# INTERIM FLOW EFFECTS FROM GLEN CANYON DAM ON THE AQUATIC FOOD BASE IN THE COLORADO RIVER IN GRAND CANYON NATIONAL PARK, ARIZONA: 1993 DRAFT ANNUAL REPORT


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IN COOPERATION WITH
THE GLEN CANYON ENVIRONMENTAL STUDIES PROGRAM
NATIONAL PARK SERVICE COOPERATIVE AGREEMENT CA 8024-8-0002


31 December 1993


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IA. COOPERATIVE AGREEMENT: CA 8024-8-0002

NAME: QUARTERLY MANAGEMENT AND TECHNICAL REPORT

PRINCIPAL INVESTIGATORS: DEAN W. BLINN and LAWRENCE E. STEVENS

GOVERNMENT TECHNICAL REPRESENTIVE: PETER ROWLANDS

SHORT TITLE OF WORK: THE ECOLOGY OF THE AQUATIC FOOD BASE IN THE COLORADO RIVER.

EFFECTIVE DATE OF COOPERATIVE AGREEMENT: 13 AUGUST 1992

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## II. INTRODUCTION:

Growing concern over the impacts of river regulation on environmental resources in the Colorado River corridor below Glen Canyon Dam prompted the Department of the Interior to develop the Bureau of Reclamation's Glen Canyon Environmental Impact Statement. Following completion of GCES Phase I, the National Academy of Science recommended that further studies integrate interactive phenomena and processes at the ecosystem level in this system (GCES Phase II). The algae and macroinvertebrates provide an important food base for fish and terrestrial fauna and link the aquatic and terrestrial components of the ecosystem. This study of the aquatic food base in the Colorado River was designed to further monitor the effects of discharge on aquatic primary producers and primary consumers in the Colorado River corridor downstream from Glen Canyon Dam through the study objectives.

### II A. MAJOR ACCOMPLISHMENTS DURING THIS QUARTER:

See enclosed Annual Report

### II B. PROBLEMS ENCOUNTERED:

No problems were encountered during this quarter.

### II C. FISCAL STATUS:

1. Cooperative Agreement Amount: $84,864 (FY92) + $171,736 (FY93) +$143,232 (FY94) TOTAL: $399,832

2. Expenditures and Commitments to Date: $249,913

3. Estimated Funds Required to Complete Work: $149,919

### II D. ACTION REQUIRED BY NPS:

No action is requested from the NPS other than continued administrative support of this report.

### II E. FUTURE PLANS:

1) January 1994 collection trip.
2) Conduct primary production experiments during February at Lees Ferry and below the confluence of the Paria River.
3) Continue recolonization and relocation efforts at Lees Ferry and Paria cobbles sites.
4) Analyze data for final report.

## II F. **Equipment Purchases**

None

## II G. **ITEMIZATION OF QUARTERLY EXPENDITURES:**

| | |
|---|---|
| Salaries: | $40,380 |
| Supplies: | 3,376 |
| Travel: | 217 |
| Equipment: | 0 |
| NAU Overhead: | 7,156 |

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## ACKNOWLEDGEMENTS

We wish to thank Mr. David Wegner and his staff in the Glen Canyon Environmental Studies Program for continuing assistance with logistics and survey-related data acquisition during this project. We appreciate the excellent logistical support provided by O.A.R.S., Inc. during research river expeditions. We thank the National Park Service for administrative support, especially Dr. Peter G. Rowlands and the National Biological Survey staff at Northern Arizona University. We also thank Wade Albrecht, Peggy Benenati, Pete Gambrill, Fred Govidich, Jeanette Macauley, Gaye Oberlin, Lorraine and Patrick Putnam, Nancy Russell, Dierdre Ryan, Mike Shaver, and Kevin Wilson for their dedicated assistance with field collections and laboratory processing. Lastly, we wish to express our deepest appreciation to the many fine students and volunteers who have contributed their time and enthusiastic support to this project.

## ABSTRACT

The purpose of this study was to provide seasonal baseline data during interim flows (140 $m^3 s^{-1}$ to 565 $m^3 s^{-1}$ or 5,000 to 20,000 cfs) on the aquatic food base in the Colorado River ecosystem in Grand Canyon downstream from Glen Canyon Dam. We examined the distribution, phenology, biomass, colonization rates, secondary production, winter desiccation, and stream drift for aquatic algal and macroinvertebrate species. This study provides an initial evaluation of interim flow effects on Colorado River benthic ecology, and can be used as baseline data for experimental flooding under consideration in 1995.

Our results indicate the following:

1) The overriding factors affecting primary producers and consumers are dam operations and tributary influence (increased turbidity) which result in a stair-step decrease in biomass below the confluence of the Paria River (5 RKM below Lees Ferry).

2) The filamentous green alga, Cladophora glomerata, is the dominant macroalga above the Paria River and Oscillatoria spp., a crustose blue-green alga (Cyanobacteria), is dominant below the Little Colorado River.

3) Algal and macroinvertebrate biomass and abundance are strongly negatively correlated with distance from the dam.

4) Reduced hydraulic variability increase macroinvertebrate, algal and aquatic macrophyte diversity and biomass downstream. Reduced flows with minimum fluctuations (for 2-3 months) following winter spates resulted in higher downstream water temperatures, reduced drift, and perhaps greater nutrient retention.

5) Aquatic macrophytes (Potamogeton) are colonizing channel bottoms due to the accumulation of fine sediments during interim flows. These plants appear to be less suitable for epiphyte colonization than Cladophora, and therefore their continued colonization of channel bottoms may reduce the overall foodbase in the Colorado River ecosystem.

6) Fluctuations between (170 $m^3 s^{-1}$ to 368 $m^3 s^{-1}$ or 6,000 to 13,000 cfs) showed at least a two-fold increase in stream drift compared to steady flows at 227 $m^3 s^{-1}$ (8,000 cfs)

7) There is at least a 90% decrease in coarse particulate organic material (CPOM) in stream drift between Lees Ferry and below the Paria River confluence (RKM 5.0).

8) Macroinvertebrates and epiphytic diatoms are quickly removed from drifting Cladophora packets while passing through rapids.

9) Recolonization rates by Cladophora are slow following desiccation. We estimate up to one year is required for recovery of standing crop on resubmerged substrates. The slow recovery may be a function of the apparent mode of recruitment (fragmentation) utilized by Cladophora in the Colorado River. Recolonization by Oscillatoria is faster than recolonization by Cladophora in the submerged turbid and fluctuation zones during interim flows.

10) Annual secondary production for Gammarus lacustris in the channel at Lees Ferry is 548 mg $m^{-2}$ $yr^{-1}$; i.e., seven-fold higher than in the fluctuating flow zone at Lees Ferry and three-fold higher than in the submerged channel below the confluence of the Paria River. Reduced food availability and physical abrasion due to high suspended sediment loads are considered to be responsible for the low production values below the Paria River. Low downstream standing stocks infer similar low annual production throughout the river corridor in Grand Canyon National Park.

11) Drawdown of river stage during the winter months exposes Cladophora to both freezing temperature and desiccation. Winter night time exposure experiments at Lees Ferry revealed significant losses in Cladophora biomass and chlorophyll a due to freezing and desiccation. Thus Cladophora is susceptible to drawdown during low nighttime flows in winter months.

## INTRODUCTION

Growing concern over the impacts of river regulation on environmental resources in the Colorado River corridor downstream from Glen Canyon Dam prompted the Department of the Interior to conduct environmental impact studies in lower Glen Canyon and in the Grand Canyon. Phase I of the Glen Canyon Environmental Studies (GCES) Program concluded that the dam exerted significant impacts on the downstream fluvial ecosystem, but higher than normal flows precluded assessment of the effects of normal dam operations. GCES Phase II integrated assessment of low and normal fluctuations with processes and resources at the ecosystem level. These studies demonstrated significant effects of normal operations on riverine resources. Interim flows were implemented on 1 August, 1991 to prevent further degradation of resources during the development of the Glen Canyon Dam Environmental Impact Statement. Interim flows consist of reduced flow fluctuations with restricted minimum (140 $m^3 s^{-1}$) and limited maximum (565 $m^3 s^{-1}$) flows, and reduced ramping rates.

Glen Canyon Dam operations strongly affect the lower trophic levels of the aquatic ecosystem in Grand Canyon National Park (Blinn et al. 1992). Aquatic algae and macroinvertebrates provide an important food base for native and game fish and terrestrial fauna, and link the aquatic and terrestrial components of the ecosystem. The aquatic food base is affected by the duration and timing of low releases from Glen Canyon Dam, as well as the range of daily fluctuations. This study of the aquatic food base in the Colorado River is designed to monitor interim flow effects on benthic distribution and production between Lees Ferry and Diamond Creek, Arizona.

A primary objective of the GCES interim flows discharge criteria is to maintain the aquatic food base in the Colorado River. The interim flow criteria are designed to stabilize the area available for colonization by benthic algae, thereby decreasing loss through exposure of the benthos, and stabilizing or increasing primary and secondary benthic production.

## OBJECTIVES

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

Objective 1: Monitor the effects of interim flows from Glen Canyon Dam on the standing stock of the lower trophic levels in the Colorado River between Lees Ferry and Diamond Creek.

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

Objective 3: Monitor the effects of interim flows on the re-colonization of substrata by primary producers and secondary consumers in the Colorado River ecosystem.

Objective 4: Monitor the effects of interim flows on organic drift in the Colorado River corridor in the Grand Canyon.

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

# CHAPTER ONE: STANDING STOCK OF LOWER TROPHIC LEVELS

(Peggy Benenati, Pete Gambrill, Joe Shannon, and Kevin Wilson)

## INTRODUCTION

The biomass and habitat requirements of aquatic macroinvertebrates were assessed seasonally during 1993 (Objective 1). This sampling frequency was employed to overlap generation times of organisms. Sampling sites included USGS synoptic study sites and the most downstream AGF tailwaters sites (Fig. 1). Five wide-reach sites and five narrow-reach sites were sampled seasonally. These ten sites each included three habitat types; river pools (low velocity sand and silt), riffles (high velocity cobble) and nearby tributaries during June 1993.

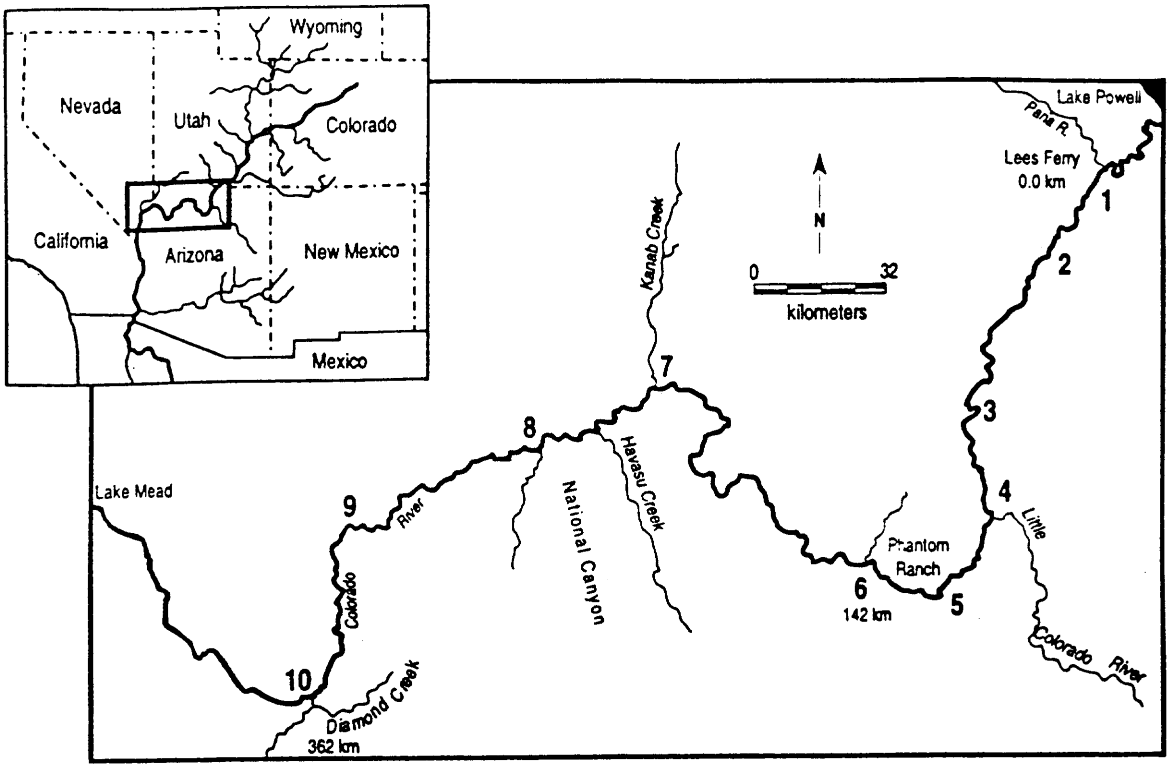
## METHODS

Sampling was conducted at three transects 30 meters apart in each habitat type. Petersen or Petit Ponar dredges were used in the fine sediment pools and Hess substrate samplers were utilized in tributaries and on cobble bars. Pool habitats were sampled at five locations along the three transects; thalweg, <28 $m^3$ $s^{-1}$, lower-littoral (approximately 140 $m^3$ $s^{-1}$), mid-littoral (approximately 280 $m^3$ $s^{-1}$), and upper littoral (800 $m^3$ $s^{-1}$). Six cobble and twelve pool sites were collected for taxonomic/abundance and biomass determinations. Cobble bar collections were taken at the lowest water flow possible with three paired samples in the mid and upper-littoral stage (zone) elevations. Adult and pharate specimens were collected with sweep nets, white and UV lights, spot samples, and Thienemann (water surface) collections.

Sediment samples were taken from dredges and mid to upper littoral collections. These samples averaged 500 gm wet weight and were oven-dried to a constant weight (60°C) and sieved for percent clast size; gravel (<3 cm), coarse sand (>1 mm), sand (>0.5 mm), silt (>0.01 mm), and clay (<0.01 mm).

Samples were sorted into the following 11 biotic categories: Cladophora, blue-green algal crust (Oscillatoria spp.), chironomids, Gammarus lacustris, gastropods, oligochaetes, simuliids, lumbricids, miscellaneous invertebrates, miscellaneous algae, and detritus. Each biotic category was oven-dried at 60°C and weighed.

The following abiotic parameters were measured at each sampling site: water temperature, dissolved oxygen (DO), pH, specific conductance, substratum,




**Legend**

| Site | Pool | Habitat Riffle | (km)* Tributary | Geomorphic Reach Width | Elevation (m s l) | Reach Orientation |
|---|---|---|---|---|---|---|
| 1 | 0.0 | 0.08/3.1 | 1.0 | Wide | 947 | Southwest |
| 2 | 50.4 | 50.8 | 50.8 | Narrow | 871 | South |
| 3 | 84.8 | 83.2 | 83.2 | Wide | 842 | Southeast |
| 4 | 98.4 | 98.7 | 98.6 | Wide | 821 | Southwest |
| 5 | 108.8 | 109.6 | 104 | Wide | 810 | Southwest |
| 6 | 140.0 | 142.4 | 140.8 | Narrow | 734 | West |
| 7 | 230.4 | 232.0 | 214.8/231.2 | Narrow | 568 | West |
| 8 | 265.5 | 240 | 249.6 | Narrow | 540 | Southwest |
| 9 | 326.4 | 328.9 | 327.2 | Wide | 450 | South |
| 10 | 360.0 | 352.0 | 361.6 | Narrow | 409 | Southwest |

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

Figure 1. Map of benthic and drift collection sites in the Colorado River through Grand Canyon including site number, habitat, geomorphic reach width, elevation and reach orientation. Drift collecting sites are within 15 km downstream from benthic collection sites.

microhabitat conditions, Secchi depth (water transparency), water velocity or stage, and depth, date, site and time of day.

## RESULTS AND DISCUSSION

During the past winter, the abnormally high precipitation resulted in flooding throughout the Colorado River drainage with the Little Colorado River reaching 425 $m^3/s$. Peak flows occurred in January and February and reduced the duration of the January and March collection trips. Effects of flooding were immediately evident in March with an increased accumulation of sand throughout the river. Data from the June collection revealed the influence of flooding on the benthic foodbase. There was a significant increase in biomass on cobble/riffles below Nankoweap over the May 1991 research flow collections (Wilks' Lambda $F_{10,178} = 2.13$, $p = 0.024$). Pool habitats were significantly different for all stations (Wilks' Lambda $F_{10,332} = 2.15$, $p = 0.003$). Cladophora glomerata biomass showed the effect of flooding at Tanner Cobble (RKM 110) with 17.8 g dry weight (dw) $m^{-2}$ (Fig. 2). This is the first station below the Little Colorado confluence and may have assimilated nutrients scoured from overland flow. Multivariate analysis of water chemistry values showed an overall significant difference in each parameter (temperature, pH, conductivity, dissolved oxygen and Secchi depth) between May 1991 and June 1993 (Wilks' Lambda $F_{5,126} = 102$, $p < 0.0001$). The Paria River was also in spate through the winter, which may have contributed to increased biomass through Marble Canyon (RKM 0.0-99). Pool habitats showed an increase of biomass primarily from the accumulation of detritus and decomposers.

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

Macroinvertebrate and algal diversity were also higher during spring 1993 season as a result of reduced flow variability. There was an increase in lentic organisms such as Hemiptera (Gerridae; water striders, Belostomidae; giant water bugs and Corixidae/Naucoridae) associated with the emergent vegetation along shorelines

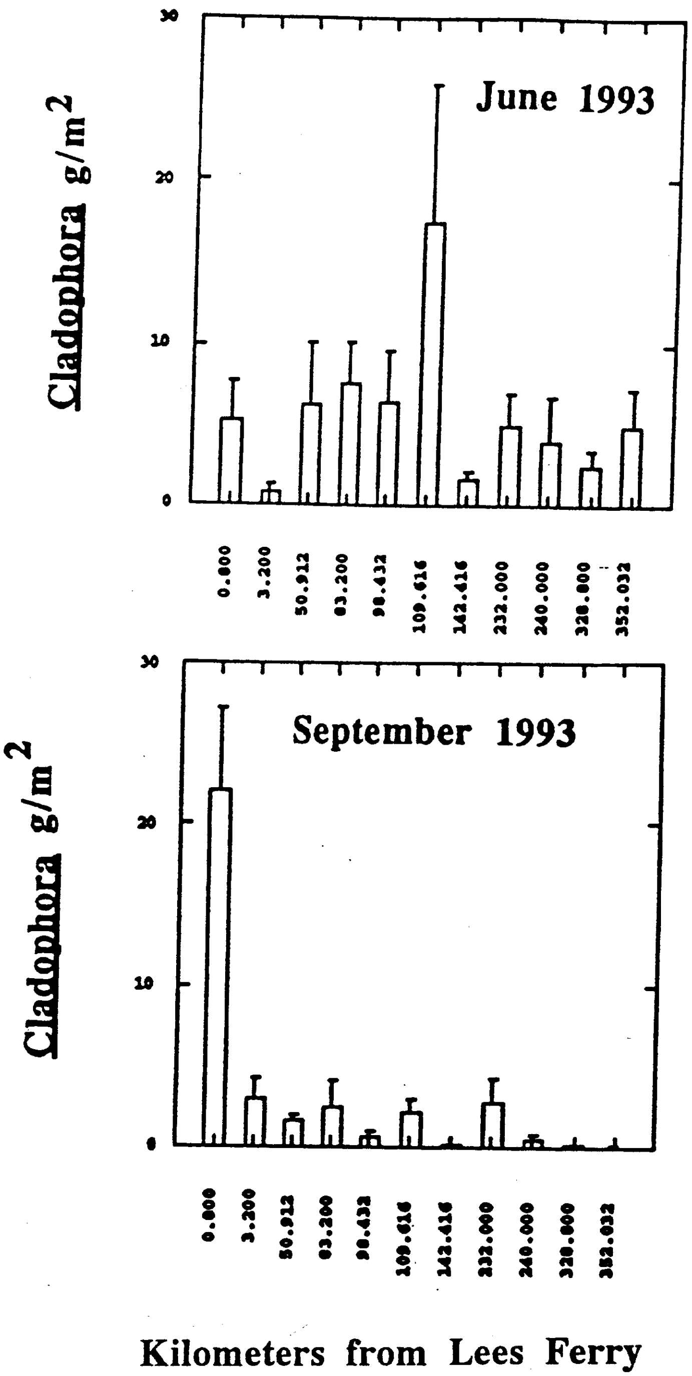



Figure 2. Cladophora glomerata biomass (g $m^{-2}$ dry wt) estimates for cobble bars in the Colorado River through Grand Canyon comparing post winter flood growth. June 1993 data follow three months of low flows (396 $m^3$ $s^{-1}$) while September 1993 follows two months of high flows (340 $m^3$ $s^{-1}$ to 565 $m^3$ $s^{-1}$). This comparison suggests that flooding increased productivity downstream of the Little Colorado River in June 1993.

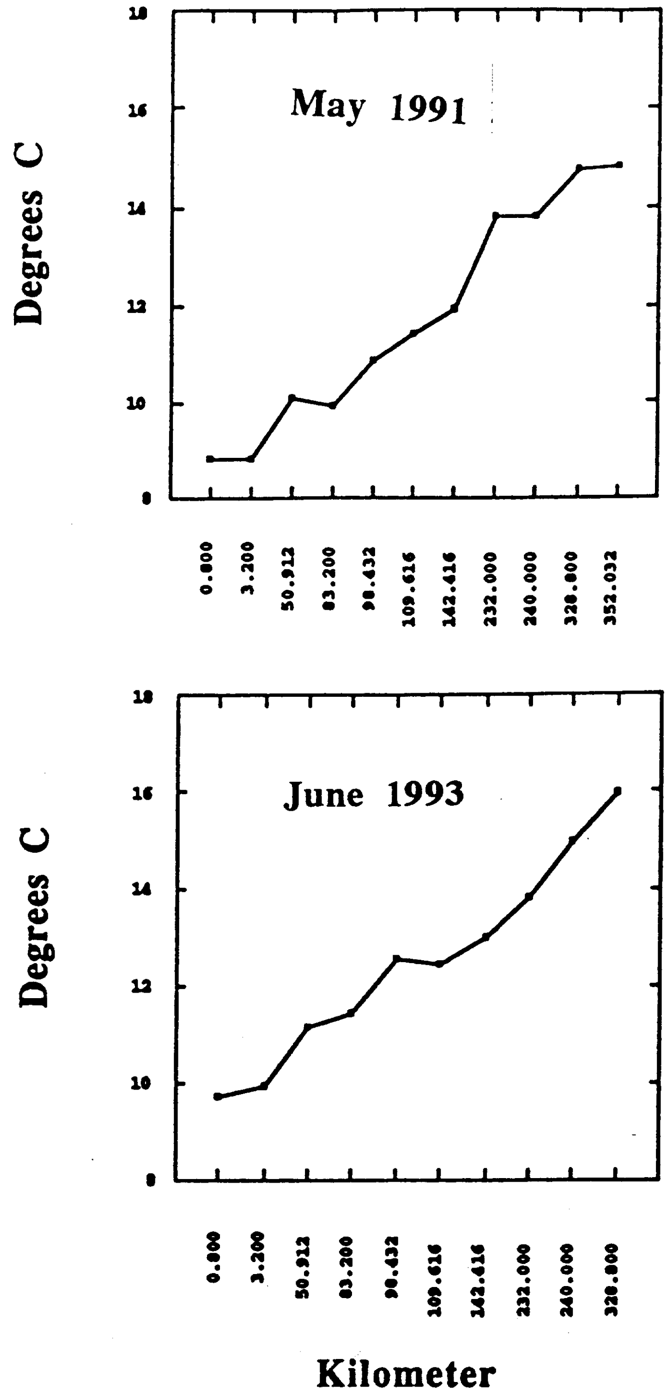



Figure 3. Longitudinal comparison of water temperatures (°C) between May 1991 research flows and June 1993 interim flows. Elevated temperatures in the lower Canyon sites allowed the expansion benthic biota. Univariate analysis shows a significant difference in water temperature for these two datasets ( $\underline{F}_{1,130} = 5.74$, $\underline{p} = .018$).

in the lower reaches of the Canyon. Macrophytes such as Potamogeton, Mimulus (Monkey Flower) and Chara continue to colonize fine sediment/low velocity areas throughout the Lees Ferry tailwater reach and sections of Marble Canyon.

We examined Potamogeton sp. stand at the Nankoweap site for epiphyton and macroinvertebrates. Six 0.02 $m^2$ samples were collected. The ash-free dry weight of periphyton was 2-fold lower than that associated with Cladophora below the Paria River confluence and only one Gammarus was found. These preliminary data suggest that Potamogeton is a poor habitat for epiphytic diatoms and macroinvertebrates.

A green tubular/filamentous alga, Enteromorpha intestinalis, was found below Middle Granite Gorge on hard substrates in the splash zones and was examined for epiphytes in the same manner as the Potamogeton. This green alga supported a similarly low epiphyte standing crop and no macroinvertebrates. Macrophytes have colonized a newly created niche (fine sediments on the channel floor), and should be monitored to see if they encroach upon nearby established Cladophora beds.

The September 1993 collection trip was completed under turbid conditions after discharge volumes during July and August of interim flow maxima (340-566 $m^3$ $s^{-1}$). Overall biomass estimates decreased by about 40% from June collections. The September biomass values were closer to those collected during previous fall seasons (Blinn et al. 1992) and may indicate that the system had stabilized from the past winter flooding. Diversity for primary and secondary producers was also reduced in comparison to June.

These data indicate that low releases from Glen Canyon Dam after a spate event may enhance production. A habitat building flood from Glen Canyon Dam, proposed for the spring of 1995, may exert similar effects on the reaches above the Little Colorado River.

Although macroinvertebrate diversity was low in September, the appearance of a small caddisfly (Trichoptera) in the Hydroptilidae Family, genus Ochrotrichia is noteworthy (Wiggins 1977). These caddisflies are free-living during their first four instars, but build a purse-case (ca 5 mm) composed of fine sand, silk and filamentous algae during the fifth and final instar. Ochrotrichia scrape diatoms from rocks and algae and are found in Cladophora filaments in densities up to 200 animals $m^{-2}$. Ochrotrichia appeared in Marble Canyon and maintained similar densities throughout the corridor. They are commonly found in erosional and depositional lotic habitats in North America (Merritt and Cummins 1978).

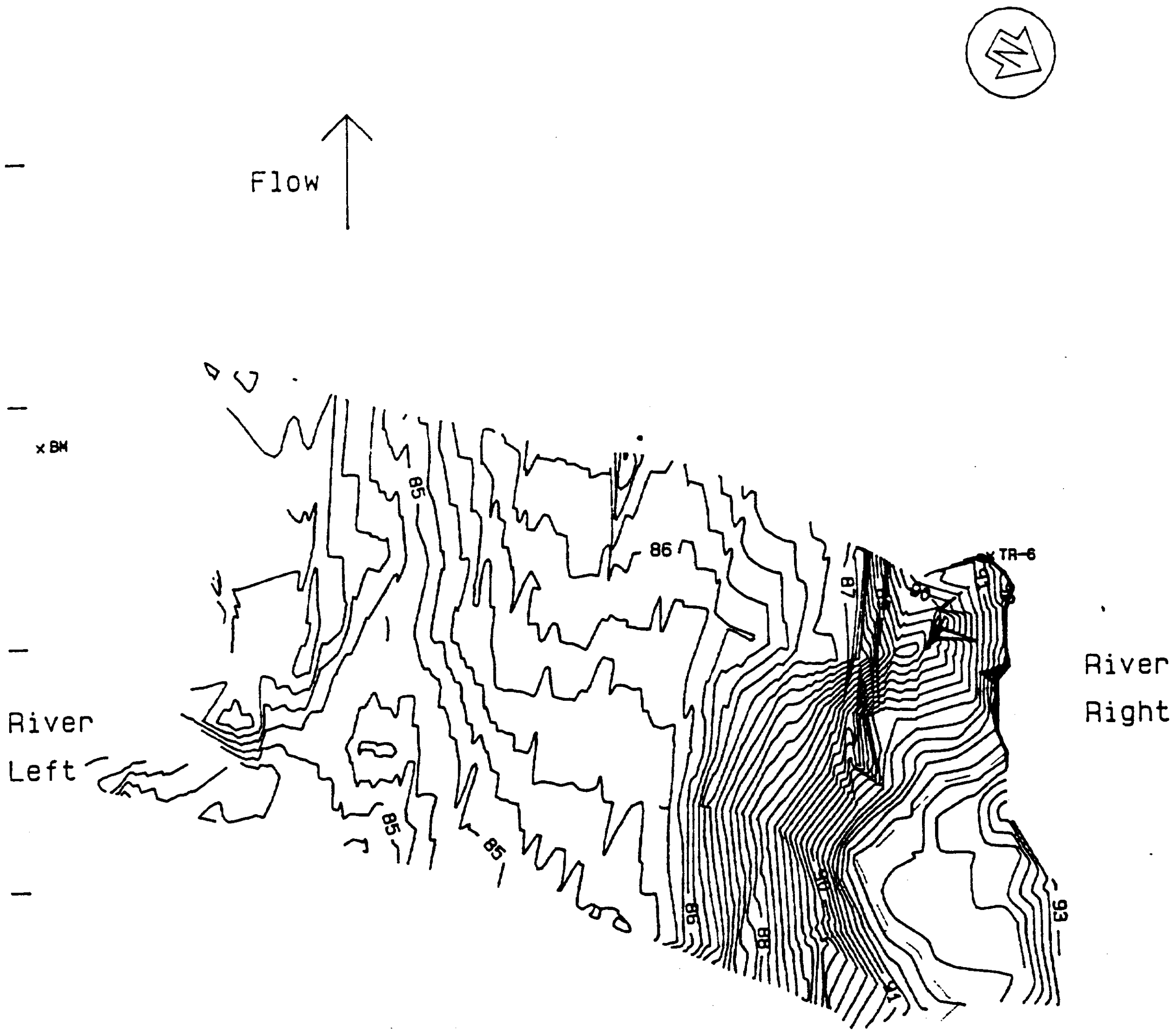
In an attempt to better understand the ecology of the biting black-fly, Simuliium arcticum, we assessed the population density and fecundity at nine cobble stations. The Lees Ferry and Paria cobble sites rarely have black-fly larvae and were therefore omitted. Thirty cobbles were sampled for larvae and viable pupal cases. Cobble measurements were taken for approximate volumetric calculations. Multivariate analysis with season and river kilometer as predictor variables indicated that larva and pupal density did not vary seasonally (Wilks' Lambda $F_{4,892} = 1.85, p = 0.11$), but did vary longitudinally (Wilks' Lambda $F_{16,880} = 6.14$, $p < 0.0001$). This preliminary analysis suggests that black flies are not confined to seasonal flights and have variable developmental times. These aquatic insects are primary colonizers after spates and have evolved fast response times to habitat changes. Flow regulation may alter developmental times for these aquatic insects. The longitudinal variation in developmental times may be explained by water temperature, reach width, and the amount of sunlight received by the river channel. Densities ranged up to 450 larvae $cm^{-2}$ with a mean of 7 animals $cm^{-2}$, while pupal densities where estimated as high as 110 $m^{-2}$ with a mean of 3.3 pupae $cm^{-2}$.

Tributaries were sampled during June and had not yet recovered from winter spates. The only exception was Spring Canyon, which had its usual high biomass/diversity of benthic organisms. Tributaries developed cemented bottoms from travertine deposition. Interstitial spaces in the substrate are reduced due to filling by $CaCO_3$. This phenomenon was observed while sampling the hyporheic zone of tributaries, where a dense coat of travertine was found below a thin layer (<30 cm) of sand, gravel and cobbles. This debris coating was probably deposited from lower magnitude spates.

Collection stations were surveyed by the GCES staff for implementation into the GIS program on the September river trip. These data were collected with the GCES survey equipment; Leitz Set 4 Total Station,Global Hydrographic Superhydrolab Bathometric Survey System and Sokkia V4.0 mapping software. Representative wide and narrow reaches are illustrated in Figs 4-7.

# NAU Aquatic Food Base Site

## Lee's Ferry Gauge




Contour Interval = 0.2m
(contour elevations from assumed benchmark)

Waters Edge Line — — — — —
(stage dicharge = 340 CMS)

Grid tic interval = 30m

1: 600

Survey Date: 931115

Location: RKM 0.0R

Elevation: 947 MSL

Canyon Orientation: Southwest

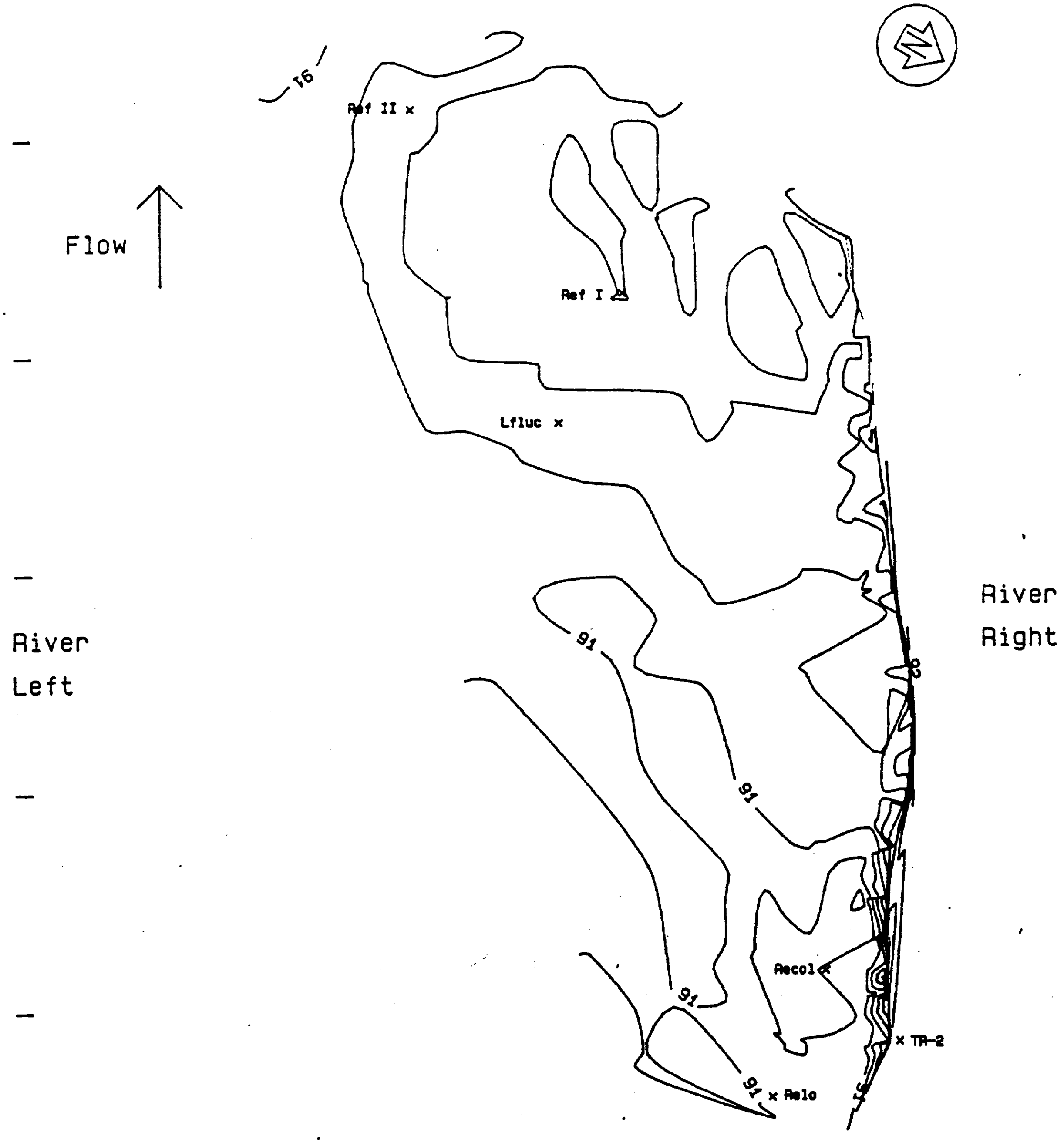
Reach Type: Wide

Habitat: Pool

Computer Operator: Pete [illegible]

# NAU Aquatic Food Base Site

## Lee's Ferry Cobble




Survey Date: 931115

Location: RKM 0.8R

Elevation: 947 MSL

Canyon Orientation: Southwest

Reach Type: Wide

Habitat: Riffle

Contour Interval = 0.2m
(contour elevations from assumed benchmark)

Waters Edge Line — — — — —
(stage discharge = 340 CMS)

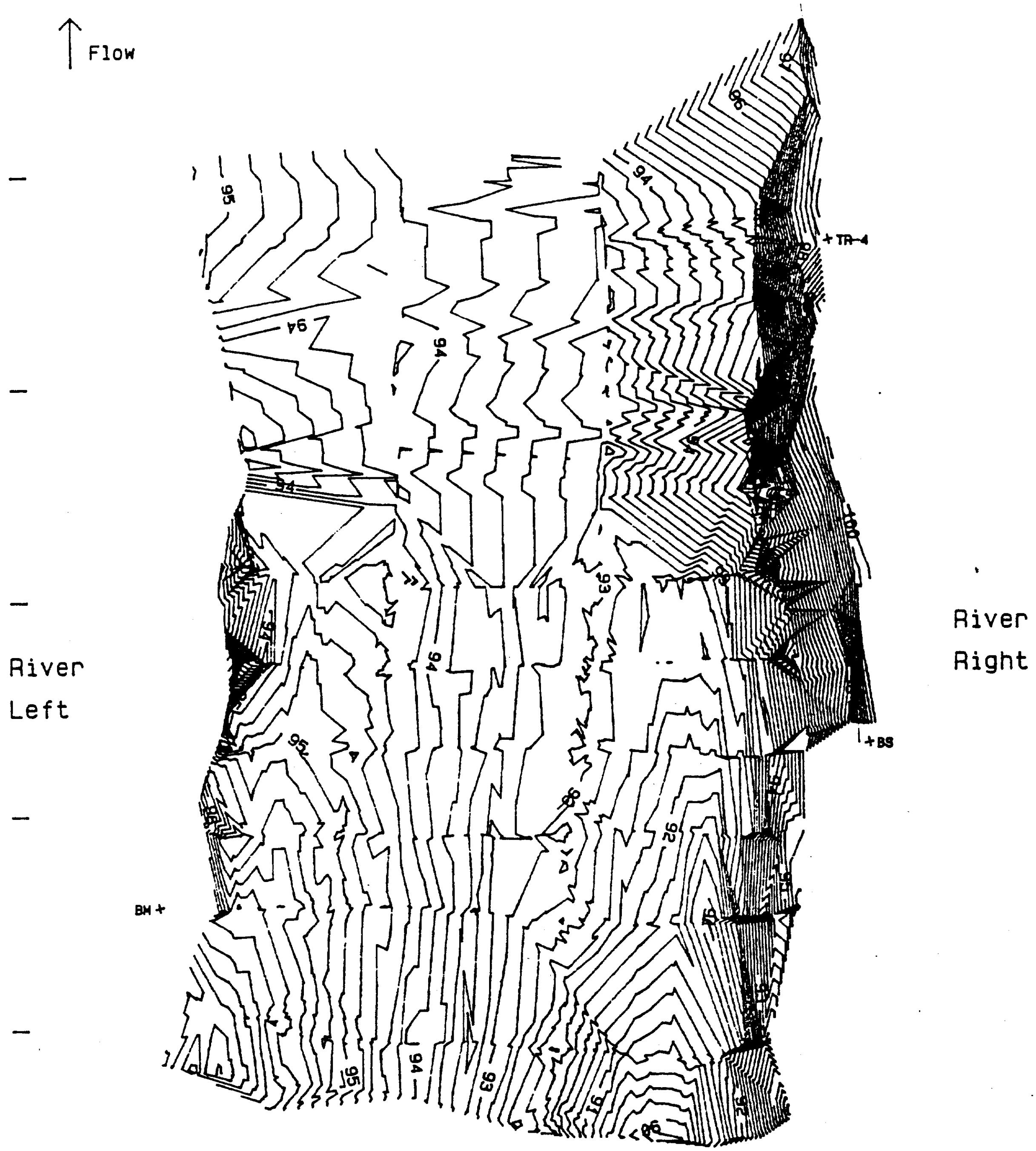
Grid tic interval = 30m

1: 600

Computer Operator: Pete [illegible]

# NAU Aquatic Food Base Site

Grand Canyon Gauge




Survey Date: 930905

Location: RKM 140.0R

Elevation: 734 MSL

Canyon Orientation: West

Reach Type: Narrow

Habitat: Pool

Contour Interval = 0.2m
(contour elevations from assumed benchmark)

Waters Edge Line — — — — —
(stage discharge = 311 CMS)

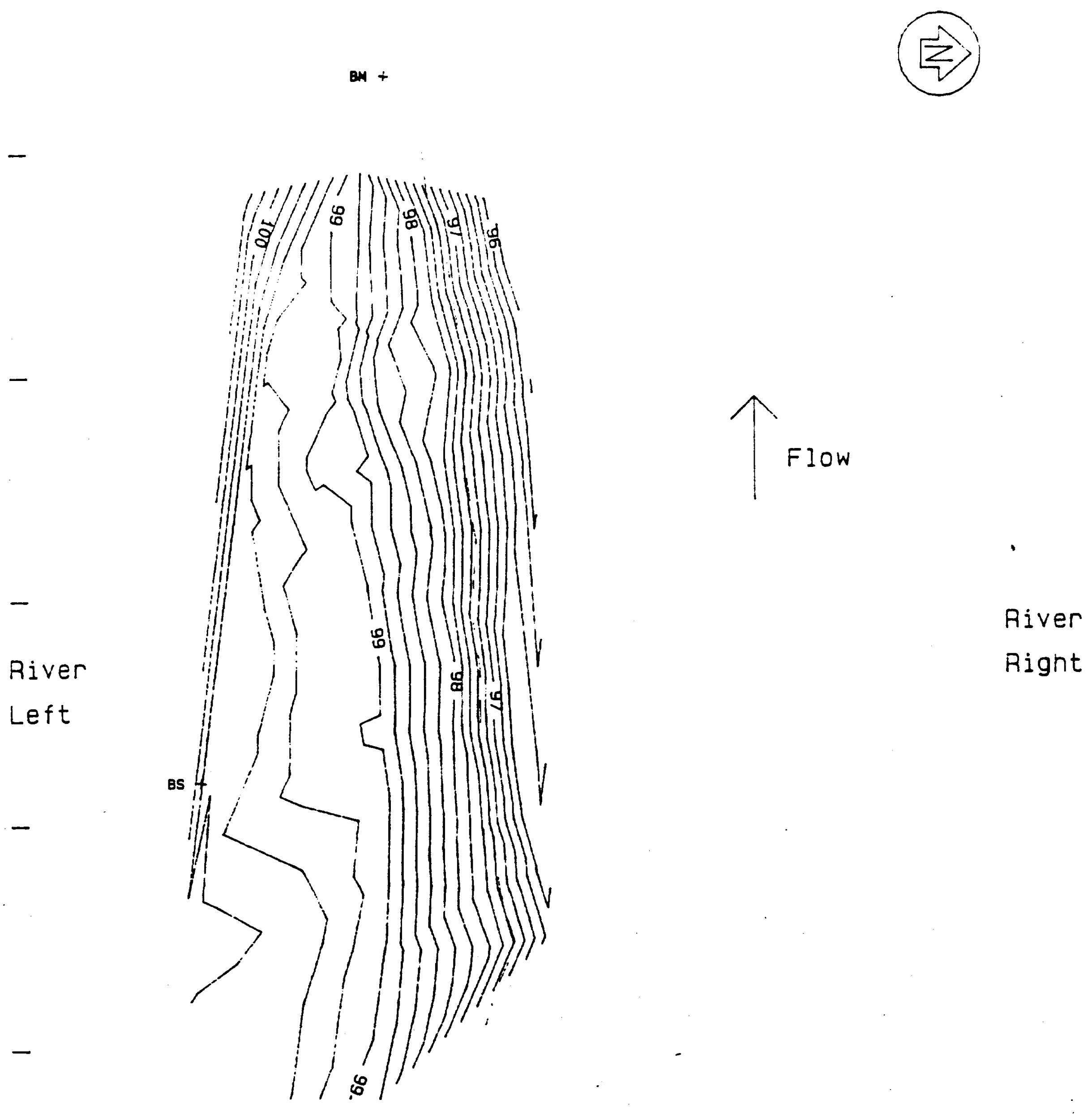
Grid tic interval = 30m

1: 600

Computer Operator: Pete Sambrill, 1993

# NAU Aquatic Food Base Site

## Phantom Cobble




Contour Interval = 0.2m
(contour elevations from assumed benchmark)

Waters Edge Line — — — — —
(stage discharge = 340 CMS)

Grid tic interval = 30m

1: 600

Survey Date: 930905

Location: RKM 142.4L

Elevation: 734 MSL

Canyon Orientation: West

Reach Type: Narrow

Habitat: Riffle

Computer Operator: Pete Gembrill, 1993

# CHAPTER TWO: PRIMARY AND SECONDARY PRODUCTION

(Dean W. Blinn, Dierdre Ryan, and Joe Shannon)

## INTRODUCTION

From the standpoint of a functioning ecosystem, production is the means by which energy is made available for conversion from one trophic level into the next. Therefore, resource managers should be concerned with the processes of production and those factors which modify the synthesis of organic matter. Flow effects on the primary production of Cladophora glomerata and Oscillatoria spp. are important because these two algal taxa are dominants in the system, and support higher trophic levels. Secondary production of Gammarus lacustris is vital to understanding energy flow within the Colorado River ecosystem because this amphipod serves as a critical intermediate link between algal and fish biomass in the Colorado River food web (Blinn et al. 1992). This study examines the effects of interim flows in combination with suspended sediment loads on the annual secondary production of G. lacustris at two sites in the Colorado River ecosystem.

## METHODS

### Primary Production

We constructed three air-tight primary production chambers out of clear acrylic that will help us determine the amount of carbon synthesis in the Colorado River at Lees Ferry, Two-Mile Wash, and Diamond Creek. These chambers are cylinders (23.5 cm in diameter and 18.5 cm deep) with a lid and an inside plunger with a gasket to prevent air exchange. Two air tight ports were installed for a circulation pump that provides a current and serves to maintain ambient water temperature as the chambers heat up in the sun. A third port was installed that accepts a dissolved oxygen (DO) probe from a Yellow Spring Instruments model 55 DO meter.

### Secondary Production

Benthic invertebrates were collected in submerged and fluctuationg zones of the Colorado River at Lees Ferry (RK 0) and Two Mile Wash (RK 3.1), Arizona, to evaluate the role of interim flows on the secondary production of Gammarus lacustris, an important amphipod in the Lees Ferry food web (Blinn et al., 1992). Twelve samples were taken with a modified mini-Hess sampler (0.031 $m^2$) at two-week intervals between 30 September 1992 and 15 September 1993 in submerged and fluctuating zones at Lees Ferry and Two Mile Wash (treatments = 4). Hess samples were collected from three randomly selected sites along four transects within each treatment. Samples within the fluctuating zone were collected during evening (after 1500 hrs) high water (≥10,000 cfs; 283 $m^3s$) and samples in the main channel (controls) were taken during the subsequent low morning flows (after 0700 hrs; ≤ 5,000 cfs; 141 $m^3s$). Benthic invertebrates and algae were removed from cobble by disturbing the substrata within the mini-Hess sampler for 60 s, after which samples were collected and placed on ice for transport back to the Aquatic Biology Laboratory at Northern Arizona University, Flagstaff, Arizona. Reference points for transects were alternated monthly to avoid oversampling local sites. All invertebrates, including lumbricids, oligochaetes, simuliids, chironomids, gastropods, and G. lacustris, were sorted and weighed from each sample. Body length of each G. lacustris instar was measured to the nearest 1 mm. Instars were separated into 19 1-mm size classes and the dry weight of each size class was determined. Eggs were removed from female brood pouches and number and weight of eggs from each mature female was determined. Also the size of females with eggs was determined for each sample. Cladophora glomerata, cyanobacteria, miscellaneous algae, and aquatic macrophytes were also sorted and weighed from each sample

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

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

where P is the annual production, $W_j$ is the mean weight of instar j, c is the number of instars, and $N_j$ is the number of individuals that developed into instar j during the year.

## RESULTS AND DISCUSSION

### Primary Production

A preliminary in situ run in November using Cladophora covered cobbles from Lees Ferry provided us with a successful sampling protocol. We plan a winter experiment in February and a summer experiment in July to test the influence of interim flows and suspended sediment on primary production of Cladophora and associated epiphytic diatoms, and Oscillatoria. Included with the various sites as predictor variables are submerged and fluctuation zones for response variables of Cladophora, Oscillatoria, and dominant macrophytes.

## Secondary Production

There were notable differences in average annual densities of Gammarus lacustris between Lees Ferry and Two Mile Wash and between continuously submerged and fluctuating flow treatments at each site. Highest average densities were recorded in the submerged channel at Lees Ferry (1,174 animals $m^{-2}$ $yr^{-1}$) , while lowest average densities were measured in fluctuating zones at Lees Ferry (184 animals $m^{-2}$ $yr^{-1}$) and Two Mile Wash (7.6 animals $m^{-2}$ $yr^{-1}$). Average annual density for G. lacustris for continuously submerged treatments at Two Mile Wash was 235 animals $m^{-2}$.

Annual secondary production for Gammarus lacustris in the continuously submerged channel (5.48 kg dw $ha^{-1}$ $yr^{-1}$) was an order of magnitude higher than values for the fluctuation zone (0.73 kg dry weight dw $ha^{-1}$ $yr^{-1}$) in the Colorado River at Lees Ferry, Arizona (Tables 1 and 2). The area of exposed cobble bar between high water (800 $m^3$ $s^{-1}$) and 425 $m^3$ $s^{-1}$ at Lees Ferry is ~8,090 $m^2$ compared to ~31,855 $m^2$ between 800 $m^3$ $s^{-1}$ and 170 $m^3$ $s^{-1}$ (Blinn et al. 1992). These data imply that regulated flows between 170 $m^3$ $s^{-1}$ and 425 $m^3$ $s^{-1}$ reduce overall annual production of G. lacustris at Lees Ferry by at least 65%, assuming relatively uniform distribution of Gammarus throughout the channel.

Annual production by G. lacustris in the continuously submerged channel (≤6,000 cfs) at Two Mile Wash , just 1.6 km below the Paria confluence, was only 1.79 kg dw $ha^{-1}$ $yr^{-1}$ (Table 3). This represents a 3-fold reduction in annual production from the corresponding clear water habitat at Lees Ferry which is 2 km upstream from the Paria River confluence (Table 3). Perhaps the periodic input of suspended sediment from the Paria River reduces annual secondary production in this region. The influence of interim flows between 170 $m^3$ $s^{-1}$ and 565 $m^3$ $s^{-1}$ was also noted at Two Mile Wash. Annual secondary production for G. lacustris was 0.04 kg dw $ha^{-1}$ $yr^{-1}$, nearly 50 times lower than that in the continuously submerged channel (≤170 $m^3$ $s^{-1}$) at Two Mile Wash (Table 4).

Assuming an energy equivalence of 16.54 j (joules) $mg^{-1}$ for G. lacustris (Blinn et al. 1992), we estimated that Gammarus collected within the benthic community provides ~90,639 kj $ha^{-1}$ $yr^{-1}$ total available energy in the submerged river channel at Lees Ferry compared to 29,606 kj $ha^{-1}$ $yr^{-1}$ in the submerged channel of Two Mile Wash. The fluctuating zones at Lees Ferry and Two Mile Wash produce 12,074 kj $ha^{-1}$ $yr^{-1}$ and 662 kj $ha^{-1}$ $yr^{-1}$, respectively.

Cho (1992) reported that it requires ~15,000 kj of energy to produce 1 kg of trout biomass. Based on these conversions and a 70% assimilation efficiency for rainbow trout (Phillips and Brockway 1959), Gammarus could support ~4.2 kg $ha^{-1}$ of trout biomass in the benthic community at Lees Ferry and ≤0.7 kg of trout in the benthic community at Two Mile Wash. Data on the foraging efficiency of trout at Lees Ferry is not available.

At all treatment sites, animals between 7-10 mm showed negative production values (Tables 1-4). Typically, negative production values imply sampling error in the field or sorting error in the laboratory. We noted that G. lacustris are typically in amplexus (sexual pairing) at 7-10 mm at Lees Ferry. Since the pattern is consistent for all site treatments, especially for 9-10 mm animals (Figs 1-4), we propose the negative production depicts a behavioral event for G. lacustris during mating that makes them more difficult to capture. If mating animals modify their swimming and/or habitat selection (i.e., move to deeper water) they may be more difficult to sample. However, if animals return to a normal behavior in the next size interval after mating, a negative production value would be recorded between successive size classes. This may help explain the consistent negative production values within the 7-10 mm size classes.

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

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

Total annual secondary production for G. lacustris in the benthic community of the Colorado River at Lees Ferry [6.21 kg dw $ha^{-1}$ $yr^{-1}$ (5.48 from submerged + 0.73 from the fluctuating zone)] is considerably lower than previous reports for congeneric amphipods in small lotic ecosystems. Waters and Hokenstrom (1980) reported between 231-271 kg dw $ha^{-1}$ $yr^{-1}$ for G. pseudolimnaeus in Valley Creek, Minnesota, among the highest single-species estimate for amphiphods in lotic ecosystems. Thus, production in the reach of Valley Creek is ~44 times higher than benthic production for G. lacustris at Lees Ferry in the Colorado River. Waters and Hokenstrom (1980) further reported the subsequent years during relatively high siltation yielded only 64 kg dw $ha^{-1}$ $yr^{-1}$, still ~10 times higher than highest values estimated in the Colorado River. Other reports on annual production by Gammarus in lotic ecosystems include 130 kg dw $ha^{-1}$ $yr^{-1}$ for G. pulex in a Dorset Chalk Stream in England (Welton 1979), and 39 kg dw $ha^{-1}$ $yr^{-1}$ for G. pulex in a small Danish stream (Mortensen 1982).

Reports on annual production for congeneric amphipods in lentic environments are also higher than estimates in the Colorado River. Tilly (1968) reported 366 kg dw $ha^{-1}$ $yr^{-1}$ for G. pseudolimnaeus in Cone Spring, Iowa, Beattie et al. 1972) estimated 130 kg dw $ha^{-1}$ $yr^{-1}$ for G. tigrinus in Tjeukemeer Reservoir in the Netherlands, and Iversen and Jessen (1977) reported 38 kg dw ha-1 yr-1 in Rold Kilde Spring, Denmark. Finally, LaFrance and Ruber (1985) estimated that production for G. mucronatus in a Massachusetts salt marsh was between 124 to 158 kg dw $m^{-2}$ $yr^{-1}$.

The relatively low secondary production for G. lacustris in the benthic community at Lees Ferry may be an underestimate. Stream drift within the river channel at Lees Ferry contained 2.3 x $10^{5}$ g dw Gammarus $yr^{-1}$ (See Section on Stream Drift) . We suggest that a large fraction of the G. lacustris biomass becomes dislodged and enters stream drift in the Colorado River. Inclusion of drift biomass at Lees Ferry substantially elevates estimates of secondary production by G. lacustris in the Colorado River. Waters and Hokenstrom (1980) also reported high annual mean drift (41-46 g $d^{-1}$ $m^{-3}$ $s^{-1}$) for G. pseudolimnaeus in Valley Creek during periods of high secondary production. Mean annual drift at Lees Ferry is ~550 g $d^{-1}$ $m^{-3}$ $s^{-1}$ at 300 $m^{3}$ at 10K.

Reports on annual secondary production for congeneric amphipods in larger river ecosystems are considerably lower than those reported in the tailwaters of Glen Canyon Dam. Mann (1971) reported 0.14 kg dw $ha^{-1}$ $yr^{-1}$ for G. pulex in the River Thames, England, nearly 40 times lower than for benthic production for G. lacustris at Lees Ferry in the Colorado River.

Table 1. Annual secondary production for Gammarus lacustris in the channel at Lees Ferry, Colorado River, Arizona , between 30 September 1992 and 15 September 1993, as estimated by the size-frequency method.

| Size Class (mm) | $N_j$ (No./m$^2$) | $\Delta N_1$ | Geometric mean weight (mg) $(M \times M_{j+1})^{0.5}$ | Production (mg m$^{-2}$ yr$^{-1}$) |
|---|---|---|---|---|
| 2-3 | 208.66 | | | |
| | | 33.60 | 0.24 | 8.06 |
| 3-4 | 175.03 | | | |
| | | 5.60 | 0.30 | 1.68 |
| 4-5 | 169.41 | | | |
| | | 38.13 | 0.48 | 18.30 |
| 5-6 | 131.28 | | | |
| | | 43.50 | 0.80 | 34.80 |
| 6-7 | 87.82 | | | |
| | | 26.99 | 1.24 | 33.47 |
| 7-8 | 60.83 | | | |
| | | 9.17 | 1.86 | 17.06 |
| 8-9 | 51.63 | | | |
| | | -2.55 | 2.59 | -6.61 |
| 9-10 | 54.19 | | | |
| | | -10.84 | 3.40 | -36.86 |
| 10-11 | 65.02 | | | |
| | | 21.67 | 4.27 | 92.53 |
| 11-12 | 43.35 | | | |
| | | 21.67 | 5.18 | 34.19 |
| 12-13 | 36.42 | | | |
| | | 7.47 | 6.18 | 46.17 |
| 13-14 | 28.93 | | | |
| | | 7.16 | 7.46 | 53.41 |
| 14-15 | 21.78 | | | |
| | | 6.33 | 8.69 | 55.01 |
| 15-16 | 15.44 | | | |
| | | 3.78 | 9.95 | 37.61 |
| 16-17 | 11.66 | | | |
| | | 3.38 | 11.50 | 38.87 |
| 17-18 | 8.28 | | | |
| | | 5.83 | 13.55 | 79.00 |
| 18-19 | 2.34 | | | |
| | | 0.81 | 15.09 | 12.22 |
| 19-20 | 1.64 | | | |
| | | 1.23 | 17.08 | 21.01 |
| 20-21 | 0.41 | 0.41 | *20.28 | 8.32 |
| TOTAL ANNUAL PRODUCTION | | | | 548.24 |

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

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

Table 2. Annual secondary production for <u>Gammarus</u> <u>lacustris</u> in the fluctuating zone at Lees Ferry, Colorado River, Arizona , between 30 September 1992 and 15 September 1993, as estimated by the size-frequency method.

| Size Class (mm) | $N_j$ (No./m2) | $\Delta N_1$ | Geometric mean weight (mg) $(M \times M_{j+1})^{0.5}$ | Production (mg $m^{-2}$ $yr^{-1}$) |
|---|---|---|---|---|
| 2-3 | 26.10 | | | |
| | | -5.50 | 0.24 | -1.32 |
| 3-4 | 31.60 | | | |
| | | -0.10 | 0.30 | -0.03 |
| 4-5 | 31.70 | | | |
| | | 4.30 | 0.48 | 2.06 |
| 5-6 | 27.40 | | | |
| | | 11.56 | 0.80 | 9.25 |
| 6-7 | 15.84 | | | |
| | | 1.83 | 1.24 | 2.27 |
| 7-8 | 14.01 | | | |
| | | 6.71 | 1.86 | 12.48 |
| 8-9 | 7.36 | | | |
| | | -1.94 | 2.59 | -5.03 |
| 9-10 | 9.30 | | | |
| | | 2.56 | 3.40 | 8.71 |
| 10-11 | 6.74 | | | |
| | | 2.65 | 4.27 | 11.32 |
| 11-12 | 4.09 | | | |
| | | 1.23 | 5.18 | 6.37 |
| 12-13 | 2.86 | | | |
| | | 1.12 | 6.18 | 6.92 |
| 13-14 | 1.74 | | | |
| | | 0.000 | 7.46 | 0.000 |
| 14-15 | 1.74 | | | |
| | | 0.21 | 8.69 | 1.82 |
| 15-16 | 1.53 | | | |
| | | 0.81 | 9.95 | 8.06 |
| 16-17 | 0.72 | | | |
| | | 0.000 | 11.50 | 0.000 |
| 17-18 | 0.72 | | | |
| | | 0.51 | 13.55 | 6.91 |
| 18-19 | 0.21 | 0.21 | *15.09 | 3.71 |
| TOTAL ANNUAL PRODUCTION | | | | 72.96 |

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

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

Table 3. Annual secondary production for Gammarus lacustris in the channel at Two Mile Wash (below Paria confluence), Colorado River, Arizona, between 30 September 1992 and 15 September 1993, as estimated by the size frequency method.

| Size Class (mm) | $N_j$ (No./m$^2$) | $\Delta N_1$ | Geometric mean weight (mg) $(M \times M_{j+1})^{0.5}$ | Production (mg m$^{-2}$ yr$^{-1}$) |
|---|---|---|---|---|
| 2-3 | 14.83 | 0.92 | 0.24 | 0.22 |
| 3-4 | 13.91 | -1.12 | 0.30 | -0.34 |
| 4-5 | 15.03 | -1.74 | 0.48 | -0.84 |
| 5-6 | 16.77 | 4.19 | 0.80 | 3.35 |
| 6-7 | 12.58 | -3.17 | 1.24 | -3.93 |
| 7-8 | 15.75 | -0.19 | 1.86 | -0.35 |
| 8-9 | 15.94 | -3.49 | 2.59 | -9.04 |
| 9-10 | 19.43 | -2.96 | 3.40 | -10.07 |
| 10-11 | 22.39 | 1.94 | 4.27 | 8.28 |
| 11-12 | 20.45 | 4.80 | 5.18 | 24.86 |
| 12-13 | 15.65 | 1.23 | 6.18 | 7.60 |
| 13-14 | 14.42 | 0.000 | 7.46 | 0.000 |
| 14-15 | 14.42 | 2.76 | 8.69 | 23.98 |
| 15-16 | 11.66 | 4.81 | 9.95 | 47.86 |
| 16-17 | 6.85 | 3.78 | 11.50 | 43.47 |
| 17-18 | 3.07 | 1.64 | 13.55 | 22.22 |
| 18-19 | 1.43 | 1.33 | 15.09 | 20.07 |
| 19-20 | 0.10 | 0.10 | *17.08 | 1.71 |
| TOTAL ANNUAL PRODUCTION | | | | 179.05 |

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

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

Table 4. Annual secondary production for Gammarus lacustris in the fluctuating zone at Two Mile Wash (below Paria confluence), Colorado River, Arizona, between 30 September 1992 and 15 September 1993, as estimated by the size frequency method.

| Size Class (mm) | $N_j$ (No./m$^2$) | $\Delta N_1$ | Geometric mean weight (mg) $(M \times M_{j+1})^{0.5}$ | Production (mg m$^{-2}$ yr$^{-1}$) |
|---|---|---|---|---|
| 2-3 | 1.74 | | | |
| | | 1.02 | 0.24 | 0.25 |
| 3-4 | 0.72 | | | |
| | | 0.31 | 0.30 | 0.09 |
| 4-5 | 0.42 | | | |
| | | -0.20 | 0.48 | -0.10 |
| 5-6 | 0.61 | | | |
| | | 0.10 | 0.80 | 0.08 |
| 6-7 | 0.51 | | | |
| | | 0.00 | 1.24 | 0.00 |
| 7-8 | 0.51 | | | |
| | | 0.51 | 1.86 | 0.95 |
| 8-9 | 0.00 | | | |
| | | -0.51 | 2.59 | -1.32 |
| 9-10 | 0.51 | | | |
| | | 0.10 | 3.40 | 0.34 |
| 10-11 | 0.41 | | | |
| | | -0.10 | 4.27 | -0.43 |
| 11-12 | 0.51 | | | |
| | | 0.00 | 5.18 | 0.00 |
| 12-13 | 0.51 | | | |
| | | 0.30 | 6.18 | 1.85 |
| 13-14 | 0.21 | | | |
| | | -0.51 | 7.46 | -3.81 |
| 14-15 | 0.72 | | | |
| | | 0.51 | 8.69 | 4.43 |
| 15-16 | 0.21 | 0.21 | 9.95 | 2.09 |
| TOTAL ANNUAL PRODUCTION | | | | 4.42 |

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

Production = $\sum_{j=1}^{c-1}$ [Nj - Nj+1) x $(M_j \times M_{j+1})^{0.5}$] + (Nc X Mc); c = number of size classes; Nj = the number of individuals that developed into instar j; * = mean individual dry weight biomass (mg) of 20-21 mm instars.

# CHAPTER THREE: RECIPROCAL-RELOCATION AND RECOLONIZATION EXPERIMENTS

(Mike Shaver, Fred Govedich, and Joe Shannon)

## INTRODUCTON

Reciprocal transplants of cobble with associated biota were conducted between Lees Ferry (0.0 km) and Cathedral Island (4.8 km downstream) to measure changes in biotic communities in reciprocal habitats. Recolonization of cobble by associated biota following desiccation is tested in the channel and zone of fluctuation at Lees Ferry and Cathedral Island.

## METHODS

### In Situ Reciprocal-Relocation Experiments

On May 17, 1993, 100 cobbles (10-30 cm diameter) with associated biota were collected from the permanently wetted channel (<142 $m^3$ $s^{-1}$) at Lees Ferry and transplanted at Cathedral Island. Cobbles were placed in a 10 x 10 grid below the zone of fluctuation (<142 $m^3$ $s^{-1}$) and the corners of the grid were painted for later location of grid. Likewise, 100 cobbles with associated biota from Cathedral Island were transplanted upstream to the Lees Ferry cobble bar. At the initial incubation, twenty additional cobble from the river channel at each site were sampled as controls. At monthly intervals for three months, 20 samples were randomly collected from each grid with a circular 20 $cm^2$ template. Collections were transported to the Aquatic Biology Laboratory at Northern Arizona University in the dark on ice for processing. At each sampling, 20 control cobble were collected from below the 142 $m^3$ $s^{-1}$ the channel at both sites.

### In Situ Recolonization Experiments

On October 10, 1992, 220 cobble each were collected from the channel (142 $m^3$ $s^{-1}$) at Lees Ferry and Cathedral Island. The bottoms of these cobbles were numbered with paint and placed above the high water mark (565 $m^3$ $s^{-1}$) to allow desiccation of associated biota. Twenty additional control cobbles from the channel were sampled at Lees Ferry and Cathedral Island. On May 17, 1993 (219 days of desiccation), samples were collected with a circular 20 $cm^2$ template from 20 cobble prior placement into grids. At both sites, 100 cobbles were submerged in the channel at <5,000 cfs to insure continuous submergence. Another 100 cobble were placed within the zone of fluctuation (140 to 565 $m^3$ $s^{-1}$) at 340 $m^3$ $s^{-1}$. Periodic submergence in the fluctuating zone was monitored with Ryan thermisters. Again, at both sites 20 control cobble were taken from the channel and sampled at the time of placing the grids.

All macroinvertebrates including lumbricids, oligochaetes, simuliids, chironomids, gastropods, and Gammarus lacustris were sorted from each sample. Macroinvertebrates were oven-dried at 60°C for 48 h to constant weights. Algal categories including Cladophora, Oscillatoria, and miscellaneous algae were saved as a composite for periphyton.

The Cladophora sample was placed in 40 ml of filtered river water and agitated for 1 min. The composite were poured through a 0.5 mm screen to separate macroalgae from epiphyton. The screen was rinsed with filtered river water to remove additional epiphyton from sample. Macroalgae (Cladophora) were remove from screen and blotted on a paper towel. Macroalgae were placed in crucibles and oven-dried to a constant weight. The epiphyton solution was swirled for 3-4 sec in beaker to suspend epiphyton. The suspended epiphyton was filtered onto Whatman GF/C glass microfibre filters (0.45$\mu$). Filters were oven-dried at 60°C for 48 h to a constant weight. Filters were ashed at 500°C for 1 h in crucibles and ash weights were obtained. Filters were saved for compositional analyses of epiphyton.

## RESULTS AND DISCUSSION

### In Situ Reciprocal-Relocation Experiments

The relocated Oscillatoria covered cobble from Cathedral Island at Lees Ferry had significantly less plant biomass ($p<0.001$) than control cobbles sampled at Lees Ferry after three months of incubation (Fig. 8). The clear water environment at Lees Ferry enabled Cladophora to replace Oscillatoria, but not to levels of control cobbles at Lees Ferry after three months. Cladophora biomass on initial substrates was neglible, but after 3 months Cladophora made up 59% of the algal community. In contrast, Oscillatoria comprised nearly 100% of the algal community on initial substrates and only 38% after three months. Furthermore, total animal biomass and epiphytic diatoms associated with Cladophora were significantly less ($p = 0.015$) on relocated substrates than these biota on control cobbles at Lees Ferry.

There was no significant difference ($p = 0.08$) in total plant biomass between Cladophora covered cobbles transplanted from Lees Ferry to Cathedral Island compared to control cobbles (Fig. 9). Cladophora and periphyton remained dominant on the relocated substrates throughout the 3 month incubation period at Cathedral Island. Cladophora biomass on initial substrates made up 96% and

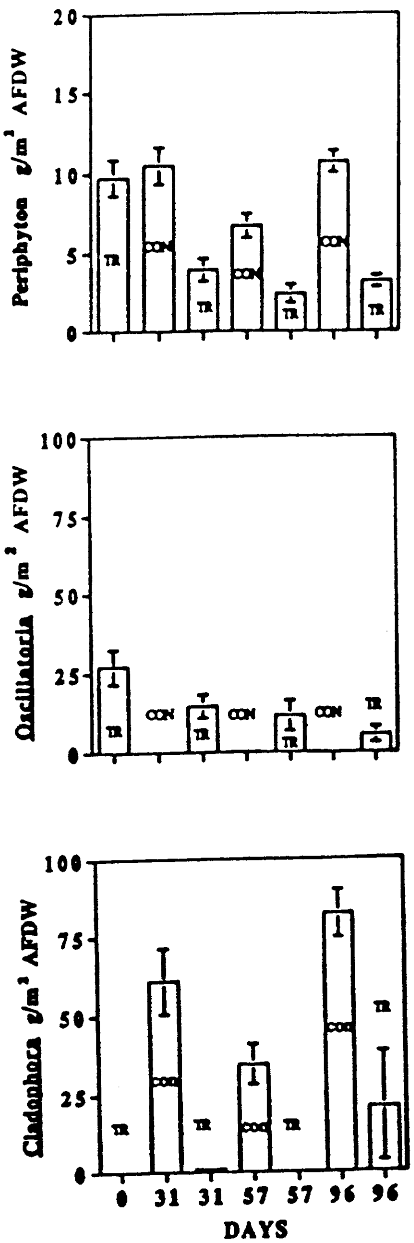



Figure 8. Relocation treatments at Lees Ferry (RKM 0.0), Colorado River, Arizona, were incubated for 96 days under clear water conditions. Cladophora has increased from negligible biomass to 59% of the algal community. Oscillatoria biomass has decreased from nearly 100% to 38% of the algal community. Epiphytic diatoms (periphyton) has decreased with the disturbance by relocation and is one/third of the control levels after the 96 days of incubation in a clear water environment.(con = controls; TR = treatments). Standard error bars are provided.

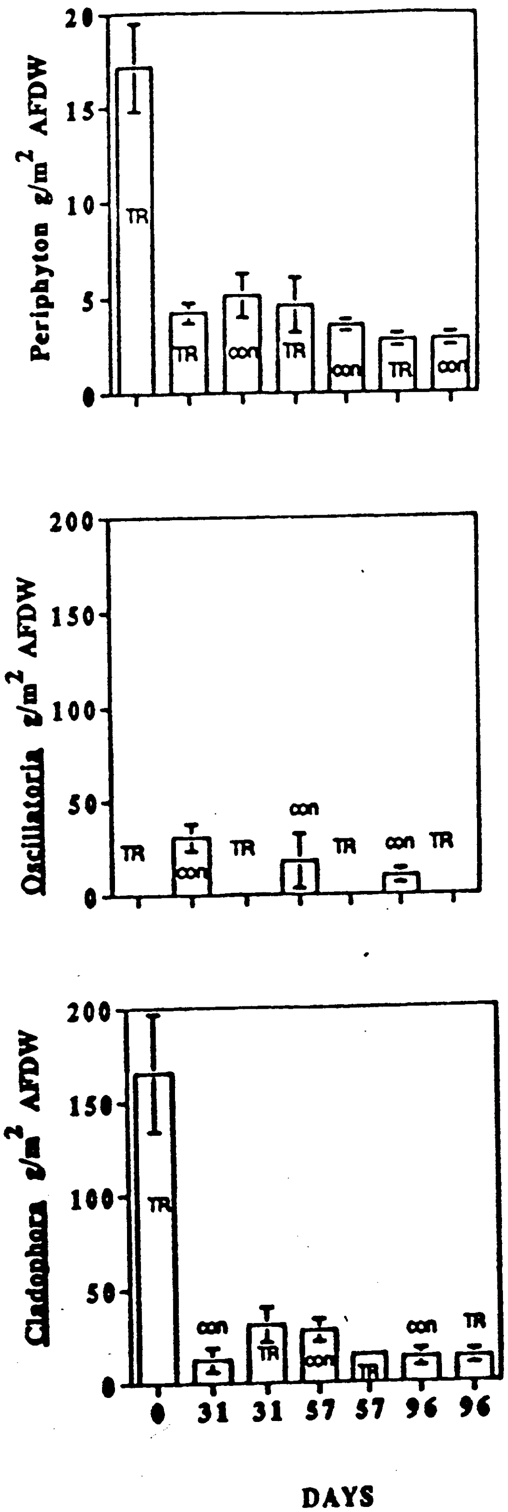



Figure 9. Relocation treatments at Cathedral Island (RKM4.8), Colorado River, Arizona, were incubated for 96 days under clear water conditions. Cladophora and its associated periphyton remained dominant on the relocated substrates. Cladophora composed 96% of the biomass at the start of the experiment and 74% after 96 days. Oscillatoria biomass has not changed significantly after 96 days. (con = controls; TR = treatments). Standard error bars are provided.

74% after three months incubation. Control substrates at Cathedral Island also showed an increase in Cladophora biomass ranging from negligible to 34% after 3 months. During the three month incubation period at Cathedral Island, water was relatively clear for 90% of the time. This suggests that Oscillatoria is unable to establish control levels under clear water conditions. At Cathedral Island, Cladophora, epiphytic diatoms and total animal biomass were similar to control substrates.

## In Situ Recolonization Experiments

After 219 days of desiccation there was negligible Cladophora biomass on cobbles. Following five months of re-submergence at Lees Ferry there was an average of 18.7 g $m^{-2}$ AFDW of Cladophora on the the desiccated cobbles; i.e., only 11% recovery of Cladophora compared to submerged controls (178.2 g $m^{-2}$ AFDW). Similar experiments at Cathedral Wash showed only a 2% recovery compared to controls.

# CHAPTER FOUR: ORGANIC DRIFT

(Peggy Benenati, Mike Shaver,
Joe Shannon, and Kevin Wilson)

## INTRODUCTION

Benthic organisms in streams are passively dislodged from substrates during both high and variable flows (Brittain and Eikeland 1988). Drift may also enable organisms to actively escape unfavorable conditions and colonize new habitats. We examined the importance of regulated flows on the abundance and composition of organic drift in the Colorado River ecosystem.

## METHODS

### Down River Drift

Drift was collected on seasonal river trips from sites at or near sampling stations in the late afternoon and early morning to examine the effect of the changing hydrograph on drift biomass. USGS drift protocol was followed in September 1992 and January and March 1993. Surface samples were collected with a circular net (140 cm long, 48 cm opening, 1 mm nylon mesh) towed behind a boat for 10 min. River bank drift collections were also made with a triple drift net with a 10 cm opening constructed of 0.5 mm nylon mesh for one h. Water velocity was recorded at the net mouth for volumetric calculations during all collections. These samples were perserved in 70% ETOH, oven-dried to a constant weight and ashed for ash-free dry weight (AFDW) calculations.

June and September 1993 collections were made with the 48 cm net from the river bank for at least 10 min. Three replicates were collected in the late afternoon and early morning and sorted in the field into the following categories; Gammarus lacustris, other macroinvertebrates, detritus, Cladophora, and other algae/macrophytes. Densities of G. lacustris, chironomids, simuliids and the remaining combined macroinvertebrates were recorded while sorting. Samples were oven-dried to a constant weight and converted to g $m^{-3}$ $s^{-1}$.

### Lees Ferry Drift

The effect of discharge on drift was examined at Lees Ferry, AZ (0.0 RKM) with a circlular net (140 cm long, 48 cm diameter opening) constructed of 1 mm nylon mesh. The net was held at the surface with a float and deployed off a navigational buoy so each set would be in the same position within the channel.

Collections were taken at six hour intervals starting at 0600 hrs for five days. For the first three days (May 29-31, 1993) discharge was held steady at 226 $m^3s$ (Fig. 10). Two days of normal flows (140 to 280 $m^3 s^{-1}$) were sampled starting at 0000 hrs on June 1. Current velocity was measured with an electronic metering device before and after each collection for volumetric calculations.

Cladophora Drift Packets

Packets of drifting Cladophora glomerata with associated macroinvertebrates and epiphyton were sampled from the tailwaters of Glen Canyon Dam in the Colorado River through Grand Canyon at six sites (Fig. 1). Collections were made at the same sites as benthic samples including an additional site the Glen Canyon gauging station (-22.4 RKM). Twelve to 20 packets were gathered with a long-handled dip net (30 X 25 cm with 1 mm mesh net) at mid-channel from the surface to a depth of 1 m. Twenty samples were also collected above and below Badger Creek Rapids (12.8 RKM) to ascertain the affect of hydraulics on Cladophora packets. Samples were sorted in accordance with benthic collections. Epiphyton samples were removed from dried Cladophora by aggitating the Cladophora packets for two minutes in 200 ml of filtered river water. Hyrax mounts were made from diluted solutions for density and composition estimates. A minimum of 200 cells/Whipple grid were counted.

RESULTS AND DISCUSSION

Down River Drift

There was a shift in composition of drift between Marble Canyon (RKM 0.0-98.9) and Grand Canyon (RKM 99-362) during interim flows. Drift through Marble Canyon was dominated by Cladophora with G. lacustris and chironomids, while drift in Grand Canyon (RKM 99-362) was dominated by detritus with simuliid larvae. Drift response to dam regulation appears to be minimal during low flow months. Our collections were made only during low flow months when we sample the benthos. Next summer we plan to match drift collections at Lees Ferry with our secondary production collections to determine the amount of G. lacustris lost to drift during a high flow month such as July.

Lees Ferry Drift

Steady flows (227 $m^3s$) at Lees Ferry were examined to deterime the rate of behavioral drift in comparison to flow related drift. Cladophora and macrophytes showed a significant diurnal shift in biomass drift ($F_{3,51} = 4.16$, p

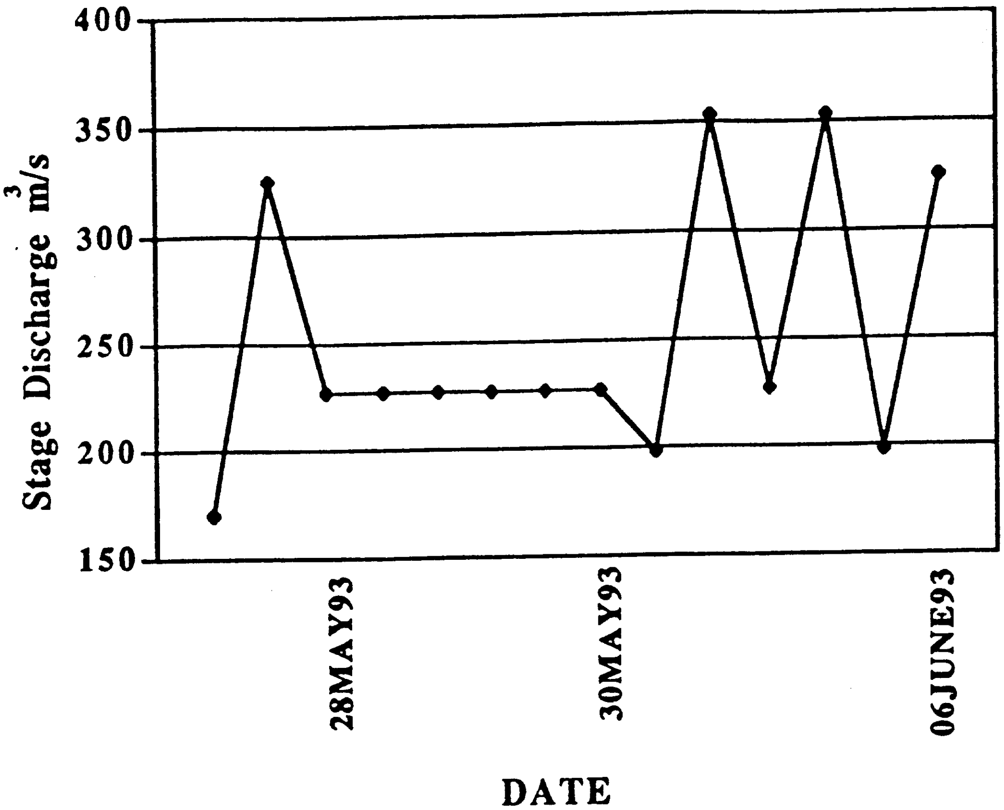



Figure 10. Colorado River stage discharge during drift collection period at Lees Ferry, AZ . USGS data courtesy of GCES office and Jeanie Korn.

= 0.01; $F_{3,51} = 2.82$, $p = 0.04$). Mean AFDW biomass of drifting Cladophora between 0600 and 1200 hrs was 1.3 g $m^{-3}$ $s^{-1}$, while collections from 1800 and 2400 hrs were 1.0 g $m^{-3}$ $s^{-1}$. Neither macroinvertebrate biomass or abundance changed significantly throughout the collection period.

Multivariate analysis of interim fluctuating flows following the three day steady flows had an overall effect on algae and macroinvertebrate biomass and density regarding stage discharge at the time of collection (Wilks' Lambda; $F_{24,70} = 2.9$, $p < 0.001$; Table 5). However, univariate analysis of categorical data was not significant for all taxonomic groups. Only macrophytes, Cladophora, detritus, Oligochaeta, and gastropods showed a significant positive correlation with stage discharge ($p < 0.001$).

Multivariate comparisons between steady and interim fluctuating flows showed a significant difference between each data set by stage for algal biomass and macroinvertebrate densities (Wilks' Lambda; $F_{(3,84)} = 33.1$, $p < 0.0001$; Fig. 11). Macroinvertebrate biomass did not show a significant change between steady and fluctuating flows.

Cladophora was the dominant plant found in the drift and composed 98.5% of the plant biomass for both steady and fluctuating flows. Potamogeton and algal fragments of Rhodochorton, Chara, and Batracospermum comprised the remaining 1.5%. We estimated approximately 428 g $s^{-1}$ of plant material drifts from Lees Ferry at a mean annual discharge of 280 $m^3$ $s^{-1}$.

Mean biomass and abundance of drifting macroinvertebrates from both collection periods were 0.015 g $m^{-3}$ and 49.5 animals $m^{-3}$. Channel wide estimates at 283 $m^{-3}$ $s^{-1}$ for drifting macroinvertebrate biomass is 4.5 g $s^{-1}$. Gammarus and chironomids comprised 33% and 62%, respectively; of the drifting biomass. These results are similar to the drift data reported by Leibfried and Blinn (1988). Perry and Perry (1986) found that macroinvertebrate drift in the Kootenai River, Montana, reached similar densities during the rising arm of the hydrograph.

Data for steady flows suggest that macroinvertebrates in the tailwaters of Glen Canyon Dam do not exhibit behavioral drift. Typically, invertebrate populations in non-regulated rivers show strong diel maxima in stream drift (Brittain and Eikeland, 1988). The dramatic diel changes in hydrographs in the tailwaters of Glen Canyon Dam may have selected against organisms that undergo diel behaviors. Substrate selection studies by Shannon et al. (1994) substantiate the lack of diel behavior by G. lacustris at Lees Ferry. Furthermore, Armitage (1977) also found that chironomids and baetids lacked a diurnal drift pattern in the regulated RiverTees in Great Britain. Diurnal drift patterns for algae may be

Table 5. Categorical comparison of biomass ($g/m^3$ ash-free dry weight) and abundance ($animals/m^3$) for aquatic benthos in stream drift during steady and interim fluctuating flows at Lees Ferry, Arizona. Multivariate analyses revealed a significant overall difference between the two collection periods (Wilks' Lambda $F_{3,85} = 44.1$, $p < 0.0001$).

| Taxonomic Catagories | Steady flows ($227\ m^3$) | Interim fluctuating flows ($158\text{-}354\ m^3$) |
|---|---|---|
| Lumbricids | 0.0 $g/m^3$<br>0.0 $animals/m^3$ | 0.00001 $g/m^3$<br>0.1 $animals/m^3$ |
| <u>Gammarus</u> | 0.00149<br>1.7 | 0.00638<br>4.8 |
| Oligochaeta | 0.00009<br>2.4 | 0.00039<br>6.6 |
| Simuliids | 0.00012<br>0.1 | 0.0<br>0.0 |
| Chironomids | 0.00449<br>31.7 | 0.00889<br>58.0 |
| Gastropods | 0.00017<br>0.08 | 0.00016<br>0.01 |
| Other Invertebrates | 0.00048<br>0.2 | 0.00047<br>0.7 |
| <u>Cladophora</u> | 0.58314 | 2.28272 |
| Detritus | 0.02491 | 0.03294 |
| <u>Oscillatoria</u> | 0 | 0 |
| Other algae | 0.01084 | 0.03574 |

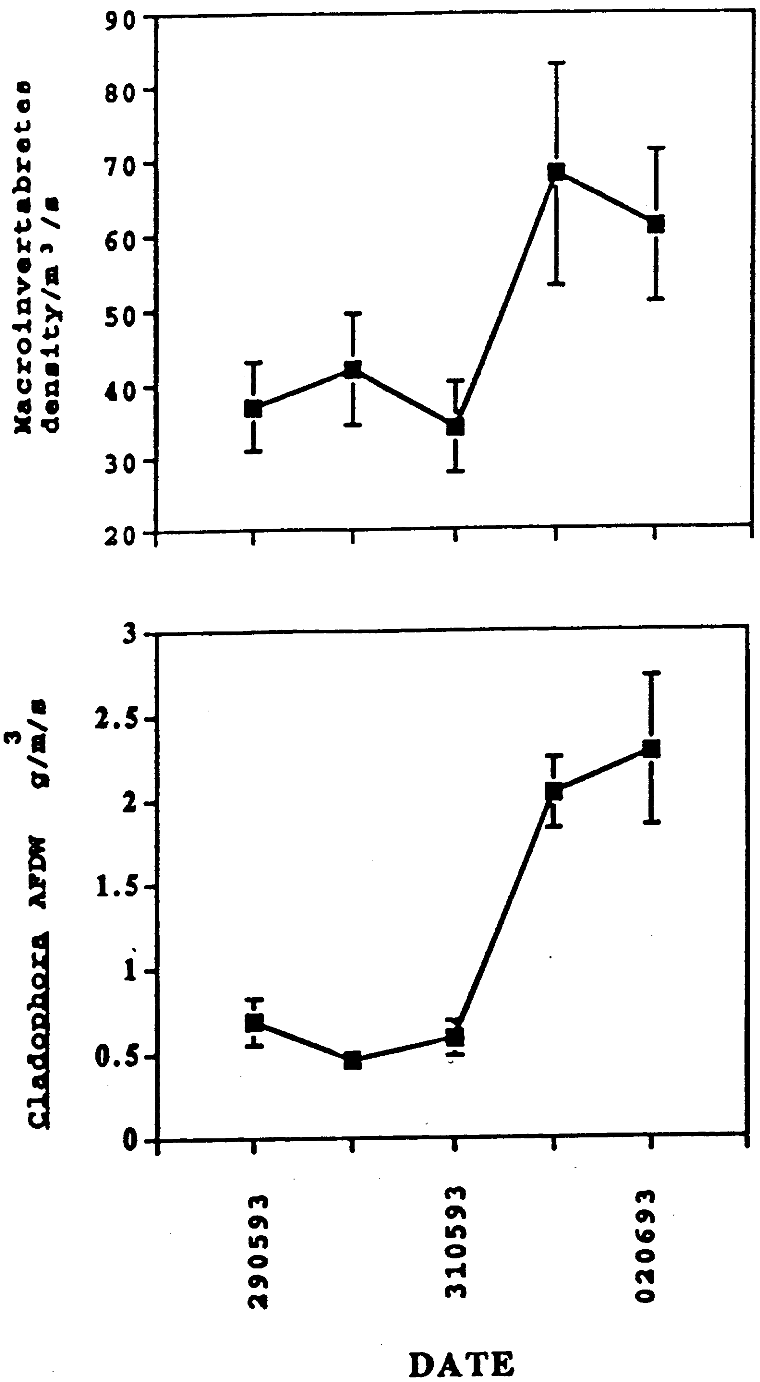



Figure 11. Comparison of steady (227 $m^3 s^{-1}$) versus interim fluctuating flows (158-354 $m^3 s^{-1}$) by daily totals for Cladophora AFDW and combined macroinvertebrate density. There was a significant overall difference between these two collection periods (Wilks' Lambda $F_{3,85} = 44.1$, $p<0.0001$). Standard error bars are provided.

explained by an increase in photosynthetic oxygen trapped by filaments thereby raising filaments into the water column where they were removed by hydraulic stress. Apparently, a large number of the macroinvertebrates enter stream drift in the tailwaters of Glen Canyon Dam while clinging to the Cladophora that has been removed by hydraulic stress.

Our data also show that terrestrial insects are not numerically important in stream drift in the mainstem of Glen Canyon Dam tributaries. In contrast, Armitage (1977) found that terrestrial insects comprised about 10% of the annual drift biomass in the regulated RiverTees in Great Britain.

Cladophora glomerata drift packets

Standing crop of Cladophora drift changed significantly both spatially ($F_{7,371} = 11.56$; $p < 0.0001$) and temporally ($F_{7,371} = 6.93$; $p = 0.013$) along the Colorado River. Highest standing crop was recorded at Lees Ferry with a significant drop below the Paria River confluence (1.0 RKM), and again at the 85.0 RKM site (Fig.1).

The effect of hydraulics on Cladophora packet processing was measured on 20 packets of Cladophora above and 20 below Badger Creek Rapids (12.8 RKM), the first large rapid (4.6 m vertical drop) below Lees Ferry (Stevens 1983). The turbulence at Badger Rapid significantly reduced the size of Cladophora packets ($F_{1,40} = 6.45$; $p = 0.015$) with mean AFDW above the rapid = 0.046 g compared to 0.012 g below. No macroinvertebrates were found in the Badger Creek Rapid collections. Chironomid biomass was the only macroinvertebrate to show a significant difference in AFDW spatially ($F_{1,371} = 3.945$; $p < 0.000$). Chironomid larvae reached maximum density at Lees Ferry (0.00014 AFDW) and dropped 10-fold by 5 RKM (0.00002 AFDW). These values were based on midge larvae, pupae, exuvea, and pharate individuals. Chironomid larvae were the only macroinvertebrates to show a significant temporal variation ($F_{4,371} = 5.992$; $p = 0.015$). Chironomid standing stock in Cladophora packets was highest in summer with 0.00602 AFDW, while other seasons showed a marked, but uniform reduction; i.e., fall 0.0009, winter 0.00012, and spring 0.00010.

There was a significant reduction in epiphyton density within Cladophora packets with distance downstream from Glen Canyon Dam ($F_{3,128} = 8.9$; $p < 0.01$, Fig. 12). Epiphyton density was highest at Lees Ferry (450,000 cells/mg, AFDW Cladophora) but dropped by 40% below the Paria confluence at Two-Mile Wash and 64% at Tanner which is below the confluence of the Little Colorado River. Glen Canyon site had similar densities as Two-Mile Wash, but was lower than

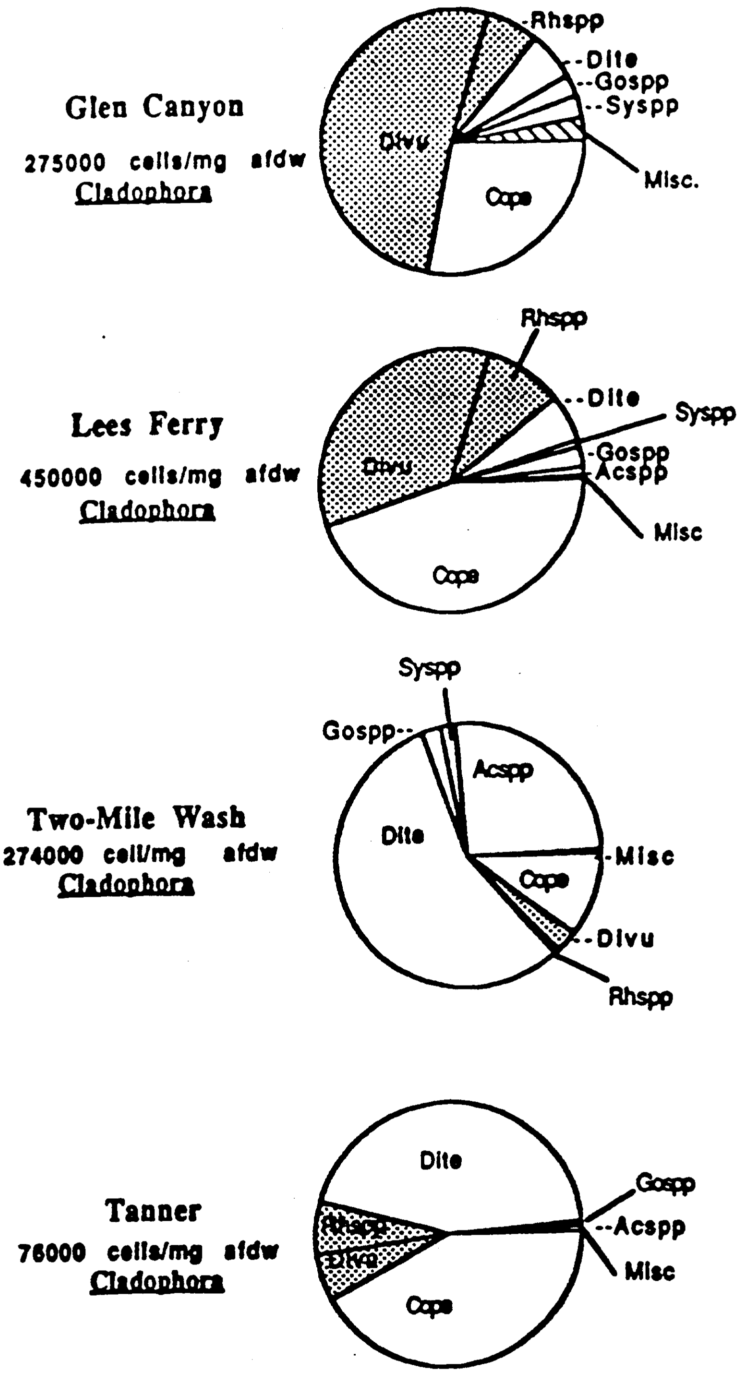



Figure 12. Comparison of epiphytic diatom densities and composition on Cladophora drift packets at four collection sites. There is a significant shift from up-right to adnate species with distance from Glen Canyon Dam, and a decrease in density from Lees Ferry ($p<0.01$). Taxonomic codes; Cope = Cocconeis pediculus, Divu = Diatoma vulgare, Rhspp = Rhoicosphenia spp., Dite = Diatoma tenue, Gospp = Gomphonema spp, Syspp = Synedra spp., Acspp = Achnanthes spp. and Misc. are for other taxa. Stippled taxa are up-right species, open taxa are more adnate and hatched are other taxa.

Lees Ferry impart due to the impact of dam regulation and variable Lake Powell water chemistry.

Diatom composition showed significant changes by site with an overall decrease in up-right compared to adnate taxa with distance downstream ($F_{7,128} = 4.88$; $p < 0.0001$). Dominant up-right taxa included Rhoicosphenia curvata and Diatoma vulgare, while Cocconeis pediculus, Gomphonema spp., Synedra spp., Diatoma tenue and Achnanthes spp. comprised taxa with more adnate and/or intermediate physiognomy. The importance of this change in diatom composition relates to the fact that up-right taxa are more easily grazed by macroinvertebrates than adnate forms (Colletti et al. 1987, Blinn et al. 1989) and are more susceptible to abrasion by suspended sediments and hydraulic stress (Hardwick et al., 1992). The greatest difference in composition by site was between Glen Canyon and Lees Ferry where Diatoma vulgare was replaced by Cocconeis pediculus at Lees Ferry. There was no significant difference in composition betweeen Two-Mile Wash and Tanner Wash ($p < 0.05$).

## CHAPTER FIVE: EFFECTS OF WINTER DESICCATION

(Joe Shannon and Dean W. Blinn)

### INTRODUCTION

The biological effects of desiccation may be confounded by freezing during winter low flows. Dudgeon et al. (1989, 1990) reported that freezing reduces photosynthesis, cell membrane permeability, frond growth, and overall biomass in marine intertidal algal communities, however, experimental investigations quantifying the effects of freezing on freshwater algae are limited. We hypothesized that freezing in the "intertidal zone" of regulated rivers has similar negative impacts on freshwater algal communities.

### METHODS

The combined result of freezing and desiccation on Cladophora glomerata biomass, chlorophyll a, and macroinvertebrate abundance was tested at Lees Ferry on 10-11 February, 1993. This protocol was designed to isolate the combined effects of freezing and desiccation from ultra violet light. Thirty cobbles (~90 cm in circumference), with an associated Cladophora community, were translocated from below the 141 $m^3/s$ stage to the 280 $m^3/s$ stage at 1500 h on 10 February. All translocated treatment cobbles were placed at a depth of 15 cm in the shade of large boulders to reduce potential U.V. damage prior to night desiccation. A Peabody Ryan scroll thermistor was secured in the middle of the treatment cobbles to determine average duration of submergence, desiccation and freezing by comparison of water and ambient temperatures. Discharge reached peak flow at 2100 h. Percent cloud cover and humdity were recorded.

On 11 February at 0800 h, prior to contact with direct sunlight, the treatment cobbles were resubmerged to a depth of about 15 cm so that cobbles would be rinsed in accordance with the raft experimental protocol (Blinn et al. 1992). Treatment cobbles were sampled at 1600 h on 11 February. Paired samples were scraped (20 $cm^2$), one for Cladophora biomass and the second for chlorophyll a and macroinvertrebrate numeration. The second sample pair was protected from direct sunlight and placed on dry ice. Controls were established from 30 cobbles randomly collected from below the 141 $m^3/s$ stage, while cobbles were being translocated on 10 February and at the completion of the experiment.

Cladophora ash-free dry weights (AFDW) were calculated from the following equation:

$$AFDW = 0.00048 + 0.35606(\text{dry wt})$$
$$F = 8336.5;\ p < 0.00001;\ r^2 = 0.934;\ n = 593$$

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

## RESULTS AND DISCUSSION

Winter desiccation (i.e., three hours of night freezing during eight hours of exposure) resulted in a significant loss of Cladophora biomass and chlorophyll a (Fig. 13). No significant difference was determined between controls for Cladophora biomass so they were combined for analysis of variance for treatment samples ($F = 0.67$; df = 1,57; $p = 0.41$). Mean AFDW for Cladophora decreased from 80.1 g in controls to 44.5 g in desiccated samples, a significant decrease ($F = 9.11$; df = 1,87; $p = 0.003$). Controls for chlorophyll a showed a significant difference ($p = 0.007$) so they were not pooled.

Chlorophyll a decreased significantly between control samples taken at the end of the experiment (8714.2 mg/$m^2$) and the treatment samples (3622.69 mg/$m^2$; $F = 12.07$; df = 1,57; $p = 0.0009$). However the control collection (3787 mg/$m^2$) taken at the start of translocation did not show a significant difference with the initial desiccation samples ($F = 0.01$; df = 1,55; $p = 0.92$).

There was no significant change in macroinvertebrate abundance between control and desiccated treatment cobbles (Wilks Lambda = 0.93; $F = 1.38$; df = 4,84; $p = 0.24$). Although there were 400 $m^{-2}$ lumbricids, 175 $m^{-2}$ Gammarus, 75 $m^{-2}$ oligochaetes, and 325 $m^{-2}$ gastropods total for control samples the desiccated samples had only 75 $m^{-2}$ Gammarus. Lack of significance can be attributed to the high variance between samples due to the patchy nature of the biotic community at Lees Ferry.

Based on thermistor readings, treatment cobbles were exposed for eight hours with only 3 hours below freezing (-2°C). Ambient temperature was always below river temperature of 6.5°C. Relative humidity was 60% at 0730 hrs at the end of the exposure period. Discharge ranged from 400 $m^3$s on February 10 to a 255 $m^3 s^{-1}$ the following day.

Nighttime winter desiccation exerts similar effects on Cladophora biomass as does summer desiccation (Blinn et al. 1992. Only 3 hrs of freezing reduced biomass by 50%, which is comparable to summer losses (48%) after a 12 hr exposure. Chlorophyll a showed a significant decrease from final controls. Dudgeon et al. (1989,1990) have shown negative effects on rates of photosynthesis, cell

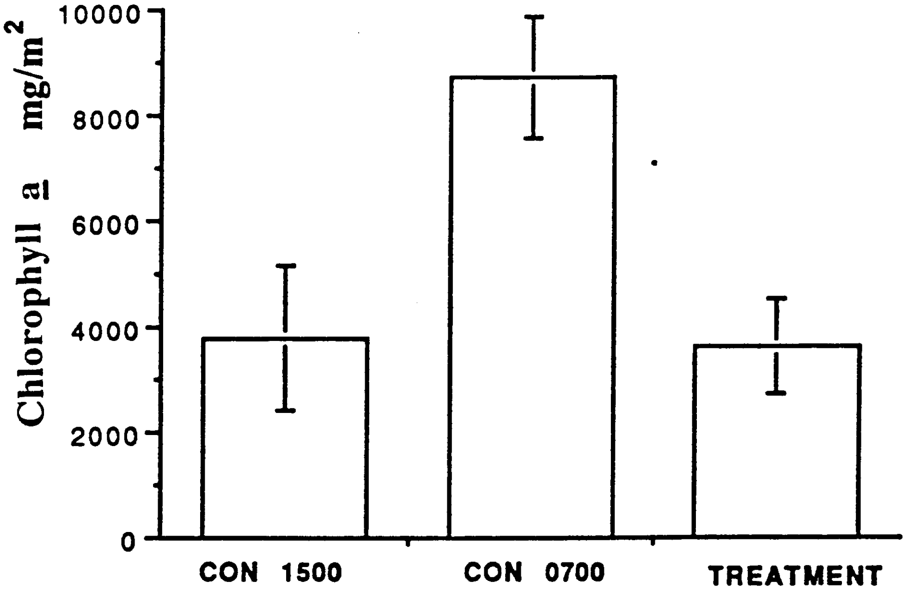



Figure 13. Winter desiccation on Cladophora glomerata biomass (AFDW) and chlorophyll a ($mg/m^2$) after eight hours of exposure and three hours of freezing. Cladophora biomass and chlorophyll a were significantly reduced ($p = 0.001$) from final control treatments. CON 1500 = initial controls at 1500 hr and CON 0700 = final controls.

membrame permeability, frond growth and overall biomass in freezing experiments with intertidal algae. Filaments were sticky to the touch, suggesting cell breakdown, but few were bleached. Data for macroinvertebrate densities were not conclusive due the patchiness in the benthic community at Lees Ferry. However, there was a strong pattern for loss of macroinvertebrate biomass (93%) following one winter night exposure. Repeated desiccation and increasing the sample size may resolve this discrepency.

## CHAPTER SIX: MANAGEMENT CONSIDERATIONS

Our data suggest that river regulation (340 $m^3 s^{-1}$ to 565 $m^3 s^{-1}$) will reduce the effect of natural flooding. Therefore, in order to obtain the maximum accumulation of benthic biota in the mainstem there should be a period of low discharge with minimal fluctuation for at least two to three months following natural peak winter flows. The direct effects of low discharge include higher water temperatures and reduced drift within the mainstem, and potentially greater light penetration to benthic substrates.

The accumulation of fine sediments through interim flows has allowed aquatic macrophytes (Potamogeton) to colonize these now soft bottom benthic substrates. Higher aquatic macrophytes have always been present at low densities in the mainstem, but with interim flows, these macrophyte populations have dramatically increased. The significance of this increase lies in the potential encroachment of Cladophora. These macrophytes host approximately two-fold fewer epiphytic diatoms than does Cladophora, and therefore provide overall less food for chironomids and Gammarus in the Colorado River ecosystem. These higher aquatic macrophytes may, however, provide improved forage for waterfowl. This modification needs to be closely assessed in the long term monitoring of this system.

River regulation has a signficant impact on downstream export of benthic biomass. Our drift studies at Lees Ferry indicate that fluctuations between 6,000 to 13,000 cfs show at least a two-fold increase in organic stream drift compared to steady 8,000 cfs flows. To the best of our knowledge this energy is not directly available to native and exotic fishes below the Paria River due to tributary influence.

Based on preliminary data, highest secondary production for Gammarus is expected to occur during low volume months. These low volume months include fluctuations between 170 $m^3 s^{-1}$ and 285 $m^3 s^{-1}$. Although higher flows provide more submerged substrates, these flows also remove Gammarus from benthic substrates due to increased shear stress. Upper threshold flow levels at which Gammarus is lost to drift needs to be established due to the importance of this invertebrate as an intermediate link between primary producers and fish. These thresholds for Gammarus and other benthos (Cladophora glomerata, epiphtyic diatoms, and associated macroinvertebrates) can be accomplished in flume experiments for predictions of planned flood effects.

Initial recolonization rates by Oscillatoria from desiccated cobbles are faster than recolonization rates for Cladophora in the submerged zone during interim flows (140 $m^3 s^{-1}$ to 565 $m^3 s^{-1}$). Oscillatoria gained 23.4 $g/m^2$ (AFDW) biomass over a 5 month period in the fluctuation zone at Lees Ferry. In contrast, there was no significant recolonization of Oscillatoria or Cladophora in the zone of fluctuation
during research flows (140 m3 s-1 to 850 $m^3 s^{-1}$). This suggests that interim flows allow productivity to increase above the minimum discharge.

Nightime desiccation during the winter is as detrimental to the aquatic benthos as summer daytime desiccation at Lees Ferry. There was a significant loss in Cladophora biomass and chlorophyll a after only 3 hours of freezing during reduced flows.

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