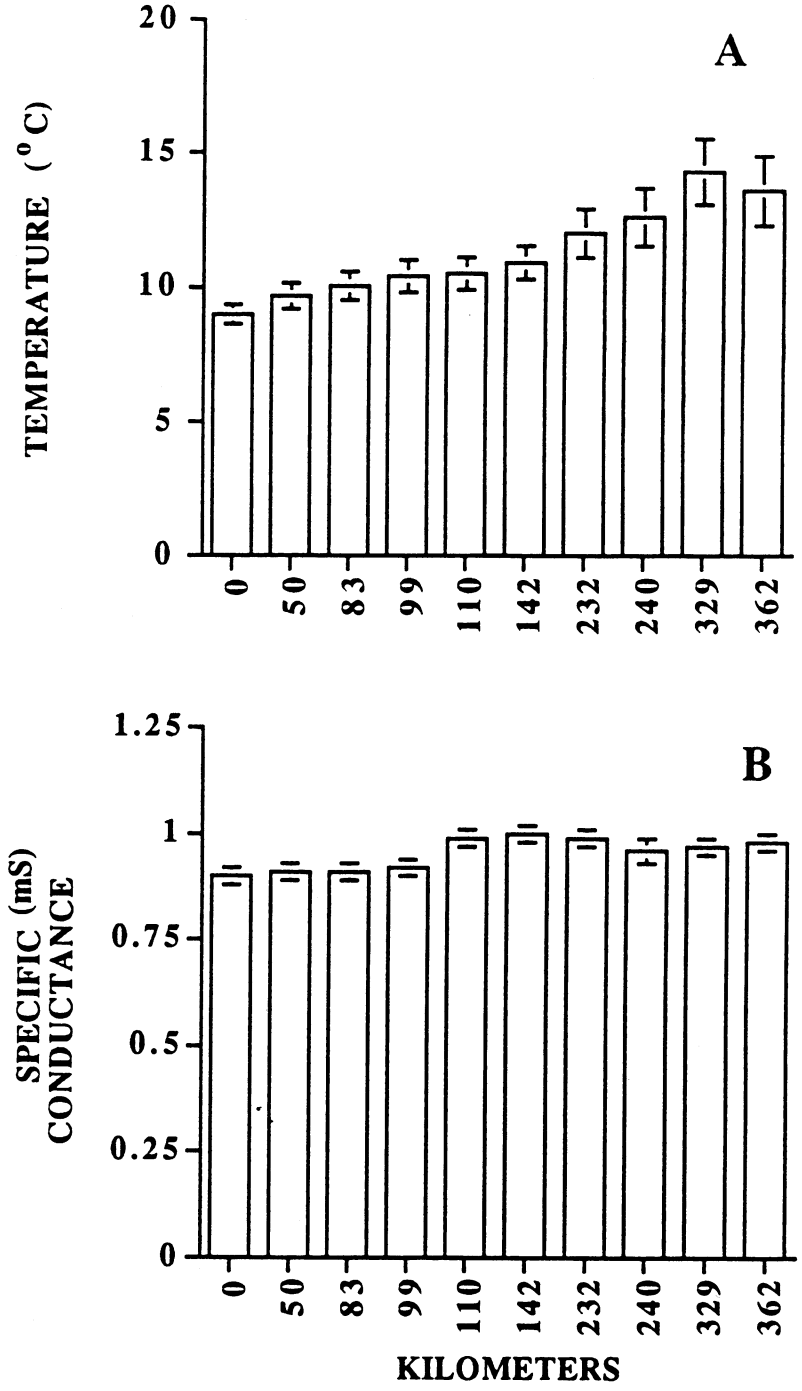


Figure 2. Average water temperature (A) and specific conductance (B) at collection sites in the Colorado River corridor between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

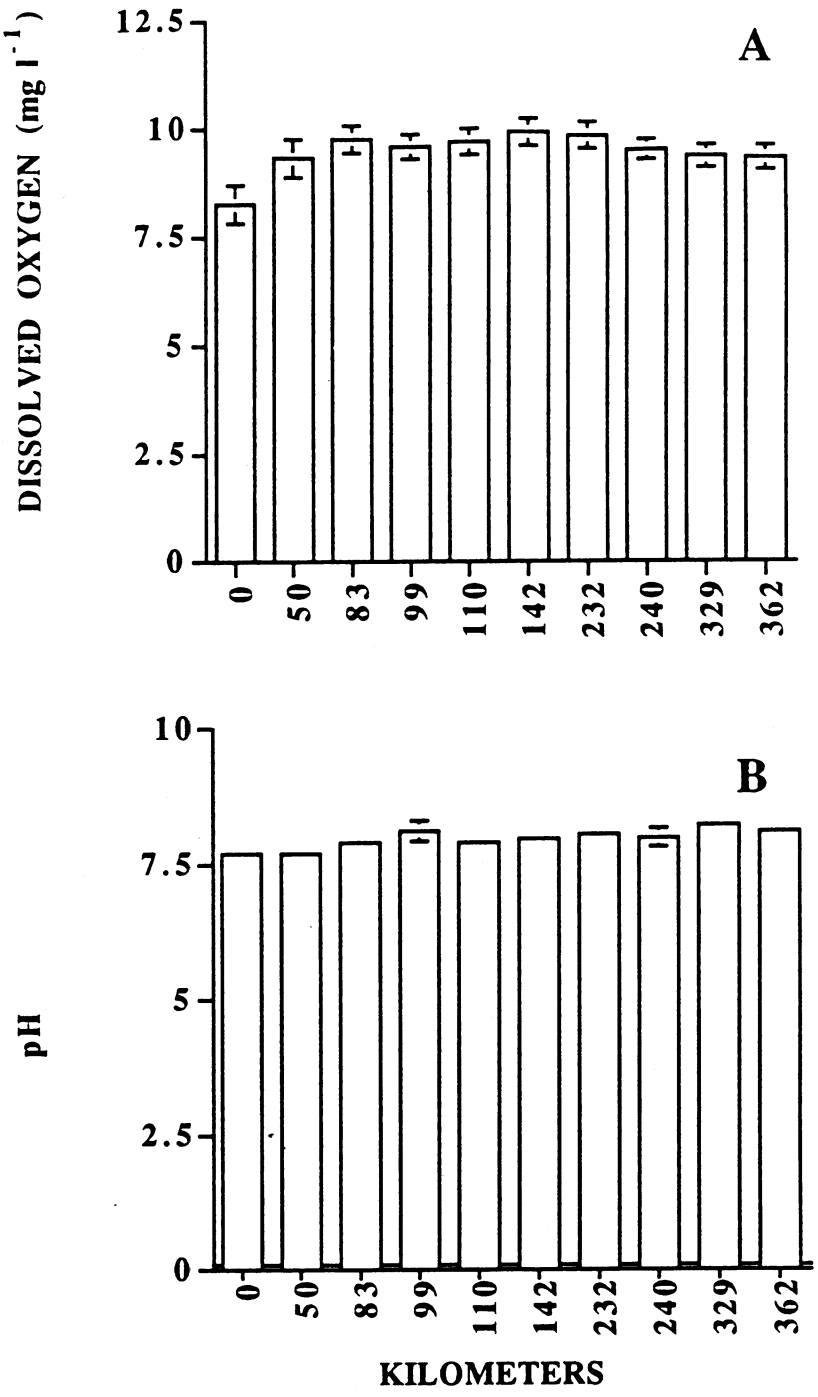


Figure 3. Average dissolved oxygen (A) and pH (B) at collection sites in the Colorado River corridor between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

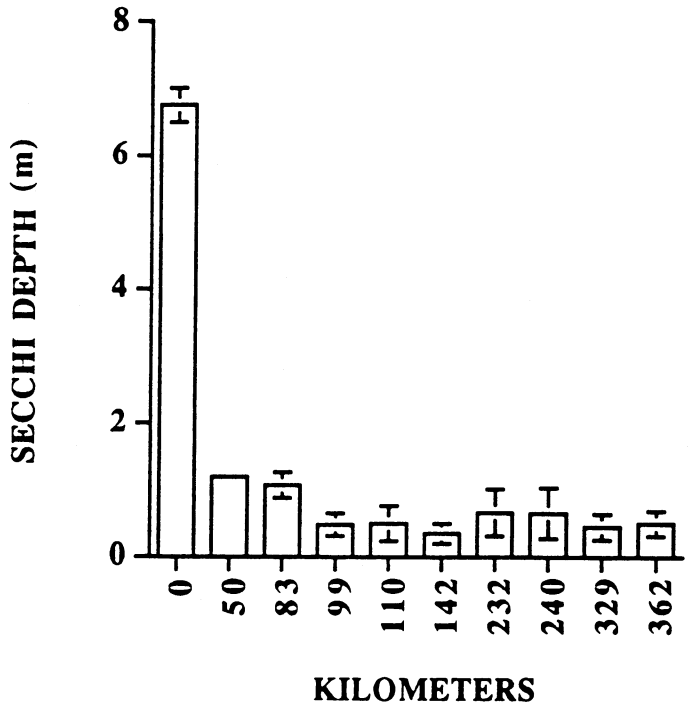


Figure 4. Average Secchi depths at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and and June 1994. Error bars represent ±1 S.E.

from an average of 7.7 (SE ±0.05) at Lees Ferry to 8.1 (SE ±0.5) at Diamond Creek (Fig. 3B).

Secchi depth (water transparency) decreased downstream and changed seasonally. Secchi depths were highest at Lees Ferry (6.75 m, SE ±0.25), decreased abruptly at RKM 50 (1.2 m), and remained low throughout the Canyon (Fig. 4). Despite the LCR floods in 1993, water transparency was 3-fold greater during Interim Flows (IF) than during GCES Research Flows (RF) (1990-1991).

SEDIMENT ANALYSES

Sediment composition was significantly altered within pool habitats during IF and varied significantly by depth (Wilk's Lambda $F_{5,408} = 4.4$, $p < 0.001$) and reach width (Wilk's Lambda $F_{5,409} = 5.2$, $p < 0.001$). Percent composition of very coarse and coarse sand and very fine sand were positively related to depth, while silt was negatively correlated with depth ($p < 0.04$). Proportions of gravel and very coarse sand increased in wide reaches, while very fine sand increased in narrow reaches ($p < 0.001$). Sediment composition did not vary significantly by transect within a site, seasonally or by discharge. During RF, gravel and very fine sand made up a higher percentage of the sediment than during IF; however, proportions of silt increased during IF (Fig. 5).

RF flows created a pool habitat that supported the highest density of life near the up-stream end of a pool/eddie complex where organic material and silt accumulated (Blinn et al. 1992). Under IF this area was built-up to produce sand islands at low water stages (<280 m^{-3}) and compacted the sediment to the point that additional weight had to be added to the Petersen dredge for dependable collecting (total weight 40 kg). This situation became so problematic during collections at Spring Canyon that this site was moved one km downstream to a larger pool that was still navigatable. The accumlation of sand has created a productive backwater the entire length of our transects. Riffle habitats have also accumulated sediment reducing the area of hard substrate available for colonization and requiring transects to be moved up river into less impacted areas.

DISTRIBUTION OF AQUATIC BENTHOS

Ash-free dry mass (AFDM) of benthic communities in the Colorado River varied significantly with dam-related, geomorphic, and temporal variables (Table 3). Significant decreases in benthic plant and animal mass occurred below the Paria River (RKM 1.5) and the Little Colorado River LCR, (RKM 98.6) in a stairstep manner as previously reported by Blinn et al. (1992). Glen Canyon (26 km) accounted for 69% of the algal and 50% of the macroinvertebrate mass collected

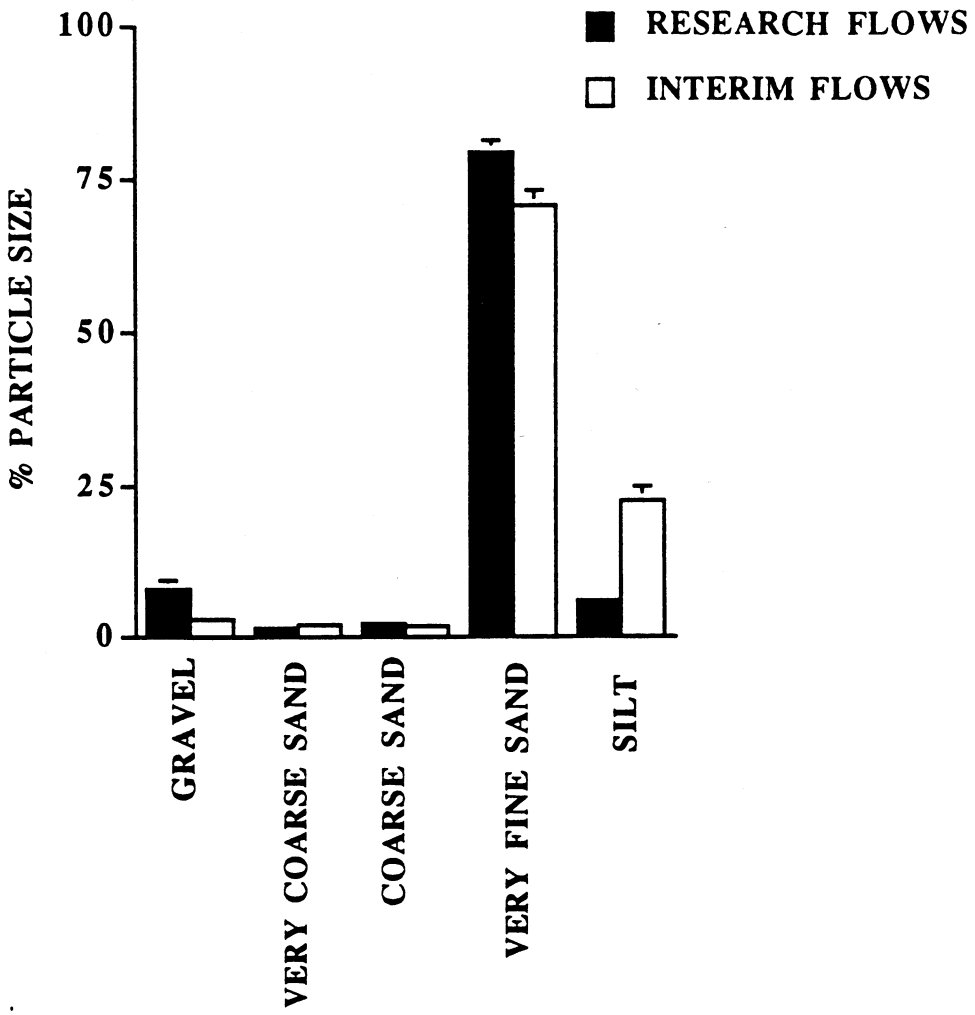


Figure 5. Comparison of particle sizes collected from pool habitats in the Colorado River through Grand Canyon comparing research flow (RF; 1991) to interim flow (IF; 1992-1994) data. Gravel and very fine sand composed a significantly higher ($p < 0.01$; $n = 412$) percentage of pool sediments during RF; however, silt deposition increased significantly during IF ($p > 0.01$; $n = 412$). No significant change was detected for distribution of coarse or very coarse sand.

Table 3. MANOVA table of abiotic predictor variables on response variables of biotic categories collected from the Colorado River through Grand Canyon from September, 1993 through June, 1994. Predictor variables include site, habitat, collection trip, season, and collection stage (< 300 $m^3 s^{-1}$). Taxonomic categories are 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). Predictor variables were analyzed as AFDM m^{-2} ln+1 transformed data. Only significant univariate response variables are listed ($p<0.01$).

Source	Wilks' Lambda	Approximate F Statistic	df	p	Significant Univariate
Site	0.25	8.9	231,>10000	0.000	C,O,A,D,M, G,S,B,L,T,
Habitat	0.75	42.4	11,1413	0.000	C,O,D,M, S,B,L,T,
Collection Trip	0.83	3.4	77,8438	0.000	C,O,A,D,M, S,L,T
Season	0.92	3.2	33,4157	0.000	C,O,M,S,L,
Zone	0.86	6.4	33,4157	0.000	C,O,A,D,M, G,S,B,L,T,I,
Reach Width	0.89	15.0	11,1413	0.000	C,A,M, G,S,L,T,

throughout the 360 km section of the river. Sites within Marble and Grand Canyons contributed 18% and 41% and 13% and 9%, respectively, of algal and macroinvertebrate AFDM (Figs. 6 & 7). This implies that Glen Canyon contributes 70% of the total benthic standing mass in only 7% of the total distance within the 360 km study area. Wide reaches are more productive than narrow, but this geomorphic difference was less during RF than IF.

PRIMARY PRODUCERS

Cladophora glomerata AFDM was consistently higher in riffle habitats as compared to pool habitats, corroborating results during RF. However, under IF C. glomerata AFDM increased downstream in riffle habitats due to higher water clarity (Fig. 8). A 27% increase in C. glomerata standing mass was detected in riffles through Marble Canyon to Tanner cobble (2.5 g m^{-2} AFDM) as compared to RF collections (0.9 g m^{-2} AFDM; Blinn et al. 1992). Pearson correlation analyses indicated that C. glomerata AFDM was positively related to Secchi depth in pool and riffle habitats and negatively correlated to specific conductance in riffles (Tables 4 & 5). Both of these relationships result in a punctuated decrease in C. glomerata standing mass due to tributary input of sediment.

Pearson correlation analyses of primary and secondary producer biomass in pools and riffles indicated C. glomerata was positively correlated with all macroinvertebrate groups in riffles ($p<0.001$; Table 6). In pool habitats chironomids, Gammarus lacustris, gastropods, and tubificid biomass were positively related to C. glomerata standing crop ($p<0.001$; Table 6). Shannon et al. (1994) demonstrated that the epiphytic diatom assemblage on C. glomerata is the preferred food of G. lacustris and these correlations further support findings for other grazing taxa in riffles. Other feeding guilds must also occur in greatest abundance on C. glomerata. Cladophora glomerata does not colonize soft substrates present in pools downstream from the Paria River, therefore the C. glomerata in the pools is likely a result of deposition or snagging of drifting C. glomerata packets on roots or beaver cuttings.

System-wide cross-channel C. glomerata distribution on cobbles increased in mean biomass with depth; <28 m^3 s^{-1}, 5.7 g m^{-2} AFDM; 140 m^3 s^{-1}, 2.5 g m^{-2} AFDM; 280 m^3 s^{-1}, 1.03 g m^{-2} AFDM. Cladophora glomerata was not collected in the varial zone above the 300 m^3 s^{-1} stage, except in large rapids where sporadic colonization was noted in the splash zone.

Cladophora glomerata is the keystone alga in the Colorado River and provides considerable autochthonous energy to the river. Data on C. glomerata collected over the past four years have shown wide variability in biomass, but a general increase in AFDM during IF (Fig. 9). September collections of C. glomerata are

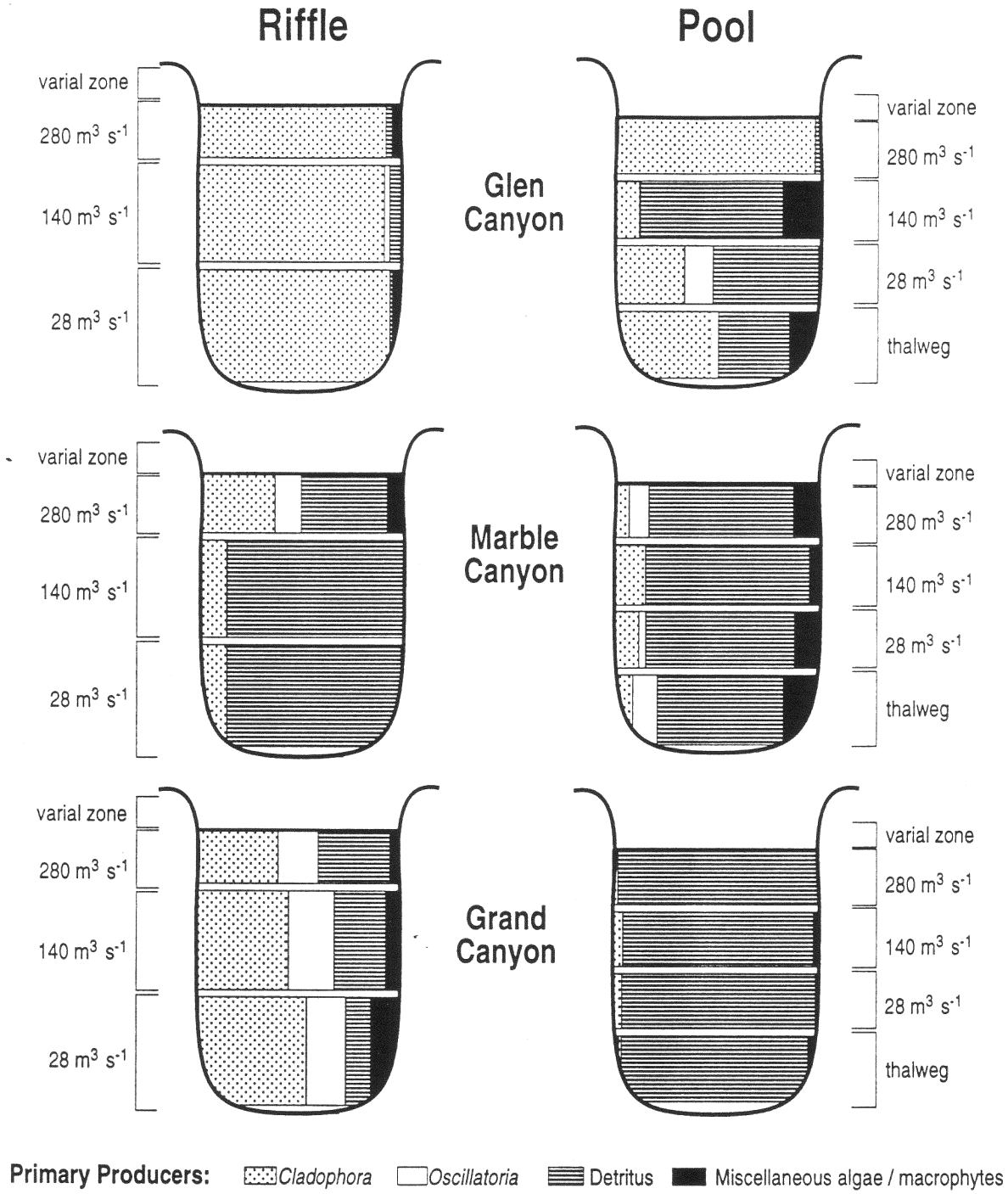


Figure 6. Percent composition of primary producers in riffle and pool habitats at different stages (280 $m^3 s^{-1}$, 140 $m^3 s^{-1}$ and 28 $m^3 s^{-1}$) for seasonal collections from September 1992 through June 1994 in the Colorado River through Grand Canyon. Study sites were divided into three major reaches separated by the Paria and Little Colorado Rivers (Fig. 1); Glen Canyon (included site 1), Marble Canyon (included sites 2-4 and Two-Mile Wash) and Grand Canyon (included sites 5-10). No primary producers were collected in the upper varial zone.

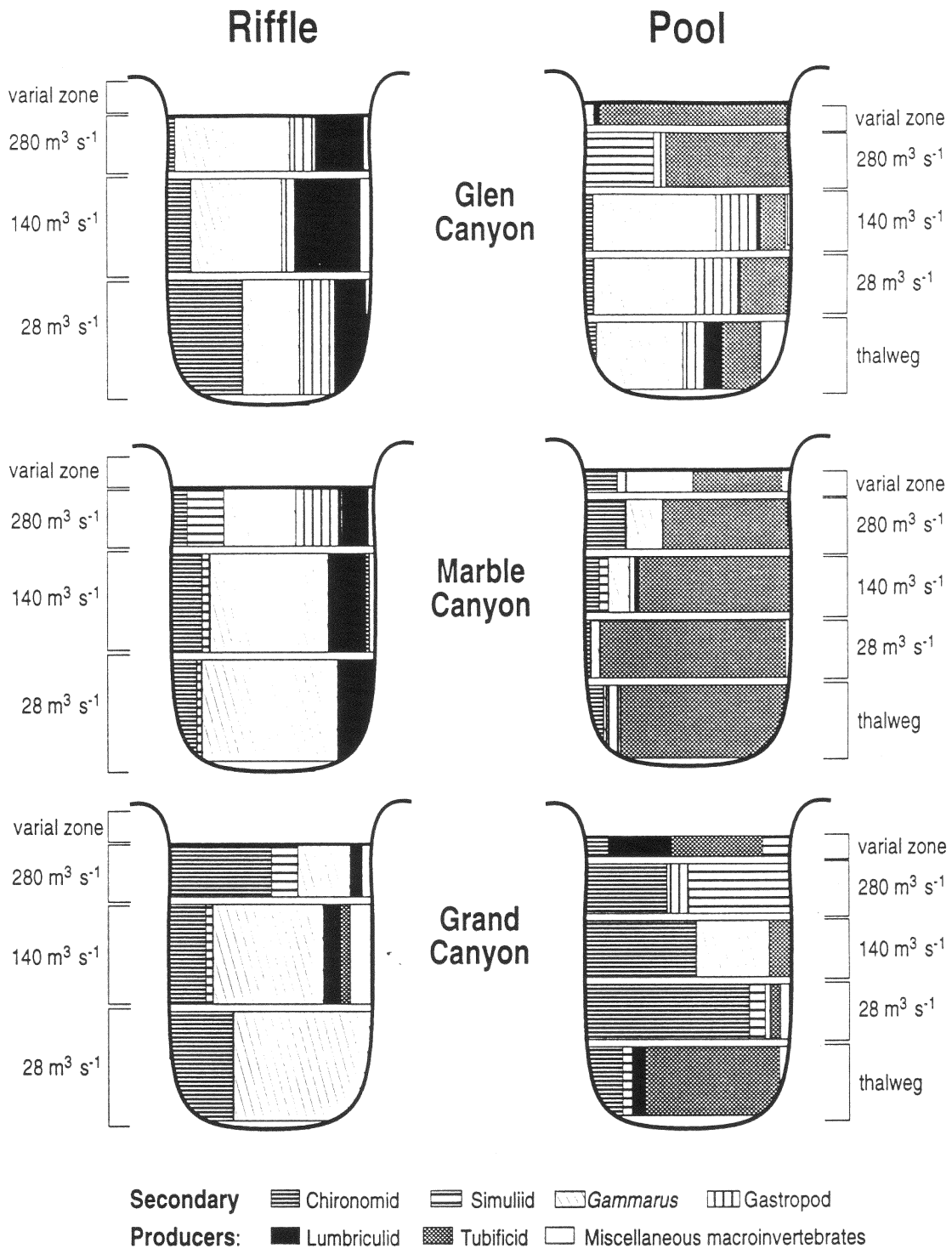


Figure 7. Percent composition of secondary producers in riffle and pool habitats at different stages (280 $m^3 s^{-1}$, 140 $m^3 s^{-1}$, and 28 $m^3 s^{-1}$) for seasonal collections from September 1992 through June 1994 in the Colorado River through Grand Canyon. Study sites were divided into three major reaches separated by the Paria and Little Colorado Rivers (Fig. 1); Glen Canyon (included site 1), Marble Canyon (included sites 2-4 and Two-Mile Wash) and Grand Canyon (included sites 5-10).

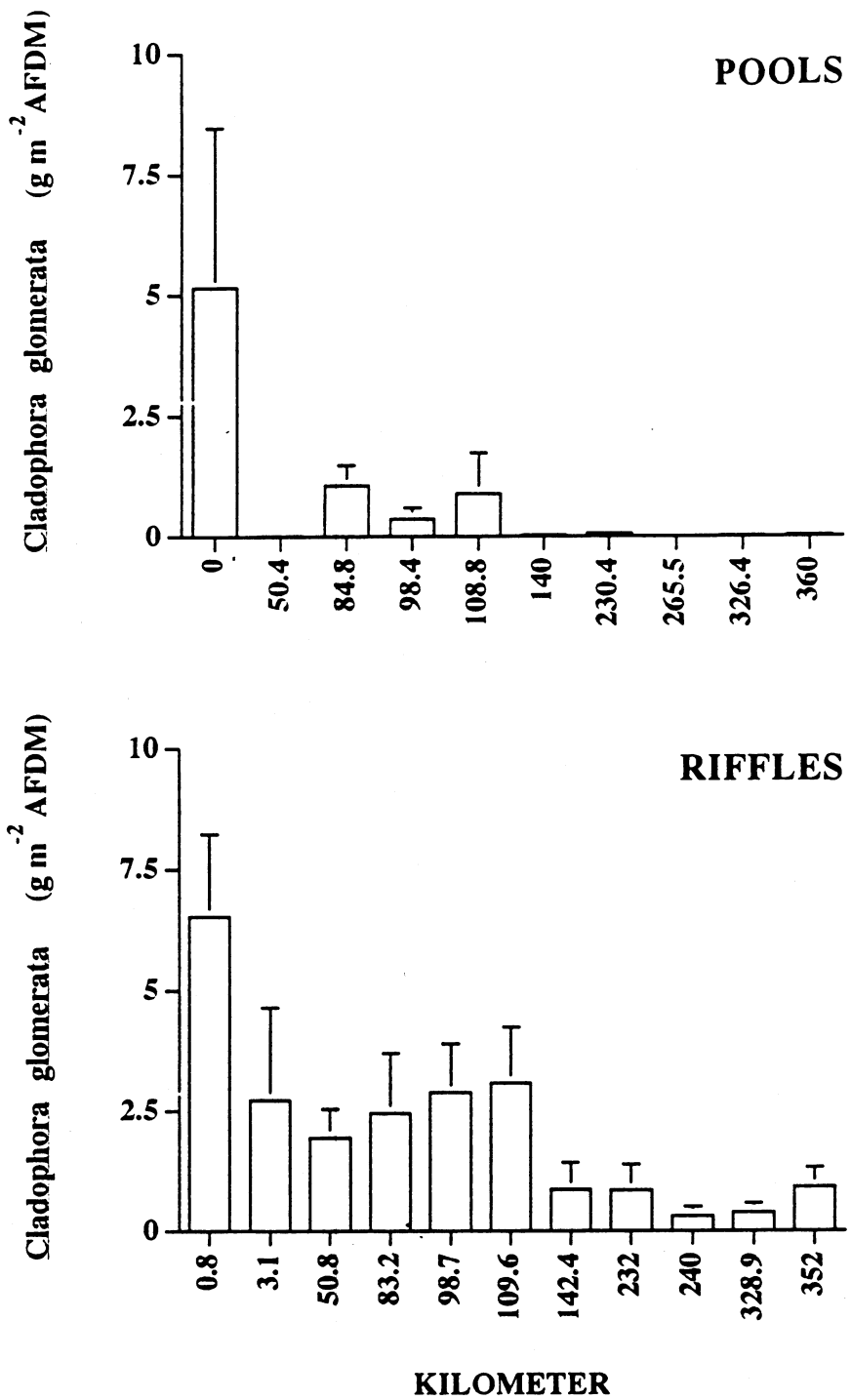


Figure 8. Average ash-free dry mass (AFDM) for Cladophora glomerata in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

Table 4. Pearson correlation matrix with Bonferroni probability adjustments between primary and secondary producers and abiotic factors from pools in the Colorado River through Grand Canyon from September, 1992 through June, 1994. Abiotic parameters include: specific conductance (C), dissolved oxygen (DO), temperature (T), pH (PH), Secchi depth (SD), and depth (D). No correlations were detected between food base components and velocity, transect and pH. Analyses were completed on AFDM m^{-2} ln+1 transformed data. Only significant correlations were reported, and both positive (+) and negative (-) responses are indicated.

	Abiotic Factors				
Primary & Secondary Producers	C	DO	T	SD	D
Cladophora				<0.0001 (+)	
Oscillatoria				<0.0001 (+)	
Misc. Algae Macrophytes	<0.01 (-)			<0.0001 (+)	
Detritus					<0.01 (+)
Chironomids				<0.0001 (+)	
Gammarus		0.04 (-)			
Gastropods				<0.0001 (+)	
Simuliids					
Lumbriculids				<0.0001 (+)	
Tubificids			0.008 (-)		

Table 5. Pearson correlation matrix with Bonferroni probability adjustments between primary and secondary producers and abiotic factors in riffles in the Colorado River through Grand Canyon from September, 1992 through June, 1994. Abiotic parameters include: specific conductance (C), dissolved oxygen (DO), temperature (T), pH (PH), Secchi depth (SD), and depth (D). No correlations were detected between food base components and transect and no abiotic correlation was detected with miscellaneous algae/macrophytes, simuliids, tubificids, and miscellaneous macroinvertebrates. Analyses were completed on AFDM m^{-2} ln+1 transformed biotic data. Only significant correlations were reported, and both positive (+) and negative (-) responses are indicated.

	Abiotic Factors						
Primary & Secondary Producers	C	DO	T	PH	SD	D	V
Cladophora	0.004 (-)				<0.0001 (+)		
Oscillatoria			0.009 (+)				0.002 (+)
Detritus						0.002 (+)	0.04 (+)
Chironomids		<0.0001 (+)			<0.0001 (+)		
Gammarus			0.04 (-)	0.003 (-)			
Gastropods					<0.0001 (+)		
Lumbriculids					<0.0001 (+)		

Table 6. Pearson correlation matrix with Bonferroni probability adjustments for primary and secondary producers from riffles in the Colorado River through Grand Canyon from September, 1992 through June, 1994. Analyses were completed on AFDM m^{-2} ln+1 transformed data. Only significant response variables are reported and all were positively correlated.

	Primary Producers			
Secondary Producers	Cladophora	Oscillatoria	Miscellaneous Algae/Macrophytes	Detritus
Chironomids	<0.0001			
Gammarus	<0.0001			<0.0001
Gastropods	0.006			
Simuliids	0.004		<0.0001	
Lumbriculids	<0.0001			
Tubificids	<0.0001			<0.0001
Miscellaneous Macroinvertebrates	<0.0001			<0.0001

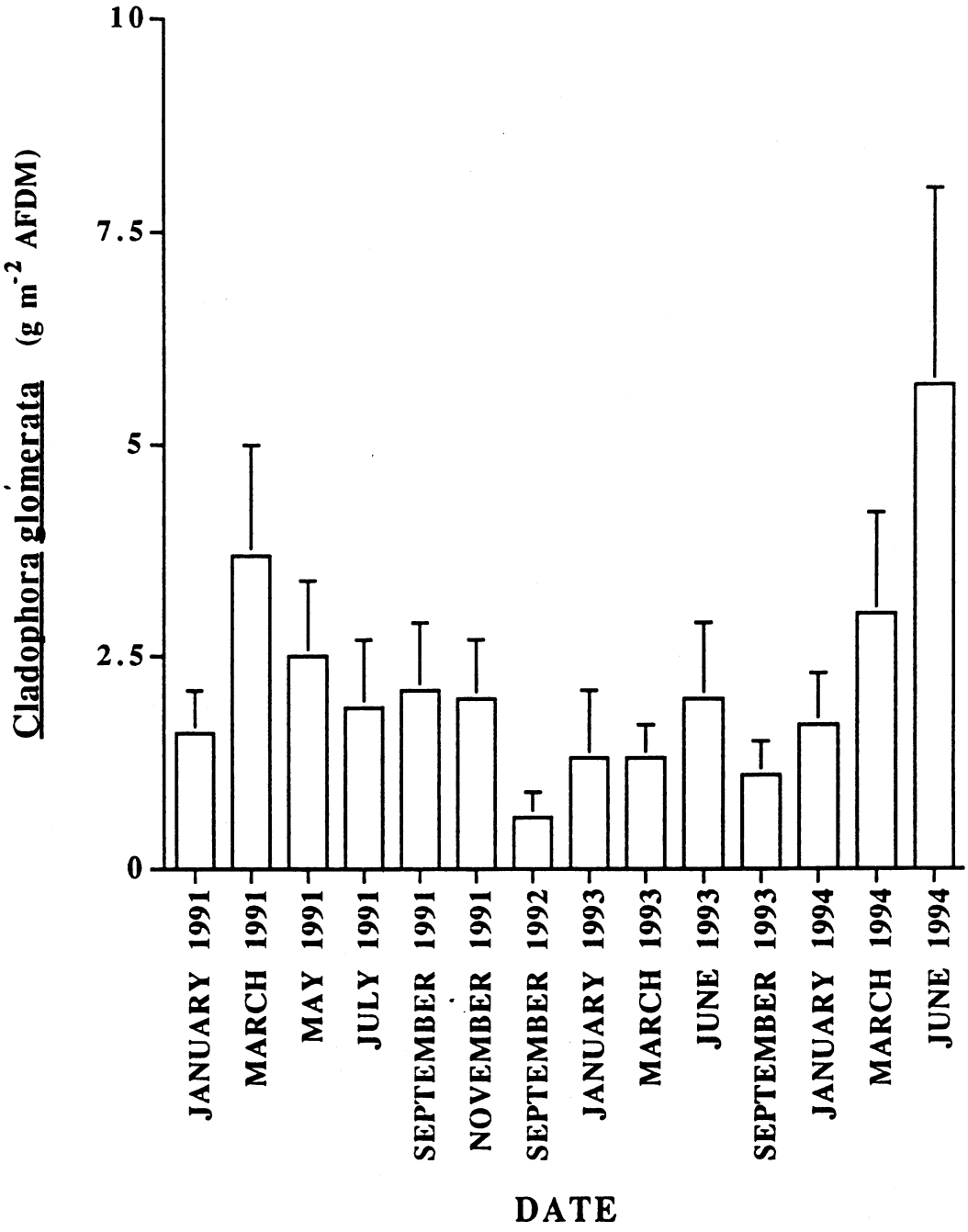


Figure 9. System-wide Cladophora glomerata ash-free dry mass (AFDM) collected with a Hess from riffle habitats in the Colorado River through Grand Canyon National Park. Biomass was averaged from 11 stations for each collection trip. Error bars represent ± 1 S.E.

reduced in the lower canyon following the peak releases during July and August. Cladophora glomerata AFDM in Glen and Marble Canyons remain consistent suggesting that river regulation increased suspended sediments from bed load accumulation in the lower canyon. September collections were made following dry summer periods eliminating the impact of tributary input. Future monitoring should continue in order to evaluate the role of dam management and climatic conditions on this keystone alga.

During IF, Oscillatoria AFDM increased downstream and remained consistently higher in riffle habitats, but Oscillatoria AFDM increased in pool habitats (especially Nankoweap eddie) as compared to RF (Fig. 10). Colonization of soft sediment by Oscillatoria occurred along the littoral zone in recently formed backwater habitats at Nankoweap (see sediment analyses section). Pearson correlations for measured abiotic and biotic categories indicated that Oscillatoria biomass was positively correlated with Secchi depth in pools and with temperature and water velocity in riffles (Tables 4 & 5). Oscillatoria in Nankoweap pool is novel because this cyanobacterian is typically associated with turbid water on cobbles. Warm water temperatures may benefit Oscillatoria growth in the river, while other algal taxa are found in the consistently cold tailwaters.

Macroinvertebrates are not generally associated with Oscillatoria in riffles; however, tubificids are positively correlated with Oscillatoria and chironomids are negatively correlated with this alga in pool environments (Tables 6 & 7). Oscillatoria is not a common substratum for macroinvertebrates because it is very compact and has little surface area for colonization and largely lacks epiphytic diatoms. The high tubificid/Oscillatoria relationship at Nankoweap was a sampling artifact, as both reach their highest biomass at this site (Figs. 10 & 16).

System-wide cross-channel distribution of Oscillatoria AFDM on cobbles was negatively correlated with stage: mean Oscillatoria AFDM at <28 $m^3 s^{-1}$ = 0.1 g m^{-2} AFDM; at 140 $m^3 s^{-1}$ = 0.8 g m^{-2} AFDM; and at 280 $m^3 s^{-1}$ = 2.1 g m^{-2} AFDM. Oscillatoria was collected in the varial zone above the 300 $m^3 s^{-1}$ stage, demonstrating a greater tolerance to desiccation than C. glomerata. We suspect motile filaments of Oscillatoria retreat into the fine sand/silt/mucilage matrix and retain water during atmospheric exposure.

Detrital AFDM remained highly variable between riffle and pool habitats throughout the river (Fig. 11). The accumulation of detritus at Lees Ferry is the result of beaver cuttings, which began before RF collections. Correlation analyses between detritus and measured abiotic variables indicated that depth was positively related to detrital mass in both pools and riffles, while water velocity showed a positive correlation to detrital mass in riffles (Tables 4 & 5). Detrital

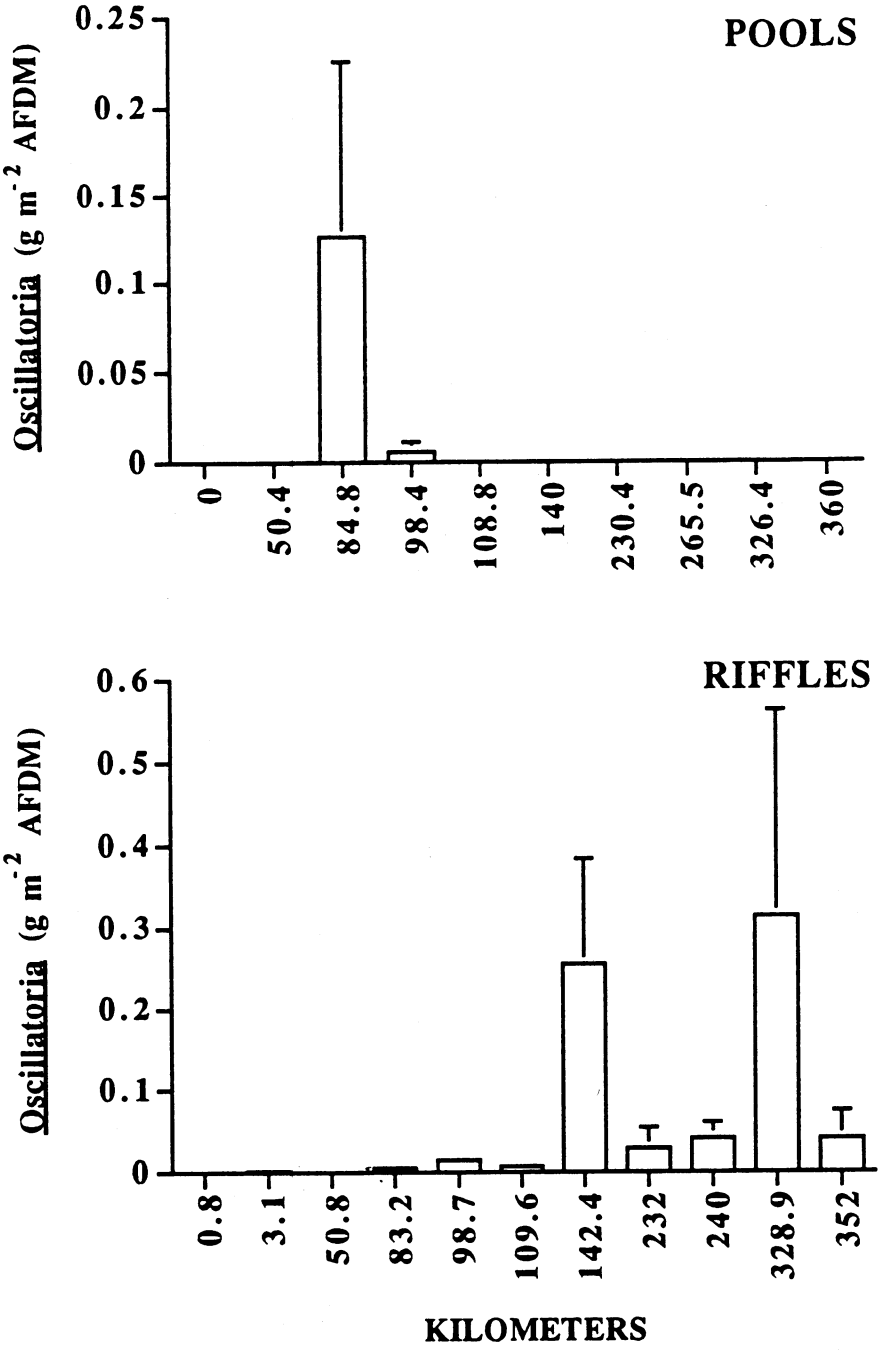


Figure 10. Average ash-free dry mass (AFDM) for Oscillatoria spp. in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

Table 7. Pearson correlation matrix with Bonferroni probability adjustments for primary and secondary producers from pools in the Colorado River through Grand Canyon from September, 1992 through June, 1994. Analyses were completed on AFDM m^{-2} ln+1 transformed data. Only significant response variables are reported, both positive (+) and negatively (-) correlated.

	Primary Producers			
Secondary Producers	Cladophora	Oscillatoria	Miscellaneous Algae/Macrophytes	Detritus
Chironomids	<0.0001(+)	<0.0001 (-)	<0.0001 (+)	<0.0001 (+)
Gammarus	<0.0001(+)		<0.0001 (+)	<0.0001 (+)
Gastropods	<0.0001 (+)		<0.0001 (+)	<0.0001 (+)
Simuliids				
Lumbriculids			<0.0001(+)	
Tubificids	<0.0001(+)	<0.0001 (+)	<0.0001 (+)	<0.0001 (+)
Miscellaneous Macroinvertebrates				

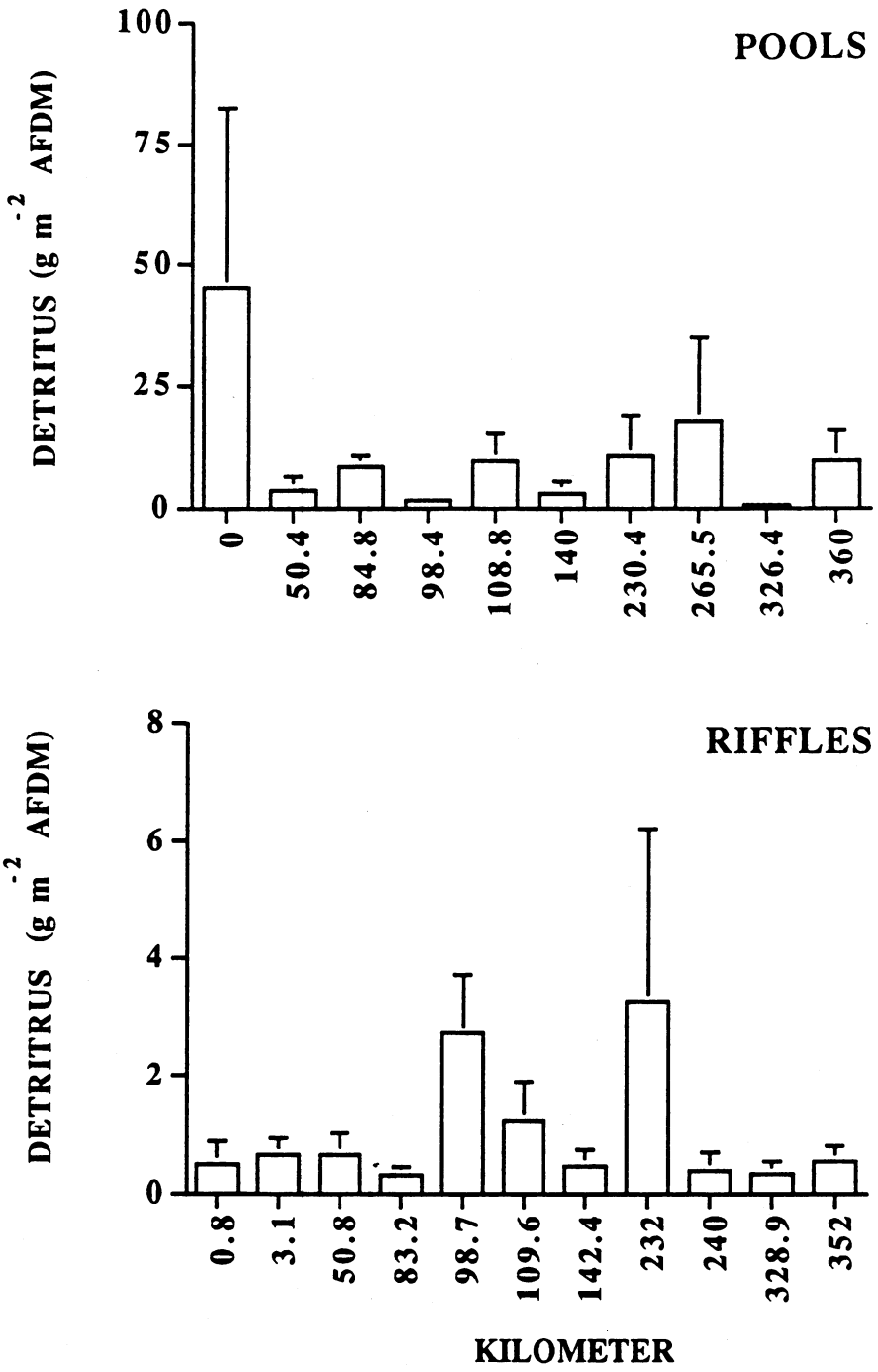


Figure 11. Average ash-free dry mass (AFDM) for detritus in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

material accumulates in deeper areas of pools away from the shore and accumulated sediment. System-wide cross-channel distribution of detritus in pools showed a negative correlation between AFDM and stage; mean detrital AFDM at <28 $m^3 s^{-1}$ = 24.1 g m^{-2} AFDM; at 140 $m^3 s^{-1}$ = 19.0 g m^{-2} AFDM; and at 280 $m^3 s^{-1}$ = 8.8 g m^{-2} AFDM.

Chironomids, G. lacustris, gastropods, and tubificids are all positively associated with detritus in pools, and G. lacustris, tubificids, and miscellaneous macroinvertebrates are also positively associated with detritus in riffles (Tables 6 & 7). These macoinvertebrates may directly consume detritus, but more likely graze on bacteria, fungi, and epiphyton associated with the detrital matter.

Standing mass and diversity of miscellaneous algae and macrophytes (MAM) increased during IF (Table 8; Fig. 12). Potamogeton, Chara, Elodea and Mimulus increased particularly in pool habitats at Lees Ferry and in Lower Marble Canyon. Bryophyte (Fontinalis spp.) AFDM increased in riffle habitats from Nankoweap (RKM 83) to Tanner (RKM 110). Pearson correlation analyses indicated that miscellaneous alga and macrophyte AFDM were positively correlated with Secchi depth (Table 4). This may help explain why these two groups were most prevalent in Glen and Marble Canyons when water was clear as compared to downstream reaches where tributary input increases water turbidity (Figs. 2 & 4).

Pearson correlation analyses also showed a positive correlation between MAM and chironomids, G. lacustris, gastropods, and tubificids in pools and for simuliids in riffles. The relationship in pools likely results from plants creating a favorable refuge from predation and current. We examined Potamogeton stands at the Nankoweap site for epiphyton and macroinvertebrates. Six 0.02 m^2 samples were collected. The ash-free dry mass of epiphyton per dry mass of plant host was 2-fold lower on Potamogeton foliage than that associated with the highly branched filaments of C. glomerata below the Paria River confluence. Only one G. lacustris was found in the Potamogeton samples. These data suggest that Potamogeton is a poor substratum for epiphytes and macroinvertebrates compared to C. glomerata, and therefore plays a lesser role in the food chain for native and exotic fish in the Colorado river. Chara has been shown to support a high abundance of epiphytic diatoms and may explain the positive relationship of some macroinvertebrates with the category of miscellaneous primary producers. Macrophytes have colonized a newly created niche (fine sediments on the channel floor), and should be monitored to see if they encroach upon nearby established C. glomerata beds.

System-wide cross-channel distribution of MAM in pools showed a positive correlation between AFDM and stage; mean MAM AFDM at <28 $m^3 s^{-1}$ =

Table 8. Miscellaneous primary and secondary producers collected in pools and riffles in the Colorado River through Grand Canyon during interim flows from September, 1992 through June, 1994. Bold notations for site numbers (Fig. 1) and season indicate highest densities.

PRIMARY PRODUCER	SITE	SEASON	SECONDARY PRODUCER	SITE	SEASON
Batrachospermum spp.	**1**,2,3,4,6,9	all	Belostomatidae	6,7	summer
Chaetophora spp.	1	all	calanoid copepod	1	all
Chara spp.	1	all	Coleoptera	2,3,9,10	summer
Draparnaldia spp.	1	all	Corixdae	6,7,8	summer
Elodea spp.	**1**,2,4	all	Diptera	1,2,3,6,**7**,8	summer
Equisetum spp.	2,9,10	summer	Ephemeroptera	5,7,10	all
Enteromorpha intestinalis	1,5,6,7,**9**, 10	summer	Hydra	**1**,3	all
			Hydropsychidae	1,6,**7**,8	all
Fontinalis spp.	1,2,**3**,4,5, 6,9,10	spring summer	Gerridae	6,7,8	summer
Microspora sp.	1	all	Naucoridae	6,7,8	summer
Mimulus sp.	3	all	nematode	2,3	fall
Potamogeton pectinatus	**1**,3,4,5,6	all	Ostracod	**1**,2,3	fall winter
			planaria	1,2,**3**,4,5,7	all
Rhizoclonium spp.	1	all			
			Plecoptera	7	winter
Rhodochorton sp.	**1**,2,4,8	spring summer	Tipulidae	5,7	fall
Spirogyra spp.	1	all	Trichoptera	3,4,5,8,9	all
Ulothrix zonata	1	all			

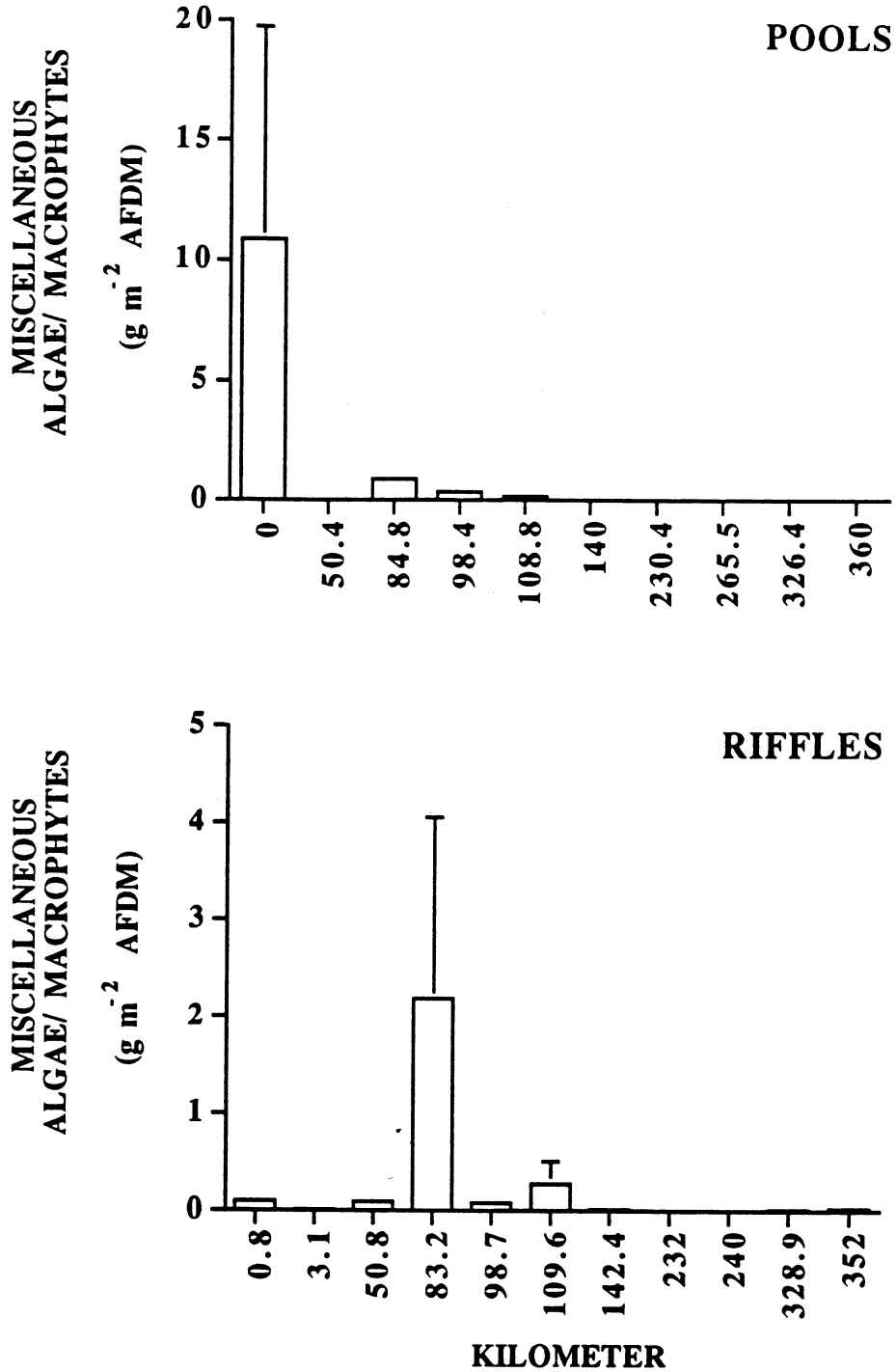


Figure 12. Average ash-free dry mass (AFDM) for miscellaneous algae and macrophytes in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

0.11 g m^{-2} AFDM; at 140 m^3 s^{-1} = 0.11 g m^{-2} AFDM; and at 280 m^3 s^{-1} = 0.27 g m^{-2} AFDM. Only the moss, Fontinalis, was collected in the varial zone above the 300 m^3 s^{-1} stage on cobbles, and in the splash zone of large rapids.

A green tubular/filamentous alga, Enteromorpha intestinalis, was also found below Middle Granite Gorge on hard substrata in the splash zones and was examined for epiphytes in the same manner as Potamogeton. This green alga supported a similarly low epiphyte standing crop and no macroinvertebrates.

SECONDARY PRODUCERS

Chironomid AFDM was consistently higher in riffle habitats compared to pool habitats during IF in accord with RF results. However, chironomid AFDM increased downstream in riffle habitats due to increased C. glomerata cover, and in lower Canyon pool habitats in response to increased deposition of fine sediments (Fig. 13). Increases in chironomids in these diverse habitats likely resulted from different chironomid assemblages with different feeding strategies.

Pearson correlation analyses of chironomid biomass and measured abiotic variables illustrated the positive association of midge larvae with increasing Secchi depth in pools and riffles. Dissolved oxygen (DO) concentrations were also positively associated with midge biomass in riffles. These data support the increased densities of chironomid larvae through Glen and Marble Canyons and are related to low suspended sediment levels and elevated DO concentrations at downriver collection sites.

System-wide cross-channel distribution of chironomids on cobbles showed a negative correlation between standing mass and stage; mean chironomid AFDM at <28 m^3 s^{-1} = 0.12 g m^{-2} AFDM; at 140 m^3 s^{-1} = 0.04 g m^{-2} AFDM; and at 280 m^3 s^{-1} = 0.02 m^{-2} AFDM. Midges were not collected in the varial zone above the 300 m^3 s^{-1} stage.

Simuliid AFDM increased through Marble Canyon to Tanner in riffle habitats, and in pool habitats in lower Grand Canyon, however a decrease in blackfly biomass was observed in riffles within the lower Grand Canyon as compared to RF (Fig. 14). The increased colonization of simuliids in Marble Canyon may be a result of IF allowing the export of particulate and dissolved organic matter from the Glen Canyon tailwaters to be processed and consumed by these filter feeders. Warm river temperatures in the lower canyon may also contribute to up-river and pool habitat shifts in standing biomass of this Nearctic blackfly. Simuliids are rare in Glen Canyon, probably due to the extensive C. glomerata cover of substratum which reduces area for settling by larvae.

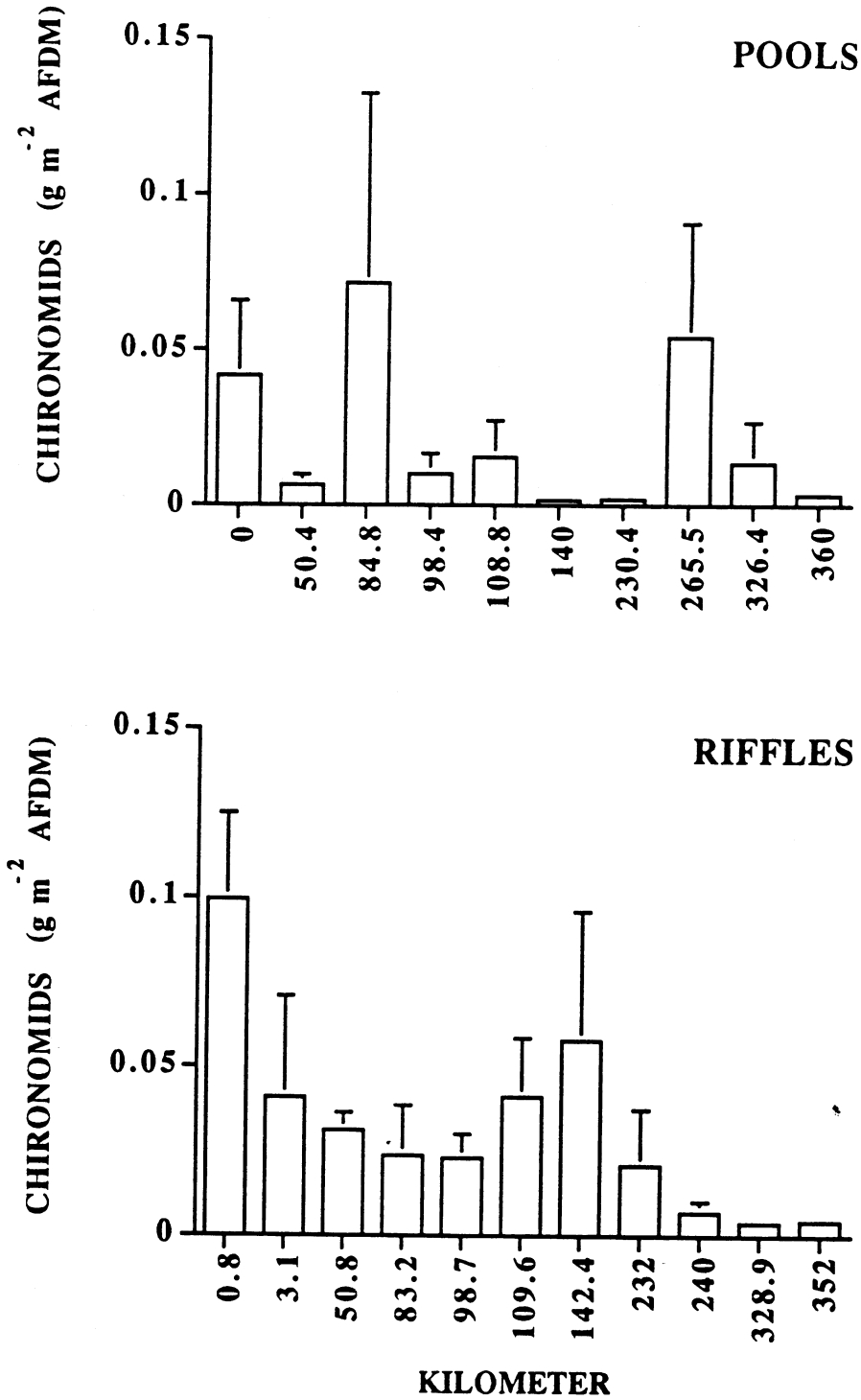


Figure 13. Average ash-free dry mass (AFDM) for chironomids in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

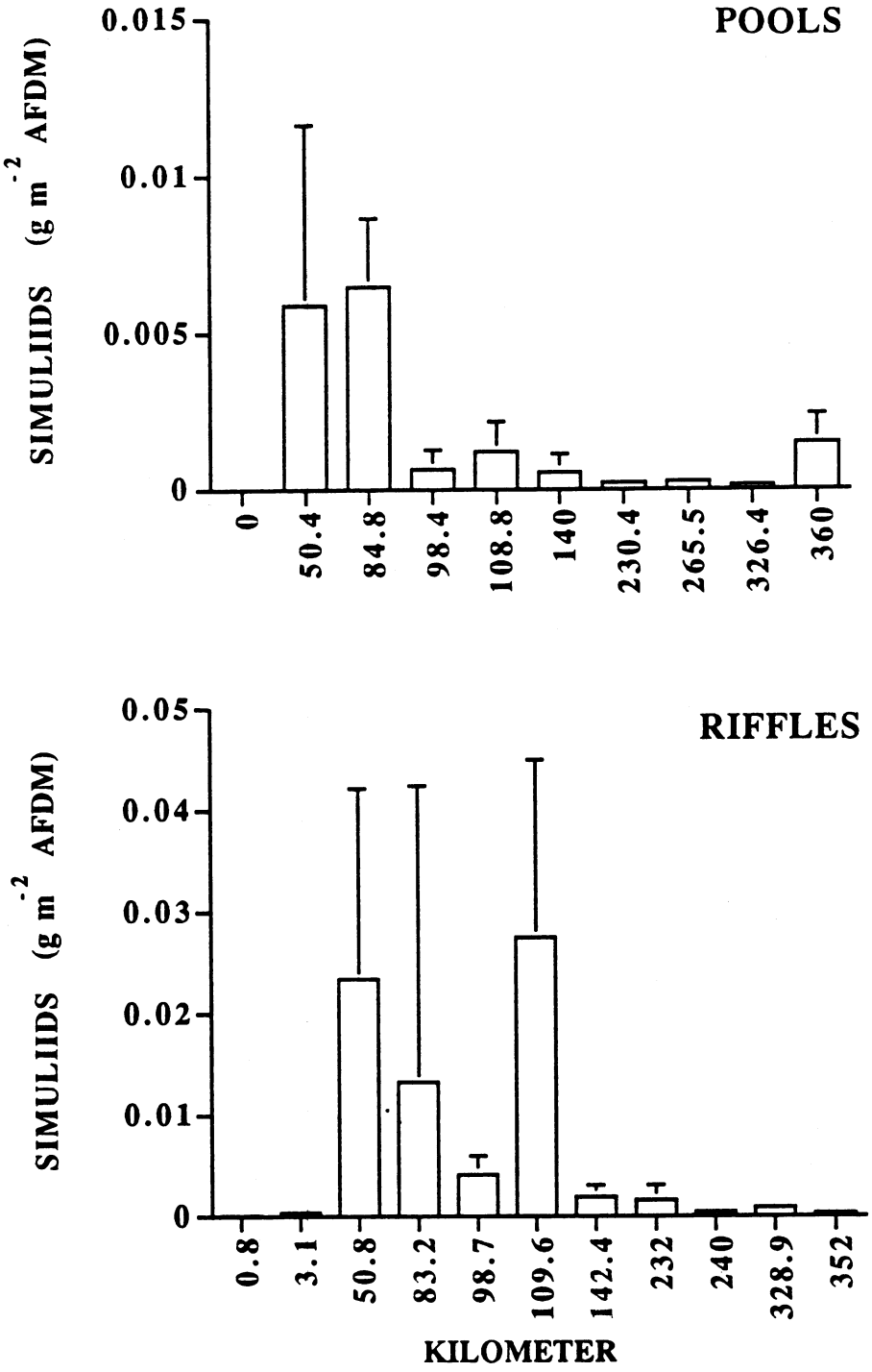


Figure 14. Average ash-free dry mass (AFDM) for simuliids in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

Riffle habitats were examined for patterns in simuliid life history from January, 1993 through March, 1994. These observations showed a significant seasonal pattern throughout the study site (MANOVA, Wilks lambda; $F_{2,1023} = 13.6$, $p < 0.0001$). Larvae metamorphosed to the pupa stage during the winter followed by adult flights in the spring. We have observed flights of adult blackflies during April since 1990. Highest densities for simuliid larvae were recorded on cobble bars at Tanner (625 larvae m^{-2}), with an average of 7 larvae m^{-2} throughout the study site. Pupal densities at Tanner were estimated at 110 pupae m^{-2} and an average of 3.3 pupae m^{-2} throughout the study area. Simuliid larvae have the ability to quickly colonize disturbed habitats and therefore are primary colonizers after spates. System-wide cross-channel distribution of simuliids on cobbles showed highest mean standing mass (0.116 g m^{-2}) at the 140 m^3 s^{-1} stage and reduced standing masses at lower (0.004 g AFDM m^{-2} at <28 m3 s-1) and higher (0.012 g m^{-2} AFDM at 280 m^3 s^{-1}) stages. Blackflies were not collected in the varial zone above the 300 m^3 s^{-1} stage.

Standing stock of Gammarus lacustris AFDM followed a similar pattern as that observed for C. glomerata AFDM; i.e., an overall increase in comparison to RF data (Fig. 15). Reproduction was also observed throughout the study site with fertile females collected during January and March of 1993. There was a decrease in G. lacustris standing crop at Lees Ferry during 1994. This reduction in standing crop may have resulted from high infection rates by a parasitic acanthocephalan during this period. Frequency of occurrence for this infection was 90% in late winter during 1993 and dropped to <1% in June 1994. Recent collections of G. lacustris at Lees Ferry and Paria Cobbles during the Fall of 1994 indicated a 15% infection rate.

Pearson correlation analyses demonstrated a negative relationship between G. lacustris and dissolved oxygen in pool habitats, and with water temperature and pH in riffle habitats (Tables 4 & 5). All three factors increased with distance downriver and may contribute, along with reduced C. glomerata AFDM, to the decline in standing stock of G. lacustris in the lower reaches of the canyon. System-wide cross-channel distribution of G. lacustris on cobbles showed a negative correlation between standing mass and stage; mean amphipod biomass at <28 m^3 s^{-1} = 0.22 g m^{-2} AFDM; at 140 m^3 s^{-1} = 0.18 g m^{-2} AFDM; at 280 m^3 s^{-1} = 0.03 g m^{-2} AFDM. Gammarus lacustris were not collected in the varial zone above the 300 m^3 s^{-1} stage.

Tubificid AFDM increased in pools, but decreased in riffles during IF in comparison to RF (Fig. 16). Tubificid standing stock at the Nankoweap pool habitat increased an order of magnitude during IF. A 60% reduction in tubificid biomass was recorded in riffles from Lees Ferry to Tanner during IF.

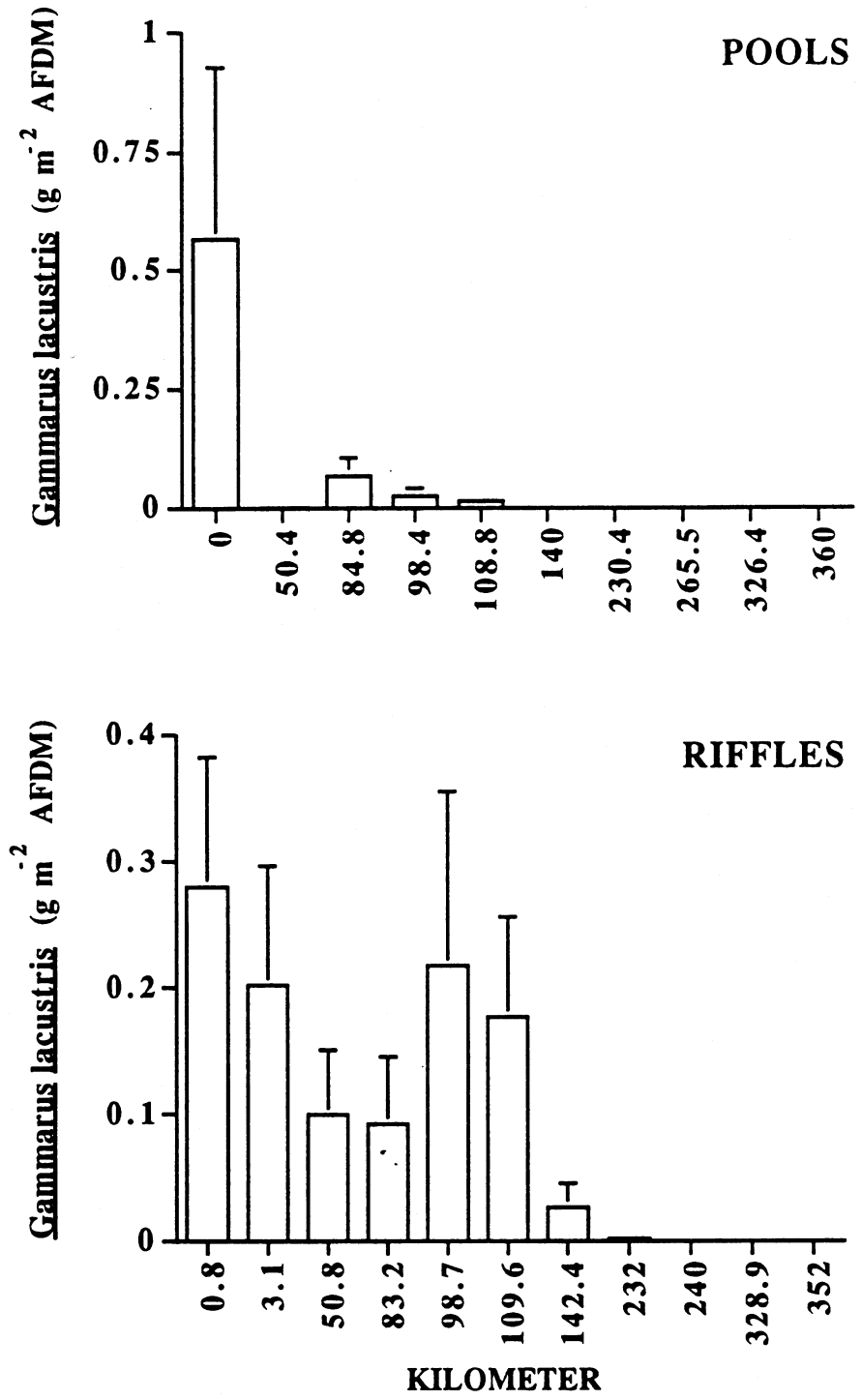


Figure 15. Average ash-free dry mass (AFDM) for Gammarus lacustris in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

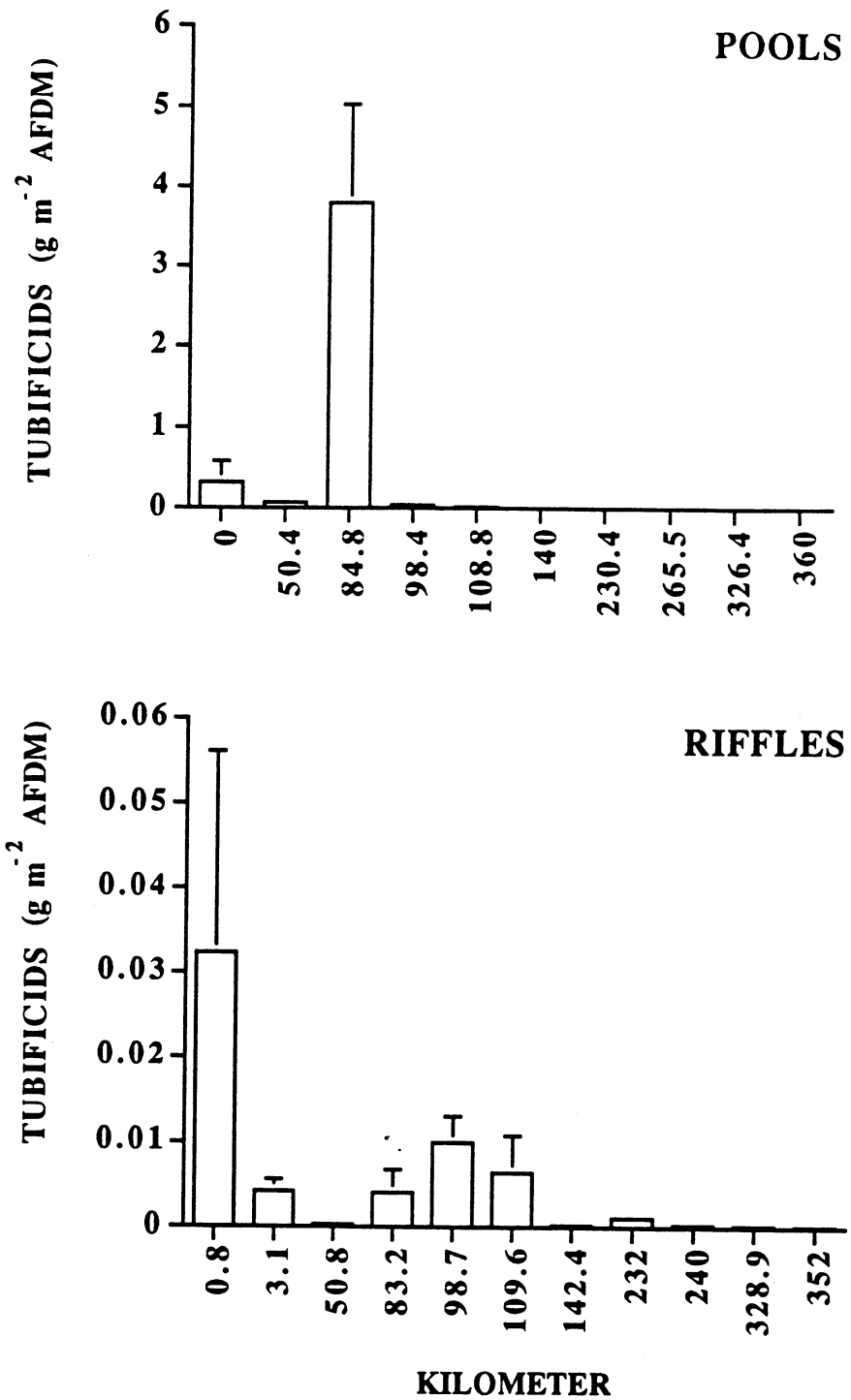


Figure 16. Average ash-free dry mass (AFDM) for tubificids in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

Pearson correlation of tubificid biomass and measured abiotic factors indicated that tubificid AFDM was negatively correlated with water temperature in pools (Table 4). This negative response to elevated water temperature by tubificids may be a contributing factor to their absence in pools, and their low densities in riffles below Tanner (Fig. 16). System-wide cross-channel distribution of tubificids in pools showed a positive correlation between standing mass and stage; mean tubificid biomass at <28 $m^3 s^{-1}$ = 0.17 g m^{-2} AFDM; at 140 $m^3 s^{-1}$ = 0.82 g m^{-2} AFDM; and at 280 $m^3 s^{-1}$ = 1.24 g m^{-2} AFDM. Tubificids were collected in the varial zone above the 300 $m^3 s^{-1}$ stage with a system mean density of 22 animals m^{-2} at the waters edge of pools and 3 animals m^{-2} at the 560 $m^3 s^{-1}$ stage. In contrast, tubificids averaged 2,168 animals m^{-2} in pool habitats below 300 $m^3 s^{-1}$ stage. During RF we collected only 11 tubificids from 900 samples within the varial zone.

During IF lumbriculid AFDM decreased in pools by 77% and in riffles by 40% in comparison with the RF period (Fig. 17). Pearson correlation analyses of lumbriculid biomass and measured abiotic parameters revealed a positive correlation between Secchi depth and earthworm standing crop in both pools and riffles (Tables 4 & 5). The relationship between clear water and earthworm AFDM may contribute to their presence in low turbidity reaches of Lees Ferry and Marble Canyon. System-wide cross-channel distribution of lumbriculid AFDM in riffles showed a negative correlation to stage; mean lumbriculid AFDM at ≤ 28 $m^3 s^{-1}$ = 0.08 g m^{-2} AFDM; at 140 $m^3 s^{-1}$ = 0.06 g m^{-2} AFDM; and at 280 $m^3 s^{-1}$ = 0.01 g m^{-2} AFDM. Lumbriculids were collected in the varial zone above the 300 $m^3 s^{-1}$ stage with a system wide mean density in riffles of 2.5 animals m^{-2} at waters edge and 0.6 animals m^{-2} at the 560 $m^3 s^{-1}$ stage. This varial zone colonization compares to a system mean density of 16.5 lumbriculids m^{-2} below the 300 $m^3 s^{-1}$ stage in riffle habitats. During RF we collected only 17 earthworms from 900 samples within the varial zone.

Gastropod AFDM remained higher in pools than riffles; however, each AFDM value increased over RF levels in lower Marble Canyon riffles (Fig. 18). Pearson correlation analyses of gastropod biomass and measured abiotic factors revealed a positive relationship between Secchi depth and gastropod AFDM in pools and riffles (Tables 4 & 5). Snail affinity for water with low turbidity may explain the high concentrations of snails at Lees Ferry and Nankoweap. System-wide cross-channel distribution of gastropods in pools showed a decrease in mean AFDM with decreasing stage, i.e., 0.02 g m^{-2} AFDM at <28 $m^3 s^{-1}$, 0.03 g m^{-2} AFDM at 140 $m^3 s^{-1}$ and 0.04 g m^{-2} AFDM at 280 $m^3 s^{-1}$. Snails were collected in the varial zone above the 300 $m^3 s^{-1}$ stage at a system-wide mean density of 1.2 animals m^{-2} at waters edge in pool habitats and 0.3 animals m^{-2} at the 560 $m^3 s^{-1}$ stage. This varial zone colonization compares to a system mean density of 141

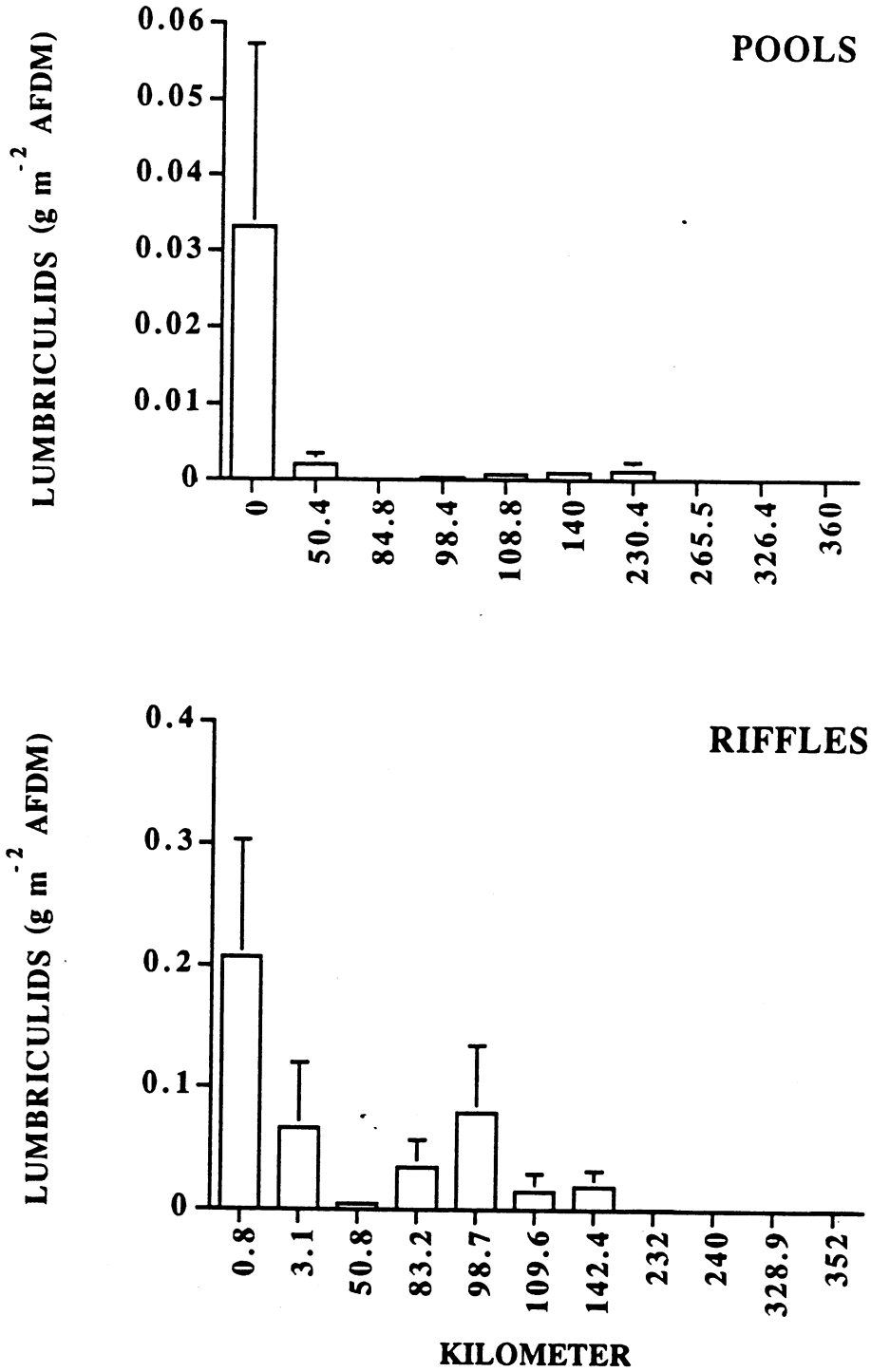


Figure 17. Average ash-free dry mass (AFDM) for lumbriculids in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

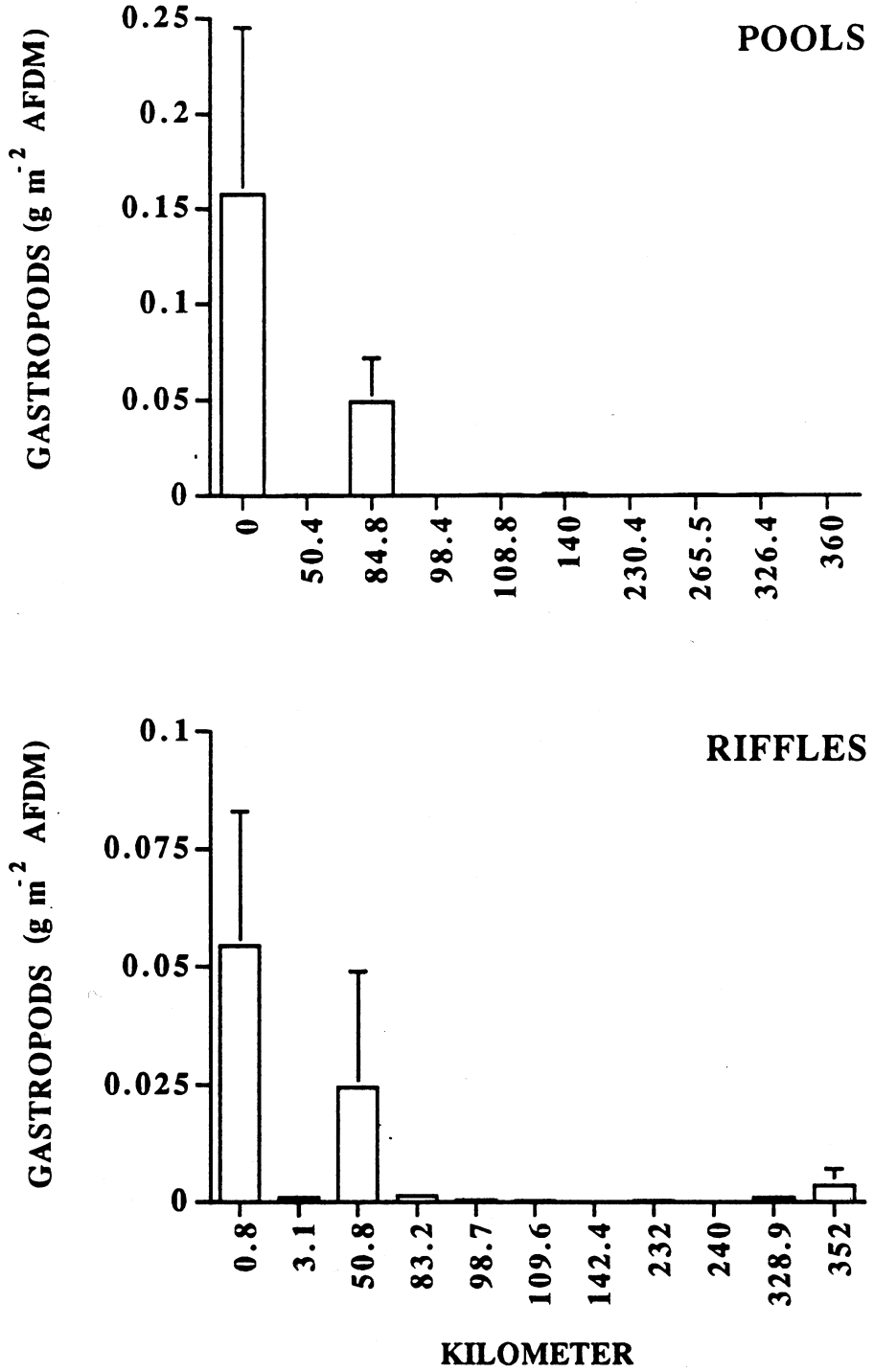


Figure 18. Average ash-free dry mass (AFDM) for gastropods in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

gastropods m^{-2} below the 300 m^3 s^{-1} stage in pool habitats. No snails were collected in the varial zone during RF.

Miscellaneous macroinvertebrate AFDM increased above RF values and was greater in pool than in riffle habitats (Fig. 19). AFDM of this biotic category decreased downstream in pool habitats, but was higher from RKM 83 to RKM 110 in riffle habitats (Fig. 19). System-wide cross-channel distribution of miscellaneous macroinvertebrate in pools showed a peak in mean AFDM in the thalweg samples; <28 m^3 s^{-1}, 0.33 g m^{-2} AFDM; 140 m^3 s^{-1}, 0.006 g m^{-2} AFDM; 280 m^3 s^{-1}, 0.009 g m^{-2} AFDM. Miscellaneous macroinvertebrates were collected in the varial zone above the 300 m^3 s^{-1} stage with a system-wide mean density in pools of 0.7 m^{-2} at waters edge and 0.4 m^{-2} at the 560 m^3 s^{-1} stage. This varial zone colonization compares to a system mean density of 34 miscellaneous macroinvertebrates m^{-2} below the 300 m^3 s^{-1} stage in pool habitats. During RF, miscellaneous macroinvertebrate were collected from 900 samples in the varial zone.

Macroinvertebrate species richness increased during IF in concert with reduced flow variability (Table 8). Taxa including aquatic heteroptera (Gerridae, Belostomatidae, Corixidae, and Naucoridae) were found in association with emergent vegetation in the lower reaches of the Canyon. Although macroinvertebrate species richness was low in September, 1993, the appearance of a small caddisfly (Trichoptera) in the family Hydroptilidae (Ochrotrichia), is noteworthy. These caddisflies are free-living during their first four instars, but build a purse-case (~5 mm) composed of fine sand, silk and filamentous algae during the fifth and final instar (Wiggins 1977). Ochrotrichia utilized diatoms on rocks and algae and occurred in filaments of C. glomerata at densities up to 200 animals m^{-2}. Ochrotrichia appeared in Marble Canyon and maintained similar densities throughout the corridor. This taxon is commonly found in erosional and depositional lotic habitats in North America (Merritt & Cummins 1984).

DISCHARGE ANALYSIS

Comparison of benthic biota AFDM collected under RF and IF at discharge stages <150 m^3 s^{-1} for pool and riffle habitats by each site demonstrated that overall biomass in riffles decreased and biomass in pools increased under IF ($p < 0.01$, Table 9, Figs 6 & 7). Benthic biota varied by category and by site. However, due to a consistent baseflow of 142 m^3 s^{-1} under IF a new channel zone was colonized by primary and secondary producers up to the 280 m^3 s^{-1} stage. IF flow changes have contributed an average of 17% to the total benthic biomass at Lees Ferry, 38% through Marble Canyon and 34% in Grand Canyon sites in this newly colonized zone (Table 10). The downriver increases are probably due to a

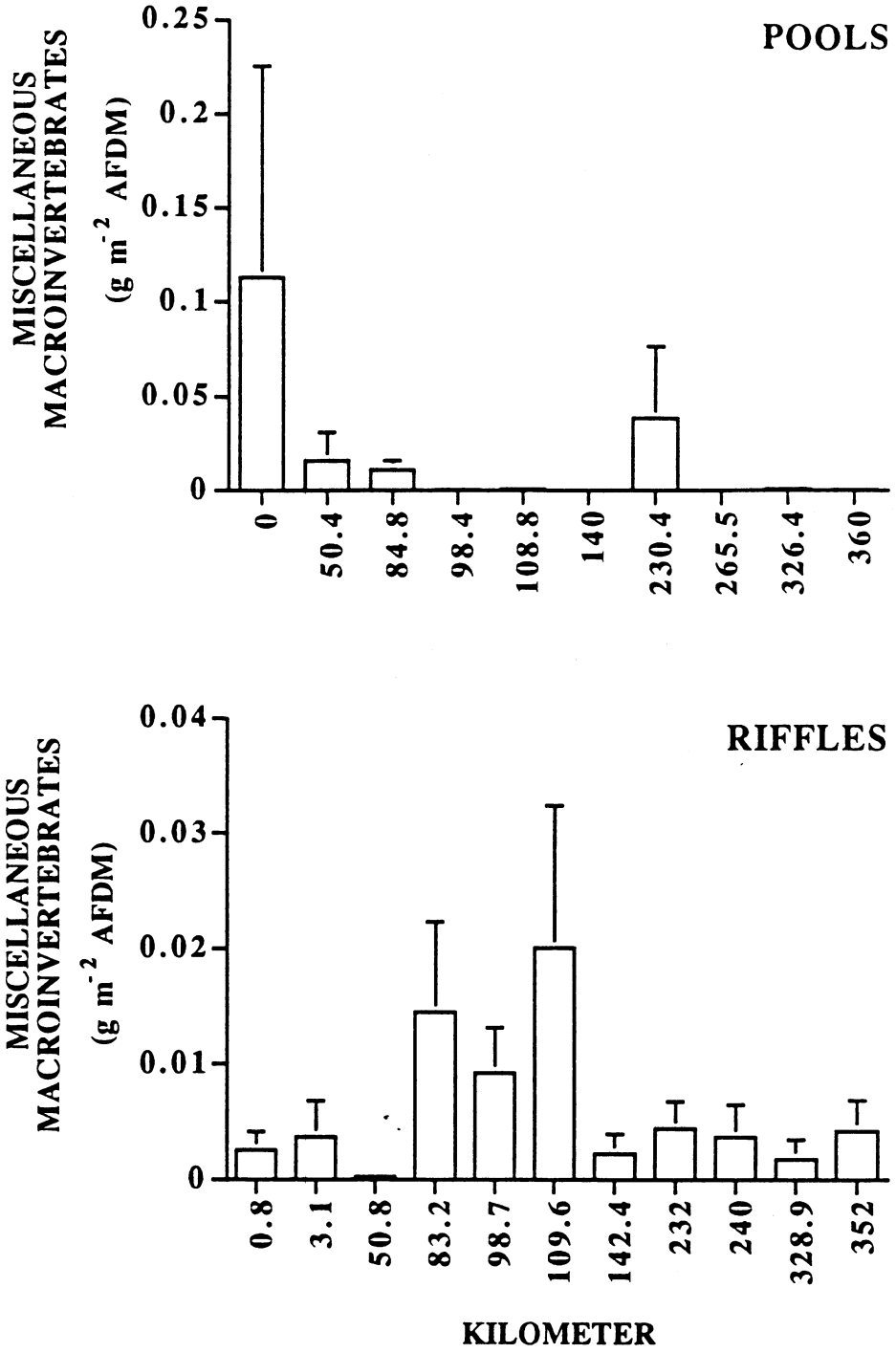


Figure 19. Average ash-free dry mass (AFDM) for miscellaneous macroinvertebrates in pools and riffles at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Seasonal collections were taken between September 1992 and June 1994. Error bars represent ±1 S.E.

Table 9. Comparison of primary and secondary producer AFDM (number on left side of slash = primary producer AFDM and number on right side of slash = secondary producer AFDM) between bimonthly research flow (RF) collections (January 1991- November, 1991; n = 6) and quarterly interim flow (IF) collections (September, 1992 - June 1994; n = 8) from both riffle and pool habitats at each collection site. These analyses compare discharge zones <170 $m^3 s^{-1}$ only because of the lack of varial zone colonization under research flows. Only significant univariate tests ($p < 0.01$) are reported from MANOVA analyses by site . Mean AFDM for each component are reported by site and habitat (RFg/IFg).

RIFFLE	SITE					
PRIMARY AND SECONDARY PRODUCERS	1.0	3.1	50.8	83.2	98.7	109.6
Oscillatoria				1.6/0.3		
Detritus	5.3/0.7		1.9/0.3			
Chironomids			0.01/0.001		0.0007/0.003	
Simuliids						0.04/0.009
Gammarus	1.7/0.2	0.7/0.2		0.003/0.1		
Gastropods	0.1/0.06					

POOL	SITE		
PRIMARY AND SECONDARY PRODUCERS	50.4	84.8	98.4
Detritus	0.003/3.9	1.7/6.2	0.4/1.4
Tubificids	0.3/3.43	0.0004/0.04	

Table 10. Average AFDM of benthic primary and secondary producers at Lees Ferry, Marble Canyon and Grand Canyon between 280 $m^3 s^{-1}$ and 180 $m^3 s^{-1}$ stages collected seasonally during interim flows from September, 1992 through June, 1994. No collections were made from this zone during research flows; bimonthly from January through November, 1991. High standard error values indicate the variablility within this zone particularly at Lees Ferry because occasional of atmospheric exposure.

Site	Habitat	Primary Producer g AFDM m^{-2} (±1se) %	Secondary Producer g AFDM m^{-2} (±1se) %
Lees Ferry	Pool (n=6)	5.8 g (4.2) 27%	0.3 g (0.2) 0.1%
	Riffle (n =2)	5.2 (0.3) 22%	0.4 (0.3) 18%
Marble Canyon	Pool (n=25)	4.3 g (0.9) 56%	1.3 g (0.5) 38%
	Riffle (n =30)	2.0 (0.2) 48%	0.13 (0.12) 10%
Grand Canyon	Pool (n=32)	5.8 g (4.2) 47%	0.3 g (0.2) 3%
	Riffle (n =80)	1.37 (0.2) 38%	0.08 (0.07) 46%

larger wetted perimeter from a reduction in the size of the hydrostatic wave due to daily fluctuations and a reduced compensation depth as a result of an increase in suspended sediments (Fig. 4). This varial zone is occasionally exposed to the atmosphere, therefore benthic variability is increased as depicted by the high standard error values in Table 10.

Multivariate analyses of water chemistry values showed an overall significant difference in each parameter (water temperature, pH, specific conductance, dissolved oxygen and Secchi depth) between May 1991 under RF and June 1993 under IF (Wilks' Lambda $F_{5,126} = 102$, $p < 0.0001$). Water temperature was slightly warmer in June 1993 as compared to May 1991 (Fig. 20), reflecting reduced flow velocity under IF.

Cladophora glomerata AFDM in riffle habitats was influenced by LCR flooding and by high midsummer flows in 1993 (Fig. 21). During the winter of 1993, abnormally high precipitation resulted in flooding throughout the Colorado River drainage with discharges from the LCR reaching 425 $m^3 s^{-1}$. Peak flows occurred in January and February and reduced the duration of the January and March collection trips. Effects of flooding were immediately evident in March with an increased accumulation of sand throughout the sampling stations. The June float trip revealed a significant increase in C. glomerata AFDM in cobble/riffle habitats below Nankoweap, as compared to the May 1991 collections (Wilks' Lambda $F_{10,178} = 2.13$, $p = 0.024$). Pool habitat AFDM (not graphed) increased significantly at all stations below the Paria River (Wilks' Lambda $F_{10,332} = 2.15$, $p = 0.003$), primarily from the accumulation of detritus and decomposers. The Paria River was also in spate during late winter 1993, which may have contributed to increased AFDM through Marble Canyon (RKM 0.0-99). Pool habitats showed an increase in AFDM primarily from the accumulation of detritus and decomposers. Cladophora glomerata AFDM increased after the LCR floods at Tanner cobble (RKM 110) to 17.8 g AFDM m^{-2} (Fig. 21). This is the first station below the confluence of the LCR and may reflect increased nutrient loads due to floods.

Dam regulation and drier than normal Springs during 1993 and 1994, may have contributed to the relatively high AFDM of aquatic benthos in the mainstem. From March through June 1993, discharge was less than normal for this period, with flows ranging from 170-396 $m^3 s^{-1}$ and a mean flow of approximately 240 $m^3 s^{-1}$. These low flows resulted in elevated water temperature downriver. For example, water temperature was 12.5°C at Tanner (RKM 110) and 17.5° C at Diamond Creek (RKM 362). These temperatures are similar to those of May 1991, which included two 140 $m^3 s^{-1}$ steady flow periods. Consistently elevated water temperatures coupled with clear water and a possible flood-induced nutrient pulse may have improved algal growth.

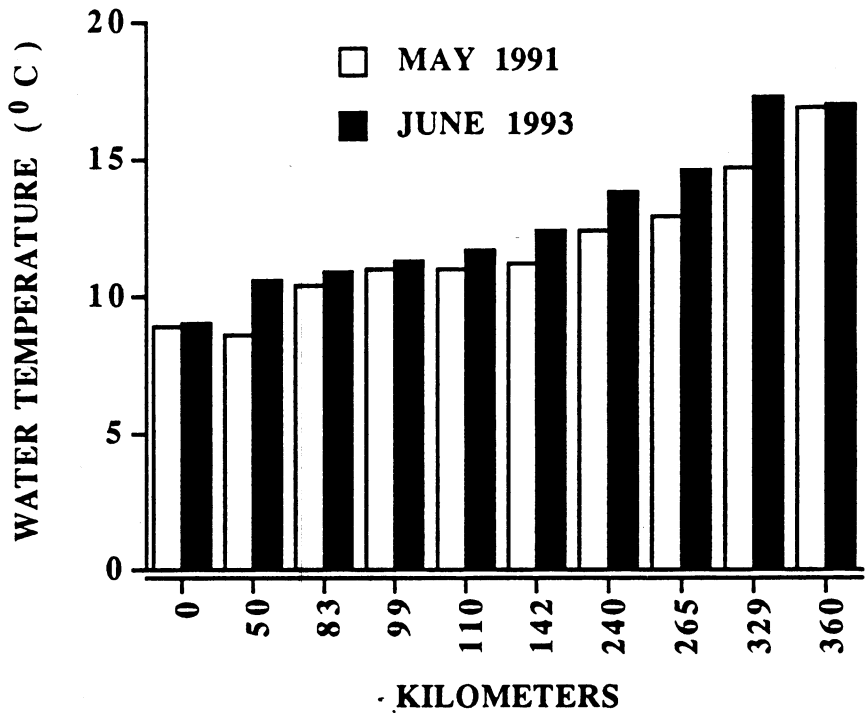


Figure 20. Water temperature at collection sites between Lees Ferry (RKM 0) and Diamond Creek (RKM 362) during float trips on May 1991 and June 1993. Note the higher temperatures for June 1993.

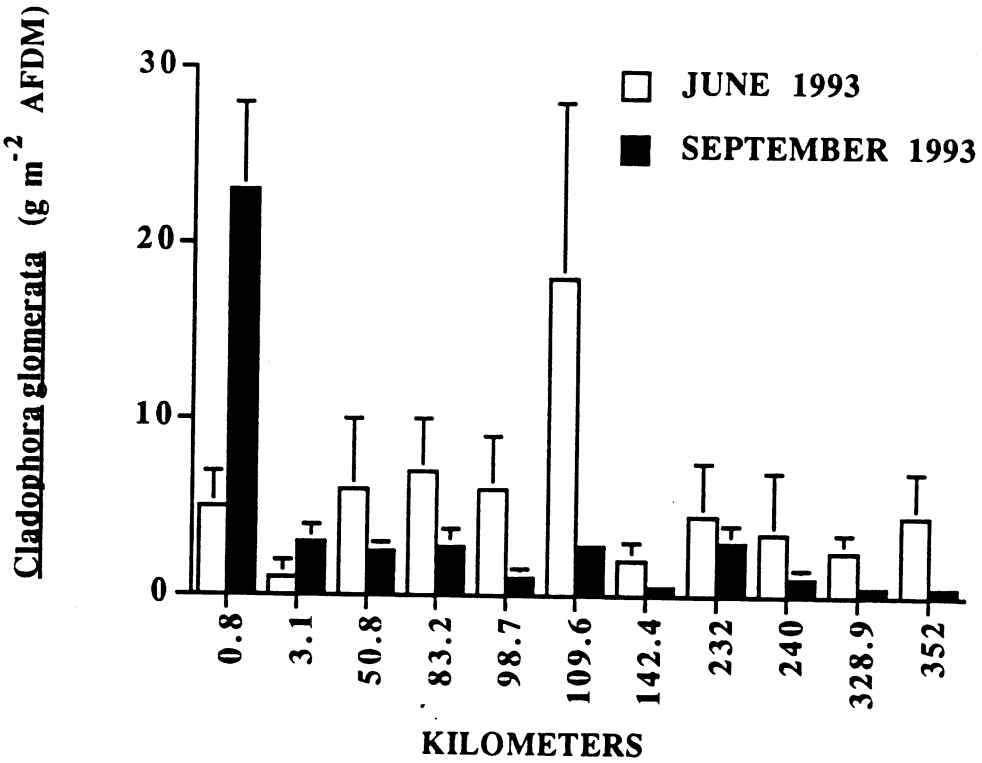


Figure 21. Average ash-free dry mass (AFDM) for Cladophora glomerata during June and September 1993 at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Error bars represent ±1 S.E.

The September, 1993 collection trip was completed under turbid conditions after July and August IF maxima (340-566 $m^3 s^{-1}$). Overall biomass estimates decreased by about 40% from June collections. The AFDM values for September were similar to those collected during previous fall seasons (Blinn et al. 1992). Species richness of primary and secondary producers was also reduced in comparison to June 1993; however, monitoring data indicated that low releases from GCD after a spate event may enhance production. We predict a Spring increase in production with subsequent reduction in AFDM influenced by higher summer release patterns if the habitat building flood from GCD, proposed for the spring of 1995, affects the benthos in a similar manner as did the 1993 LCR floods.

TRIBUTARY BENTHOS

MANOVA of benthic AFDM from 11 tributaries sampled in June of 1993 and 1994 indicated a significant difference between collection years and sites (Figs. 22 & 23; Wilks' Lambda = 0.8; $F_{10,120} = 2.9$, $p = 0.01$; Wilks' Lambda = 0.8; $F_{10,120} = 2.3$, $p = 0.01$, respectively). Only detritus ($p < 0.01$) and MAM ($p < 0.01$) were significantly different by collection year in a univarite context. Univariate analysis of taxonomic categories showed that only the miscellaneous macroinvertebrates varied significantly between sites ($p = 0.03$). Further analyses of miscellaneous macroinvertebrate density at the ordinal level for both collection trips revealed a significant overall difference (Wilks' Lambda < 0.01; $F_{1,129} = 5.3$, $p = 0.01$). Univariate analysis determined that the site variability is limited to Odonata ($p < 0.001$), Heteroptera ($p = 0.02$), Megoloptera ($p < 0.01$) and unidentified macroinvertebrates ($p < 0.001$), while Coleoptera, Plecoptera, Ephemeroptera, and Trichoptera abundance remained constant between sites (Fig. 23).

Dissolved oxygen, water temperature and pH were all significantly different in tributaries from the mainstem between collection trips ($p < 0.001$), while only DO and water temperature were different between tributaries ($p < 0.05$). Water velocity and depth of collections did not vary significantly between collection trips or tributaries indicating consistent sampling protocol.

Tributaries were sampled during June, 1993, and had not yet recovered from winter spates. The only exception was Spring Canyon, which revealed high benthic AFDM. This same pattern was observed in June, 1994. Tributaries developed cemented bottoms from travertine deposition. Interstitial spaces in the substrate were reduced due to filling by $CaCO_3$. This phenomenon was observed while sampling the hyporheic zone of tributaries (Blinn et al., 1992) where an impervious layer of travertine was found below a thin layer (<30 cm) of sand,

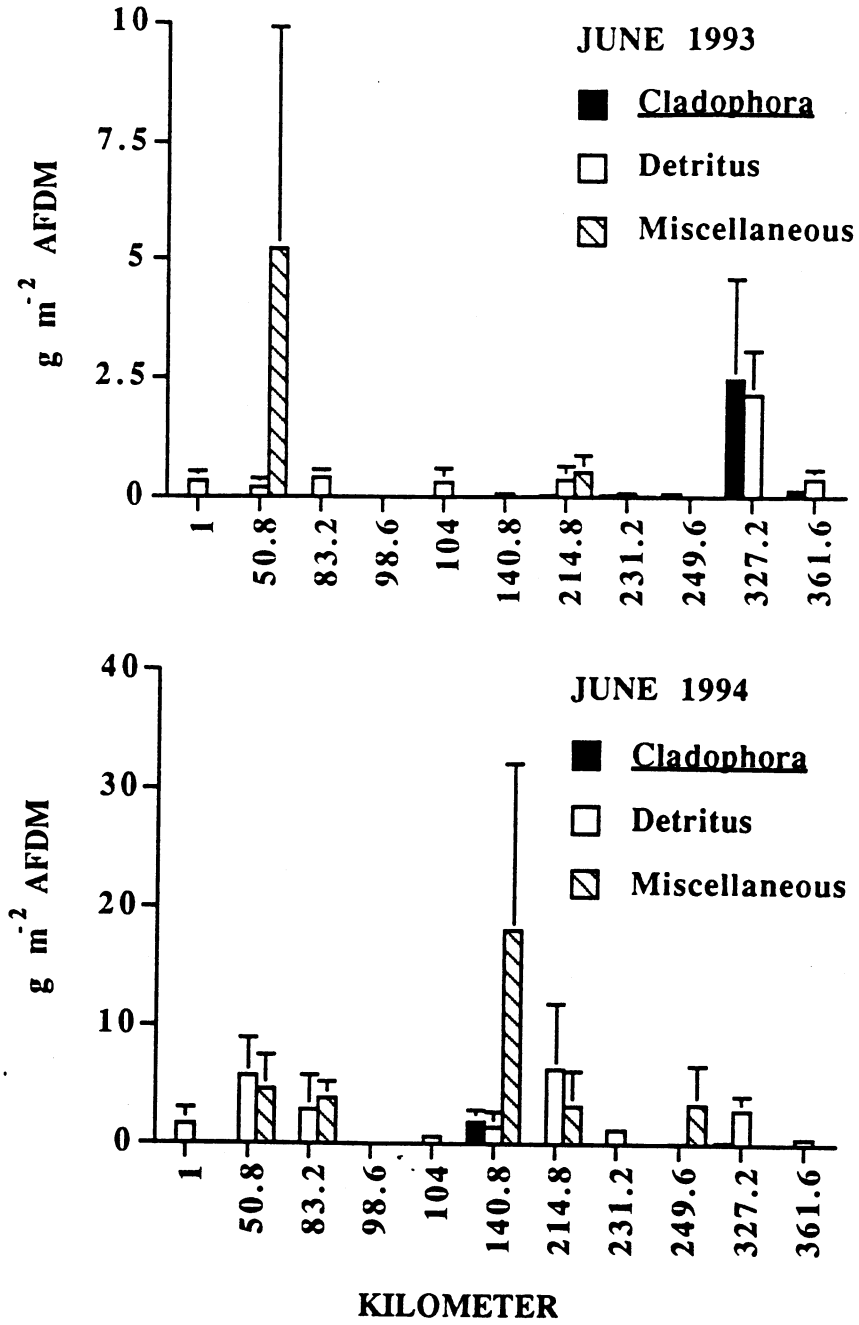


Figure 22. Average AFDM of benthic primary producers in tributaries entering the Colorado River between the Paria River (RKM 1.0) and Diamond Creek (RKM 362). Collections were made in June 1993 and 1994. Miscellaneous category is composed primarily of bryophytes, macrophytes and Nostoc. Error bars represent ±1 S.E.

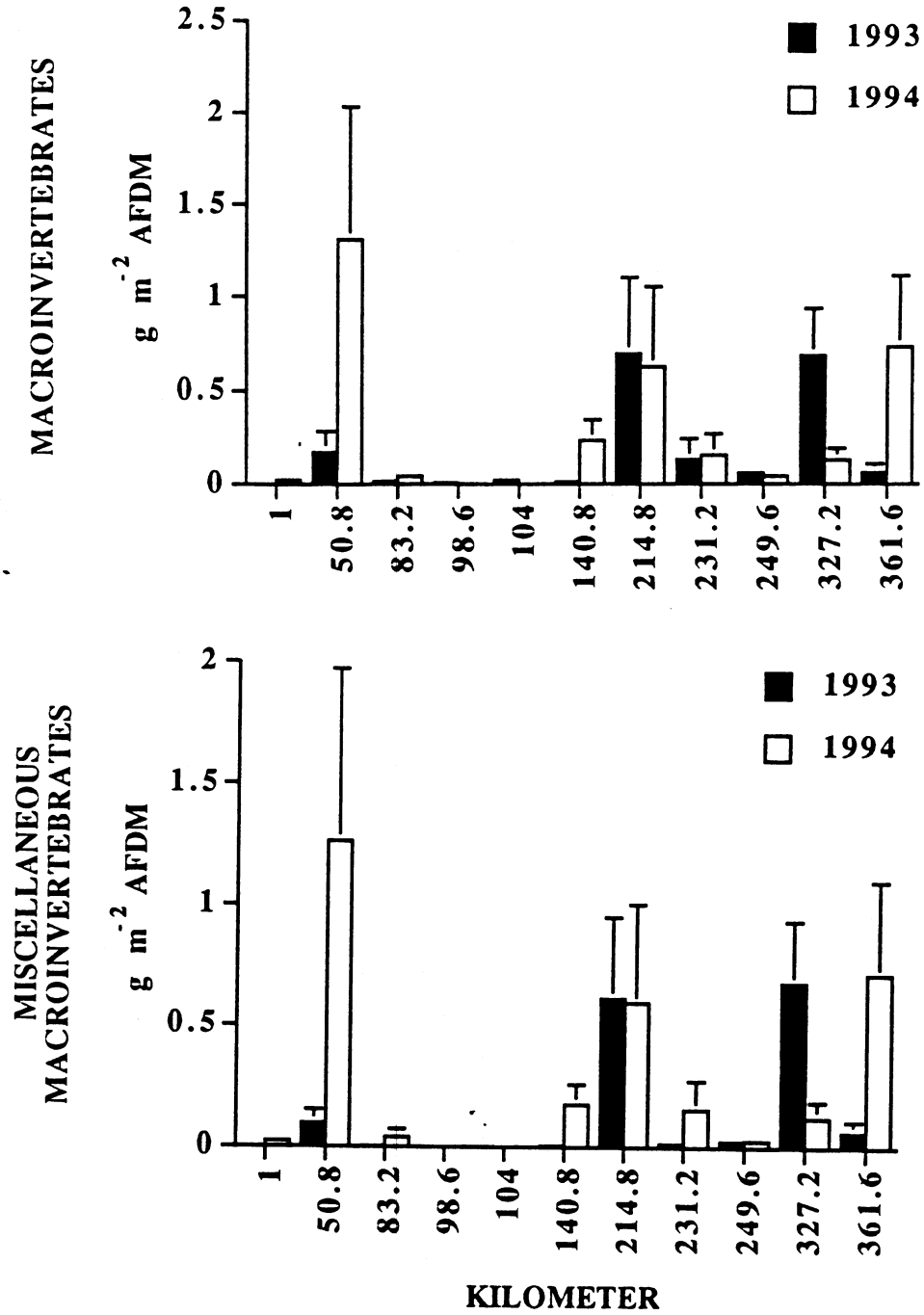


Figure 23. Average AFDM of benthic macroinvertebrates in tributaries entering the Colorado River between the Paria River (RKM 1.0) and Diamond Creek (RKM 362). Collections were made in June 1993 and 1994. Macroinvertebrates include aquatic diptera, gastropods and oligochaetes, while miscellaneous macroinvertebrates are primarily aquatic insects. Error bars represent ±1 S.E.

gravel and cobbles. The debris coating was probably deposited from lower magnitude spates. Spawning gravels required by trout for successful reproduction have also been cemented in Nankoweap Creek

Water analyses of a spate entering the Colorado River 1 km below Glen Canyon Dam, draining the northwest section of Page, AZ., revealed unnaturally high levels of nitrate (0.9 mg L^{-1}), ammonia (0.87 mg L^{-1}) and ortho-phosphate (>1.36 mg L^{-1}). Ambient concentrations in rivers are typically 0.1 mg L^{-1} NO_3, 0.015 mg L^{-1} NH_3, and 0.025 mg L^{-1} P-PO_4 (Meybeck & Helmer 1989). These preliminary data suggest the city of Page may be contributing nutrients to the tailwater reach. Further investigations are warranted to determine if sewage, heavy metals and pathogens are also carried into the Colorado River from Page during storms.

Collection stations were surveyed by the GCES staff for implementation into the Global Information System (GIS) program on September, 1993. These data were collected with GCES survey equipment: i.e., Leitz Set 4 Total Station, Global Hydrographic Superhydrolab Bathymetric Survey System and Sokkia V4.0 mapping software. Representative wide and narrow reaches are illustrated in Appendix Figures 1-17. We have provided data on benthos, drift and water chemistry to the GCES staff for inclusion into the LCR and Tanner GIS data base.

SUMMARY

Benthic primary and secondary producer standing mass was assessed seasonally from September 1992 through June 1994 betweeen Lees Ferry and Diamond Creek. Interim Flows and seasonal and climatic variation altered benthic community structure. In general algal and macroinvertebrate AFDM and species richness increased through time in downstream reaches. We attribute these changes to reduced daily discharge fluctuation and ramping rates, and exceptionally clear water flows. Aquatic habitats have also been altered during this period by both the operation of GCD and variability in tributary inflow.

Pool and riffle habitats have accumulated fine sediments reducing the area of hard substrates for colonization. Pool habitats have also accumulated fine sediments that have created a productive littoral zone along the length of the pool/eddie complexes sampled and decreased the total volume of water circulating within pools. This has reduced the accumulation of detritus during low flow months. Macrophyte biomass has also increased in depositional areas within Glen and Marble Canyons. Bryophyte biomass increased in erosional zones throughout the study site.

The winter of 1993 had large spates from watersheds extending beyond the Grand Canyon rim, while a summer monsoon in 1993 produced a debris flow in Tanner Wash, which restructured the pool and riffle habitats at that site. Both events were followed by an overall increase in benthic AFDM, perhaps a result of nutrient increase from tributary flows.

Interim Flows have allowed natural patterns in primary and secondary producer distribution to be recognized which were previously diluted by normal dam operations. This flow regime has also allowed sporadic colonization into the previously depauperate varial zone. Pools of water in the varial zone left after high flow months have provided spawning habitats for mosquitos, particularly in the lower Canyon, which were previously rare along the mainstem.

CHAPTER TWO: PRIMARY AND SECONDARY PRODUCTION

INTRODUCTION

From the standpoint of a functioning ecosystem, production is the process through which energy is converted from one trophic level to the next. Therefore, resource managers must be concerned with the processes of production and those factors which modify the synthesis of autochthonous organic matter. Disturbance effects on Cladophora glomerata, Oscillatoria spp. and associated epiphytes are important because these algal groups are the dominant primary producers in the Colorado River ecosystem and therefore support higher trophic levels. Secondary production by Gammarus lacustris and chironomid larvae are vital to understanding energy flow within the Colorado River ecosystem because these macroinvertebrates serve as critical intermediate links between algal and fish trophic levels in the Colorado River food web (Blinn et al. 1992). This study examines the effects of regulated flows in combination with suspended sediment loads on the primary and secondary production of benthos in the Colorado River ecosystem.

METHODS

PRIMARY PRODUCTION

Primary production estimates were calculated for benthic algae at Lees Ferry (RKM 0.0), Cathedral Island (RKM 4.8) and Gorilla Island (RKM 352) during the winter and summer of 1994 (Fig. 1). Three circular chambers were designed and constructed of Lexan acrylic with a diameter of 23.5 cm and height of 18.5 cm. Each chamber was sealed with a lid and an air-tight circular plunger (0.5 cm thick). Three air-tight ports were placed 5 cm above the bottom: two for water circulation and a third for a dissolved oxygen probe (YSI model 55). Three L of river water were added to each chamber. Three cobbles approximately 25 cm in circumference were placed into each chamber and the plunger was lowered to the top of each cobble to eliminate gas exchange with the atmosphere. Electric submersible pumps circulated the water in each chamber at a flow rate of 0.5 L s^{-1}. Chambers were placed in the river at a depth of 15 cm to maintain chamber water within 3°C of ambient river water temperature. Water temperature and dissolved oxygen (mg L^{-1}) were recorded every 5 min. until approximately 2 mg L^{-1} dissolved oxygen were produced in each chamber for standardization of production calculations. River water chemistry (DO, specific conductance, water temperature and pH) was measured with a Hydro-Lab Scout II. Light intensity

(μE m^{-2} s^{-1}) was measured at the water surface and the depth of cobbles at five minute intervals with a Li-Cor photometer (Model 185-B). Respiration estimates were measured in chambers placed in a 164 L cooler with 80 L of river water; chamber water was maintained near river temperature (9-11°C). The lid was covered with black plastic and a silver blanket to achieve total darkness and to reflect solar radiation, respectively. A photometer was placed in the cooler to monitor light energy. After completion of respiration experiments the pH of the water was measured in each chamber. Turbidity of the river water was determined in each experiment with a Hach® turbidometer (NTU) and Secchi depths were recorded. Suspended sediment samples (n = 3) were taken at Gorilla Island (RKM 352) along with a light profile in order to establish light extinction coefficients.

After each production measurement, primary producers were scrapped from each cobble and sorted on site into the following categories: Cladophora glomerata, Oscillatoria spp., and miscellaneous algae. Samples were oven-dried at 60°C to a constant weight. Ash-free dry mass (AFDM) was measured after one hour at 500°C in an ash furnace.

We examined the contribution of epiphytes to community primary production in the clear tailwaters of Glen Canyon Dam at Lees Ferry during winter and summer. Cladophora covered cobbles with and without epiphytes were analyzed separately with the above outlined protocol. Epiphyton AFDM estimates were made after agitating cobbles for one minute in a plastic container with 500 ml of river water. Epiphyton suspensions were immediately filtered onto glass fiber filters (Whatman GF/C) with a 47 mm Millipore syringe filter system. Filters were dried at 60°C to constant weight, and epiphyte ash-free dry mass (AFDM) was estimated after one hour at 500°C.

The impact of suspended sediment on primary production was measured with colonized cobbles from Cathedral Island (RKM 4.8) on February 1994, which is located below the Paria River confluence (Fig. 1). Cobbles with Oscillatoria spp. and C. glomerata were placed in clear water (NTU = 1; light energy =1321 μE m^{-2} s^{-1}) collected at Lees Ferry to determine photosynthesis. These same chamber/cobbles were monitored for dissolved oxygen production with turbid water (NTU = 90; light energy = 800 μE m^{-2} s^{-1}) added to the chambers. A similar experiment was conducted during August 1994 with three turbidity treatments: NTU = 6.5, light energy = 2102 μE m^{-2} s^{-1}; NTU = 90, light energy = 1225 μE m^{-2} s^{-1}; NTU = 146, light energy = 290 μE m^{-2} s^{-1}.

Cross-channel primary production estimates were determined on August 1994 at Lees Ferry by incubating cobbles collected from the following stages;

1) 400 $m^3 s^{-1}$ and desiccated for 12 h, 2) 280 $m^3 s^{-1}$ and desiccated for 12 h, 3) 280 $m^3 s^{-1}$ while submerged, and 4) <140 $m^3 s^{-1}$ continually submerged, control treatment from June data. Desiccation experiments were conducted at night to mimic typical Lees Ferry discharge patterns. Both desiccation periods were conducted during the monsoon period therefore relative humidity was high (>70%) and air temperatures were low (<25°C).

Phytoplankton and lotic bacteria can alter benthic primary production estimates (Greenberg et al. 1992). Unfiltered river water was used in the chambers for nutrient assimilation by the epiphyton, therefore a control run was conducted to determine the contribution of phytoplankton and lotic bacteria to production estimates. The same protocol was followed as with other experiments but without cobbles and with 5 L of water in each chamber. We did not detect any net primary production from river water. An average of 0.3 mg L^{-1} O_2 was lost during the light portion and 0.3 mg L^{-1} O_2 was produced in the dark portion of the experiment. These variations may be attributed to changes in water temperature during the experimental periods.

Reach-wide calculations for primary production followed those outlined in Greenberg et al. (1992).

$$\text{Primary Production (PP)} = \frac{V(\Delta DOp)B}{t(b)}$$
$$(g\ O_2\ m^{-2}\ h^{-1})$$

$$\text{Respiration (R)} = \frac{V(\Delta DOr)B}{t(b)}$$
$$(g\ O_2\ m^{-2}\ h^{-1})$$

Where : V = volume of water in chamber
ΔDOp = Final DO - Initial DO reading (O_2 L^{-1}) - during photosynthesis
ΔDOr = Initial DO - Final DO reading (O_2 L^{-1}) - during respiration

B = average epiphyton estimated for the study reach (g m^{-2} AFDW)
t = duration period (h)
b = total biomass of epiphyton in chamber

Gross Primary Production (GPP) = NPP + R
($g\ O_2\ m^{-2}\ h^{-1}$)
Net Primary Production (NPP) = GPP - R
($g\ O_2\ m^{-2}\ h^{-1}$)

Reach-wide estimates for biomass (B) were obtained from Hess substrate collection data gathered from river trips. Lees Ferry and Cathedral Island winter biomass values were estimated by averaging January and March data because production measurements were conducted in February. Both gross and net production were measured in grams of oxygen per square meter per hour (g O_2 m^{-2} h^{-1}). These values were converted to carbon (g C m^{-2} h^{-1}) by multipling the gross and net dissolved oxygen production by the constant 1.146 (Cole 1983). This conversion assumes a photosynthetic quotient (PQ) of 1.2. Energy values were obtained by multiplying net and gross oxygen data by 3.51 (Blinn et al. 1992), again assuming a PQ of 1.2 (Cole 1983).

Statistical Analyses

Multivariate analysis of variance tests were run to determine if predictors (season and location) influenced gross and net primary production. The impact of increased water turbidity and epiphytes on primary production was analyzed with a Student t Test. Regression analysis was run to define the relationship between light intensity and primary production. All statistical investigations were performed on SYSTAT (V 5.1) computer software (Wilkinson 1989).

SECONDARY PRODUCTION

Benthic invertebrates were collected in submerged and varial (fluctuating) zones of the Colorado River at Lees Ferry (RKM 0) and Two Mile Wash (RKM 3.1), Arizona, to evaluate the role of regulated flows and suspended sediments on the secondary production of Gammarus lacustris and chironomid larvae, two important macroinvertebrate groups in the Lees Ferry food web (Blinn et al. 1992). Samples were taken at two-wk intervals with a modified mini-Hess sampler (0.031 m^2) in submerged and varial zones at Lees Ferry and Two Mile Wash between 29 September 1992 and 15 September 1993. Samples were collected in the varial zone [5,000 cfs (140 m^3 s^{-1}) to 20,000 cfs (566 m^3 s^{-1})] at two time periods over a diel cycle; i.e., periods of drawdown (exposed; $\leq$140 m^3 s^{-1}) and re-submergence ($\geq$10,000 cfs or $\geq$283 m^3 s^{-1}). Therefore, we had three treatments at each site; i.e., a control submerged channel ($\leq$140 m^3 s^{-1}) and a submerged and exposed varial zone. Hess samples were collected from four randomly selected sites along three transects within each treatment at each site (n = 12 from each treatment). Benthic invertebrates and algae were removed by disturbing the substrata within the mini-Hess sampler for 60 s, afterwhich samples were collected and placed on ice for transport back to the Aquatic Biology Laboratory at Northern Arizona University, Flagstaff, Arizona. Reference points for transects were alternated monthly to avoid oversampling

local sites. Instars of G. lacustris were sorted from each sample and body length of each instar was measured to the nearest 1 mm. Instars were separated into 19 1-mm size classes and the dry weight of each size class was determined. Eggs were removed from female brood pouches and number and weight of eggs from each mature female was determined. Also the size of females with eggs was determined for each sample. Unlike the protocol for G. lacustris, the combined weight of chironomid larvae from each sample was determined; instars and taxa were not separated.

The size-frequency method (Benke 1984) was used to estimate the annual production of G. lacustris within each treatment. We followed procedures of Menzie (1980, 1981), Dehdashti & Blinn (1991) and Runck & Blinn (1990, 1993):

$$P = \sum_{j=1}^{c} (N_1 - N_{j+1}) \cdot (W_j \cdot W_{j+1})^{1/2},$$

where P is the annual production, W_j is the mean weight of instar j, c is the number of instars, and N_j is the average density m^{-2}.

RESULTS AND DISCUSSION

PRIMARY PRODUCTION

Primary production estimates for algal benthos at Lees Ferry, Cathedral Wash (RKM 4.8) and Gorilla Island (RKM 352) varied significantly both seasonally ($F = 3.14$; $df = 4,72$; $p = 0.013$) and by site ($F = 5.32$; $df = 2,36$; $p = 0.009$; Table 11). There was an overall decrease in primary production with distance downriver. These findings do not concur with the generally accepted pattern in nonregulated rivers of a positive correlation between autotrophic production and stream order (Wetzel & Ward 1992, Thorp & Delong 1994). Differences along the stream continuum for the Colorado River and other rivers may be due to the highly constricted river channel resulting in high hydraulic stress and seasonally high levels of suspended sediments from tributaries thereby reducing light for photosynthesis at downstream sites (Blinn et al. 1992, Yard et al. 1992).

Estimates for primary production during the summer did not change significantly downriver (Wilks' Lambda, $F = 2.18$; $df = 4,3$; $p = 0.09$), however univariate analysis showed a significant decrease for both gross ($p = 0.02$) and net production ($p = 0.03$) estimates (Table 11). Differences between multivariate and univariate statistics may be explained by the unusually transparent water at

Table 11. Primary production (gross/net) estimates in the Colorado River at Lees Ferry, Cathedral Island (RKM 4.8) and Gorilla Island (RKM 352). Primary production values for both gross and net primary production differed by site (Wilks' Lambda, F = 3.14; df 2,32; p = 0.01) and season (Wilks' Lambda, F = 5.32; df 2,36; p = 0.009). Mean values were estimated from air-tight in-situ production chambers. Light values were collected underwater at the same depth as the chambers.

SITE	DATE	OXYGEN PRODUCTION g O_2 m^{-2} h^{-1} gross/net (±se/±se)	CARBON PRODUCTION g C m^{-2} h^{-1} gross/net (±se/±se)	ENERGY kcal gross/net (±se/±se)	MEAN LIGHT μE $m^{-2}s^{-1}$ (±se)
Lees Ferry (n = 6)	02/94	0.89/0.34 (0.3/0.4)	0.28/0.11 (0.01/0.01)	3.15/1.23 (0.2/0.15)	1009 (26)
Lees Ferry (n = 6)	06/94	0.774/0.284 (0.06/0.04)	0.241/0.089 (0.02/0.01)	0.84/0.3 (0.2/0.1)	2303 (147)
Cathedral Island (n = 6)	02/94	0.414/0.16 (0.16/0.08)	0.129/0.048 (0.05/0.03)	1.45/0.56 (0.56/0.3)	800 (88)
Cathedral Island (n = 3)	06/94	0.338/0.91 (0.05/0.03)	0.105/0.028 (0.02/0.01)	1.18/0.31 (0.18/0.11)	1927 (14)
Gorilla Island (n = 3)	02/94	0.016/0.0008 (0.01/0.003)	0.005/0.0002 (0.002/0.0001)	0.06/0.0007 (0.02/0.0001)	207 (11)
Gorilla Island (n = 6)	06/94	0.355/0.123 (0.22/0.09)	0.095/0.033 (0.06/0.02)	0.72/0.37 (0.8/0.3)	2576 (30)

Gorilla Island (RKM 352); i.e., 2576 μE m^{-2} s^{-1} compared to more typical values of ≤500 μE m^{-2} s^{-1}.

Seasonal variation in net primary production (NPP) at Gorilla Island ranged from 0.0008 g O_2 m^{-2} h^{-1} in the winter to 0.12 g O_2 m^{-2} h^{-1} in the summer, while production estimates at Cathedral Island ranged from 0.91 to 0.16 g O_2 m^{-2} h^{-1} for summer and winter, respectively. At Lees Ferry, 4.8 km upstream from Cathedral Island, net primary production estimates were 0.89 g O_2 m^{-2} h^{-1} during the winter and 0.77 g O_2 m^{-2} h^{-1} in the summer. Low winter estimates can be explained by reduced light energy and low algal biomass (Table 11).

Lees Ferry had the highest gross (GPP = 0.774 g O_2 m^{-2} h^{-1}) and net (NPP = 0.284 g O_2 m^{-2} h^{-1}) primary production for the three sites measured in this study (Table 11). Angradi and Kubly (1993) reported dramatically higher levels of gross primary production (5 g O_2 m^{-2} h^{-1}) at 14 Mile Bar in the Colorado River, which is 2 km below Glen Canyon Dam. The higher production levels measured by Angradi and Kubly (1993) may be explained by variations in methodology and/or the closer proximity of their study site to higher nutrient levels released from Glen Canyon Dam. Our primary production equation employed reach-wide (B) estimates, while Angradi and Kubly (1993) used estimates from 35 cm^{-2} scrapings which may have inflated their production estimates due to the patchy distribution of benthos (Blinn et al. 1992). We estimated 7.5 g AFDM m^{-2} in the winter and 15.9 g AFDM m^{-2} in the summer at Lees Ferry, while Angradi and Kubly (1993) estimated 148 g AFDM m^{-2} from scrapings during the summer at 14 Mile Bar.

Other investigators have reported mean annual net primary production ranging from 1.0 g c m^{-2} d^{-1} or 3.2 g O_2 m^{-2} d^{-1} (NPP) in a northern cool desert stream with no canopy (Bott 1983) to 0. 41 g.c m^{-2} d^{-1} or 1.33 O_2 m^{-2} d^{-1} (NPP) for a similar stream in Idaho (Minshall 1978). Jonsson (1992) reported Cladophora NPP in Lake Thingvallavatan, Iceland produced 0.005 g O_2 m^{-2} h^{-1} with a similar light intensity as found at Lees Ferry in the summer. This lake is cold with a maximum summer temperature of 10.5°C, also comparable to Lees Ferry.

There was no significant difference in primary production at Lees Ferry for C. glomerata with and without epiphytes (p >0.05; Table 12). Cladophora glomerata with epiphytes had a mean NPP of 0.219 g O_2 m^{-2} h^{-1}, while C. glomerata without epiphytes produced 0.236 g O_2 m^{-2} h^{-1}. An average of 0.723 g and 0.601 g AFDM of epiphytes per chamber was removed from each treatment, respectively. Cladophora glomerata filaments may be more photosynthetically

Table 12. Primary production (gross and net) estimates for Cladophora glomerata with and without epiphytes in the Colorado River at Lees Ferry, Arizona during winter (February) and summer (June) 1994. Comparison of primary production under clear and turbid water conditions in the Colorado River at Cathedral Island, Arizona during June and August 1994. June estimates did not vary significantly because of turbidity. August estimates did vary by turbidity. Significant differences in oxygen production are indicated by bold letters ($p < 0.001$). Mean values were estimated from air-tight in-situ production chambers. Carbon estimates were based on conversion factors in Cole (1983). Light values were collected under water at the same depth as chambers.

TREATMENT	DATE	OXYGEN PRODUCTION $g\ O_2\ m^{-2}\ h^{-1}$ gross/net (±se/±se)	CARBON PRODUCTION $g\ C\ m^{-2}\ h^{-1}$ gross/net (±se/±se)	MEAN LIGHT $\mu E\ m^{-2}\ s^{-1}$ (±se/±se)
Cladopha with epiphytes (n=6)	02/94	0.217/0.127 (0.06/0.04)	0.06/0.04 (0.02/0.02)	1009 (26)
	06/94	0.774/0.284 (0.06/0.04)	0.241/0.01 (0.02/0.01)	2303 (147)
Cladophora without epiphytes (n=6)	02/94	0.416/0.155 (0.06/0.07)	0.129/0.05 (0.02/0.03)	737 (239)
	06/94	0.732/0.155 (0.06/0.06)	0.23/0.11 (0.02/0.02)	2346 (203)
Cathedral Island 1 ntu (n=3)	02/94	0.663/0.145 (0.18/0.11)	0.21/0.05 (0.06/0.05)	1321 (35)
Cathedral Island 90 ntu (n=3)	02/94	0.413/0.159 (0.05/0.03)	0.13/0.05 (0.02/0.01)	800 (14)
Cathedral Island 6.5 ntu (n=3)	08/94	**A** 0.05/0.020 (0.008/0.01)	0.016/0.006 (0.003/0.004)	2102
Cathedral Island 90 ntu (n=3)	08/94	**B** 0.03/0.002 (0.006/0.006)	0.01/0.0006 (0.01/0.002)	1225
Cathedral Island 146 ntu (n=3)	08/94	**B** 0.021/0.013 (0.004/0.007)	0.007/0.004 (0.001/0.003)	290

efficient without the epiphytic diatoms, possibly due to light interference and competition for nutrients by epiphytes. Low sample size and a high variance of GPP/NPP estimates indicate the need for further sampling in order to determine a significant pattern.

Experimentally increased suspended sediment loads at Cathedral Island, in February 1994, did not significantly reduce the GPP or NPP ($p = 0.8$). Although the light was reduced by 40% from 1321 to 800 $\mu E\ m^{-2}\ s^{-1}$, it did not have an adverse affect on photosynthesis (Table 13). The cobbles used in these experiments were composed of 85% C. glomerata and 15% Oscillatoria spp. However a similar series of experiments was conducted in August 1994 and a significant difference was found between all runs (<0.001, Table 13). The summer experiment indicated respiration was the dominant process at 90 and 146 NTU treatments. Percent composition was similar between seasons and summer algal AFDM was elevated by 65%. A comparison between June and August 1994 primary production estimates showed an 80% reduction in NPP by August (Table 12). During this period the Paria River was often in spate due to an active monsoon period and river discharge was increased. These and other factors make it difficult to understand the effects of turbidity on primary production. Graham et al. (1982) reported that optimum net photosynthesis for C. glomerata occurred between 13-17°C and 300-600 $\mu E\ m^{-2}\ s^{-1}$ in laboratory experiments.

Cross-channel primary production estimates at Lees Ferry varied significantly by stage ($p < 0.001$) with 80% of the production below the minimum discharge of 140 $m^3\ s^{-1}$ (Table 13). Submerged cobbles collected from the 280 $m^3\ s^{-1}$ stage were 91% more productive than desiccated cobbles (12 h desiccation) from the same stage. This experiment was conducted during summer high volume releases to investigate optimum conditions within the varial zone at Lees Ferry. Algal composition varied by site or position of collection from 100% C. glomerata below 140 $m^3\ s^{-1}$ to almost 100% Oscillatoria spp. with some tufts of moss at the 400 $m^3\ s^{-1}$ stage. Cladophora glomerata contributed 45% of algal biomass at the 280 $m^3\ s^{-1}$ stage and Oscillatoria spp. made up the remaining biomass. Dam regulation and the cross-channel algal composition contribute to the decrease of primary production in the varial zone.

Regression analysis between mean light energy and GPP and NPP production ($p = 0.34$ and $p = 0.89$, respectively) did not reveal the expected significant positive relationship. Possible explanations include the variability in algal composition, biomass and river temperature between sites. Higher water temperature and C. glomerata biomass may counter reduced light levels. Cladophora glomerata and Oscillatoria spp. were the most common algae and their contribution to GPP and NPP estimates ranged from 100% to negligible depending on site and season.

Table 13. Primary production estimates for the varial zone at Lees Ferry cobble bar (RKM 0.8) in the Colorado River during August, 1994. Three examinations were conducted; (1) cobbles were collected from the 400 $m^3 s^{-1}$ water line and desiccated for 12 h a night prior to incubation, (2) cobbles were collected from the 280 $m^3 s^{-1}$ water line and desiccated for 12 h at night prior to incubation, (3) submerged cobbles were collected from the 280 $m^3 s^{-1}$ water line and directly incubated, 4) June 1994 estimates from below the 140 $m^3 s^{-1}$ water line were used for comparison. Significant differences in primary production (NPP) estimates based on oxygen production are indicated by bold letters ($p < 0.001$). Mean values were estimated from air-tight in-situ production chambers. Carbon estimates were based on conversion factors from Cole (1983). Light values were collected under water at the same depth as the chambers.

TREATMENT		OXYGEN PRODUCTION g $O_2 m^{-2} h^{-1}$ gross/net (±se/±se)	CARBON PRODUCTION g C $m^{-2} h^{-1}$ gross/net (±se/±se)	ENERGY kcal gross/net (±se/±se)	MEAN LIGHT μEin $m^{-2}s^{-1}$
		A			
1)	400 $m^3 s^{-1}$ desiccated (n = 3)	0.02/0.004 (0.006/0.001)	0.006/0.001 (0.002/0.001)	0.07/0.02 (0.02/0.007)	1190
		A			
2)	280 $m^3 s^{-1}$ desiccated (n = 3)	0.02/0.006 (0.003/0.003)	0.005/0.002 (0.001/0.001)	0.05/0.02 (0.02/0.01)	1914
		B			
3)	280 $m^3 s^{-1}$ submerged (n = 3)	0.11/0.06 (0.03/0.02)	0.03/0.02 (0.01/0.01)	0.38/0.22 (0.12/0.07)	1787
		C			
4)	<140 $m^3 s^{-1}$ submerged (n=6) 06/94	0.774/0.284 (0.06/0.04)	0.241/0.089 (0.02/0.01)	2.7/0.25 (0.2/0.1)	2303

This variability was most evident at Gorilla Island (RKM 352) in June. In the first experiment (n = 3), cobbles were composed of 51% C. glomerata and 49% Oscillatoria spp. and had an NPP of 0.185 g O_2 m^{-2} h^{-1}. In the second experiment (n = 3) cobbles were composed of 0.05% C. glomerata and 95% Oscillatoria spp. and had an NPP of 0.031 g O_2 m^{-2} h^{-1}. Furthermore, mean light intensity in the experiment dominated by Oscillatoria was 2576 μE m^{-2} s^{-1}; similar to that of experiment one. The 83% reduction in NPP for the second experiment suggests that the Oscillatoria assemblage is not as productive as C. glomerata. Additional experiments need to be conducted to verify these results.

An increase in water temperature can off-set algal composition and biomass differences in production estimates. When comparing summer experiments at Lees Ferry with cobbles containing 100% C. glomerata (0.669 g AFDM) to those with similar composition at Gorilla Island (0.177 g C. glomerata AFDM), we find only a 34% reduction in NPP (0.280 g O_2 m^{-2} h^{-1} at Lees Ferry compared to 0.185 g O_2 m^{-2} h^{-1} at Gorilla Island). Although there was a 52% reduction in total algal biomass at Gorilla Island and a 72% decrease in C. glomerata mass, the NPP difference is not linear. The similar mean light energy for both runs eliminates light as an independent variable. In contrast, water temperature in the incubation chambers averaged 14.3°C at Lees Ferry and 20.3°C at Gorilla Island. These data suggest that elevated water temperature can off-set variations in algal composition and biomass, thereby mitigating the negative impact of turbid water on primary production. Several investigators have suggested that irradiance is the dominant factor controlling primary production (Calow & Petts 1992).

SECONDARY PRODUCTION

Secondary Production Estimates for Gammarus lacustris: Average annual densities of Gammarus lacustris decreased between Lees Ferry (RKM 0.0) and Two Mile Wash (RKM 3.0) and from continuously submerged to fluctuating flow treatments at each site. Highest average densities (1,174 animals m^{-2} yr^{-1}) were recorded in the continuously submerged channel (controls, ≤140 m^3 s^{-1}) at Lees Ferry, while lowest average densities were measured in the varial zone (140 to 565 m^3 s^{-1}) at Two Mile Wash. Negligible densities of G. lacustris were collected in the exposed varial zone (≥283 m^3 s^{-1}) while 184 animals m^{-2} yr^{-1} were collected in the re-submerged varial zone (140 to 283 m^3 s^{-1}) at Lees Ferry. Average annual densities of G. lacustris at Two Mile Wash were 235 animals m^{-2} yr^{-1} and 7.6 animals m^{-2} yr^{-1} in the continuously submerged (controls) and exposed varial zone. No animals were recovered from within the exposed varial zone.

Annual secondary production for G. lacustris (104.2 kg dm ha^{-1} yr^{-1}) in the continuously submerged channel was an order of magnitude higher than values for the varial zone (13.9 kg dry dm ha^{-1} yr^{-1}) in the Colorado River at Lees Ferry (Tables 14-15). The area of cobble bar exposed within the varial zone (565 and 800 m^3 s^{-1}) at Lees Ferry is ~8,090 m^2 compared to ~31,855 m^2 for the combined continuously submerged and varial zone between 140 m^3 s^{-1} and 800 m^3 s^{-1} (Blinn et al. 1992). These data imply that regulated flows between 140 m^3 s^{-1} and 565 m^3 s^{-1} reduce overall annual production of G. lacustris at Lees Ferry by 65%, assuming relatively uniform distribution of G. lacustris throughout the channel.

Annual production by G. lacustris in the continuously submerged channel (≤140 m^3 s^{-1}) at Two Mile Wash, just 1.6 km below the Paria confluence, was only 34 kg dm ha^{-1} yr^{-1} (Table 16). This represents a 3-fold reduction in annual production from comparable clear water habitats at Lees Ferry just 2 km upstream from the Paria River confluence (Table 14). Periodic input of suspended sediment from the Paria River greatly reduced annual secondary production at Two Mile Wash; suspended sediment and turbidity are the only measured variables that changed between the two sites. Annual secondary production for G. lacustris in the continuously submerged channel was nearly 50 times higher than that in the re-submerged varial zone (0.8 kg dm ha^{-1} yr^{-1}) at Two Mile Wash (Table 17).

Assuming an energy equivalence of 16.54 j (joules) mg^{-1} for G. lacustris (Blinn et al. 1992), we estimated that G. lacustris in the benthic community provides ~1.7 x 10^6 kj ha^{-1} yr^{-1} available energy in the submerged river channel at Lees Ferry compared to ~5.6 x 10^5 kj ha^{-1} yr^{-1} in the submerged channel of Two Mile Wash. Also, G. lacustris in the varial zones at Lees Ferry and Two Mile Wash produce ~2.3 x 10^5 kj ha^{-1} yr^{-1} and ~1.4 x 10^4 kj ha^{-1} yr^{-1}, respectively. Thus, the fully submerged clearwater habitat at Lees Ferry is 137-fold more productive than the varial zone at Two Mile Wash.

Cho (1992) reported that it requires ~15,000 kj of energy to produce 1 kg of trout biomass. Based on these conversions and a 70% assimilation efficiency for rainbow trout (Phillips & Brockway 1959), G. lacustris could support ~113 kg of trout biomass ha^{-1} yr^{-1} in the benthic community at Lees Ferry and ≤37 kg of trout ha^{-1} yr^{-1} in the benthic community at Two Mile Wash. Data on foraging efficiencies of trout at Lees Ferry are not presently available.

At all treatment sites, animals between 7-10 mm showed a negative production (Tables 14-17). Typically, negative production values imply field sampling error and/or laboratory sorting error. We noted that G. lacustris is typically in

Table 14. Annual secondary production for Gammarus lacustris in the continuously submerged channel (≤140 $m^3 s^{-1}$) at Lees Ferry, Colorado River, AZ, between 30 September 1992 and 15 September 1993, as estimated by the size-frequency method.

Size Class (mm)	N_j (No./m^2)	ΔN_1	Geometric mean weight (mg) $(M \times M_{j+1})^{0.5}$	Production (mg m^{-2} yr^{-1})
2-3	208.66			
		33.60	0.24	8.06
3-4	175.03			
		5.60	0.30	1.68
4-5	169.41			
		38.13	0.48	18.30
5-6	131.28			
		43.50	0.80	34.80
6-7	87.82			
		26.99	1.24	33.47
7-8	60.83			
		9.17	1.86	17.06
8-9	51.63			
		-2.55	2.59	-6.61
9-10	54.19			
		-10.84	3.40	-36.86
10-11	65.02			
		21.67	4.27	92.53
11-12	43.35			
		21.67	5.18	34.19
12-13	36.42			
		7.47	6.18	46.17
13-14	28.93			
		7.16	7.46	53.41
14-15	21.78			
		6.33	8.69	55.01
15-16	15.44			
		3.78	9.95	37.61
16-17	11.66			
		3.38	11.50	38.87
17-18	8.28			
		5.83	13.55	79.00
18-19	2.34			
		0.81	15.09	12.22
19-20	1.64			
		1.23	17.08	21.01
20-21	0.41	0.41	*20.28	8.32
TOTAL ANNUAL PRODUCTION				548.24
TOTAL ADJUSTED PRODUCTION (PRODUCTION · c) =				10,416 mg m^{-2} yr^{-1}

Geometric mean weight (mg) = $(M_j \times M_{j+1})^{0.5}$; M = individual dry weight (dw) biomass (mg) of size class j.

Production = $\sum_{j=1}^{c-1} [Nj - Nj+1) \times (M_j \times M_{j+1})^{0.5}] + (Nc \times Mc)$; c = number of size classes; Nj = the average density m^{-2} ; * = mean individual dry weight biomass (mg) of 20-21 mm instars.

Table 15. Annual secondary production for Gammarus lacustris in the varial zone (140-283 $m^3 s^{-1}$) at Lees Ferry, Colorado River, Arizona, between 30 September 1992 and 15 September 1993, as estimated by the size-frequency method.

Size Class (mm)	N_j (No./m^2)	ΔN_1	Geometric mean weight (mg) $(M \times M_{j+1})^{0.5}$	Production (mg m^{-2} yr^{-1})
2-3	26.10			
		-5.50	0.24	-1.32
3-4	31.60			
		-0.10	0.30	-0.03
4-5	31.70			
		4.30	0.48	2.06
5-6	27.40			
		11.56	0.80	9.25
6-7	15.84			
		1.83	1.24	2.27
7-8	14.01			
		6.71	1.86	12.48
8-9	7.36			
		-1.94	2.59	-5.03
9-10	9.30			
		2.56	3.40	8.71
10-11	6.74			
		2.65	4.27	11.32
11-12	4.09			
		1.23	5.18	6.37
12-13	2.86			
		1.12	6.18	6.92
13-14	1.74			
		0.000	7.46	0.000
14-15	1.74			
		0.21	8.69	1.82
15-16	1.53			
		0.81	9.95	8.06
16-17	0.72			
		0.000	11.50	0.000
17-18	0.72			
		0.51	13.55	6.91
18-19	0.21	0.21	*15.09	3.71
TOTAL ANNUAL PRODUCTION				72.96
TOTAL ADJUSTED PRODUCTION (PRODUCTION · c) =				1,386 mg m^{-2} yr^{-1}

Geometric mean weight (mg) = $(M_j \times M_{j+1})^{0.5}$; M = individual dry weight (dw) biomass (mg) of size class j.

Production = $\sum_{j=1}^{c-1} [Nj - Nj+1) \times (M_j \times M_{j+1})^{0.5}] + (Nc \times Mc)$; c = number of size classes; Nj = the average density m^{-2}; * = mean individual dry weight biomass (mg) of 20-21 mm instars.

Table 16. Annual secondary production for Gammarus lacustris in the continuosly submerged channel (≤140 $m^3 s^{-1}$) at Two Mile Wash (below Paria confluence), Colorado River, AZ, between 30 September 1992 and 15 September 1993, as estimated by the size frequency method.

Size Class (mm)	N_j (No./m^2)	ΔN_1	Geometric mean weight (mg) $(M \times M_{j+1})^{0.5}$	Production (mg m^{-2} yr^{-1})
2-3	14.83			
		0.92	0.24	0.22
3-4	13.91			
		-1.12	0.30	-0.34
4-5	15.03			
		-1.74	0.48	-0.84
5-6	16.77			
		4.19	0.80	3.35
6-7	12.58			
		-3.17	1.24	-3.93
7-8	15.75			
		-0.19	1.86	-0.35
8-9	15.94			
		-3.49	2.59	-9.04
9-10	19.43			
		-2.96	3.40	-10.07
10-11	22.39			
		1.94	4.27	8.28
11-12	20.45			
		4.80	5.18	24.86
12-13	15.65			
		1.23	6.18	7.60
13-14	14.42			
		0.000	7.46	0.000
14-15	14.42			
		2.76	8.69	23.98
15-16	11.66			
		4.81	9.95	47.86
16-17	6.85			
		3.78	11.50	43.47
17-18	3.07			
		1.64	13.55	22.22
18-19	1.43			
		1.33	15.09	20.07
19-20	0.10	0.10	*17.08	1.71

TOTAL ANNUAL PRODUCTION 179.05

TOTAL ADJUSTED PRODUCTION (PRODUCTION · c) = 3,402 mg m^{-2} yr^{-1}

Geometric mean weight (mg) = $(M_j \times M_{j+1})^{0.5}$; M = individual dry weight (dw) biomass (mg) of size class j.

Production = $\sum_{j=1}^{c-1} [Nj - Nj+1) \times (M_j \times M_{j+1})^{0.5}] + (Nc \times Mc)$; c = number of size classes; Nj = the average density m^{-2}; * = mean individual dry weight biomass (mg) of 20-21 mm instars.

Table 17. Annual secondary production for Gammarus lacustris in the varial zone (140-283 $m^3 s^{-1}$) at Two Mile Wash (below Paria confluence), Colorado River, Arizona, between 30 September 1992 and 15 September 1993, as estimated by the size frequency method.

Size Class (mm)	N_j (No./m^2)	ΔN_1	Geometric mean weight (mg) $(M \times M_{j+1})^{0.5}$	Production (mg m^{-2} yr^{-1})
2-3	1.74			
		1.02	0.24	0.25
3-4	0.72			
		0.31	0.30	0.09
4-5	0.42			
		-0.20	0.48	-0.10
5-6	0.61			
		0.10	0.80	0.08
6-7	0.51			
		0.00	1.24	0.00
7-8	0.51			
		0.51	1.86	0.95
8-9	0.00			
		-0.51	2.59	-1.32
9-10	0.51			
		0.10	3.40	0.34
10-11	0.41			
		-0.10	4.27	-0.43
11-12	0.51			
		0.00	5.18	0.00
12-13	0.51			
		0.30	6.18	1.85
13-14	0.21			
		-0.51	7.46	-3.81
14-15	0.72			
		0.51	8.69	4.43
15-16	0.21	0.21	9.95	2.09

TOTAL ANNUAL PRODUCTION 4.42

TOTAL ADJUSTED PRODUCTION (PRODUCTION · c) = 84 mg m^{-2} yr^{-1}

Geometric mean weight (mg) = $(M_j \times M_{j+1})^{0.5}$; M = individual dry weight (dw) biomass (mg) of size class j.

Production = $\sum_{j=1}^{c-1} [Nj - Nj+1) \times (M_j \times M_{j+1})^{0.5}] + (Nc \times Mc)$; c = number of size classes; Nj = the average density m^{-2}; * = mean individual dry weight biomass (mg) of 20-21 mm instars.

amplexus (sexual pairing) at 7-10 mm at Lees Ferry. Since the pattern is consistent for all site treatments, especially for 9-10 mm animals (Tables 14-17), we propose the negative production depicts a behavioral response for G. lacustris during mating. If mating animals modify their swimming and/or habitat selection (i.e., move to deeper water) they may be more difficult to sample. However, if animals return to a normal behavior in the next size interval after mating, a negative production value would be recorded between successive size classes. This may help explain the consistent negative production values within the 7-10 mm size classes.

Average annual biomass of eggs in brood pouches of female G. lacustris was 118.5 mg m^{-2} in the continuously submerged channel at Lees Ferry compared to 3.9 mg m^{-2} in the corresponding varial zone. At Two Mile Wash, the continuously submerged zone had an average of 33.9 eggs m^{-2}, while the varial zone had only 2.5 eggs m^{-2}. This infers a dramatic reduction in fecundity in the varial zone compared to the submerged channel at Lees Ferry. Eggs were first observed in females ≥7 mm in length.

Gammarus lacustris reproduction at Two Mile Wash was greatly reduced from that at Lees Ferry. Average annual mass contributed by eggs in the submerged channel was only 22.7 mg m^{-2} (12.5 eggs m^{-2}) while no female brood pouches had eggs in the varial zone at Two Mile Wash.

Our production estimates for G. lacustris in the benthic community of the Colorado River at Lees Ferry (104.8 kg dm ha^{-1} yr^{-1}) is lower than some previous reports for congeneric amphipods in small lotic ecosystems. Waters and Hokenstrom (1980) reported between 231-271 kg dm ha^{-1} yr^{-1} for G. pseudolimnaeus in Valley Creek, Minnesota, among the highest single-species estimate for amphiphods in lotic ecosystems. Thus, production in the reach of Valley Creek is 2-fold higher than benthic production for G. lacustris in the Colorado River at Lees Ferry. Waters and Hokenstrom (1980) further reported subsequent years, during relatively high siltation, G. pseudolimnaeus yielded only 64 kg dm $ha^{-1}yr^{-1}$. Other reports on annual production by Gammarus in lotic ecosystems include 130 kg dm ha^{-1} yr^{-1} for G. pulex in a Dorset Chalk stream in England (Welton 1979) and 39 kg dm ha^{-1} yr^{-1} for G. pulex in a small Danish stream (Mortensen 1982).

Reports on annual production for congeneric amphipods in lentic environments are also higher than estimates in the Colorado River. Tilly (1968) reported 366 kg dm ha^{-1} yr^{-1} for G. pseudolimnaeus in Cone Spring, Iowa, while Beattie et al. (1972) estimated 130 kg dm ha^{-1} yr^{-1} for G. tigrinus in Tjeukemeer Reservoir in

the Netherlands, and LaFrance and Ruber (1985) estimated that production for G. mucronatus in a Massachusetts salt marsh was between 124 to 158 kg dm m^{-2} yr^{-1}. However, Iversen and Jessen (1977) reported only 38 kg dm ha^{-1} yr^{-1} for Gammarus in Rold Kilde Spring, Denmark.

In contrast, reports on annual secondary production for congeneric amphipods in large river ecosystems are considerably lower than those reported in the tailwaters of Glen Canyon Dam. Mann (1971) reported 0.14 kg dm ha^{-1} yr^{-1} for G. pulex in the River Thames, England, several orders of magnitude lower than values for benthic production for G. lacustris in the Colorado River at Lees Ferry.

Our secondary production values for G. lacustris in the benthic community at Lees Ferry may underestimate actual production. We propose that nearly all the G. lacustris mass in the varial zone becomes dislodged daily and enters stream drift during the rising limb of the hydrograph. The high levels of stream drift at Lees Ferry support this conclusion (See Chapter Three: Organic Stream Drift). For example, mean annual drift at Lees Ferry is 2.3 x 105 g dm G. lacustris yr^{-1} or ~550 g d^{-1} m^{-3} s^{-1} at 300 m^3 at 284 m^3 s^{-1}. Leibfried and Blinn (1986) also reported that G. lacustris drift increased during the rising limb of the hydrograph in the Colorado River. Also, Waters and Hokenstrom (1980) reported high annual mean drift (41-46 g d^{-1} m^{-3} s^{-1}) for G. pseudolimnaeus in Valley Creek during periods of high secondary production. The fact that neglible animals are collected in the varial zone during exposed periods further supports high downstream losses in this unstable habitat. Recruitment into the re-submerged varial zone occurs from the continuously submerged river channel and downstream drift. Therefore, inclusion of drift biomass (or production in the varial zone) at Lees Ferry elevates estimates of secondary production by G. lacustris to 6.21 kg dm ha^{-1} yr^{-1} in the submerged zone ($\leq$140 m^3 s^{-1}) at Lees Ferry, or an annual P/$\bar{B}$ ratio of ~3.2.

Secondary Production Estimates for Chironomid Larvae: Estimates on secondary production for the chironomid community at Lees Ferry showed similar patterns to G. lacustris under regulated flows and elevated suspended sediments. The total annual biomass for the chironomid community in the continuously submerged clear water zone at Lees Ferry was 4.3 g dm m^{-2} compared to 0.56 g dm m^{-2} in the varial zone at Lees Ferry. Downstream in the more turbid water at Two Mile Wash, the total annual biomass was 0.58 and 0.068 g dm m^{-2} in the continuously submerged and varial zones, respectively.

In contrast to G. lacustris, larval size classes for taxa within the chironomid community at Lees Ferrry and Two Mile Wash were not separated. Therefore,

we were not able to use the size frequency method as outlined for G. lacustris. Instead, production estimates were converted from annual P/$\bar{B}$ values taken from Berg and Hellenthal (1991). After extensive studies, these investigators reported the average annual P/$\bar{B}$ ratio was 9.5 for 14 chironomid larval species. Therefore by knowing the average annual chironomid biomass for each treatment [mean total biomass/number of sampling intervals (n = 26)], we calculated P. Although this application does not yield as high a resolution as the size frequency method, it does provide general estimates of production.

Therefore using this application (P/$\bar{B}$ = 9.5) we estimated production values of 15.7 kg dm ha^{-1} yr^{-1} for the chironomid community in the continuously submerged zone at Lees Ferry compared to 2.0 kg dm ha^{-1} yr^{-1} for the varial zone at the Ferry. Likewise, production estimates in the control submerged zone at Two Mile Wash were 2.1 kg dm ha^{-1} yr^{-1} compared to 0.25 kg dm ha^{-1} yr^{-1} in the varial zone at the same site.

Production estimates for chironomids in other studies have ranged from 4.7 kg dm ha^{-1} yr^{-1} in Factory Brook, Massachusetts (Neves 1979) to 190 kg dm ha^{-1} yr^{-1} in the Hudson River (Menzie 1981). Recently Berg and Hellenthal (1991) reported a community chironomid production of 297 kg dm ha^{-1} yr^{-1} in a north temperate stream, the highest value reported to this time.

Although the production estimates for chironomids in the Colorado River are relatively high it is likely that these estimates are conservative because some investigators propose that annual P/$\bar{B}$ ratios may be >100 (Hauer & Benke 1991). Assuming an annual P/$\bar{B}$ ratio of 100, community chironomid production in the Colorado River may reach 165 kg dm ha^{-1} yr^{-1} in the continuously submerged zone at Lees Ferry. We propose that community production by chironomids may be somewhere between our low estimate (16 kg dm ha^{-1} yr^{-1}) and high estimate (165 kg dm ha^{-1} yr^{-1}).

As reported for G. lacustris, large amounts of chironomid biomass enter stream drift within varial zones of Lees Ferry and Two Mile Wash. This again is witnessed by the dynamic recruitment of chironomid larvae in the exposed varial zone following re-submergence. We estimated ~8.9 mg m^{-3} enter stream drift during fluctuating flows at Lees Ferry. If stream drift were taken into account, we estimate that an additional 2.0 kg dm ha^{-1} yr^{-1} production (production in the Lees Ferry varial zone) or 17.7 kg dm ha^{-1} of chironomid biomass is produced at Lees Ferry each year, assuming a P/$\bar{B}$ ratio of 9.5.

The high occurrence of chironomid larvae in the diets of exotic and native fishes in the Colorado River (Leibfried, personal communication) further supports our high production estimates for midge larvae in the river. Blinn et al. (1992) reported the dense epiphyton associated with C. glomerata yields ~1.72 x 10^6 kj ha^{-1} at Lees Ferry, which appears to provide adequate energy to support chironomid mass at the next trophic level. Chironomid larvae graze the abundant epiphytic community and provide a critical intermediate link between primary producers and fish in the Colorado River ecosystem (Blinn et al. 1992). The high production values for chironomids in the Colorado River results, in part, from the high turnover rates for midges. It typically requires G. lacustris >12 mo to complete a life cycle (Pennak 1989), while some midge species complete larval development in as little as 2 wk (Hauer & Benke 1991). Preliminary results from midge rearing studies in our laboratory indicate Cricotopus annulator completes larval development within 30 to 50 d at 11-12°C, and this species makes up ~80% of the midge population at Lees Ferry (Blinn et al. 1992)

SUMMARY

Benthic primary production decreased downstream as turbidity increased, due to tributary input, and phytobenthos decreased. In general, higher production was measured during the summer compared to winter months. Higher downstream water temperature may offset this spatial pattern and should be considered when planning for a multiple level intake system. No significant difference occurred in production between C. glomerata with epiphytes versus Cladophora without epiphytes, suggesting that C. glomerata NPP may increase if epiphyte density decreases. Optimum light conditions for C. glomerata growth in this system requires further study.

Both G. lacustris and the chironomid community have high production rates in the submerged zone (≤140 m^3 s^{-1}) at Lees Ferry. However, both invertebrates are strongly affected by regulated flows from Glen Canyon Dam and suspended sediment input from tributaries. Gammarus lacustris and chironomid production was reduced by over 80% in the tailwater varial zone at Lees Ferry. Further reductions (≥80%) in downstream production at the somewhat turbid habitat of Two Mile Wash were caused by suspended sediments entering from the Paria River. Considerable mass of both invertebrates enter stream drift on a daily basis. Inclusion of stream drift in production estimates increases overall production values for each invertebrate. Both G. lacustris and chironomid larvae play an important role as intermediate links in the Colorado River food web.

CHAPTER THREE: ORGANIC STREAM DRIFT

INTRODUCTION

Stream drift in natural lotic ecosystems has received considerable attention over the past several decades (Waters 1972, Allan & Russek 1985, Brittain & Eikeland 1988, Wilzbach et al. 1988), while only a few studies have focused on similar behavior in regulated running waters, especially in arid biomes. In general, a positive correlation exists between invertebrate drift and discharge (Pearson et al. 1968, Brooker & Hemsworth 1978, Leibfried & Blinn 1986, Blinn & Cole 1991), with a change in flow after long periods of stable discharge yielding greatest organic transport (Irvine 1985; Perry & Perry 1986). Elevated discharges increase scouring potential and may exert strong selective pressures on benthic organisms (Brittain & Eikeland 1988). Reduced flow can increase stream drift through behavioral factors such as crowding, reduced gas concentration, and avoidance of desiccation (Minshall & Winger 1968, MacPhee & Brusven 1973, Armitage 1977, Corrarino & Brusven 1983, Perry & Perry 1986, Blinn et al. 1992).

Algal drift in regulated streams has received less attention than invertebrate drift. Armitage (1977) reported filamentous algae and moss dominated the non-faunal drift in the regulated River Tees below Cow Green Dam, Great Britain. Leibfried & Blinn (1986) also reported increased algal drift during the rising arm of the hydrograph from Glen Canyon Dam (GCD) in the Colorado River, Arizona.

Over sixty percent of the algal standing stock (primarily Cladophora glomerata) in the Colorado River corridor (386 km) is produced in 26 km between GCD and the Paria River, the first significant tributary (Blinn et al. 1992). The dramatic decrease in downriver standing crop of C. glomerata results from heavy input 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. The clear, cold tailwaters immediately below GCD and abundant armoured substrates provide excellent habitat for C. glomerata. This highly branched filamentous green alga provides refugia and food for the macroinvertebrate assemblage in the tailwaters of GCD (Blinn et al. 1992, Hardwick et al. 1992, Shannon et al. 1994).

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, especially during regulated fluctuating flows associated with hydroelectric power production (Leibfried & Blinn 1986),

and become part of downstream drift. Due to the cessation of normal allochthonous riverine drift by Glen Canyon Dam and the overall limited downstream production in the Grand Canyon reach (Blinn et al. 1992), it has been proposed that stream drift, and especially C. glomerata drift packets with associated epiphyton and macroinvertebrate communities, provide food in the form of coarse particulate organic matter (CPOM) to downstream biotic communities in the Colorado River.

We examined several aspects of organic drift in a large regulated river in an arid biome. Specifically, we 1) examined the quantity and composition of stream drift over distance 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 (TOC) during regulated and steady flows, and 4) determined the effects of river hydraulics (rapids) on the mass, macroinvertebrate composition, and food value of C. glomerata drift packets throughout the Colorado River corridor.

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. 1). Lees Ferry, located 24 km below GCD, is designated 0.0 river kilometer (RKM).

GCD releases water from the hypolimnion of Lake Powell with a maximum power plant discharge of 934 $m^3 s^{-1}$ (Stanford & Ward 1991). Operation of GCD is governed by Interim Flow criteria until the GCD Environmental Impact Statement is completed and operation decisions are finalized (Randle et al. 1993, U.S. Bureau of Reclamation 1994). Interim Flows have a peak discharge of 566 $m^3 s^{-1}$ and a minimum of 141 $m^3 s^{-1}$ with a maximum up-ramp of 71 $m^3 s^{-1}$ and a maximum down-ramp of 42 $m^3 s^{-1}$. Maximum ranges of daily fluctuations vary from 170 $m^3 s^{-1}$ to 226 $m^3 s^{-1}$ based on projected monthly water allotments.

The biotic characteristics of the study site throughout the canyon are shaped by discharge regulation, channel morphology, and biome effects via tributary inputs of suspended sediments (Blinn et al. 1992). Waters above the Paria River (1.0 RKM) support high standing crops of Cladophora glomerata and a macroinvertebrate assemblage of Gammarus lacustris, chironomid larvae, and gastropods (Blinn et al. 1992). The consistently clear, cold tailwaters (8-12°C) below GCD are dramatically altered at the Paria River confluence where a mean

of 3.02 x 10^6 tons of suspended sediments annually enter the Colorado River (Andrews 1991). Due to rapid light extinction, mean annual standing mass of C. glomerata and associated macroinvertebrates are dramatically reduced throughout the remainder of the river corridor (Blinn et al. 1992, Yard et al. 1992). The Colorado River within Glen and Grand Canyons is a run-pool-drop river with a shallow gradient of 1.5 m 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 temperatues drop below 0°C at night.

METHODS

Drift Collections: Near-shore surface drift samples (0.0-0.5 m deep) were collected on September 1993, January, March, and June 1994 at the 10 downriver sites used by Blinn et al. (1992; Fig. 1). Collections were made with a circular tow nèt (48 cm diameter opening, 0.5 mm nylon mesh) held in place behind a moored pontoon raft or secured to the river bank if the raft was in an eddie. Collections were taken in triplicate at approximately 0600 h and 1800 h at each site to establish the extent to which velocity affects drift. September samples were preserved with AFA (alcohol, formalin, and acetic acid) and sorted into six categories including: Gammarus lacustris, chironomid larvae, simuliid larvae, other macroinvertebrates, Cladophora glomerata and detritus. Animals 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 (Table 1). All collection and sorting techniques followed this protocol unless ortherwise noted. Current velocity was measured for volumetric calculations using a Marsh McBirney electronic flow meter (Model # 201). River discharge was determined in reference to U.S.G.S. periods by time of day at the nearest stream gauges for each collection. The duration of all collections (n = 276) averaged four 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 material (0.054 g m^{-3} s^{-1}, S.E. ± 0.005; Culp et al. 1994)

Twelve to 20 packets of drifting C. glomerata were randomly collected during 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 Rapids (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 11 biotic categories: C. glomerata, Oscillatoria spp., detritus, miscellaneous algae and macrophytes, G. lacustris, chironomids, simuliids, tubificids, lumbriculids, gastropods, and miscellaneous macroinvertebrates. Densities for oligochaetes were established through regression analysis of biomass because of fragmentation while sorting. The resulting equation was:

$$\text{Tubificid density} = 2418.5709\ (\text{Ash-free Dry Mass}) + 14.9265$$
$$(R^2 = 0.887;\ F_{1,138} = 1066.044;\ p < 0.0001).$$

Epiphyton was removed from C. glomerata by agitating algal filaments in WhirlPacs® containing 200 ml of filtered river water for two min (Blinn et al. 1992). Hyrax® mounts were made to determine diatom density and composition from a minimum of 200 cells at 1000x magnification for each sample.

We examined the influence of steady versus repeated fluctuating flows on stream drift at Lees Ferry, AZ, 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 six-h intervals starting at 0600 h for five days. Discharges from Glen Canyon Dam were held steady (226 $m^3 s^{-1}$) the first three days (May 29-31, 1993) followed by two days of fluctuating flows (discharges from 141 to 283 $m^3 s^{-1}$). Water velocity was measured with a Marsh McBirney electronic flow meter (Model 201) before and after each collection period for volumetric calculations. Samples were preserved in AFA and sorted using the above protocol.

Total organic carbon (TOC) concentrations were also measured at Lees Ferry during a steady and fluctuating flow regime in May 1994. Drift and TOC samples were collected at 0600 h and 1800 h (low and high water) at Lees Ferry and at Paria River cobble (RKM 3.2) on the third and final day of 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 L^{-1}) was measured for each sample.

Tributary Drift Collections: We examined the contribution of organic drift into the Colorado River from 11 tributaries between Lees Ferry and Diamond Creek in January, March, and June, 1994 (Fig. 1). These tributaries were the same as those used by Blinn et al. (1992). A rectangular drift net (0.363 mm mesh) was positioned for 10 min (n = 3 replicates) 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 Survery (Glen Canyon Environmental Studies, personal communication).

In-situ Desiccation Experiments: This experiment was designed to determine the effect of repeated 12-h night exposure periods on C. glomerata and macroinvertebrate 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, AZ. 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, 81 cm apart. Tops and upstream ends of each sluiceway were covered with nylon mesh (0.5 mm) net to enhance water flow through each sluice and were hung into 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 randomly divided into two treatments, eight continuously submerged controls and eight that were pulled out of the water nightly for 12 h (1800-0600 h) for three consecutive days. This cycle was designed to simulate fluctuating flow dam operations, in which low water occurs during the night in the tailwaters of GCD. Four cobbles with C. glomerata and an associated macroinvertebrate assemblage (30 cm in circumference) were placed into each sluice. These cobbles were gathered from below the 141 m^3s^{-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. 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 scrapped clean.

The following physical parameters were recorded at 0600 h, 1200 h, and 1800 h: % cloud cover, % humidity, water temperature, daily minimum and maximum air temperatures, Secchi depth, and river discharge. Discharge information 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 (Model # 201).

Statistical Analyses: Multivariate analyses of variance (MANOVA) were used to analyze categorical predictor variables (biomass estimates) and multiple response variables (physical parameters/treatment) for benthic, drift, and sluiceway experiments. Multivariate repeated measures analyses were also perfomred on

sluiceway data. Hydraulic impact on C. glomerata drift packets were analyzed with a Student t-test. All calculations were performed with SYSTAT computer software on ln+1 transformed data (Version 5.1, Wilkinson, 1989).

RESULTS

Downriver Drift: Multivariate analysis showed a significant positive correlation between biomass of stream drift and discharge (Wilks' Lambda, $F = 4.2$, $p < 0.001$, $n = 132$; Figs. 24 - 28) and distance from Glen Canyon Dam (GCD) (Wilks' Lambda, $F = 2.79$, $p < 0.001$, $n = 276$). Discharge (226 to 510 $m^3 s^{-1}$) had a selective effect on drift components. Univariate analysis showed that detritus was positively influenced by discharge ($F = 5.5$, $p < 0.0001$), in contrast all other biotic categories (Gammarus lacustris, Cladophora glomerata, chironomids, simuliiids, oligochaetes, and gastropods) had a significant negative relationship with discharge ($F = 2.7$, $p < 0.001$, all categories). The relationship between detritus and discharge is not linear with a drop in biomass between 350 and 450 $m^3 s^{-1}$ (Fig. 24). Discharges between 340 and 395 $m^3 s^{-1}$ increased detrital drift by 55%, with another 80% increase above 450 $m^3 s^{-1}$.

Drift composition changed with distance from GCD. There was a significant increase of drifting material through the Grand Canyon, however, G. lacustris and miscellaneous algae/macrophytes did not show a significant difference between sites ($F = 0.43$, $p = 0.99$, $n = 276$; $F = 1.38$, $p = 0.09$, $n = 276$, respectively). Other categories varied significantly between sites ($F = 3.3$, $p < 0.001$), but increased with distance. Terrestrial insects collected in drift samples comprised only 0.001% of the total number of animals collected (11 of 10,708 animals).

Drift composition and biomass varied significantly by season (Wilks' Lambda, $F = 10.5$, $p < 0.00001$, $n = 276$; Figs. 25-28). Univariate analyses showed a lack of seasonal variation for G. lacustris and miscellaneous algae/macrophytes ($F = 0.19$, $p = 0.82$, $n = 276$; $F = 1.25$, $p = 0.28$, $n = 276$, respectively), while all other biomass categories varied seasonally ($F = 10.8$, $p < 0.0001$, all categories). Collections during September 1993 had the highest mean total organic drift (0.08 $g\ m^{-3} s^{-1}$ AFDM) and were composed primarily of detritus, probably due to tributary input. Cladophora glomerata drift increased through the spring to a maximum of 0.015 $g\ m^{-3} s^{-1}$ AFDM in June (Fig. 28). This may have been due to an abnormally dry year which reduced tributary input and caused unusually clear water. Macroinvertebrate biomass, density and diversity also increased between March and June collections; i.e, a 55% increase in aquatic dipterans and a 66% increase in miscellanous macroinvertebrates. Macroinvertebrate AFDM

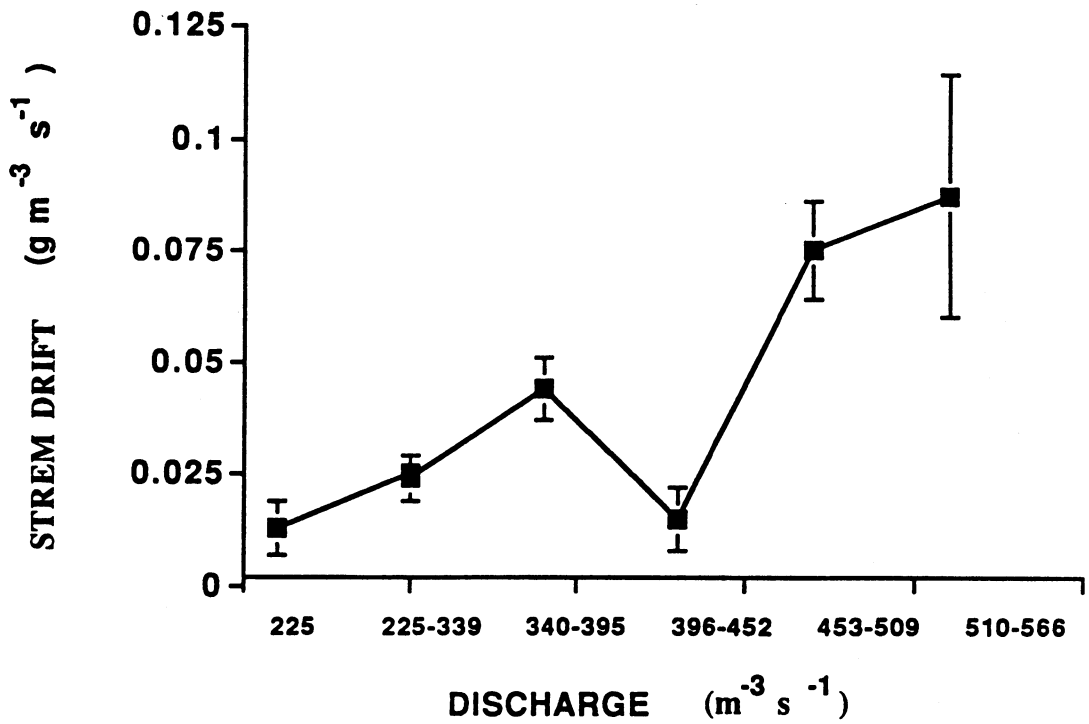


Figure 24. Comparison of near-shore stream drift collections (g AFDM m^{-3} s^{-1}) and discharge (m^3 s^{-1}) in the Colorado River corridor through Grand Canyon National Park, Arizona.

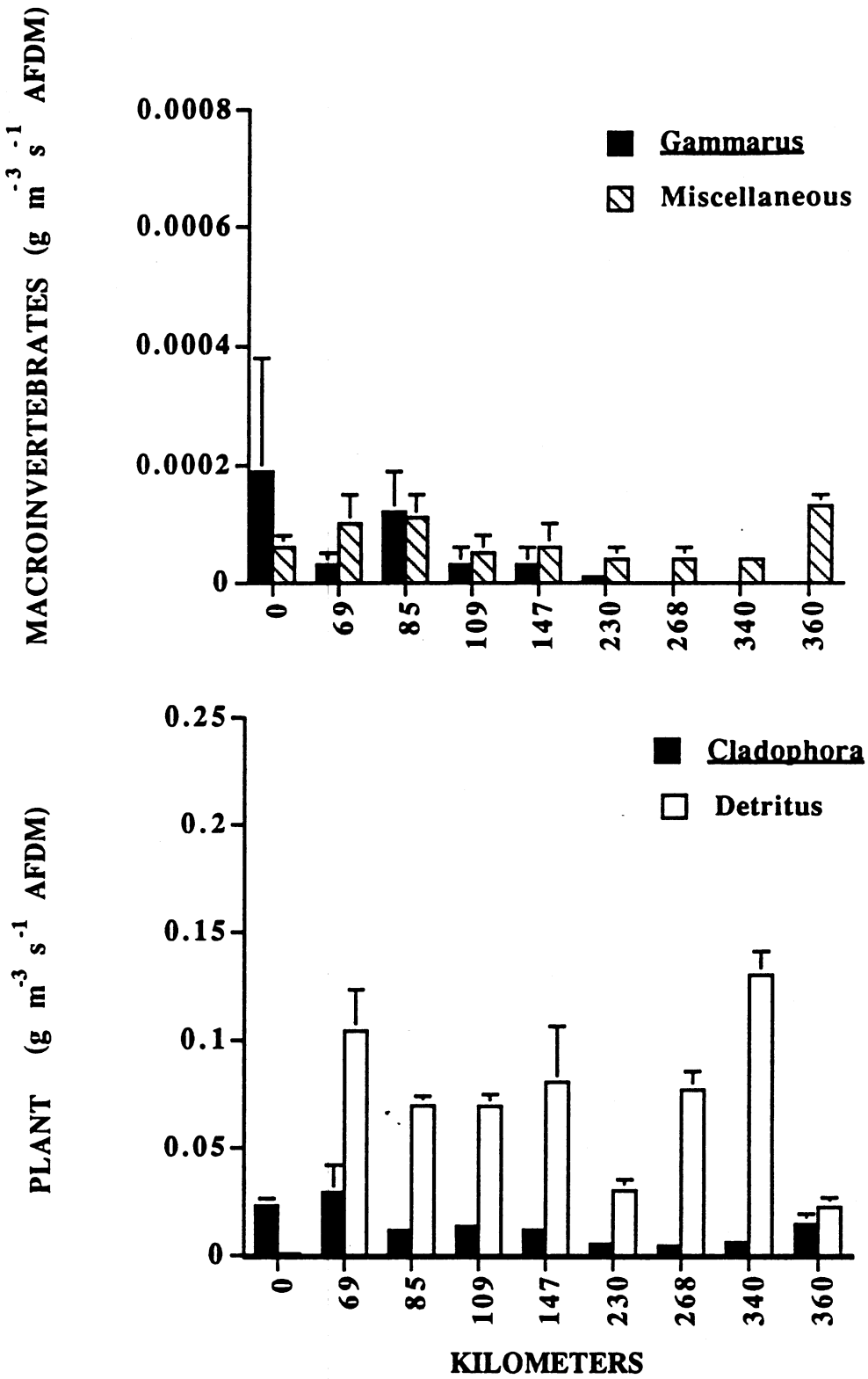


Figure 25. Average mass (g AFDM m^{-3} s^{-1}) of plants, macroinvertebrates and detritus in stream drift at collection sites in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362) during September 1993. Error bars represent ± 1 S.E.

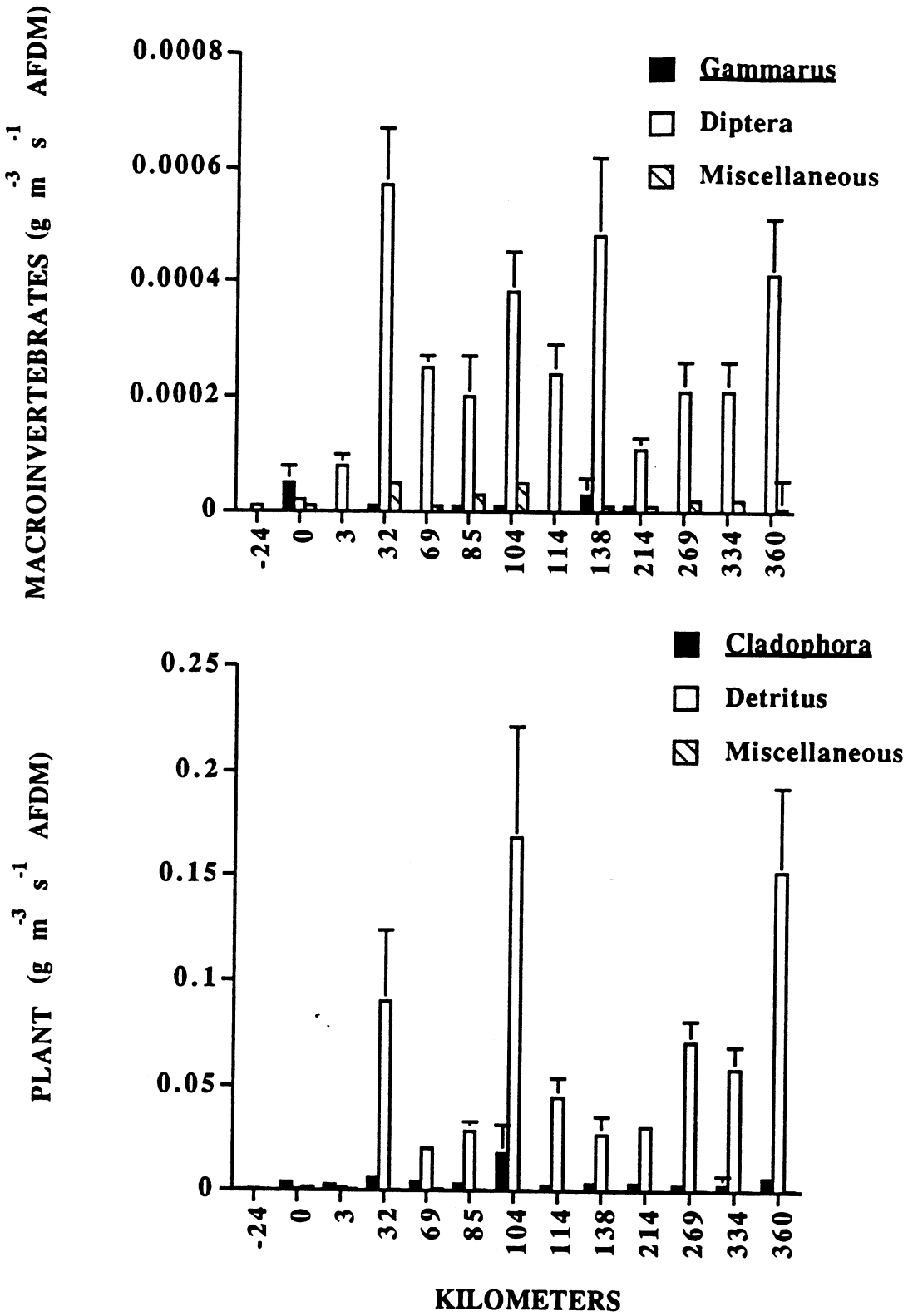


Figure 26. Average mass (g AFDM m^{-3} s^{-1}) of plants, macroinvertebrates and detritus in stream drift at collection sites in the Colorado River between Glen Canyon Dam (RKM -24) and Diamond Creek (RKM 362) during January 1994. Error bars represent ±1 S.E.

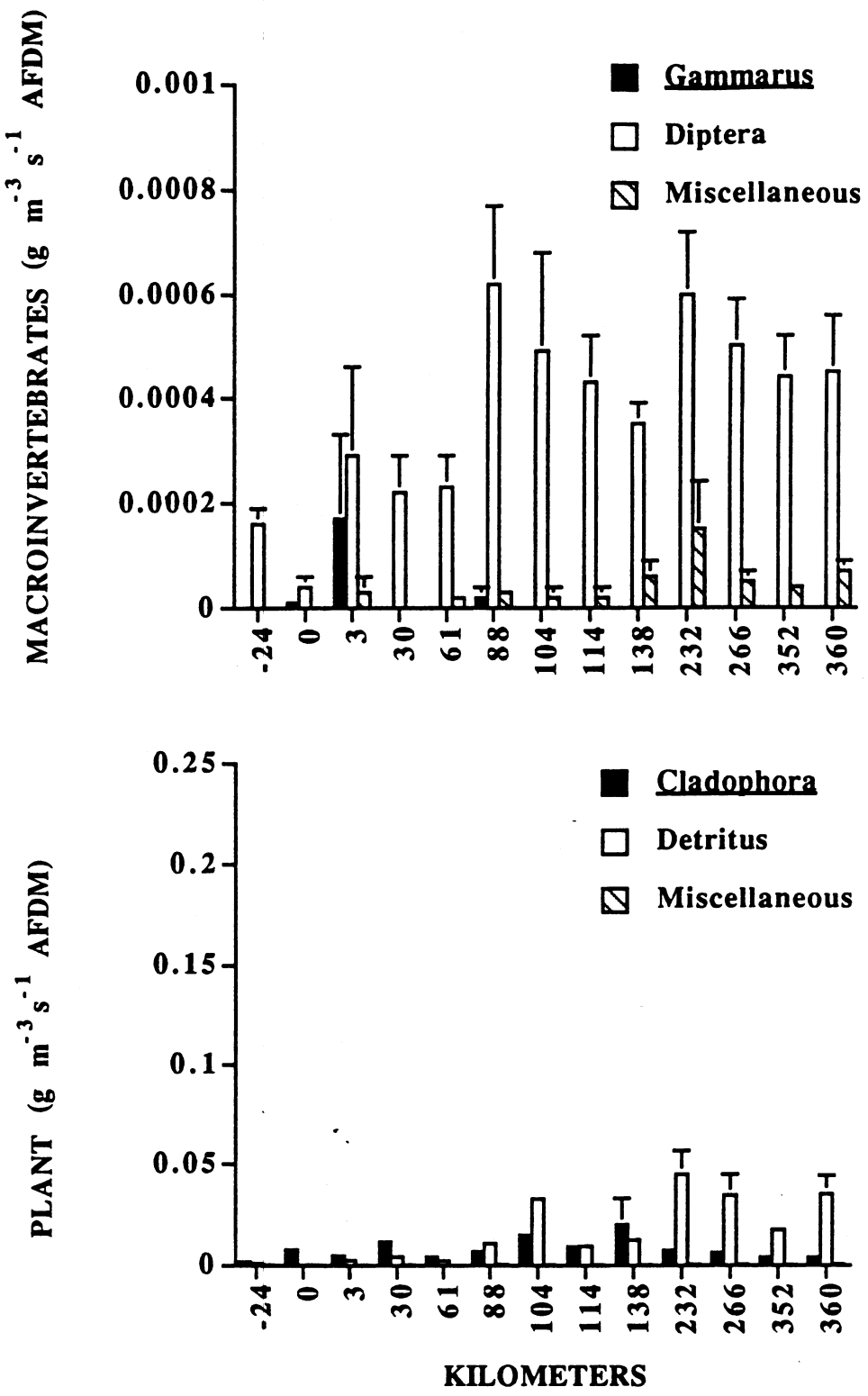


Figure 27. Average mass (g AFDM m^{-3} s^{-1}) of plants, macroinvertebrates and detritus in stream drift at collection sites in the Colorado River between Glen Canyon Dam (RKM -24) and Diamond Creek (RKM 362) during March 1994. Error bars represent ± 1 S.E.

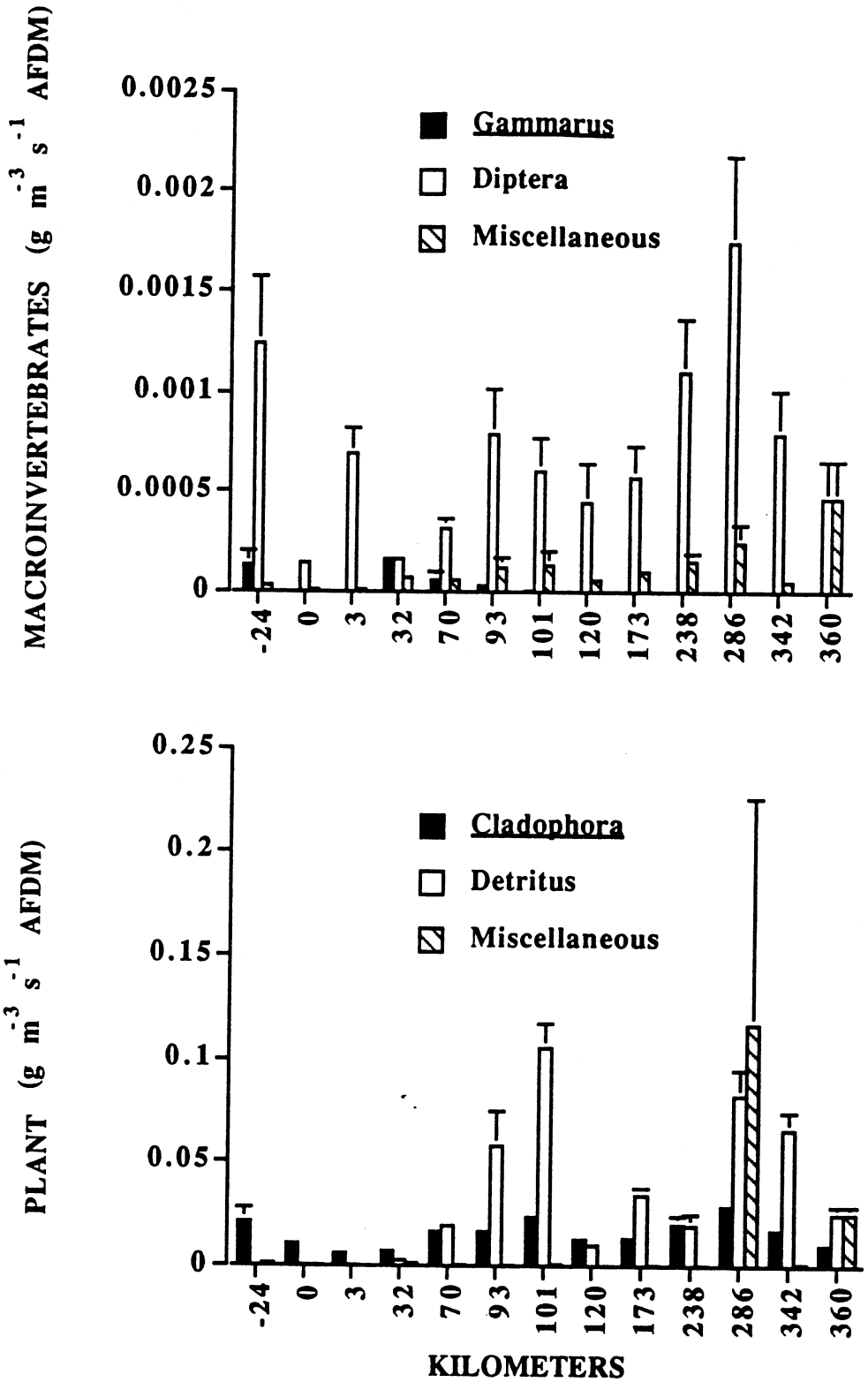


Figure 28. Average mass (g AFDM m^{-3} s^{-1}) of plants, macroinvertebrates and detritus in stream drift at collection sites in the Colorado River between Glen Canyon Dam (RKM -24) and Diamond Creek (RKM 362) during June 1994. Error bars represent ±1 S.E.

drift was 2.3 g m^{-3} s^{-1} (S.E. ±0.3) in March (Fig. 27), compared to 5.9 g m^{-3} s^{-1} (S.E. ±0.8) in June (Fig. 28).

Seasonal and longitudinal variations in organic drift are influenced by suspended sediments and debris from tributary input, which is dependant on climatic conditions. Detritus in the Colorado River is comprised primarily of finely ground allochthonous material derived from riparian vegetation and tributary spates.

Cladophora glomerata Drift Packets: The mass of C. glomerata drift packets changed significantly both spatially ($F_{7,371} = 11.56$, $p < 0.0001$) and temporally ($F_{7,371} = 6.93$, $p = 0.013$) in the Colorado River through Grand Canyon. Maximum AFDM for C. glomerata 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. Cladophora glomerata drift packets had the highest mass during September (0.6 g AFDM, S.E. ±0.2), while March drift packets had the lowest AFDM (0.01 g, S.E. ±0.002)

In a separate experiment to examine the effects of rapids on the integrity of C. glomerata packets, we noted a significant ($F_{1,40} = 6.45$, $p = 0.015$) 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 macroinvertebrates were found in the Badger Creek Rapid collections; they had apparently been 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 (Stevens 1983, Kieffer 1985).

Densities of epiphytic diatoms in drifting C. glomerata packets changed significantly with distance from GCD ($F_{3,128} = 8.9$; $p < 0.01$, Fig. 29). 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). Furthermore, the proportion of up-right diatom taxa diatom decreased with distance downstream ($F_{7,128} = 4.88$; $p < 0.0001$; Fig. 29). The more prostrate taxa include Cocconeis pediculus, Gomphonema spp., Diatoma tenue, and Achnanthes spp., while up-right taxa included Rhoicosphenia curvata and Diatoma vulgare. The greatest difference in composition by site was between GCD tailwaters (GCD/Lees Ferry) and Marble Canyon (Paria/Tanner Washes) where D. vulgare was replaced by C. pediculus. There was no significant difference in composition of epiphytic diatoms ($p > 0.05$) between GCD and Lees Ferry or Two-Mile Wash and Tanner Wash (RKM 108).

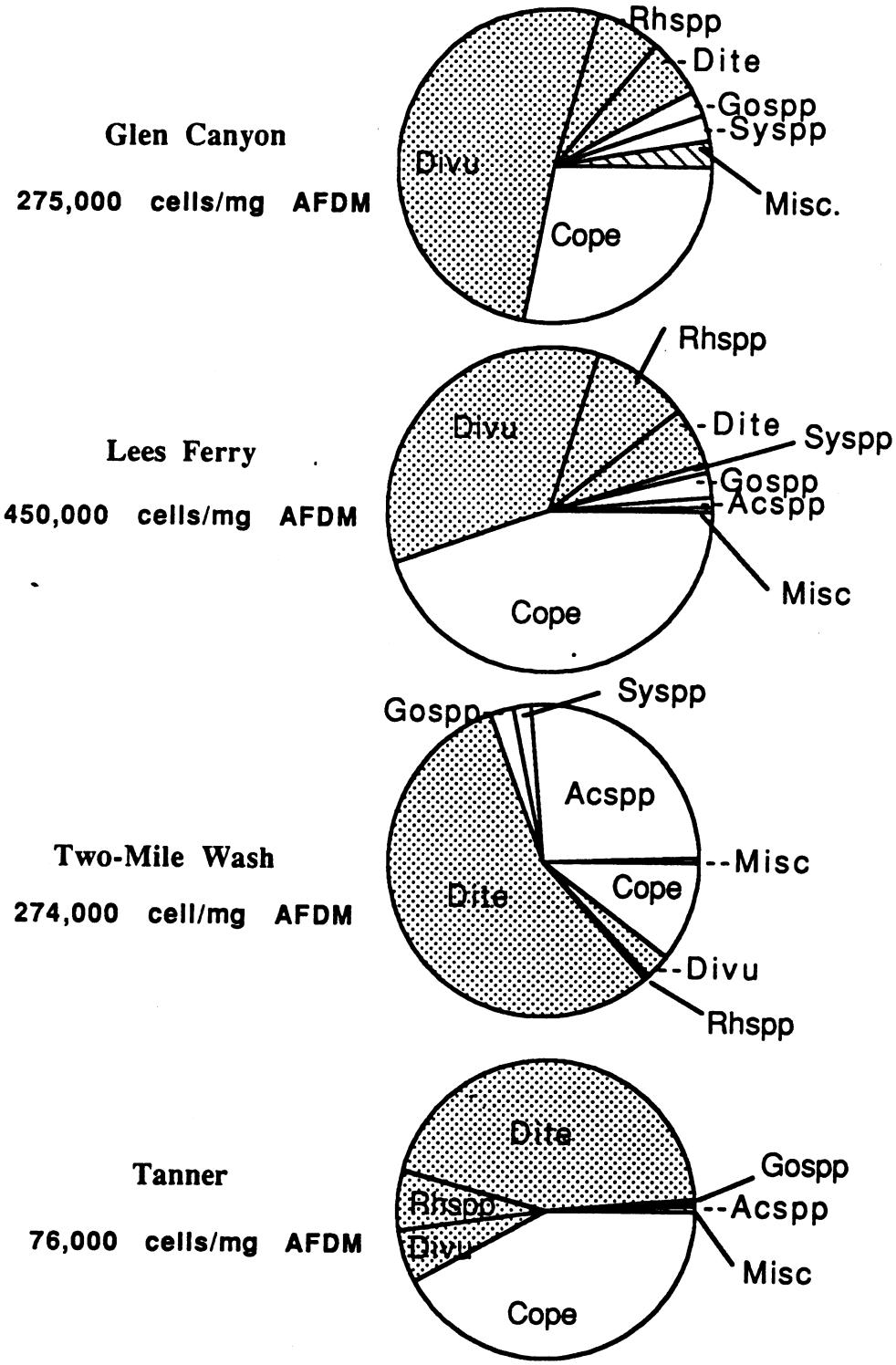


Figure 29. Density and composition of epiphytic diatoms on Cladophora glomerata drift packets at Glen Canyon (RKM -24), Lees Ferry (RKM 0), Two-Mile Wash (RKM 3.1), and Tanner (RKM 109) in the Colorado River, Arizona. Stippled sections represent upright diatom taxa, while unstippled sections represent more prostrate taxa. Divu=Diatoma vulgare, Cope=Cocconeis pediculus, Rhspp=Rhoicosphenia spp., Dite=Diatoma tenue, Gospp=Gomphonema spp., Syspp=Synedra spp., Acspp=Achnanthes spp., Misc=miscellaneous diatom species.

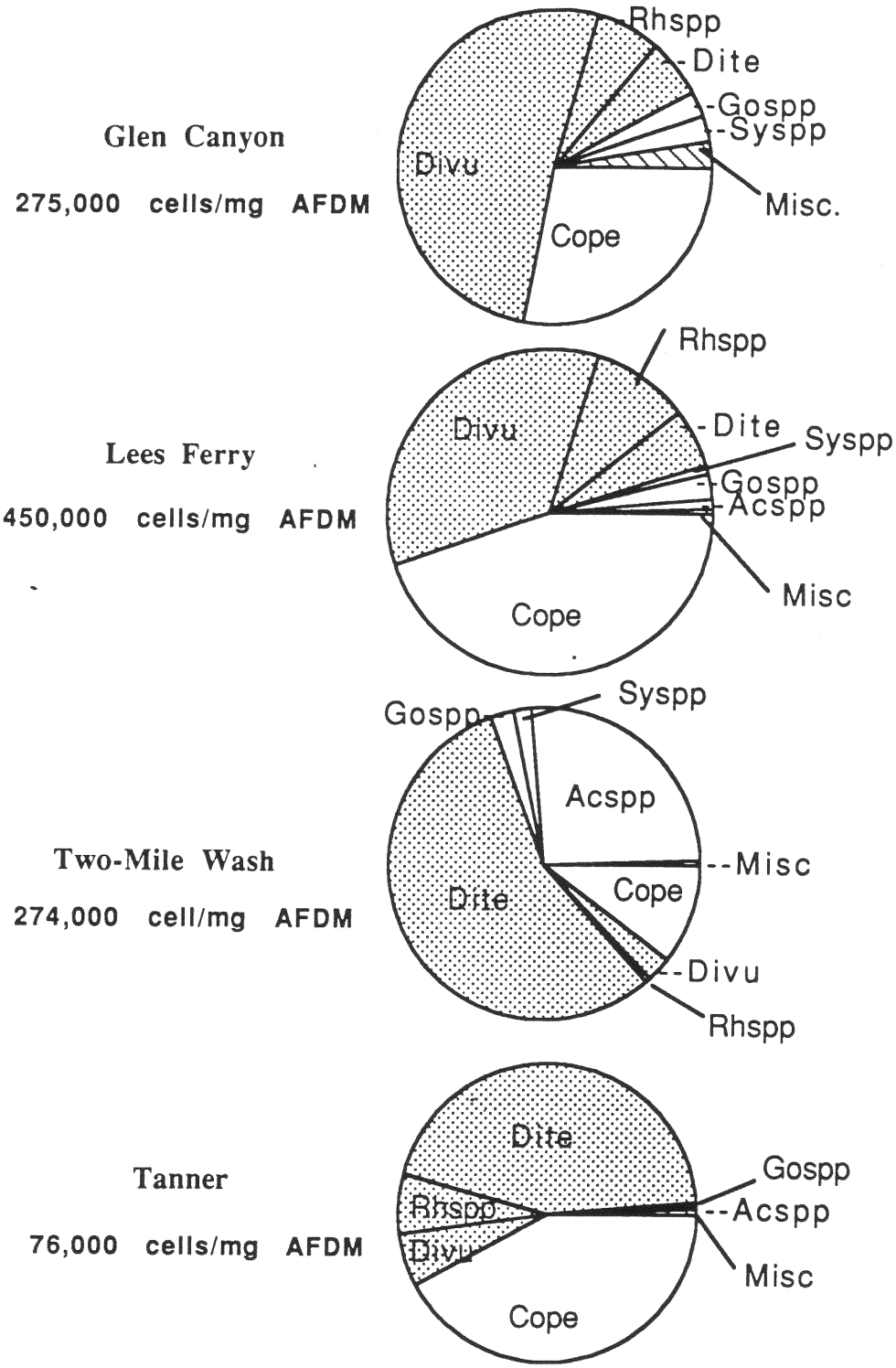


Figure 29. Density and composition of epiphytic diatoms on Cladophora glomerata drift packets at Glen Canyon (RKM -24), Lees Ferry (RKM 0), Two-Mile Wash (RKM 3.1), and Tanner (RKM 109) in the Colorado River, Arizona. Stippled sections represent upright diatom taxa, while unstippled sections represent more prostrate taxa. Divu=Diatoma vulgare, Cope=Cocconeis pediculus, Rhspp=Rhoicosphenia spp., Dite=Diatoma tenue, Gospp=Gomphonema spp., Syspp=Synedra spp., Acspp=Achnanthes spp., Misc=miscellaneous diatom species.

Invertebrate AFDM in C. glomerata drift packets changed over space and time. These values include midge larvae, pupae, exuviae, and pharate material. Average chironomid larvae standing mass in C. glomerata packets was highest during the summer ($\bar{x}$ = 0.00602 g AFDM, S.E. ±0.002), while other seasons were substantially reduced; 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). Chironomid larvae in C. glomerata drift packets showed a significant difference in AFDM spatially ($F_{1,371} = 3.945$, $p < 0.000$) and seasonally ($F_{4,371} = 5.992$, $p = 0.015$). Maximum standing mass of chironomid larvae occurred in drift packets at Lees Ferry ($\bar{x}$ = 0.00014 g AFDM), but decreased 10-fold at RKM 5 (0.00002 g AFDM). Other macroinvertebrates were absent from drift packets by RKM 5.

Tributary Drift: Contribution of tributary drift to the Colorado River varied significantly between streams (Wilks' Lambda, $F_{72,446} = 4.9$, $p < 0.0001$, $n = 99$, Fig. 30); however, no significant seasonal pattern was detected under baseflow conditions during January, March, June, and September ($F_{6,81} = 1.0$, $p = 0.4$, $n = 99$). Lack of seasonal drift patterns may be attributed to unseasonably dry weather patterns that maintain baseflows.

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} 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. Mean organic drift (AFDM) from tributaries was 0.13 g m^{-3} s^{-1} (S.E. ±0.04), compared with 0.5 g m^{-3} s^{-1} (SE ±0.004) in the mainstem. Based on mean discharges for tributaries (1.1 m^{-3} s^{-1}) and the mainstem (374 m^{-3} s^{-1}), we estimate that ~0.14 g of organic drift is contributed by tributaries to the Colorado River (drift = 167 g). We estimate that tributaries release an average of 2.76 animals m^{-3} s^{-1} (3 animals at 1.1 m^{-3} s^{-1}), while the mainstem transports 3.2 animals m^{-3} s^{-1} (1,200 animals at 374 m^{-3} s^{-1}).

Aquatic dipterans, C. glomerata and detritus vary significantly by tributary ($F = 4.5$, $p < 0.0001$), while other biotic categories do not significantly vary between tributaries ($F = 1.8$, $p > 0.06$; Fig. 30). Diamond Creek released the most aquatic dipteran larvae (0.001 g m^{-3} s^{-1}; 0.05 simuliids m^{-3} s^{-1} and 7 chironomids m^{-3} s^{-1}), compared with 0.02 g m^{-3} s^{-1} (4.8 animals m^{-3} s^{-1}) for other macroinvertebrates. Aquatic macroinvertebrates in other tributaries consisted of Plecoptera, Trichoptera, Ephemeroptera, Odonata, gastropods, lumbricids and assorted terrestrial insects. These macroinvertebrates were the dominant components in tributary stream drift (0.002 g m^{-3} s^{-1}; 1.2 animals m^{-3}

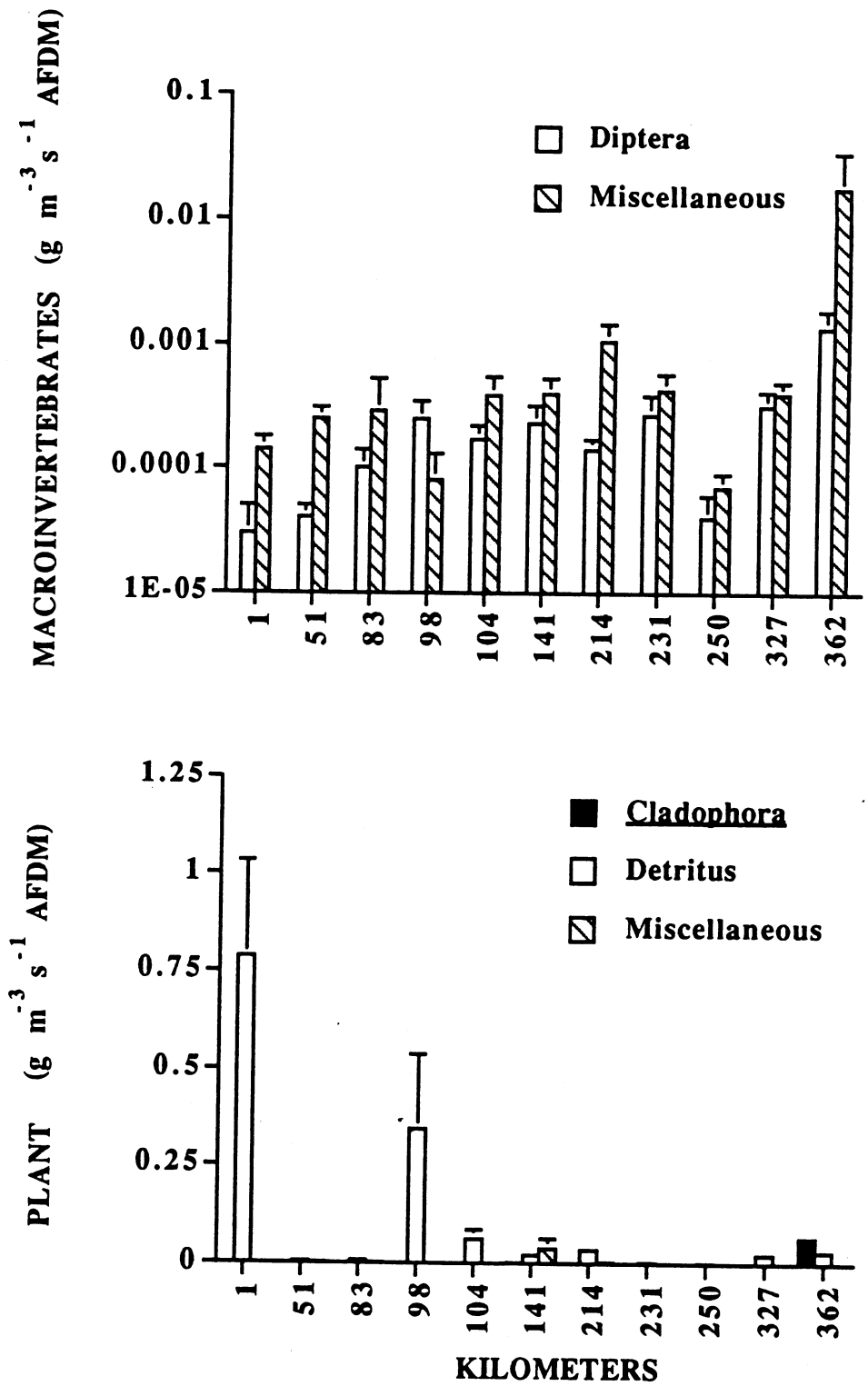


Figure 30. Average mass (g AFDM m^{-3} s^{-1}) of plants, macroinvertebrates and detritus in stream drift at selected tributaries in the Colorado River between Lees Ferry (RKM 0) and Diamond Creek (RKM 362). Values represent means for samples collected during January, March and June 1994.

s^{-1}), but contributed the least to the overall drift biomass in the mainstem (0.0007 g m^{-3} s^{-1}; 0.38 animals m^{-3} s^{-1}).

Organic Drift in Steady Versus Fluctuating Flows: We examined 3 days of steady (227 m^3 s^{-1}) flows followed by 2 days of fluctuating flows (141-283 m^3 s^{-1}) at Lees Ferry to determine the rate of organic drift for each treatment. Fluctuating flows had an overall significant positive effect on algal and macroinvertebrate drift mass and density (Wilks' Lambda; $F_{24,70} = 2.9$, $p < 0.001$; Table 18). However, univariate analysis showed that only macrophytes, C. glomerata, detritus, oligochaetes, and gastropods had a significant positive correlation with stage discharge ($p < 0.001$).

Cladophora glomerata was the dominant primary producer found within the drift and composed 98.5% of the biomass for both steady and fluctuating flows (Table 18). 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 s^{-1} AFDM at a discharge of 283 m^3 s^{-1}.

Cladophora glomerata and macrophyte AFDM changed significantly on a diurnal basis ($F_{3,51} = 4.16$, $p = 0.01$; $F_{3,51} = 2.82$, $p = 0.04$, respectively). Mean AFDM of drifting plants from 0600 and 1200 h was 1.3 g m^{-3} s^{-1} (S.E. ±0.3), while collections from 1800 and 2400 h were 1.0 g m^{-3} s^{-1} (S.E. ±0.2). Neither macroinvertebrate AFDM or abundance changed diurnally through the collection period.

Mean biomass and abundance of macroinvertebrate drift from steady and fluctuating flows were 0.015 g m^3 (S.E. ±0.008) and 49.5 animals m^{-3} (S.E. ±9.0), respectively (Table 18). We calculated a channel wide estimate of 4.5 g s^{-1} of macroinvertebrate drift mass at a discharge of 283 m^3 s^{-1}. Gammarus lacustris and chironomids comprised 33% and 62%, respectively, of the drifting macroinvertebrate biomass.

During a similar discharge regime on May 1994, organic drift followed the same pattern as stated above, while Total Organic Carbon (TOC) averaged 39.5 mg L^{-1} (S.D. ±0.6, $n = 12$) during steady flows and 32.6 mg 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 the associated macroinvertebrate assemblage resulted in a significant loss in

Table 18. Comparison of mass (g m^{-3}) and abundance (animals m^{-3}) in stream drift during steady versus fluctuating flows in the Colorado River at Lees Ferry, Arizona. Mass values are AFDM. 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 s^{-1})	INTERIM FLUCTUATING FLOWS (158-354 m^3 s^{-1})
Cladophora glomerata	0.58314 g m^{-3}	2.28272 g m^{-3}
Oscillatoria spp.	0	0
Other algae	0.01084	0.033574
Chironomids	0.00449 31.7 animals m^{-3}	0.00889 58.0 animals m^{-3}
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 Invertebrates	0.00048 0.2	0.00047 0.7
Detritus	0.02491	0.03294

biomass to stream drift (Wilks' Lambda, $F_{24.1}$, $p < 0.0001$, $n = 58$, Fig. 31). 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 flora did not show a significant loss due to exposure ($p > 0.2$) and were found in only trace amounts, i.e, cumulative average for all contols was 0.78 g m^{-2} AFDM.

Daily loss of macroinvertebrates from treatment sluiceways due to desiccation 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. 32). Univariate analysis of macroinvertebrate composition showed a significant loss of lumbriculids ($F = 4.82$, $p < 0.05$, $n = 14$; 0.0004 g AFDM) and G. lacustris ($F = 7.9$, $p < 0.2$, $n = 14$; 0.028 g AFDM) after a 1-d exposure, and a significant loss of gastropods ($F = 10.6$, $p < 0.001$, $n = 14$, 0.0008 g AFDM) after two successive days of exposure.

Continuously submerged control sluiceways did not show a significant loss in AFDM for algae or macroinvertebrates (Wilks' Lambda, $F = 1.32$, $p = 0.24$, $n = 58$; Fig. 31). There were no significant differences between initial and final controls for algae and macroinvertebrates (Wilks' Lambda, $F = 1.08$, $p = 0.38$, $n = 58$, Fig. 31). All univariate analysis 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 there was a significant difference between controls and exposed sluiceways by each day ($p < 0.0001$), supporting the MANOVA analyses.

Air temperatures during the sluiceway experiment ranged from 13° to 46° C with a mean of 25.5°C. Humidity ranged from 19% to 62% with a mean of 35.8%. Cloud cover increased significantly ($F = 51.4$, $p < 0.01$, $n = 9$) 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 >5 m. Discharge ranged from 141 to 566 $m^3 s^{-1}$ ($\bar{x} = 387$ $m^3 s^{-1}$), and changed by as much as 424 $m^3 s^{-1}$ in 12 h. However, current velocity taken at the up-stream end of each sluiceway averaged 0.38 m s^{-1} and did not vary significantly during the course of the experiment ($F = 0.003$, $p = 1.0$, $n = 16$).

DISCUSSION

The large benthic standing mass in the immediate tailwaters of Glen Canyon Dam (GCD) contributes negligible coarse particulate organic carbon (CPOM) to downstream aquatic communities in the Colorado River corridor through Grand

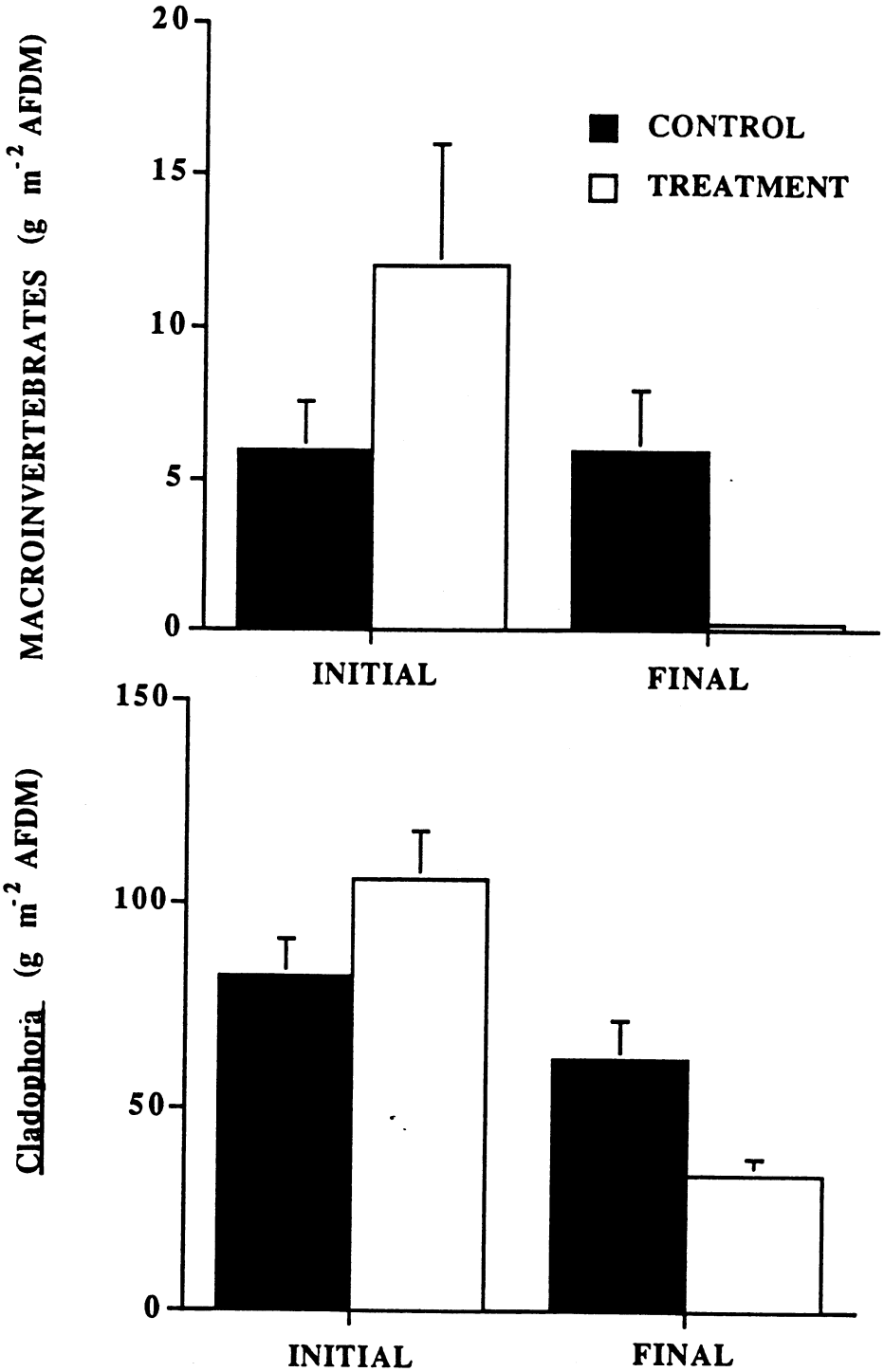


Figure 31. Ash-free dry mass (AFDM) values for Cladophora glomerata and macroinvertebrates benthos lost to stream drift in sluiceway experiments. Treatments were subjected to 3 consecutive nights of exposure compared to continuously submerged controls. Control AFDM was collected at the start and end of the experiment.

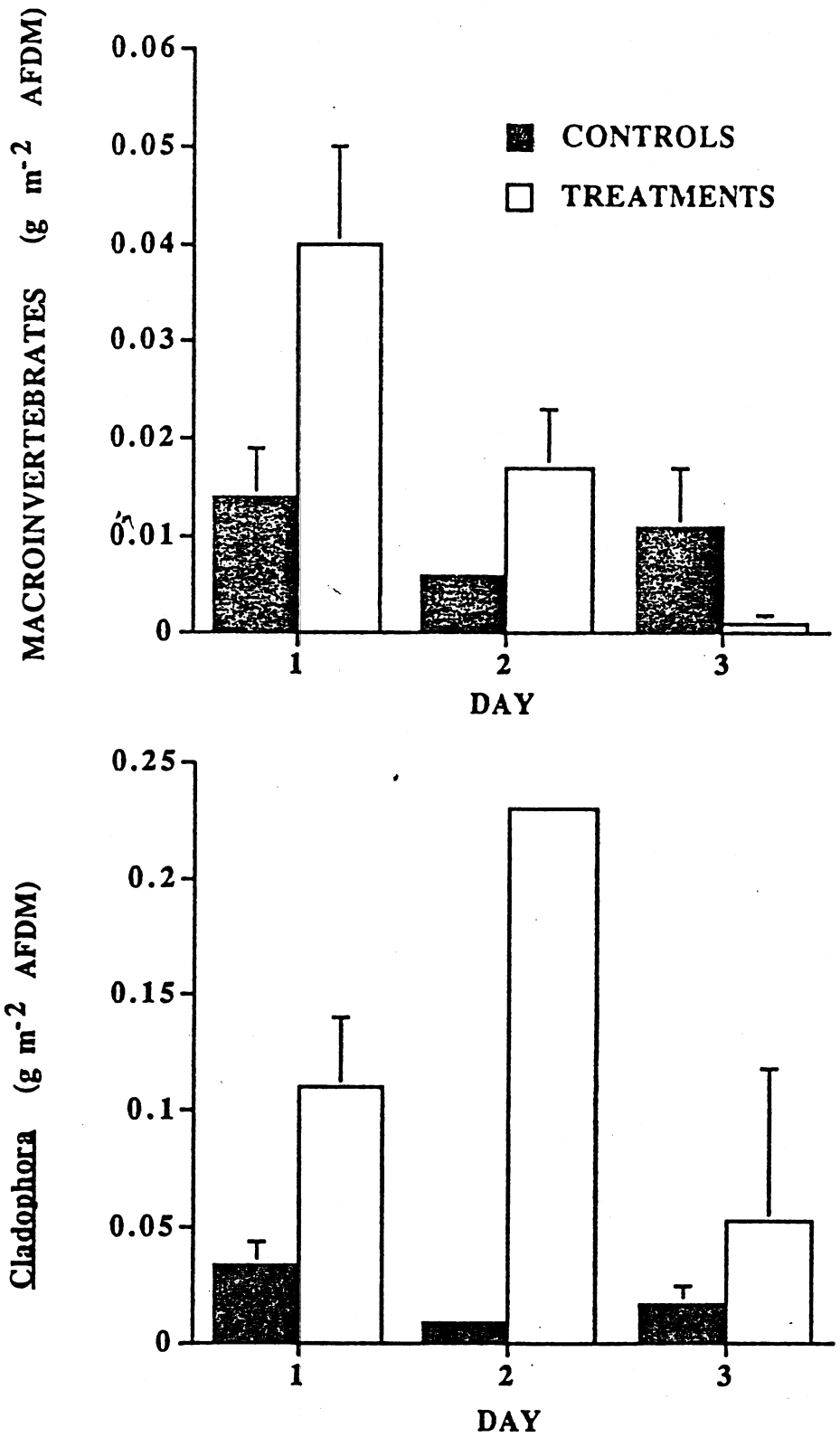


Figure 32. Daily loss of ash-free dry mass (AFDM) for Cladophora glomerata and macroinvertebrates collected in experimental sluiceway drift nets. Treatments were subjected to 3 consecutive nights of exposure compared to continuously submerged controls.

Canyon. Although operations of GCD dislodge packets of C. glomerata and associated communities through variable discharge volumes and periods of desiccation of colonized cobble bars (Leibfried & Blinn 1986, Blinn et al. 1992, Angradi & Kubly 1993), rapids along the river corridor quickly pulverize packets and limit transport of CPOM to downstream 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 glomerata averaged 0.17 g AFDM (~2,000 joules based on energy equivalents derived by Blinn et al. 1992) in drift packets at Lees Ferry (RKM 0.0) and was reduced by 22% below the confluence of the Paria River, just 1.0 km downstream. There was an additional 26% reduction in drifting C. glomerata mass and energy below Badger Rapid (RKM 12.8). The Paria riffle is a minor rapid with a vertical drop of less than one m, while Badger Rapid is the first major rapid with a vertical drop of 2.0 m (Keiffer 1990).

Cell densities of epiphytic diatoms associated with C. glomerata are reduced by 83% by Tanner Wash (RKM 110) and changed from an up-right to a prostrate assemblage upon exiting the Lees Ferry reach. This change in diatom community physiognomy may be important to downstream macroinvertebrate communities because up-right taxa are more readily available to macroinvertebrate grazers than prostrate forms (Colletti et al., 1987, Steinman et al. 1987, Blinn et al. 1989, Peterson et al. 1992), and perhaps are more susceptible to abrasion by suspended sediments and hydraulic stress (Hardwick et al. 1992).

Macroinvertebrates associated with the C. glomerata packets displayed an even greater distance-related reduction in AFDM than algal components through the first two rapids (12.8 km). Macroinvertebrates 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). These data do not conform with the river continuum theory (Vannote et al. 1980), but instead support the riverine productivity model of Thorp and Delong (1994) which states that reach productivity may not be entirely dependent on up-stream carbon sources.

Power (1990) reported high densities of insect larvae associated with 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 of small rivers, however in lotic ecosystems with hydralic turbulence, rapids greatly reduce downstream transport of CPOM and stream gradient is negatively correlated with autochthonous CPOM drift.

Zooplankton drift in the Colorado River through Grand Canyon remains relatively constant (100 animals m^{-3} s^{-1}), but decreases in condition downstream (parasites, body structures missing, etc.) between GCD to Diamond Creek (Haury 1988). Sabri et al. (1993) reported that copepod larvae declined only slightly with distance from the impoundment in the River Tigris and appeared to be more resilent in lotic conditions over numerically dominant rotifers. Haury (1988) did not report a correlation between densities of zooplankton drift and increased discharge in the Colorado River. In contrast, Sabri et al. (1993) reported a positive relationship between increased zooplankton density and discharge in the 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. The trophic role of lentic zooplankton in the food web of the regulated Colorado River is not fully understood (Haury 1988); however, Ward (1975) reported that hypolimnial released zooplankton do not contribute appreciable amounts of organic matter to the downstream communities in a Colorado mountain reservoir.

During the June 1994 collection trip, L. Haury collected zooplankton with a 13 cm diameter opening plankton net (243 µm mesh) in the mainstem as well as in several backwater sites These data showed similar patterns to collections taken during the 1980's when densities dropped by 80% after RKM 120. Diversity appears to be lower overall during Interim Flows (IF) than in the past, particularly noticeable is the absence of large (>1-2 mm) copepods and Daphnia. However, collections at Nankoweap pool revealed a dominance of Bosmina longirostris; the only site this cladoceran was collected. These preliminary results suggest that further collections are needed to better understand the distibutional patterns of zooplankton through Grand Canyon National Park.

Our data indicate that terrestrial insects are not important in stream drift in the Colorado River corridor through Grand Canyon National Park. Yet Valdez (personal communication) reports high numbers of terrestrial insects in stomachs of humpback chubs. Perhaps the 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 National Park. Furthermore, the narrow band of riparian vegetation along the shores of the Colorado River, arid climate and river regulation may provide limited habitat for insects (Stevens 1989). In contrast, Armitage (1977)

reported that terrestrial insects contributed ~10% of the annual drift biomass 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 biomass entered drift after 3 nights of repeated exposure. Other investigators (Usher & Blinn 1990, Blinn et al. 1992, Angradi & Kubly 1993) reported comparable losses in C. glomerata biomass after successive exposures in laboratory stream tanks and in the tailwaters of GCD. Furthermore, in-situ drift experiments demonstrated significant differences between steady and fluctuating flows. Fluctuating flows (141-283 $m^3 s^{-1}$) showed a 20% increase in C. glomerata drift at 1600 and 2400 h compared to steady flows (226 $m^3 s^{-1}$). The peak hydrostatic wave from GCD reaches Lees Ferry at approximately 1600 h which accounts for the evening increase in C. glomerata drift (U.S. Bureau of Reclamation 1994).

Comparisons between steady and fluctuating flows suggest that macroinvertebrates do not exhibit behavioral drift in the tailwaters of GCD. Tailwater conditions, with dramatic daily changes in velocity, may have selected for organisms that do not change their behavior on a diurnal basis as noted in unregulated streams (Waters 1972). Shannon et al. (1994) observed G. lacustris in a series of in-situ experiments and found no significant differences in feeding behavior between day and night experiments. Armitage (1977) also reported that chironomids and baetids lacked a diurnal drift behavior in the regulated River Tees, Great Britain.

The composition of downstream aquatic benthic communities was similar to C. glomerata drift packets collected within each corresponding reach. Tailwater communities (RKM 26 below GCD) have high standing crops of C. glomerata and associated G. lacustris and chironomid larvae (e.g. Cricotopus annulator). Blinn et al. (1992) reported a reduction in C. glomerata and macroinvertebrate standing stock in downstream reaches due to elevated suspended sediments from tributaries draining arid landscapes. Elevated suspended sediments reduce photosynthetic available radiation (PAR) in the water column with distance downstream and cause a negative bottom-up response in the trophic structure of the Colorado River ecosystem (Blinn et al. 1992, Yard et al. 1992). The decrease in light energy results in an overall reduced algal biomass and a compositional change from C. glomerata to Oscillatoria spp. This compositional change in primary producers is reflected by a reduction in grazers (chironomid larvae and G. lacustris) and an increase in filter-feeders (Simulium arcticum; Blinn et al. 1992). Changes in composition of 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. The close relationship between composition of C. glomerata drift packets and the benthic community within each corresponding reach suggests that drift composition and quantity is reach specific and not cumulative throughout the study site. It also supports the importance of rapid hydraulics in restricting the transport of CPOM in the Colorado River corridor.

Downstream dipteran insects may be foraging on the fine particulate organic matter (FPOM) generated from the disintegration of drifting C. glomerata packets. Organic drift from tributaries contributes to both CPOM and FPOM as the contribution from tributaries appears to diminish at the rapid adjacent to the confluence of each tributary. Data for TOC collected downriver during the May 1993 steady flows by the staff from Glen Canyon Environmental Studies (W.S. Vernieu, personal communication, GCES, Flagstaff, AZ) reported no significant differences in TOC concentrations downstream (33 mg L^{-1}) between Lees Ferry and Diamond Creek (RKM 362). Cellot and Rostan (1993) reported no significant variation in dissolved organic carbon (DOC) 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.

Total volume of stream drift increased with distance down river from GCD, but changed in composition from C. glomerata to detritus, particularly when the Paria and Little Colorado Rivers were flooding. Detrital drift collected near cobble bars is not correlated with benthic mass of macroinvertebrates in the Colorado River, but instead showed a positive correlation with slow velocity depositional pools (Blinn et al. 1992). Corkum (1993) reported a similar relationship between velocity, detritus and macroinvertebrate abundance in accordance with drainage biome effects. Tributaries don't account for the total amount of detritus collected in the mainstem drift samples. Riparian vegetation must be the source for the net difference between tributary and mainstem detrital loads during periods of low precipitation as was reported in the lower Colorado River by Lieberman and Burke (1993)

Down river detrital drift, which represents a large portion of the total biomass, was the only component to show a positive correlation with discharge. This is in contrast to drift collected in the 1980's by Leibfried and Blinn (1986) under higher flow regimes (85 - >566 m^{-3} s^{-1}). They reported a positive correlation between discharge and G. lacustris and C. glomerata but not for chironomids. Detrital drift was not reported. Interim flows are less energetic than the high

flows and erratic ramping rates of the past decade may result in detritus being the only component directly affected, perhaps due to buoyancy. The non-linear relationship of total drift and discharge (Fig. 23) may be a function of eddie/pools emptying during discharges above 450 m^{-3} s^{-1} and below 400 m^{-3} s^{-1}, and filling between 400 and 450 m^3 s^{-1}. Our data also indicate a threshold of about 300 m^{-3} s^{-1} at which point total drift biomass dramatically increases (Fig. 23). As water stage increases, mostly the base littoral zone is swept, reducing the ratio of drift to flow volume. A threshold of ~450 m^3 s^{-1} probably begins to entrain pool-stored drift. Leibfried & 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 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 s^{-1} and an average channel width of 67 m (Randle & Pemberton 1987). Therefore, the magnitude of annual discharges (283 m^3 s^{-1}) are great enough to eliminate debris dams which play an important role in resource processing in 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 m of the water column (Shannon, personal observations). 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 we saw large rafts of organic flotsam, largely composed of sticks and logs, at times covering the surface of 500 m^2 eddies. Benthic sampling during the subsequent year recovered minor percentages of the flotsam.

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. Continued research on microbial processing and DOC is essential to better understand the organic budget of the Colorado River through Grand Canyon National Park.

SUMMARY

A strong positive correlation exists between detrital drift and discharge in the Colorado River corridor, while other biotic components show a strong negative correlation to discharge. Drift components vary seasonally; e.g., September collections show highest drift mass. The high autochthonous production between Glen Canyon Dam (GCD) and Lees Ferry supply little coarse particulate organic matter (CPOM) to downstream reaches. Rapid hydraulics quickly pulverize packets of drifting C. glomerata into fine particulate organic matter (FPOM). Packets of C. glomerata and associated communites are reduced by 4-fold below the Paria confluence (RKM 1.0) and 10-fold by RKM 85. The activity of downstream microbial loops on FPOM and the role of these microbes in the Colorado River food web need study. Tributaries provide ≤25% of the total organic stream drift in the Colorado River through Grand Canyon National Park. Regulated flows significantly increase stream drift of aquatic benthos in the tailwaters of GCD.

CHAPTER FOUR: ACCOMODATION AND RECOVERY OF COLORADO RIVER BENTHOS TO FLOW REGULATION IMPACTS

INTRODUCTION

The abundant standing stock of Cladophora glomerata at Lees Ferry is strongly reduced below the confluence of the Paria River and the cyanobacteria assemblage (Oscillatoria spp.) becomes an important component of the phytobenthos standing stock in the Colorado River through Grand Canyon National Park (Blinn et al. 1992, Shannon et al. 1994). The transition in algal community structure coincides with abrupt increases in suspended sediment load accompanied by reduced water clarity at the Paria River and subsequent tributaries (Yard et al. 1992). Recent studies have indicated that C. glomerata supports significantly higher epiphytic diatom and macroinvertebrate communities than Oscillatoria assemblages (Pinney 1991, Blinn et al. 1992, Shannon et al. 1994). Therefore, replacement of C. glomerata habitats with those more suitable for Oscillatoria has major bottom-up implications on the aquatic food web in the Colorado River through Grand Canyon National Park. Elevated suspended sediment loads are likely more detrimental to the exposed filamentous streamers of C. glomerata than to compact mucilagenous assemblages of Oscillatoria (Davies-Colley et al. 1992, Dodds & Gudder 1992, Sze 1993).

Diel and seasonally variable flows are common in regulated rivers with phytobenthos communities periodically exposed to desiccation (Lowe 1972, Lillehammer & Saltveit 1984, Peterson 1986, 1987). Oscillatoria mats have been shown to survive desiccation, recovering rapidly upon rehydration (Vincent & Howard-Williams 1986, Hawes 1993), while C. glomerata has been shown to lose significant amounts of chlorophyll a after six or more hours of atmospheric exposure in field and laboratory experiments (Usher & Blinn 1990, Angradi & Kubly 1993).

We distinguished distance-related tributary influences from diel flow effects on Colorado River phytobenthos. Reciprocal translocation experiments with cobble and associated biota between Lees Ferry (RKM 0.8) and Cathedral Island (RKM 4.8) were conducted to measure the rate of accommodation among C. glomerata and Oscillatoria communities in high and low sediment habitats. The term "accommodation" has been used to describe the adjustment of an established biotic community to a long-term incubation in an alternative environment (Crossman et al. 1973, Yount and Niemi 1990). We tested the ability of C. glomerata and Oscillatoria to accomodate in alternative clear and turbid environments. We then measured the recolonization of desiccated cobbles by benthic communities in continuously submerged and varial zones at Lees Ferry and Cathedral Island. "Recolonization" refers to the resilience of

a community to recover from a disturbance such as desiccation (Yount and Niemi 1990).

METHODS

In-Situ Reciprocal Translocation Accommodation Experiments

On May 17, 1993, 100 cobbles (20-50 cm diam) with associated biota were collected from the permanently wetted channel (<142 $m^3 s^{-1}$ stage) in the clear-water reach of Lees Ferry (RKM 0.8) and transplanted into a more turbid reach at Cathedral Island (RKM 5). Cobbles were placed in a 10 x 10 grid beneath the varial zone (<142 $m^3 s^{-1}$ stage) and the corners of the grid were painted for later recovery of the grid. Likewise, 100 cobbles with associated biota from Cathedral Island were translocated upstream to the clear-water reach at Lees Ferry. At the start of the experiment, 20 additional submerged cobbles were sampled once and used as initial controls. One 20 cm^2 quadrat of algae and macroinvertebrates was collected from each of 20 randomly selected cobbles in each grid at approximate monthly intervals for three months, and at 9 and 11 mo. After sampling these rocks were replaced within the grid to reduce sampling disturbance. No samples were taken at 11 mo at Cathedral Island due to loss of cobbles during high flows. At each sampling date, 20 additional control cobbles were collected from below the 142 $m^3 s^{-1}$ stage in the channel at both sites for comparison with reciprocal translocated cobbles. Macroinvertebrates, including chironomids, gastropods, lumbriculids, tubificids, simuliids, and Gammarus lacustris, were sorted from each algal sample (C. glomerata and Oscillatoria) and oven-dried at 60°C for 48 h to constant mass. Ash-free dry mass (AFDM) conversions were calculated from Table 1.

The algal mass was placed in a bag with 40 ml of filtered river water and agitated for 1 min. The composite was poured through a 0.5 mm screen to separate macroalgae from epiphyton. The macroalgae on the screen were rinsed with filtered river water to remove additional epiphyton from samples. Macroalgae were removed from the screen and sorted to genus and oven-dried at 60°C for 48h or to a constant mass. The epiphyton solution was swirled for 3-4 s in a beaker and filtered onto Whatman GF/C glass microfiber filters (0.45μm). Filters were oven-dried at 60°C to a constant mass. Filters were ashed at 500°C for 1 h in crucibles and ash-free dry mass (AFDM) was determined. Filters were saved for compositional analyses of diatom epiphyton.

In-Situ Recolonization Experiments

On October 10, 1992, 440 cobbles were collected from the submerged channel (<142 $m^3 s^{-1}$ stage) at Lees Ferry. The bottoms of the cobbles were numbered with paint and placed above the high water mark (565 $m^3 s^{-1}$ stage) to allow desiccation of associated biota. Twenty additional control cobbles from the channel were sampled at Lees Ferry. On May 17, 1993 (219 d of desiccation), samples were collected with a circular 20 cm^2 template from 20 desiccated cobbles prior to placement in the channel. At both sites, 100 cobbles were submerged in the channel at the <140 $m^3 s^{-1}$ stage to insure continuous submergence. An additional 100 cobbles were placed in the varial zone (140 to 565 $m^3 s^{-1}$ stage) at 340 $m^3 s^{-1}$ at Lees Ferry and Cathedral Island. Twenty samples (20 cm^2) were randomly collected from cobbles at 2 mo, 5 mo, 9 mo and 11 mo. On each sampling date, 20 control cobbles were collected from below the 142 $m^3 s^{-1}$ stage in the channel at both sites for comparison with recolonizing desiccated cobbles. Algae (C. glomerata and Oscillatoria) and macroinvertebrates including chironomids, gastropods, lumbriculids, tubificids, simuliids, and G. lacustris were sorted from each sample, oven-dried at 60°C to constant mass, and converted to AFDM estimates (Table 1).

RESULTS AND DISCUSSION

In-Situ Reciprocal-Translocation Accommodation Experiments at Lees Ferry

At the start of the translocation experiment (0 MO), Cladophora glomerata colonized cobbles from Lees Ferry had a 6-fold higher algal AFDM (165 g m^{-2}, SE ± 31) than Oscillatoria assemblages (27 g m^{-2}, SE ± 5) collected at Cathedral Island ($F = 41.4$, $n = 40$, $p < 0.001$, Fig. 33A). Accommodation by C. glomerata was slow on the translocated cobbles in the clear-water habitat at Lees Ferry (Fig. 33A). Even after 11 mo, relocated cobbles at Lees Ferry had only one-third (21 g m^{-2}, SE ± 5, $F = 38.9$, $n = 40$, $p < 0.001$) the C. glomerata AFDM as compared to control cobbles (80 g m^{-2}, SE ± 8). In contrast, other filamentous green algae with extensive mucilage (Mougeotia and Spirogyra) have been shown to reach full growth in 33 d in lotic habitats (Peterson & Stevenson 1992). The compact mucilagenous matrix of sand and Oscillatoria appears to restrict the accommodation of rhizoidal holdfast cells of C. glomerata. Furthermore, holdfast cells of C. glomerata prefer solid substrata for attachment in lotic environments (Dodds & Gudder 1992). Therefore, cobbles covered by Oscillatoria in varial zones and/or turbid waters may retard the rate of colonization by C. glomerata and potentially modify the foodweb in the Colorado River.

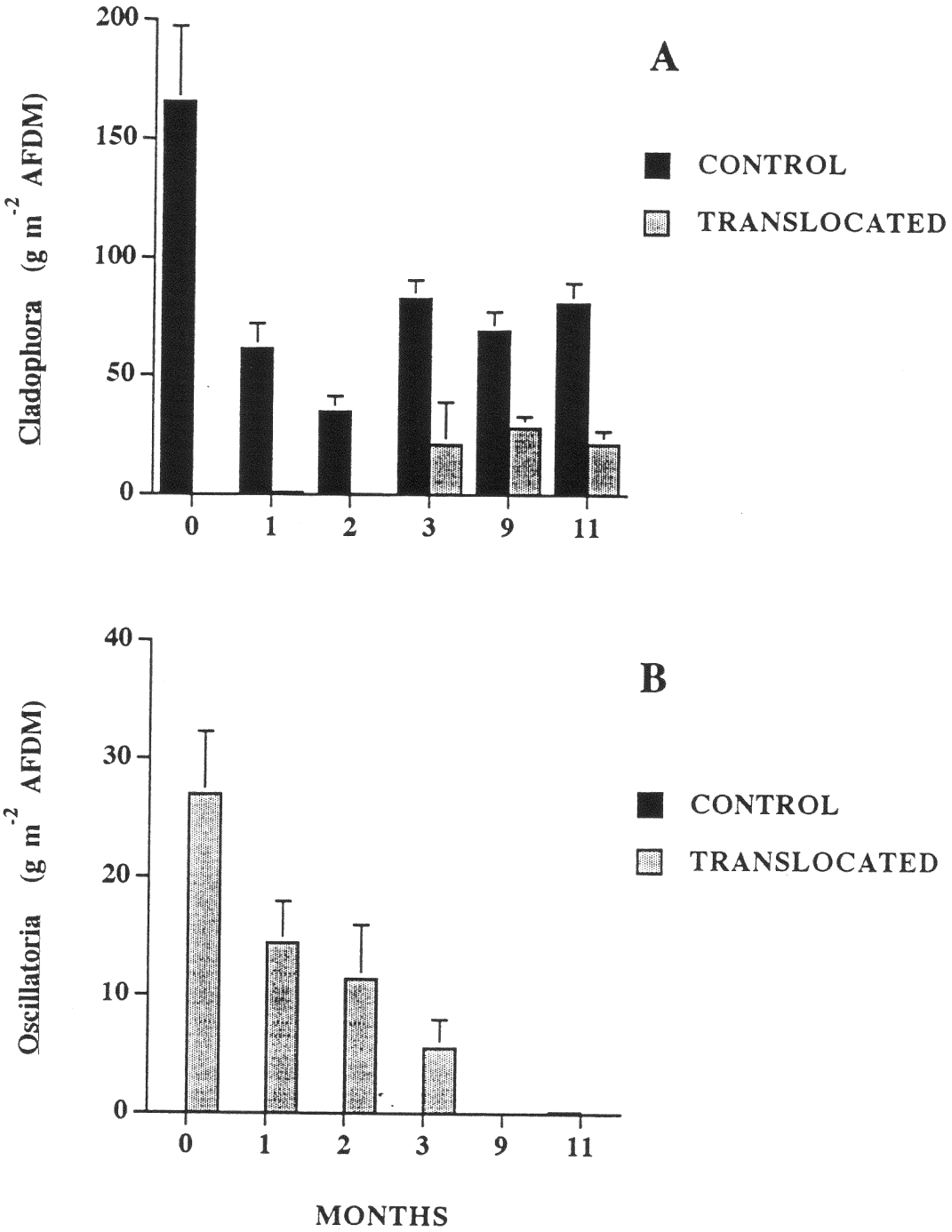


Figure 33. Accomodation rates (days) as g m^{-2} AFDM for Cladophora glomerata (A) and Oscillatoria spp. (B) on the cobbles translocated from a turbid habitat at Cathedral Island (RKM 4.8) in the Colorado River to an upstream clear water habitat at Lees Ferry, Arizona (RKM 0.8). Controls represent collections from resident submerged cobbles at Lees Ferry.

Oscillatoria AFDM on cobbles translocated to Lees Ferry decreased in AFDM by half to one-fifth per month, virtually disappearing within six mo (Fig. 33B). This suggests the permanently submerged, clear-water habitat at Lees Ferry is less suitable for Oscillatoria than for C. glomerata. The lack of sediment and shading by filaments of C. glomerata may have retarded the development of Oscillatoria mats at Lees Ferry.

Epiphyton AFDM associated with C. glomerata remained 25 to 70% lower on translocated cobbles compared to controls throughout the study period at Lees Ferry (Fig. 34). This pattern correlates with the reduced AFDM (60% lower) of C. glomerata on relocated cobbles compared to controls and a positive correlation between epiphyton AFDM and C. glomerata. Although epiphyton increased on both control and translocated cobbles, high mid-winter epiphyton AFDM on control cobbles suggest seasonal influences on this food source.

At the start of the experiment, macroinvertebrate AFDM on cobbles from Lees Ferry was significantly higher on C. glomerata covered cobbles (2.6 g m^{-2}, S.E. ± 0.8) than on Oscillatoria covered cobbles (0.14 g m^{-2}, S.E. ± 0.11) from Cathedral Island ($F = 10.3$, $n = 40$, $p < 0.003$). Chironomid AFDM increased quickly at Lees Ferry with no significant difference in AFDM after 1 mo (Fig. 35A), while G. lacustris did not significantly colonize until 9 mo had elapsed (Fig. 35B). Macroinvertebrate recolonization has been shown to be rapid (10 to 30 d) in other lotic ecosystems (Mackay 1992). The relatively rapid recruitment of macroinvertebrate mass compared to algal benthos was probably due to the high drift rates and/or mobility of benthic invertebrates (Mackay 1992, Yount & Niemi 1990). The fact that chironomid AFDM on translocated cobbles reached control levels in one mo in the presence negligible C. glomerata AFDM suggests that chironomids are capable of utilizing Oscillatoria-dominated benthic communities and/or are able to feed on periphytic diatoms, or biofilm, associated with cobble surfaces. In contrast, Gammarus lacustris was shown to be more dependent on the presence of C. glomerata with recruitment remaining negligible until the establishment of C. glomerata cover. Differences in colonization rates are likely attributed to differences in mouthpart morphology and/or foraging strategies between chironomids and Gammarus. The high variability in AFDM for both chironomids and G. lacustris may be due to lower food quantity (epiphyton AFDM remained significantly less) and possibly lower food quality on relocated, as compared to control cobbles. Based on energy equivalents derived for the macroinvertebrate community in the Colorado River (Blinn et al. 1992), we estimate that animal energy associated with C. glomerata benthic communities yields ~46,000 joules m^{-2} compared to only 2,500 joules m^{-2} in Oscillatoria assemblages.

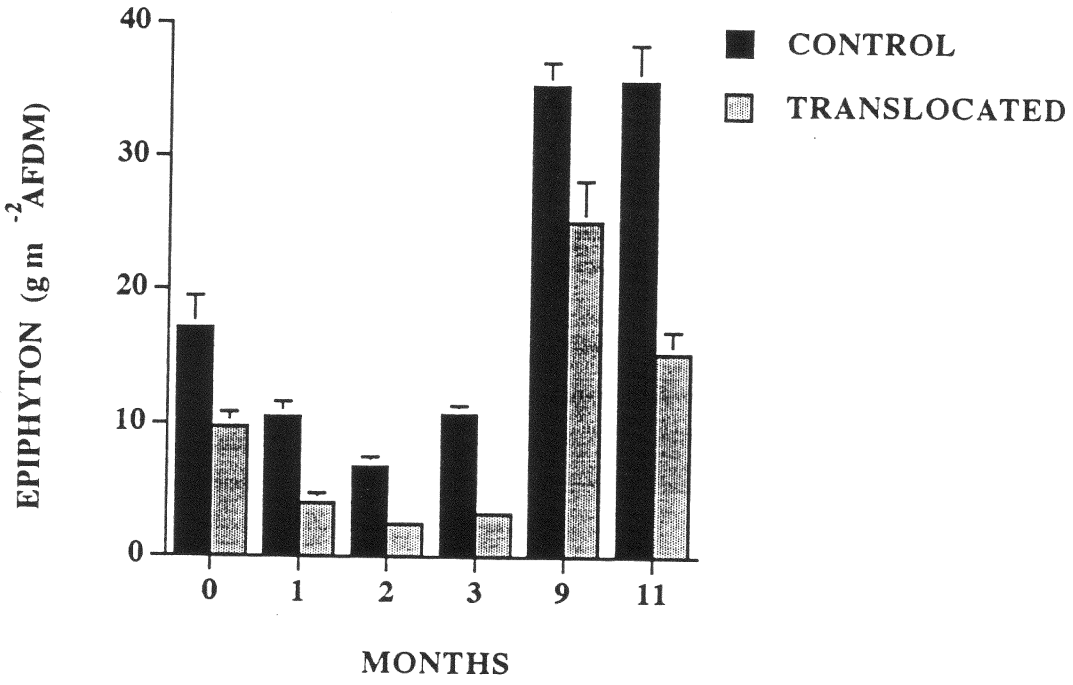


Figure 34. Accomodation rates (days) for epiphyton (g m^{-2} AFDM) on cobbles translocated from a turbid habitat at Cathedral Island (RKM 4.8) in the Colorado River to an upstream clear-water habitat at Lees Ferry, Arizona (RKM 0.8). Controls represent collections from resident submerged cobbles at Lees Ferry.

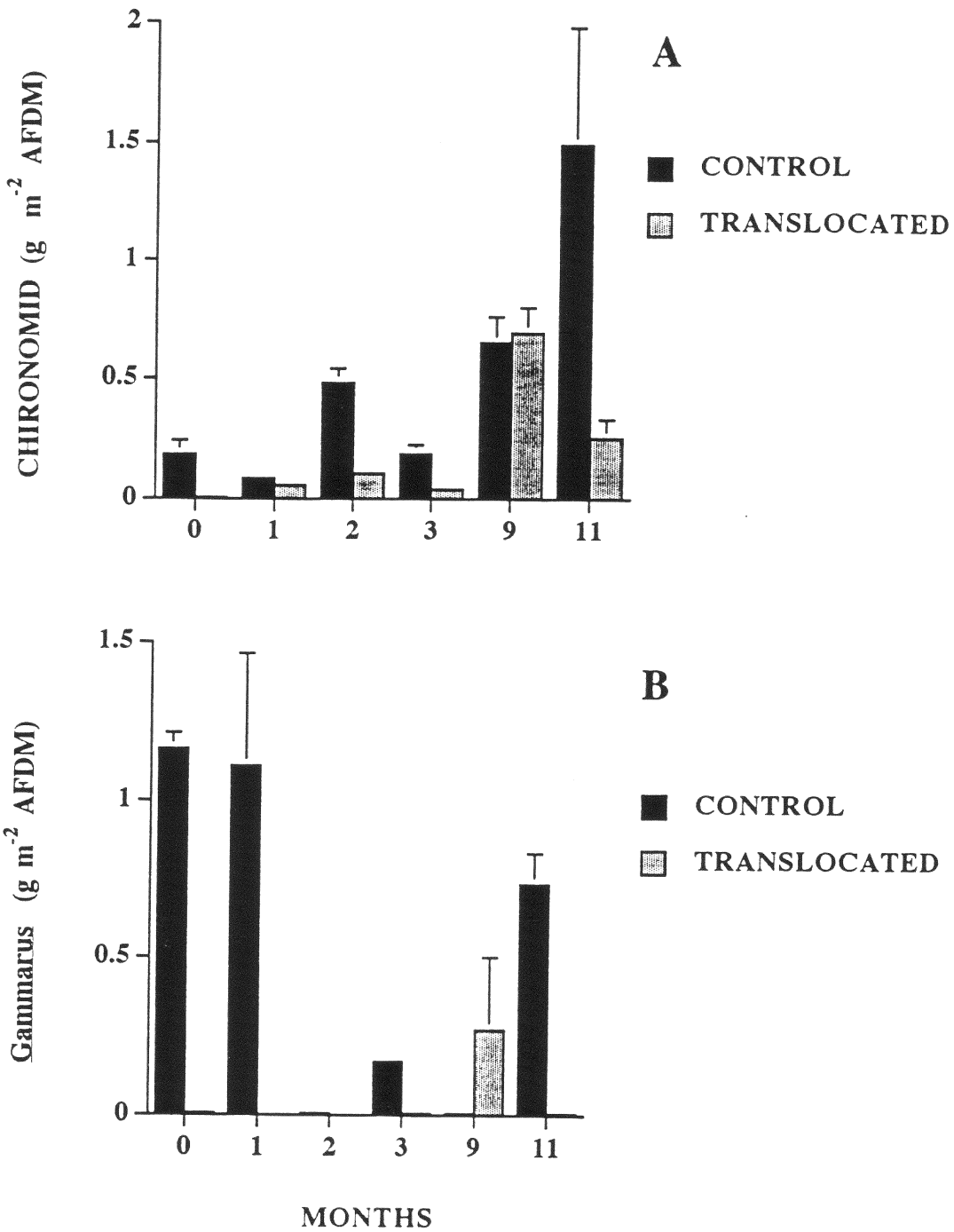


Figure 35. Accomodation rates (days) as g m^{-2} AFDM for chironomid larvae (A) and Gammarus lacustris (B) on the cobbles translocated from a turbid habitat at Cathedral Island (RKM 4.8) in the Colorado River to an upstream clear-water habitat at Lees Ferry, Arizona (RKM 0.8). Controls represent collections from resident submerged cobbles at Lees Ferry.

In-Situ Reciprocal-Translocation Accommodation Experiments at Cathedral Island

Benthic AFDM on translocated cobbles at Cathedral Island rapidly changed to control levels. Cladophora glomerata AFDM decreased by 80% of initial translocated cobbles within one mo and remained near control levels thereafter (Fig. 36A). This reduction is even more dramatic than the 15 to 57% loss in algal mass reported in six New Zealand streams following increased turbidity (Davies-Colley et al. 1992). The rapid loss of C. glomerata AFDM under elevated turbidity at Cathedral Island is in contrast to the rather slow increase in AFDM of C. glomerata on translocated cobbles under low turbidity at Lees Ferry (Fig. 33A). This implies that even under optimum conditions, recruitment by C. glomerata requires nearly one year to recover after a major turbidity disturbance. The gradual increase in C. glomerata AFDM on controls was attributed to the low sediment inflow from the Paria River during the study period, which created relatively clear-water conditions approximately 80% of the time in this reach.

Oscillatoria AFDM increased on translocated cobbles at Cathedral Island and reached control levels after 9 mo under turbid water conditions (Fig. 36B). The overall decrease in Oscillatoria AFDM on control cobbles over the course of the experiment was likely due to the relatively clear flows during the experiment.

In accord with reduced C. glomerata, epiphyton AFDM was rapidly reduced to levels of controls after 1 mo (Fig. 37). AFDM values for epiphyton were significantly lower at Cathedral Island (5.2 g m^{-2}, SE ±1.2) compared to those in the clear-water habitat at Lees Ferry (11.0 g m^{-2}, SE ±1.1; Fig. 34). The difference in epiphyton mass between Lees Ferry and Cathedral Island reciprocal transplants is likely due, in part, to differences in mass of C. glomerata substrata between the two sites. The relatively high levels of epiphyton AFDM after 9 mo on both control and translocated cobbles is unexplainable at this time (Fig. 37).

Patterns in macroinvertebrate AFDM varied between chironomid and G. lacustris on transplants at Cathedral Island. Increased development of C. glomerata through the experiment (related to increased light availability), led to increased mass on control cobbles. Chironomid AFDM increased on both control and translocated cobbles throughout the experiment (Fig. 38A). In contrast, G. lacustris AFDM rapidly decreased on treatment cobbles, and therefore varied seasonally (Fig. 38B). Macroinvertebrate densities have been shown to be reduced by >50% due to catastrophic drift within 24 h of the addition of fine sediments (Culp et al. 1986). The reduction in G. lacustris AFDM by >80% after one mo was consistent with this pattern. The high variability in chironomid AFDM at both the Lees Ferry and Cathedral Island sites may be the result of seasonality and/or dam

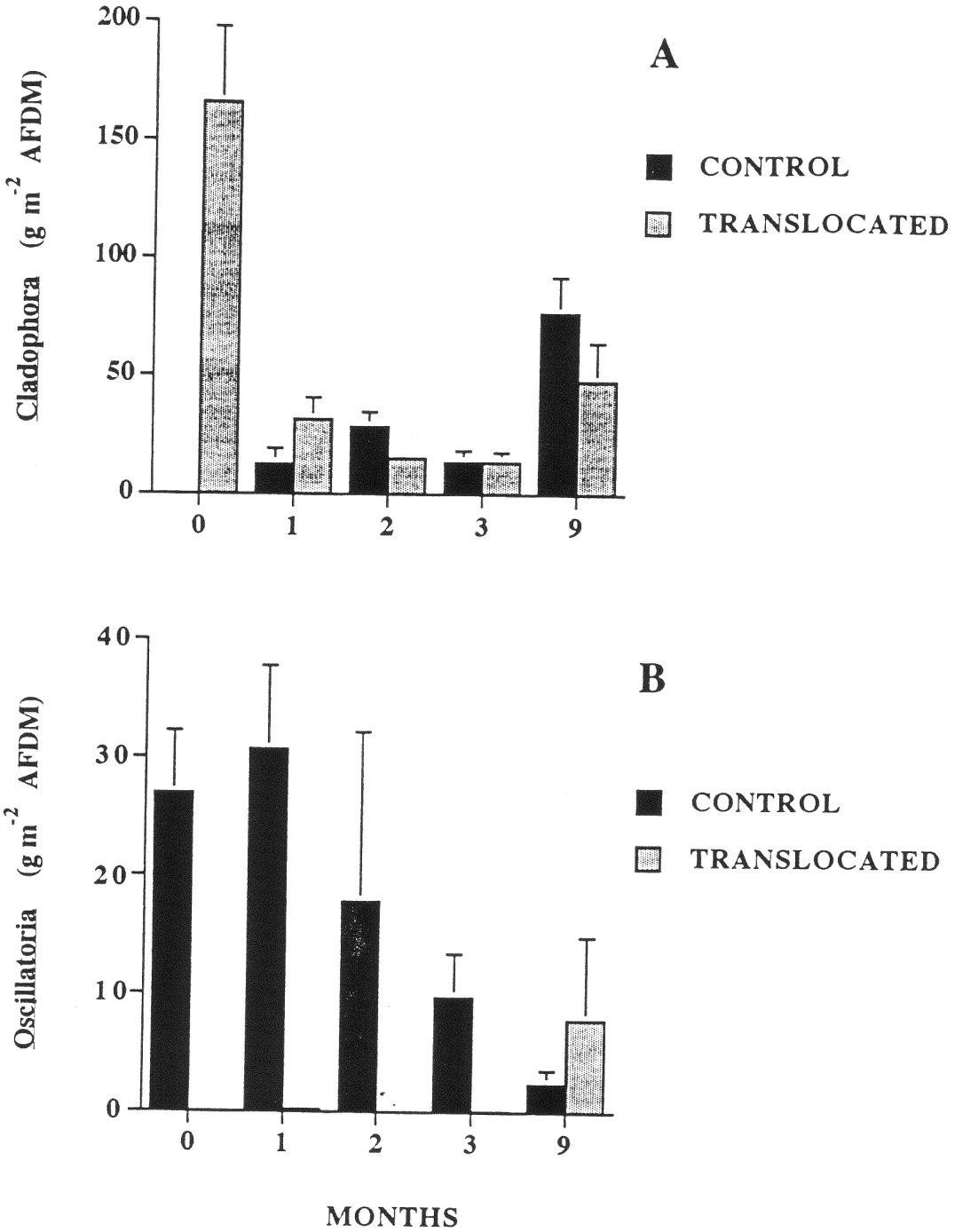


Figure 36. Accomodation rates (days) as g m^{-2} AFDM for Cladophora glomerata (A) and Oscillatoria spp. (B) on the cobbles translocated from a clear-water habitat at Lees Ferry (RKM 0.8) in the Colorado River to a more turbid downstream habitat at Cathedral Island, Arizona (RKM 4.8). Controls represent collections from resident submerged cobbles at Cathedral Island.

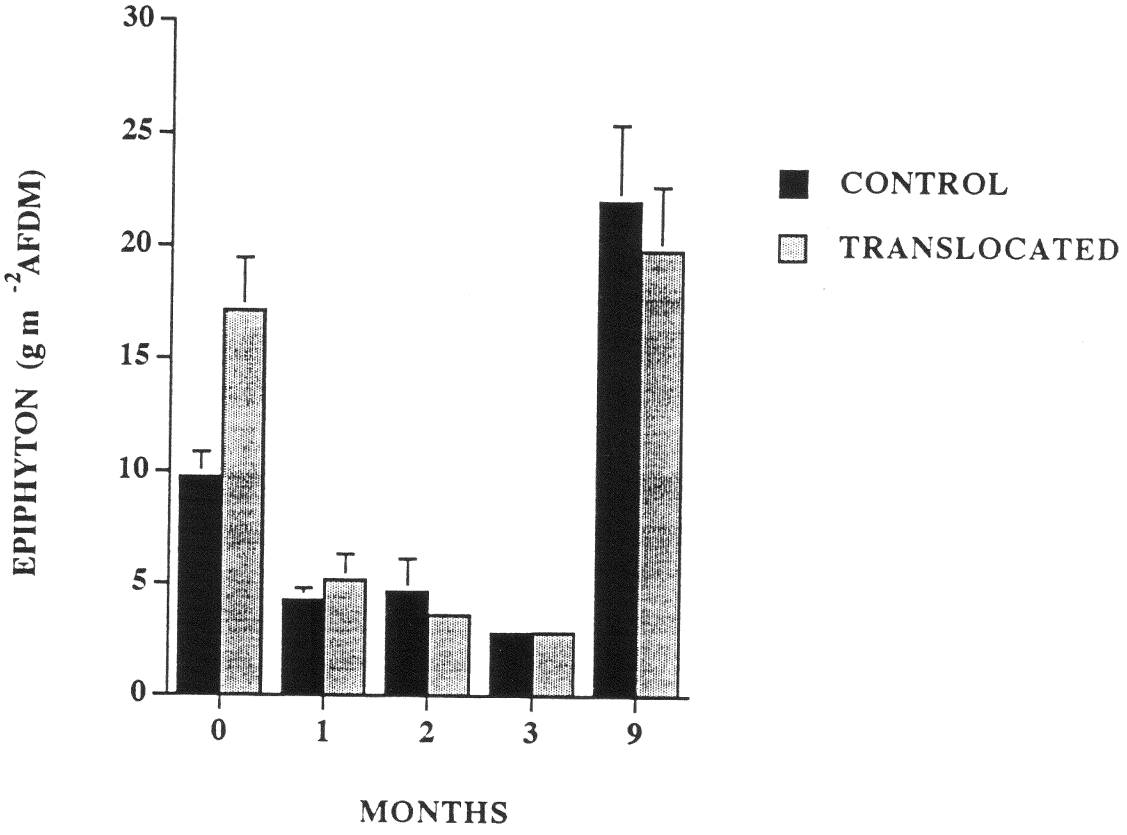


Figure 37. Accomodation rates (days) for epiphyton (g m^{-2} AFDM) on cobbles translocated from a clear-water habitat at Lees Ferry (RKM 0.8) in the Colorado River to a more turbid downstream habitat at Cathedral Island, Arizona (RKM 4.8). Controls represent collections from resident submerged cobbles at Cathedral Island.

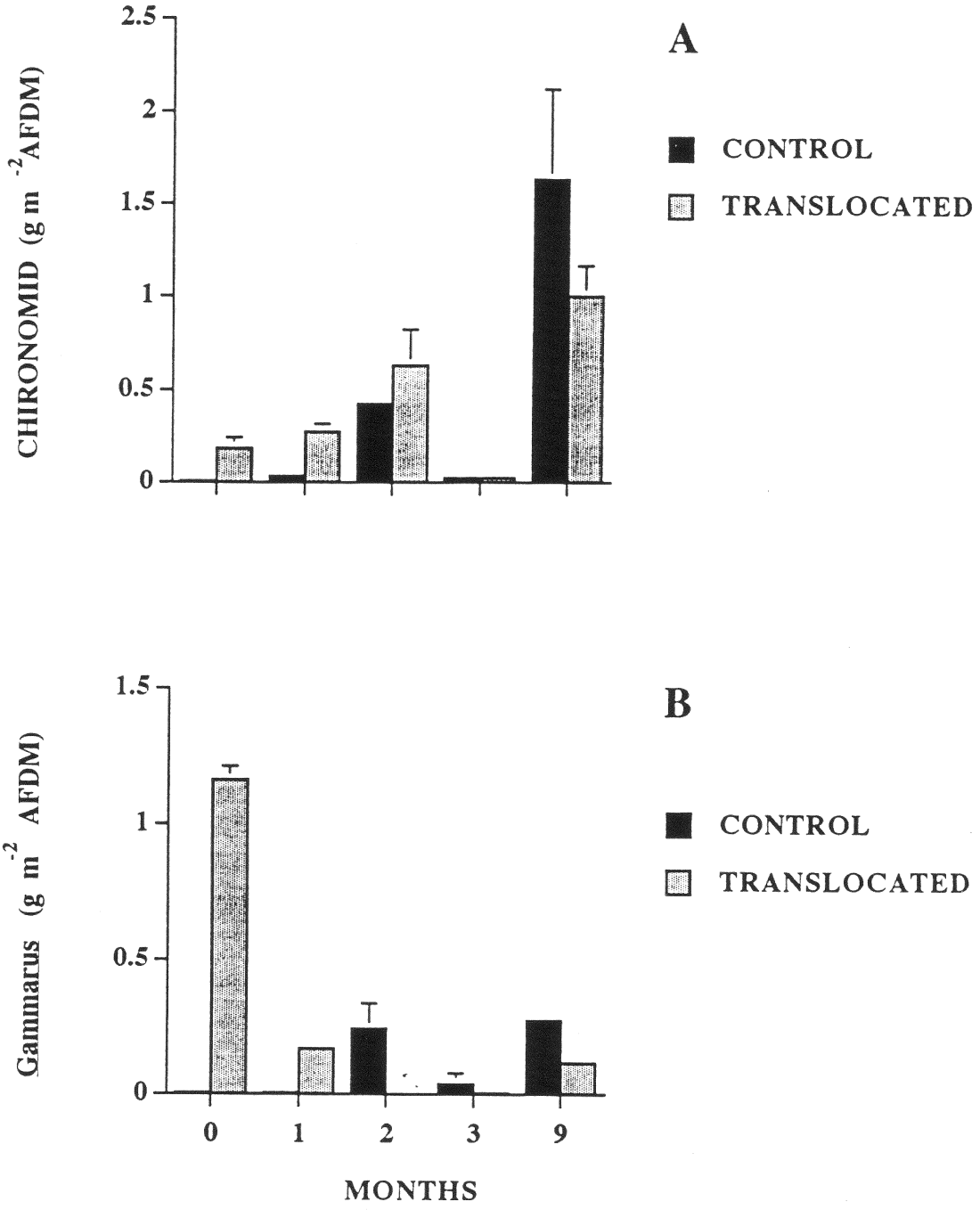


Figure 38. Accomodation rates (days) as g m^{-2} AFDM for chironomid larvae (A) and Gammarus lacustris (B) on cobbles translocated from a clear-water habitat at Lees Ferry (RKM 0.8) in the Colorado River to a more turbid downstream habitat at Cathedral Island, Arizona (RKM 4.8). Controls represent collections from resident submerged cobbles at Cathedral Island.

discharge (hydraulic stress) and therefore had a stronger influence on chironomid AFDM than water clarity and/or feeding strategies.

In-Situ Recolonization Experiments at Lees Ferry

Phytobenthic recolonization rates varied between the continuously submerged and varial zone at Lees Ferry. Cladophora glomerata recolonized desiccated cobbles in the submerged zone, while Oscillatoria was the dominant alga on desiccated cobbles in the varial zone (Fig. 39). Cladophora glomerata AFDM was negligible in the varial zone and generally remained significantly less on submerged cobbles in this zone compared to control cobbles over a 9-mo period (Fig. 39A). In contrast, Oscillatoria spp. reached highest mass in the varial zone (Fig. 39B). Our work is in agreement with previous reports on the ability of Oscillatoria mats to tolerate periodic desiccation (Vincent and Howard-Williams 1986, Hawes 1993) and the ability of C. glomerata to be better suited to grow on stable substrata in non-varial, tailwaters with high transparency (Dodds and Gudder 1992).

The rapid recovery by C. glomerata on treatment cobbles compared to Oscillatoria assemblages (See accommodation experiments) may suggest a strong interaction for substrata between these two benthic algae. Competition between these two benthic algae may result from allelochemicals released by Oscillatoria (Sze 1993) or more likely the inability of C. glomerata to physically establish rhizoidal hold-fasts on sand-impregnated mucilage crusts of Oscillatoria (Dodds and Gudder 1993).

Macroinvertebrate communities showed faster recolonization rates in the continuously submerged zone at Lees Ferry than did benthic algae. Chironomid mass on submerged desiccated cobbles (0.34 g m^{-2}, SE ±0.27) was not significantly different from chironomid AFDM on controls (0.14 g m^{-2}, SE ± 0.04) after 5 mo ($F = 0.11$, $n = 40$, $p = 0.74$); however, both treatment and controls showed wide fluctuations over the next two sampling periods (Fig. 40A). Similarly, G. lacustris AFDM was highly variable but quickly achieved levels equal to or higher than controls in the submerged zone after 1 mo (Fig. 40B).

Gammarus lacustris AFDM remained negligible in the varial zone through the experiment; however, chironomid AFDM increased to control levels at 11 mo. This pulse coincided with the temporary inundation of cobbles in the varial zone and demonstrates the ability of chironomids to rapidly colonize substrata. The slow recolonization by G. lacustris on cobbles located in the varial zone suggests that chironomids are better adapted to utilizing resources in the Oscillatoria community and/or the mouthparts of G. lacustris may be less efficient in utilizing

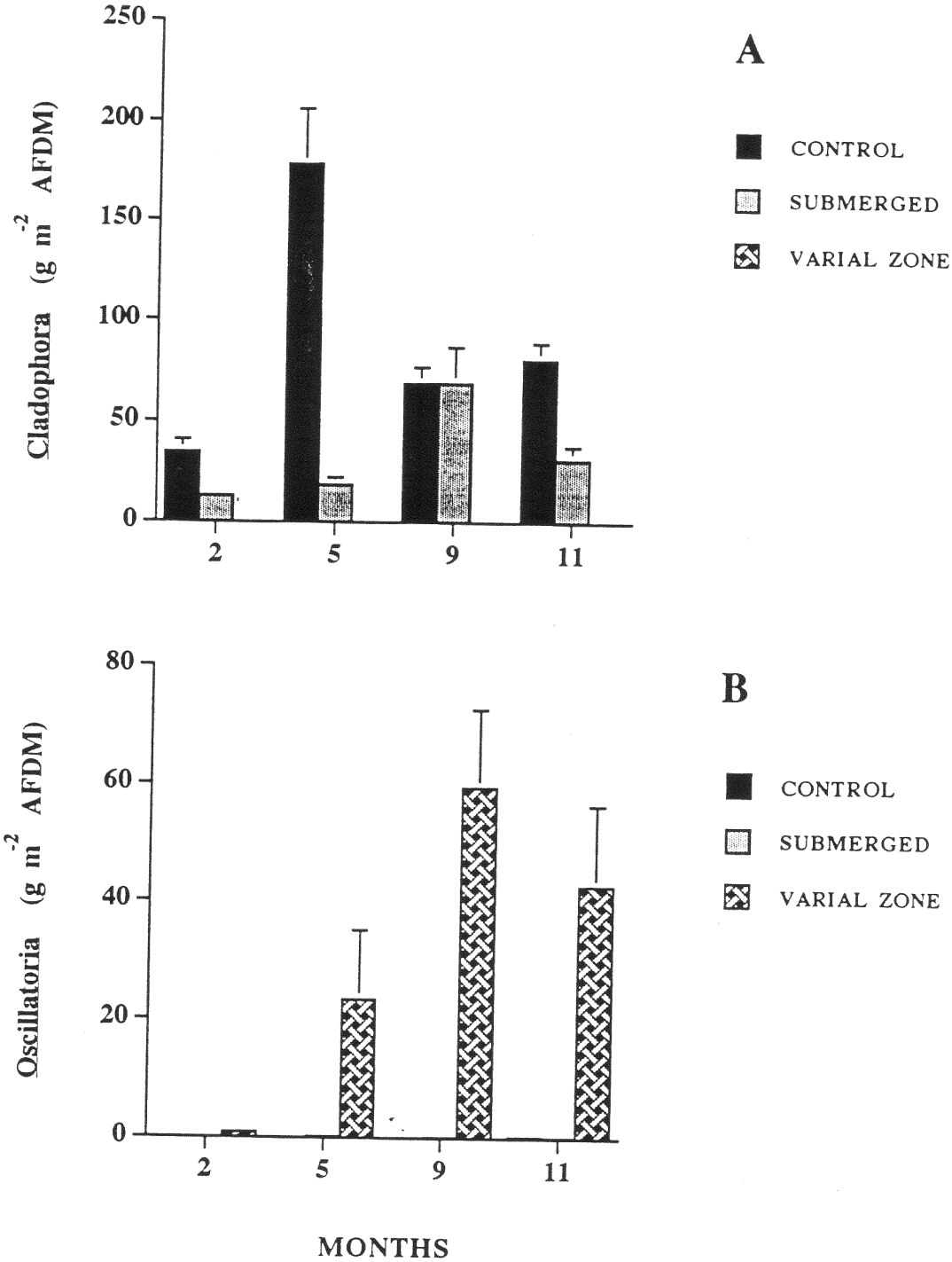


Figure 39. Recolonization rates (months) as g m^{-2} AFDM for Cladophora glomerata (A) and Oscillatoria spp. (B) on desiccated cobbles placed in continuously submerged ($\leq$140 m^3 s^{-1}) and varial zones (140 to 283 m^3 s^{-1}) of the Colorado River at Lees Ferry, Arizona (RKM 0.8). Cobbles were desiccated for 219 days.

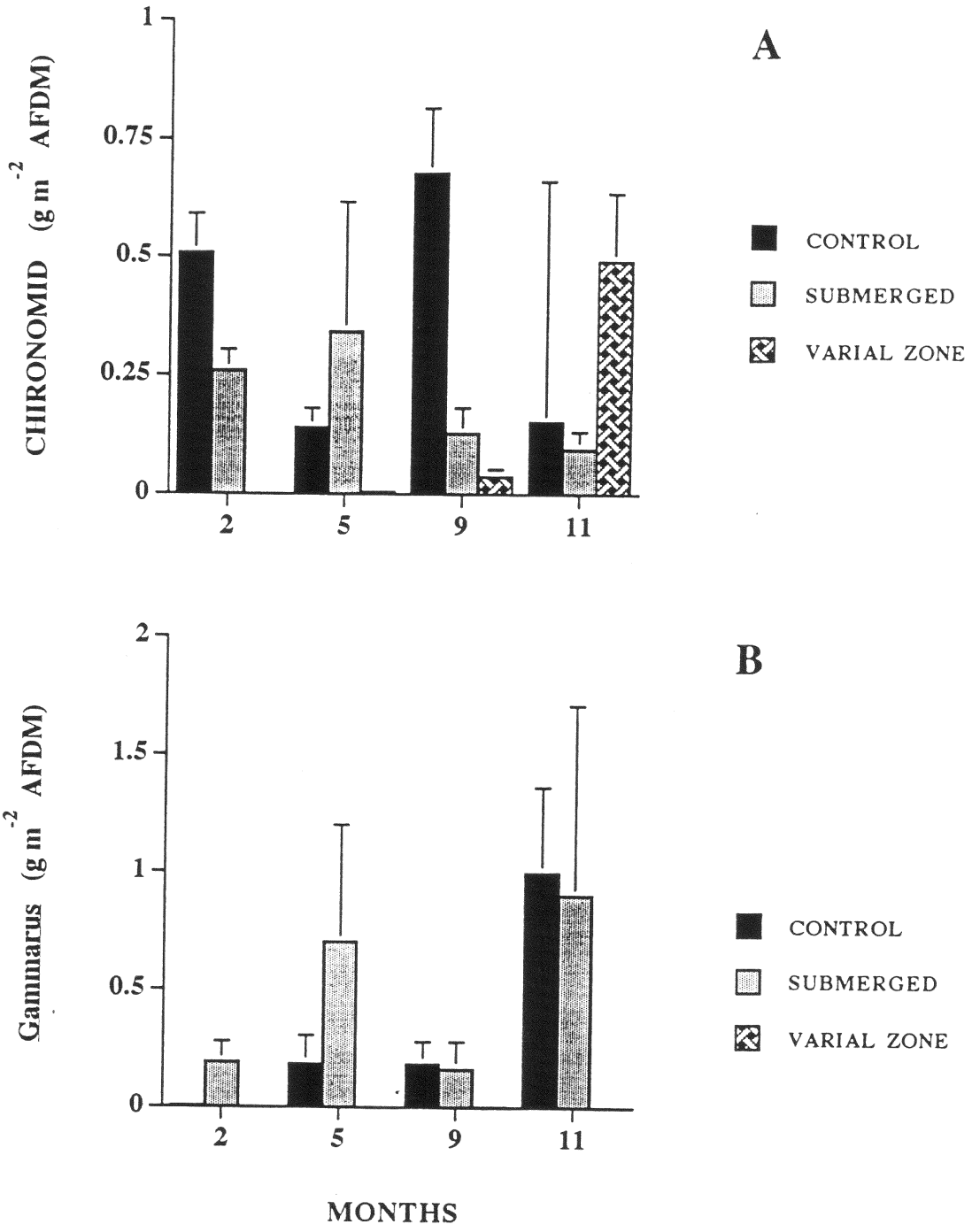


Figure 40. Recolonization rates (months) as g m^{-2} AFDM for chironomid larvae (A) and Gammarus lacustris (B) on desiccated cobbles placed in continuously submerged ($\leq$140 m^3 s^{-1}) and varial zones (140 to 283 m^3 s^{-1}) of the Colorado River at Lees Ferry, Arizona (RKM 0.8). Cobbles were desiccated for 219 days.

periphyton on rock surfaces as compared to epiphyton associated with C. glomerata.

In-Situ Recolonization Experiments at Cathedral Island

The pattern for recolonization of desiccated cobbles in the more turbid Cathedral Island habitat is less well defined than that in the clear-water habitat at Lees Ferry. Cladophora glomerata AFDM developed slowly in the submerged zone, attaining control levels by the end of the experiment (11 mo; Fig. 41A). Cladophora glomerata AFDM also increased on control cobbles as a result of low suspended sediment levels, but development in the varial zone was minor (Fig. 41A). Oscillatoria AFDM colonization in the varial zone exceeded submerged controls by 9 mo (Fig. 41). These experiments imply that C. glomerata is better adapted to submerged, clear-water zones and Oscillatoria is more successful at colonizing substrata in varial zones and/or turbid water habitats, which agrees with our previously described results from translocation experiments.

In association with the low AFDM of C. glomerata, recruitment by macroinvertebrate AFDM was slower at Cathedral Island than Lees Ferry throughout most of the study period; probably due to low AFDM of C. glomerata. In the submerged zone, chironomid AFDM increased slowly, but dropped after 9 mo (Fig. 42A). Gammarus lacustris AFDM reached control levels in the submerged zone in 11 months (Fig. 42B), but neither chironomid or G. lacustris AFDM developed to any extent in the varial zone. The low macroinvertebrate mass in Oscillatoria mats at Cathedral Island may have resulted from the limited number of macroinvertebrates available for recruitment in the surrounding area at Cathedral Island.

We calculated animal energy equivalents associated with C. glomerata and Oscillatoria benthic communities along the Colorado River corridor using data by Blinn et al. (1992). Our estimates indicate that 1 g of C. glomerata yields ~0.1g of macroinvertebrate mass compared to ~0.015 g of macroinvertebrates in a comparable mass of Oscillatoria. Data for C. glomerata communities were derived from collections (n = 96) at Lees Ferry and Tanner (RKM 108), while values for Oscillatoria assemblages were taken from two downstream sites (n = 90) at RKM 205 and RKM 220 (See Chapter One). Based on average energy equivalents derived for the macroinvertebrate community in the Colorado River (Blinn et al. 1992), these values yield 1,800 joules of energy g^{-1} of Cladophora mass compared to only ~270 joules of energy g^{-1} of Oscillatoria mass.

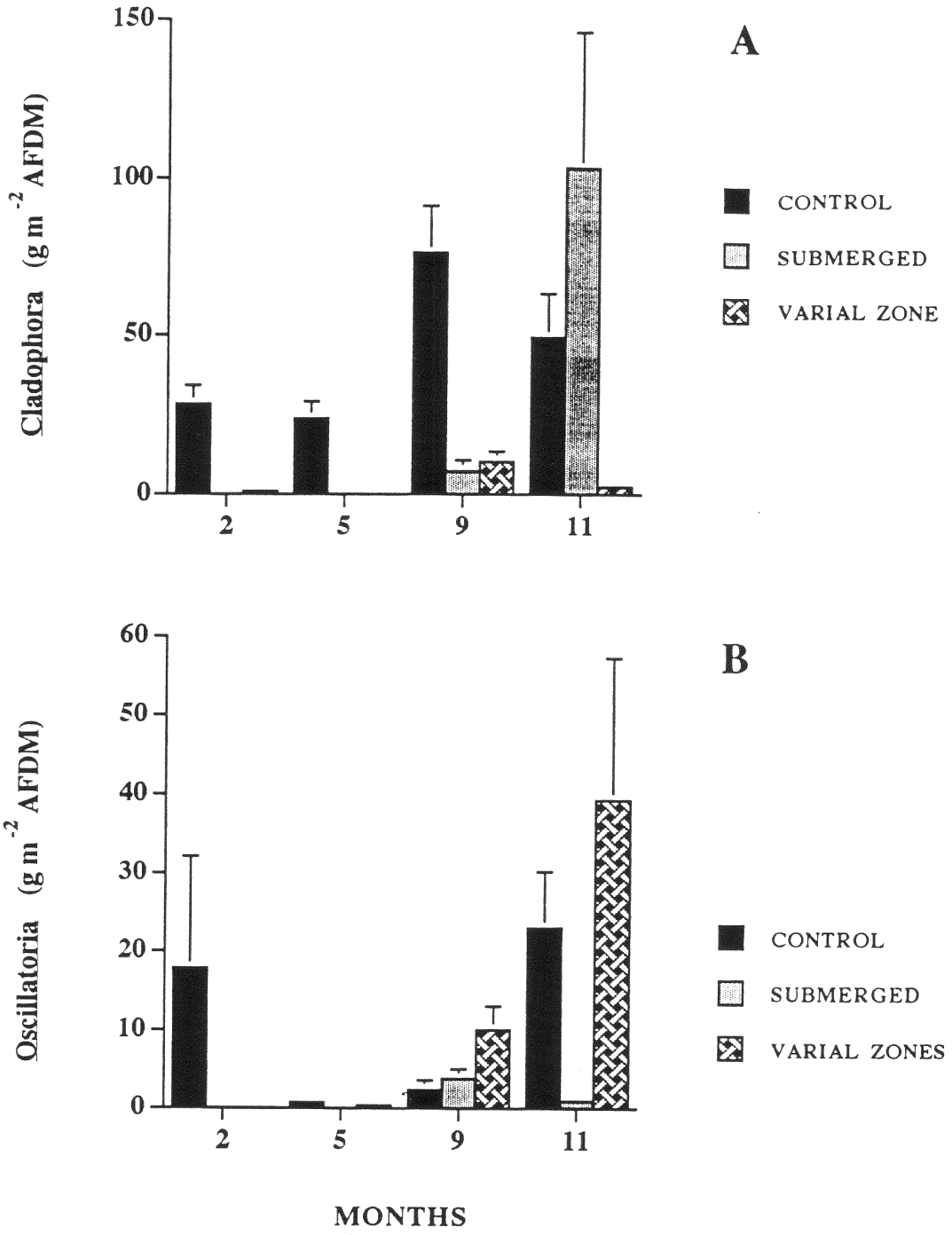


Figure 41. Recolonization rates (months) as g m^{-2} AFDM for Cladophora glomerata (A) and Oscillatoria spp. (B) on desiccated cobbles placed in continuously submerged ($\leq$140 m^3 s^{-1}) and varial zones (140 to 283 m^3 s^{-1}) of the Colorado River at Cathedral Island, Arizona (RKM 4.8). Cobbles were desiccated for 219 days.

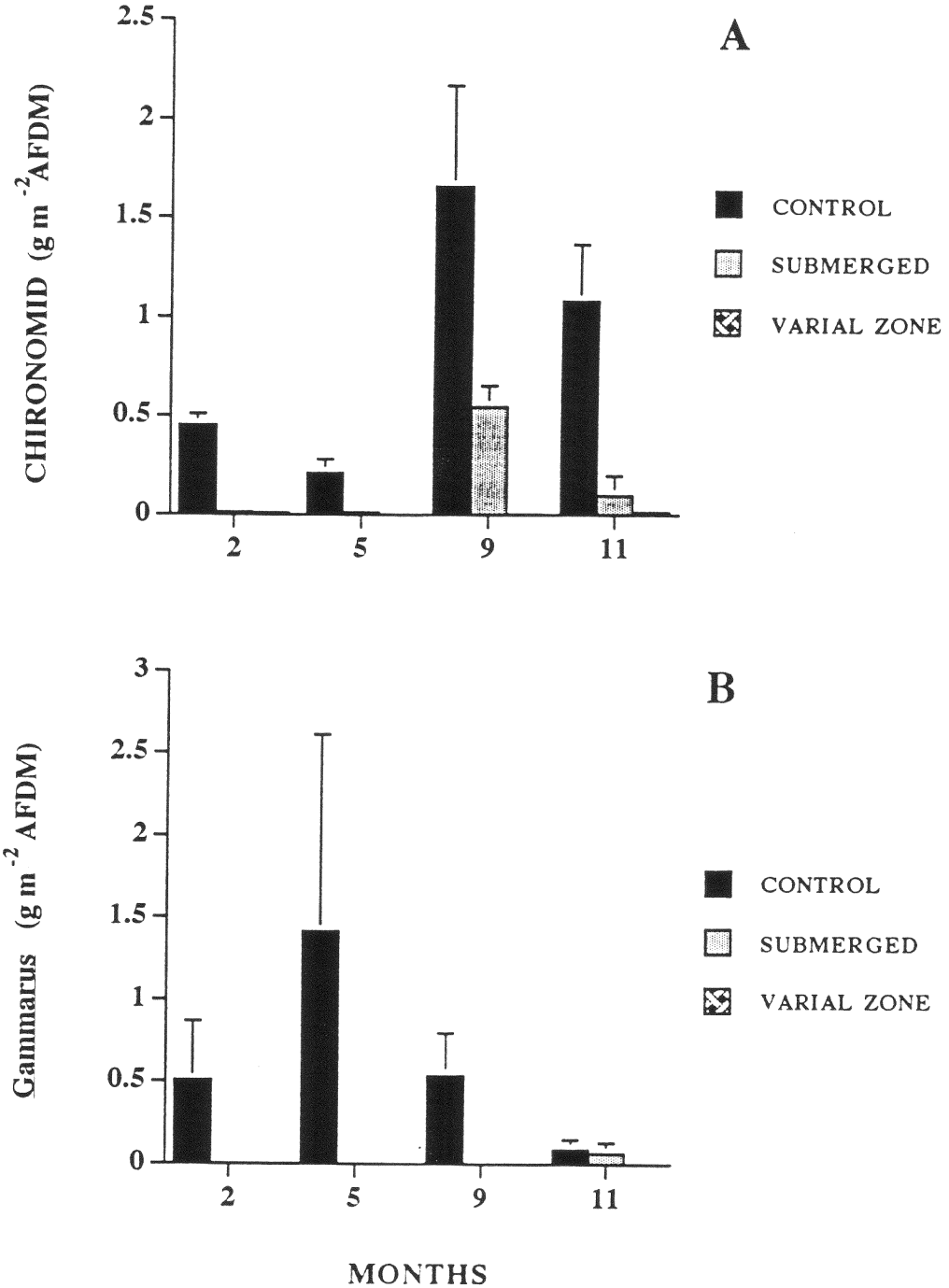


Figure 42. Recolonization rates (months) as g m^{-2} AFDM for chironomid larvae (A) and Gammarus lacustris (B) on desiccated cobbles placed in continuously submerged ($\leq$140 m^3 s^{-1}) and varial zones (140 to 283 m^3 s^{-1}) of the Colorado River at Cathedral Island, Arizona (RKM 4.8). Cobbles were desiccated for 219 days.

SUMMARY

The above experiments indicate that both variable water levels and elevated suspended sediment are less suitable conditions for C. glomerata than for Oscillatoria phytobenthic communities. These observations are generally supported by patterns displayed by phytobenthic communities located downstream from Glen Canyon Dam (See Chapter One, Blinn et al. 1992, Angradi and Kubly 1993, Shannon et al. 1994). Chironomid AFDM increased more quickly than G. lacustris AFDM on translocated cobbles at Lees Ferry, and chironomid recruitment appeared to be less dependent on C. glomerata than recruitment by G. lacustris. Macroinvertebrates showed faster recolonization of desiccated cobbles in the continuously submerged zone than did benthic algae. In general, cobbles in the varial zone showed limited recruitment by macroinvertebrates compared to submerged and control cobbles.

We estimate the energy derived from animal mass associated with C. glomerata communities to be nearly an order of magnitude higher than energy derived from macroinvertebrate mass in Oscillatoria communities. Therefore, loss of C. glomerata habitat and the replacement by habitat more suitable for Oscillatoria reduces the overall food value of the phytobenthic community in the Colorado River through Grand Canyon National Park.

CHAPTER FIVE: EFFECTS OF WINTER FREEZING ON FLUVIAL BENTHOS

INTRODUCTION

Fluctuating flows in regulated rivers may expose the benthos to desiccation and ultraviolet radiation; and also to winter freezing. Dudgeon et al. (1989, 1990) reported that freezing reduces photosynthesis, cell membrane permeability, frond growth, and overall biomass in marine intertidal algal communities; however, experimental investigations quantifying the effects of freezing on fluvial benthos are limited. We hypothesized that freezing in varial zones of regulated rivers exerts similar negative impacts on freshwater algal communities.

Although Interim Flows (IF) reduced the extent of littoral exposure, IF's still permit flow levels to drop to 140 $m^3 s^{-1}$ for 6-h periods during the night. Because of the deformation of the release wave in the tailwaters of the system, exposure is greatest at Glen Canyon Dam and in the Glen Canyon Reach and decreases downstream. Exposure of the Glen Canyon Reach is critical because this upper reach supports more than 60% of the benthic algal and macroinvertebrate communities in our study area. Brief daytime exposures have been shown to affect Cladophora glomerata viability (Usher & Blinn 1990, Angradi & Kubly 1993). We asked whether this nocturnal exposure during cold winter months affects the viability of C. glomerata/epiphyte/macroinvertebrate assemblages.

METHODS

The combined result of freezing and desiccation on Cladophora glomerata mass, chlorophyll a, and macroinvertebrate abundance was tested at Lees Ferry on 10-11 February 1993. This protocol was designed to isolate the combined effects of freezing and desiccation from those of ultraviolet light. Thirty cobbles (~90 cm in circumference), each supporting an associated C. glomerata community, were translocated from below the 141 $m^3 s^{-1}$ stage to the 280 $m^3 s^{-1}$ stage at 1500 h on 10 February. All translocated treatment cobbles were placed at a depth of 15 cm in the shade of large boulders to reduce potential ultraviolet light damage prior to night desiccation. A Peabody Ryan scroll thermistor was secured in the middle of the treatment cobbles to determine average duration of submergence, desiccation and freezing by comparison of water and ambient air temperatures.

Discharge reached peak flow at 2100 h and percent cloud cover and humdity were recorded.

Prior to contact with direct sunlight on 11 February (0800 h), the treatment cobbles were resubmerged to a depth of about 15 cm so cobbles would be rinsed in accordance with the experimental protocol of Blinn et al. (1992). Treatment cobbles were sampled at 1600 h on 11 February. Paired samples of 20 cm^2 were collected: one for C. glomerata mass and the second for chlorophyll a and macroinvertebrate numeration. The second sample pair was protected from direct sunlight and placed on dry ice. Unexposed control samples were collected from 30 cobbles randomly selected from below the 140 $m^3 s^{-1}$ stage at the completion of the experiment on 11 February.

Macroinvertebrates were separated from C. glomerata in the laboratory and oven-dried at 60°C to a constant weight. Animals were sorted and counted into the following groups: Gammarus lacustris, gastropods, lumbriculids, and tubificids. Chlorophyll a was calculated using the methanol extraction procedure (Tett et al. 1975).

RESULTS AND DISCUSSION

Winter desiccation (i.e., three h of night freezing during eight hours of exposure) resulted in a significant loss of C. glomerata biomass and chlorophyll a. Mean AFDM of C. glomerata decreased from 80.1 g in controls to 44.5 g in desiccated/frozen treatments, a highly significant decrease ($F = 9.11$; $df = 1,87$; $p = 0.003$). Chlorophyll a also decreased significantly between control samples (8,700 mg m^{-2}) and frozen/desiccated treatment samples (3.600 mg m^{-2}; $F = 12.07$; $df = 1,57$; $p = 0.0009$; Fig. 43).

Although control samples averaged 400 lumbriculids m^{-2}, 175 G. lacustris m^{-2}, 75 tubificids m^{-2}, and 325 gastropods m^{-2} compared to only 75 G. lacustris m^{-2} in frozen/desiccated samples, there was no significant change in macroinvertebrate abundance between control and treatment cobbles (Wilks' Lambda = 0.93; $F = 1.38$; $df = 4,84$; $p = 0.24$). The lack of significance can be attributed to the high variance between samples due to the patchy nature of the biotic community at Lees Ferry.

Based on thermistor readings, treatment cobbles were exposed for eight h with only three h below freezing (-2°C). Ambient air temperature was always below river temperature of 6.5°C. Relative humidity at the end of the exposure period

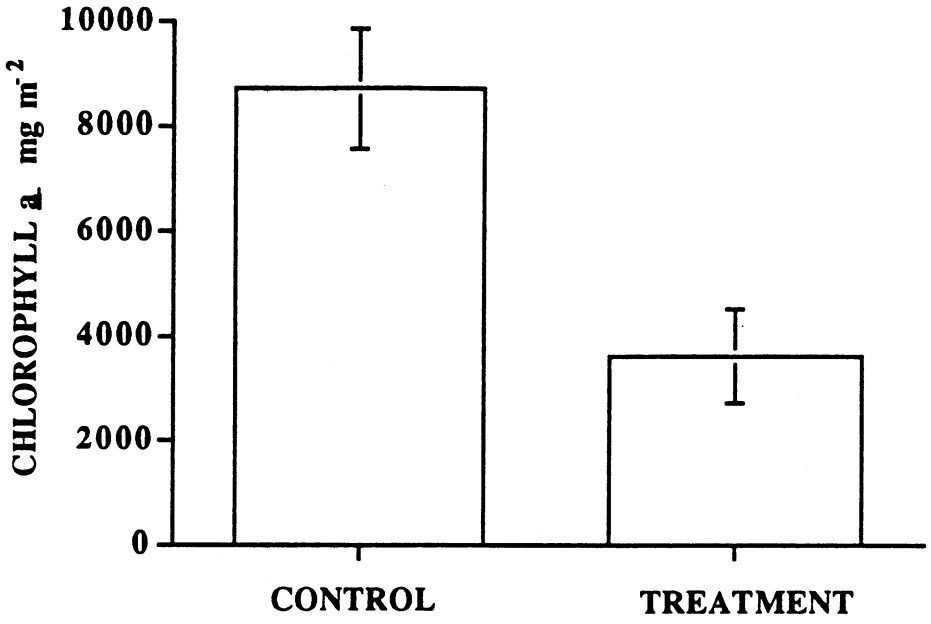


Figure 43. Impacts of winter freezing/dessication on chlorophyll a (mg m^{-2}) in Cladophora glomerata after eight hours of exposure and three hours of freezing. Control values were taken at the end of the experiment from continuously submerged cobbles.

was 60% (0730 h). Discharge ranged from 400 $m^3 s^{-1}$ on February 10 to 255 $m^3 s^{-1}$ on the following day.

SUMMARY

Winter nighttime desiccation exerts similar effects on the mass of C. glomerata as does summer desiccation (Usher & Blinn 1990, Blinn et al. 1992, Angradi & Kubly 1993). Three h of nighttime freezing reduced biomass by 50%, which is comparable to summer losses (48%) after a 12-h exposure. Chlorophyll a also showed a significant decrease from controls. Data for macroinvertebrate densities were not conclusive due to the patchiness of the benthic community at Lees Ferry. However, there was a strong pattern for loss of macroinvertebrate biomass (93%) following one winter night exposure. Repeated desiccation and larger sample sizes may resolve this discrepency.

CHAPTER SIX: MANAGEMENT CONSIDERATIONS

Reduction in flow dynamics of the Colorado River under Interim Flows (IF) has initiated a series of potentially long-lasting changes in the benthos and patterns of drift in the Colorado River through Grand Canyon. These patterns are initiated by inflow from Lake Powell, dam operations and downstream tributary inflow at several temporal scales. Our monitoring results demonstrated that reduction in flow velocity, accumulation of fine sediments and exceptionally prolonged periods of low tributary inflow under IF allowed aquatic plants (especially Potamogeton and Chara sp.) to colonize soft-bottom habitats throughout the wide reaches upstream from the Little Colorado River. Aquatic macrophytes have been reported at low densities in the Glen Canyon reach to the Paria River since the mid-1970's, but under IF Potamogeton has dramatically increased in Marble Canyon and is now distinctly visible on aerial photographs. In addition to Potamogeton, the ranges of several other macrophyte taxa have been extended in the Colorado River under IF.

Physical changes that shift the dominance of benthic flora away from the filamentous green alga, Cladophora glomerata to other taxa may exert profound changes on the aquatic food base in this system. Other macrophytes host fewer epiphytes, which are the primary food source for benthic invertebrates (Czarnecki and Blinn 1978, Blinn et al. 1986, Blinn et al. 1989, Pinney 1991, Hardwick et al. 1992, Blinn et al. 1992, Shannon et al. 1994, Stevens et al. in review) and some fish species (Leibfried, personal communication) in this system. Benthic macrophytes (Potamogeton, Chara) and bryophytes are well established and may not be scoured by planned flooding. Because the benthos is changing rapidly it is not possible to predict the long-term developmental trajectory of the river benthos.

Our monitoring results and experiments indicate that both fluctuating water levels and elevated suspended sediments are less suitable habitats for C. glomerata than for Oscillatoria. Cladophora glomerata colonizes cobbles in the continuously submerged zone, while Oscillatoria colonizes substrates in zones of fluctuating flow and reaches with elevated suspended sediments. Recolonization by C. glomerata is very slow in submerged zones (≥1 yr), with negligible recolonization in varial (fluctuating) zones. In general, loss of C. glomerata habitat greatly reduces overall energy as animal mass in the benthic algal community. Thermal responses of C. glomerata and Oscillatoria should be investigated in more detail.

Nightime freezing and desiccation during the winter is as detrimental to the aquatic benthos as summer daytime desiccation at Lees Ferry. There was a significant loss in C. glomerata mass and chlorophyll a after 3 h of freezing during reduced flows. This means that if the management strategy is to maximize production of C. glomerata for the fisheries, wintertime, nighttime flows of ≤141 $m^3 s^{-1}$ (5,000 cfs) for 6 h should be avoided. Collectively these monitoring results support a minimum 24 h flow of 225 $m^3 s^{-1}$ to provide maximum habitat for C. glomerata colonization.

Both the chironomid larval community and Gammarus lacustris have relatively high production rates in the submerged zone (≤140 $m^3 s^{-1}$) of the Colorado River. Highest production by these two invertebrate groups is expected to occur during low volume months. These low volume months include fluctuations between 170 $m^3 s^{-1}$ and 285 $m^3 s^{-1}$. Although higher flows provide more submerged channel, these flows also remove chironomid larvae and G. lacustris from benthic substrates due to increased shear stress. Upper threshold flow levels at which G. lacustris and chironomid larvae are lost to drift needs to be established due to the importance of these invertebrates as intermediate links between primary producers and fish. Determination of these thresholds for G. lacustris and other benthos (C. glomerata, epiphytic diatoms, and associated macroinvertebrates) should be more carefully studied in flume experiments as well as in situ experiments for predictions of planned flood effects.

River regulation has a signficant impact on downstream export of benthic biomass. Our monitoring studies at Lees Ferry showed at least a two-fold increase in organic stream drift between 170 to 370 $m^3 s^{-1}$ (6,000 -13,000 cfs) compared to steady 225 $m^3 s^{-1}$ (8,000 cfs) flows. This energy is probably not directly available to native and exotic fishes below the Paria River. The extent to which the coarse particulate matter (CPOM) generated from Lees Ferry is processed by the microbial loop or transported as fine particulate organic matter (FPOM) through the river corridor is unclear. Therefore, the role of bacteria, and perhaps fungi, in the food web of downstream aquatic communties needs further research.

Sediment-related turbidity is the single most important factor influencing productivity in the Colorado River ecosystem. The clear-water Glen Canyon reach supports most of the benthic standing crop (>60%) in the system (Blinn et al. 1992), with limited downstream transport of C. glomerata and associated communities (See Chapter Three on Organic Drift). Prolonged clear-water flows during IF has allowed production to increase on a system-wide basis; however, this increased standing crop is subject to the vagaries of mainstream

floods and tributary-related turbidity from sediment inflow. At present the EIS Preferred Alternative calls for flow levels that preserve or enhance a mass balance of sediments, coupled with occasional (2-10 yr) floods to redistribute those sediments. Therefore, no sediment augmentation is planned. This means that the upper reaches of the river will remain dominantly as partially clear-water sections, and therefore will remain highly productive. Management strategies may change in response to proposed regulation of river temperature.

Proposed warming of the river during the summer months may initiate substantial changes in phytobenthos, epiphyton, zooplankton, and macroinvertebrate assemblages. Numerous taxa are presently excluded from the system by cold temperatures which reduce growth rates and prohibit completion of invertebrate life cycles. However, modification of the river temperature may modify selected trophic levels which, in turn, may affect the Colorado River food web. Blinn et al. (1989) reported that upright diatom taxa, available to grazers including G. lacustris and chironomid larvae, decreased when water temperature was elevated to ≥18°C, while the more adnate, less available, taxa increased. This compositional shift in the physiognomy of epiphytic diatom communities may potentially reduce the availability of food to macroinvertebrate grazers (Steinman et al. 1987, Colletti et al. 1987) and modify the aquatic food web, especially in the clear-water reach below Glen Canyon Dam. Present discussions regarding construction of a multiple level intake structure (MLIS) indicate that it may not be possible to warm the river to pre-dam conditions. Maximum pre-dam summer temperatures exceeded 29°C at Lees Ferry. Even if design modification to the MLIS withdraws surface water temperatures, the river would not be warmed to more than 18°C at Lees Ferry. This means that only partial recovery of natural conditions may be possible in the Marble Canyon reach, the section of the river which supports the greatest concentration of native fish, especially humpback chub.

Provided that tributary inflow patterns remain consistent (highly variable), the future of the Colorado River benthos will be determined by management of Lake Powell and operations of Glen Canyon Dam. Most of the variability in benthic standing mass and productivity is related to water clarity and temperature, factors which may change under different management options. Whereas benthic production is influenced by water clarity, benthic diversity is influenced by water temperature.

Our monitoring data on natural flooding from the LCR (January-February 1993) indicates that maintenance floods as outlined in the Glen Canyon Dam Environmental Statement (U.S. Bureau of Reclamation 1994), may exert an

overall beneficial effect on the aquatic food base. Cobble and pool habitats have been reduced in size due to sedimentation under IF, and the extent of firm substrates would be increased.

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 and higher aquatic trophic levels. Mainstream 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 a comprehensive analysis 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). 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 all macroinvertebrate taxa presently in the mainstream. These studies should be conducted first in a laboratory environment, and subsequently in field experiments. Thermal modification studies should be initiated as soon as possible so that an adequate database can be developed, and so issues surrounding assemblage change 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 to riparian trophic levels.

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CHAPTER EIGHT: PRESENTATIONS AND PUBLISHED ARTICLES RELATED TO THIS STUDY

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Shaver, M.L., F.G. Govedich, J.P. Shannon, K.P. Wilson, & D.W. Blinn. 1994. Reciprocol transplants in clear and turbid water habitats in the regulated Colorado River, Grand Canyon, Arizona. 38th Annual Meeting of the Arizona-Nevada Academy of Science. Glendale Community College, Glendale Arizona.

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Yard, M., D.W. Blinn, L.E. Stevens, & J. Shannon. 1994. Limnology and lower trophic levels of the Colorado River from Lake Powell through the Grand Canyon. Abstract. American Fisheries Society, Flagstaff, AZ.

APPENDIX FIGURES

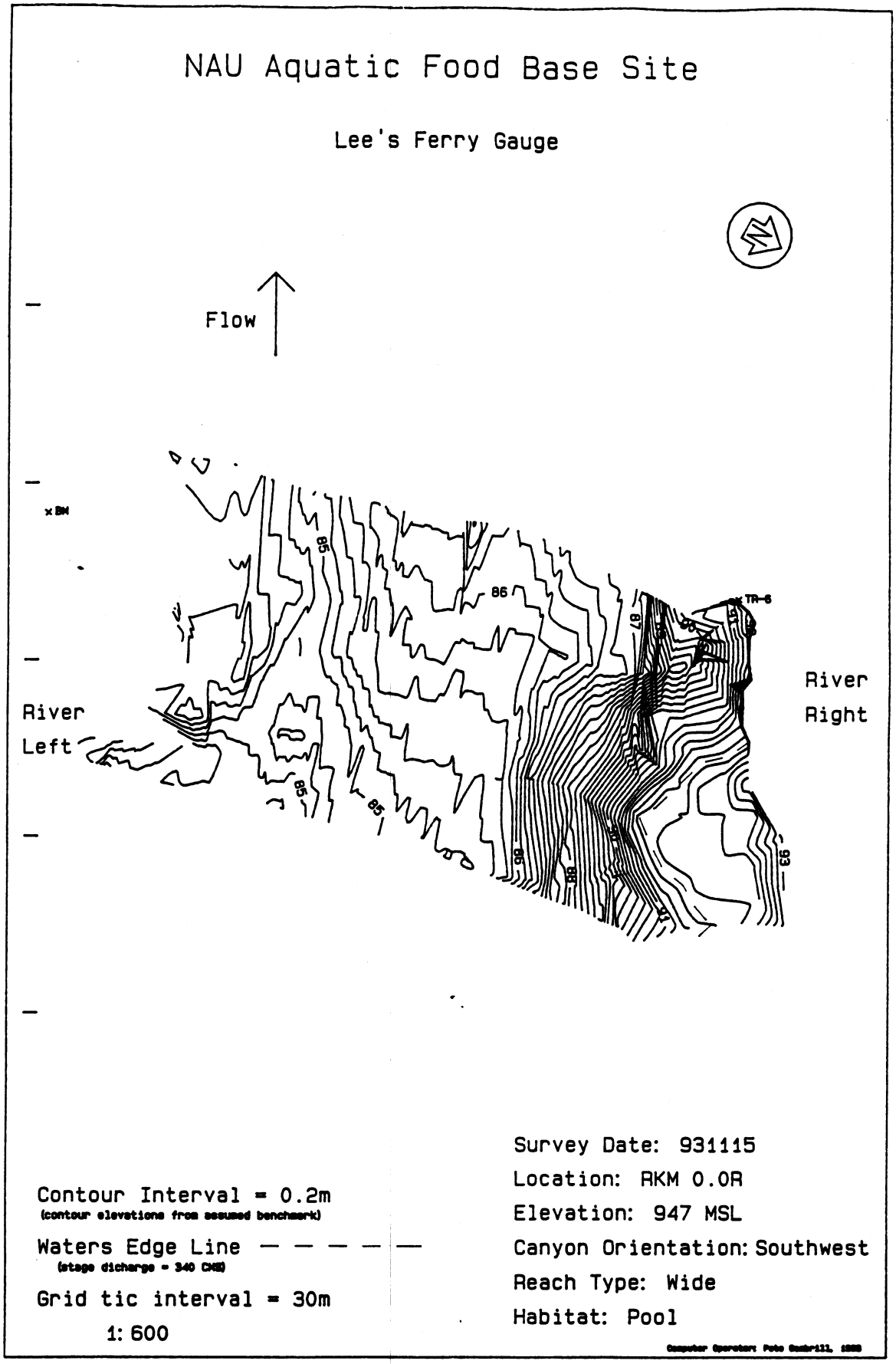

Figure 1. Bathymetric map of Lees Ferry Gauge (RKM 0.0), a wide pool.

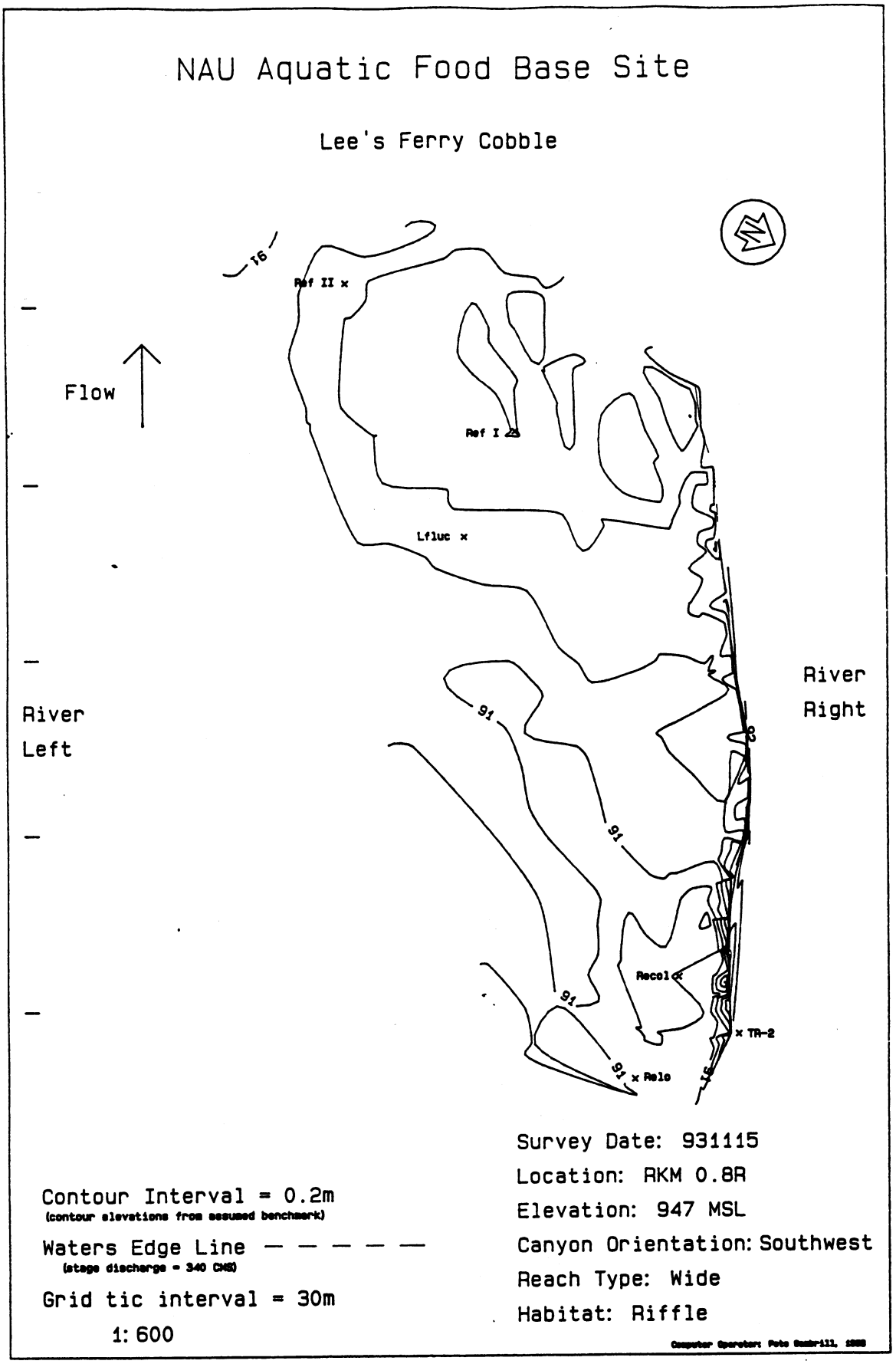

Figure 2. Bathymetric map of Lees Ferry cobble (RKM 0.8), a wide reach.

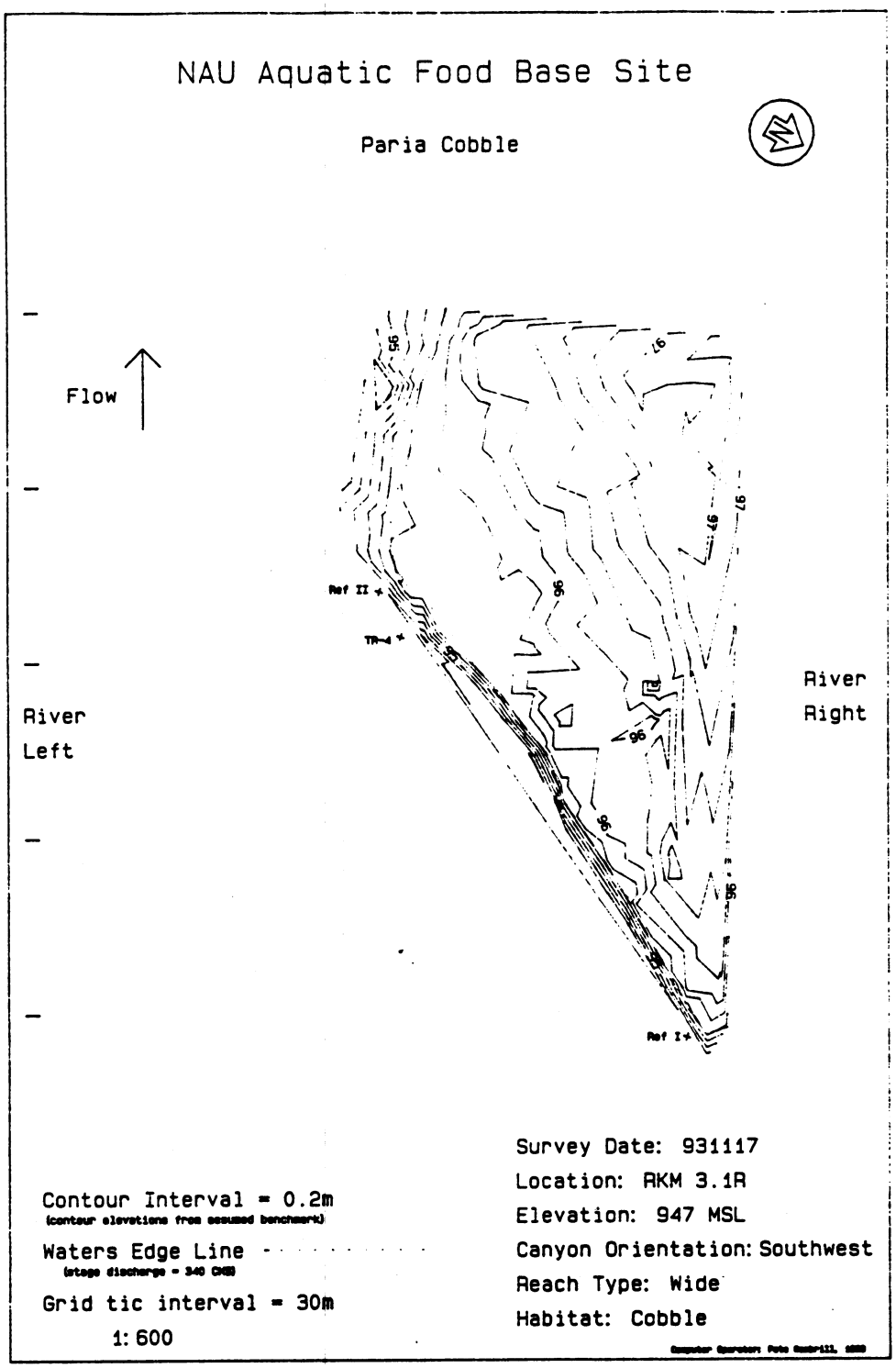

Figure 3. Bathymetric map of Paria cobble (RKM 3.1), a wide reach riffle

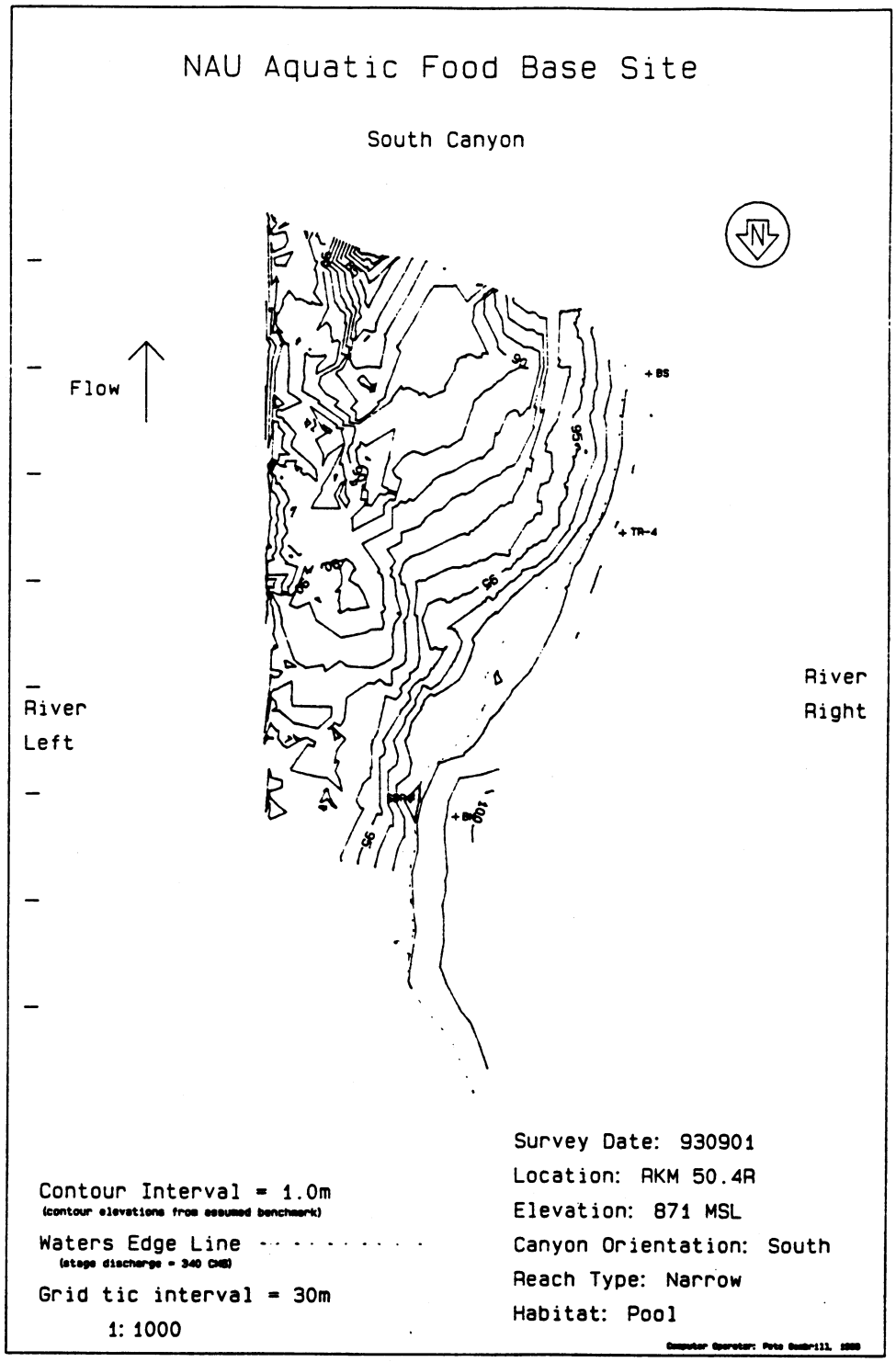

Figure 4. Bathymetric map of South Canyon (RKM 50.4), a narrow pool.

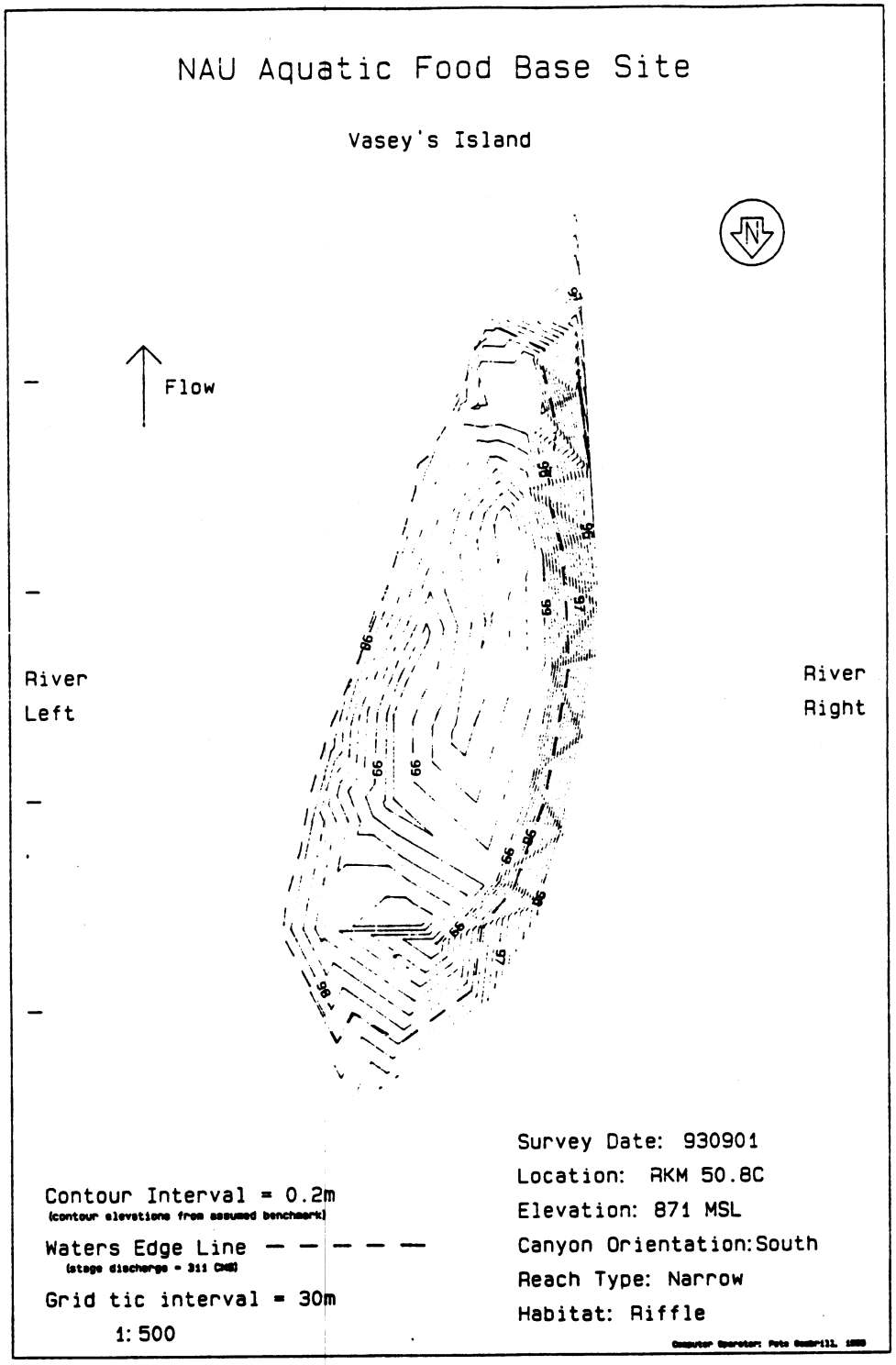

Figure 5, Bathymetric map of Vasey's Island (RKM 50.8), a narrow riffle.

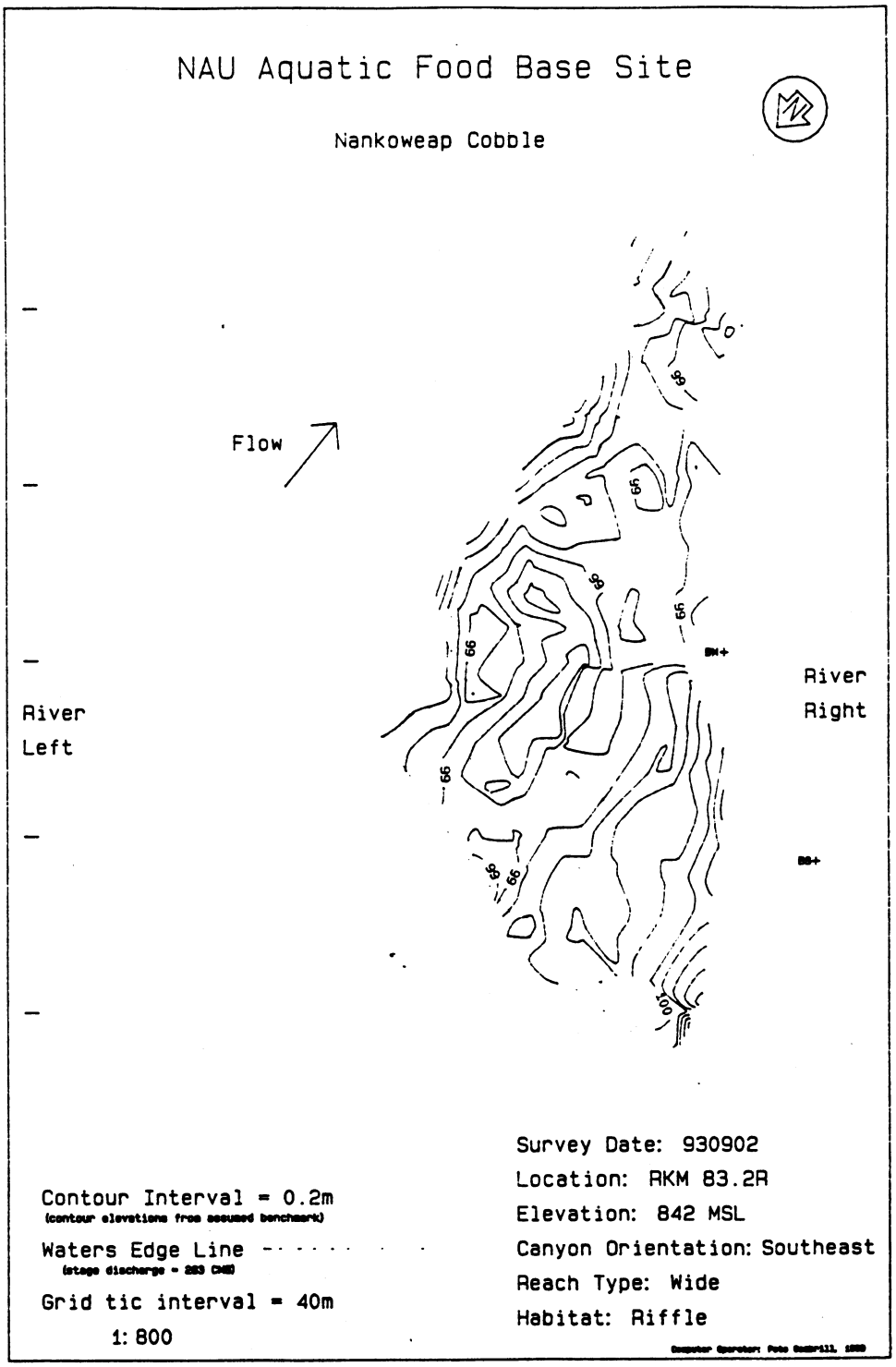

Figure 6. Bathymetric map of Nankoweap (RKM 83.2), a wide riffe.

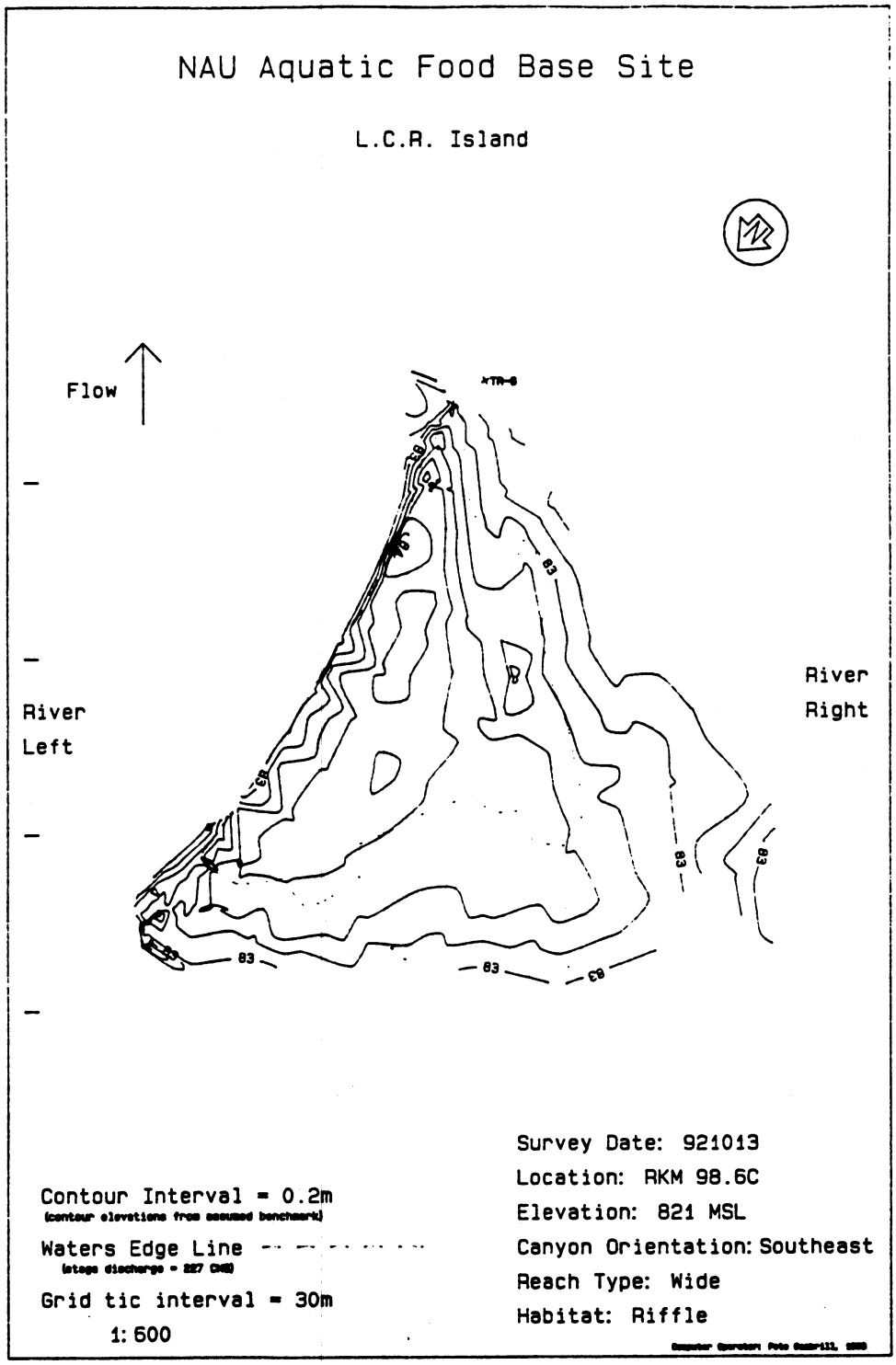

Figure 7. Bathymetric map of Little Colorado River (RKM 98.6), a wide riffle site.

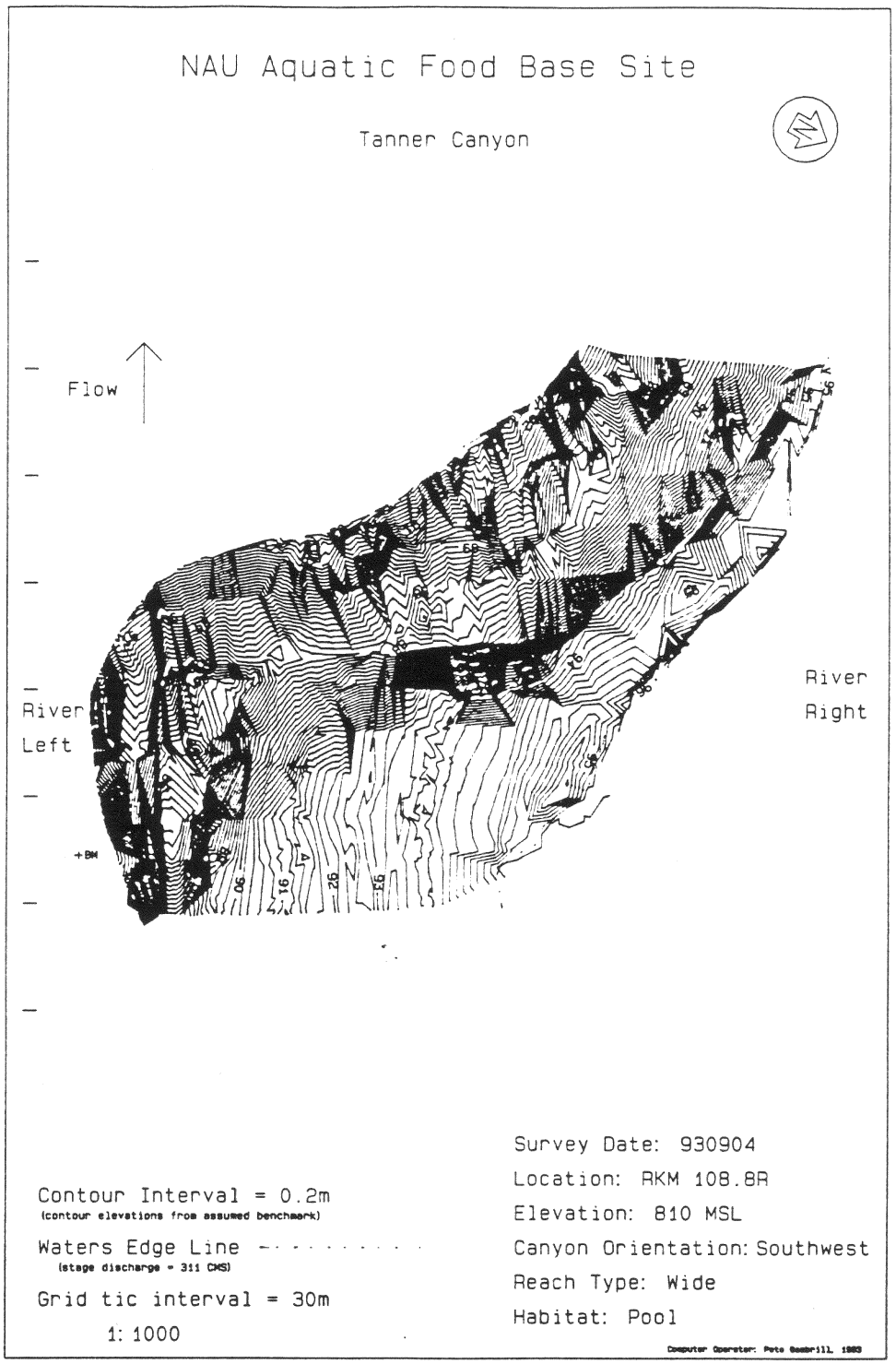

Figure 8. Bathymetric map of Tanner Canyon (RKM 108.8), a wide pool site.

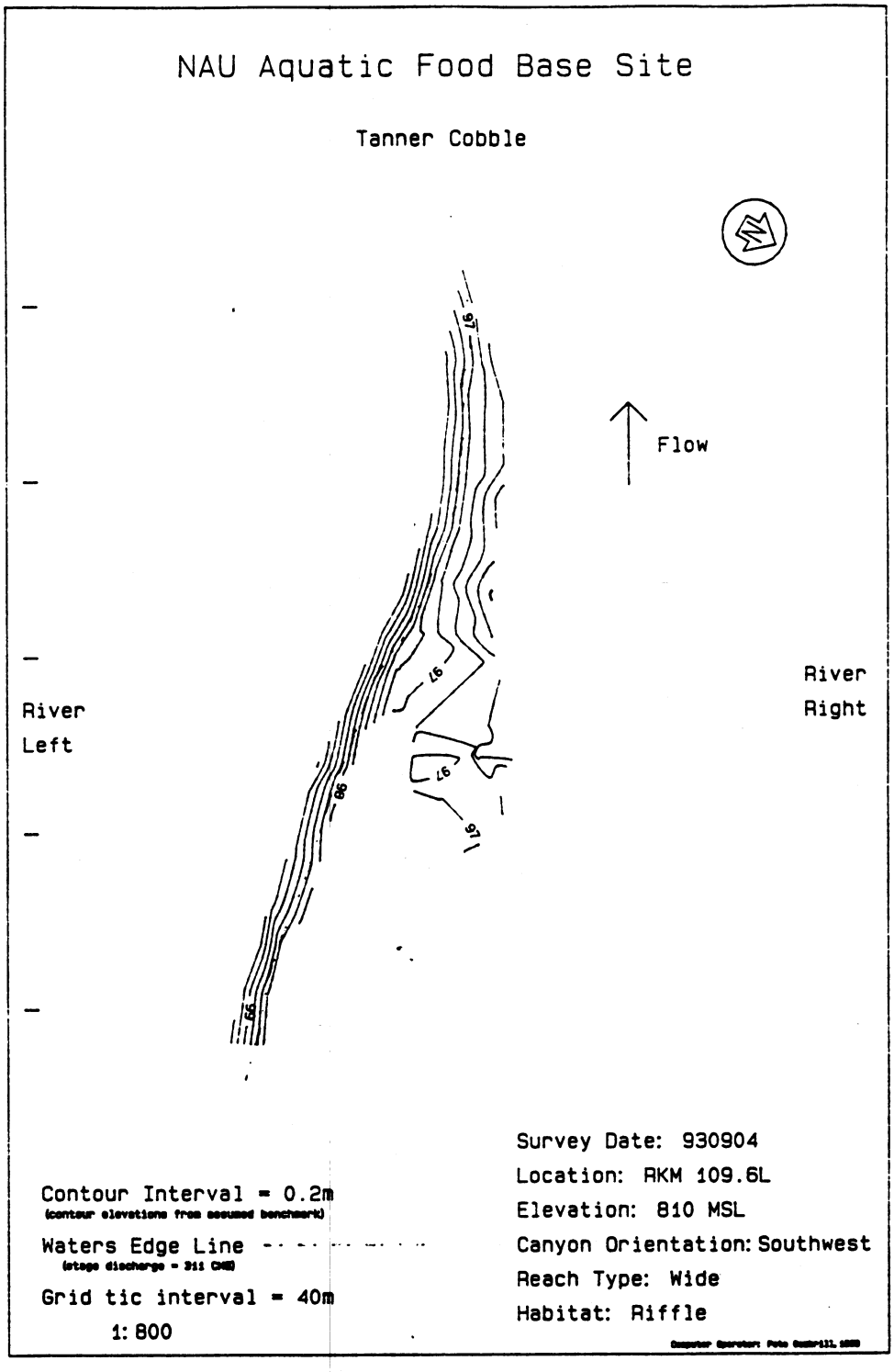

Figure 9. Bathymetric map of Tanner Canyon (RKM 109.6), a wide riffle site.

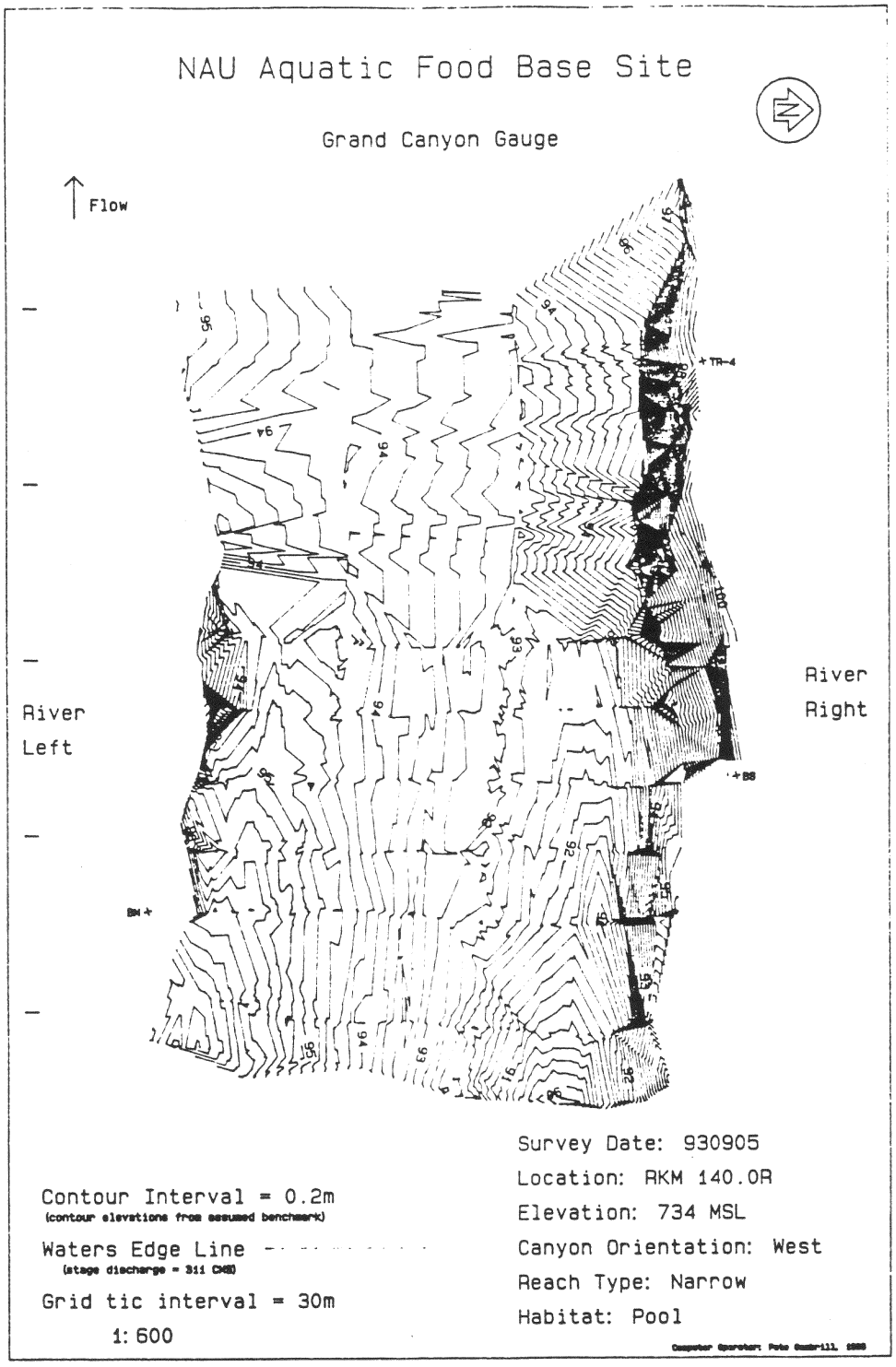

Figure 10. Bathymetric map of Grand Canyon Gauge (RKM 140.), a narrow pool site.

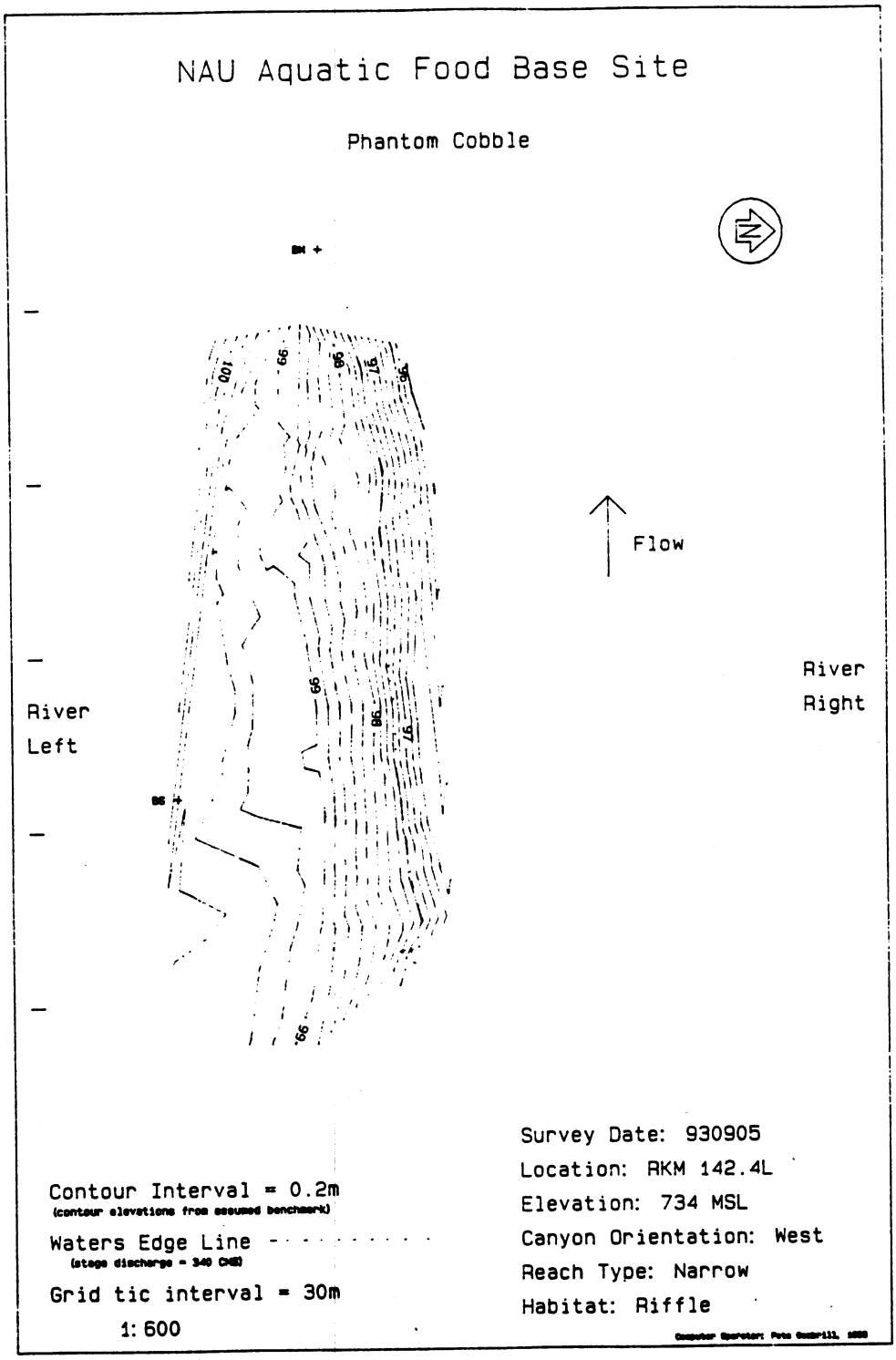

Figure 11. Bathymetric map of Phantom cobble (RKM 142.4), a narrow riffle site.

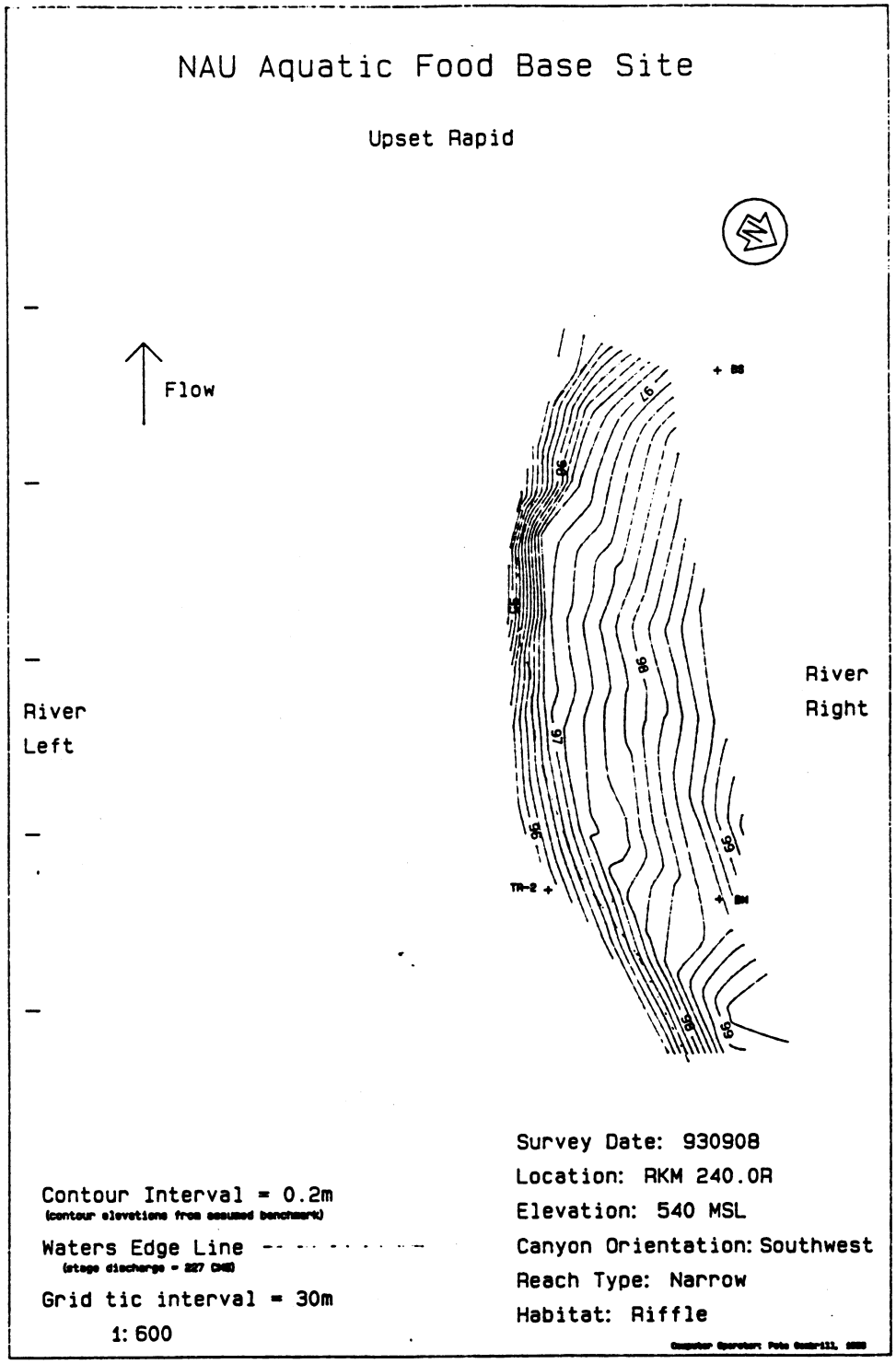

Figure 12. Bathymetric map of Upset Rapid (RKM 240.0), a narrow riffle site.

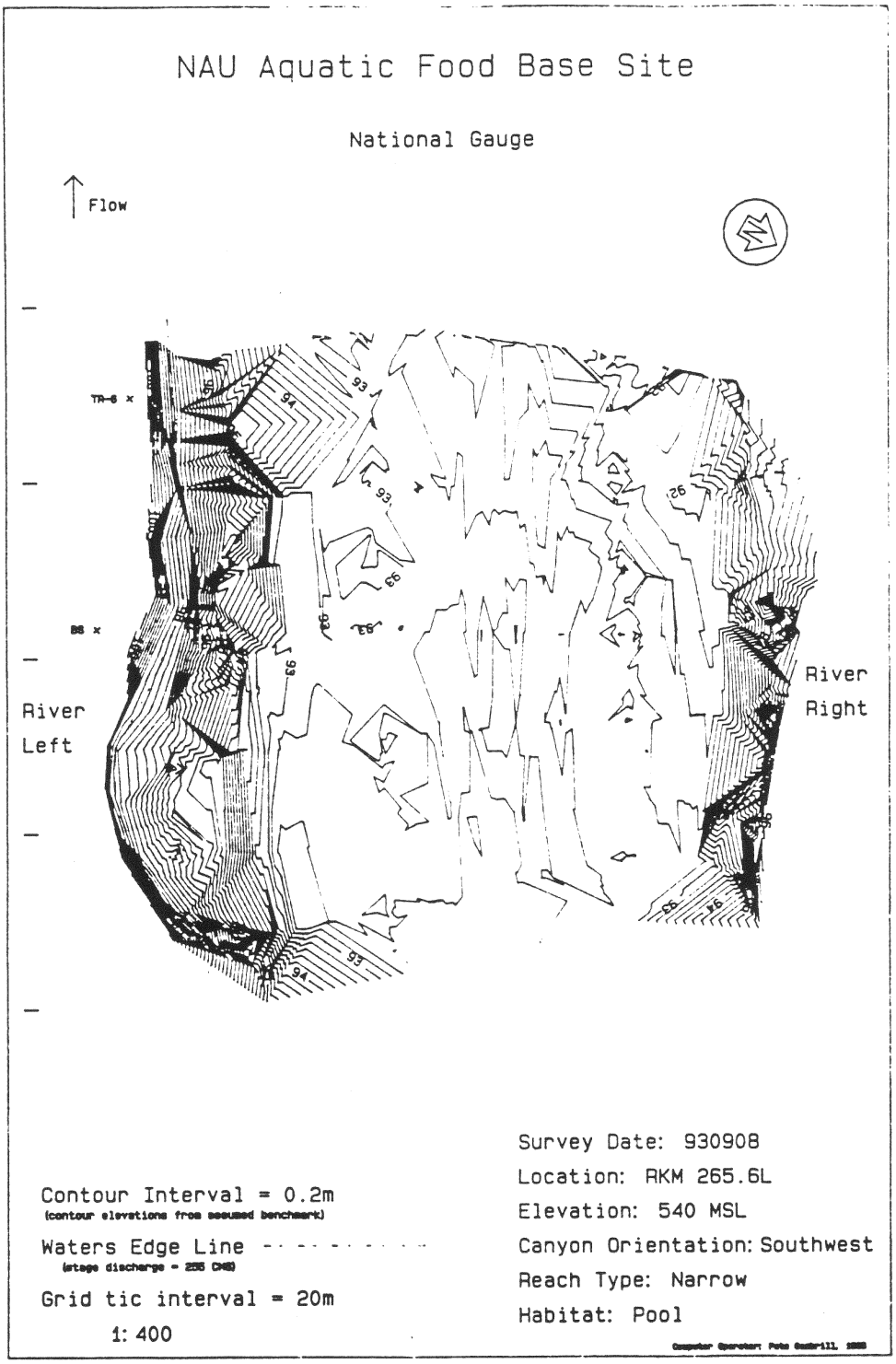

Figure 13. Bathymetric map of National Gauge (RKM 265.6), a narrow pool site.

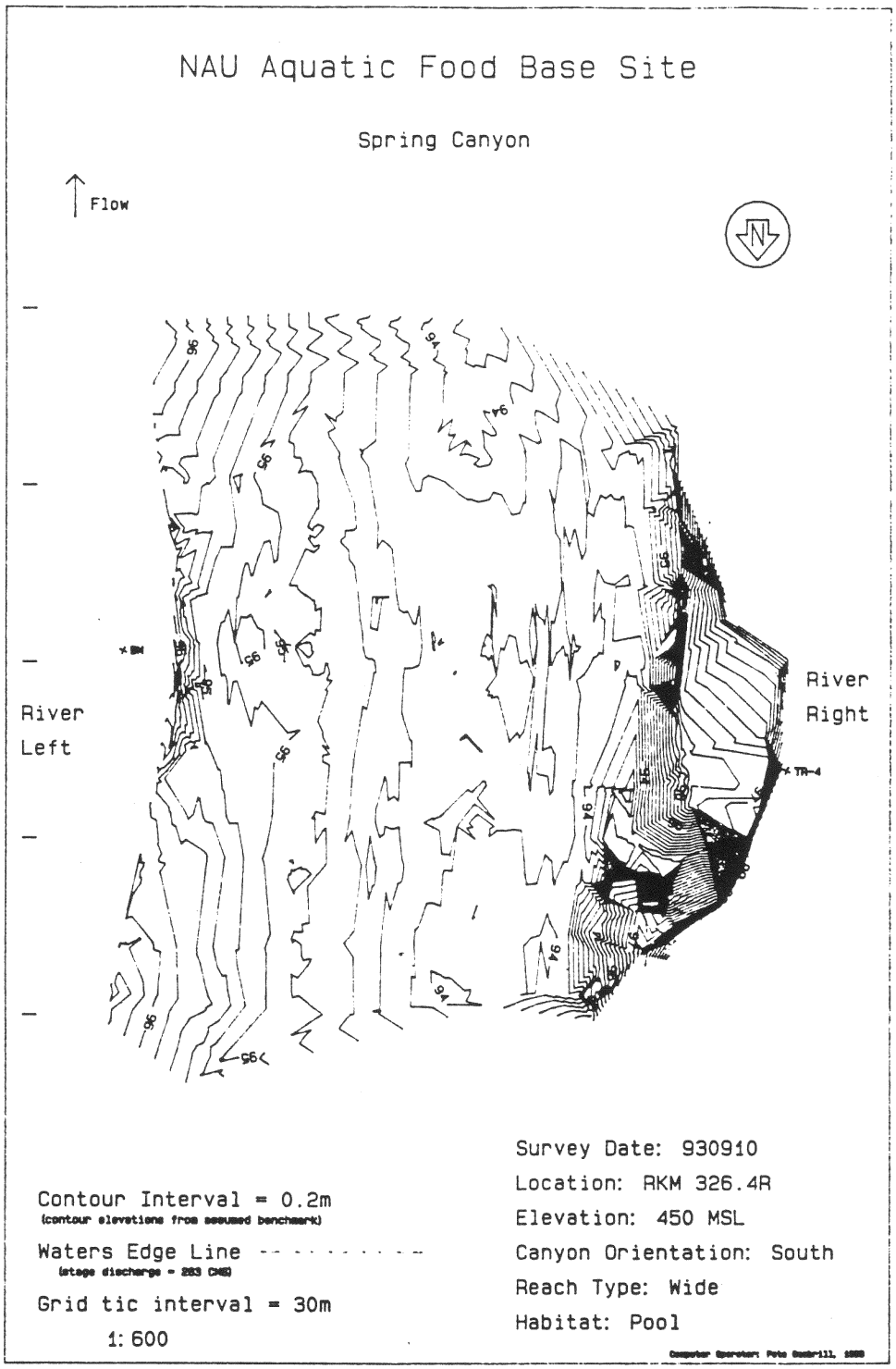

Figure 14. Bathymetric map of Spring Canyon (RKM 326.4), a wide pool site.

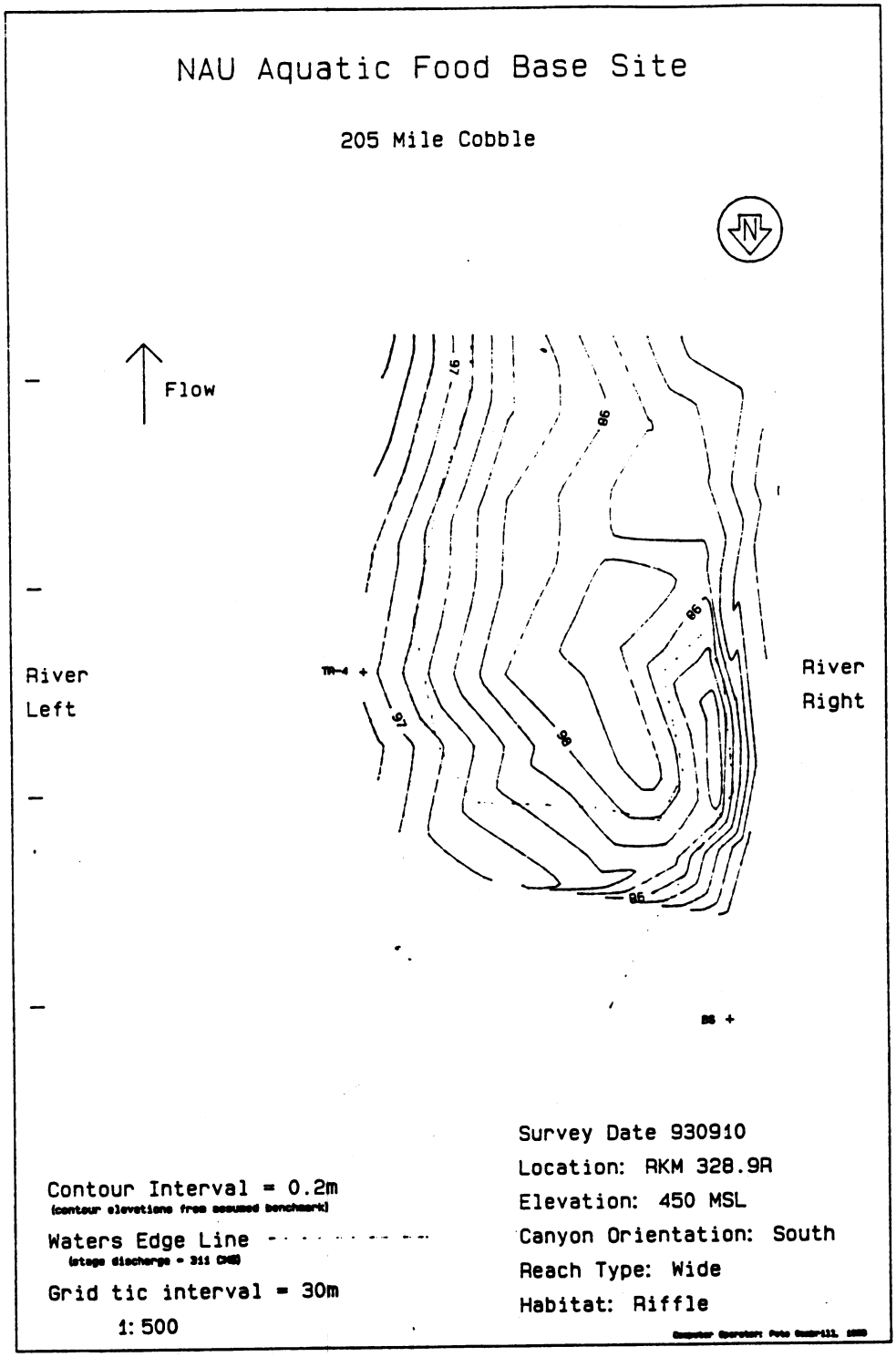

Figure 15. Bathymetric map of 205 Mile cobble (RKM 328.9), a wide riffle site.

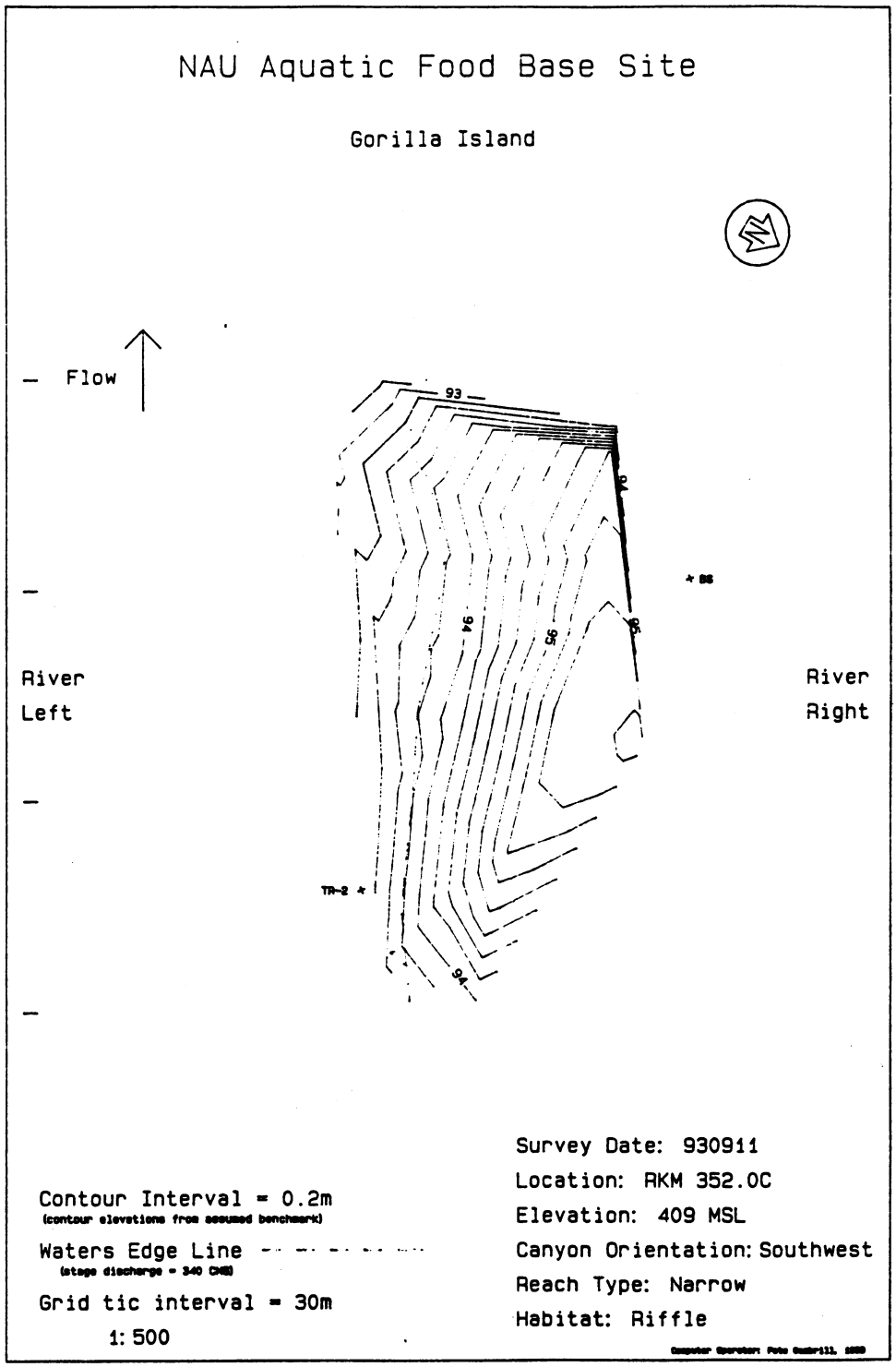

Figure 16. Bathymetric map of Gorilla Island (RKM 352), a narrow riffle site.

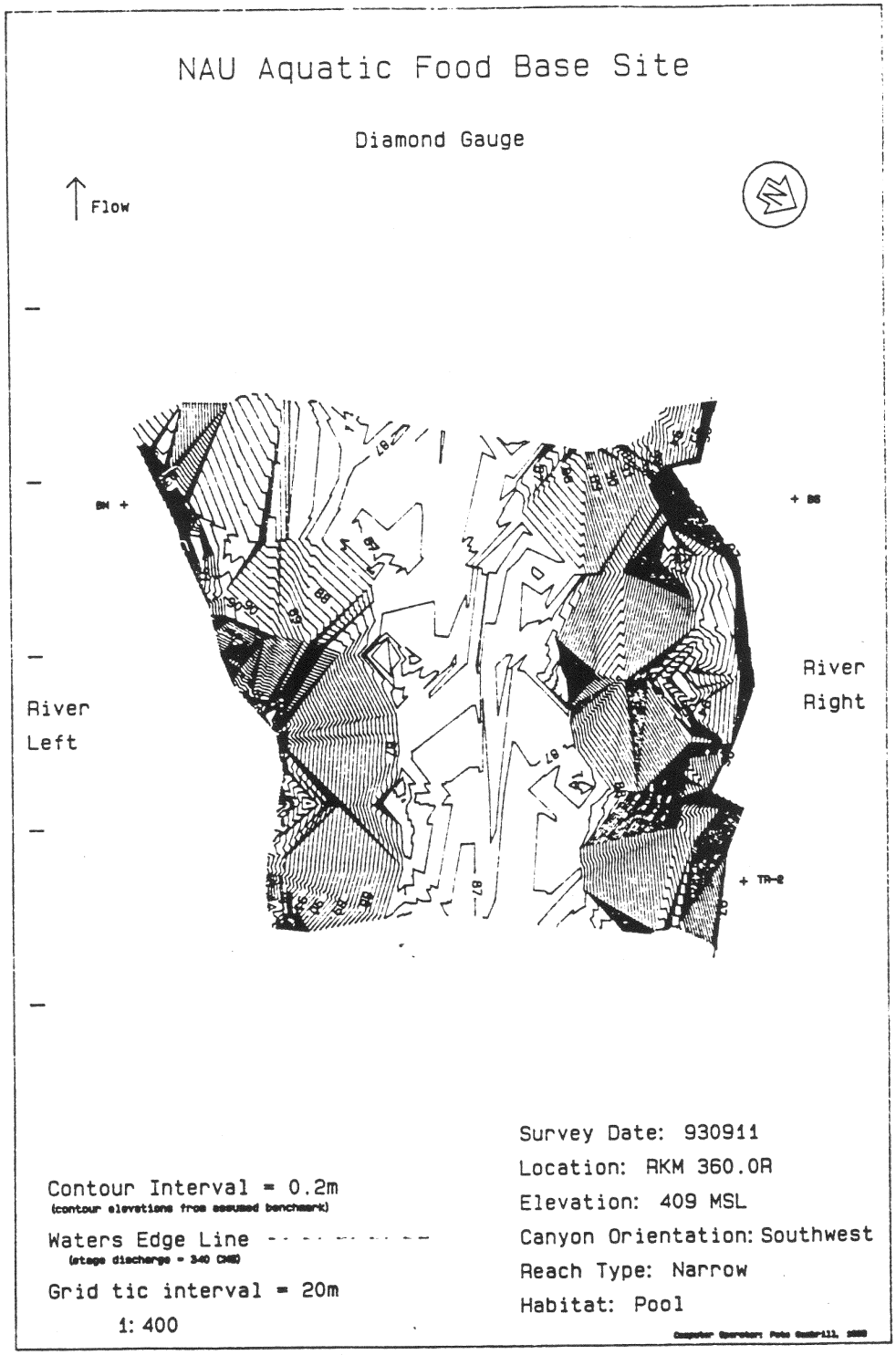

Figure 17. Bathymetric map of Diamond Gauge (RKM 360.0), a narrow pool site.