1997 - 1998 Response Of The Aquatic Food Base To Elevated Discharges And Three-Day Low Flows In The Colorado River Below Glen Canyon Dam, Arizona

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TABLE OF CONTENTS

PAGE

ABSTRACT

We estimated primary productivity and algal and macroinvertebrate biomass at monthly intervals from March through December 1997 in the Colorado River at Lees Ferry, Arizona, 25 km below Glen Canyon Dam. Discharge from Glen Canyon Dam during 1997 was above normal due to high snow pack (~130% of average) in the upper-Colorado River basin. Measurements and collections were taken below baseflow (<142 $m^3 \cdot s^{-1}$) in the river channel and within the varial zone (~400 $m^3 \cdot s^{-1}$) where discharge ranged from 227 to 780 $m^3 \cdot s^{-1}$. The phytobenthic assemblage on cobble was comprised of a mixture of bryophytes, chlorophytes, cyanobacteria, rhodophytes and diatoms which supported a macroinvertebrate community primarily of grazers and collectors.

Net primary production (NPP) estimates were not significantly different between the varial and channel zones ($\underline{x}$ = 0.6 g $O_2 \cdot m^{-2} \cdot h^{-1}$ NPP) from March through August 1997. However, the varial zone had a negative NPP (-0.05 g $O_2 \cdot m^{-2} \cdot h^{-1}$) after a 60% reduction in discharge for 3 d during areal photography of the river channel due to rotting algae. Phytobenthic biomass remained about the same after the reduced discharge, but was not viable. Channel NPP was also reduced by 20%. Recovery was complete within 60 d for both phytobenthic biomass and NPP which was driven by the colonization of periphytic diatoms. In November, a 3-d flow of ~850 $m^3 \cdot s^{-1}$ had no discernable effect on the phytobenthos.

Comparison between turbid and clear site recovery from the 3-d low flow indicated the turbid site was four times as long as the clear Lees Ferry site.

Our study provides evidence that dramatic changes in discharge for terrestrial resource monitoring will have negative impacts on the aquatic food base and that well-defined resource priorities are fundamental to sound ecosystem level management. We conclude that consistent high flows have a positive influence on

the aquatic food base, while short term low flows have protracted negative consequences on the aquatic food base below Glen Canyon Dam.

INTRODUCTION

Discharge manipulation has been described by many authors as the most pervasive aspect of river regulation regarding benthic vitality (Blinn et al. 1995; Petts 1996; Stanford et al. 1996; Valentine et al. 1995). Hydroelectric peaking power dams have not only removed the natural annual hydrograph (Stevens et al. 1997), but have also added variable daily discharges (Angradi and Kubly 1993). This temporal alteration in discharge range has resulted in the recognition that base flows are a critical component of dam operations (Benenati et al 1998; Shaver et al. 1997; Valentin et al. 1995). In natural streams, Statzner and Higler (1986) also argue that hydrologic regime is the most critical abiotic factor structuring stream benthos.

Benenati et al. (1998) reported that periphyton responded positively to continual inundation, but daily fluctuations reduced periphyton biomass below base flow (Also see reviews in Lowe 1979 and Blinn et al. 1998). Benthic macroinvertebrates have been shown to respond positively to increases in baseflow in large rivers (peak flows >1000 $m^3 \cdot s^{-1}$; Weisberg et al. 1990) and in streams (peak flows < 40 $m^3 \cdot s^{-1}$; Malmqvist and Englund 1996; Nymann 1995). Other researchers are investigating the role of regulated discharges across trophic levels through intensive field collections (Shannon et al. 1996; Stevens et al. 1997; Valentin et al. 1995) and with in-situ controlled experiments (Blinn et al. 1995; Petersen and Stevenson 1992; Shaver et al. 1997)

Suspended sediments are also paramount in determining benthic community structure in arid regions (Fisher and Minckley, 1978; Newcombe and MacDonald, 1991). Reduction in photosynthetically available radiation (Davies-

Colley et al., 1992), scour (Shannon et al. 1994) and reduction in diversity through substrate homogeneity (Shaver et al. 1997) are some of the negative features of suspended sediment. Corresponding alterations occur through the food chain with an inverse correlation reported between suspended sediment levels and macroinvertebrate biomass as well as taxa richness (Culp et al. 1986; Stevens et al. 1997a). Tertiary consumers, such as fish (Valdez and Ryle 1997) and water fowl (Stevens et al. 1997b) have also responded negatively to elevated suspended sediments in regards to abundance and diversity.

Many hydrological investigations are concerned with some variation of mean monthly or annual discharges as it relates to benthic community structure (Clausen and Biggs 1998). In the Colorado River below Glen Canyon Dam annual releases are mandated at 8.23 million acre feet (MAF) and may average slightly higher in high run-off years. The average discharge is about 350 $m^3 \cdot s^{-1}$ which is the pre-impoundment average discharge (Stevens et al 1997a). Understanding this artifical ecosystem and its relationship to water hydraulics via dam operations is valuable to the basic understanding of benthic community structure. In this regulated river several factors controlled for. Temperature and annual flow variability are two such parameters. The role of suspended sediments can be examined between adjacent clear and turbid reaches below the confluence of the Paria River (Shaver et al. 1997) We used monthly field collections assessing phytobenthic biomass and productivity along with macroinvertebrate biomass to determine the influence of discharge on the benthic trophic structure in the tailwaters of the Colorado River below Glen Canyon Dam. Collections were made at two stage elevations within the wetted perimeter: below baseflow (<142 $m^3 \cdot s^{-1}$), and within the varial zone (~ 400 $m^3 \cdot s^{-1}$). Discharge ranged from 227 to 780 $m^3 \cdot s^{-1}$. Abrupt changes in the hydrograph by dam operators, in an effort to manage above normal in-flows and for science purposes, provided the predictor for our biotic response variables.

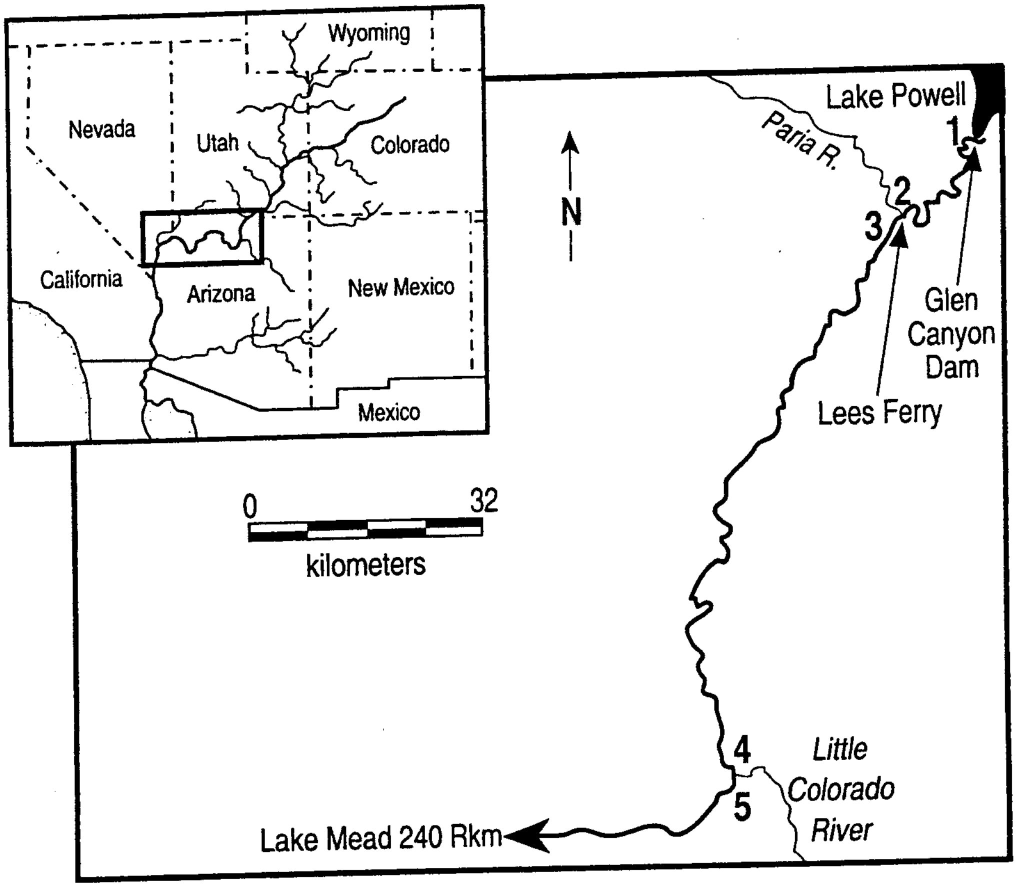
The interactions between suspended sediments, discharge and benthic biomass was examined at three sites down river of Lees Ferry. These sites were periodically turbid from the input of suspended sediments from tributaries during storms, thereby adding turbidity was as a predictor variable.

METHODS

Study Area

Samples were collected from the Colorado River below Glen Canyon Dam which forms Lake Powell, a 300 km long reservoir (Stanford and Ward 1991; Fig. 1). This reach of the Colorado River is influenced by the interaction of hypolimnetic discharges of cold clear water (~10°C) for daily hydroelectric peaking power and monthly water allotments and tributary input of suspended sediments (Blinn and Cole 1991; Shannon et al. 1996, Stevens et al. 1997). As the Colorado traverses the narrow walls of Glen Canyon National Recreation Area and Grand Canyon National Park there is little warming of water even during hot summer months (>35°C air temperature). Stevens et al. (1997) estimated that the Colorado River would have to extend an additional 500 km, given a summer warming rate of 0.023°C/km, to match the pre-impoundment high of 29.5°C. This is not possible because of multiple river impoundments further downstream.

Daily and monthly fluctuations in discharge defines the area of benthic colonization across the channel (Blinn et al. 1995; Hardwick et al. 1992; Usher and Blinn 1992), while spates from tributaries increase the suspended sediment load reducing overall benthic biomass due to abrasion and light attenuation with distance from the dam (Shaver et al. 1997; Stevens et al.1997a). However, recent reductions in daily ramping rates from June 1995 through March 1998 and high



LEGEND

Site	RKM	Collection type	Habitat
1 Glen Canyon Dam Gauge	-23.2	Drift	Clear
2 Lees Ferry	0.8	Drift/Benthic Primary Production	Clear
3 Two-Mile Wash	3.1	Drift/Benthic	Turbid
4 Little Colorado Island	98.6	Drift/Benthic	Turbid
5 Tanner Canyon	109.6	Drift/Benthic	Turbid

Figure 1. Collection sites in the Colorado River below Glen Canyon Dam through Grand Canyon National Park, Arizona. Lees Ferry is designated river kilometer 0.0 (RKM) and Glen Canyon Dam is located 23.2 RKM up-river.

consistent flows (~ 560 $m^3 \cdot s^{-1}$) between months have resulted in greater biomass and biodiversity in the algal and macroinvertebrate community than was described by Stevens et al. (1997) from a 1991 data set. This probably is due to habitat stability and dilution of turbid water (Shannon et al. 1998).

Biotic responses to Glen Canyon Dam include a change from pre-impoundment allochthonous to autochthonous carbon sources primarily from periphyton on cobble bars. After 30 years of phytobenthic dominance by Cladophora glomerata this filamentous green algahas been seasonally replaced by a mixture of bryophytes and filamentous chlorophytes, rhodophytes, and diatoms (Benenati, et al. 1997). This compositional shift is attributed to a combination of factors involving the filling of Lake Powell in 1995, which resulted in a reduction in nutrients, an increased discharge regime, and corresponding change in light availability (Blinn et al. 1998). The secondary producer assemblage is comprised primarily of the amphipod, Gammarus lacustris, a nearctic complex of simuliids and chironomids and trichopteran and gastropod grazers that utilize epiphytic and epilithic diatoms (Shannon et al. 1994; Stevens et al. 1997a). Lumbriculid and tubificid mud-dwelling worms are common in pools and near shore vegetation habitats of Equisetem spp., Phragmites and Carex.

Glen Canyon Dam is operated by the U.S. Department of Interior through the Bureau of Reclamation under guidelines established through an environmental impact study completed in 1995 (U.S. Department of Interior 1995). Operation criteria includes a baseflow of 142 $m^3 \cdot s^{-1}$ and maximum flows of 710 $m^3 \cdot s^{-1}$ with daily fluctuations of 142, 170 or 227 $m^3 \cdot s^{-1}$ depending on monthly water allotments with hourly ramping rates not to exceed 112 $m^3 \cdot s^{-1}$ up and 43 $m^3 \cdot s^{-1}$ down. During this study the maximum flows were exceed twice because an emergency was declared concerning the filling of Lake Powell and dam safety and a third time in an attempt to conserve sand from a Paria River spate (Fig. 2). From 1995 through 1998 dam operators have had to contend with above normal snow packs ranging from 100 to 140% of normal within the Lake Powell drainage basin (USBOR WWW).

Field Data Collection

Phytobenthic and macroinvertebrate samples were collected at four sites using a modified Hess substrate sampler in the varial zone (Fig. 1). These sites bracketed the two largest tributaries; Paria River and Little Colorado River. The varial zone is defined as the channel area that is periodically desiccated or inundated due to dam operations (Stanford and Hauer 1992). The modification consisted of a cloth covering secured over the top of the Hess so that samples could be taken at depths >0.45 m. In order to assess the role of variable discharges, collections were made at two stage elevations within the wetted perimeter i.e., below baseflow or channel (<142 $m^3 \cdot s^{-1}$) and within the varial zone (~400 $m^3 \cdot s^{-1}$). Discharge ranged from 227 to 810 $m^3 \cdot s^{-1}$ during the study (Fig. 2). The Hess substrate sampler was used in the varial zone for both phytobenthic and macroinvertebrate biomass estimates. Collections were taken at approximately monthly intervals for one year starting in March 1997. These samples were placed on ice and sorted within 24 h into the following biotic categories: macroinvertebrates, Cladophora, detritus, and miscellaneous algae/macrophytes/bryophytes (MAMB). These samples were oven-dried at 60°C, weighed to the nearest μg and converted to ash-free dry mass (AFDM) estimates using the results from regression analysis for each category (p <0.001; R^2 >0.85; n=325). Macroinvertebrates were also numerated for Gammarus lacustris, chironomids, simuliids, tubificids, lumbriculids, gastropods and all

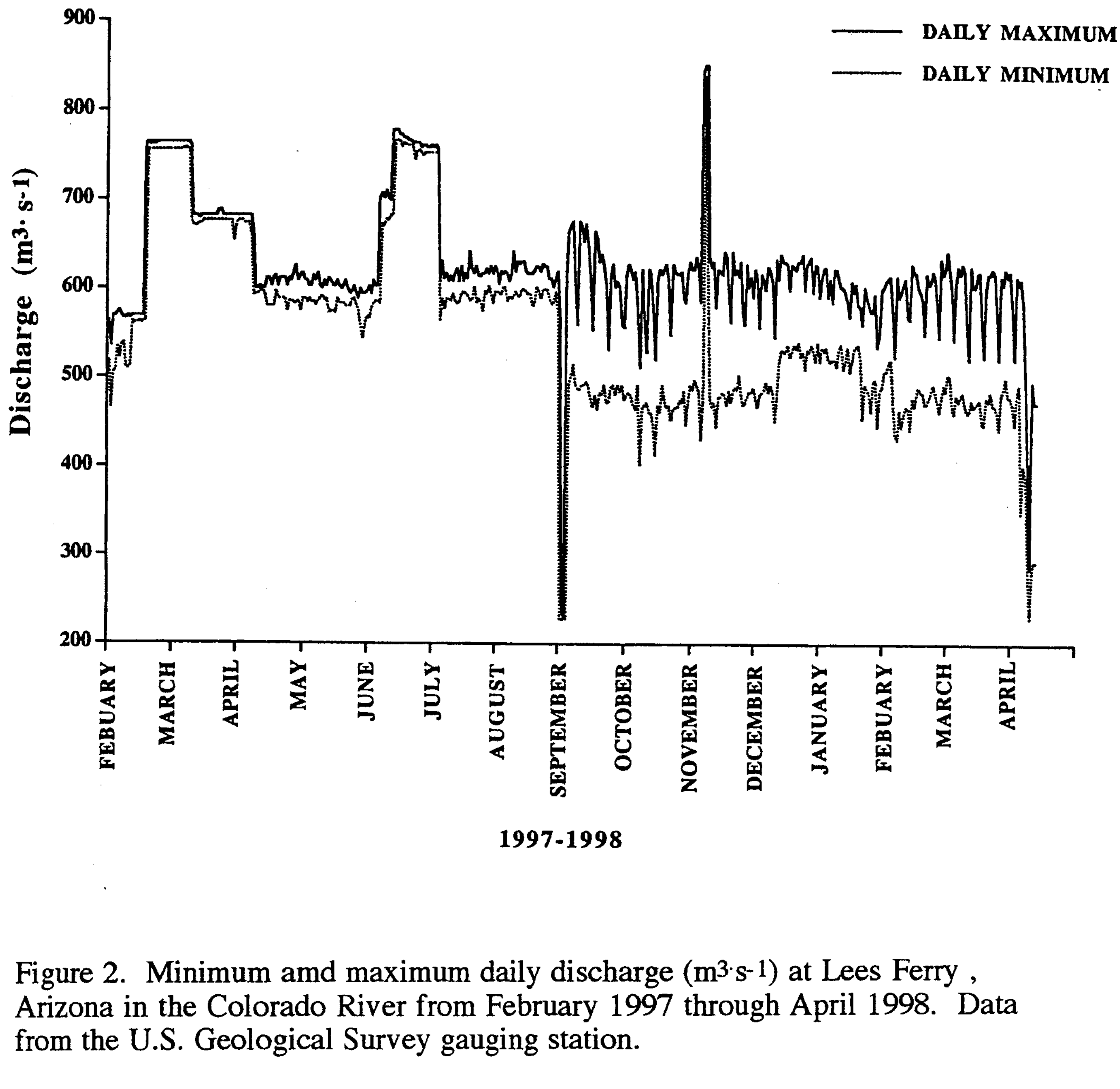


Figure 2. Minimum amd maximum daily discharge ($m^3 \cdot s^{-1}$) at Lees Ferry, Arizona in the Colorado River from February 1997 through April 1998. Data from the U.S. Geological Survey gauging station.

other taxa encountered. See Stevens et al. (1997a) and Shannon et al. (1998) for taxa descriptions.

Primary productivity estimates were taken from cobbles randomly grabbed from the varial zone while cobbles were collected by SCUBA in the channel. Cobbles were held in buckets of river water prior to placement in clear plastic metabolic chambers ($\underline{n} = 3$). Chambers were designed after Bowden et al. (1992) consisting of a plunger made air-tight with a rubber o-ring and a lid to keep water from filling the chamber (dia. 23.5 cm). Each chamber had three air tight ports placed 5 cm above the bottom, two for water circulation via electrical pumps and one for a dissolved oxygen probe (YSI™ Model 55). The circulation pumps maintained a current of 0.2 to 0.3 $m^3 \cdot s^{-1}$, which approximates typical current speeds on the cobble bar (see technique review, Botts et al. 1997). Three liters of river water were added to each chamber along with three cobbles. Each chamber was incubated in daylight in a 164-L cooler with river water and ice to maintain chamber temperatures within 3°C of the ambient river water. The cooler was covered with a black plastic sheet and reflective blanket during the dark treatment to assure total darkness for respiration estimates. Light climate for both daylight and respiration treatments were monitored with a photometer (LiCor™ 250). Trials were run until approximately a 2 $mg \cdot L^{-1}$ change was detected in both light and dark treatments. Ambient light was measured with the photometer during each trial and all trials were conducted between 1000 h and 1500 h and ranged from 505 to 4778 μmols $m^{-2} \cdot s^{-1}$.

After each trial was completed the cobbles were scraped of all periphyton and sorted into the biotic categories listed above for AFDM estimates. Reach-wide calculations followed those outlined by APHA (1992). A trial was run with unfiltered river water to determine if phytoplankton and lotic bacteria would effect the results. We did not detect any net primary production from river water with an average of 0.3 $mg \cdot L^{-1}$ gained and lost during photosynthesis and respiration, respectively.

Organic drift biomass was assessed at each benthic station with an additional site just below Glen Canyon Dam (Fig. 1). Triplicate samples were taken with a circular tow net (48 cm in diam., 0.5 mm mesh) for coarse particulate organic matter (CPOM) at each site. Drift nets were held in place behind a moored pontoon raft or secured to the river bank (0 - 0.5 m depth). Volumetric calculations (mass $\cdot m^{-3} \cdot s^{-1}$) were determined using set duration and velocity with a Marsh-McBirney electronic flow meter.

Water quality was measured at each collection period with a Hydrolab™ H2O multiple parameter probe for the following indicators; temperature (°C), conductivity (mS), pH and dissolved oxygen concentration (mg/l). Light intensity was continously monitored from August 1997 through March 1998 with a HOBO® light intensity logger (Lumens/0.1 m^2) at four stations. These locations correspond with the down river benthic and drift collection sites; Lees Ferry, Two-Mile Wash which bracketed the Paria River and at the gauging station above the Little Colorado River confluence and Tanner Canyon which is below the Little Colorado River confluence. Three loggers were placed at each station one on land that served as control for ambient light and two attached to a chain 50 cm above and below the 227 m^3/s stage. These arrangements allowed for data collection within all ranges of dam operations.

Discharge data from Glen Canyon Dam was retrieved from the U.S. Geological Survey database on the internet from the Lees Ferry gauging station.

Analysis

A mulitivariate approach was used to determine patterns in benthic biomass in response to discharge and suspended sediments. Data were transformed (1+

nlog) to ensure constancy of variance. Biotic response variables, both benthic and drift data, was analyzed with MANOVA to determine response to abiotic variables. Principal component analysis (PCA) was performed on benthic biomass estimates at all sites in an effort to explore whether a combination of abiotic variables best explains the variance in benthic estimates (Clausen and Biggs, 1998). A correlation matrix PCA with varimax rotation created the largest percent of explainable variance.

Light intensity data were reduced to ranked data by calculating the mean for each 55 - 66 d period prior to benthic collection. This was done by taking the daily peak light intensity from all three sensors and determining the percentage of light intensity at each depth from the terrestrial sensor. These two percent values were then averaged and used as the light intensity for that day. This calculation was then averaged across the deployment period to quantify the light regime prior to collecting. This protocol limits the validity of the light information to the immediate area of data logger deployment because of river channel orientation, cloud cover, canyon wall shading and seasonal light patterns.

Discharge values from the United States Geological Survey gauging station at Lees Ferry was used as a direct value at the time of collection. A discharge fluctuation factor (DFF) for the month preceeding collections was calculated by determining the daily discharge range. This simple hydrological value was used to characterize discharge from Glen Canyon Dam instead of the more traditional factors such as flow median and mean (Poff and Ward, 1989) , coefficient of variation (Jowett and Duncan 1990), flood frequency and duration (Fisher and Grimm, 1988; Townsend and Hildrew, 1994) in natural stream studies because this is a regulated river. Blinn et al. (1995) determined that the daily low flow or wetted perimeter defines the area of benthic colonization over a period of several months. Within this study area water velocity changes from hourly, weekly and montly discharge fluctuations which can impact the benthos below baseflow (Statzner et al., 1988; Biggs and Thomsen, 1995). Flooding was not a factor during the sampling period therefore a monthly range of discharge was the chosen hydrologic descriptor.

All calculations and analyses were performed on SYSTAT™ Ver. 5.2.1 software (SYSTAT, Inc., 1992).

RESULTS AND DISCUSSION

Water Quality

Water quality factors were typical of the study site during the period of collection. Water temperture ranged from 8.6 °C at Lees Ferry in October 1997 to 11.8 °C at Tanner Canyon in August 1997 in response to the steady 227 m^3/s discharge. Conductivity increased with distance from Glen Canyon Dam from 0.59 mS in January 1998 at Lees Ferry to 0.89 mS at Tanner Canyon in October 1997. Dissolved oxygen (DO) concentration also increased with distance from the dam and varied seasonally. The DO ranged from 9.09 mg/l in October 1997 at Lees Ferry to 13.41 mg/l in March 1997 at Tanner Canyon.

Light intensity ranged from 1447 lumens /0.1m^2 on the terrestrial sensor in March 1998 at several locations to 0 lumens /0.1m^2 in the water column. Average light intensity for the sampling period was 397 lumens/0.1m^2 on the terrestrial sensor, 120 lumens / 0.1m^2 at 0.5 m above the 227 m^3/s stage and 34 lumens /0.1m^2 at 0.5 m below 227 m^3/s stage. Discharge fluctuation factor (DFF) ranged from a low of 42 m^3/s in June 1997 to 380 m^3/s in October 1998. Depth of benthic collections ranged from 0.2 to 1.5 m while water velocity ranged from 0.1 to 1.7 m/s.

Lees Ferry Primary Production

Primary productivity varied in response to discharge and collection site (Table 1). The highest net primary productivity (NPP) occurred in April for both varial (1.83 g $O_2 \cdot m^{-2} \cdot h^{-1}$) and channel (1.11 g $O_2 \cdot m^{-2} \cdot h^{-1}$) estimates (Fig. 3). This was the only time the varial zone had greater NPP than the channel and coincides with the first emergency high discharge of a steady 780 $m^3 \cdot s^{-1}$ in March (Fig. 2) These estimates for each collection site are an order of magnitude higher than previously reported for this reach using the same protocol (Blinn et al. 1998). Blinn et al. (1998) reported NPP of 0.40 g $O_2 \cdot m^{-2} \cdot h^{-1}$ from the varial zone in August 1995 and 0.17 g $O_2 \cdot m^{-2} \cdot h^{-1}$ in the channel.

Angradi and Kubly (1993) reported gross primary productivity (GPP) of 5 g $O_2 \cdot m^{-2} \cdot h^{-1}$ in 1991 from the channel 2 km below Glen Canyon Dam. This is 3-fold higher production than we estimated (1.5 g $O_2 \cdot m^{-2} \cdot h^{-1}$) in 1997 and may be due to several factors. Variation in methodology can make cross comparison difficult when using metabolic chambers (Botts et al. 1997). Angradi and Kubly's sites were closer to the dam which may have increased nutrient availability. Also, estimates for algal biomass were derived differently. They used algal AFDM scrapings from 35 cm^2 templates which may have inflated their estimates (148 g AFDM$\cdot m^{-2}$) due to the patchy nature of the benthos (Stevens et al. 1997). Our algal AFDM estimates (63 g AFDM$\cdot m^{-2}$) were from Hess samplers (0.1 m^2) and provide a reach-wide estimate that takes into account the area between cobbles.

Jonsson (1992) reported a NPP of 0.005 g $O_2 \cdot m^{-2} \cdot h^{-1}$ for Cladophora in Lake Thingvallavataan, Iceland which has a summer maximum of 10.5°C and similar light intensity as Lees Ferry. In a cool desert stream in Idaho, Minshall

Table 1. Analysis of variance for primary productivity estimates in the Colorado River at Lees Ferry, Arizona from March 1997 through December 1998. Collection date and location significantly influenced primary productivity with the peak in NPP corresponding with highest and most steady flows from Glen Canyon Dam in March and April.

Source	df	MS	F	P
Collection Location	1	0.065	6.43	0.015
Collection Date	7	0.168	16.52	0.000
Location X Date	7	0.054	5.37	0.000

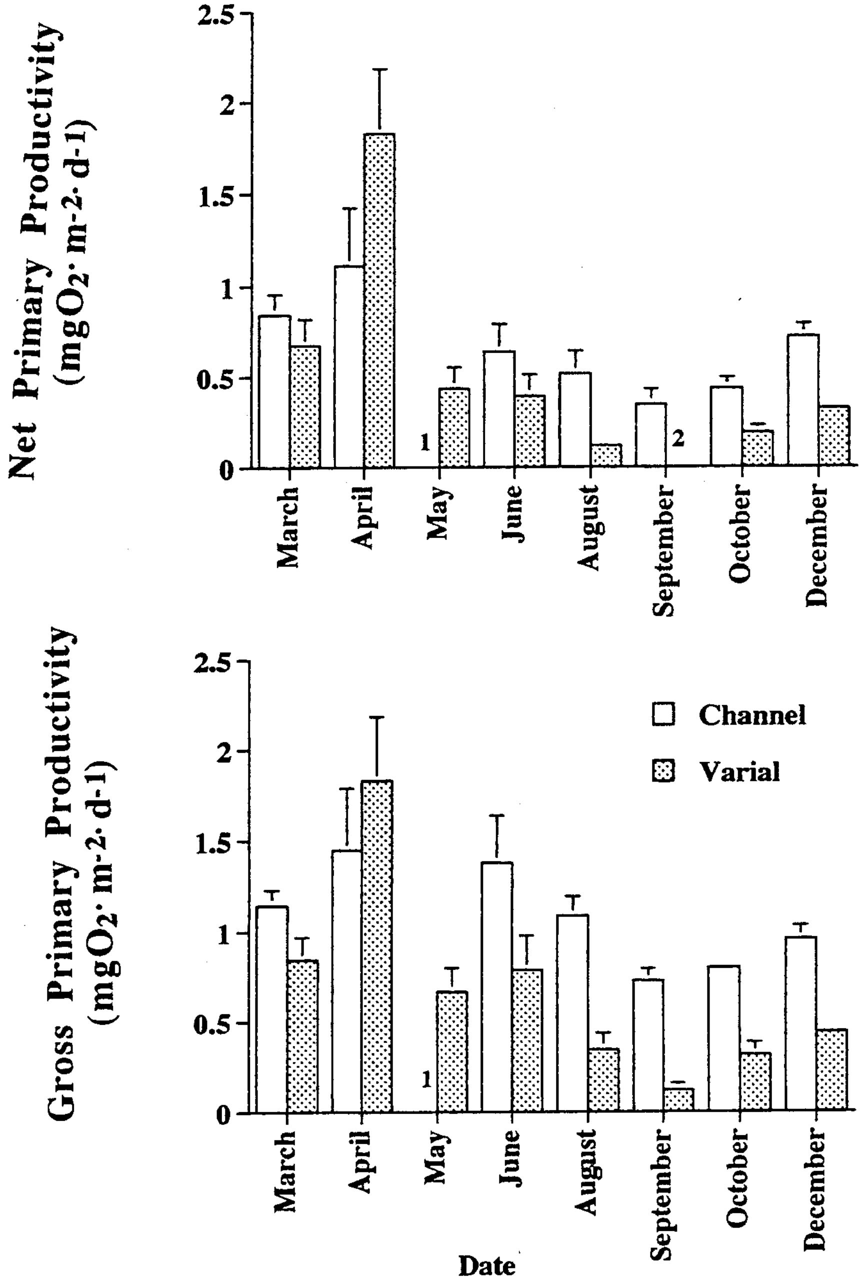


Figure 3. Net and gross primary production estimates at Lees Ferry in the Colorado River from March to December 1997. Two habitats were examined, below baseflow (channel) and within the channel margin above baseflow (varial). August estimates were prior to the 3-d flow of 227 $m^3 \cdot s^{-1}$. (1) no channel collection in May. (2) respiration exceeded production. ($\pm$ 1 SE).

(1978) reported a NPP range of 0.41 to 1.33 g $O_2 \cdot m^{-2} \cdot h^{-1}$, while Bott (1983) estimated NPP from 1.0 to 3.2 g $O_2 \cdot m^{-2} \cdot h^{-1}$ in a similar habitat.

Primary productivity was negatively affected by the 3 d of reduced steady flows (227 $m^3 \cdot s^{-1}$) conducted for areal photography of the river channel from 30 August through 1 September (Fig. 3). NPP for the varial zone in August was 121 (± 25) g $O_2 \cdot m^{-2} \cdot h^{-1}$ compared to a negligible NPP in September. Based on conversion values from Cole (1994), we estimated that 0.05 g $C \cdot m^{-2} \cdot h^{-1}$ was lost as a result of this 3 d draw down. The reduced steady flows exposed the varial zone for 3 d under cloudy skies with light rain which probably dampened the impacts of atmospheric exposure. Although there was 17 g $AFDM \cdot m^{-2}$ of phytobenthos in the varial zone, it was decomposing. Even the channel NPP estimates were impacted by the 3 d draw down as evidenced by a 33% reduction in biomass between August and September. This pattern is supported by Benenati et al. (1998) in a phytobenthic recolonization study at Lees Ferry where controls placed in the channel lost biomass after a similar period of low flow. Recovery of NPP for both the channel and varial collections was complete by October 1997 or within 45 d (Fig. 3).

The loss of NPP in the varial zone in June may be attributed to monsoon storms that created arroyo flash floods and over-land flow delivering suspended sediments into the water column between the Glen Canyon Dam and Lees Ferry (K. Wilson pers. observations). This suggests that a low flow for areal photography during the annual monsoon season, which commonly extends through August, only adds additional stress to the tailwater food base and is not conducive to quality areal photography.

Lees Ferry Phytobenthic Biomass

Phytobenthic estimates varied significantly ($p<0.01$) between collection date and location (Fig. 4). Maximum phytobenthic biomass was not reached until August in the channel. However, the varial zone peaked in April, exceeding channel estimates in the channel and equalling NPP data. The maximum phytobenthic biomass in the channel can be explained by following the summer solstice and the August estimate was statistically the same as June and September. The August drawn down had more of an impact on channel NPP than on phytobenthic biomass with no significant decrease until December.

The varial zone had 17 g AFDM$\cdot$m^{-2} in September, 12.5 g AFDM$\cdot$m^{-2} in October and 12 g AFDM$\cdot$m^{-2} in December, but NPP increased through this period. This increase in NPP probably resulted from epiphytic and epilithic diatoms that colonized the cobbles and rotting algae. Diatoms are capable of high rates of photosynthesis even in the waning light regime of fall because of their accessory photosynthetic pigments; chlorophyll A, C_1, C_2 and fucoxanthin (Sze 1993). This may also explain the high NPP estimates in March and April, while phytobenthic biomass was relatively low. Epilithic biofilms can account for the majority of primary production in clear low order streams (Naiman 1983). Guacsh and Sabater (1998) documented biofilm primary production of 0.1 to 0.006 g $O_2\cdot m^{-2}\cdot h^{-1}$ in two second order streams in NE Spain.

Phytobenthic composition followed the pattern described by Benenati (1997) of increasing Cladophora biomass through June replacing MAMB which dominated from March until June. This was particularly evident in the varial collections where MAMB made up 80% of the biomass in March and 10% in June, while the channel followed the same overall pattern. MAMB never exceeded 55% of the assemblage.

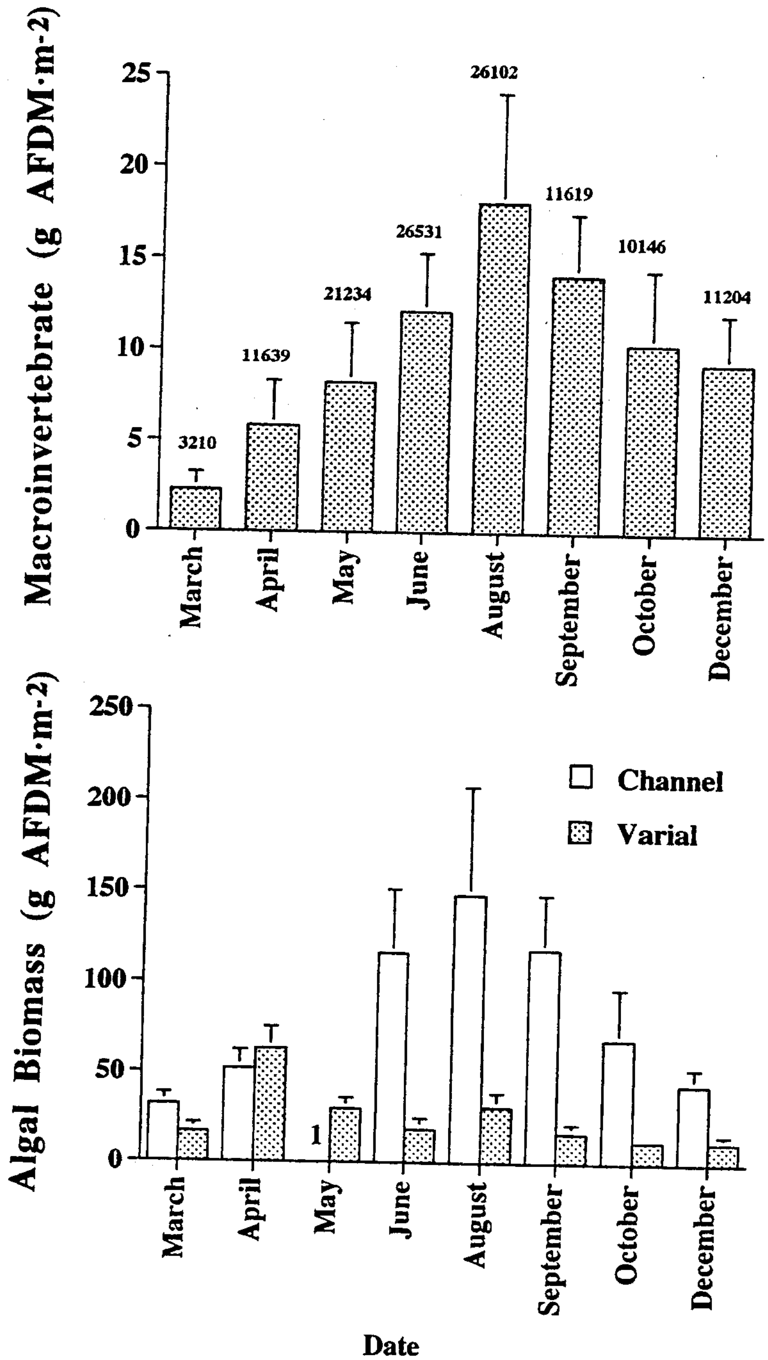


Figure 4. Algal and macroinvertebrate biomass estimates (g AFDM·m^{-2}) at Lees Ferry Arizona in the Colorado River. Two habitats were examined, below baseflow (channel) and within the channel margin above baseflow (varial) for algal biomass estimates. August estimates were prior to the three day flow of 227 $m^{3} \cdot s^{-1}$. Numbers above bars indicate abundance of macroinverterbates (#·m^{-2}) (1) no channel collection in May. ($\pm$ 1 SE).

Lees Ferry Macroinvertebrate Biomass and Density

Varial zone macroinvertebrate biomass varied significantly ($p<0.01$) through the study period reaching a peak of 18.1 g AFDM·m^{-2} in August (Fig. 4). This is the maximum macroinvertebrate biomass reported for the Lees Ferry reach. Previously, Stevens et al. (1997) reported 3.6 g AFDM·m^{-2} in 1991 and Shaver et al. (1997) found >3.0 g AFDM·m^{-2} in 1994, probably due to the relatively consistent flows since 1995. Macroinvertebrate biomass more closely followed a seasonal growth pattern of channel periphyton than the varial zone periphyton (Figs. 3 and 4). This pattern may be explained by the close relationship between Cladophora and macroinvertebrate biomass (Shannon et al. 1994). Cladophora is the structural host for epiphytic diatoms which provides food for grazers and shelter from current and predators. However, the majority of the macroinvertebrate biomass is made up of snails (Physella sp. and Fossaria obrussa). Starting in April, snails composed 50% of the biomass and peaked in September at 90% of the biomass (Fig. 4). Although the rapid recolonization of snails is a positive step in the colonization of the varial zone, these invertebrates apparently provide limited energy to upper trophic levels in the Colorado River food web, because <1% of the trout diet at Lees Ferry is made up of snails (Department of Arizona Game and Fish; pers. comm. 1998). Snails are early colonizers after a disturbance such as desiccation (Blinn et al. 1995). They graze on the microbial biofilm on cobbles and decomposing filamentous algae in the Lees Ferry reach. Snails also tolerate atmospheric exposure better than other invertebrates because they can seek refuge in their shell. Therefore, if snails were disregarded and only chironomids, Gammarus, oligochaetes and other invertebrates were considered, complete recolonization by the original assemblage would not have occurred until December.

The 3 d flow of ~850 $m^3 \cdot s^{-1}$ on the November 3, 4 and 5 November did not have any discernible impact on the benthos at Lees Ferry, Arizona.

Interaction of Discharge and Suspended Sediments

Benthic biomass estimates at the turbid down river collection sites varied significantly (MANOVA; $p < 0.001$) by collection trip, site, daily fluctuation factor (DFF) and light (Table 2). Not all biotic categories responded the same to each of these abiotic predictor variables with detritis and Oscillatoria AFDM estimates the most stable. Cladophora, MAMB and macroinvertebrate AFDM estimates all responded to the four abiotic variables in the same pattern. All were negatively correlated with distance from the dam and increasing DFF, positively correlated with light intensity with corresponding seasonal peaks in AFDM estimates.

Benthos down river of the Paria River were negatively impacted by the combination of hydrologic variability and suspendend sediments reducing benthic biomass and recovery after the 3-d low flow (Fig. 5 -7). Impact of the 3-d low flow in August 1997 reduced all biotic categories in the varial zone by at least 50% for primary producers and > 90% for macroivertebrates. The benthic biomass at these down river sites peaked in June/August prior to the 3-d low flow then showed variable recovery through the winter. We estimate benthic recovery in the varial at these turbid sites took ~ 200 d or four times as long as the clear Lees Ferry site (~ 45 d). These turbid sites are important habitats for native fish such as the flannelmouth sucker (Catostmous discobolus) which inhabitats the area around the Paria River confluence and is represented by the Two Mile Wash site (Valdez and Ryel 1995). Little Colorado River Island and Tanner Canyon sites are within the critical habitat reach for the endangered native humpback chub (Gila cypha) as designated by the U. S. Fish and Wildlife Service.

Table 2. Results of MANOVA for benthic biomass estimates from three turbid water sites in the Colorado River through Grand Canyon National Park. Biotic response variables were Cladophora (C), miscellaneous algae, macrophytes and bryophytes (M), Oscillatoria (O), detritus (D) and macroinvertebrate (B) biomass estimates. Overall these benthic categories varied with collection location, date of collection, discharge fluctuation factor (DFF), and turbidity.

Source	Wilks' Lambda	Approximate F-Statistic	df	p	Significant Response Variable
Collection Location	0.57	9.89	10,310	<0.000	C,M,D,B
Collection Date	0.23	4.90	50,673	<0.000	C,M,B
DFF	0.24	4.86	50,673	<0.000	C,M,B
Turbidity	0.29	3.61	40,443	<0.000	C,M,O,D,B

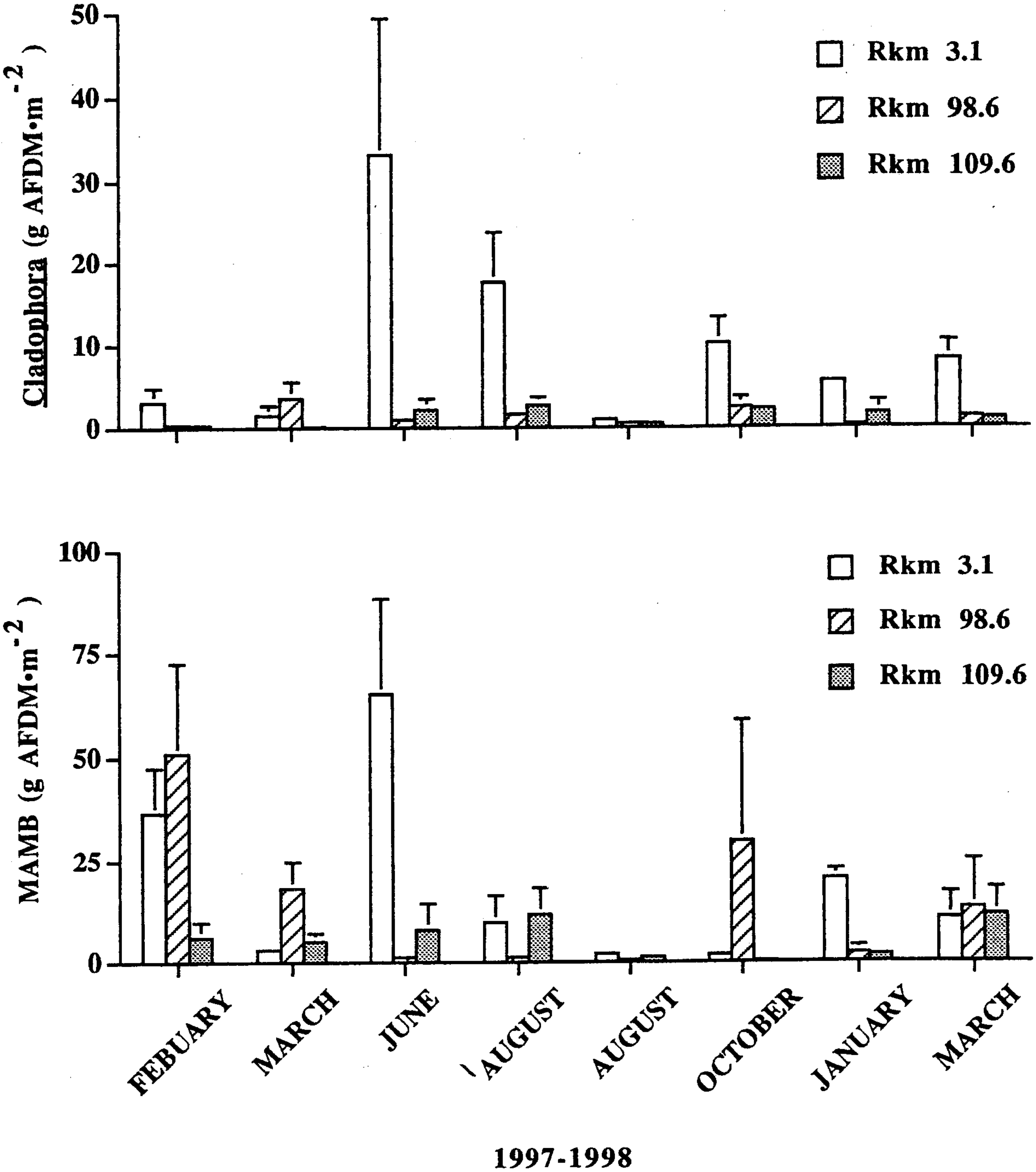


Figure 5. Miscellaneous algae, macrophytes and bryophyte (MAMB) and <u>Cladophora</u> biomass estimates (g AFDM·m^{-2}) at three sites in the Colorado River from February 1997 to March 1998. [1]August estimates were prior to the three day flow of 227 m^{3}·s^{-1}. (± 1 SE).

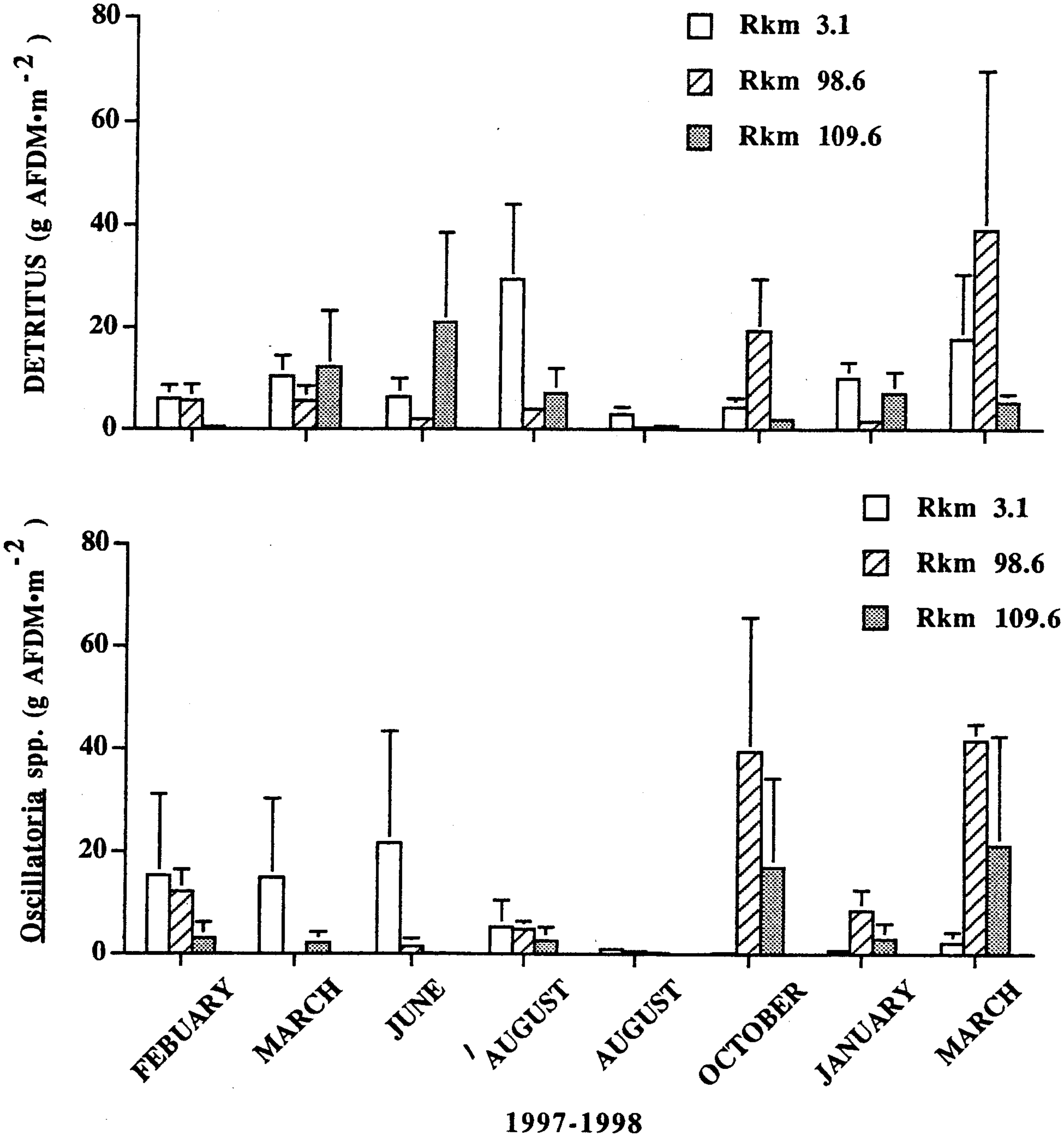


Figure 6. Oscillatoria and detrital biomass estimates (g AFDM·m^{-2}) at three sites in the Colorado River from February 1997 to March 1998. [1]August estimates were prior to the three day flow of 227 m^{3}·s^{-1}. ($\pm$ 1 SE).

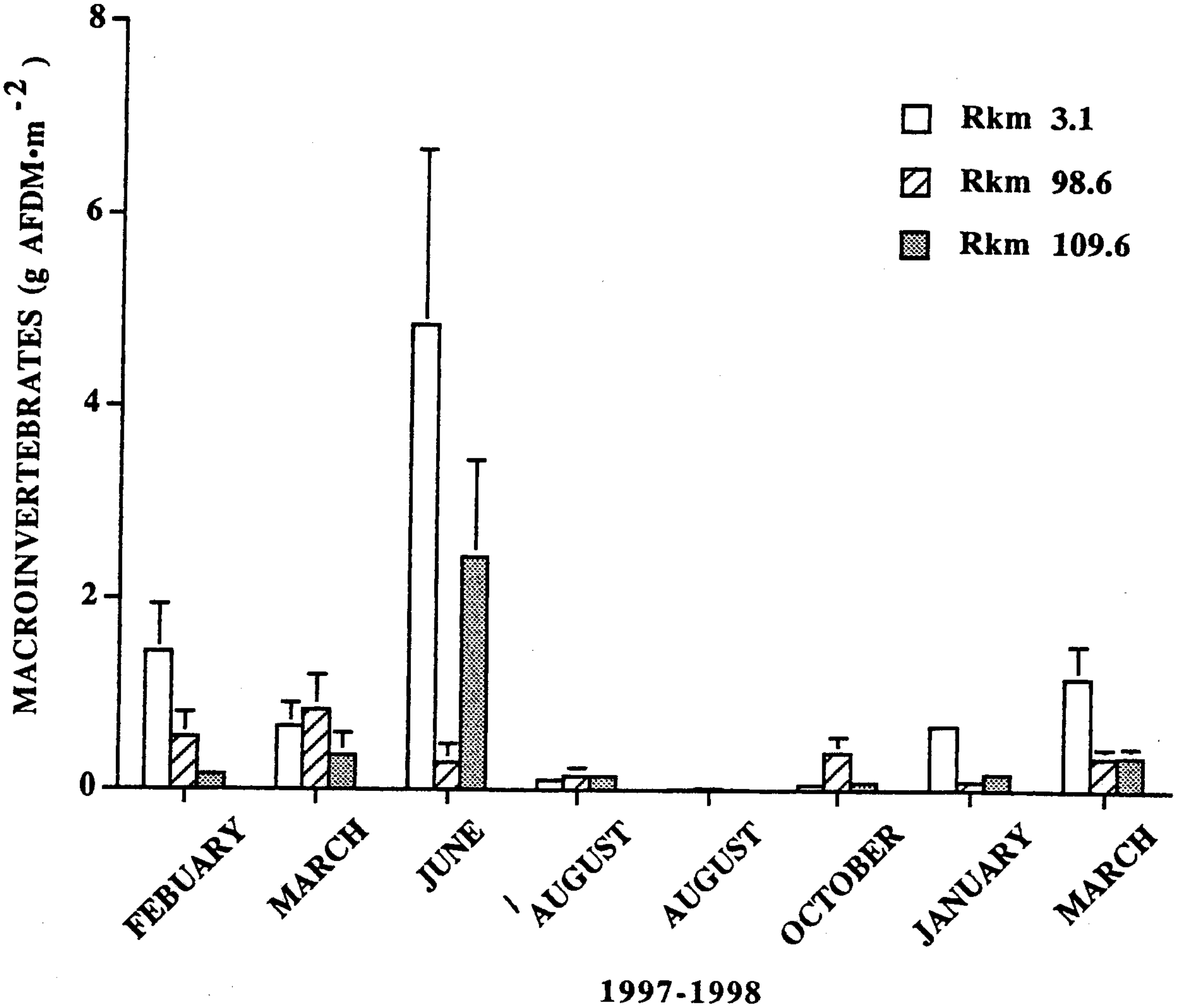


Figure 7. Macroinvertebrate biomass estimates (g AFDM·m^{-2}) at three sites in the Colorado River from February 1997 to March 1998. [1]August estimates were prior to the three day flow of 227 m^3·s^{-1}. ($\pm$ 1 SE).

Biomass estimates during this period of collection were the greatest reported for the down river sites and probably results from limited fluctuations in discharges starting in 1995. The Paria River was in spate periodically in August 1997 and several convective storms also resulted in overland flow throughout the reach between GCD and Lees Ferry. The accompanying suspended sediments from these events reduced benthic biomass prior to the 3-d low flow.

Cladophora biomass followed a similar patterns as the macroinvertebrates showing positive increases between the two time periods, 1991 and 1997-1998; Two-Mile Wash (94%), LCR Island (68%) and Tanner Canyon (99%). Oscillatoria biomass was more variable with a decrease of 24% at Two-Mile Wash which from an energetics stand point is a favorable change due to it's lack of vertical structure and low epiphytic diatom assemblage (Shaver et al. 1998; Blinn et al 1995). MAMB was not documented in 1991 by Stevens et al. (1997a) due to low biomass. MAMB biomass was on the average 54% higher than Cladophora at the three down river sites. MAMB is positively correlated with lower GCD discharges (Shannon et al. 1998)

Macroinvertebrate biomass ranged from < 0.01 to 4.87 g AFDM/m^2 at Two-Mile Wash averaging 2.13 (SE $\pm$ 0.76) g AFDM/m^2 which is an 80% greater than the 0.50 ($\pm$ 0.23) g AFDM/m^2 that Stevens et al. (1997) reported for 1991 bimonthly collections. Macroinvertebrate biomass also increased at LCR Island (95%) and Tanner Canyon (99%) in comparison to the 1991 data reported by Stevens et al. (1997a). Numerically gastropods did not contribute to the biomass of the macroinvertebrates at the down river sites as they did at Lees Ferry. Chironomids were the dominate taxa in the turbid study sites averaging 1638/m^2 ($\pm$ 514) peaking in June at Two Mile-Wash with 12,164/m^2. This reduction in gastropod numbers is probably a result of the turbidity in the down river sites decreasing the feeding effiecency of these grazers.

Recovery in the down river turbid sites results not just from the suspended sediments but also because of the reduce benthic biomass as a source for recolonization (Fig. 8). Shaver et al (1997) through a series of desiccation and translocation experiments between clear and turbid habitats near Lees Ferry reported that recovery was 5 times faster within in the within the clear habitats than the turbid habitats. These recovery rates are similar to those in this investigation. Sources of recolonization for recovery from disturbance is from local benthic regions. Shannon et al. (1996) deterimined that drifting macroinvertebrates do not travel far because of the molar action of hydraulics within in the rapids Turbid sites probably have less than a 30% of the benthic area available for recolonization of the varial zone, in comparison to the clear water benthic pool below baseflow (Fig. 8). Below baseflow average total benthos at Lees Ferry in August 1998 was 16.12 g/m^2 and the turbid sites were less with 7.90 and 12.67 g/m^2 at Little Colorado Island and Tanner Canyon, respectively. Although the difference between clear and turbid habitats is small in terms of biomass the productive benthic area difference is large because of reduced light availibilty in the turbid sites. The benthos cannot survive at the same depths in turbid water as compared to clear and therefore is limited to a smaller band along the channel margin.

Organic Drift

Coarse particulate organic matter (CPOM) drift varied by collection site, and date and in response to the three flow of 227 $m^3 \cdot s^{-1}$ (Table 3). This varibality in drift is a reflection of the benthic biomass patterns. The seasonal changes in drift and differences between sites follows the same pattern as reported by Shannon et al. (1996) for 1993 and 1994.

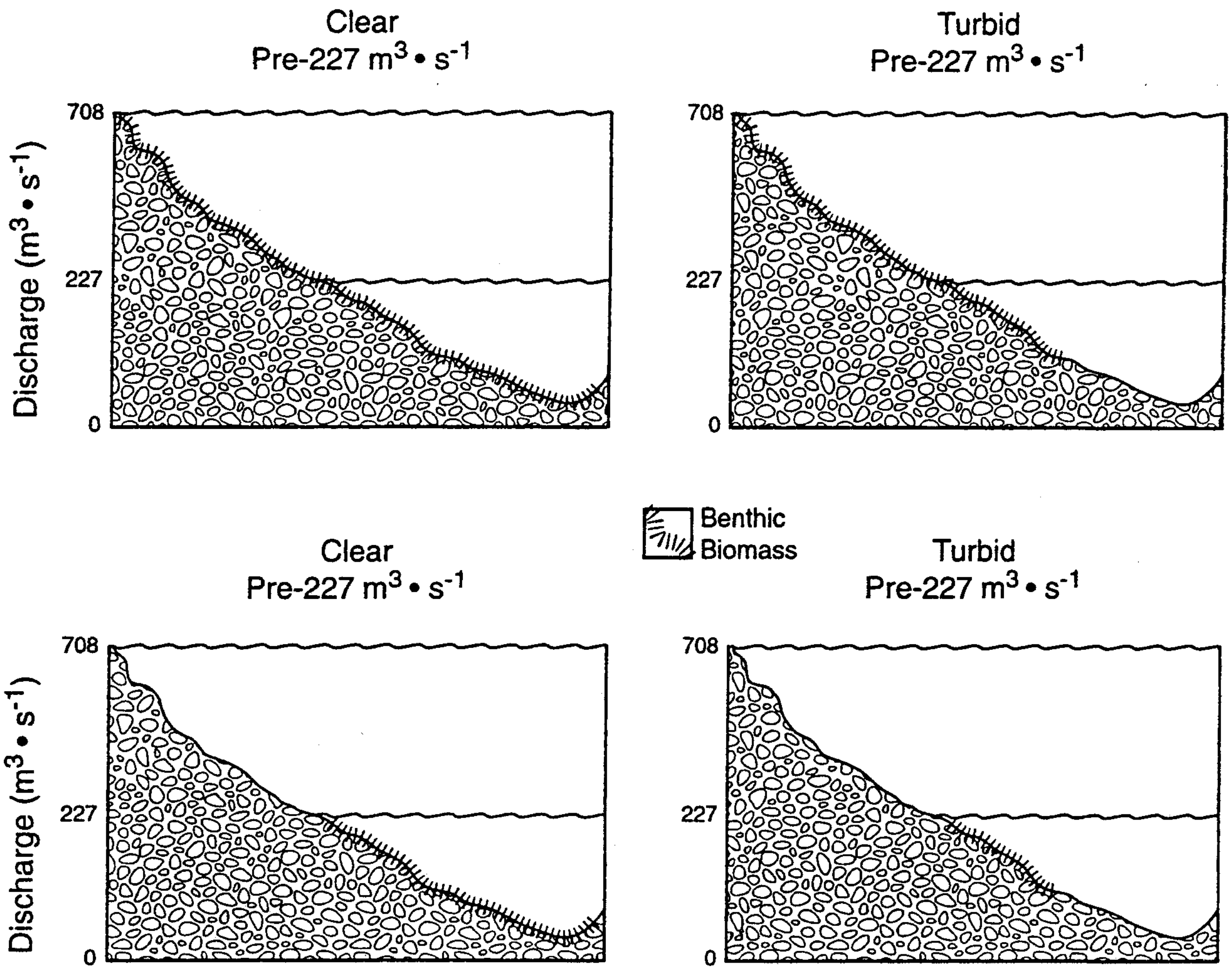


Figure 8. Conceptual illustration of benthic distribution between a clear and turbid water habitat. The pre-227 $m^{-3} \cdot s^{-1}$ diagrams have flows of 708 $m^{-3} \cdot s^{-1}$ and show benthic cover through the channel in the clear habitat and a reduced benthic cover deep in the channel in the turbid habitat because of light attenuation and scouring by suspended sediments. The post-227 $m^{-3} \cdot s^{-1}$ diagrams have flows of 708 $m^{-3} \cdot s^{-1}$ and shows benthic cover has been eliminated from the channel above the 227 $m^{-3} \cdot s^{-1}$ stage elevation for both habitats. Recolonization into the varial zone above the 227 $m^{-3} \cdot s^{-1}$ stage elevation will occur faster in the clear habitat because there is a greater benthic nucleus than in the turbid habitat.

Table 3. Results of MANOVA for organic biomass estimates from five sites in the Colorado River through Grand Canyon National Park. Biotic response variables were Cladophora (C), miscellaneous algae, macrophytes and bryophytes (M), detritus (D), aquatic diptera (A), Gammarus (G) and macroinvertebrate (B) biomass estimates. Overall these benthic categories varied with collection location, date of collection, and between pre-and post 3 d of 227 $m^3 \cdot s^{-1}$ flows in August 1997.

Source	Wilks' Lambda	Approximate F-Statistic	df	p	Significant Response Variable
Collection Location	0.23	4.40	60,817	<0.000	C,D,A,B
Collection Date	0.33	3.15	60,817	<0.000	C,M,D,B
3 d 227 $m^3 \cdot s^{-1}$	0.85	4.76	6,164	<0.000	A,D

However, Cladophora, miscellaneous macroinvertebrates, and MAMB have all increased during this study probably in response to the reduced DFF. Average Cladophora biomass in the drift during this study period was higher (0.025 g $\cdot m^{-3} \cdot s^{-1}$AFDM) than the highest reported by Shannon et al. (1996) in 1994 (0.015 g $\cdot m^{-3} \cdot s^{-1}$AFDM). The peak Cladophora biomass 1997-1998 was 0.412 ($\pm$ 0.008; g $\cdot m^{-3} \cdot s^{-1}$AFDM) in August 1998 at Lees Ferry before the 3- d steady flow of 227 $m^{-3} \cdot s^{-1}$. In 1993-1994 miscellaneous macroinvertebrates and aquatic diptera biomass contribution to drift was always < 0.0002 g $\cdot m^{-3} \cdot s^{-1}$AFDM. Miscellaneous macroinvertebrates and aquatic diptera were higher in 1997-1998 with a mean of 0.00046 g $\cdot m^{-3} \cdot s^{-1}$ AFDM and peak of 0.00734 g $\cdot m^{-3} \cdot s^{-1}$ AFDM for miscellaneous macroinvertebrates and an a mean of 0.00040 g $\cdot m^{-3} \cdot s^{-1}$ AFDM and peak of 0.00228 g $\cdot m^{-3} \cdot s^{-1}$ AFDM for aquatic diptera. These results indicate how reduced daily fluctuations in flow can not only increase drifting organic matter, but increase in biotic richness in organic drift.

Daily flow fluctucation has been reported by Anagradi (1994) and Valdez and Ryle (1997) as a positive attribute which can enhance the amount of CPOM drift below a hydropower dam. However, during this study period we determined that with a reduced daily fluctuation and an increase in benthic productivity high drift rates can be achieved without the habitat degradation of high daily flow fluctuation. Drift induced by daily flow fluctuation probably reduces resilance of the benthos to recovery from disturbance such as a 3-d low flow through depelting local benthic stocks. This may explain the negative impact that the highly variable research flows in 1991 (Patton, 1991) had the benthic commuity (Stevens et al. 1997a).

The 3-d low steady flow had an inverse affect on CPOM drift biomass for aquatic diptera and detritus (Table 3). Aquatic diptera biomass in the CPOM drift was 60% higher prior to the 3-d steady flow, while detritus was 70%

higher after the 3-d steady flow. The aquatic diptera biomass peak occured in April and May during a period of low daily flow fluctuations (DFF of 76; Fig. 2). This further supports the positive result of low daily flow fluctuations. Detritus increased during the period of highest daily flow fluctuation (DFF of 353 - 380) in September and October 1998 but dropped in November as this CPOM was flushed through the study site.

Principal Component Analysis Summary

Many patterns relating hydraulics, turbidity and benthic biomass have been presented from this study. As a way of summarizing the patterns in this study we ran PCA on the benthic data and the primary abiotic factors (Fig. 9). Factor one explains 25% of the variance and illustrates the correlation between Cladophora, MAMB, macroinvertebrate biomass and the abiotic factors of turbidity and daily flow fluctuations which change with collection site. Oscillatoria and detritus are related to velocity at the time of collection and only slightly by depth. Factor two explains 16% of the variance and how collection date and discharge are unrelated because you can have repeated disharges at the time of collection. These is further support that the interaction of daily flow fluctuation and suspended sediments have major roles in the benthic community structure of the Colorado River through Grand Canyon National Park.

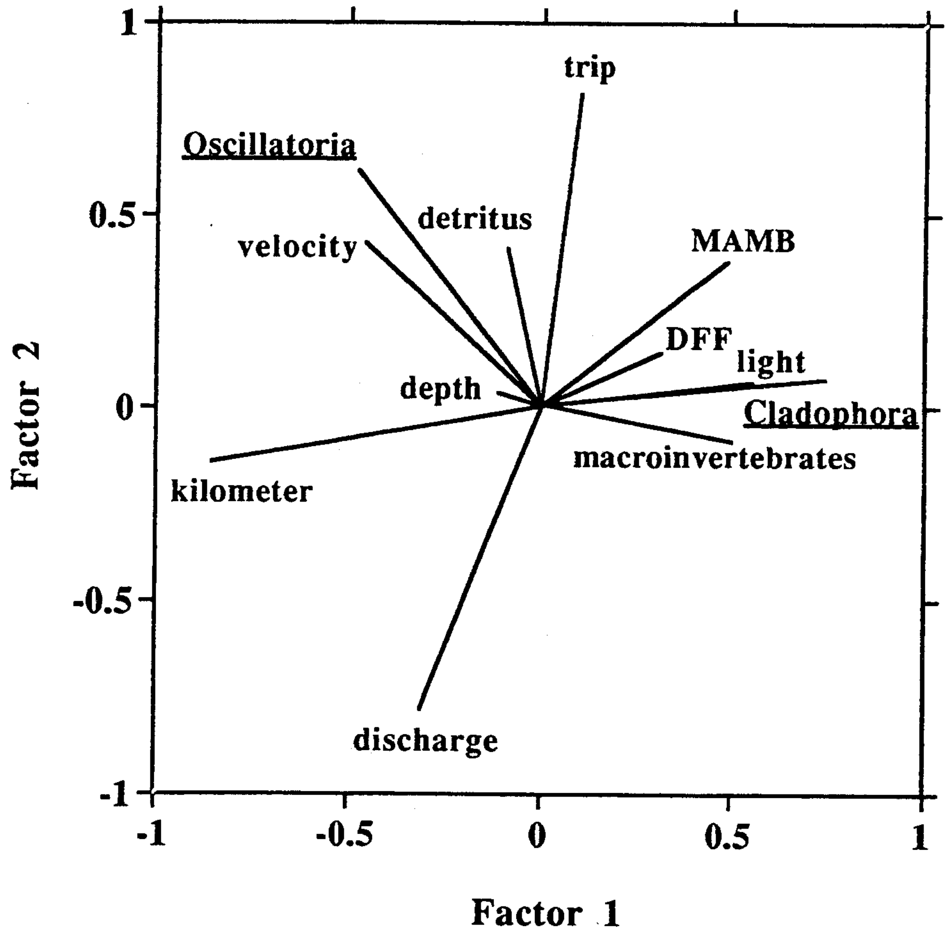


Figure 9. Principal component analysis (PCA). Factor one explains 25% of the variance and illustrates the correlation between Cladophora, MAMB, macroinvertebrate biomass and the abiotic factors of turbidity and daily flow fluctuations which changes with collection site. Factor two explains 16% of the variance and how collection date and discharge are unrelated because you can have repeated disharges at the time of collection. This PCA is further support for the interaction of daily flow fluctuation and turbidity as a function of suspended sediments and benthic community structure.

CONCLUSIONS

Analyses of monthly collections of the aquatic benthos at two stage elevations at Lees Ferry, AZ, below Glen Canyon Dam on the Colorado River indicated that dam releases have positive and negative impacts. The high steady flows in winter and early summer (~760 $m^3 \cdot s^{-1}$) in conjunction with flows averaging 580 $m^3 \cdot s^{-1}$ with little daily fluctuations provided favorable conditions for phytobenthos and macroinvertebrate growth. However, a 3 d draw down (227 $m^3 \cdot s^{-1}$) in August 1997 for resource surveillance negatively impacted the benthos and took more than 45 d for recovery. Areal surveillance as a monitoring tool should not compromise aquatic resources especially since these food resources may be critical to threatened native fishes that occupy downstream habitats. We recommend these photographic surveillance flights be conducted at the prevailing discharge if they are to be sustain after the surveillance. During normal release years (8.23 maf) the over flight should coincide with months that the daily flows are close to 127 $m^3 \cdot s^{-1}$ such as May or October. The increase in daily fluctuations after the drawn down is also disruptive to the benthic habitat. High discharges with daily fluctuations of 200 $m^3 \cdot s^{-1}$, although within current operation criteria, are too energetic and unstable. These flows are slowly eroding the favorable habitat that dam operations provided from June 1995 to August 1997.

Impact of the 3-d low flow in August 1997 reduced primary producers biomass by at least 50% and > 90% for macroinvertebrates within the varial zone. The benthic biomass of these down river sites peaked in June/August prior to the 3-d low flow then showed variable recovery through the winter. We estimate that varial zone benthic recovery at these turbid sites (~ 200 d) took four times as long as the clear Lees Ferry site (~ 45 d).

Daily flow fluctucation has been reported by Anagradi (1994) and Valdez and Ryle (1997) as a positive attribute which can enhance the amount of CPOM drift below a hydropower dam. However, we determined that reduced daily fluctuations and high benthic productivity induce high drift rates without the habitat degradation of high daily flow fluctuation.

This study was done with additional funding to the NAU Aquatic Food Base Program from the Grand Canyon Monitoring and Research Center and clearly demonstrates the need for investigative work beyond annual monitoring protocols when novel changes in dam operations are announced.

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