

# COLORADO RIVER BENTHIC ECOLOGY IN GRAND CANYON, ARIZONA, USA: DAM, TRIBUTARY AND GEOMORPHOLOGICAL INFLUENCES

LAWRENCE E. STEVENS<sup>1</sup>, JOSEPH P. SHANNON<sup>2</sup> AND DEAN W. BLINN<sup>2</sup>

<sup>1</sup>*Applied Technology Associates, Inc., PO Box 22459, Flagstaff, AZ 86002-2459, USA*

<sup>2</sup>*Department of Biological Sciences, Box 5640, Northern Arizona University, Flagstaff, AZ 86011, USA*

## ABSTRACT

The serial discontinuity concept (SDC; Ward and Stanford, in *Ecology of River Systems*, 1983) predicts that recovery of large regulated rivers over distance downstream from a dam is limited by relative tributary size; however, channel geomorphology may also influence the recovery process. We examined the spatial variation in water quality, benthic composition and ash-free dry standing biomass (AFDM) among the bedrock-defined geomorphological reaches in three turbidity segments of the Colorado River between Glen Canyon Dam and Diamond Creek, Arizona, including most of the Grand Canyon. This 387-km long study area supported virtually no Ephemeroptera, Plecoptera or Trichoptera, probably because cold, stenothermic, hypolimnetic releases limited maximum aestival warming to 17.1°C. The benthos displayed abrupt, physically related decreases in AFDM over distance from the dam and in the varial zone. The 26-km long clear water segment between the dam and the Paria River supported a depauperate *Cladophora glomerata*/epiphyte/chironomid/*Gammarus lacustris*/lumbricine/*Physella* sp. assemblage, and ooze-dwelling oligochaetes. This segment contained 6.9% of the aquatic habitat below the 140 m<sup>3</sup>/s (normal minimum) discharge stage of the Colorado River study area, but supported 63.5% of the benthic primary producer AFDM and 87% of the benthic consumer AFDM in the entire study area. Turbidity increased and light penetration decreased immediately downstream from the confluence of the small, turbid Paria River, and further downstream from the Little Colorado River confluence. The benthos downstream from the Paria River was abruptly replaced by an *Oscillatoria/Simulium* assemblage with a mean AFDM of <0.12 g C/m<sup>2</sup>.

Dam-related effects on water clarity, varial flow and water temperature overrode geomorphological influences on habitat availability. These results generally support the SDC, in that recovery of the benthos did not take place over distance in this large river ecosystem; however, geomorphological differences in substratum availability between reaches mediated dam and tributary effects on water clarity and benthic AFDM. Interactions between flow regulation and geomorphology produce a pattern of circuitous recovery of some physical river ecosystem characteristics over distance from the dam, but not of the benthos. Improving discharge management for endangered native fish populations requires detailed understanding of existing and potential benthic development, and trophic interactions, throughout the geomorphological reaches and turbidity segments in this river. ©1997 by John Wiley & Sons, Ltd.

*Regul. Rivers*, **13**, 129–149, (1997)

No. of Figures: 8. No. of Tables: 3. No. of Refs: 91.

KEY WORDS: benthic ecology; *Cladophora*; Colorado River; geomorphology; Glen Canyon Dam; large rivers; reaches; serial discontinuity concept; spatial scale; substrata; tailwaters; tributaries; turbidity;

## INTRODUCTION

Flow regulation affects the distribution of river benthos over distance downstream from dams by altering turbidity, water temperature and other discharge-related variables, and the roles of tributaries and natural channel

Correspondence to: Lawrence E. Stevens  
Contract grant sponsor: National Park Service, USA  
Contract grant number: CA 8009-8-0002

geomorphology (Ward, 1976; Ward and Stanford, 1979; Armitage, 1984). The serial discontinuity concept (SDC; Ward and Stanford, 1983, 1995) proposes that flow regulation interrupts river continua, resetting physical and biological conditions to those of lower stream order. Restoration (recovery) of ecological characteristics that typify comparable unregulated rivers occurs over distance downstream from the flow regulation point, and as a result of interactions between the size and location of the dam in the drainage basin, the location and size of tributaries, and geomorphological characteristics. Tributaries exert regional or 'biome' effects on rivers (Minshall *et al.*, 1983; Corkum, 1991) and may contribute suspended load and/or thermal variability, which are often reduced in the tailwaters of large dams (Bruns *et al.*, 1984; Rader and Ward, 1988; Storey *et al.*, 1991; Roos and Pieterse, 1994; Johnson *et al.*, 1995). Consequently, small regulated rivers joined by one or more large tributaries may be physically and biologically indistinguishable from comparable unregulated rivers, whereas large rivers in arid biomes with few, small tributaries may remain highly altered over long distances downstream from the point of flow regulation.

Flow regulation and tributary inflow effects are superimposed on the template of existing mainstream channel geomorphology, which may mediate distance-related benthic changes. In the topographically and geologically diverse terrains that characterize many large river basins, tectonics and bedrock geology influence channel geometry, velocity and substrate distribution across microsite, local, reach-based and system-wide spatial scales (Schmidt and Graf, 1990; Schmidt and Rubin, 1995). Geomorphological factors may strongly affect the distribution of the benthos, fisheries and floodplain vegetation development (Hupp, 1988; Gregory *et al.*, 1991; Newcombe and MacDonald, 1991; Stevens *et al.*, 1995). However, channel geomorphology influences on the benthos may be overridden by regulated flow effects, and may therefore exert only weak influences on distance-related benthic change.

Most data used to test the SDC have been collected from smaller, montane streams and in mesic regions (e.g. Culp and Davies, 1982; Cushing *et al.*, 1980; Munn and Brusven, 1983; Miller, 1985; Rader and Ward, 1988; Ryder and Scott, 1988; Volez and Ward, 1989; but see Stanford *et al.*, 1988). Few studies have attempted to quantify the influence of flow regulation on downstream benthic change in relation to reach-based channel geomorphology, particularly in large, regulated rivers in arid regions (but see supporting data in Grimm and Fisher, 1989; Minshall *et al.*, 1992; Roos and Pieterse, 1994; Helsen and Sedlack, 1995; Johnson *et al.*, 1995). Such studies are important because economic development has led to extensive modification of water supplies in arid regions, thereby altering fluvial habitats, benthos, autochthonous production, fish populations and other ecosystem components and processes (e.g. Blinn and Cole, 1991; Minckley, 1991; Molles, 1992).

Management of high-order, regulated rivers is often compromised by a lack of data on the pre-impoundment condition, and distance-related changes in, water quality related and benthic variables (Allen and Flecker, 1993). In ecosystems, such as the Colorado River in Grand Canyon, within-system, distance-related analyses may offer some insight into pre-impoundment conditions. The role of flow regulation on Colorado River benthic ecology has been examined in headwater reaches (Pearson, 1967; Ross and Rushforth, 1980; Rader and Ward, 1988), in the remaining flowing reaches downstream from Grand Canyon (Winget, 1984; Lieberman and Burke, 1993), and in the tailwaters of Glen Canyon Dam (Blinn *et al.*, 1989, 1995; Angradi and Kubly, 1993; Angradi, 1994; Shannon *et al.*, 1994); however, data on the mainstream benthos in Grand Canyon are limited (Czarnecki and Blinn, 1978; Blinn and Cole, 1991; Hardwick *et al.*, 1992; Shannon *et al.*, 1996). Such data are required to develop management strategies and monitoring programmes. Such temporal and spatial data are needed to understand the potential development of the benthos and the aquatic food base for fisheries, and to infer management strategies for benthic recovery (Gore and Shields, 1995; Ligon *et al.*, 1995).

In this paper we have tested the SDC and evaluated the rate of benthic recovery in the large, geomorphologically complex Colorado River downstream from Glen Canyon Dam. We used a within-system, distance-related approach to examine the effects on the benthos of physical, dam-related factors (distance-related turbidity and variational flows) and channel geomorphology (riffle versus pool habitats, and variation between reaches) on the temporal variation of the benthos. We also present dietary data, and review existing dietary literature, on the dominant aquatic macroinvertebrates in this system, in order to assess the structure of the aquatic food-web. We conclude by relating benthic structure to the predictions of the SDC, and we discuss potential management strategies and effects in relation to proposed changes in dam operations.

METHODS

Study area

The Colorado River is the main river system in the American South west, draining one-twelfth of the coterminous United States. It is one of the most thoroughly controlled American rivers, and it is regulated by more than 40 large flow regulation structures (Hirsch *et al.*, 1990). The river flows 472 km through northern Arizona between Glen Canyon Dam and Lake Mead, including lower Glen Canyon and all of Grand Canyon (Figure 1). River locations are designated by distance from Lees Ferry, Arizona (river kilometre, km 0, 36°52'03"N, 111°35'40"W), which lies 24.5 km downstream from the dam. The river descends from an elevation of 947 m at Lees Ferry to 404 m at Diamond Creek (km 363, 35°46'0"N, 113°22'30"W), with a mean gradient of 1.52 m/km and with most of its descent occurring in more than 165 white water rapids. The river is deeply incised into the uplifted Colorado Plateau, and it flows through Sonoran and Mohave desert scrub vegetation (Johnson, 1991). Mean annual precipitation on the canyon floor is 215 mm/year, bimodally distributed between winter and summer (Sellers and Hill, 1974). Additional geographical information on this system is presented in Stevens *et al.* (1995).

The Colorado River is a debris fan-dominated river constrained by talus slopes and cliffs of Proterozoic and Paleozoic bedrock strata, including resistant sandstones, limestones, igneous and crystalline strata, as well as softer shales and siltstones (Howard and Dolan, 1981). Variation in bedrock hardness creates distinctive wide-

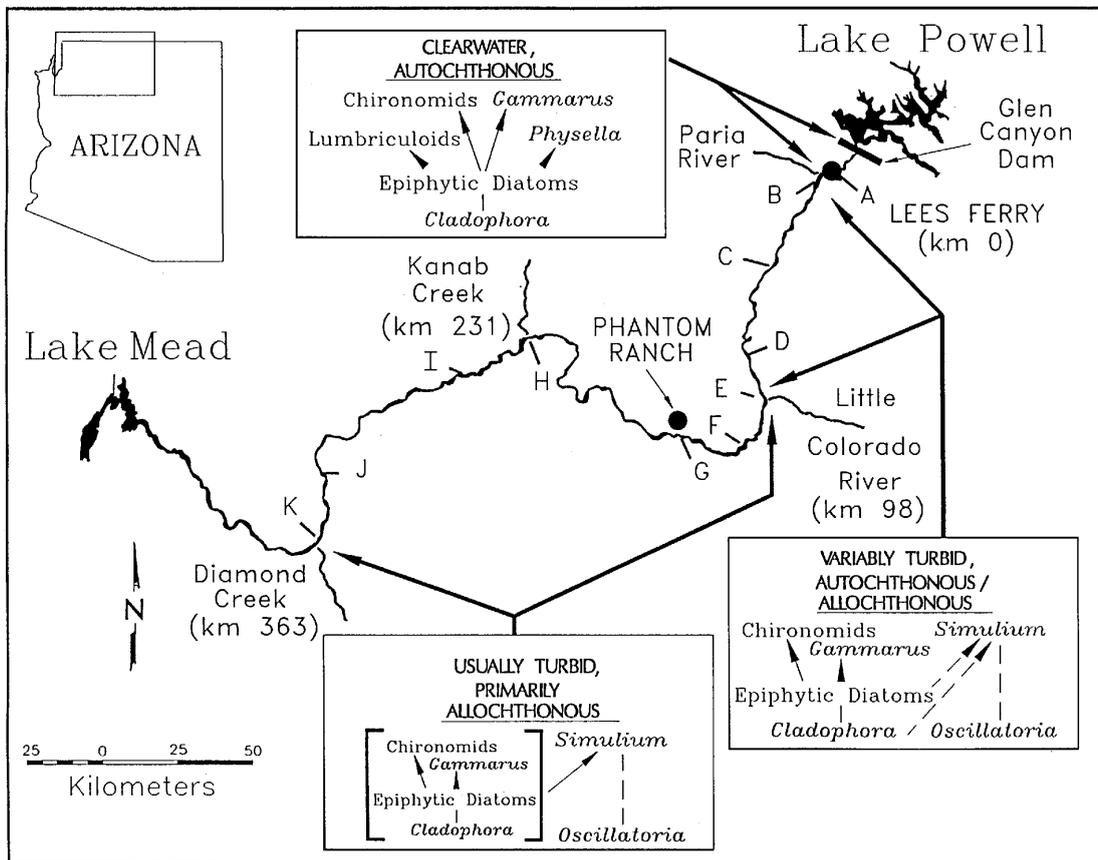


Figure 1. Map of the Colorado River in Grand Canyon National Park, Arizona. Study sites are designated by letter and are described in Table I. Benthic assemblages varied between three major turbidity segments of the river: the clear water Glen Canyon reach (CW), the variably turbid Marble Canyon segment (VT), and the usually turbid Lower Grand Canyon segment (UT). Boxes show river ecosystem energy shifting from autochthonous sources in the CW segment to largely allochthonous sources in the downstream turbid reaches. Dashed lines without arrows in the boxes indicate weak linkage between trophic levels

Table I. Study sites in the Colorado River in the Grand Canyon. Study site letters pertain to Figures 1 and 8. Distance (km) is measured from Lees Ferry, Arizona which lies 24.6 km downstream from Glen Canyon Dam. Turbidity segments include the clear water (CW), variably turbid (VT) and usually turbid (UT) segments. Reach names have been modified from Schmidt and Graf (1990) and reach width was measured at 680 m<sup>3</sup>/s by Schmidt and Graf (1990). Sample size is six for all water quality parameters at each site

Site	Distance from Lees Ferry (km)	Turbidity segment	Reach number (Figure 8) and name	Mean reach width (m)	Elevation (m AMSL)	Mean DO (mg/l) (mg/l; SD)	Mean specific conductivity ( $\mu$ S; SD)	Mean temp. ( $^{\circ}$ C; SD)	Mean pH (SD)	Mean Secchi depth (m; SD)
A	0	CW	1. Glen Canyon	85.3	947	8.1 (1.16)	0.91 (0.02)	9.2 (2.20)	7.7 (0.19)	5.35 (1.01)
B	3	VT	2. Permian Gorge	70.0	940	8.3 (1.38)	0.90 (0.04)	9.6 (2.17)	7.8 (0.34)	4.30 (2.12)
C	50	VT	4. Redwall Gorge	67.1	871	10.2 (1.18)	0.79 (0.35)	10.0 (2.92)	7.6 (0.47)	1.02 (1.01)
D	83	VT	5. Marble Canyon	106.7	842	10.7 (0.66)	0.92 (0.04)	10.5 (2.38)	8.0 (0.26)	1.05 (1.15)
E	98	VT	5. Marble Canyon	106.7	821	10.5 (0.42)	0.94 (0.05)	10.8 (2.07)	7.9 (0.28)	1.38 (1.04)
F	110	UT	6. Furnace Flats	118.9	810	10.6 (0.82)	1.00 (0.06)	10.5 (2.37)	7.9 (0.21)	0.97 (1.36)
G	142	UT	7. Upper Granite Gorge	57.9	734	10.9 (0.20)	1.02 (0.05)	10.8 (2.34)	8.1 (0.13)	1.15 (1.80)
H	232	UT	10. Muav Gorge	54.9	568	10.7 (0.77)	1.01 (0.06)	11.4 (2.42)	8.1 (0.13)	0.37 (0.42)
I	240	UT	11. Lower Canyon Reach	54.9	540	11.0 (0.77)	0.99 (0.05)	10.2 (1.97)	8.2 (0.12)	0.15 (0.03)
J	329	UT	11. Lower Canyon Reach	94.5	450	10.8 (0.28)	0.98 (0.03)	11.6 (3.03)	7.9 (0.30)	0.85 (0.77)
K	352	UT	12. Lower Granite Gorge	73.2	409	11.2 (0.37)	1.00 (0.05)	12.7 (3.97)	8.0 (0.23)	0.20 (0.10)

shallow and narrow-deep geomorphological reaches (Schmidt and Graf, 1990; Table I; Figure 1). The uppermost Glen Canyon reach is wide (mean width  $>85$  m); two wide and two narrow ( $<85$  m wide) reaches occur in Marble Canyon between the Paria River (km 1) and the Little Colorado River (km 98) confluences; and the Grand Canyon section between km 98 and Lake Mead contains three wide and five narrow reaches. The number of sand-bar deposits and fluvial marshes, and the percentage cover of soft versus firm substrata on the channel bed, are positively correlated with reach width (Schmidt and Graf, 1987, 1990; Stevens *et al.*, 1995). Debris-fan eddy complexes exist at each tributary confluence, creating spatially fixed and geomorphologically distinctive pool, riffle and return current channel (backwater) habitats (Howard and Dolan, 1981; Kieffer, 1985; Webb *et al.*, 1989; Schmidt and Graf, 1990).

The unregulated Colorado River was flood-prone, turbid, and warmed during summer. The mean daily pre-dam flow from 1922 to 1962 was  $470.4 \text{ m}^3/\text{s}$ , with a mean annual flood peak of  $2450 \text{ m}^3/\text{s}$ , a 10-year flow return frequency of  $3540 \text{ m}^3/\text{s}$ , an historic peak flow of  $8500 \text{ m}^3/\text{s}$  and a paleo-flood peak flow of  $14\,000 \text{ m}^3/\text{s}$  (Howard and Dolan, 1981; O'Conner *et al.*, 1994). The river transported a highly variable mean sediment load of  $6.0 \times 10^{10} \text{ kg/year}$  past Lees Ferry (Andrews, 1991) and was virtually always turbid. Pre-dam water temperature ranged from freezing in winter to  $29.4^\circ\text{C}$  in the summer at Lees Ferry (W. Vernieu, US Bureau of Reclamation, Flagstaff, AZ, personal communication), and the river supported a largely endemic, warm water fish assemblage (Blinn and Cole, 1991; Minckley, 1991). Numerous pre-dam photographs reveal little benthic algal cover on rocks during low flows (Turner and Karpiscak, 1980; Stephens and Shoemaker, 1987; Webb, 1996), suggesting that scouring floods limited the colonization and growth of benthic macroalgae.

The 200-m high Glen Canyon Dam was completed in 1963, creating Lake Powell reservoir and regulating the Colorado River through Grand Canyon (Stanford and Ward, 1991). Although mean daily flow ( $412.2 \text{ m}^3/\text{s}$ ) did not change greatly, impoundment greatly reduced flood frequency and magnitude, increased hourly varying flow, decreased sediment transport and created cold, stenothermic conditions (Andrews, 1991; Blinn and Cole, 1991). Post-dam river flows from 1965 to 1991 fluctuated widely on an hourly basis but little seasonally. During normal inflow years, the maximum range of daily flows exceeded  $750 \text{ m}^3/\text{s}$  every month of the year. This large range in daily flow approximated the post-dam annual discharge range, and exposed the benthos along the shoreline to daily desiccation (Angradi and Kubly, 1993; Blinn *et al.*, 1995).

Impoundment reduced sediment transport at Lees Ferry to  $<1\%$  of pre-dam levels (Howard and Dolan, 1981), and mainstream turbidity is now largely determined by tributary-derived suspended sediment contributions. More than 490 ephemeral and 40 perennial tributaries join the Colorado River in Grand Canyon, but only six perennial tributaries have mean flows  $>1 \text{ m}^3/\text{s}$ . Although the base flow of the Paria River (the most upstream perennial tributary) is only  $0.2 \text{ m}^3/\text{s}$  ( $<0.002\%$  of the mean mainstream flow), it contributes an average of  $2.75 \times 10^6$  tonnes of suspended sediment/year, with concentrations of up to  $780\,000 \text{ mg/l}$  (Graf *et al.*, 1991). The Little Colorado River annually supplies three times more suspended sediment than the Paria River, and Kanab Creek (km 230) provides additional sediment in the lower Canyon (Andrews, 1991; Figure 1). Turbid inflow from the Paria River reduces maximum benthic light availability between km 1 and 98 approximately 70% of the time on an erratic, seasonal basis. Cumulatively, the Paria River, Little Colorado River and subsequent tributaries reduce maximum light availability in the middle and lower Grand Canyon 80% of the time (M. Yard, Bureau of Reclamation biologist, Flagstaff, AZ, written communication).

Sediment retention by Glen Canyon Dam and the locations of sediment-contributing tributaries have created three mainstream turbidity segments (Table I; Figure 1): the clear water segment (the Glen Canyon reach) lies between Glen Canyon Dam and the Paria River confluence; the variably turbid segment includes the four reaches between the Paria River and the Little Colorado River in Marble Canyon; and the usually turbid middle and lower Grand Canyon segment includes the seven reaches between the Little Colorado River and Lake Mead.

#### *Field data collection*

We sampled water quality variables and benthic algal and macroinvertebrate standing biomass at bimonthly intervals in 1991 at 11 stations between Lees Ferry and Diamond Creek (Table I; Figure 1). We sampled pool (velocities  $<1.0 \text{ m/s}$ ) and riffle/rapid ( $>1.0 \text{ m/s}$ ) habitats in six wide and five narrow reaches, using petit Ponar ( $0.02 \text{ m}^2$  area) or Peterson ( $0.09 \text{ m}^2$  area) dredges in pool environments, and Hess samplers ( $0.11 \text{ m}^2$  area) in cobble-bottomed riffle habitats. Three to six samples were collected in each of three stage zones: the deep

submerged zone ( $<80\text{ m}^3/\text{s}$ , pools only), the shallow submerged zone ( $80\text{--}142\text{ m}^3/\text{s}$ ) and the varial zone ( $142\text{--}792\text{ m}^3/\text{s}$ , near the maximum power plant release stage). Samples were collected at the lowest daily discharge level. Although we sampled during US Bureau of Reclamation test flows (Patten, 1991), releases were within the range of normal dam operations and were as variable as those of previous years.

Water quality was measured at each study site six times in 1991 using a Hydrolab<sup>TM</sup> portable field sensor. Water quality variables included dissolved oxygen (DO), specific conductance ( $\mu\text{S}$ ), temperature ( $^{\circ}\text{C}$ ) and pH. Sample depth, Secchi depth (water transparency) and velocity (measured with a Marsh–McBirney<sup>TM</sup> #201 velocity meter) or stage were also measured. Substrate was noted for each sample.

Benthic standing mass was sorted into primary producers (*Cladophora glomerata*, *Oscillatoria* spp.), consumers (molluscan grazers, chironomids, *Gammarus lacustris*, simuliid filter feeders, megadrile and microdrile oligochaete ooze feeders, and other aquatic macroinvertebrates) and detritus. Samples were dried at  $60^{\circ}\text{C}$  to constant mass and weighed. Subsamples were ashed at  $500^{\circ}\text{C}$  for 1 h and dry mass was converted to  $\text{g C}/\text{m}^2$  ash-free dry mass (AFDM). Linear regression equations between standing dry biomass and AFDM values were developed for large samples of each category, and used to convert dry mass values to AFDM.

We analysed the gut contents of chironomid midge larvae, the numerically dominant benthic macroinvertebrate taxon in this system, to determine the trophic role of benthic algae (*Cladophora glomerata* and *Oscillatoria* spp.). Chironomid larvae collected from the mainstream at Lees Ferry ( $n=10$ ), km 51 (15), and km 361 (21) were placed in 70% EtOH. Specimens were soaked in 10% KOH for 3–12 h (depending on larval size) to clear the integument while maintaining the integrity of the gut and its contents. Cleared specimens were inspected under 1000 magnification for frequency of diatoms, *Cladophora*, *Oscillatoria*, detritus and inorganic particles. *Gammarus* diet data were derived from Pinney (1991) and Shannon *et al.* (1994).

### Analyses

We described relationships between AFDM of biotic components and the physical, chemical, spatial and temporal variables using multivariate canonical correspondence analysis (CANOCO; Ter Braak, 1992). This direct gradient ordination approach is a widely used principal components-style analysis (Palmer, 1993). CANOCO employs data on species distributions in sampling units to define multivariate axes, and uses multiple regression analysis to correlate factor loading scores for samples in species space with environmental predictor variables. We also used Pearson correlation analysis with serial Bonferroni-adjusted probabilities (Rice, 1989) statistically to describe the correlations between physical and biotic variables and CANOCO factor scores (SYSTAT 5.03; Wilkinson, 1991).

We analysed the effects and interactions of impoundment, geomorphology and season on  $\log_e(\text{AFDM}+1)$  transformed values of 10 biotic response variables using multiple analysis of variance (MANOVA; Wilkinson, 1991). An overall impoundment factor was created using the three turbidity segments of the river and three stage zones, creating nine treatment levels. The three stage zones (deep and shallow submerged, and the varial zone) provided an exposure gradient resulting from dam-created varial flow. The frequency of daily exposure of these zones under normal dam operations at Lees Ferry was 2, 40 and 97%, respectively.

An overall geomorphology factor was generated using local habitat (pool versus riffle/rapid settings) and reach width (narrow versus wide), producing four treatment levels. Pair-wise interactions between dam and geomorphological effects with season were also tested, and MANOVA and univariate ANOVA tests were employed to explore predictor effects on individual biotic components. We corroborated MANOVA results with separate Mann–Whitney or Kruskal–Wallis tests, and using serial Bonferroni analyses.

We estimated total benthic AFDM of algae and macroinvertebrates below the  $142\text{ m}^3/\text{s}$  stage (the normal low water stage) in the 10 geomorphological reaches sampled during this study. This involved combining channel floor surface area, per cent cover of firm and soft substrata and benthic AFDM in each reach. We coupled wetted perimeter measurements from 730 river cross-sections and additional bathymetric data from the Glen Canyon reach (M. Yard, US Bureau of Reclamation, Flagstaff, Arizona, unpublished data) to estimate bed surface area  $<142\text{ m}^3/\text{s}$ , the normal low discharge level. We multiplied surface area values by the percentage firm (boulder or bedrock) or sand cover in each reach, derived from analysis of side-scan SONAR (Schmidt and Graf, 1987). We then multiplied these values by mean annual benthic AFDM estimates for firm and soft substrata, respectively.

RESULTS

*Water quality parameters*

Water quality variables changed over distance from Glen Canyon Dam, and seasonally (Tables I and II; Figure 2). Temperature ranged from 6.5°C in January 1991 at km 3 (Site B) to 17.1°C in late May at Diamond Creek (Figure 2A). Water temperatures were stenothermic or declined slightly during the winter months, but increased by 9°C through the Grand Canyon during summer. The maximum temperature recorded in the lower Canyon occurred during a constant 142 m<sup>3</sup>/s test flow. Overall, the annual, system-wide post-dam summer temperature range (10.6°C) was approximately one third of the pre-dam range at Lees Ferry (29.4°C).

Dissolved oxygen (DO) concentration varied significantly over distance from the dam (Tables I and II; Figure 2B). Values of DO were relatively low ( $\geq 6.6$  mg/l) at Lees Ferry and increased significantly to saturation as the river passed through the first few large rapids. DO increased during the middle of the summer at Lees Ferry, and also varied hourly at this location. Specific conductance (not shown) varied in a similar fashion to DO, ranging from a low of 0.83 to 1.10  $\mu S$ , increasing slightly downstream.

Hydrogen ion concentration (pH) varied from 6.8 to 8.4, shifting slightly between seasons, but not greatly between study sites (Figure 2C). The trend of increasing pH during autumn, 1991 may be attributable to decreased mainstream flows in the autumn of 1991 (which allowed carbonate-rich tributary baseflows to influence the mainstream) or to variation in Lake Powell's volume.

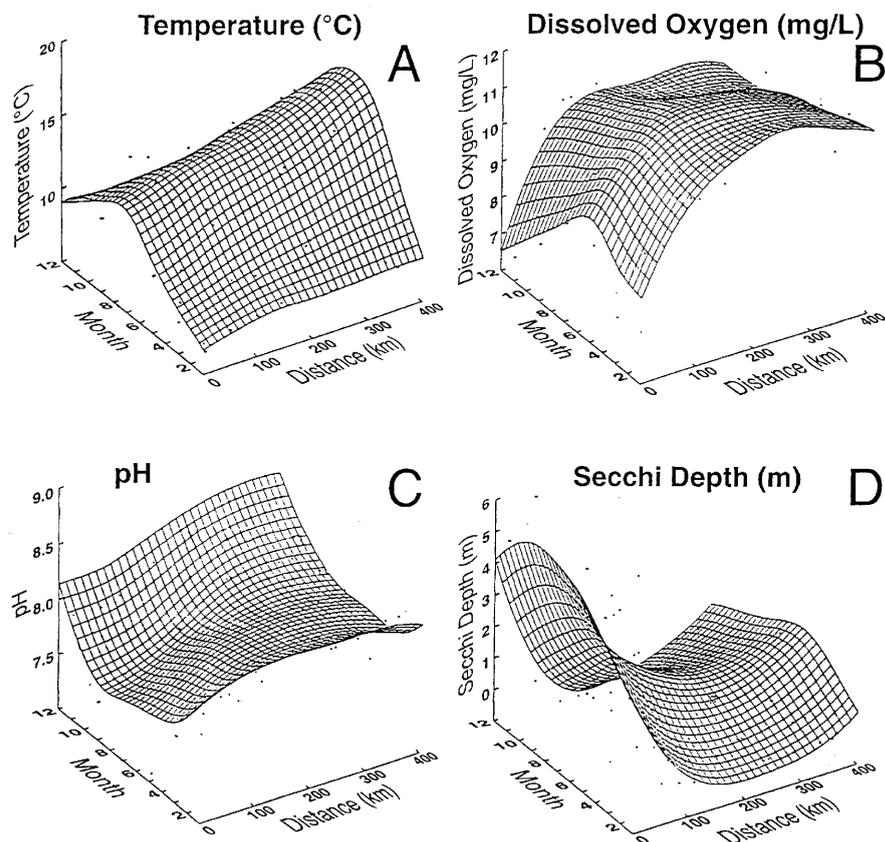
Secchi depth (water transparency) was strongly negatively correlated with distance from Glen Canyon Dam (Figure 2D). Secchi depths ranged from 7.0 m at Lees Ferry to 0.02 m at downstream sites. Secchi depth declined after km 1, and again at the Little Colorado River confluence. Monsoonal precipitation and greater-than-baseflow discharge from tributaries decreased Secchi depth slightly but not significantly during the summer months. The

Table II. Pearson correlation analysis of physical and selected biotic variables through the 11 Colorado River study sites in the Grand Canyon, Arizona. Variables include: dissolved oxygen (DO, mg/l), specific conductance (SC,  $\mu S$ ), temperature (T, °C), pH, Secchi depth (S, m), estimated velocity (V, m<sup>2</sup>/s), distance from Lees Ferry (km0), detrital mass (D, AFDM g C/m<sup>2</sup>), Julian day (JD), total primary producer standing biomass (TPP, AFDM g C/m<sup>2</sup>) and total macroinvertebrate standing mass (TM, AFDM g C/m<sup>2</sup>). A serial Bonferroni analysis (Rice, 1989) at  $p \leq 0.05$  was used to evaluate the statistical significance of pair-wise correlations

	DO	SC	T	pH	S	V	KM	D	JD	TPP	TM
DO	1.000										
SC	0.367	1.000									
	*										
T	0.111	-0.021	1.000								
	nsd	nsd									
pH	0.360	0.396	-0.157	1.000							
	nsd	*	nsd								
S	-0.623	-0.226	0.023	0.337	1.000						
	*	nsd	nsd	nsd							
V	-0.183	0.124	-0.099	0.037	-0.044	1.000					
	nsd	nsd	nsd	nsd	nsd						
KM	0.555	0.320	0.360	0.310	-0.604	-0.326	1.000				
	*	nsd	nsd	nsd	*	nsd					
D	-0.233	-0.037	-0.169	-0.044	0.143	-0.163	-0.151	1.000			
	nsd										
JD	-0.454	-0.007	0.301	-0.344	0.199	-0.113	-0.109	0.189	1.000		
	*	nsd									
TPP	-0.234	0.005	-0.115	-0.275	0.373	0.016	-0.240	-0.035	0.030	1.000	
	nsd	nsd	nsd	nsd	*	nsd	nsd	nsd	nsd		
TM	-0.406	-0.085	-0.137	-0.238	0.509	-0.116	-0.304	0.099	0.104	0.547	1.000
	*	nsd	nsd	nsd	*	nsd	nsd	nsd	nsd	*	

nsd  $p > 0.05$

\*  $p \leq 0.05$



summer of 1991 was relatively dry and the pattern of tributary-related turbidity over distance downstream is expected to be more pronounced in normal, wetter years.

Serial Bonferroni-adjusted Pearson correlation analysis revealed that DO increased significantly with distance downstream from Lees Ferry (Table II). Both DO and pH were positively correlated with specific conductance, and DO was negatively correlated with Julian day. DO was negatively correlated with Secchi depth, an artefact of proximity to both the dam and the Paria River.

#### The benthos

*Cladophora glomerata* strongly dominated the clear water reach upstream from the Paria River, with a mean AFDM of  $15.5 \text{ g C/m}^2$  in the deep-submerged and shallow-submerged zones at Lees Ferry ( $SD \pm 24.76 \text{ g C/m}^2$ ; Table II; Figure 3A). Average *Cladophora* AFDM abruptly decreased by 33.7-fold to  $0.5 \text{ g C/m}^2$  at Site B, just downstream from the Paria River confluence. Average *Cladophora* AFDM in cobble bars rose slightly to  $3.0 \text{ g C/m}^2$  near the Little Colorado River, and then decreased to  $0.9$  ( $SD \pm 1.63 \text{ g C/m}^2$ ) in the middle and lower Grand Canyon. Mean *Cladophora* AFDM rarely exceeded  $0.1 \text{ g C/m}^2$  in pool environments downstream from the Paria River confluence, and *Cladophora* did not occur to any significant extent above the normal minimum stage. Other, comparatively rare, primary producers were collected near Lees Ferry but not downstream, including *Oedogonium* spp., *Draparnaldia* spp., *Potamogeton* and *Stigeoglonium* spp.

Crustose *Oscillatoria* spp. mats strongly dominated firm-bottomed substrata downstream from the Paria River (Table II; Figure 3B). Mean *Oscillatoria* AFDM abruptly increased from  $0.003$  ( $SD \pm 0.012$ )  $\text{g C/m}^2$  at Lees Ferry to  $0.6$  ( $SD \pm 1.46$ )  $\text{g C/m}^2$  at km 3. Mean *Oscillatoria* AFDM increased to  $7.3 \text{ g C/m}^2$  downriver from the

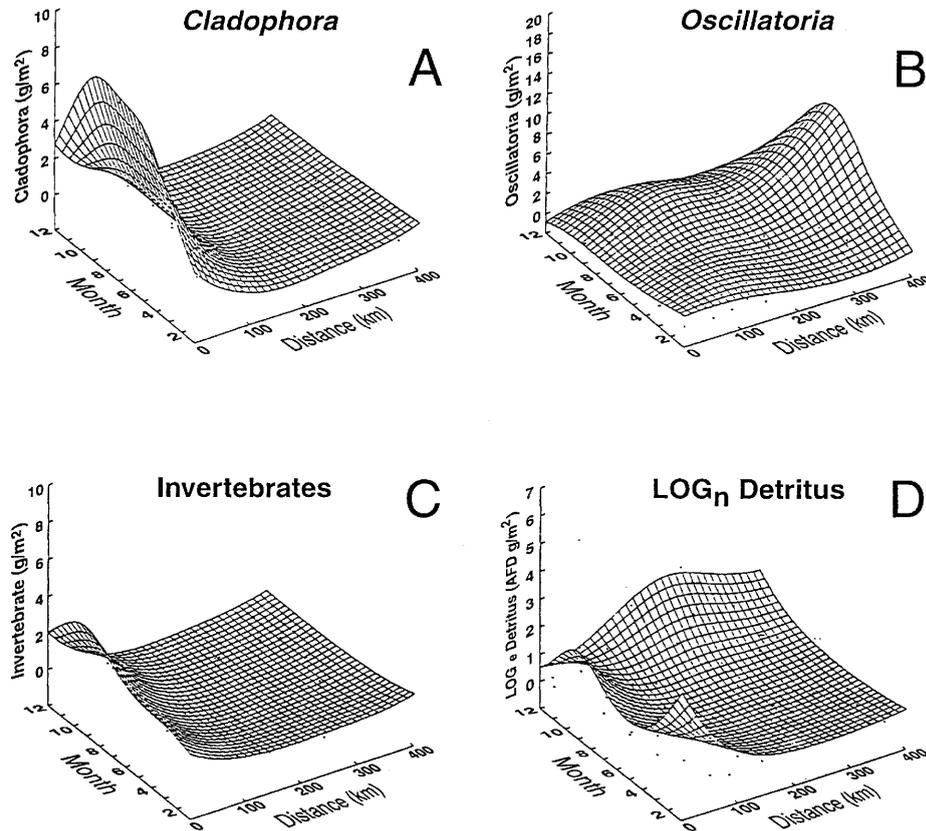


Figure 3. Spatial and temporal distribution of biotic variables through the study area in 1991: (A) total mean *Cladophora glomerata* AFDM ( $\text{g C/m}^2$ ); (B) total mean *Oscillatoria* spp. AFDM; (C) mean total aquatic macroinvertebrate AFDM; and (D) total mean detrital AFDM

Little Colorado River on cobble-bars, but was virtually absent in pool environments, except at the km 97 station, which was partially floored with cobble. In contrast to *Cladophora*, we observed that *Oscillatoria* remained viable in the lower varial zone, surviving relatively long periods of exposure. Total autotroph AFDM was positively correlated with Secchi depth, with much higher AFDM in the clear water Glen Canyon Reach (Table II).

Macroinvertebrate composition and AFDM varied over distance downstream and in relation to reach, local habitat and stage elevation gradients (Table II; Figure 3C). Abundant aquatic macroinvertebrates at Lees Ferry included *Gammarus lacustris*, various Chironomidae (especially *Cricotopus annulator*, *C. globistylus* and *Orthocladius rivicola*), snails (*Physella* sp. and *Fossaria obrussa*) and megadrile worms (especially Lumbricidae and Lumbricullidae), which were associated with the *Cladophora* beds, as well as ooze- and gravel-dwelling oligochaetes (Naididae and Tubificidae) and sphaeriid clams (*Pisidium variable* and *P. walkeri*).

Lees Ferry supported an annual mean invertebrate AFDM of  $2.9 \text{ g C/m}^2$  ( $\text{SD} \pm 4.01 \text{ g C/m}^2$ ). Macroinvertebrate AFDM was positively correlated with autotroph AFDM ( $p \ll 0.05$ ; Table II). Macroinvertebrate AFDM was also significantly positively correlated with Secchi depth, but was negatively correlated with DO concentration, an artefact of the relatively low DO in the Glen Canyon Reach.

Downstream from the Paria River, *Simulium arcticum* (Simuliidae) and lumbriculoid worms were the dominant macroinvertebrates in riffle habitats, especially on firm substrata, including lodged driftwood, and chironomids were erratic. Ten additional macroinvertebrate orders were encountered in the river in 1991, but these were rare, comprising  $<0.1\%$  of the AFDM at any sampling site. Pool habitats downstream from km 50 were virtually devoid of macroinvertebrates.

Table III. MANOVA table of the effects of dam impacts (distance and stage zone), geomorphology (pool versus riffle/rapid habitats and wide versus narrow reaches), and season (winter, spring, summer, autumn) on  $\log_e$ -transformed (AFDM +1) of two benthic algal taxa (Cl=*Cladophora glomerata*, Os=*Oscillatoria* spp.) and seven invertebrate taxa (L=lumbricine worms, G=*Gammarus lacustris*, Ol=other oligochaetes, Si=*Simulium arcticum*, Ch=chironomid midges, P=*Physella* sp. and OIn=other invertebrates)

Source	Wilks lambda	Approx		Response variables									
		<i>F</i>	<i>p</i>	Cl	Os	L	G	Ol	Si	Ch	P	OIn	
Overall model:		<i>F</i> <sub>63,2495</sub>											
Dam(D) + Geo(G) + Season(S) + (D*G) + (D*S) + (G*S)	0.341	8.349	<0.0001	***	***	***	***	***	*	***	***	***	
Primary effects		<i>F</i> <sub>9,442</sub>											
D	0.955	2.322	0.014	*	nsd	nsd	*	t	*	nsd	nsd	*	
G	0.908	4.983	0.000	***	nsd	***	***	nsd	*	t	nsd	nsd	
S	0.972	1.418	0.178	nsd	nsd	nsd	nsd	t	nsd	nsd	nsd	nsd	
Two-way interactions													
D × G	0.897	5.635	0.000	***	nsd	***	***	nsd	*	t	nsd	**	
D × S	0.948	2.677	0.005	nsd	nsd	*	nsd	*	nsd	t	nsd	*	
G × S	0.964	1.800	0.065	nsd	nsd	nsd	nsd	nsd	nsd	nsd	nsd	t	

nsd  $p > 0.1$

t  $0.05 < p < 0.10$

\*  $p < 0.05$

\*\*  $0.01 < p < 0.05$

\*\*\*  $p < 0.001$

Mean macroinvertebrate AFDM on cobble-bars decreased 8.3-fold immediately downstream from the Paria River confluence, and an additional three-fold downstream from the Little Colorado River confluence. The Lees Ferry cobble-bar supported a 2.7-fold higher (not significantly different) invertebrate AFDM than did the pool environment, whereas cobble-bars supported increasingly greater (>20-fold) AFDM and different composition of invertebrates with distance downstream from the Paria River, as compared to pools.

Benthic detrital carbon (>1 mm) AFDM was highly variable, and demonstrated no statistical difference over distance downstream or between seasons (Tables I and III; Figure 3D). Detritus was particularly abundant in the Lees Ferry pool where beaver (*Castor canadensis*) introduced substantial masses of wood to the river floor. A trend of increased detritus accumulation in autumn 1991 may have been related to lower flows.

#### *Trophic relations*

As demonstrated for *Gammarus* by Pinney (1991) and Shannon *et al.* (1994), chironomid larval diet predominantly consisted of epiphytic diatoms, bacteria and limited detritus. Algae made up 61.4% (SD  $\pm$ 29.73) of the intestinal tract contents of chironomid larvae at Lees Ferry, 30.7% (SD  $\pm$ 34.08) at km 51, and 7.5% (SD  $\pm$ 9.17) at km 361. Diatoms comprised >95% of the algae in chironomid larvae guts at each location, and *Cladophora* fragments comprised <1% of the total gut contents. The diatom genera most frequently encountered in chironomid guts were *Achnanthes*, *Cocconeis*, *Cymbella*, *Diatoma* and *Rhoicosphenia*, all of which are common epiphytes associated with *Cladophora* in this system (Czarnecki and Blinn, 1978; Blinn *et al.*, 1989; Hardwick *et al.*, 1992). Chironomid larvae >4 mm in length averaged 1013 diatom cells per larva, while larvae  $\leq$ 4 mm averaged 41.3 diatom cells per larva. The average cell dimensions for diatoms in the GI tract were  $9.4 \mu\text{m}$  (SD  $\pm$ 8.14)  $\times$   $51.2 \mu\text{m}$  (SD  $\pm$ 167.52). Detritus, bacteria and sand comprised the balance of the diet, and no *Oscillatoria* filaments occurred in chironomid gut samples. Larger chironomids consumed higher quantities of sand.

#### *Ordination*

Ordination analyses revealed that flow regulation overrode geomorphological influences on the benthos. The first two CANOCO axes explained 80.8% of the species–environment relationship of benthic species in samples space (Figure 4). Axis 1 (eigenvalue = 0.586, species–environment variance contribution = 62.2%) was strongly positively correlated with distance downstream and stage zone, and negatively correlated with Secchi depth. These three variables are the dam-related predictors. *Cladophora* and most aquatic macroinvertebrates had low negative scores on axis 1, while *Oscillatoria* had a high positive score.

The second CANOCO axis was correlated with geomorphological factors, as well as with season and interactions between geomorphic and dam-related variables. Axis 2 (eigenvalue = 0.175, species–environment variance contribution = 18.6%) was negatively correlated with habitat type, velocity and DO concentration. *Simulium arcticum* and lumbriculoid worms were distributed erratically throughout the river corridor in riffle habitats, and had relatively high positive scores on axis 2.

Analyses of samples in species space likewise revealed strong correlations of sites with physical gradients in this system (Figure 5). The individual study sites and centroids of the turbidity segments revealed a sigmoidal pattern over distance downstream from the dam (Figure 5A). This ‘circuitous recovery’ pattern indicates that increasing turbidity exerts the greatest influence on the benthos in this nearly stenothermic river; wide geomorphological reaches (e.g. A, D, E in Figure 5A) support higher benthic AFDM than do narrow reaches (e.g. B, C, F–H), and benthic AFDM decreases over distance downstream. Therefore, geomorphological reaches mediate turbidity effects. Pool and riffle habitat differences in AFDM were not significant at the Lees Ferry site, and increased in difference over distance downstream (Figure 5B). Stage elevation zones (Figure 5C) strongly influenced benthic composition; however, the influence of seasonality on the benthos was weak (Figure 5D).

#### *Dam, geomorphological and seasonal effects*

MANOVA analysis of dam-related factors (D) and geomorphological factors (G), and D  $\times$  G and D  $\times$  season (S) interactions corroborated the ordination patterns described above (overall MANOVA  $p < 0.0001$ ), and indicated that seasonal effects alone were not significant (Table III). Significant D effects ( $p = 0.014$ ) involved

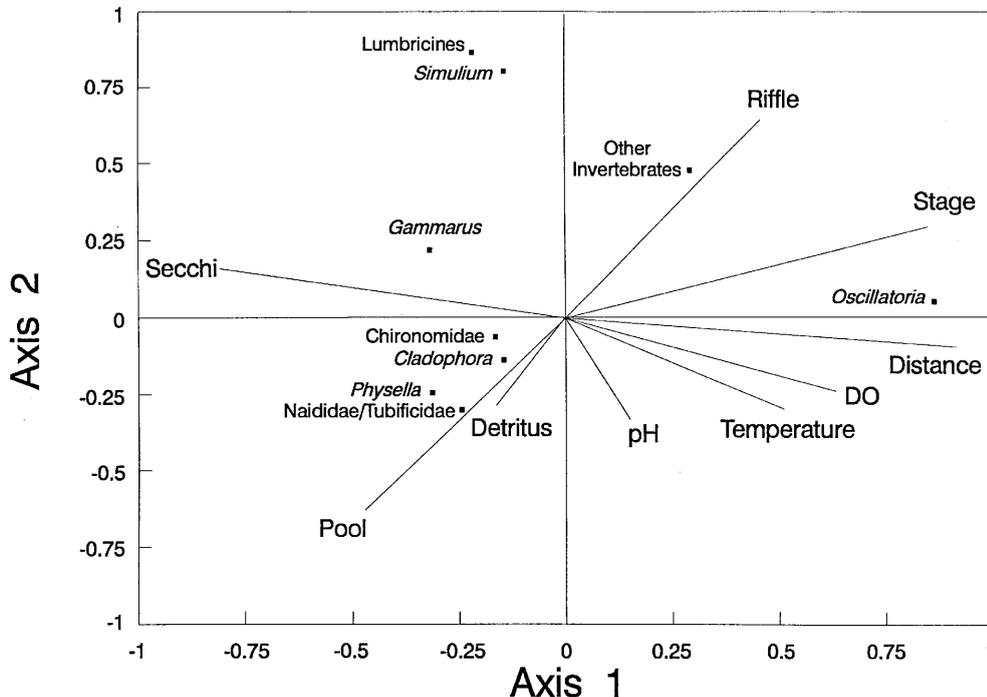


Figure 4. Canonical community correspondence analysis (CANOCO, Ter Braak, 1992) showing species and environmental variable factor loading scores on the two axes. Axis 1 was positively correlated with dam-induced alteration of the Colorado River, including gradients of distance-related water clarity (Secchi depth) and stage elevation. Axis 2 was correlated with geomorphological variables at local (pool versus riffle habitats) and reach-based (reach width) spatial scales

reduced benthic ADFM at downstream sites compared with Lees Ferry, particularly of *Cladophora* and *Gammarus*, as well as a negative correlation between ADFM and stage zone (Table III; Figure 6). The varial zone contained little life, with only 34 organisms collected in 396, 0.002 m<sup>3</sup> samples in that zone during a full year of intensive sampling. MANOVA results were supported by serial Bonferroni-adjusted Kruskal–Wallis tests on each biotic component across the nine dam-related treatment levels ( $t_{KW, 8 df} > 77.137$ ,  $p < 0.0001$ ,  $n = 458$ , for each biotic component respectively).

Geomorphology influenced the distribution of the benthos, but to a much lesser extent than did dam effects ( $p < 0.001$ ; Table III; Figure 7). Wide reaches supported increasingly greater proportions of benthic ADFM over distance downstream than did narrow reaches. At the local geomorphological scale, firm-bottomed riffle/rapid habitats supported increasingly greater proportions of total benthic ADFM over distance downstream than did soft-bottomed pool habitats. These results were supported by separate Kruskal–Wallis tests on each biotic component across the four geomorphologically related treatment levels ( $t_{KW, 3 df} > 22.045$ ,  $p < 0.0001$  for each biotic component, respectively), except for the naidd/tubificid oligochaetes and *Physella* snails ( $t_{KW, 3 df} = 10.889$  and  $13.065$ , and  $p = 0.012$  and  $p = 0.004$ , respectively).

The significant D  $\times$  G interaction effect was attributable to distance-related decreases in ADFM in the deep-submerged zone compared with the shallow submerged zone (Table III; Figure 6); and to high and statistically equivalent pool and riffle benthic ADFM at Lees Ferry, but higher riffle than pool ADFM in downstream reaches (Figure 7).

Season did not play a role in predicting ADFM by itself; however, the significant S  $\times$  D interaction (Table III) was attributable to summertime increases in oligochaete and chironomid populations in the shallow-submerged zone at Lees Ferry, as well as increased occurrence of the few other invertebrate taxa at middle and lower canyon sites. The absence of direct seasonal effects was further supported by separate Kruskal–Wallis tests on each biotic component in summer versus winter ( $t_{KW, 8 df} < 0.279$ ,  $p > 0.095$ , for each biotic component, respectively).

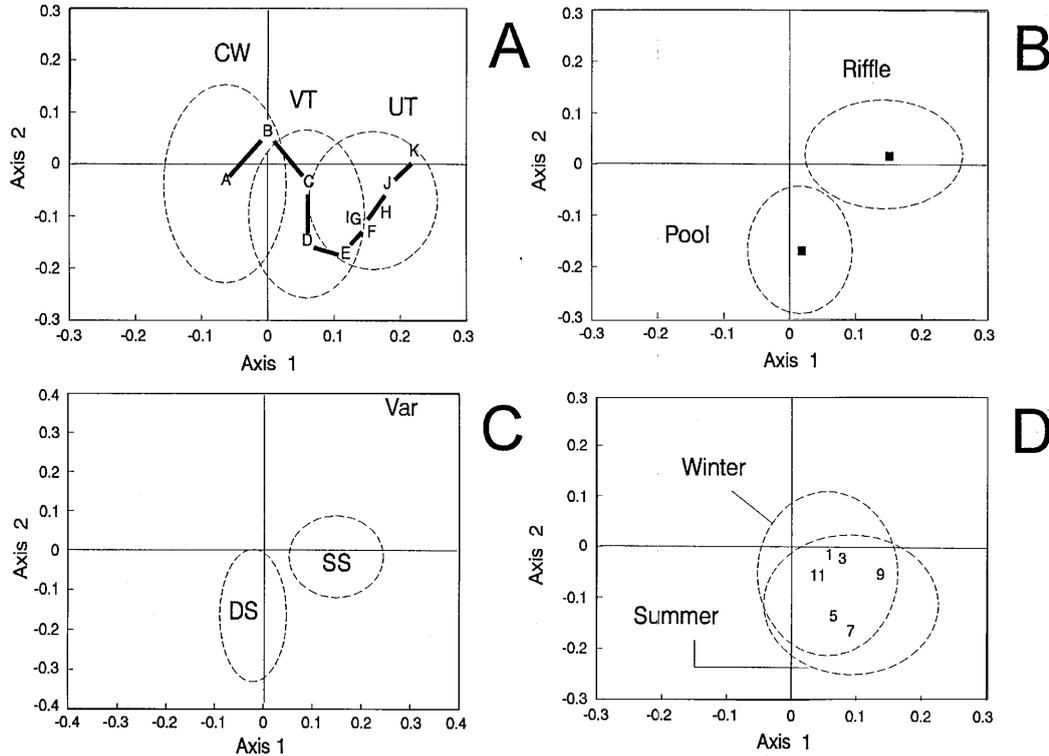


Figure 5. Canonical community correspondence analysis (Ter Braak, 1992) of factor loading scores for samples in species space on axes 1 and 2. Dashed circles represent 1 SD around the mean sample scores in relation to each gradient or factor. (A) A sigmoidal distance and turbidity-related shift in assemblage structure occurred between Lees Ferry (Site A) and Diamond Creek (Site K; Table I). Centroids for turbidity segments include: CW = the clear water Glen Canyon segment; VT = the variably turbid Marble Canyon segment; UT = the usually turbid Grand Canyon segment. (B) Benthic composition shifted in relation to habitat and velocity between pool and riffle habitats. (C) Benthic composition shifted in relation to stage zone from deep submerged (DS) to shallow submerged (SS) to varial (Var) habitats. (D) Winter and summer centroid mean and standard deviations demonstrate that little change in benthic composition occurred on a seasonal basis (numbers represent months)

*Reach-based benthic standing mass*

The total estimated AFDM of benthic algae and macroinvertebrates differed strongly between reaches (Figure 8). The clear, cold, stenothermic 26.1-km long Glen Canyon reach comprised approximately 6.9% of the total channel bed area lying below the 142 m<sup>3</sup>/s stage, yet it supported an estimated 63.3% of the total benthic algal mass and 86.9% of the total aquatic invertebrate mass of the 385-km long river corridor between Glen Canyon Dam and Diamond Creek. Downstream from the Paria River, *Cladophora* and, to a lesser extent, macroinvertebrate AFDM were higher in wide reaches (Figure 8A and C, respectively), while reach-based estimated *Oscillatoria* mass generally increased over distance downstream (Figure 8B). Estimated total detrital mass was somewhat higher at Lees Ferry, but showed no consistent pattern with respect to the other reaches (Figure 8D).

DISCUSSION

*Overview*

Benthic assemblage composition and structure in the Colorado River is primarily determined by flow regulation effects on water clarity and stage elevation, and is secondarily influenced by geomorphological effects of substratum distribution and reach width. The reduction of seasonal warming, another flow regulation effect, probably also dramatically altered the benthic invertebrate composition in this system. These physically induced

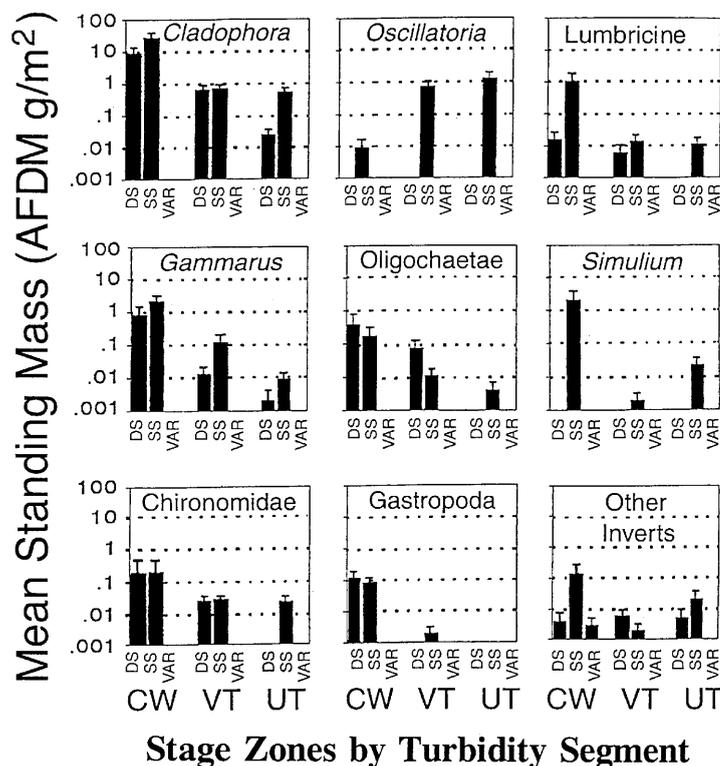


Figure 6. Flow regulation affects biotic components across three stage zones (DS = deep-submerged, SS = shallow-submerged, Var = varial zone of hourly flow fluctuation) in the clear water (CW), variably turbid (VT) and usually turbid (UT) segments (see Table I). Data are pooled within reaches and zones, and the y-axis is log<sub>10</sub> transformed. Biotic components are AFDM g C/m<sup>2</sup> of two algal and seven aquatic invertebrate taxa, and error bars are 1 SE

(bottom-up) patterns provide support for the serial discontinuity concept (Ward and Stanford, 1983) in this large, arid-lands river; however, reach-based geomorphological influences on channel width and substratum availability mediate benthic community characteristics.

#### The clear water benthos

The clear water segment upstream from the Paria River supported an autochthonous, tightly linked assemblage of *Cladophora*, epiphytes and grazing macroinvertebrates (*Cricotopus* spp. and *Orthocladus* spp. chironomids; *Gammarus lacustris*; lumbriculoids; *Physella*), with a mean total standing mass of 18.5 g C/m<sup>2</sup> below the 80 m<sup>3</sup>/s stage (Figure 1). Standing mass varied little between clear water riffle and pool habitats, or between soft and firm substrata, because *Cladophora* colonized nearly all of the channel floor below the varial zone. Therefore, geomorphological influences were reduced in importance in this reach.

*Cladophora glomerata* is a widely distributed, filamentous green alga (Whitton, 1970; Graham *et al.*, 1982; Dodds, 1991) which does not directly provide nutrition to macroinvertebrates in this system; rather, it provides cover for macroinvertebrates and habitat structure for the algal epiphytes (mostly diatoms) that comprised the majority of the diet of those invertebrates (Shannon *et al.*, 1994). Pinney (1991) reported that diatoms comprised >90% of the diet of *Gammarus lacustris* at Lees Ferry, with the balance consisting of cyanobacteria and detritus, but not *Cladophora*. *Gammarus* selected upright periphytic diatom taxa (e.g. *Rhoicosphenia* and *Diatoma*) over adnately attached genera (e.g. *Cocconeis*) on *Cladophora*, despite the great abundance of adnate diatoms on *Cladophora*. Shannon *et al.* (1994) corroborated this finding and documented experimentally that *Gammarus* detected chemical cues from diatoms. Our dietary data further corroborate the reliance of chironomid larvae on epiphytes, but not on *Cladophora*.

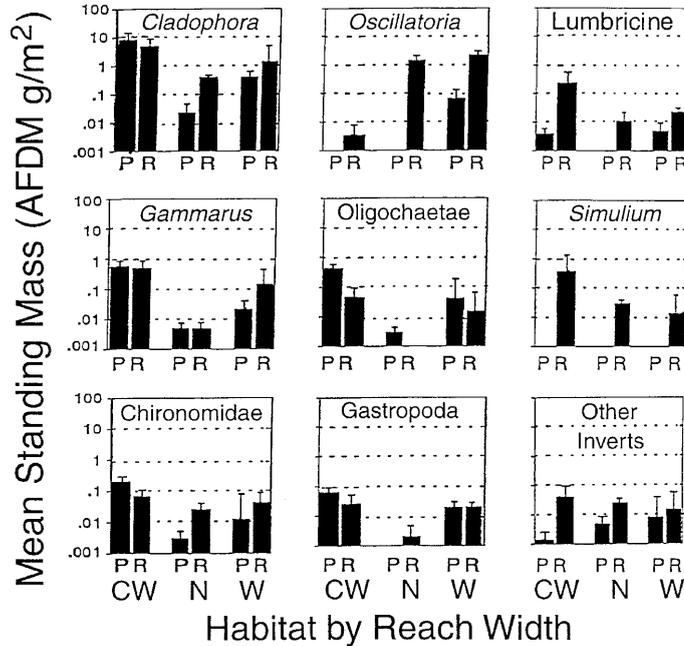


Figure 7. Effects of geomorphology on nine biotic variables, with habitat (P=pool versus R=riffle/rapid) coupled with reach width at the clear water (CW) Lees Ferry site, and in downstream narrow (N) and wide (W) reaches (Schmidt and Graf, 1990). These data include only the deep and shallow submerged zones, not the varial zone. The y-axis is log<sub>10</sub> transformed. Pool and riffle data at Lees Ferry are presented separately because standing biomass was substantially higher there than downstream from the Paria River confluence (univariate  $F_{1,208} = 73.312, p < 0.0001$ ). Error bars are 1 SE

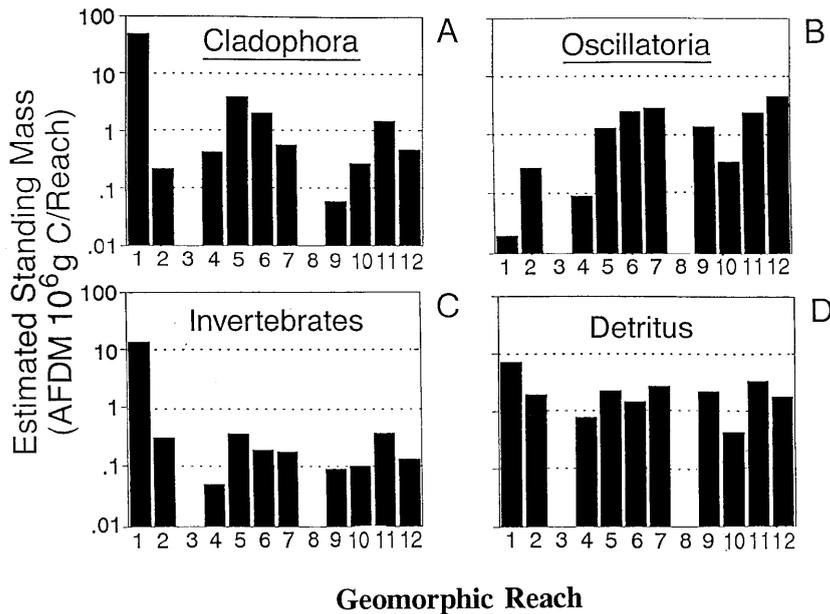


Figure 8. Total estimated AFDM of biotic components in 10 of the 12 bedrock-defined geomorphological reaches of the Colorado River between Glen Canyon Dam and Lake Mead, Arizona (modified from Schmidt and Graf, 1990; Table I): (A) *Cladophora glomerata*, (B) *Oscillatoria* spp., (C) invertebrates, (D) benthic detritus. The y-axis is log<sub>10</sub> transformed. Reaches 3 and 8 are short, narrow reaches that were not sampled, but are likely to be similar to adjacent reaches.

Dam-related increased water clarity strongly altered benthic composition and standing mass in the clear water reach. Stone and Rathbun (Arizona Game and Fish Department, Phoenix, AZ, unpublished data) reported that *Cladophora* rapidly colonized the river floor between the dam and the Paria River confluence in 1966 and 1967. The short clear water segment supported the majority of the algal and macroinvertebrate AFDM in the 389-km long study area.

The clear water benthos is strongly linked to higher trophic levels, including the fisheries (Leibfried, 1988; Blinn *et al.*, 1995) and riparian insectivores, which feed on the aerial life stages of aquatic Diptera (Blinn and Cole, 1991). In addition, drifting organic matter is transported into the less productive reaches downstream from the Paria River (Angradi and Kubly, 1994). Angradi (1994) suggested that material spirals in this system were relatively short, a prediction consistent with the concepts of Elwood *et al.* (1983) in regulated rivers; however, Graf (1995) demonstrated experimentally, relatively rapid movement of dye clouds through this system, and little retention by eddies. The importance of organic drift from the Glen Canyon reach to downstream decomposers requires further investigation.

#### *The benthos in turbid reaches*

Mainstream turbidity was substantially and consistently altered by downstream tributaries (Table I). Tributary-derived suspended sediment loads reduced *Cladophora* AFDM in an abrupt, 'stairstep' fashion, with a 37-fold decrease in mean AFDM at the Paria River confluence, and further at the Little Colorado River and subsequent tributary confluences. Hardwick *et al.* (1992) reported that epiphytic diatom densities on *Cladophora* decreased by >25% from Lees Ferry to km 364. Similarly, *Gammarus* AFDM decreased 22-fold in riffle habitats from Lees Ferry to the Little Colorado River, and to near negligible levels further downstream, and the AFDM of other macroinvertebrates also decreased sharply downstream from the Paria River confluence.

*Oscillatoria* spp. replaced *Cladophora* as the dominant firm-substratum benthic algal taxon downstream from the Paria River. We observed that *Oscillatoria* exhibited a greater tolerance to desiccation under daily and monthly fluctuating flows, conferring on it a selective advantage under highly varying flows. Crustose *Oscillatoria* mats provide less surface area for diatom attachment and colonization, and were not utilized as food by macroinvertebrates. Consequently, *Oscillatoria* supported little invertebrate standing mass. The lack of *Oscillatoria* crusts in pre-dam photographs (Turner and Karpiscak, 1980; Webb, 1996), suggests that regular scour limited its colonization in the pre-dam river.

Unlike the tightly linked *Cladophora* assemblage in the clear water segment, the benthos downstream from the Paria River consisted of a loose association between *Oscillatoria*, and filter-feeding *Simulium* and ooze-feeding chironomids. Filter-feeding *Simulium* larvae are often abundant primary colonizers on firm substrata in rivers, such as recently disturbed rock surfaces and driftwood in moderate to high velocity settings (e.g. Ulfstrand *et al.*, 1974). At the scale of bedrock-defined reaches, estimated total *Oscillatoria* standing mass increased over distance downstream. At the microsite scale, *Oscillatoria* cover tends to be negatively correlated with *Simulium* because both taxa require firm substrata. Food resources for other downstream macroinvertebrates appear to be limited by reduced *Cladophora* AFDM and consequent reduction in epiphyte densities, as demonstrated by low estimated total invertebrate standing mass values.

#### *An altered benthos*

Dam-related increased water clarity and temperature have overridden local geomorphological influences on the Colorado River benthos, as demonstrated by the following observations. (1) The tailwaters benthos is incrementally affected by baseflow stage, flow fluctuations and seasonal aspects of the flow regime (Usher and Blinn, 1990; Angradi and Kubly, 1993; Blinn *et al.*, 1995). (2) Cobble-bar AFDM decreased by more than 37-fold downstream from the Paria River confluence, and two-fold more past the Little Colorado River confluence, in concert with reduced water clarity. However, standing mass was only two-fold higher in wide versus narrow reaches downstream from the Paria River, indicating that geomorphological influences were weaker than turbidity-related effects. (3) Differences between standing mass on firm- versus soft-bottomed habitats increased from three-fold at Lees Ferry to more than 20-fold in the lower Canyon, indicating increased importance of riffle/rapid habitats to the benthos over distance downstream. (4) Lastly, dam-induced erosion of fine sediments has

exposed additional coarse substrata in the Lees Ferry area (Howard and Dolan, 1981), increasing the habitat available for *Cladophora glomerata* colonization.

The post-dam aquatic macroinvertebrate fauna in the Grand Canyon portion of the Colorado River is remarkably depauperate compared with other rivers. Virtually no Ephemeroptera, Plecoptera or Trichoptera were collected in the mainstream in 1991. Cold-stenothermic releases may not permit these taxa to complete their life cycles in the river. These taxa are abundant in unregulated streams throughout this region, including Colorado River tributaries in Grand Canyon (Hofknecht, 1981) and in the less regulated reaches of the Colorado, San Juan and lower Green rivers upstream from Lake Powell (Ward and Stanford, 1991; L.E.S. and J.P.S., personal observations). Ephemeroptera and other taxa should be abundant in the clear water segment, but are apparently excluded by the stenothermic releases (Hauer and Stanford, 1982, 1991). The pre-impoundment Colorado River may have been characterized by low benthic standing mass as a result of high turbidity and high flood-disturbance intensity, as reported in other large, turbid rivers (Junk *et al.*, 1989); however, pre-dam aquatic invertebrate species diversity was probably higher than that following flow regulation.

Temperature and turbidity regimes strongly influence benthic assemblages in regulated rivers (Ward, 1976; Ward and Stanford, 1982; Armitage, 1984). Cold, stenothermic temperatures probably reduced the Colorado River macroinvertebrate diversity by eliminating key developmental cues (*sensu* Vannote and Sweeney, 1980), while increased benthic light availability has increased benthic standing mass, and production (*e.g.* Angradi and Kubly, 1993), especially in the clear water reach. Although a small tributary, the Paria River dramatically reduces benthic light availability; however, no tributary in this system is large enough to influence mainstream temperature. Given a maximum aestival warming rate of 0.023°C/km in 1991, recovery to the annual pre-dam summer maximum water temperature of 29.4°C would require a mainstream run of 930 km, but such a run is prevented by other downstream dams.

The role of coarse detritus in this river has also been substantially altered by flow regulation. Large amounts of driftwood accumulated in specific eddies in the pre-dam river, as attested to by the diaries of numerous pre-dam river-runners. Large woody debris is now derived from tributaries during floods, or from occasional scouring flows of the profusely vegetated post-dam shorelines (Stevens *et al.*, 1995). Flow regulation reduced organic as well as inorganic sediment transport. Our data (Figure 3D) and reach-based estimates (Figure 8D), and those of Shannon *et al.* (1996), demonstrate that post-dam benthic detrital standing mass is generally low and variable, increasing through the more turbid downstream reaches.

#### *Relationships to river models*

Within the conceptual framework of the river continuum model (RCM) and its corollaries (Vannote *et al.*, 1980; Minshall *et al.*, 1985; Elwood *et al.*, 1983; Sedell *et al.*, 1989; Thorp and DeLong, 1994), the SDC (Ward and Stanford, 1983) emphasizes the role of dam size and location in the drainage in the resetting process in regulated rivers. Recent consideration of the SDC in relation to alluvial rivers further draws attention to the role of floodplains, which may affect channel stability, thermal regime, biodiversity and FPOM/CPOM ratios in regulated rivers (Ward and Stanford, 1995), and the difficulties of restoring large regulated rivers (Ligon *et al.*, 1995).

Our study demonstrates that reach-based channel geometry mediates distance-related restoration of ecosystem components and processes in this large, geomorphologically complex regulated river. The circuitous 'recovery' of the Colorado River may best be explained by coupling model predictions related to dam-induced reduction of flood disturbance and thermal variability (Ward and Stanford, 1982; Junk *et al.*, 1989), reach-based channel geometry influences (Sedell *et al.*, 1989; Brussock and Brown, 1991), and localized autochthonous production (Townsend, 1989; Thorp and DeLong, 1994), with SDC predictions. Rather than being reset to an equivalent, lower stream order, the Grand Canyon section of the Colorado River displays regionally unusual temperature, flow and turbidity regimes which reduce benthic diversity but increase standing biomass in clear water and variably turbid segments.

#### *Management considerations*

Managing dams to maintain or improve riverine fish populations requires a sound understanding of benthic assemblage structure and food base responses to flow characteristics (Armitage *et al.*, 1987; Gore, 1989). Our

data demonstrate that dam influences on water clarity, temperature and substratum availability exert strong effects on assemblage composition and standing mass, with potentially large effects on fish (Blinn *et al.*, 1995). Designed to protect river resources, we predict that the recently implemented flow regime of reduced flow velocity and variability, will increase water clarity and fine sediment deposition, and will reduce benthic scour, on a system-wide basis. These effects may increase benthic algal colonization in upper reaches, and may permit downstream expansion of other aquatic plant populations.

The US Bureau of Reclamation has proposed intentional warming of the river by construction of a multi-level withdrawal structure on the upstream face of the dam. Warmer summer river temperatures may increase benthic invertebrate, and possibly macrophyte, diversity and production. However, warmer temperatures may also alter competitive hierarchies and the distribution of *Cladophora*, *Oscillatoria*, epiphytes and other macrophytes, thereby affecting the invertebrate food base and non-native fish populations in unpredictable ways (Blinn *et al.*, 1989).

Natural ecological analogues of regulated rivers may provide insight into management options and potential development in this river system. Except for flow magnitude and hourly variation, conditions in the tailwaters reach resemble those of cold, stenothermic spring-fed tributaries in Grand Canyon, which support abundant invertebrates not presently found in the tailwaters reach. In contrast, mainstream thermal and benthic light conditions downstream from the Paria River resemble those of turbid glacial rivers (e.g. Milner, 1987) for which no regional analogue exists. Where pre-impoundment conditions are unknown and where no natural ecological analogues exist, management must be based on clearly articulated evaluation of resources and trade-offs. Such practices will limit undesired changes in the benthos, fisheries and riparian biota.

#### ACKNOWLEDGEMENTS

This project was largely sponsored by the US Bureau of Reclamation Glen Canyon Environmental Studies Program and we thank David Wegner, Michael Yard and William Vernieu. This project was conducted under the auspices of the National Park Service (NPS, contract no. CA 8009-8-0002). We thank several taxonomists who assisted in this project: Robert Peterson (Simuliidae), Earle Spamer (Mollusca), James Sublette (Chironomidae) and Mark Wetzel (Oligochaetae). Laboratory assistance was provided by E. Autenreith, P. Benenati, J. Carder, G. Oberlin, J. Macaulley, T. Martin, L. Putnam, M. Shaver, D. Silva, T. Yates and 38 NPS volunteers. We thank J. Carder for assistance with diet analyses, and R. Davis and V. Saylor for assistance with graphics. Dr Jack A. Stanford and two anonymous reviewers provided valued comments on earlier versions of the manuscript.

#### REFERENCES

- Allen, J. D. and Flecker, A. S. 1993. 'Biodiversity conservation in running waters', *BioScience*, **43**, 32–43.
- Andrews, E. D. 1991. 'Sediment transport in the Colorado River basin', in Marzolf, G. R. (Ed.), *River Ecology and Dam Management*. National Academy Press, Washington D.C. pp. 54–74.
- Angradi, T. R. 1994. 'Trophic linkages in the lower Colorado River: multiple stable isotope evidence', *J. North Am. Benthol. Soc.*, **13**, 479–495.
- Angradi, T. R. and Kubly, D. M. 1993. 'Effects of atmospheric exposure on chlorophyll *a*, biomass and productivity of the epilithon of a tailwater river', *Regul. Riv.*, **8**, 345–358.
- Angradi, T. R. and Kubly, D. M. 1994. 'Concentration and transport of particulate organic matter below Glen Canyon Dam on the Colorado River, Arizona', *J. Arizona-Nevada Acad. Sci.*, **28**, 12–22.
- Armitage, P. D. 1984. 'Environmental changes induced by stream regulation and their effects on lotic macroinvertebrate communities', in Lillehammer, A. and Saltveit, S. J. (Eds), *Regulated Rivers*. Universitetsforlaget AS, Oslo. pp. 139–165.
- Armitage, P. D., Gunn, R. J. M., Furse, M. T., Wright, J. F., and Moss, D. 1987. 'The use of prediction to assess macroinvertebrate response to river regulation', *Hydrobiologia*, **144**, 25–32.
- Blinn, D. W. and Cole, G. A. 1991. 'Algae and invertebrate biota in the Colorado River: comparison of pre- and post-dam conditions', in Marzolf, G. R. (Ed.), *Colorado River Ecology and Dam Management*. National Academy Press, Washington, D.C. pp. 85–104.
- Blinn, D. W., Truitt, R., and Pickart, A. 1989. Responses of epiphytic diatom communities from the tailwaters of Glen Canyon Dam, Arizona, to elevated water temperature. *Regul. Riv.*, **4**, 91–96.
- Blinn, D. W., Shannon, J. P., Stevens, L. E., and Carder, J. P. 1995. 'Consequences of fluctuating discharge for lotic communities', *J. North Am. Benthol. Soc.*, **14**, 233–248.
- Bruns, D. A., Minshall, G. W., Cushing, C. E., Cummins, K. W., Brock, J. T., and Vannote, R. L. 1984. 'Tributaries as modifiers of the river-continuum concept: analysis by polar ordination and regression models', *Arch. Hydrobiol.*, **99**, 208–220.

- Brussock, P. P. and Brown, A. V. 1991. 'Riffle-pool geomorphology disrupts longitudinal patterns of stream benthos', *Hydrobiologia*, **220**, 109–117.
- Corkum, L. D. 1991. 'Spatial patterns of macroinvertebrate distributions along rivers in eastern deciduous forest and grassland biomes', *J. North Am. Benthol. Soc.*, **10**, 358–371.
- Culp, J. M. and Davies, R. W. 1982. 'Analysis of longitudinal zonation and the river continuum concept in the Oldham–South Saskatchewan River system', *Can. J. Fish. Aquat. Sci.*, **44**, 832–845.
- Cushing, C. E., McIntire, C. D., Sedell, J. R., Cummins, K. W., Minshall, G. W., Petersen, R. C., and Vannote, R. L. 1980. 'Comparative study of physical-chemical variables of streams using multivariate analysis', *Archiv fur Hydrobiologia*, **89**, 343–352.
- Czarnecki, D. B. and Blinn, D. W. 1978. 'Diatoms of the Colorado River in Grand Canyon National Park and vicinity. Diatoms of Southwestern U.S.A.' *Bibliotheca Phycologia*, **38**, 1–182.
- Dodds, W. K. 1991. 'Factors associated with dominance of the filamentous green alga *Cladophora glomerata*', *Wat. Res.*, **25**, 1325–1332.
- Elwood, J. W., Newbold, J. D., O'Neill, R. V., and Van Winkle, W. 1983. 'Resource spiraling: an operational paradigm for analyzing lotic ecosystems', in Fontaine, T. D. and Bartell, S. M. (Eds), *Dynamics of Lotic Ecosystems*. Ann Arbor Science, Ann Arbor, MI. pp. 3–27.
- Gore, J. A. 1989. 'Models for predicting benthic macroinvertebrate habitat suitability under regulated flows', in Gore, J. A. and Petts, G. E. (Eds), *Alternatives in Regulated River Management*. CRC Press Inc., Boca Raton, LA. pp. 253–265.
- Gore, J. A. and Shields, F. D., Jr. 1995. 'Can large rivers be restored?', *BioScience*, **45**, 142–152.
- Graf, J. B. 1995. 'Measured and predicted velocity and longitudinal dispersion at steady and unsteady flow, Colorado River, Glen Canyon Dam to Lake Mead', *Wat. Resour. Bull.*, **31**, 265–281.
- Graf, J. B., Webb, R. H., and Hereford, R. 1991. 'Relation of sediment load and flood-plain formation to climatic variability, Paria River drainage basin, Utah and Arizona', *Geol. Soc. Am. Bull.*, **103**, 1405–1415.
- Graham, J. M., Auer, M. T., Canale, R. P., and Hoffmann, J. P. 1982. 'Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: photosynthesis and respiration as functions of light and temperature', *J. Great Lakes Res.*, **8**, 100–111.
- Gregory, S. V., Swanson, F. J., McKee, W. A., and Cummins, K. W. 1991. 'An ecosystem perspective of riparian zones', *BioScience*, **41**, 540–551.
- Grimm, N. B. and Fisher, S. G. 1989. 'Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream', *J. North Am. Benthol. Soc.*, **8**, 293–307.
- Hardwick, G., Blinn, D. W., and Usher, H. D. 1992. 'Epiphytic diatoms on *Cladophora glomerata* in the Colorado River, Arizona: longitudinal and vertical distribution in a regulated river', *The Southwestern Naturalist*, **37**, 148–156.
- Hauer, F. R. and Stanford, J. A. 1982. 'Ecology and life histories of three net-spinning caddisfly species (Hydropsychidae: *Hydropsyche*) in the Flathead River, Montana', *Freshwat. Invert. Biol.* **1**, 18–29.
- Hauer, F. R. and Stanford, J. A. 1991. 'Distribution and abundance of Trichoptera in a large regulated river', *Verh. Internat. Verein. Limnol.* **24**, 1636–1639.
- Helsesic, J. and Sedlack, E. 1995. 'Downstream effect of impoundments on stoneflies: case study of the epipotamal reach of the Jihlava River, Czech Republic', *Regul. Riv.*, **10**, 39–49.
- Hirsch, R. M., Walker, J. F., Day, J. C., and Kollio, R. 1990. 'The influence of man on hydrologic systems', in Wolman, M. G. and Riggs, H. C. (Eds), *Surface Water Hydrology. Geologic Society of America Decade of North American Geology*, Vol. 0–1. pp. 329–359.
- Hofknecht, G. W. 1981. 'Seasonal community dynamics of aquatic invertebrates in the Colorado River and its tributaries within Grand Canyon, Arizona', *M.S. Thesis*, Northern Arizona University, Flagstaff, AZ.
- Howard, A. and Dolan, R. 1981. 'Geomorphology of the Colorado River in Grand Canyon', *J. Geol.*, **89**, 269–298.
- Hupp, C. R. 1988. 'Plant ecological aspects of flood geomorphology and paleoflood history', in Baker, V. R. (Ed.), *Flood Geomorphology*. John Wiley & Sons, New York. pp. 335–357.
- Johnson, B. L., Richardson, W. B., and Naimo, T. J. 1995. 'Past, present, and future concepts in large river ecology: how rivers function and how human activities influence river processes', *BioScience*, **45**, 134–141.
- Johnson, R. R. 1991. 'Historic changes in vegetation along the Colorado River in the Grand Canyon', in Marzolf, G. R. (Ed.), *Colorado River Ecology and Dam Management*. National Academy Press, Washington, D.C. pp. 178–206.
- Junk, W. J., Bayley, P. B., and Sparks, R. E. 1989. 'The flood pulse concept in river-floodplain systems', in Dodge, D. P. (Ed.), *Proceedings, International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci.*, **106**, 110–127.
- Kieffer, S. 1985. 'The 1983 hydraulic jump in Crystal Rapid: implications for river-running and geomorphic evolution in the Grand Canyon', *J. Geology*, **93**, 385–406.
- Leibfried, W. C. 1988. 'The utilization of *Cladophora glomerata* and epiphytic diatoms as a food source by rainbow trout in the Colorado River below Glen Canyon Dam, Arizona'. *M.S. Thesis*, Northern Arizona University, Flagstaff, AZ.
- Lieberman, D. M. and Burke, T. A. 1993. 'Particulate organic matter transport in the lower Colorado River, south-western USA', *Reg. Riv.*, **8**, 323–334.
- Ligon, F. K., Dietrich, W. E., and Trush, W. J. 1995. 'Downstream ecological effects of dams', *BioScience*, **45**, 183–192.
- Miller, C. 1985. 'Correlates of habitat favorability for benthic macroinvertebrates at five stream sites in an Appalachian mountain drainage basin, U.S.A.', *Freshwat. Biol.*, **15**, 709–733.
- Milner, A. M. 1987. 'Colonization and ecological development of new streams in Glacier Bay National Park, Alaska', *Freshwat. Biol.*, **18**, 53–70.
- Minckley, W. L. 1991. 'Native fishes of the Grand Canyon region: an obituary?', in Marzolf, G. R. (Ed.), *Colorado River Ecology and Dam Management*. National Academy Press, Washington, D.C. pp. 124–177.
- Minshall, G. W., Petersen, R. C., Cummins, K. W., Bott, K. W., Sedell, J. R., Cushing, C. E., and Vannote, R. L. 1983. 'Interbiome comparison of stream ecosystem dynamics', *Ecol. Monographs*, **53**, 1–25.
- Minshall, G. W., Cummins, K. W., Petersen, R. C., Cushing, C. E., Bruns, D. A., Sedell, J. R., and Vannote, R. L. 1985. 'Developments in stream ecosystem theory', *Can. J. Fish. Aquat. Sci.*, **42**, 1045–1055.
- Minshall, G. W., Petersen, R. C., Botts, T. L., Cushing, C. E., Cummins, K. W., Vannote, R. L., and Sedell, J. R. 1992. 'Stream ecosystem dynamics of the Salmon River, Idaho: an 8th-order stream', *J. North Am. Benthol. Soc.*, **11**, 111–137.
- Molles, M. C. Jr. 1992. 'The benthic habitats and aquatic invertebrate communities of the middle Rio Grande landscape, New Mexico', *Bull. North Am. Benthol. Soc.*, **9**, 71.

- Munn, M. D. and Brusven, M. A. 1983. 'Discontinuity of trichopteran (caddisfly) communities in regulated waters of the Clearwater River, Idaho, USA', *Regul. Riv.*, **1**, 61–69.
- Newcombe C. P. and MacDonald, D. D. 1991. 'Effects of suspended sediments on aquatic ecosystems', *North Am. J. Fish. Manage.*, **11**, 72–82.
- O'Conner, J. E., Ely, L. L., Wohl, E. E., Stevens, L. E., Melis, T. S., Kale, V. S., and Baker, V. R. 1994. 'A 4500-year record of large floods on the Colorado River in the Grand Canyon, Arizona', *J. Geol.*, **102**, 1–9.
- Palmer, M. W. 1993. 'Putting things in even better order: the advantages of canonical correspondence analysis', *Ecology* **74**, 2215–2230.
- Patten, D. T. 1991. 'Glen Canyon Environmental Studies research program: past, present, and future', in Marzolf, G. R. (Ed.), *Colorado River Ecology and Dam Management*. National Academy Press, Washington, D.C. pp. 85–104.
- Pearson, W. D. 1967. 'Distribution of macroinvertebrates in the Green River below Flaming Gorge Dam, 1963–1965', *M.S. Thesis*, Utah State University, Logan, UT.
- Pinney, C. A. 1991. 'The response of *Cladophora glomerata* and associated epiphytic diatoms to regulated flow and the diet of *Gammarus lacustris*, in the tailwaters of Glen Canyon Dam', *M.S. Thesis*, Northern Arizona University, Flagstaff, AZ.
- Rader, R. B. and Ward, J. V. 1988. 'Influence of regulation on environmental conditions and the macroinvertebrate community in the upper Colorado River', *Regul. Riv.*, **2**, 597–618.
- Rice, W. R. 1989. 'Analyzing tables of statistical tests', *Evolution*, **43**, 223–225.
- Roos, J. C. and Pieterse, A. J. H. 1994. 'Light, temperature and flow regimes of the Vaal River at Balkfontein, South Africa', *Hydrobiologia*, **277**, 1–15.
- Ross, L. E. and Rushforth, S. R. 1980. 'The effects of a new reservoir on the attached diatom communities in Huntington Creek, Utah, U.S.A.' *Hydrobiologia*, **68**, 157–165.
- Ryder, G. I. and Scott, D. 1988. 'The applicability of the river continuum concept to New Zealand streams', *Verh. Internat. Verein. Limnol.*, **23**, 1441–1445.
- Schmidt, J. C. and Graf, J. B. 1987. 'Aggradation and degradation of alluvial sand deposits, 1965–1986, Colorado River, Grand Canyon National Park, Arizona—executive summary', *US Geological Survey Open File Report 87–561*. US Geological Survey, Washington, D.C.
- Schmidt, J. C. and Graf, J. B. 1990. 'Aggradation and degradation of alluvial sand deposits, 1965–1986, Colorado River, Grand Canyon National Park, Arizona', *US Geological Survey Professional Paper 1493*. US Geological Survey, Washington, D.C.
- Schmidt, J. C. and Rubin, D. M. 1995. 'Regulated streamflow, fine-grained deposits and effective discharge in canyons with abundant debris fans', *Am. Geophys. Union Monograph*, **89**, 177–195.
- Sedell, J. R., Richey, J. E., and Swanson, F. J. 1989. 'The river continuum concept: a basis for the expected ecosystem behavior of very large rivers?', in Dodge, D. P. (Ed.), *Proceedings, International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci.* **106**, 49–55.
- Sellers, W. D. and Hill, R. H. (Eds) 1974. *Arizona climate 1931–1972*, 2nd edn. University of Arizona Press, Tucson, AZ.
- Shannon, J. P., Blinn, D. W., and Stevens, L. E. 1994. 'Trophic interactions and benthic animal community structure in the Colorado River, Arizona, U.S.A.', *Freshwat. Biol.*, **31**, 213–220.
- Shannon, J. P., Blinn, D. W., Benenati, P. L., and Wilson, K. P. 1996. 'Organic drift in a regulated desert river', *Can. J. Fish. Aquat. Sci.* **53**, 1360–1369.
- Stanford, J. A. and Ward, J. V. 1991. 'Limnology of Lake Powell and the chemistry of the Colorado River', in Marzolf, G. R. (Ed.), *Colorado River Ecology and Dam Management*. National Academy Press, Washington, D.C. pp. 75–123
- Stanford, J. A., Hauer, F. R., and Ward, J. V. 1988. 'Serial discontinuity in a large river system', *Verh. Internat. Verein. Limnol.*, **23**, 1114–1118.
- Stephens, H. G. and Shoemaker, E. M. 1987. *In the Footsteps of John Wesley Powell*. Johnson Books, Boulder, CO.
- Stevens, L. E., Schmidt, J. C., Ayers, T. J., and Brown, B.T. 1995. 'Flow regulation, geomorphology and Colorado River marsh development in the Grand Canyon, Arizona'. *Ecol. Appl.*, **6**, 1025–1039.
- Storey, A. W., Edward, D. H., and Gazey, P. 1991. 'Recovery of aquatic macroinvertebrate assemblages downstream of the Canning Dam, Western Australia', *Regul. Riv.*, **6**, 213–224.
- Ter Braak, C. J. F. 1992. *CANOCO, a FORTRAN program for canonical community ordination by [partial] [detrended] correlation analysis, principal components analysis and redundancy analysis*. Microcomputer Power, Ithaca, NY.
- Thorp, J. H. and DeLong, M. D. 1994. 'The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems', *Oikos*, **70**, 305–308.
- Townsend, C. R. 1989. 'The patch dynamics concept of stream community ecology', *J. North Am. Benthol. Soc.*, **8**, 36–50.
- Turner, R. M. and Karpiscak, M. M. 1980. 'Recent vegetation changes along the Colorado River between Glen Canyon Dam and Lake Mead, Arizona', *US Geological Survey Professional Paper 1132*. US Geological Survey, Washington, D.C.
- Ulfstrand, S. L., Nilsson, L. M., and Stergar, A. 1974. 'Composition and diversity of benthic species collectives colonizing implanted substrates in a south Swedish stream', *Entomol. Scand.*, **5**, 115–122.
- Usher, H. D. and Blinn, D. W. 1990. 'Influence of various exposure periods on the biomass and chlorophyll *a* on *Cladophora glomerata* (Chlorophyta)', *J. Phycol.*, **26**, 244–249.
- Vannote, R. L. and Sweeney, B. 1980. 'Geographic analysis of thermal equilibria: a conceptual model for calculating the effect of natural and modified thermal regimes on aquatic insect communities', *Am. Naturalist*, **115**, 667–695.
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., and Cushing, C. E. 1980. 'The river continuum concept', *Can. J. Fish. Aquat. Sci.*, **37**, 130–137.
- Volez, N. J. and Ward, J. V. 1989. 'Biotic and abiotic gradients in a regulated high elevation Rocky Mountain river', *Regul. Riv.*, **3**, 143–152.
- Ward, J. V. 1976. 'Effects of flow patterns below large dams on stream benthos: a review', in Osborn, J. F. and Allman C. H. (Eds), *Instream Flow Needs Symposium*. American Fisheries Society, Bethesda, MD. pp. 235–253.
- Ward, J. V. and Stanford, J. A. 1979. 'Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams', in Ward, J. V. and Stanford, J. A. (Eds), *The Ecology of Regulated Streams*. Plenum Publishing, New York.
- Ward, J. V. and Stanford, J. A. 1982. 'Thermal responses in the evolutionary ecology of aquatic insects', *Ann. Rev. Entom.*, **27**, 97–117.
- Ward, J. V. and Stanford, J. A. 1983. 'The serial discontinuity concept of lotic ecosystems', in Fontaine, T. D. and Bartell, S. M. (Eds), *Ecology of River Systems*. Dr. W. Junk Publishers, Dordrecht, The Netherlands. pp. 29–42.

- Ward, J. V. and Stanford, J. A. 1991. 'Benthic faunal patterns along the longitudinal gradient of a Rocky Mountain river system', *Verh. Internat. Verein. Limnol.*, **24**, 3087–3094.
- Ward, J. V. and Stanford, J. A. 1995. 'The serial discontinuity concept: extending the model to floodplain rivers', *Regul. Riv.*, **10**, 159–168.
- Webb, R. H. 1996. *A century of change in the Grand Canyon*. University of Arizona Press, Tucson.
- Webb, R. H., Pringle, P. T., and Rink, G. R. 1989. 'Debris flows from tributaries of the Colorado River, Grand Canyon National Park, Arizona', *US Geological Survey Professional Paper 1492*. US Geological Survey, Washington, D.C.
- Whitton, B. A. 1970. 'Biology of *Cladophora* in freshwaters', *Wat. Res.*, **4**, 457–476.
- Wilkinson, L. 1991. *SYSTAT: The system for statistics, version 5.03*. SYSTAT, Inc. Evanston, IL.
- Winget, R. N. 1984. 'Ecological studies of a regulated stream: Huntington River, Emery County Utah', *Great Basin Naturalist*, **44**, 231–256.