THE EFFECTS OF GLEN CANYON DAM ON THE AQUATIC FOOD BASE IN THE COLORADO RIVER CORRIDOR IN GRAND CANYON, ARIZONA

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ABSTRACT

The purpose of this study was to provide seasonal baseline data on the aquatic food base in the Colorado River ecosystem in Grand Canyon downstream from Glen Canyon Dam. We examined the taxonomy, distribution, phenology, biomass, dietary requirements, and ecological roles of aquatic algal and macroinvertebrate species to assess the impacts of dam operations on this fluvial ecosystem. This study will serve as a key element for the Glen Canyon Environmental Study (GCES) Interim Flow Aquatic Food Base Monitoring Program for the Colorado River ecosystem.

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. 2) The filamentous green alga, Cladophora glomerata, was dominant above the Paria River and Oscillatoria spp., crustose blue-green algae (Cyanobacteria), was dominant below the Little Colorado River. 3) Macroinvertebrate biomass and abundance are strongly negatively correlated with distance from the dam, and are positively correlated with Cladophora. 4) Wide reaches had higher standing stocks of macroinvertebrates than narrow reaches for both pool and riffle habitats. 5) The aquatic Diptera assemblage was dominated by chironomids (8 common species) and Simuliium arcticum, the principal simuliid species. 6) Aquatic Diptera diversity is influenced by channel geomorphology. 7) Gammarus lacustris (Amphipoda) is largely replaced by chironomid larvae below the Paria River, and by simuliid larvae below the Little Colorado River. 8) Cladophora serves as a substratum for epiphytic diatoms which make up a major portion of the diet of chironomid larvae and Gammarus. 9) Over 50% of the algal biomass and at least 75% of macroinvertebrate biomass were removed after repeated 12-hr exposures over a five-day period in both day and night experimental treatments at Lees Ferry. 10) Daily observations revealed a significant reduction in macroinvertebrate biomass after the first day and a significant loss in algal biomass after the second day of experimental exposure treatments. 11) After five days of recovery, there was no significant difference in macroinvertebrate biomass on control rocks and re-submerged treatment rocks, however, there was significantly lower Cladophora biomass on re-submerged treatments compared to controls. 12) Potential ecosystem energy for epiphytic diatoms, Gammarus, and chironomid larvae were estimated for the Lees Ferry reach for low, medium, and high flows.

To evaluate the impacts of the EIS flow alternatives on the lower aquatic trophic levels, we developed a stage to area model of ecosystem energy for the Lees Ferry cobble bar (RK 0.6). This site was selected because it is representative of the tailwaters fishery and because cobble bars are biologically productive habitats in the Colorado River ecosystem. We used the Map and Image Processing System (MIPS), to estimate the area inundated by flows of 142 m^3/s (5,000 cfs), 227 m^3/s (8,000 cfs), 425 m^3/s (15,000 cfs) and approximately 807 m^3/s (28,000 cfs).

Approximately 67,981 m^2 of river channel occurs below 142 m^3/s at Lees Ferry, while 44,100 m^2, 34,571 m^2, and 12,220 m^2 of cobble bar area occurs between 142-227 m^3/s, 227-425 m^3/s, and 425-807 m^3/s, respectively. We used standing crop/m^2 field data and energy/gm ash-free dry mass data (Chapter 5) for food base components (epiphytic diatoms, chironomid larvae, Gammarus) to estimate ecosystem energy/m^2 for this cobble bar. This model assumes that the aquatic habitat below 142 m^3/s (our lowest cobble bar collection stage) is uniform.

The projected amount of energy (joules) available as epiphytic diatoms, chironomid larvae, and Gammarus from this wide reach at three different flow stages is illustrated in Figure 5.6. The stage elevation below 142 m^3/s supports an estimated ecosystem energy of 18.1 x 10^9 joules, while a base flow stage of 227 m^3/s supports 28.5 x 10^9 joules, a base flow of 425 m^3/s supports 37.6 x 10^9 joules, and that of 807 m^3/s supports 40.9 x 10^9 joules. Thus the highest potential amount of ecosystem energy (epiphytic diatoms, chironomid larvae, Gammarus) occurs at high water flows (807 m^3/s), i.e., the greatest area of river channel is unundated. There is >2 times more potential ecosystem energy at flows of 807m^3/s than at 142 m^3/s and nearly 1.5-fold and 2-fold more energy at flows of ≤227 m^3/s and ≤425 m^3/s, respectively, for each biotic component at Lees Ferry (Fig. 5.6).

This model provides a preliminary estimate of potential biomass for major components of the food base at various research flows at Lees Ferry. These estimates may serve as a minimum estimate for the cobble bars in the reach from Glen Canyon Dam to Lees Ferry. This model does not apply to reaches downstream of Lees Ferry, where detailed areal analyses have yet to be applied to ecosystem energy estimates. The aquatic food base in downstream reaches is, at present, far less affected by exposure.

The protocol employed in this study is recommended for implementation as part of the interim and long-term monitoring program in the Colorado River ecosystem through Grand Canyon. This study will assist the National Park Service and the Bureau of Reclamation develop a comprehensive understanding of aquatic ecosystem dynamics under alternative flow regimes for the Glen Canyon Environmental Studies Phase II Environmental Impact Statement.

ACKNOWLEDGEMENTS

The Aquatic Diptera Project was a cooperative effort between several agencies and many talented researchers; we are grateful for their contributions. Glen Canyon Environmental Studies (GSES) provided the primary funding for the study. The Northern Arizona University "midge" staff was the cornerstone of our work. Jeanette Macauley supervised the chironomid preparation team of Teresa Del Vecchio, Gaye Oberlin, and Teresa Yates. Shawn Browning, Amis Holm, Lorraine Putnam, Mike Shaver, and Holly Williams were responsible for collection processing. Justin Carder and Clay Runck processed the trophic linkage portion of the study. The field staff completed seven river trips under the supervision of Dennis Silva with help from Doug Bechtel, Peggy Benenati, Allan Craig, Natasha Kline, P.A. Lauman, Thomas Martin, Norca Moore-Craig, Mary Moran, J.G. Schultz, J.A. Thomas, Perry Thomas, D.H. Willis, and Brenda Witsell. Peter Gambrill assisted with the Lees Ferry in situ experimentation. Grand Canyon Resource Management (NPS) staff assisted with the following activities: MIPS mapping, Lisa Kearsley; overflight photographs, Brian Cluer. GRCA NPS also provided 48 volunteers for field work. Glen Canyon Environmental Studies (BOR) staff of Judy Brown and Karal Malloy helped with logistical support. Allan Hayden, Bill Vernieu, and Mike Yard supplied light and water chemistry equipment and expertise. David Wegner arranged use of the MIPS system and project logistics. Earle Spammer from the Academy of Natural Sciences of Philadelphia completed a gastropod inventory of the river and tributaries, while Mark Wetzel from the Illinois Natural History Survey surveyed the annelids of the river and tributaries. James Sublette of Pueblo Science Associates, Pueblo, Colorado, identified chironomid larvae and R.V. Peterson of the Systematics Entomology Laboratory in Beltsville, Maryland identified simuliid specimens. Finally, we would like to thank Lorraine Putnam for her editorial comments on the final version of this document.

CHAPTER ONE: INTRODUCTION

Overview

Growing concern over the impacts of river regulation on environmental resources in the Colorado River corridor below Glen Canyon Dam encouraged the Department of Interior to initiate the Bureau of Reclamation's Glen Canyon Environmental Studies Phase II (GCES-II) and, most recently, the 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 (National Research Council 1987). Although management has focused on the stability of sediment deposits and fisheries, other critical ecological components of this system include the aquatic food base, especially phytobenthos, periphyton, and macroinvertebrates. Cladophora and its associated epiphyton have been identified as the trophically significant primary producers in the tailwaters reach (Usher and Blinn 1990, Hardwick et al. 1992). Among the macroinvertebrates, chironomid midges and simuliid black flies are cornerstone resource species, providing food for fish and terrestrial fauna. These taxa and introduced Gammarus lacustris link the aquatic and terrestrial components of this ecosystem (Stevens and Waring 1988). Management strategies for the aquatic trophic structure may differ from those for sediment or recreation. Consequently, the aquatic food base was examined to increase the data base on aquatic/terrestrial trophic relationships in the Colorado River ecosystem.

Studies in Grand Canyon

Blinn and Cole (1991) reviewed the literature on pre-and post-impoundment conditions in the Colorado River through Grand Canyon and reported no comprehensive food base collections from the river prior to Glen Canyon Dam, and relatively few published articles on the food base following closure of the dam in 1963. River regulation by Glen Canyon Dam decreased turbidity in the tailwaters and permitted increased algal growth on Colorado River-bottom substrata, changes which have apparently been responsible for the increased expansion of macroinvertebrate populations in the tailwater reach of Glen Canyon Dam.

The algal community in the Colorado River is made up of a diverse assemblage of diatoms that grow as epiphytes on the filamentous green alga, Cladophora glomerata (Czarnecki and Blinn 1978, Hardwick et al. 1992). Oscillatoria spp. (cyanobacteria or blue-green algae) are also important in the middle and lower reaches of Grand Canyon (Czarnecki et al. 1976). Few studies have examined the effects of river regulation on primary producers in the Colorado River ecosystem. Peterson (1986, 1987) reported that biomass and density of diatoms were reduced in the tailwaters of Hoover Dam as a result of disturbance from regulated flow. Blinn et al. (1989) examined the composition of the epiphytic diatom community on Cladophora in the tailwaters of Glen Canyon Dam at ≤12°C (hypolimnial) and >18°C (epilimnial) in laboratory circulation chambers. They reported a significant decrease in density for two numerically important diatoms (Rhoicosphenia curvata and Diatoma vulgare) when water temperature was elevated to >18°C. Both diatom species are important food for chironomids and Gammarus in the Colorado River ecosystem. Also, Usher and Blinn (1990) reported a significant loss in Cladophora from substrata in laboratory stream tanks after repeated 12-hr day exposures.

The Arizona State Game and Fish Department (AGF) was involved in a six-year program to investigate the fishery potential of the Colorado River after completion of Glen Canyon Dam (Stone and Queenan 1967; Stone and Rathbun 1968, 1969). In 1968, AGF biologists Stone and Rathbun (1968) reported 43 chironomid larvae in 102 Ekman dredge samples, equivalent to 10.2 midges/m^2 or a biomass of approximately 0.001 gm/m^2. Because of this low benthic food base, the AGF engaged in a program to introduce macroinvertebrates into the Colorado RIver. The organisms introduced into the Lees Ferry reach included: Decapoda (Orconectes, crayfish), Gastropoda (Physa and Stagnicola, snails), Odonata, Trichoptera, Diptera (Tipulidae and Chironomidae), Hemiptera (Notonectidae, Corixidae and Gerridae), Coleoptera (Hydrophilidae), and Annelida (Hirundinea). These introductions were not monitored for a sufficient duration to determine the success, and most taxa have not persisted in the river.

Presently, the aquatic macroinvertebrate fauna of the Colorado River corridor in the Grand Canyon is considered to be depauperate as compared to the fauna in tributaries within Grand Canyon and other river systems (Polhemus and Polhemus 1976, Stevens 1976 and pers. obs., Hofknecht 1981, Leibfried and Blinn 1988). Larval aquatic Diptera (Chironomidae and Simuliidae) in the Colorado River and its tributaries in the Grand Canyon play a large, if not over-whelmingly important role as food for fish, and adult Diptera feed hundreds of terrestrial insectivore species in the dam-regulated river corridor (Stevens and Waring 1988). Leibfried and Blinn (1986) reported: 1) chironomids made up more than half the biomass of macroinvertebrates in the river, 2) macroinvertebrate biomass decreased below the Little Colorado River (RM 98), from summer to winter, and was low in creek mouths relative to the mainstem, and 3) macroinvertebrate biomass was positively correlated with Cladophora biomass spatially and seasonally. They also observed that chironomid larvae were numerically dominant over Gammarus in Colorado River drift and comprised as much as 85% of drifting invertebrates.

Studies on River Regulation in the American Southwest.

Studies on the effects of river regulation on lower trophic levels in the southwestern United States are few, especially information on pre-impoundment conditions. McDonald and Dotson (1959) summarized physico-chemical and biological pre-impoundment conditions in the Green and Colorado Rivers prior to completion of Flaming Gorge Dam and Glen Canyon Dam, respectively and Woodbury (1959) summarized the flora and fauna in Glen Canyon prior to impoundment. Both reviews reported high summer water temperatures (>21°C) and wide seasonal and yearly fluctuations in turbidity which restricted algal and macroinvertebrate populations. Channel catfish were dominant in the Colorado River and redside shiner was the most abundant in the Green River. Pearson (1967) compared the macroinvertebrate fauna of lotic environments in the Green River below Flaming Gorge Dam, Utah, before and after impoundment. Macroinvertebrate densities were highest immediately below the dam (mean density = 68,321/m^2), but the macroinvertebrate community consisted of few species. A Baetis mayfly, chironomid midges, simuliid gnats, and oligochaetes strongly dominated the tailwater macroinvertebrate community. Species richness increased strongly with distance from the dam. Of a total of 76 taxa collected in the river prior to impoundment, nine species (mostly previously rare species) were extirpated, and 10 to 21 new species colonized the dam-altered environment. New arrivals to the system included taxa such as Arcynopteryx sp., Paraleptophlebia pallipes, and Hyalella sp. which colonized from nearby cool-water tributaries.

Ross and Rushforth (1980) compared periphyton assemblages before and after the construction of the dam below Electric Lake on the Huntington River in eastern Utah. They concluded the dam had little effect on attached diatoms in Huntington Creek; the primary difference was an increase in the planktonic diatom Cyclotella meneghiniana below Electric Lake. Winget (1984) studied changes in macroinvertebrates below Electric Lake. He reported that smaller animals increased over larger-sized animals, namely mayflies and stoneflies were replaced by Arctopsyche grandis (caddisfly), Chironomidae, and Simuliidae. Changes were most notable near the dam, but progressively decreased with distance (>20 km) from the dam.

Studies on the effects of regulated rivers in other regions of North America and the world are reviewed in Baxter (1977), Ward and Stanford (1979), Obeng (1981), Lillehammer and Saltveit (1984), Petts (1984), Stanford and Ward (1986), Craig and Kemper (1987), Henriques (1987), and Blinn and Cole (1991).

Hypotheses Tested

This project was designed to address hypotheses proposed by Patten (1991). Research Question (RQ) 7, and specifically H_o 7.1 c-d questions whether a relationship exists between aquatic algal and macroinvertebrate productivity and dam operations (Patten 1991: 248).

Objectives

Objective 1 Use existing collections and the present study to identify the species of aquatic Diptera that occupy the Colorado River corridor in Grand Canyon National Park, determine phenology, and provide the NPS with a reference collection.

Objective 2 Use biomass studies in wide versus narrow reaches of the Colorado River (Schmidt and Graf 1990) to determine biomass, dominance, phenology, and habitat requirements of the dominant aquatic macroinvetebrates.

Objective 3 Determine the trophic significance of aquatic Diptera in this fluvial ecosystem.

Objective 4 Determine the potential impacts of dam operations on the aquatic food base using survey and observational data, and experimental techniques.

Objective 5 Develop protocol to assist the NPS in monitoring aquatic Diptera in this system.

Format of the Report

This report is divided into seven chapters, each addressing a project objective. Following this introduction we discuss macroinvertebrate taxonomy and phenology. Chapter Three discusses the distribution and biomass of benthic algae and macroinvertebrates. Chapter Four discusses trophic linkage and macroinvertebrate diets. Chapter Five discusses results of in situ experimental simulation of disharge fluctuation at Lees Ferry and synthesizes these results with field studies. In Chapter Six we discuss a recommended monitoring approach. Lastly, in Chapter Seven we present our conclusions and evaluation of GCD/EIS alternatives.

CHAPTER TWO: TAXONOMY AND PHENOLOGY OF MACROINVERTEBRATE FAUNA

INTRODUCTION

Macroinvertebrate diversity in the Colorado River is generally believed to be low (Stevens 1976, Carothers and Minckley 1981, Hofknecht 1981, Leibfried and Blinn 1986), but longitudinal and temporal patterns in diversity have not been thoroughly examined. An essential portion of any aquatic trophic study is identification of principal taxa. Therefore, the purpose of this objective of the study was to identify the macroinvertebrate fauna within the Colorado River ecosystem through Marble and Grand Canyons.

METHODS

Taxonomy of Macroinvertebrates

Macroinvertebrate specimens were obtained through present collections (Chapter 3) and past studies (Objective 1). Macroinvertebrate samples were collected throughout the river corridor in 1990-1991 using sweep nets, Thienemann collections, light traps, and spot collection techniques. Larval aquatic Diptera were also reared to adults in the laboratory. More than 200 sweep-net and white light samples of adult Chironomidae and 96 spot-collected adult simuliids were collected throughout the seasons and throughout the river corridor between 1990-1991. Specimens were recovered from each sample, prepared, and sent to taxonomists for identification. In addition, gastropod and oligochaete specimens obtained from systematic samples were sent to specialists for identifications. More than 2000 specimens have been identified to species. Relative frequency data for taxa of aquatic Diptera were developed from these data sets.

The sweep-net collections were used to evaluate adult chironomid midge distribution and phenology in the river corridor. This technique provided the largest sample of midges collected during 1990-1991. Approximately five individuals were removed from each sweep-net collection and prepared for identification. A total of 1,062 chironomid specimens were identified from throughout the Canyon and over the full sampling period. Sweep-net samples made up approximately one-half of the total number of chironomid individuals collected. In addition, approximately 100 adult simuliid specimens were prepared and sent for identification.

Chironomid larvae were reared at 21°C, to enhance development, in an incubator with a 12:12 h light:dark cycle. Larvae were placed in screw-top glass vials (50 ml) containing 40 ml of river water and a tuft of Cladophora for food and substratum for pupation. Water was changed at least every three days and the developmental stage noted in each vial. Complete metamorphosis occurred ≤58 days. All pupal cases and exuvia were gathered and mounted for species identification.

RESULTS AND DISCUSSION

Macroinvertebrate Diversity

Table 2.1 lists all macroinvertebrate species collected in the mainstem of the Colorado River during this study. This list includes 35 chironomid species, one simuliid, two gastropods, two bivalves, at least 16 annelids, and Gammarus lacustris. Other invertebrate taxa were collected in small numbers.

Grand Canyon Chironomidae

The Chironomidae are small (adults <20 mm), non-biting flies usually with aquatic fossorial ("bloodworms"), grazing or, rarely, predaceous or leaf-mining, larvae. Larvae are often abundant in flowing, lacustrine or littoral aquatic habitats. After several molts, the larvae form silk cocoons and pupate under stones, in algae or elsewhere. Adults of many species emerge first in a pharate form and then emerge as winged adults at the water surface. Males of many species engage in swarming behavior and swarms (leks) are most often seen in the morning or evening hours, particularly above light-colored backgrounds. Reproductive phenology varies tremendously depending on the life history of the species.

A total of 35 chironomid midge species were collected by various techniques during this study, and more than 1,000 individual specimens have been identified to species. These data indicate that diversity of the chironomid midge assemblage in the Colorado River changed longitudinally and seasonally, and perhaps over time during the post-dam period. Species richness was relatively high through Upper Granite Gorge, particularly in the wide reaches of the river, and diversity generally declined somewhat in the lower Grand Canyon (Fig. 2.1). This pattern suggests that the dam may have enhanced chironomid diversity because species richness declined in the lower Canyon where river conditions more nearly approximate pre-dam conditions.

Sweep-net data were used to evaluate adult chironomid species' distributions through the river corridor. Eight chironomid species comprised approximately one-half of the specimens collected by sweep-netting (Fig. 2.1). Cricotopus spp. dominated the upper Canyon, but declined somewhat longitudinally. Cricotopus annulator was strongly dominant at Lees Ferry, but declined in relative abundance in wide, slow reaches downstream. Eukiefferiella ilkleyensis and E. coerulescens were most common in the middle Canyon reaches. Eukiefferiella claripennis, Orthocladius rivicola, and Tvetenia discoloripes co-dominated the middle and lower Canyon reaches.

At least one common chironomid species was under-represented in sweep-net samples because of a complex life history. Only six of 101 C. globistylus specimens collected at Lees Ferry were taken in the adult stage. The others were collected in the larval form and were reared for identification. This species is

Table 2.1. Macroinvertebrate taxa collected in the Colorado River corridor in Grand Canyon. Site designation numbers refer to Table 3.1.

ANNELIDA (Identified by Mark J. Wetzel, Illinois Natural History Survey)

Enchytraeidae (1,2,4)

Hirudinoidae (2,6,10)

Lumbricidae (2,6,10)

Lumbriculidae (1,3,4,5,6,10)

Naididae
- Unidentified (2,3)
- Chaetogaster diaphanus (1)
- Nais communis (1)
- Nais elinguis (1,2,3,4)
- Nais pardalis (1,3)
- Nais pseudobtusa (2)
- Nais variabilis (1,2,4)
- Nais sp. (2,3)
- Ophidonais serpentina (1)
- Pristina sp. (2)

Tubificidae
- Limnodrilus hoffmeisteri (2,3,6)
- Tubifex tubifex (1,2,3)

GASTROPODA (Identified by Dr. Earle Spamer,The Academy of Natural Sciences of Philadelphia)

Physidae
- Physella sp. (1-10)

Lymnaeidae
- Fossaria obrussa (1,2,3,4)

BIVALVIA

Sphaeriidae
- Pisidium variable (1)
- Pisidium walkeri (1)

Table 2.1 (Cont.): Macroinvertebrate Taxa.

AMPHIPODA

Gammaridae
<u>Gammarus</u> <u>lacustris</u> (1-10)

HYDRACARINA (4)

OSTRACODA (1)

INSECTA

COLEOPTERA: (6,8,9)

DIPTERA:

Ceratopogonidae (4)

Chironomidae (Identified by Dr. James Sublette, Pueblo Science Associates, Pueblo, Colorado)

<u>Apedilum</u> <u>subcinctum</u>

<u>Cardiocladius</u> <u>platypus</u> (1,3,4,5,6,8,9)

<u>Chironomus</u> sp. (3,4,6,10)
<u>Chironomus</u> utahensis (1)

<u>Cladotanytarsus</u> n.sp. 5 (3,4,6,10)

<u>Cricotopus</u> <u>annulator</u> (1-10)
<u>Cricotopus</u> <u>globistylus</u> (1,3,6)
<u>Cricotopus</u> <u>trifascia</u> (3,4,5,6,7,8,9)
<u>Cricotopus</u> <u>infuscatus</u> (5,9)
<u>Cricotopus</u> n.sp. 6 (1,2,3,6,7,8)

<u>Cyphomella</u> <u>gibbera</u> (4,6,9)

<u>Diamesa</u> <u>heteropus</u> (4)

<u>Eukiefferiella</u> <u>claripennis</u> (1-10)
<u>Eukiefferiella</u> <u>coerulescens</u> (1,2,3,4,5,6)
<u>Eukiefferiella</u> <u>devonica</u> (5,8)

Table 2.1 (Cont.): Macroinvertebrate Taxa.

Eukiefferiella ilkleyensis (1,2,3,4,5,6,7,8,9)
Eukiefferiella n.sp. 3 (1)
Eukiefferiella n.sp. 9 (1)

Limnophyes sp. (7)

Metriocnemus n.sp. 3 (3)

Microspectra sp. (1)

Chironomidae

Orthocladius consobrinus (7)
Orthocladius frigidus (1)
Orthocladius luteipes (2)
Orthocladius mallochi (9)
Orthocladius rivicola (1-10)

Parakiefferiella sp.2 (2,6,7)

Paraphaenocladius exagitans (3)

Phaenopsectra profusa (3,4,8,10)

Polypedilum obelos (3,4,6,8,9)
Polypedilum apicatum (9)

Pseudosmittia sp. (2)

* Rheotanytarsus n.sp. 2 (7)
Rheotanytarsus n.sp. 3 (7)

Tvetenia discoloripes (1,3,4,5,6,7,8,9,10)

Simuliidae (Identified by Dr. R.V. Peterson, Systematic Ecology Laboratory, Beltsville, Maryland)

Simuliium arcticum (1-10)
Simuliium argus (7,8,9,10)
Simuliium griseum (10)
Simuliium petersoni (10)
Simuliium vittatum (1)

Table 2.1 (Cont.): Macroinvertebrate Taxa.

Tipulidae (4,7,9)
EPHEMEROPTERA (1,2,6,7,9)
HEMIPTERA (1,9)
ODONATA (2,9)
TRICHOPTERA (1,2,5,6,8,9)

* New to science, not collected since 1976.

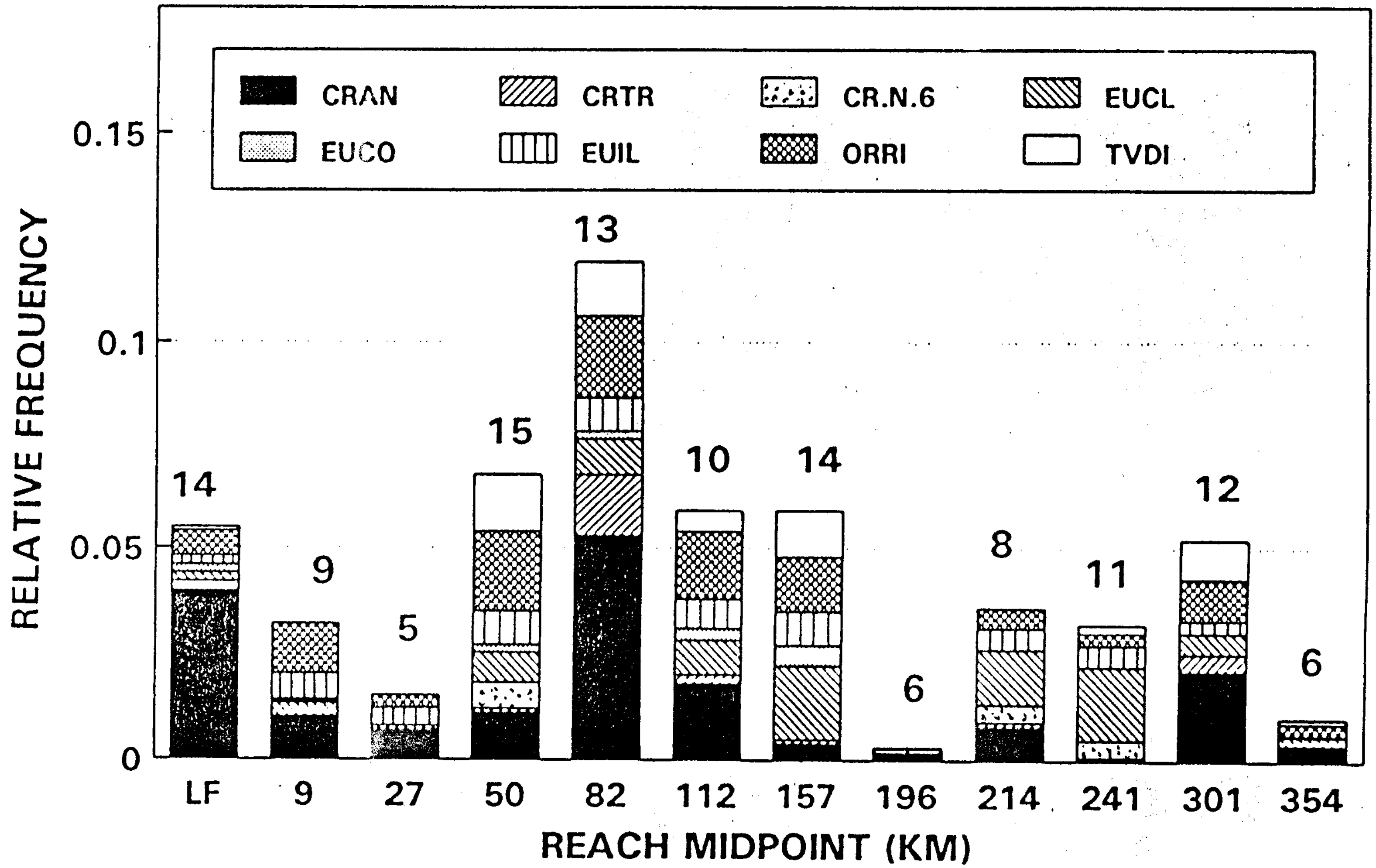


Figure 2.1. Relative frequency of dominant Chironomidae in the 11 geomorphic reaches (Schmidt and Graf 1990) through the Colorado River corridor in Grand Canyon National Park. Numbers above the columns indicate the total number of midge species encountered in each reach. CRAN = Cricotopus annulator, CRTR = Cricotopus trifascia, CR.N.6 = Cricotopus n.sp. 6, EUCL = Eukiefferiella claripennis, EUCO = Eukiefferiella coerulescens, EUIL = Eukiefferiella ilkleyensis, ORRI = Orthocladius rivicola, TVDI = Tvetenia discoloripes. N = 1,062 specimens

abundant at Lees Ferry in the larval form, but probably drifts downstream during pupation and/or eclosion. Thus, although it is an abundant species, adult forms were not well represented at Lees Ferry where it spends its larval phase.

The adult chironomid assemblage changed seasonally as well as longitudinally (Fig. 2.2). The sweep-net data were sorted according to occurrence by season: spring (March - May), summmer (June - August), autumn (September - November), and winter (December - February). These data indicate that overall species richness is greatest during the autumn months. The assemblage is dominated by Cricotopus spp., particularly C. annulator, during the spring, summer, and autumn, and that dominance shifts to E. claripennis and E. ilkleyensis, and O. rivicola during the winter months. Tvetenia discoloripes is dominant during the fall, winter, and spring, but is absent in adult form during the summer months.

There is some evidence that the chironomid fauna in the Colorado River changed during the post-dam period with both losses and gains of taxa. Stone and Rathbun (1968) noted only "blood worms" from extensive collections in the river at Lees Ferry immediately after impoundment. In 1991, 14 chironomid species were collected at Lees Ferry. Identification of 49 adult specimens collected by Stevens (unpublished data) in the mid-1970's suggested that the assemblage was dominated at that time by small-bodied Cladotanytarsus and Tvetenia. Rheotanytarsus n. sp. 2 and Apedilum subcinctum were collected in the mid-1970's in the middle and lower Canyon, but were not encountered in 1991. The status of the former taxon as an extant species is presently in question. Like the other mid-1970's dominants, their body sizes tend to be smaller than the Cricotopus-dominated assemblage of 1990-91.

A dichotomous key to the generic level was prepared for the adult male chironomids of the Grand Canyon by Ms. J. Macauley in our laboratory (Table 2.2, Fig. 2.3-2.5). This key was developed after Oliver (l981) and can be used by future researchers as an aid to identifying Chironomidae of Grand Canyon.

Grand Canyon Simuliidae

Buffalo gnats (Simuliidae) in the Colorado River constitute an important source of food for native and non-native fish. Because they are biting flies, this family is also important in recreation planning and management. The simuliids are associated with hard, smooth substrata (cobble and boulders) in fast-flowing water where the larvae feed by filtering plankton and bacteria. Because of specialized habitat requirements, simuliids are more dominant in high velocity reaches with little algal cover, such as the narrower reaches of the river. During this survey, buffalo gnats were most commonly collected on driftwood sticks and logs lodged among rocks in cobble bars.

Numerous larval simuliids were collected through the river corridor, but taxonomy of this family is presently based on pharate and adult features and larval taxonomic

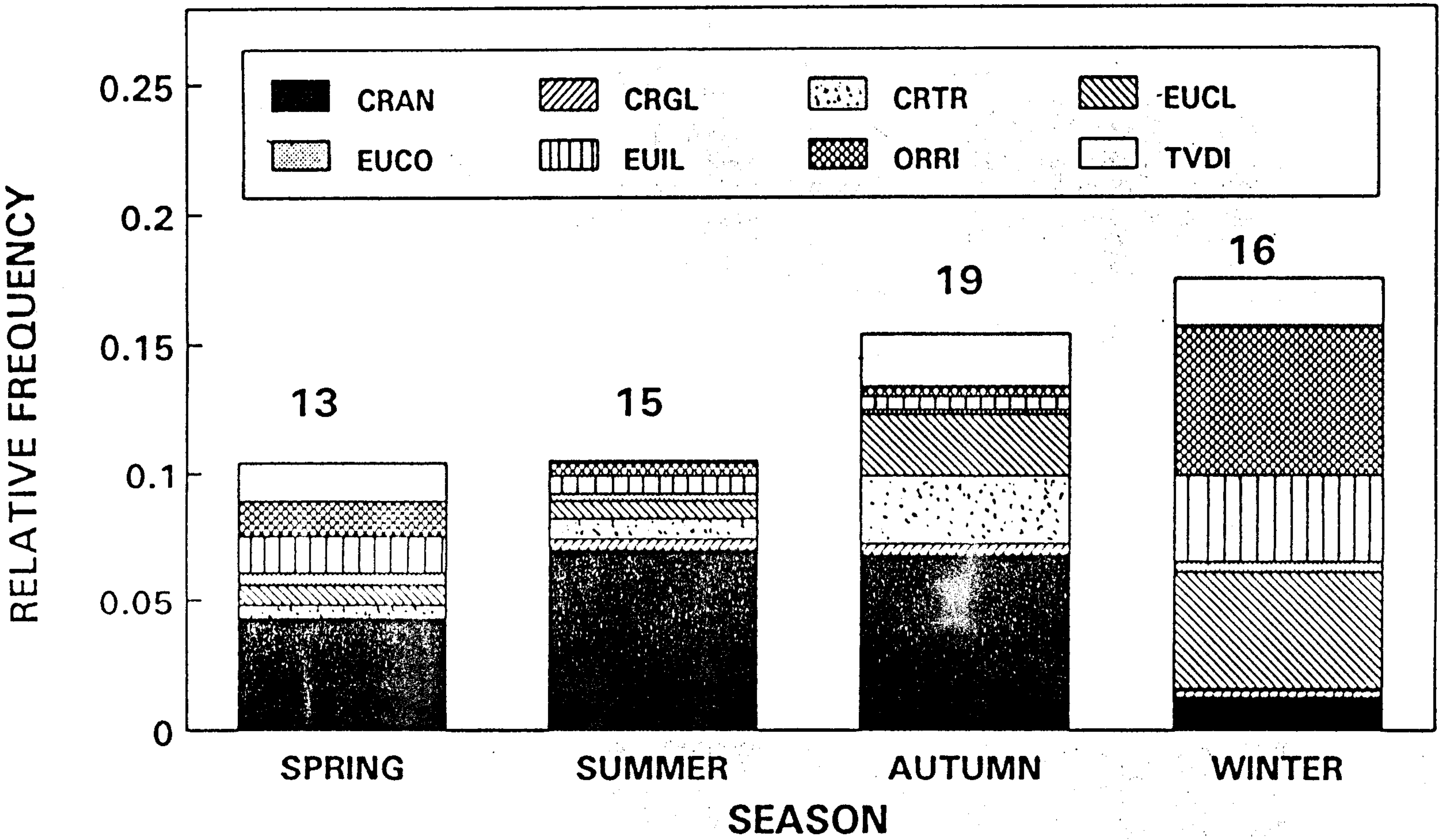


Figure 2.2. Relative frequency of dominant Chironomidae through the four seasons in the Colorado River corridor in Grand Canyon National Park. Numbers above the columns indicate the total number of midge species encountered in each season. CRAN = Cricotopus annulator, CRTR = Cricotopus trifascia, CR.N.6 = Cricotopus n.sp. 6, EUCL = Eukiefferiella claripennis, EUCO = Eukiefferiella coerulescens, EUIL = Eukiefferiella ilkleyensis, ORRI = Orthocladius rivicola, TVDI = Tvetenia discoloripes. N = 1,062 specimens

Table 2.2 Dichotomous key to adult male chironomids in Marble and Grand Canyon, Arizona in the Colorado River ecosystem. Key modified from Oliver (l981) by J. Macauley.

1a. M-Cu crossvein present (Fig.2.4A),vertical setae present (Fig.2.4L), 4th tarsomere cordiform (heart-shaped) (Fig. 2.5E)........ Diamesa
1b. M-Cu crossvein lacking 2

2a. Male gonostyll infolded (Fig. 2.5M) .... **(ORTHOCLADINAE)**...3
2b. Male gonostyll erect (Fig. 2.5N)........ **(CHIRONOMINAE)**.....13

3a. 4th tarsomere cordiform (Fig. 2.5E)........ Cardiocladius
3b. 4th tarsomere cylindrical........ 4

4a. Wings with macrotrichia on membrane, at least at tip 5
4b. Wing membrane bare; setae may be present on long veins (Fig. 2.4B)........ 6

5a. R_{4+5} over or distal to M_{3+4}; costa strongly extended past R_{4+5} (Fig. 2.4C)........ Metriocnemus
5b. R_{4+5} ends distinctly proximal to M_{3+4}; costal extention short (Fig. 2.4D)........ Paraphaenocladius

6a. Eyes hairy (Fig. 2.4K)........ 7
6b. Eyes bare........ 8

7a. Dorsocentral setae minute (Fig. 2.5A); legs and abdomen may be yellow- and black banded........ Cricotopus
7b. Dorsocentral setae coarse; legs and body black .... Eukiefferiella (part, i.e., E. coerulescens Kieffer)

8a. R_{2+3} close to R_{4+5}, or absent........ 9
8b. R_{2+3} distinct, near middle of distance between R_1 and R_{4+5} (Fig. 2.4E)........ 10

9a. Anal point present (Fig. 2.5O)........ Tvetenia
9b. Anal point absent........ Eukiefferiella (part)

10a. Tubercle or tuft of coarse microtrichia absent from center of mesoscutum........ 11
10b. Small tubercle or a tuft of coarse microtrichia present.in the center of mesocutum (Fig. 2.5B)........ 12

11a. Thorax with lanceolate setae (Fig. 2.5C); anal point absent, ninth tergum may be conical...Limnophyes

11b. Thorax with filiform setae (Fig. 2.5D); slender anal point present (Fig. 2.5O)...Orthocladius

12a R_{4+5} ends over or distal to M_{3+4} (Fig. 2.4F); eyes with a short wedge-shaped medial extension...Parakiefferiella

12b R_{4+5} ends distinctly proximal to M_{3+4} (Fig. 2.4G); eyes reniform...Pseudosmittia

13a. r-m crossvein distinctly oblique to R_{4+5} (Fig. 2.4H); tibial combs with spurs (Fig. 2.5H)...14

13b. r-m crossvein almost parallel with R_{4+5} (Fig. 2.4I); middle third of tibial combs without spurs...16

14a. Large species; wing length >2.5 mm; foretibial apex without a small spur (Fig. 2.5F)... Chironomus

14b. Small species; wing length <2.5 mm (Fig. 2.4J); foretibial apex with a small spur (Fig. 2.5G)..15

15a. Base of sternum 8 of male triangularly produced (Fig. 2.5K)............Polypedilum

15b. Base of sternum 8 of male subtruncate (Fig. 2.5L)........................Phaenopsectra

16a. Combs of mid and hind tibia with spines (Fig. 2.5I)................Cladotanytarsus

16b. Combs of mid and hind tibia without spines (Fig. 2.5J)................Micropsectra

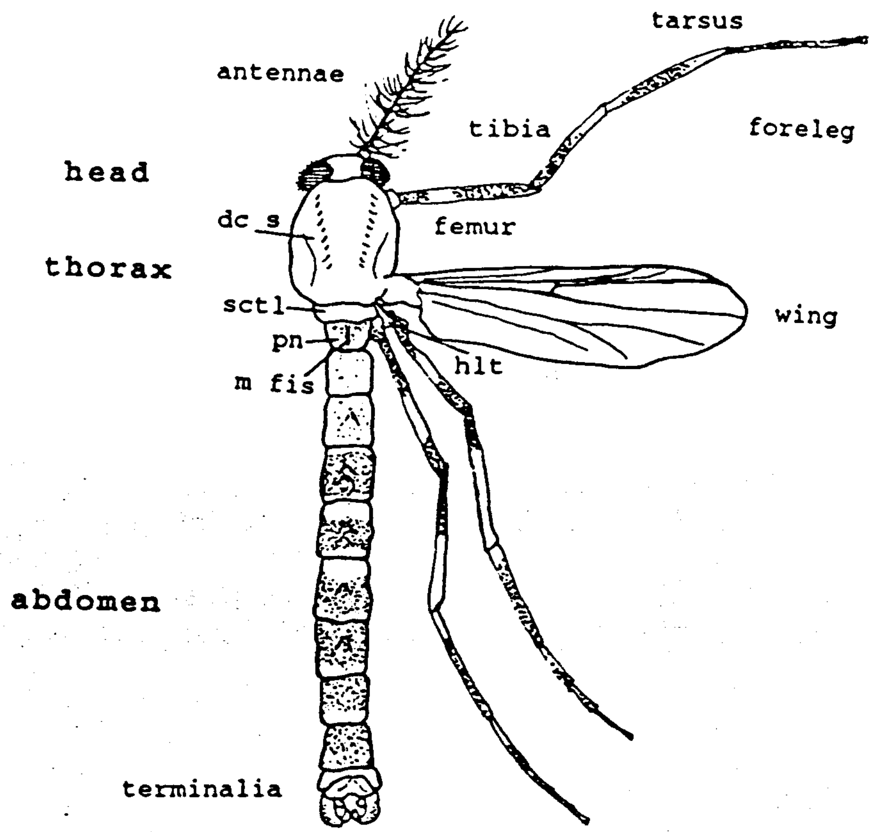


Figure 2.3 Adult chironomid male Cricotopus annulator Goetghebuer, dorsal view. Abbreviations: dc s, dorsocentral setae; sctl, scutellum; pn, postnotum; m fis, median fissure; hlt, halter.

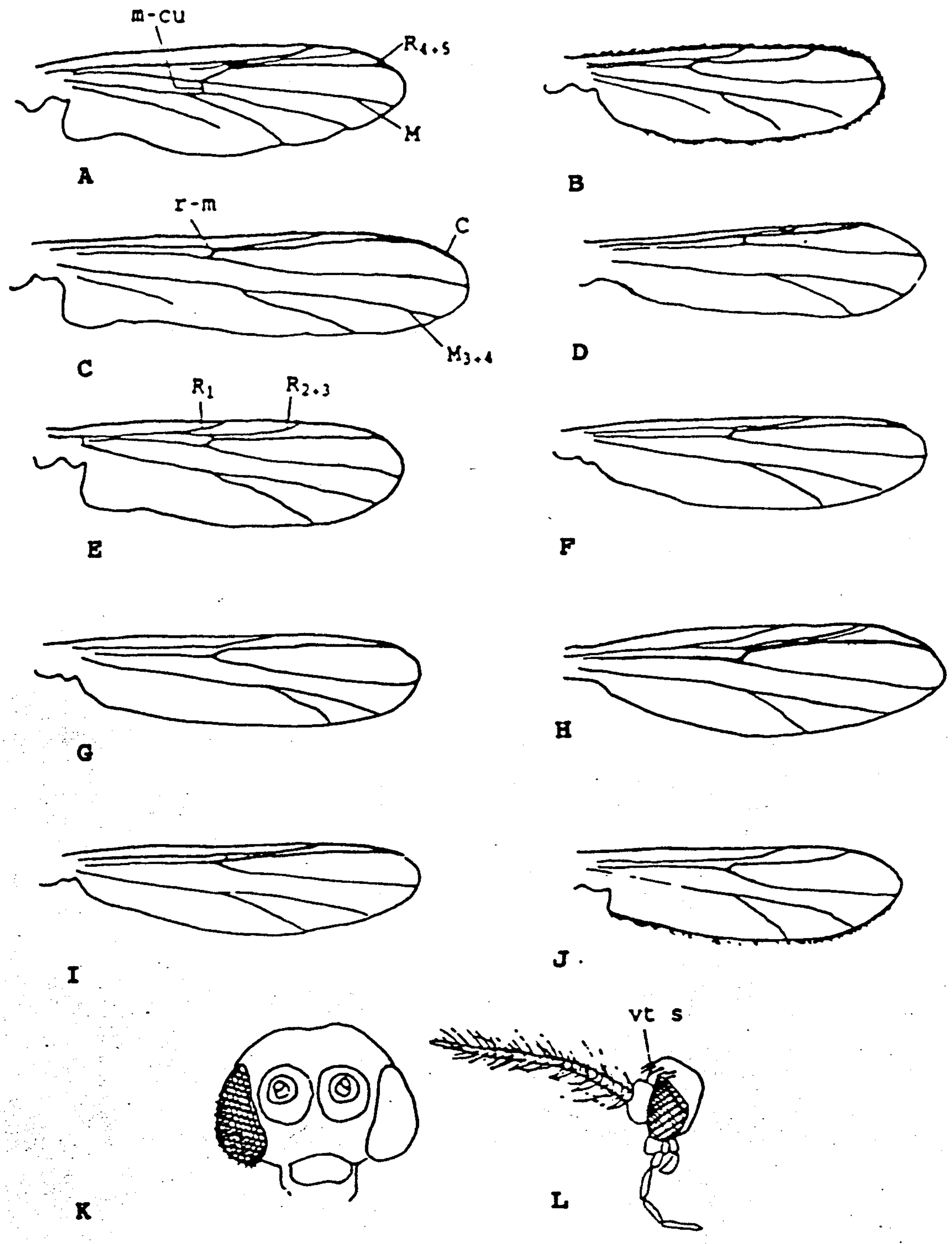


Figure 2.4. Wings and details of male chironomid heads; wing of (A) Diamesa sp.; (B) Eukiefferiella claripennis; (C) Metriocnemus sp.; (D) Paraphaenocladius exagitans; (E) Orthocladius rivicola; (F) Parakiefferiella sp.; (G) Pseudosmittia sp.; (H) Chironomus sp.; (I) Micropsectra sp.; (J) Polypedilum obelos; (K) anterior view of head with flagellum removed; (L) lateral view of head (A,G,I,K,L) redrawn from McAlpine et al. (1981).

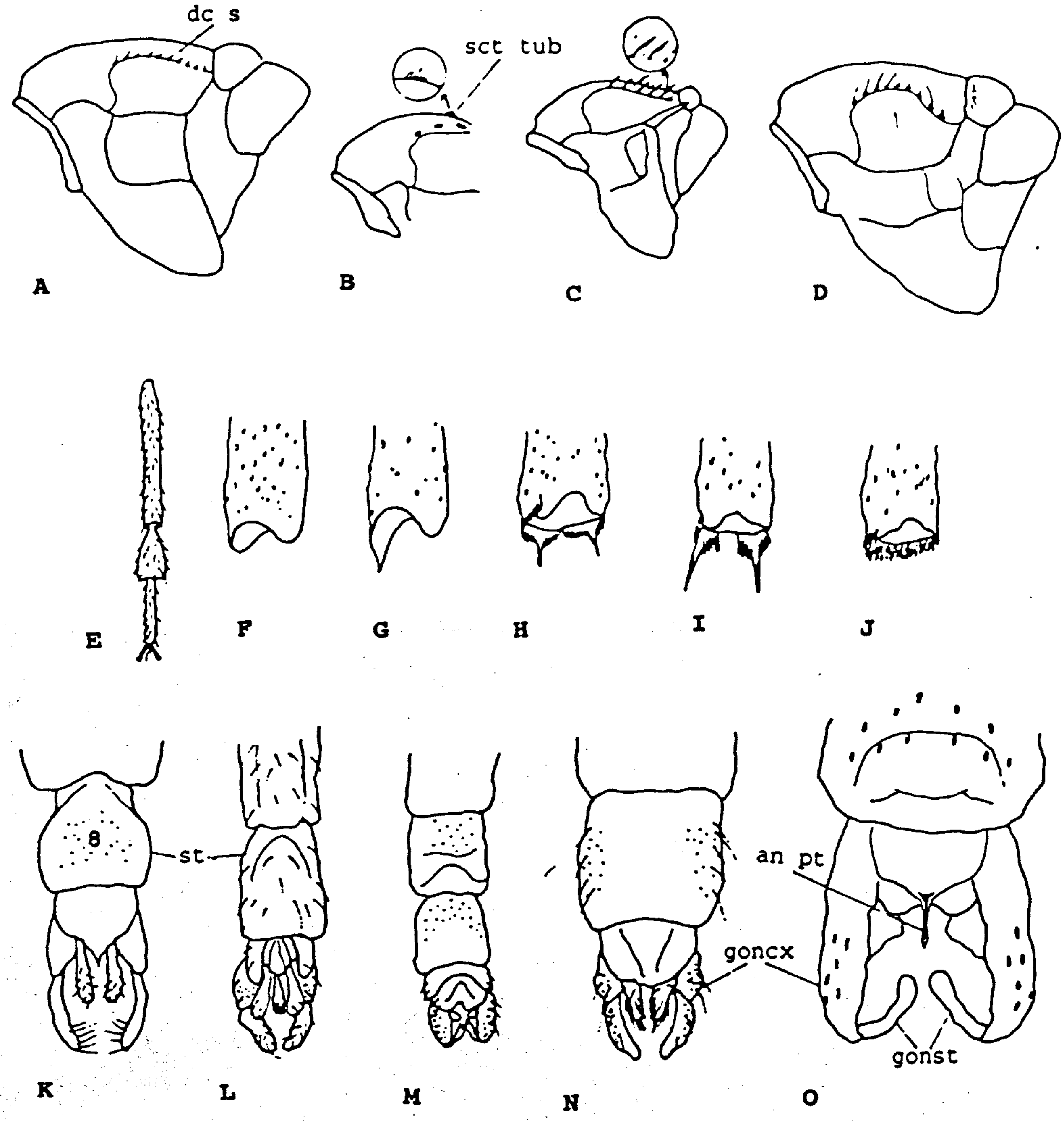


Figure 2.5. Thoraces, details of legs, and terminalia of male chironomids: thorax of (A) Cricotopus annulator, (B) Parakiefferiella sp., (C) Limnophyes sp., (D) Orthocladius rivicola; (E) terminal three tarsomeres of Cardiocladius sp; foretibial apex of (F) Chironomus sp., (G) Polypedilum sp.; hindtibial apex of (H) Chironomus sp., (I) Tanytarsus sp., (J) Micropsectra sp.; terminalia of (K) Polypedilum sp., (L) Phaenopsectra profusa, (M) Cricotopus annulator, (N) Chironomus sp.; anal point of (0) Tvetenia discoloripes (B,C,E-J) redrawn from McAlpine et al. (l981). Abbreviations: m-cu, medial-cubital crossvein; r-m, radial-medial crossvein; C, costa; R_1, first radial; R_{2+3}, second and third radials; R_{4+5}, fourth and fifth radials; M, media; M_{3+4}, posterior branch of media; vt s, vertical setae; dc s, dorsoventral setae; sct tub, scutal tubercle; st, sternite; goncx, gonocoxite; gonst, gonostylus; an pt, anal point.

characteristics have not been well established. Simuliids are typically solitary as adults and were collected by spot sampling through the river corridor. A sample of 57 adult specimens from this project, as well as 75 specimens collected from previous entomological surveys in the river corridor (Stevens 1976, Stevens and Waring 1988), were sent to R. Peterson (U.S.D.A. Beltsville, MD) for identification. The Stevens (1976) and Stevens and Waring (1988) specimens were spot collections made throughout the river corridor from 1974 through 1987.

Of the 132 adult simuliid specimens identified in this project, 110 (83.3%) were Simuliium arcticum, while four other species (S. argus, S. griseum, S. petersoni and S.vittatum) comprised the remaining species (Table 2.1; Fig. 2.6). In 1990-1991, S. arcticum was by far the most common species in this system, but this pattern of dominance appears to have shifted through post-dam time. The simuliid fauna collected during this study consisted of 93% S. arcticum, while that of 1975 to 1986 (Stevens 1976; Stevens and Waring 1988) consisted of 76% S. arcticum, a significantly greater proportion of the S. arcticum in 1990-91 ($X^2 = 4.93$, $p < 0.05$, df =1). This limited data set suggests that the simuliid assemblage in the Colorado River corridor has changed from at least a five-species assemblage to a near monoculture during the post-dam period.

A strong spring (March-April) flight of S. arcticum was observed in both 1991 and 1992, and we observed a weaker autumn (September-October) flight of this species those years. These observations suggest that availability of larval and pharate simuliids as prey for fish (e.g. trout and native species) may be limited during May-June and, to a lesser extent, December.

Grand Canyon Mollusca

Dr. Earle E. Spamer and Dr. Arthur E. Bogan (The Academy of Natural Sciences of Philadelphia) identified collections of mollusks (snails and clams) from the Colorado River and tributaries. This survey was the first inventory of Grand Canyon mollusks since Pilsbry and Ferriss (1911). Seventeen species were identified in 12 families during this reconnaissance (Table 2.1). Ten of the 17 species were new records for Grand Canyon, including two which are new to Arizona. Two species of freshwater clam (Pisidium variabile and P. walkeri) occur in the Lees Ferry area.

We analyzed seasonal changes in the Kanab amber snail (Oxyloma haydeni kanabensis) population at Vasey's Paradise from January to November, 1991 (Fig. 2.7). The Kanab ambersnail was collected at Vasey's Paradise and was officially listed as a rare and endangered species on 17 April, 1992 (U.S. Fish and Wildlife Service l992). It was previously only known from two small springs near Kanab, Utah, where its population was reported declining. A Hess sampler was used at randomly spaced intervals in one pool habitat at the base of the Vasey's Paradise falls at the downriver end of the cascade. The bi-monthly mean values of velocity, depth, dissolved oxygen, water temperature, pH, and Secchi depth, as well as biomass of primary producers (moss) and biomass of macroinvertebrates, are

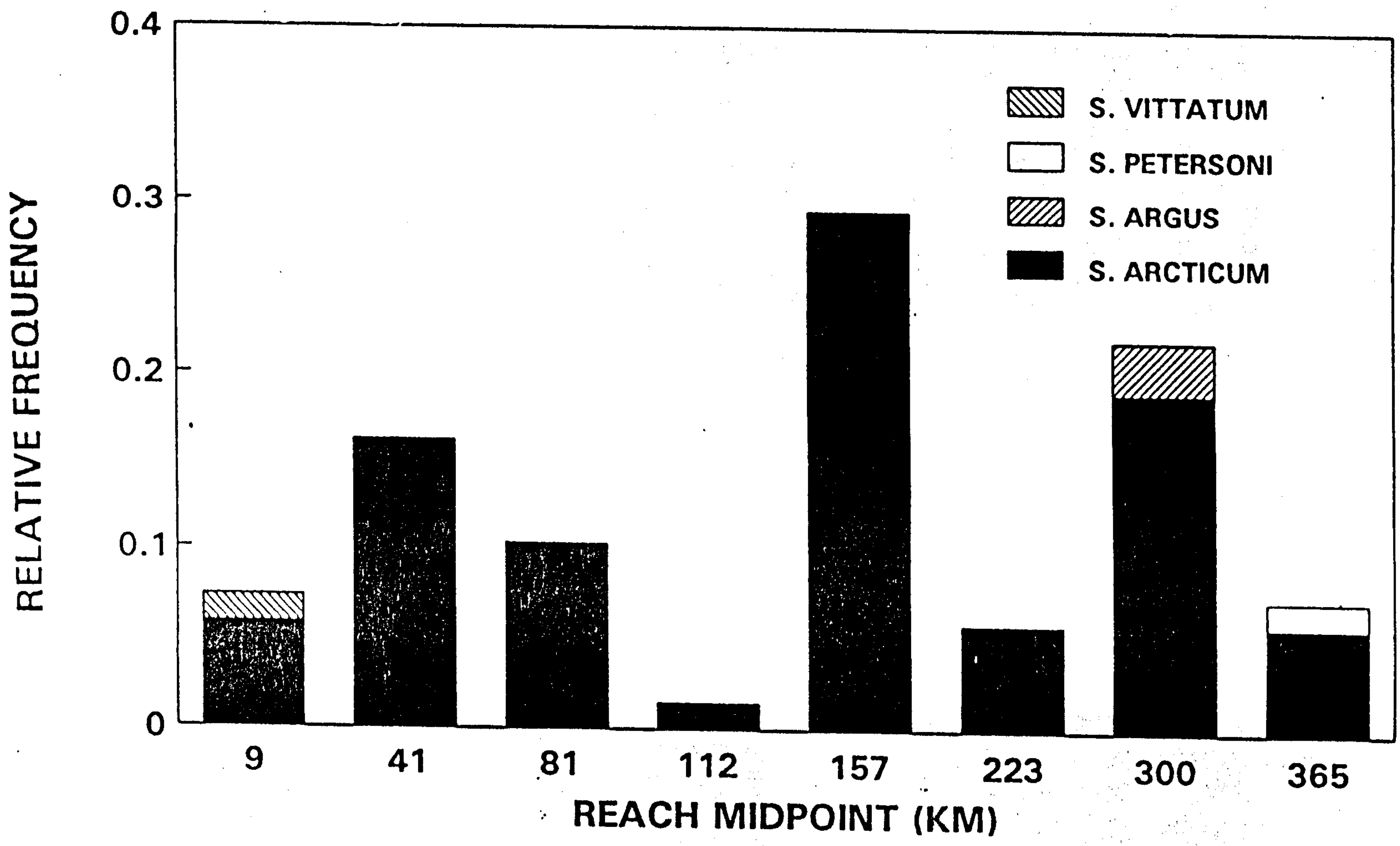


Figure 2.6. Distribution of Simuliidae through the Colorado River corridor in Grand Canyon National Park. Only S. arcticum was collected during 1990-1991, and all other species were collected in the mid-l970's by Stevens (1976). N = 96 specimens.

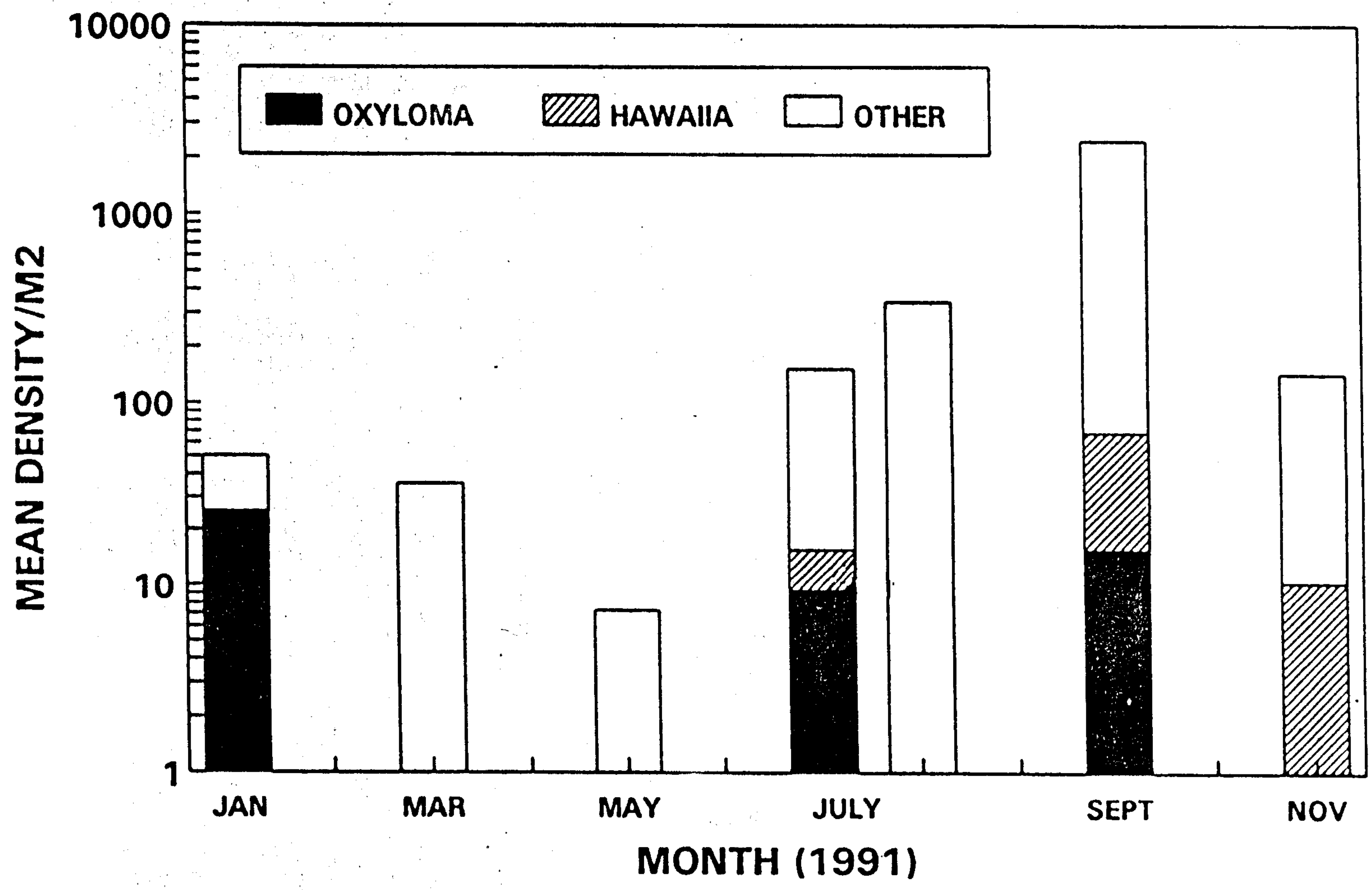


Figure 2.7. Bimonthly densities/m² of snails (Oxyloma, Hawaiia, and other) at Vasey's Paradise in 1991. Three samples/month were collected with a Hess sampler.

shown in Table 2.3. The pool is bordered by a dense stand of Mimulus Cardinalis (crimson monkey-flower) and is surrounded by Toxicodendron radicans, (poison ivy) making it generally of low interest to river runners. This pool was filled with gravel during flash floods on 1 April 1992 and the status of this population is unknown. A monitoring program is needed to document population changes of this species.

The density of the Kanab ambersnail population in 1991 was low and inconsistent (Fig. 2.7). The limited data suggest that ambersnail density may peak in summer and autumn, along with primary producer biomass; however, only 18 ambersnails were collected during this random sampling effort, and conclusions from such a small data set should be regarded as speculative. All but two of the shells collected in this habitat appeared to be dead individuals, suggesting that the snails may not prosper in the pool environment, but may occur in surrounding littoral habitats. Ambersnails have not been observed in the zone of fluctuation in the mainstem of the Colorado River.

Grand Canyon Annelida

The identifications, by Mark Wetzel, of specimens of Annelida (segmented worm) from the Colorado River corridor are the first surveys of this phylum for Grand Canyon. Twelve species have been identified in five families (Table 2.1). Enchytraeids, naidids, and tubificids were the dominant oligochaetes. Two earthworm families were common, and several leeches were collected.

Other Invertebrates

The category labelled "miscellaneous invertebrates" represented 5.3% (0.043 gm/m^2) of the total mean biomass in the Colorado River corridor (0.806 gm/m^2), but made up 47% (0.031 gm/m^2) of the total mean biomass in the tributaries. These invertebrates include members of Coleoptera, Ephemeroptera, Hemiptera, Hydracarina, Odonata, Ostracoda, and Trichoptera (Table 2.1). Ephemeroptera (mayflies) was the most abundant taxon in the miscellaneous category with the May collection on cobble riffles at Phantom (RK 142.2) yielding 89 animals or 56% of total number of the miscellaneous invertebrates during the year. Cobble riffles contained 0.72 gm/m^2 or 89% of the total mean annual biomass for miscellaneous invertebrates. We suspect most taxa in the miscellaneous category occur as drift from nearby tributaries. Fecundity for these taxa in the river corridor may be low for the following reasons: 1) sustained cold water curtails egg and larval development, 2) lack of continuously stable substrata due to river fluctuation, 3) lack of appropriate food, and 4) high suspended sediment loads.

Table 2.3 Mean water chemistry and physical conditions of the Vasey's Paradise sampling station (Colorado River kilometer 50.7R) by month in 1991. Three samples were collected per month.

PARAMETER	JANUARY	MARCH	MAY	JULY	SEPTEMBER	NOVEMBER
Velocity (m/sec)	0.25	0.38	0.38	0.34	0.46	0.18
Depth (m)	0.18	0.19	0.35	0.17	0.17	0.14
DO (mg/L)	10.4	---	9.8	9.8	8.4	8.3
Temperature (°C)	7.4	---	15.2	15.2	18.2	14.9
pH	8.3	---	8.2	8.2	8.1	8.5
Primary Producer Crop (gm/m^2)	3.97	0.64	0.56	6.33	8.62	20.46
Macroinvertebrate Stock (gm/m^2)	0.12	0.28	0.05	4.34	1.65	2.48

CHAPTER THREE: TROPHIC STRUCTURE OF THE AQUATIC FOOD BASE IN GRAND CANYON

INTRODUCTION

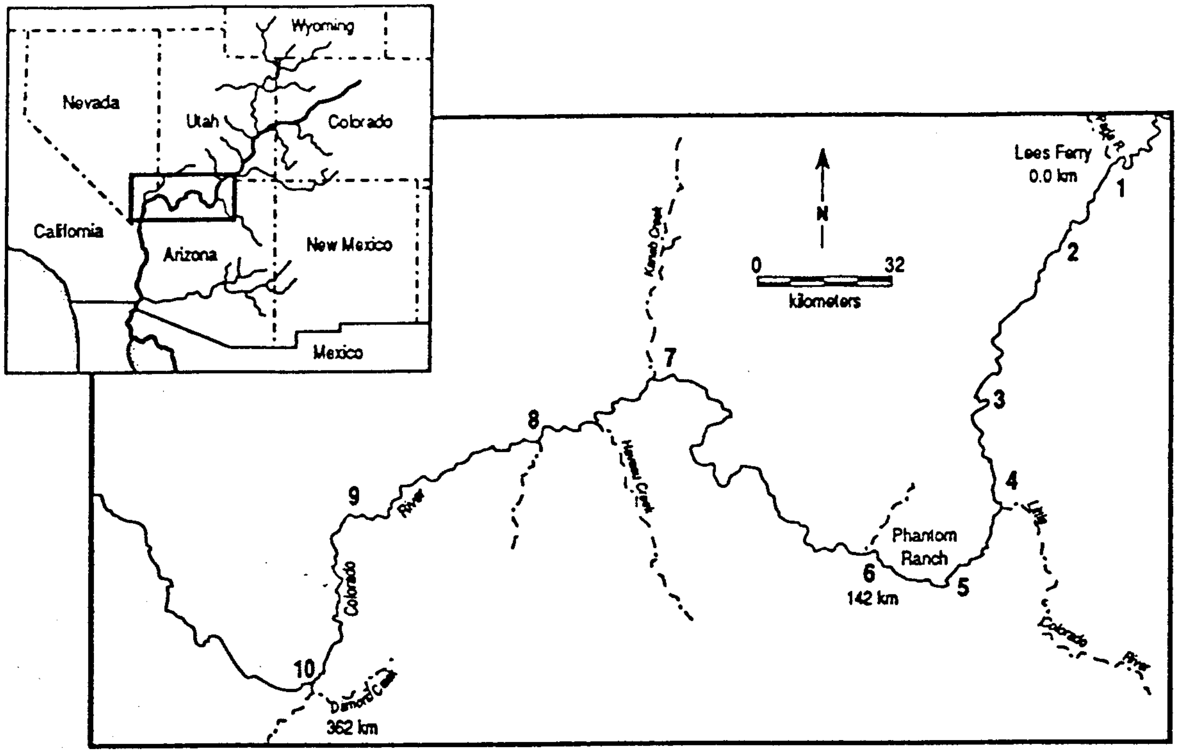
This element of the study is essential for understanding how geomorphology and upstream production influence the distribution of primary and secondary producers in the Colorado River aquatic ecosystem. The high productivity in the Lees Ferry tailwater reach can be attributed to stable cobble substrates and the continuously clear, and perhaps, nutrient-rich, hypolimnetic water released from Glen Canyon Dam (Stanford and Ward, 1991). Lack of aquatic macro-herbivores in the tailwater reach adds to the high biomass of Cladophora. The absence of tributary sediments at Lees Ferry results in light penetration >7 m, while suspended sediments below the confluence of the Paria River reduce Secchi depth to < 1 m (Yard et al. 1992). These diminished light levels at downstream sites reduce both primary and secondary production. The contribution of the tailwater reach on the downriver ecosystem is under investigation by the U.S. Geological Survey. The purpose of this objective of the study was to quantify the biomass and abundance of the food base in the Colorado River ecosystem through Grand Canyon.

METHODS

Distribution of Biomass

The biomass and habitat requirements of aquatic macroinvertebrates were assessed bimonthly between January and November, 1991 (Objective 2). This sampling frequency was employed to overlap generation times of organisms. Sampling sites included USGS synoptic study sites and AGF tailwaters sites (Fig. 3.1). Five wide-reach sites and five narrow-reach sites were investigated. These ten sites each included three habitat types; river pools (low velocity sand and silt), riffles (high velocity cobble) and nearby tributaries.

Following an October 1990 pilot trip, 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, lower-littoral (approximately 142 m^3/s), mid-littoral (approximately 283 m^3/s), and upper littoral (807 m^3/s). Three samples 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.



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 3.1. Map of study sites in the Colorado River corridor, Grand Canyon National Park, including site number, habitat, geomorphic reach width, elevation, and reach orientation.

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), course sand (>1 mm), sand (> 0.5 mm), silt (> 0.01 mm), and clay (< 0.01 mm).

Samples were sorted into the following 10 biotic categories: Cladophora, blue-green algal crust (Oscillatoria spp.), chironomids, Gammarus lacustris, gastropods, oligochaetes, simuliids, lumbricids, miscellaneous invertebrates, and detritus. Each biotic category was oven-dried at 60°C and weighed. An ash-free dry mass conversion was developed for Cladophora by ashing (500°C) and re-weighing 60 samples of this alga collected throughout the river corridor. The resulting equation was: $Y = 0.34825 X + 0.04912$ ($R^2 = 0.923$; $F = 707.8$, $df = 1{,}58$, $p < 0.001$). This equation was used to convert all Cladophora dry weight values to ash-free dry mass. All Oscillatoria samples were ashed and data are reported as ash-free dry mass.

The following abiotic parameters were measured at each sampling site: water temperature, dissolved oxygen (DO), pH, specific conductance, substratum, microhabitat conditions, Secchi depth (water transparency), water velocity or stage, depth, date, site, and time of day. Water quality data are presented in Table 3.1.

Statistical Analyses

Multivariate analysis of variance (MANOVA) was used to analyze these data for relationships between categorical predictor variables and multiple response variables. This robust multivariate analysis of variance approach provides information on how related response variables are correlated with categorical predictors and interaction effects.

RESULTS AND DISCUSSION

Colorado River Water Chemistry

Multivariate analyses (MANOVA) showed that water temperature, specific conductance, dissolved oxygen (DO), pH, and Secchi depth changed in response to month and sampling location (distance downstream from Lees Ferry; Table 3.2).

1) The pH values of the river did not change significantly downstream between seasons (Fig. 3.2). (2) DO showed a pattern of low values (≤ 7.0 mg L^{-1}) at Lees Ferry, increasing with distance downstream with an overall increase during the summer months (Fig. 3.3). All DO readings at Lees Ferry were taken before 1200 h and some diel variation in DO may occur, however, this pattern deserves further study. DO levels emerging from Glen Canyon Dam are relatively low, and oxygen saturation may not occur until below the confluence of the Paria River. (3) Water temperature increased significantly downstream especially during the summer months (Fig 3.4). A significant month by location interaction effect was observed for

Table 3.1. Average values for selected water quality parameters (mean, minimum, maximum, standard error, variance) from Lees Ferry to Diamond Creek in the Colorado River through Grand Canyon. Data were collected from ten stations at bimonthly intervals from January 1991 to November 1991.

	Dissolved Oxygen (mg/L)	Conductivity (mS)	Temperature (°C)	pH
Mean	10.3	0.96	10.6	7.9
Minimum	6.6	0.84	7.1	6.8
Maximum	12.0	1.1	17.1	8.3
Standard Error	0.07	0.003	0.15	0.012
Variance	1.58	0.004	7.40	0.10

Table 3.2. MANOVA of water chemistry data in the Colorado River downstream from Glen Canyon Dam. Data collected from riffles throughout the Grand Canyon from January - November, 1991. Predictor variables include month and station location (see Figure 3.1). Response variables include: dissolved oxygen = O (mg/L), water temperature = T (°C), pH = H, and Secchi depth = S (m). Only statistically significant responses are indicated.

SOURCE	WILK'S LAMBDA	APPROXIMATE F STATISTIC	DF	p	SIGNIFICANCE OF RESPONSE VARIABLES
Month	0.661	33.25	5,324	0.000	T***, H***,
Location	0.662	33.05	5,324	0.000	O***, T***, S***
Month*Location	0.838	12.54	5,324	0.000	T***

*** p <0.001

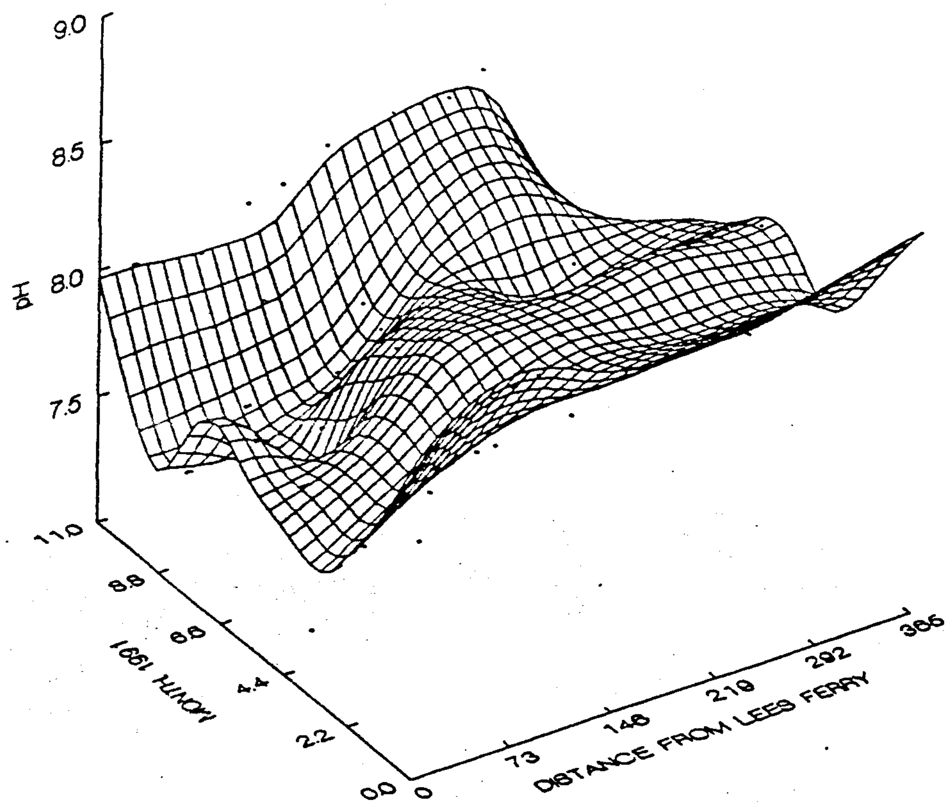


Figure 3.2. Temporal and spatial patterns for pH in the Colorado River through Grand Canyon, Arizona during 1991.

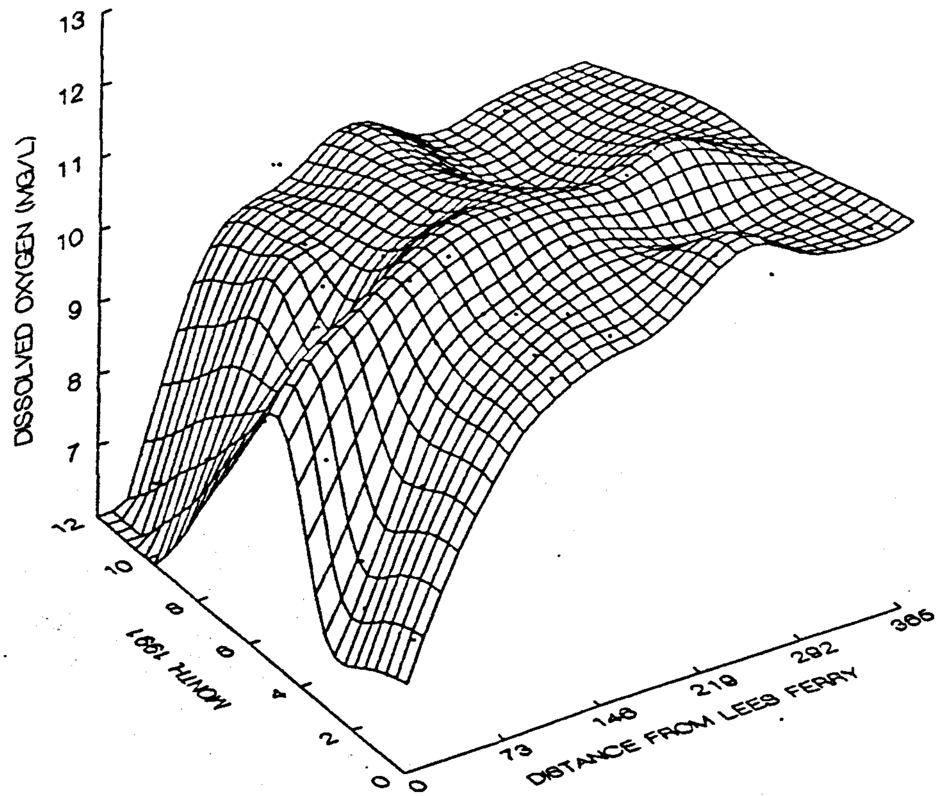


Figure 3.3. Temporal and spatial patterns for dissolved oxygen in the Colorado River through Grand Canyon, Arizona during l991.

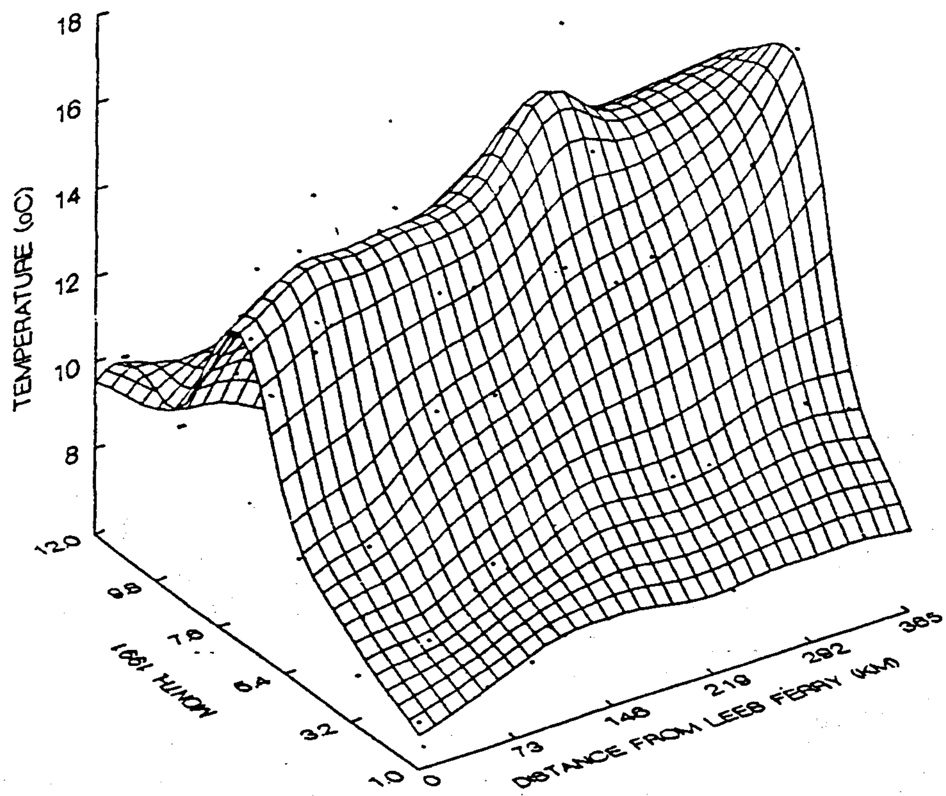


Figure 3.4. Temporal and spatial patterns for water temperature in the Colorado River through Grand Canyon, Arizona during 1991.

temperature, which was attributable to the increase in water temperature with distance downstream during the summer, but not during the winter. The peak of water temperature in the mid-Canyon during July, 1991 took place during a constant 141 m^3/s test flow. (4) Secchi depth declined with distance downstream from the dam and during tributary inflow periods (fall through spring, Fig. 3.5). The mid-Canyon, mid-summer peak in Secchi depth was attributed to lower velocities during GCES constant test flows that permitted suspended particles to settle out of the water column.

Values for specific conductance and water temperature for this study are somewhat elevated compared to values reported in Phase I GCES (April 1984-June 1986; Maddux et al. 1988). Conductivity values in Phase I ranged from 0.71 to 0.74 mS from Lees Ferry to Diamond Creek, while we report a range from 0.84 to 0.96 mS. Also, water temperature ranged from 6 to 12°C from Lees Ferry to Diamond Creek in Phase I compared to 7.1 to 17.1°C in this study. Increases in both abiotic parameters may result from lower discharge volumes during Phase II and lower water levels in Lake Powell. Elevated solute concentration from reduced reservoir levels would increase specific conductance and the three day (142 m^3/sec) beach survey low flows during the summer may account for higher maximum water temperature.

Distribution of Biomass

Multivariate analysis (MANOVA) was used to assess the bimonthly biomass data collected during field survey trips (Table 3.3). This statistical analysis allows simultaneous analysis of multiple, related response variables. Month, station, habitat, and zone significantly influenced benthic algal, macroinvertebrate, and/or detrital biomass (gm/m^2) and each predictor is discussed in relation to the response variable categories:

Month: Sampling was conducted in January, March, May, July, September and November, 1991. Monthly differences in biomass were not statistically significant in this data set. Only the univariate test effect on detritus was statistically significant in the month by station interaction. This effect was attributed to a large pulse of detritus following fall rains in 1991, and/or from the low ramping rate of the interim flows. However, the overall interaction test between month and station was not significant. Several trends require further investigation, including a midsummer reduction in Cladophora in the upper Canyon and a corresponding increase in Oscillatoria in mid-summer (Figs. 3.6-3.7). Also, detritus appears to increase during seasonal tributary input (Fig. 3.8).

Station: Stations were located between Lees Ferry (RK 0) and Diamond Creek (RK 363, Fig. 3.1). Macroinvertebrate and Cladophora biomass declined significantly downstream, and detrital biomass varied significantly between stations (Figs. 3.6-3.19). Oscillatoria biomass did not change between stations. These response variables were also significantly influenced by the interaction between

Table 3.3. MANOVA table and univariate test results of aquatic food base response variables as influenced by abiotic predictor variables in the Colorado River in Grand Canyon. Predictor variables include month in 1991 (M), study station (S), habitat (H: pool or riffle), stage zone (Z) and all possible two-way interactions. Response variables include ln-transformed total macroinvertebrate biomass gm/m² (1), associated ln-transformed biomasses of <u>Cladophora</u> gm/m² (2) and <u>Oscillatoria</u> gm/m² (3), and detritus gm/m² (4).

SOURCE	WILK'S LAMBDA	APPROX. F STATISTIC	df	p	UNIVARIATE TESTS OF SIGNIF. RESPONSE VARIABLES
Month (M)	0.986	1.243	4,360	0.292	---
Station (S)	0.868	13.692	4,360	0.000	1,2,4***
Habitat (H)	0.913	8.553	4,360	0.000	3*
Zone (Z)	0.845	16.472	4,360	0.000	1,2,4***
M*S	0.982	1.692	4,360	0.151	(4*)
M*H	0.994	0.587	4,360	0.672	---
M*Z	0.992	0.750	4,360	0.559	---
S*H	0.990	0.936	4,360	0.443	---
S*Z	0.843	16.810	4,360	0.000	1,2,4***
H*Z	0.911	8.749	4,360	0.000	1*

* $p < 0.05$
*** $p < 0.001$

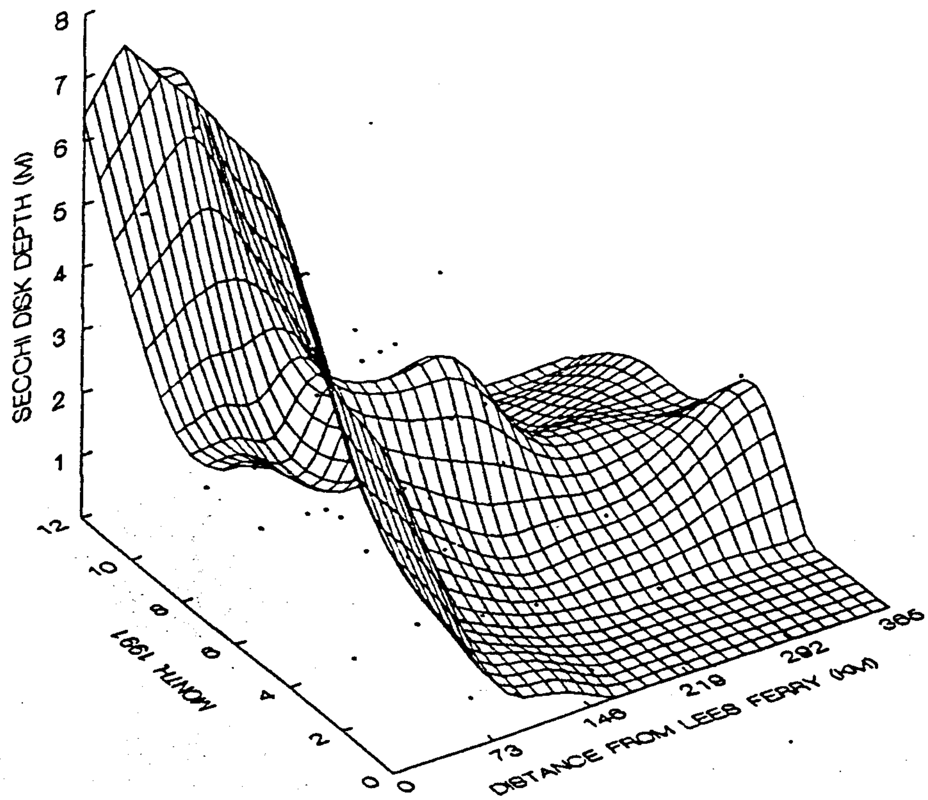
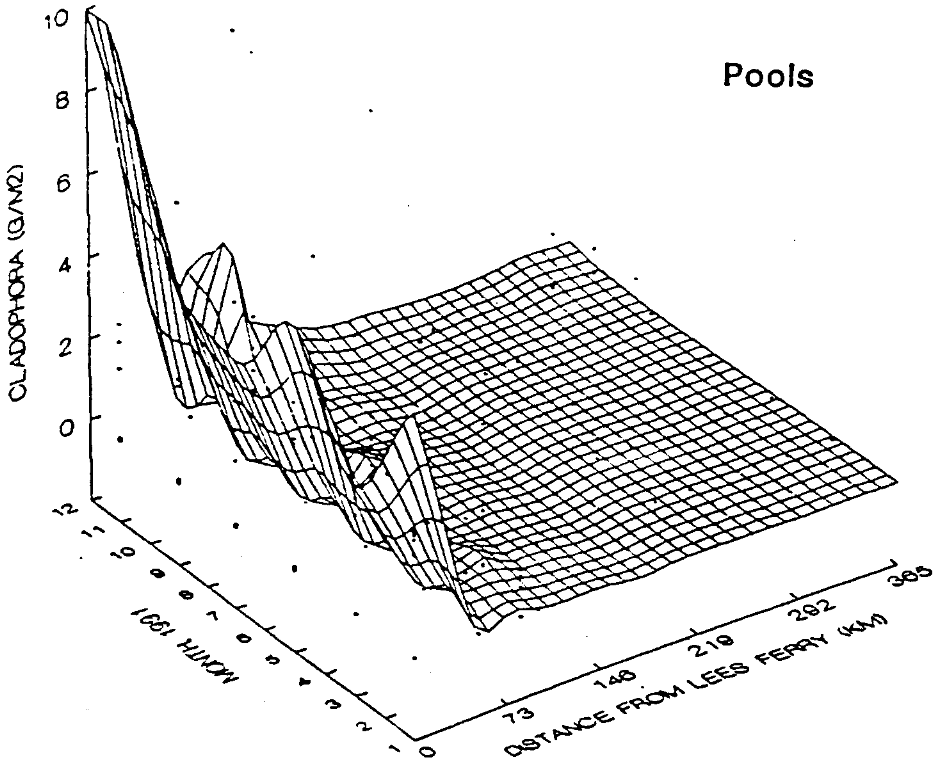


Figure 3.5. Temporal and spatial patterns for Secchi depth in the Colorado River through Grand Canyon, Arizona during 1991.



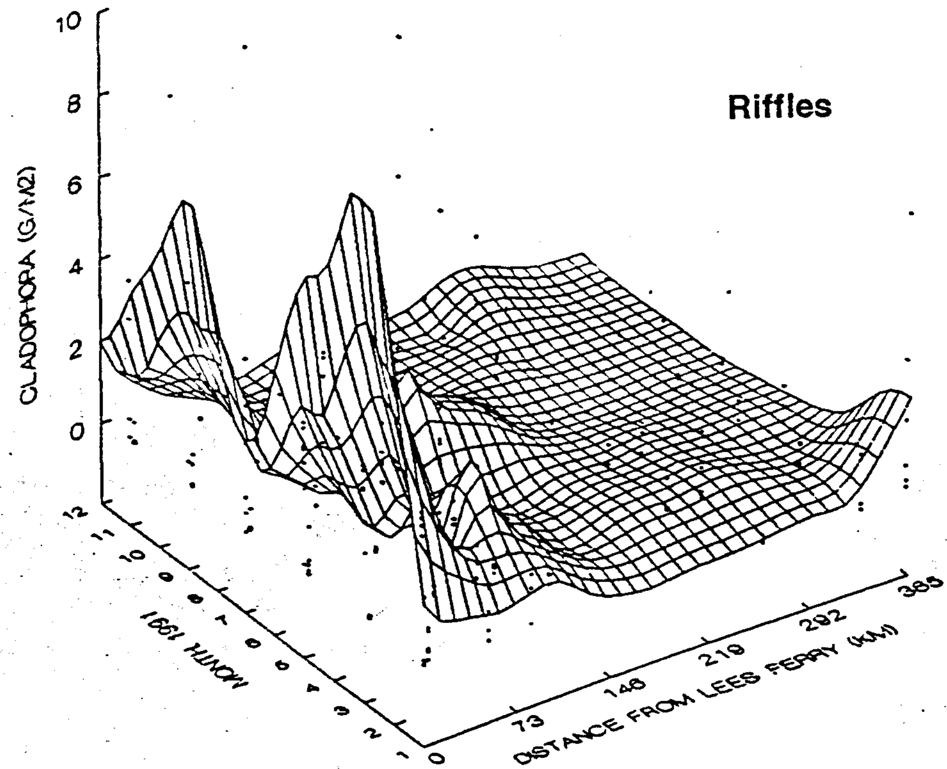


Figure 3.6. Temporal and spatial variation in Cladophora glomerata biomass (gm/m^2) in pools and riffles in the Colorado River, Arizona during 1991.

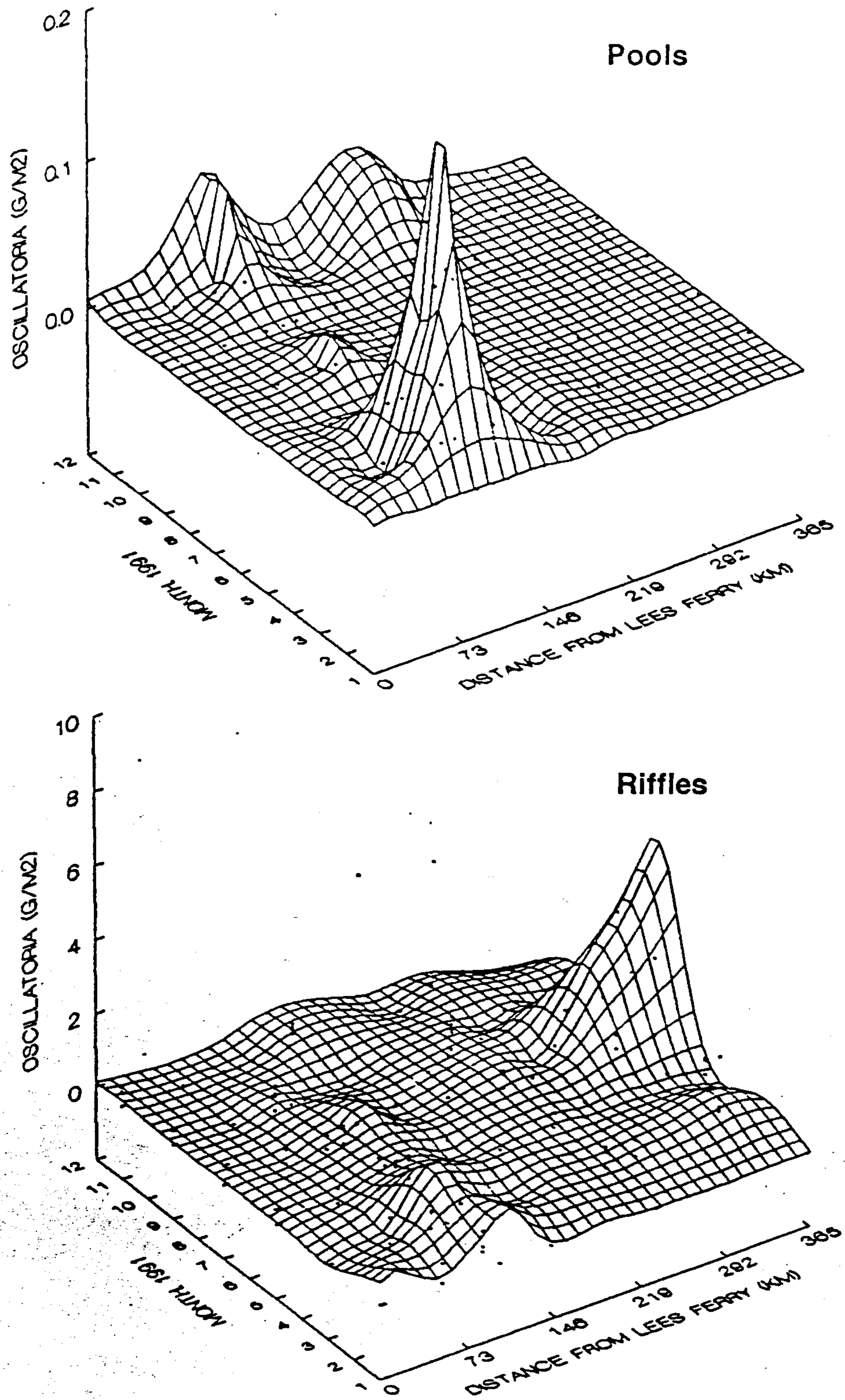


Figure 3.7. Temporal and spatial variation in Oscillatoria spp. biomass (gm/m^2) in pools and riffles in the Colorado River, Arizona during 1991. Note difference in scale between pools and riffles.

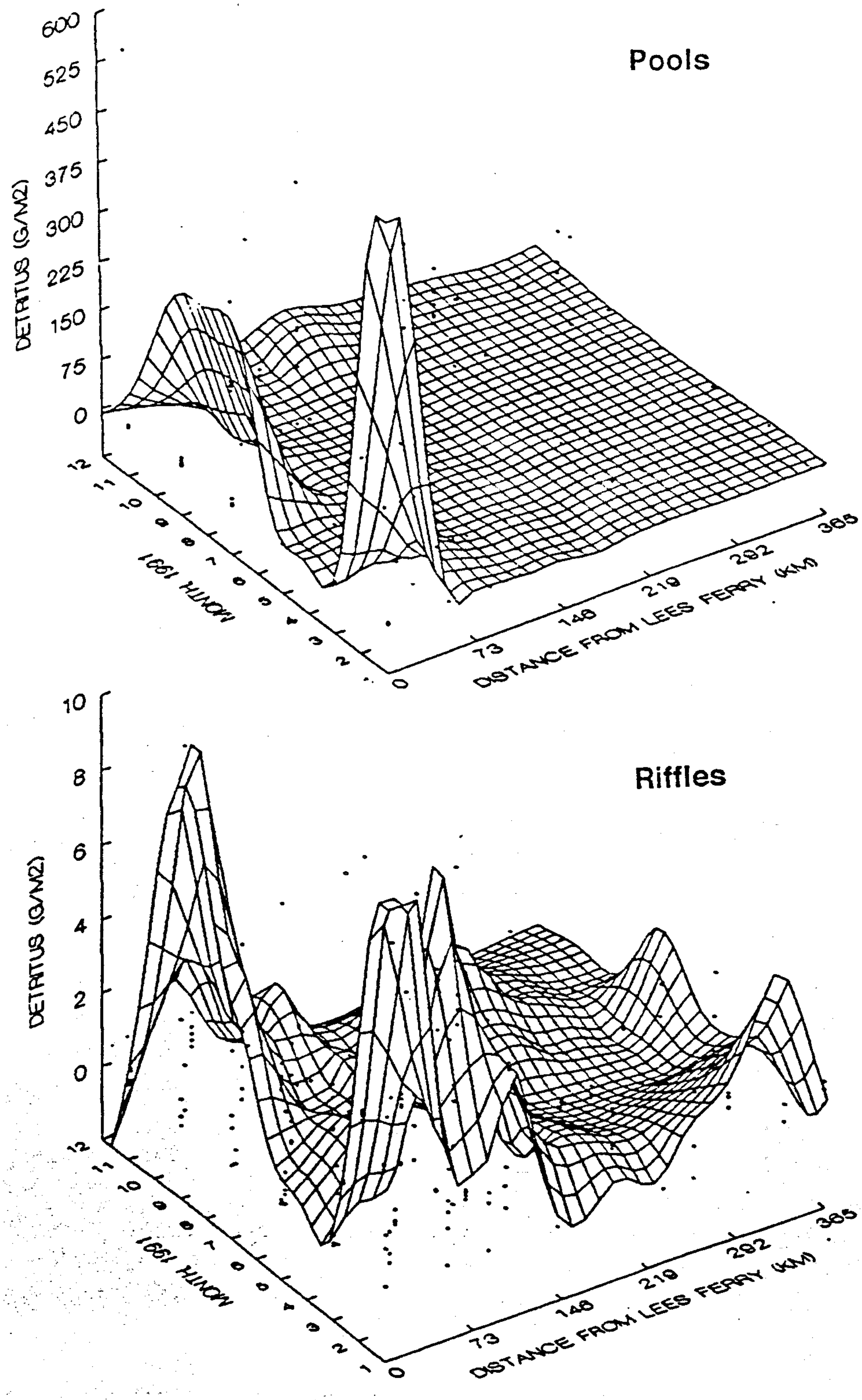


Figure 3.8. Temporal and spatial variation in detritus (gm/m2) in pools and riffles in the Colorado River, Arizona during 1991. Note difference in scale between pools and riffles.

station and zone, an effect attributed to the decreased biomass in the <150 m^3/s zone below Lees Ferry.

Habitat: We evaluated differences in biomass data in pools and riffles. Oscillatoria biomass was significantly lower in pools than in riffles. Cladophora was significantly greater below the 150 m^3/s stage in pools, than in riffles, and was especially pronounced at Lees Ferry, yielding a significant interaction effect between habitat and zone (Figs. 3.6-3.7, 3.9-3.10).

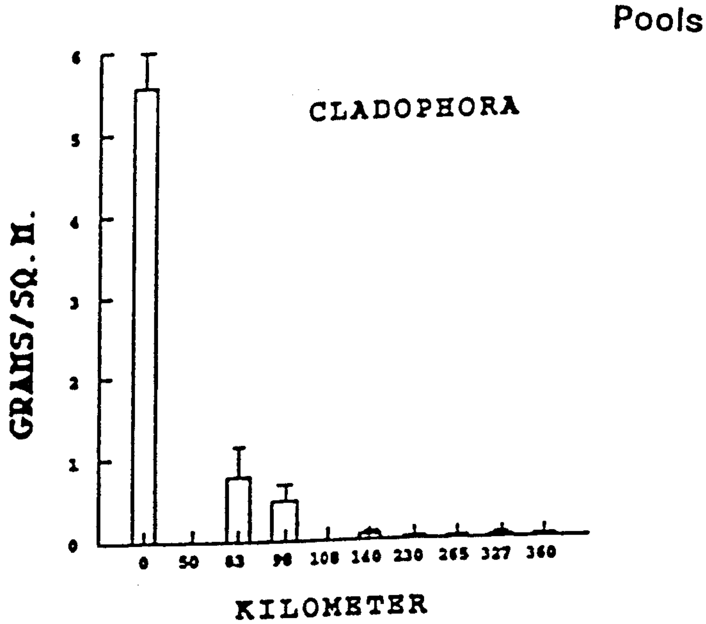
Zone: Biomass patterns were evaluated in three zones: the lower littoral zone below the 150 m^3/s stage elevation, the 150 m^3/s to ca. 350 m^3/s mid-littoral zone, and the 350 m^3/s to 700 m^3/s upper littoral zone (Figs. 3.19-3.21). Detritus, as well as macroinvertebrate and Cladophora biomasss, were significantly greater below the 150 m^3/s stage. Oscillatoria showed a uniform response over stage, suggesting that this alga may tolerate exposure.

Algal Biomass

Cladophora and Oscillatoria are the dominant benthic algae in this system; however, these two taxa occurred in different reaches of the river. Several factors significantly affected the distribution of benthic river algae, and the algal data set was further analyzed to explore those relationships in detail.

Cladophora is the dominant benthic algal species in the tailwater reach of Glen Canyon Dam. This species has a "stairstep" distribution in relation to the major tributaries downstream from Glen Canyon Dam. Cladophora cover was uniformly distributed in pools and riffles between Glen Canyon Dam and RK 1.5. Mean ash-free dry mass at Lees Ferry was 8.6 gm/m^2 (n = 45, SE = 3.0) in pools, with a maximum of 65.2 gm/m^2, and a mean of 15.5 gm/m^2 (n = 18, SE = 2.9) in riffles (Fig. 3.6). Immediately below the Paria River confluence, Cladophora biomass dropped to 0.7 gm/m^2 (n = 16, SE = 0.2), nearly a 15-fold decrease. Downstream of the Paria River, Cladophora cover became restricted to patches in riffle and boulder habitats, as indicated by the relative increase in standard error at downstream locations. During 1991, a relatively low-precipitation and low turbidity year, mean Cladophora biomass remained between 0.0 gm/m^2 and 3.2 gm/m^2 throughout the river corridor. There was less biomass in narrow reach pools and more in wide reach riffles (Fig. 3.6), and 10-fold more Cladophora biomass in riffles than in pool habitats (Fig. 3.9). During 1991, Cladophora was restricted to below the 150 m^3/sec stage.

In contrast to Cladophora, the blue-green alga, Oscillatoria, dominates the hard substrata of the middle and lower Grand Canyon. Mean ash-free dry mass values ranged from <0.01 gm/m^2 (n = 19) at Lees Ferry to 0.3 gm/m^2 (n = 16, SE = 0.3) at RK 3, and 1.1 gm/m^2 (n = 14, SE = 0.7) at RK 355 (Fig. 3.7 and 3.10). Oscillatoria was found in the Lees Ferry reach, but was relatively rare in comparison with Cladophora.



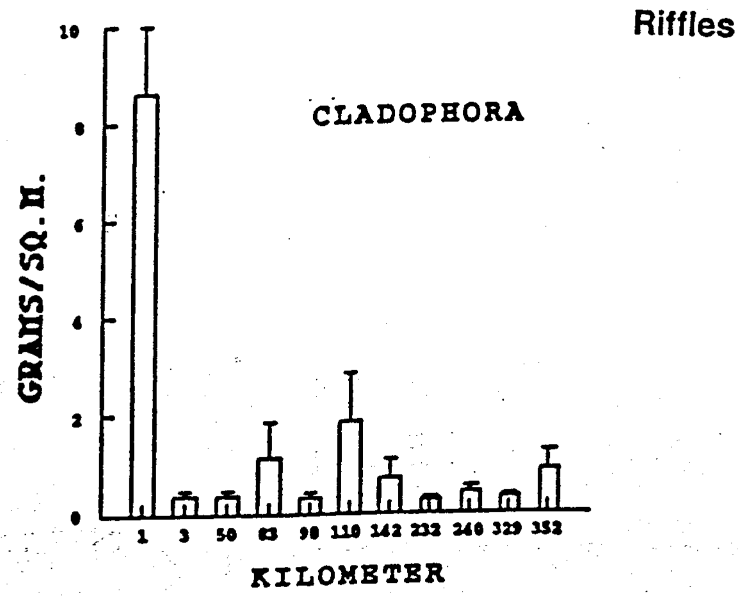
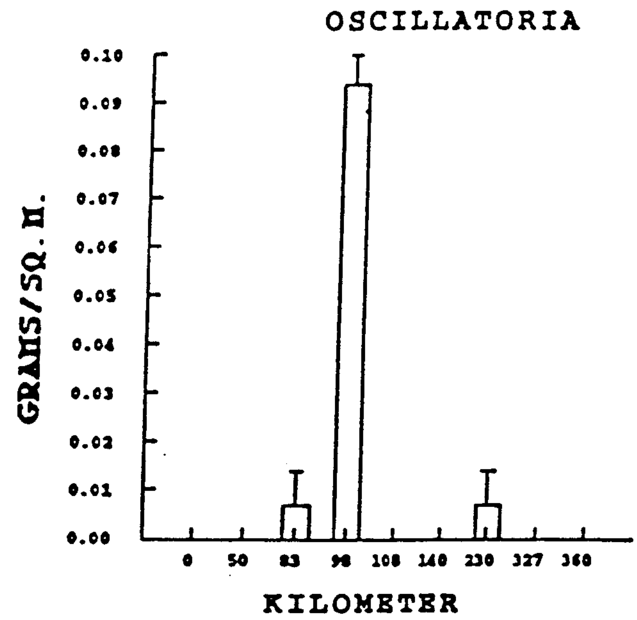


Figure 3.9. Annual summary of spatial variation in Cladophora glomerata biomass (gm/m^2, SE) in pools and riffles in the Colorado River, Arizona during 1991. Note difference in scale between pools and riffles.

Pools



Riffles

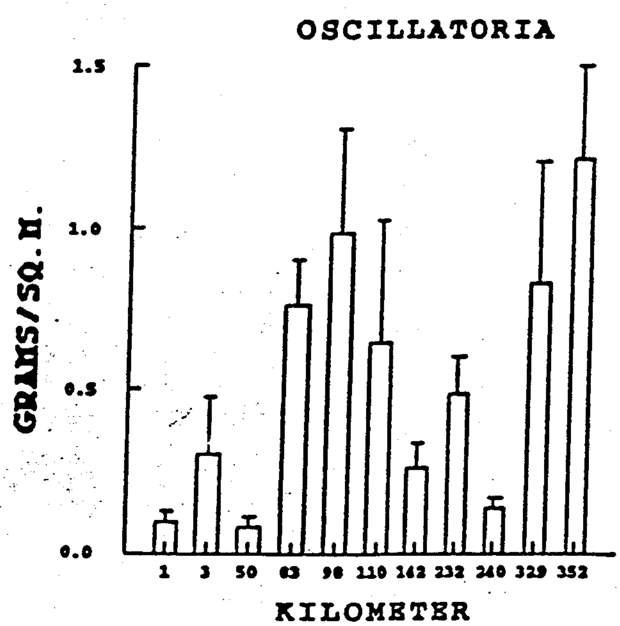


Figure 3.10. Annual summary of spatial variation in <u>Oscillatoria</u> spp. biomass (gm/m2, SE) in pools and riffles in the Colorado River, Arizona during 1991. Note difference in scale between pools and riffles.

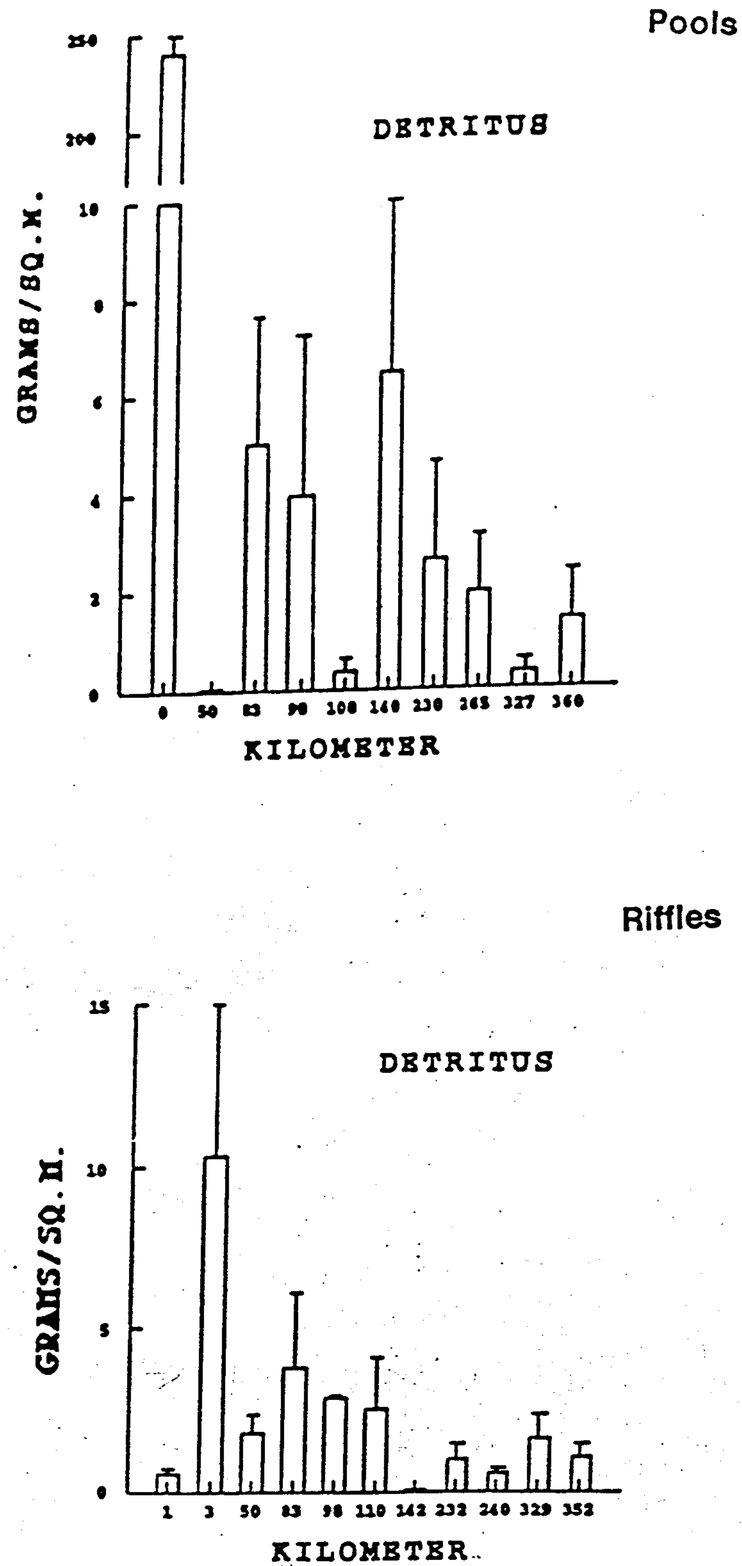


Figure 3.11. Annual summary of spatial variation in detritus (gm/m2, SE) in pools and riffles in the Colorado River, Arizona during 1991. Note difference in scale between pools and riffles.

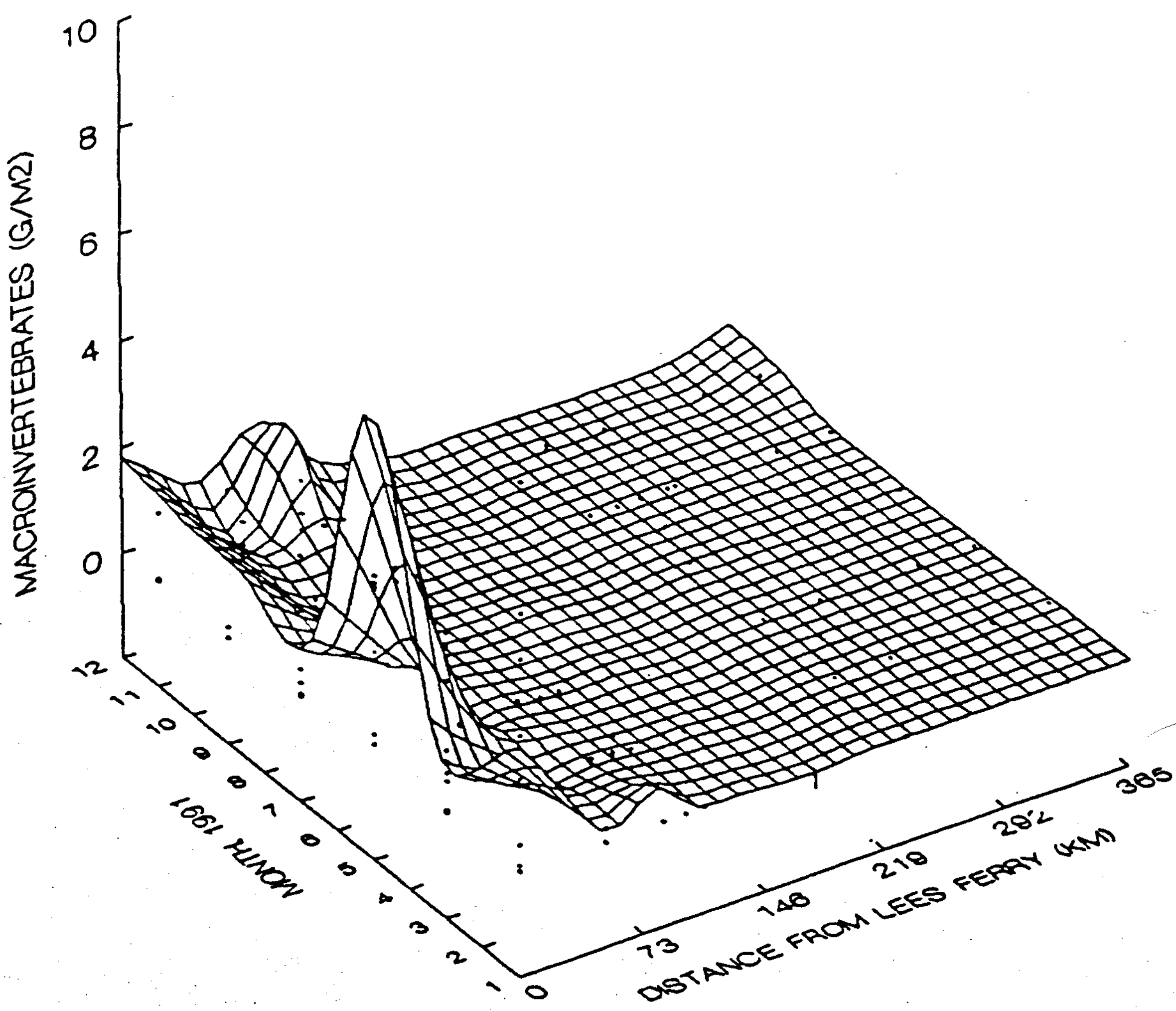
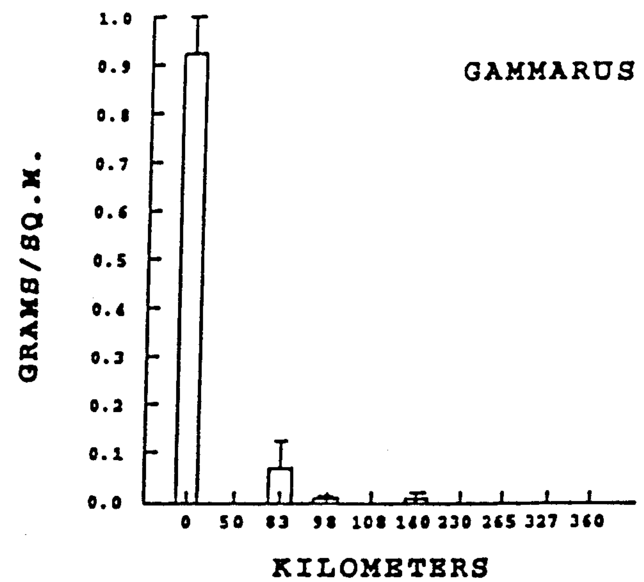


Figure 3.12. Temporal and spatial variation in macroinvertebrate biomass (gm/m2) in pools in the Colorado River, Arizona during 1991

Pools



Riffles

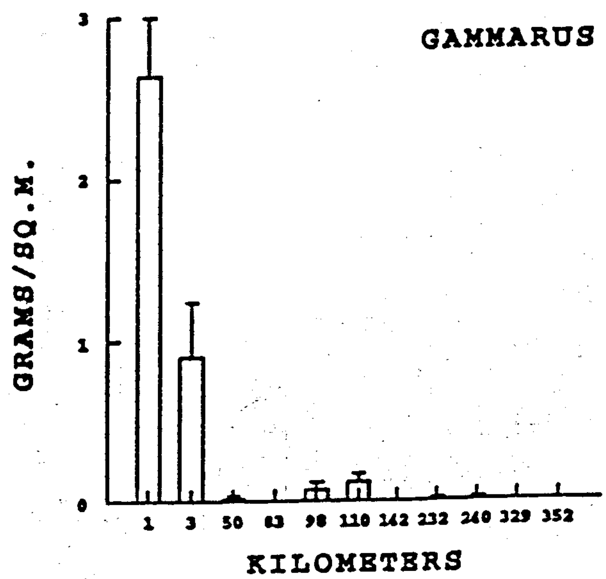
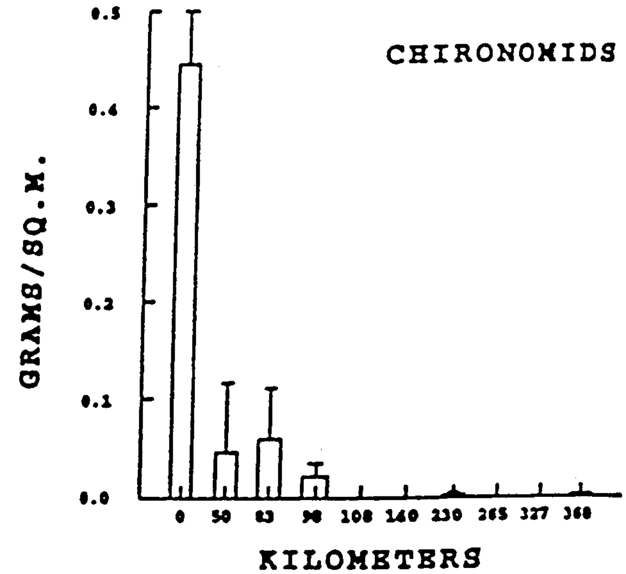


Figure 3.13. Annual summary of spatial variation in Gammarus lacustris biomass (gm/m^2, SE) in pools and riffles in the Colorado River, Arizona during 1991. Note difference in scale between pools and riffles.

Pools



Riffles

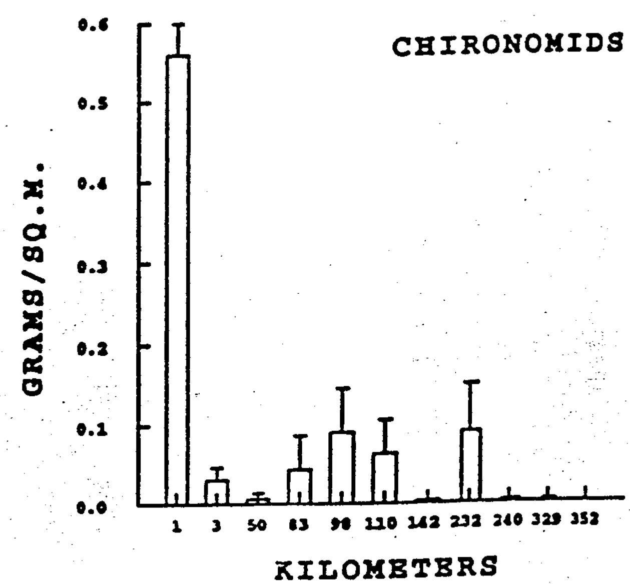
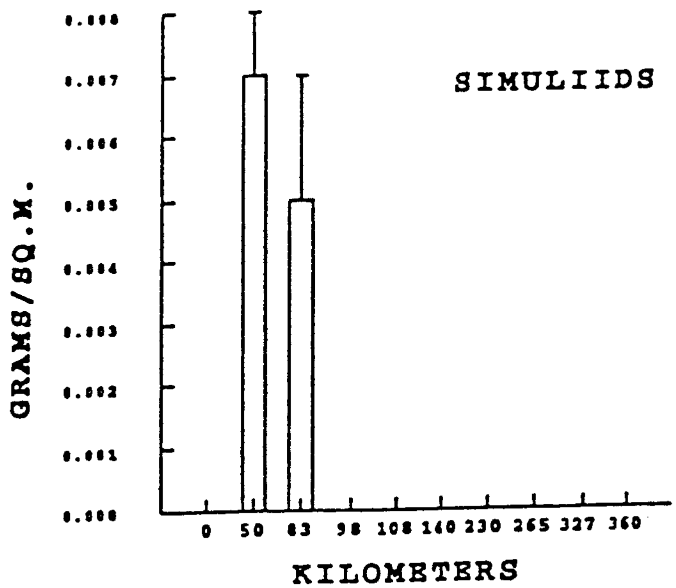


Figure 3.14. Annual summary of spatial variation in chironomid biomass (gm/m^2, SE) in pools and riffles in the Colorado River, Arizona during 1991.

Pools



Riffles

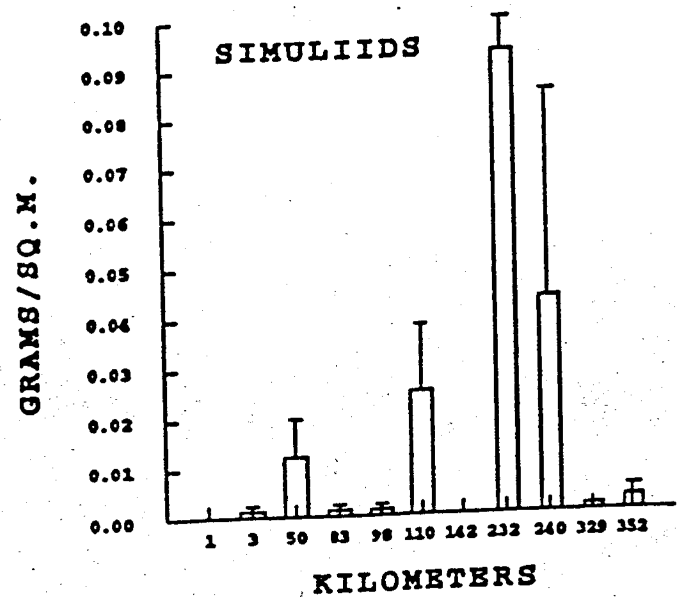
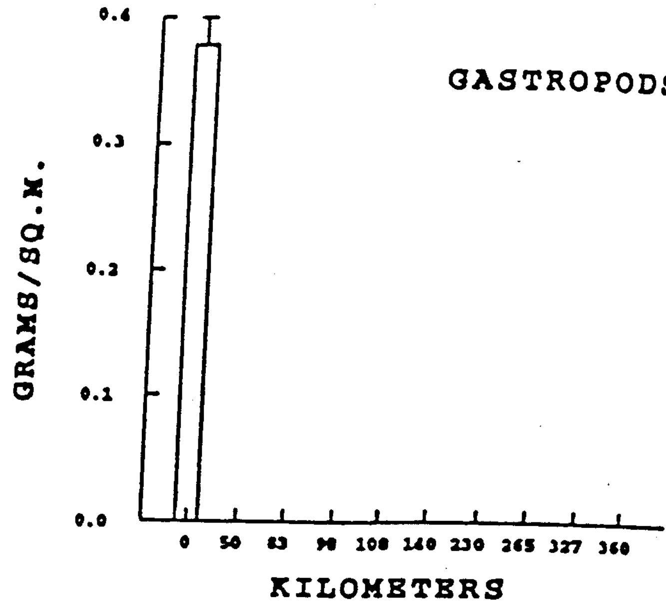


Figure 3.15. Annual summary of spatial variation in simuliid biomass (gm/m^2, SE) in pools and riffles in the Colorado River, Arizona during 1991. Note difference in scale between pools and riffles.

Pools



Riffles

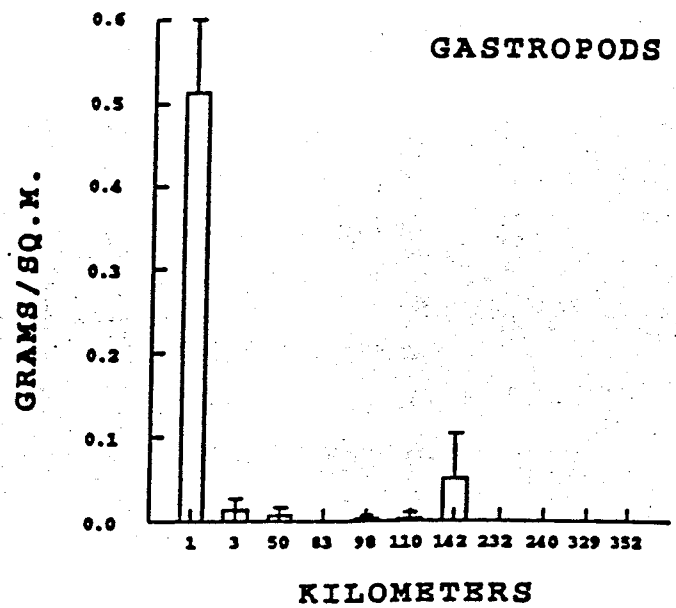
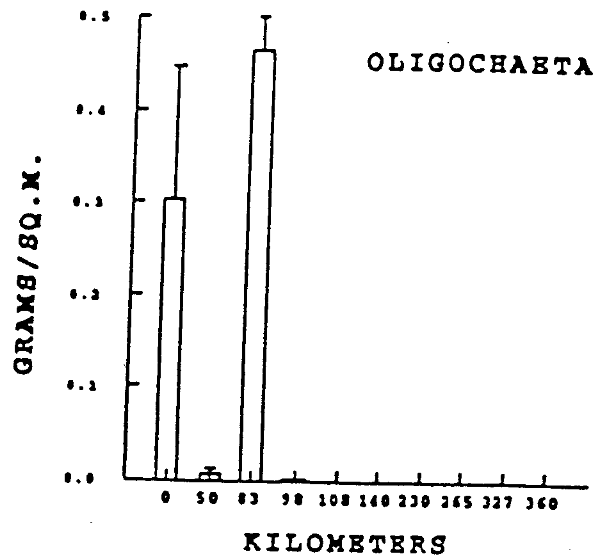


Figure 3.16. Annual summary of spatial variation in gastropod biomass (gm/m^2, SE) in pools and riffles in the Colorado River, Arizona during 1991.

Pools



Riffles

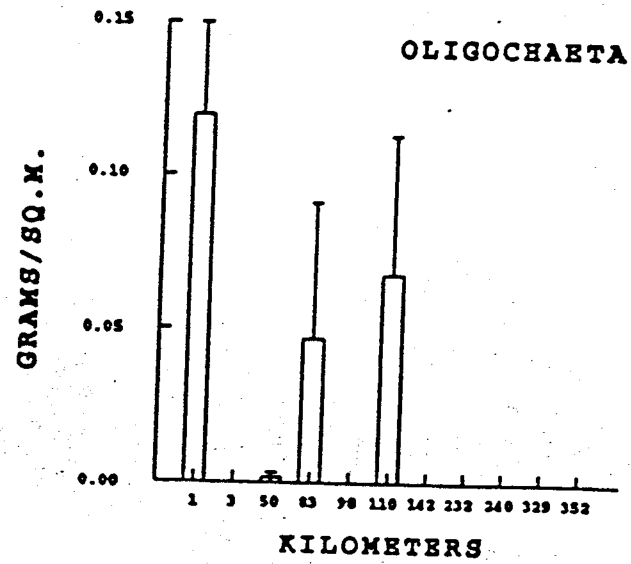
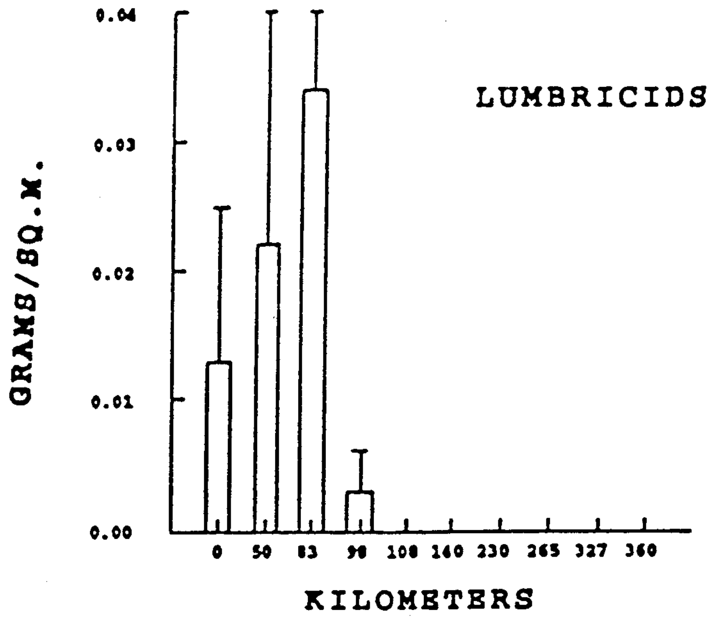


Figure 3.17. Annual summary of spatial variation in oligochaete biomass (gm/m^2, SE) in pools and riffles in the Colorado River, Arizona during 1991.

Pools



Riffles

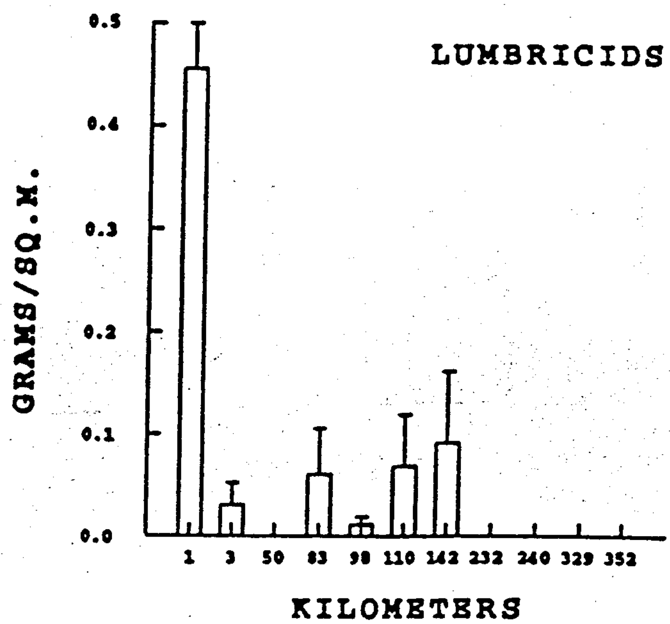


Figure 3.18. Annual summary of spatial variation in lumbricid biomass (gm/m^2, SE) in pools and riffles in the Colorado River, Arizona during 1991. Note difference in scale between pools and riffles.

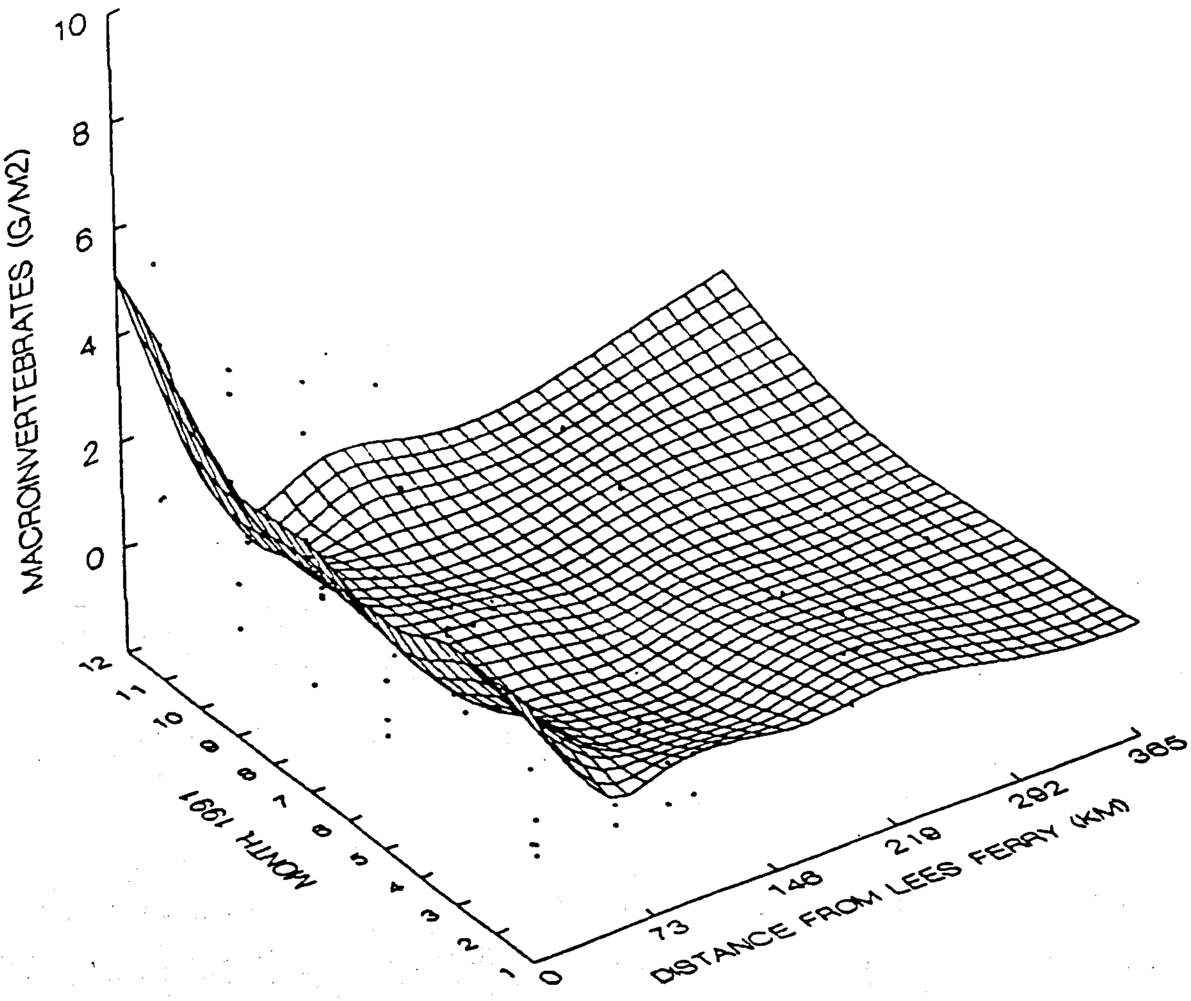


Figure 3.19. Temporal and spatial variation in macroinvertebrate biomass (gm/m2) in riffles in the Colorado River, Arizona during 1991.

RIFFLE

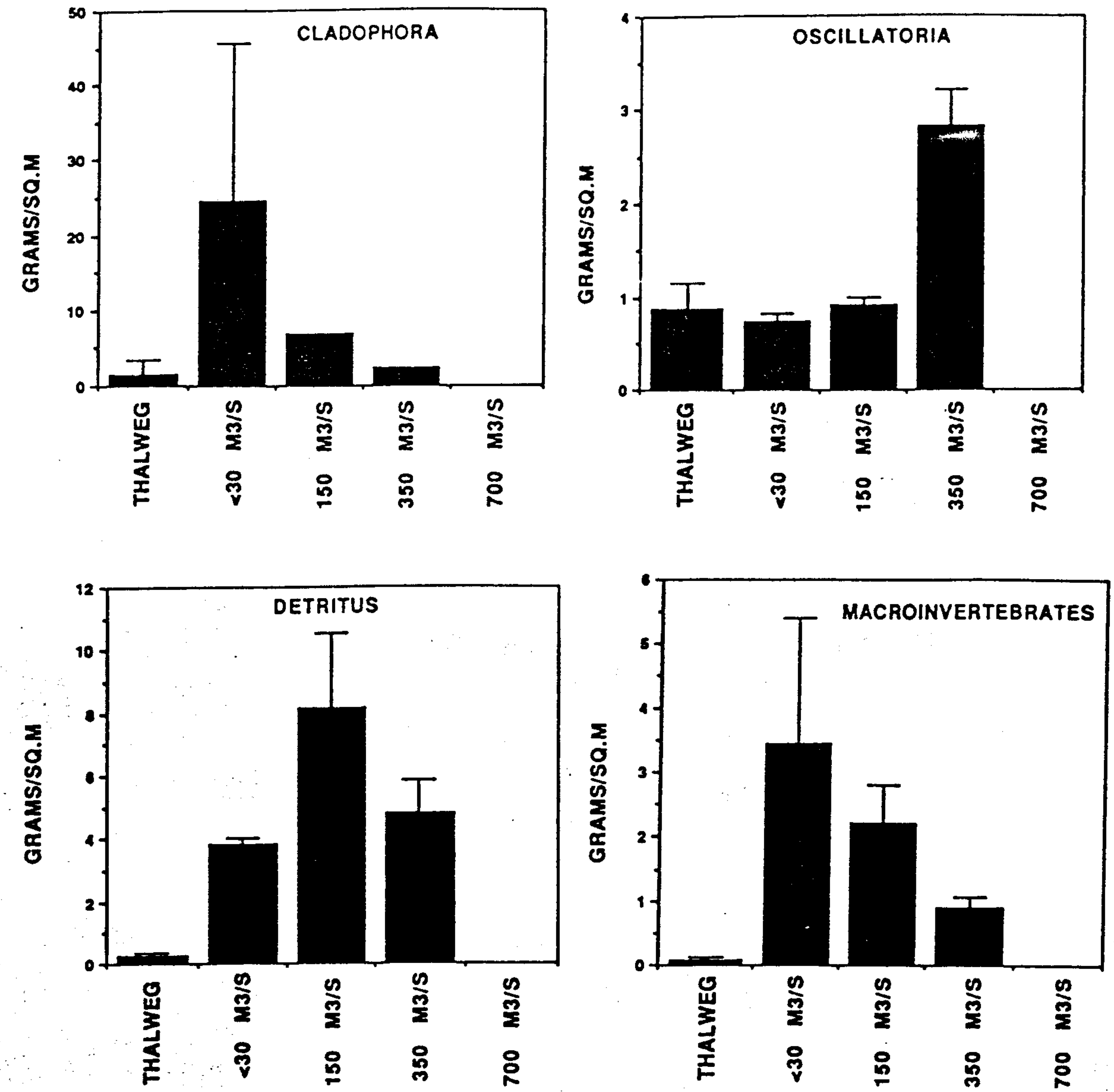


Figure 3.20. Annual biomass (gm/m2, SE) for selected biota in riffles from five discharge zones sampled in the Colorado River during 1991. Note differences in scale (gm/m2) between biota.

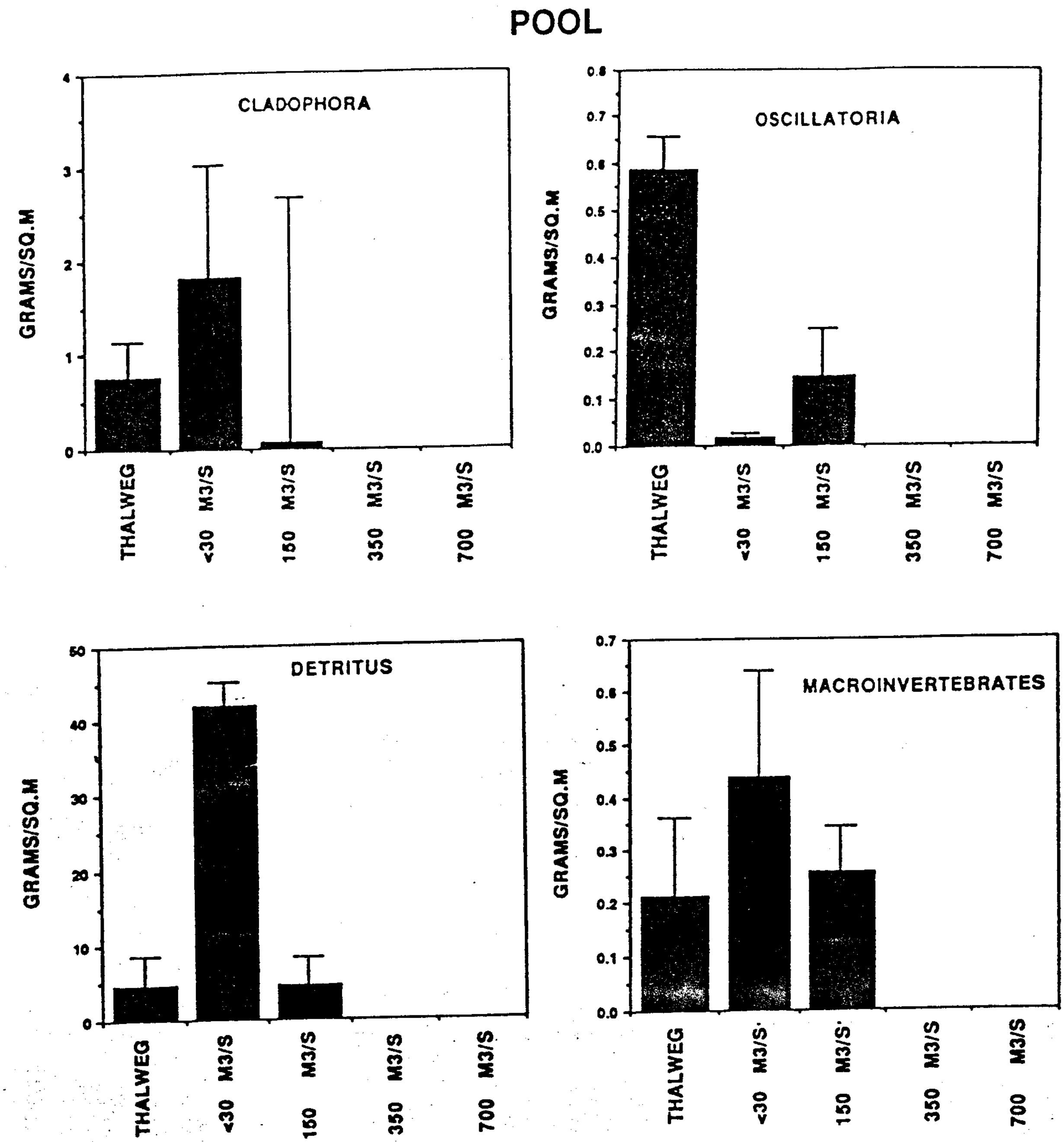


Figure 3.21. Annual biomass (gm/m2, SE) for selected biota in pools from five discharge zones sampled in the Colorado River during 1991. Note differences in scale (gm/m2) between biota.

Separate multiple stepwise regressions were performed to determine whether water chemistry parameters (DO, pH, Secchi depth, specific conductance, and temperature) were correlated with the distribution of Cladophora and Oscillatoria in river cobble bar (high velocity) habitats on hard substrates. Cladophora biomass was weakly but significantly negatively correlated with water temperature, and was positively correlated with Secchi depth, a measure of water transparency ($R^2 = 0.11$, $F = 22.464$, $df = 2{,}344$, $p < 0.001$).

$$\mathrm{Log}_n (B_{Clgl} + 1) = -0.045T + 0.097S + 0.738$$

where $\mathrm{Log}_n (B_{Clgl} + 1)$ is the natural log transformed biomass of Cladophora/m^2, T = water temperature (°C), and S is Secchi depth (m). Cladophora distribution was not correlated with DO or specific conductance ($p > 0.05$); these factors apparently do not limit Cladophora distribution in the Colorado River.

In contrast, Oscillatoria biomass was slightly but significantly negatively correlated with Secchi depth ($R^2 = 0.089$, $F = 10.15$, $df = 2{,}278$, $p < 0.001$):

$$\mathrm{Log}_n (B_{Oscil} + 1) = -0.041S - 0.06$$

where $\mathrm{Log}_n (B_{oscil} + 1)$ is the natural log transformed biomass of Oscillatoria/m^2. Oscillatoria distribution was not correlated with water temperature or specific conductance ($p > 0.05$), but showed a non-significant trend of positive correlation with DO ($p = 0.066$). The uncorrelated factors apparently do not limit the distribution of Oscillatoria in river cobble bars. From this analysis it appears that water temperature and Secchi depth may influence the distribution of these two algal species, and more research on thermal regulation of growth rates and light requirements of these two species is warranted.

Although the Lees Ferry reach is dominated by Cladophora, several other plants are associated with Cladophora in pools and riffles. In addition to epiphytic diatoms, several species of filamentous green algae including, Chaetophora, Draparnaldia, Mougeotia, Oedogonium, Rhizoclonium, Spirogyra, Stigeoclonium, and Ulothrix are associated with Cladophora tufts. These algae are most common during the summer months and can change the overall appearance of the algal cover to a light green color. Likewise, high densities of epiphytic diatoms can change the algal cover to a light brown color. The macroalga, Chara sp., along with the macrophytes, Potamogeton and Elodea, are found in fine sediments throughout Lees Ferry. Several species of Oscillatoria are also present at Lees Ferry, however, there appears to be a monoculture of this blue-green alga below the confluence of the Paria River. Also, isolated patches of aquatic moss (Bryophyta) are found throughout the river corridor and are common in tributaries with low specific conductance.

Detritus

Detritus varied signficantly between stations and between stage elevations (Table 3.3, Figs. 3.8 and 3.11). High values of detritus at Lees Ferry are attributed to beaver caching. Most of the detritus at Lees Ferry consisted of willow and tamarisk branches that were cut by beaver and stripped of bark. Downstream, large amounts of detritus were collected in pools at South Canyon and Nankoweap stations during November, 1991. These accumulations may have been attributable to tributary input during early fall monsoons and to reduced velocity during interim flows. Chironomids, simuliids, and oligochaetes were observed to colonize waterlogged driftwood in this system. Monitoring efforts presently planned will provide further data on detrital accumulation.

Macroinvertebrate Biomass

Macroinvertebrate biomass was greatest at Lees Ferry and decreased downstream. Mean biomass (dry wt.) at RK O.O ranged from 2.1 gm/m^2 (n = 45, SE = 0.6) in pools (with a maximum of 17.9 gm/m^2) to 4.3 gm/m^2 in riffles. These values were reduced nearly 4-fold immediately below the confluence of the Paria River to a mean of 1.1 gm/m^2 (n = 16, SE = 0.4). Biomass values declined downstream, typically with up to 10-fold higher values in riffles as compared to pools, and with highest values comparable to the Lees Ferry riffle in tributaries (Figs. 3.12-3.19).

Subsequent MANOVA analyses demonstrated that the macroinvertebrate assemblage was significantly influenced by time, distance, habitat type, and zones in the Colorado River (Wilk's lambda <0.955, df = 7,357, p <0.018 for each factor). The following patterns are illustrated in Figs. 3.12-3.19. This analysis showed that chironomid populations decreased significantly from January through autumn, 1991. The biomass of all macroinvertebrate categories except Simuliidae and "miscellaneous invertebrates" decreased in density with distance from Glen Canyon dam. Thus, Gammarus, oligochaetes, and chironomid biomass decreased in downstream reaches, and chironomids and Gammarus made up a significantly larger proportion of the macroinvertebrate biomass in the reach above the Paria River (univariate, df = 1,363, p = 0.008). Oligochaetes and Gammarus made up significantly more of the macroinvertebrate biomass in pools, whereas lumbricids and simuliids made up significantly more of the overall biomass in riffles (df = 1,363, p = 0.042, 0.025, respectively). Gammarus, oligochaetes, Chironomidae, and gastropods (largely Physella) contributed significantly more biomass to the lower littoral zone, almost never occurring above the 350 m^3/sec stage (Figs. 3.19-3.20).

Samples within the zone of fluctuation (middle and upper littoral habitats; n = 900) generated a total of 33 macroinvertebrates. Of this, the Lees Ferry station contributed 17 lumbricids, Site 10 cobble bar contributed 11 oligochaetes, and the Phantom rapid and Kanab Creek stations each contributed one chironomid and one simuliid larvae. In addition, three unidentified pupae were collected in Marble Canyon.

Geomorphic Patterns

Our results indicate that >50% of the aquatic food base in the 357 km stretch of river is produced between Glen Canyon Dam and Lees Ferry (17 km), which is <5% of the study area. Results from the FY90 and FY91 collections indicate the Lees Ferry reach made up >56% of the algal and >52% of the macroinvertebrate biomass between Glen Canyon Dam and Diamond Creek. Based on average areal comparisons for the river, we calculated an annual mean biomass of 8.7 gm/m^2 algae (ash-free dry mass) per kilometer distance and 0.2 gm/m^2 macroinvertebrates/km (dry wt.) for the Lees Ferry reach compared to an average of 0.1 gm/m^2 algae/km and 0.02 gm/m^2 macroinvertebrates/km for the remainder (330 km) of the river through Grand Canyon. These data were derived from the combined mean annual biomass estimates at each site.

Wide reaches comprised 98% of the total biomass of plants and animals in pool habitats, and 73% in riffle habitats. Lees Ferry was by far the most productive single station for both riffle and pool habitats yielding 32% of the total biomass for plants and animals as compared to the average biomass for the remaining 9 downstream sites. Narrow reaches, with higher water velocities and hard, bare substrata, provide more conducive habitats for filter feeders such as simuliids and certain chironomid taxa. Also, the incised narrow reaches in the Grand Canyon corridor have a southwest orientation which limits solar insolation and ultimately primary and secondary production.

Riffles provide a more heterogeneous substratum and therefore increase surface area for primary producers and food and refugia for macroinvertebrates. Although riffles constitute only a small percentage (<10%, Carothers and Brown 1991) of the overall stream bed, they are areas of highest biomass. Pools are important as depositional areas and for nutrient mineralization as shown by the high biomass (0.45 gm/m^2) of oligochaete detrital feeders. Oligochaetes were especially abundant in a well developed eddy-pool at Nankoweap (RK 83.4).

Nankoweap stations (RK 83.2 and RK 83.4) demonstrate a strong geomorphic influence on biotic biomass. There is a significant increase in plant and animal biomass at the wide and southeast oriented Nankoweap stations compared to the more narrow upstream sites through Marble Canyon. The overall increase in annual solar insolation, general slowing of water flow and increased nutrient retention time, and a reduction in the effect of fluctuating flows on the littoral zone result from a relatively low channel depth to width ratio at wide reaches. Further support for the positive influence of wide reaches on biotic communities is provided by: 1) an increase in species richness of Chironomidae (13) at Nankoweap, and 2) numerical dominance of the midge, Cricotopus annulator, which is also dominant in the wide Lees Ferry reach.

Analyses of substrata (MANOVA) illustrated that riffle/cobble (>3.0 cm diameter) and pool/silt were the most productive substrata (Wilk's Lambda = 0.763; df = 5,121; $p<0.001$) for each biotic factor. Sediment analysis of pools throughout Grand Canyon revealed that silt rather than sand, cobble, fine gravel, and course gravel supported the highest biomass of macroinvertebrates, however, silt makes up only 5.2% by dry weight of the substrata collected in pools. Sand was the most common pool sediment (94.2%), but supported little animal life.

Transect, depth, and reach width were examined for effect on sediment accumulation. Reach width was positively correlated with sand (univariate, df = 121; F = 17.5; p = <0.001) and silt (univariate, df = 121; F = 3.6; p = 0.05). Fine gravel was the only depth related clast size. Silt was positively correlated with transect (univariate, df = 121; F = 4.74; p = 0.03), that is the upstream transect within the pools had the highest accumulation of silt and macroinvertebrate biomass. This reflects the area of greatest deposition within the eddie-pool systems in Grand Canyon. These data illustrate the importance of large hard and stable substrata for primary and secondary production, and fine sediment depositional pools for the decomposers like oligochaetes and certain chrionomid larvae.

CHAPTER FOUR: MACROINVERTEBRATE DIETS

INTRODUCTION

Aquatic Diptera and Gammarus lacustris are keystone resource species for higher aquatic and riparian trophic levels in the Colorado River corridor between Glen Canyon Dam and Lake Mead, Arizona. Food resource availability is critical to macroinvertebrates, fish populations, and terrestrial ecosystem linkages in fluvial systems. These two groups play a large, if not over-whelmingly important, role as food resources for exotic and native fish, as well as hundreds of terrestrial species in the dam-regulated river corridor. Little literature exists on the dietary requirements and ecological role of these macroinvertebrates.

To address trophic linkages in this system, we analyzed the gut contents of chironomids and Gammarus lacustris to determine dietary requirements, and the extent to which Cladophora glomerata was utilized as a food source.

METHODS

Macroinvertebrate Diet

Chironomid larvae, collected in the mainstem at Lees Ferry (RK 0.0; n = 10), Vasey's Paradise (RK 50.8; n = 15), and Diamond Creek (RK 361; n = 21), were analyzed for diet (Objective 3). Each larva was placed into a separate vial containing 70% EtOH. In the laboratory, larvae were soaked in a 10% solution of KOH for 3-12 hrs (depending on larval size) prior to observation of the gastrointestinal tract (GI). This procedure cleared the outer body integument of chironomids, but maintained the integrity of the GI tract and gut contents. Observations on size of chironomid larvae; frequency of diatoms, Cladophora glomerata, Oscillatoria, detritus, bacteria, and sand; as well as dimensions of food particles were recorded at 1000x. Diet information for Gammarus was taken from Pinney (1991).

RESULTS

Macroinvertebrate Diet

Algae made up 61.4% (SE ± 9.4) of the diet in the intestinal tract of chironomid larvae at Lees Ferry (RK 0.0), 30.7% (SE ± 8.8) at Vasey's Paradise, and 7.5% (SE ± 2) at Diamond Creek (RK 361). Inorganic constituents (sand grains), detritus, and bacteria typically made up the balance of the diet at each location. Diatoms comprised >95% of the algal component at each location, with fragments of Cladophora cells typically making up <1%. The diatom genera most frequently encountered in guts were Achnanthes, Cocconeis, Cymbella, Diatoma, and Rhoicosphenia, all of which are common epiphytes associated with Cladophora in the Colorado River (Hardwick et al. 1992). Chironomids >4mm averaged 1013 (SE ± 325) diatom cells per larva, while chironomids ≤4mm averaged 41.3 (SE ± 7.8) diatom cells (up to 200 μm in length) per larva. The average cell dimension for diatoms in the GI tract was 9.4 μm (SE ± 1.2) x 51.2 μm (SE ± 24.7); the largest diatom cell observed in the G.I. tract was 6.0 μm x 120 μm. There were no Oscillatoria filaments (blue-green algae) observed in chironomid diets.

Pinney (1991) reported that diatoms comprised >90% of the diet for Gammarus at Lees Ferry. The balance of the diet included blue-green algae and detritus. Gammarus selected upright periphytic diatom taxa (Rhoicosphenia and Diatoma) over diatoms that were adnately attached (e.g. Cocconeis) to Cladophora. This observation was based on the relatively low numbers of Cocconeis in the gut of Gammarus compared to numbers of Cocconeis estimated on Cladophora cells in the field (Mann-Whitney U, $w = 26.0$, $p < 0.03$). In contrast, there were no significant differences between densities of Rhoicosphenia and Diatoma in the field and in the guts of Gammarus.

DISCUSSION

The primary food items for Gammarus and chironomid larvae in the Colorado River ecosystem are epiphytic diatoms, bacteria, and to a lesser extent detritus. Few Cladophora cells were observed in the digestive tracts of Gammarus and chironomid larvae. Diatoms are likely a cornerstone food in the tailwaters of Glen Canyon Dam, but become less important downstream, where bacteria may play a more important role in the food web.

The change in diet for downstream macroinvertebrates results from a decrease in epiphytic diatoms due to reduced Cladophora substrata. Reduction in Cladophora over distance from Glen Canyon Dam is linked to turbidity, increased water temperature, and limited stable substrata in the photic zone (Chapter 3, this report; Yard et al. 1992). Higher downstream suspended sediment loads, due to tributary inputs, reduce available light energy for both Cladophora and associated epiphytic diatoms. Hardwick et al. (1992) reported a progressive decrease in downstream densities of epiphytic diatoms with >4 times fewer diatoms/m^2 of Cladophora substratum at Diamond Creek than in the tailwaters of Glen Canyon Dam.

Oscillatoria crusts (blue-green alga) replace Cladophora as the dominant filamentous alga at downstream sites due to change in stable substrata, high suspended sediment loads, and the ability of Oscillatoria to tolerate exposed, dry periods during drawdown (Carr and Whitton 1973, Bold and Wynne 1985). The compact blue-green algal crusts have substantially less surface area for diatom attachment and colonization, and therefore contribute to the decrease in available diatoms at downstream sites. The overall role of bacteria in the food web of downstream macroinvertebrates, and the source(s) of these bacterial substrata needs further study.

CHAPTER FIVE: IN SITU SIMULATION OF REGULATED FLOW

INTRODUCTION

Regulated flow has the potential to reduce the aquatic food base in the Colorado River ecosystem. The purpose of this element of the study was to determine the potential impacts of dam operations on the aquatic food base in the Colorado River ecosystem using experimental techniques.

METHODS

Energy Measurements

Energy values (joules) were determined for selected biota in the Colorado River with a Phillipson microbomb calorimeter (Phillipson 1964) (Objective 3). Algae and macroinvertebrates used in these measurements were collected from the mainstem at Lees Ferry (Table 5.1). The gut contents of Gammarus lacustris, simuliid larvae, oligochaetes, and chironomid larvae were cleared by starving animals for 20-24 hrs. Animals were dried in a desiccator and prepared into pellets (13.5-14.5 mg). Epiphyton was removed from Cladophora glomerata by vigorous agitation for one minute in a bag filled with 50 ml of filtered (0.45 μm pore) Lees Ferry water. The epiphyton suspension was poured into a container through a clean fiberglass screen (1 mm mesh) to separate epiphyton from Cladophora. The Cladophora on the screen was thoroughly rinsed with filtered Lees Ferry water into the container to separate remaining epiphyton. This procedure removed at least 85% of the epiphyton, based on microscopic examination, and was the most efficient and effective technique for separating epiphytic diatoms from Cladophora. Only cells of the closely adnate Cocconeis remained attached to Cladophora. The epiphyton suspension was swirled within the container, thus suspending the epiphyton in the water and depositing a small cone of more dense sand in the bottom of the container. The suspended epiphyton was quickly drawn into a syringe and filtered onto a 0.45 μm glass membrane. This procedure was conducted through several rinses with filtered Lees Ferry water until the sand matrix was free of epiphyton. The epiphyton was scraped from the membrane after the suspension dried to a moist paste. Epiphyton suspensions and Cladophora filaments without associated epiphyton were dried in a desiccator and prepared into pellets (13.5-14.5 mg) for microbomb calorimetry. The epiphyton pellet contained a 5% concentration of benzoic acid to insure complete burning. All samples were compared to standard benzoic acid ignitions. These energy units (joules/gm; 1 joule = 0.239 calories) for biotic categories were used in experimental exposure studies [See Results: In Situ Simulation of Regulated Flow Experiments and Estimates of Energy Loss at Selected Research Flows (joules/m^2)]. In other words, the energy (joules/mg, in Table 5.1) for a given biotic component was multiplied by the loss in biomass (mg/m^2) for a given biotic component.

Table 5.1. Energy values (joules/mg dry wt; ± S.D., n = 3) for Cladophora glomerata, diatom epiphytes, and various macroinvertebrates collected from Lees Ferry in the Colorado River, AZ. One joule = 0.239 calories.

BIOTIC CATEGORY	ENERGY
Cladophora glomerata	11.75 (± 0.68)
Diatom epiphyte assemblage	14.43 (± 0.72)
Chironomid assemblage	21.38 (± 0.40)
* Simuliid assemblage	22.64 (± 0.30)
Gammarus lacustris	16.54 (± 0.61)
Oligochaete assemblage	20.45 (± 0.64)
Annelid assemblage	15.22 (± 1.11)

* Value taken from Cummins and Wuycheck (l971)

In Situ Experiments

A series of five experiments were conducted at Lees Ferry, Arizona between 31 May and 12 July 1991 to determine the importance of regulated flow on aquatic plant and animal biota (Objective 4, Table 5.2). Four experiments were conducted on an open-frame floating raft (2.7 x 4.3 m) anchored at Lees Ferry, and one experiment was conducted in the channel of the Colorado River at Lees Ferry. The raft was constructed from a rectangular frame of 2 x 12 dimensional lumber strapped down on two mini-snout tubes, 4.3 m in length. Baskets were suspended from five 2 x 4 cross members set 82 cm apart, starting with one at the center, along the 4.3 m structure. Two cross members were used, one was screwed into the main 2 x 12 frame, the other was set on 2 x 4 supports 61 cm off the main frame and staggered so the baskets could be hung outside of the tubes to randomize for raft effect. Low flows are the most favorable for raft experiments because baskets ride in the current better and Cladophora accumulation on the baskets is reduced. High flows can add over 8 kg wet wt. of Cladophora to the forward baskets, thereby requiring regular maintenance to reduce fouling. The raft was anchored at Lees Ferry to the downstream wake buoy, river left. Two stern lines were used, one tied off to the Lees Ferry gauging station and the other to a hinge anchor off the starboard side. With this configuration the raft could be adjusted to maintain position during changing flows.

Experiments I (1-5 June 1991) and II (12-16 June 1991) Thirty-six open-mesh baskets (17 x 20 x 11 cm) were arranged in five rows and suspended from a floating raft at Lees Ferry. One hundred and eight rocks colonized by Cladophora and associated plant and animal communities were selected from the river channel at Lees Ferry. Three rocks were randomly placed in each basket. The experimental treatment baskets included, (1) control treatments with colonized rocks continuously submerged for the entire experiment, (2) day treatments with colonized rocks exposed for 12 hr (0600-1800 hr) during the day, and (3) night treatments with colonized rocks exposed for 12-hr (1800-0600 hr) during the night. All baskets were submerged to a depth of 75 cm and treatment baskets were raised 20 cm above the water during each 12-hr day or night exposure period for five consecutive days. The above experimental protocol was designed to simulate water releases from Glen Canyon Dam with 12-hr exposure periods. Water temperature, air temperature, relative humidity (20 cm above the water surface with a sling pyschrometer), and cloud cover were monitored three times each day (0600 hr, 1200 hr, 1800 hr) during each experiment. Three random 5 x 5 cm quadrats of Cladophora and associated biota were harvested from the three rocks in each treatment basket at the start (initials) and at the end (after 5 days) of experiment I. The sampling protocol for Experiment II (conducted 12-16 June l991) was modified, whereby one 2 x 2 cm quadrat of Cladophora and associated biota was harvested from each rock in each treatment basket at the start and at the end of the experiment. Samples were sorted into periphyton plus the 10 biotic categories listed in Chapter 3. Each biotic category, except periphyton, was oven-dried (60°C) to a constant weight. Periphyton was removed from Cladophora as

Table 5.2. Experiment #, date of experiment, structure of experiment, and hypothesis for experiments conducted at Lees Ferry, Arizona.

Experiment #	Dates	Structure of Experiment	Hypothesis
I	June 1-5, 1991	Experiment conducted on raft; 12-h day and night exposures for five day period; plant and animal biomass collected after five days.	Fluctuating treatments will have greater losses of plant and animal biomass than non-fluctuating control treatments.
II	June 12-16, 1991	Experiment conducted on raft; 12-h day and night exposures for five day period; plant and animal biomass collected after five days.	Fluctuating treatments will have greater losses of plant and animal biomass than non-fluctuating control treatments.
III	June 29-July 3, 1991	Experiment conducted on raft; 12-h day and night exposures; plant and animal biomass collected daily for five day period.	There will be a progressive reduction in plant and animal biomass on substrates each day.
IV	June 30-July 16, 1991	Colonized rocks were submerged in river channel (controls) and shore (fluctuating treatment); plant and animal biomass collected after five days and 11 days; shore treatments were then submerged in channel for five days to measure recover; plant and animal biomass collected after five day resubmergence.	Rocks in fluctuating treatments will show significantly higher losses of plant and animal biomass than control non-fluctuating treatments.

Table 5.2 (Cont.)

Experiment #	Dates	Structure of Experiment	Hypothesis
V	July 12-14, l991	Experiment conducted on raft; Samples were collected in sluice channels exposed to day and night fluctuations in water.	Rocks exposed to fluctuating flows will show significantly higher losses of plant and animal biomass than control non-fluctuating control treatments.

described above. The periphyton suspension was filtered onto a pre-weighed glass fiber membrane (0.045 μm pore size). Each membrane containing periphyton was oven-dried at 102°C and weighed. Membranes were then ashed at 500°C for 1 hr in an ashing oven and weighed. Finally, distilled water was added to membranes and each membrane was re-dried at 102°C to determine final ash-free dry mass.

Experiment III (29 June to 3 July 1991) This experiment was conducted on the floating raft at Lees Ferry and entailed harvesting Cladophora and associated biota at daily intervals from night and day exposed treatments (12-hr each) over a 5-day period. In this experiment two biotic categories were estimated; i.e., plant (Cladophora and epiphytic diatoms) and animal biota. Otherwise the protocol was similar to Experiments I and II.

Experiment IV (30 June to 16 July 1991) This experiment was conducted in situ at Lees Ferry during experimental flows (141 m^3/s to 850 m^3/sec over a 24-hr period) to determine the influence of regulated flows on plant and animal biomass. Thirty-six rocks (ca. 110 cm circumference) colonized by Cladophora and associated biota were collected from the channel (85 m^3/s level) and placed at the 425 m^3/s level (shore). An additional 36 rocks in the channel were used as controls (continually submerged). One 2 x 2 cm quadrat of Cladophora and associated biota was harvested from each rock on days 5 and 11 during experimental flows. Experimental rocks positioned along the shore (425 m^3/s level) were typically exposed for 10-12 hrs each night, while control rocks in the channel (85 m^3/s level) were submerged throughout the entire experiment. After 11 days, shore rocks were returned to the channel (resubmerged at the 85 m^3/s mark) to determine recovery of plant and animal biota. One 2 x 2 cm quadrat of Cladophora and associated biota was harvested from each original channel rock (controls) and from each transplanted rock from the shore (experimental exposed treatments) after 5 days of submergence. Plant and animal biota were separated and oven-dried at 60°C to a constant weight.

Experiment V (12-14 July 1991) This experiment was designed to determine the effect of repeated 12-hr day or night exposure periods on Cladophora and invertebrate drift. This experiment was conducted in sluice channels (15 x 60 cm) secured to the floating raft and positioned parallel to flow. Three experimental channels were used with rocks exposed for 12 hrs during the night, three channels with rocks exposed for 12 hrs during the day, and three control channels, i.e. rocks continually submerged. The downstream end of each sluiceway had a removable net (156 μm mesh) to collect drift from each treatment channel. Four rocks colonized by Cladophora and associated biota were placed in each channel. Drift samples were collected from each treatment channel at the end of each day and night exposure period over a 3-day period. Control (continually submerged) treatments were collected with day treatments. River flow was constant at 141 m^3/s during the 3-day experiment. Plant and animal biota were separated and oven-dried at 60°C to a constant weight.

Statistical Analyses for In Situ Experiments Analyses were conducted on ln-transformed data (Zar 1984). Multivariate analyses (MANOVA) were used to determine the effects of repeated 12-h day or night exposures on *Cladophora*, chironomid larvae, *Gammarus*, oligochaetes, and blue-green algal crusts in Experiment I, and on *Cladophora*, epiphytic diatoms, chironomid larvae, and *Gammarus* in Experiment II. The effect of daily exposures over a 5-d period (Experiment III) was tested using an analysis of variance (ANOVA). A Tukey Test was then used to determine significant differences in plant and animal biomass between each day for day or night treatments. An analysis of variance was used to test the effect of repeated 12-h exposures after 5-d, 11-d, and recovery after a 5-d resubmergence treatment (Experiment IV). A multivariate analysis (MANOVA) was used to test the effect of 12-h day or night exposures on plant and animal drift (Experiment V).

Estimates of Cobble Bar Areas The cobble bar area at Lees Ferry was measured from aerial videotapes taken during constant research flows at 141 m^3/s, 227 m^3/s, 425 m^3/s, and the high water line of approximately 807 m^3/s (Glen Canyon Environmental Studies). Cobble bars were selected for measurement because they represent areas of greatest biotic biomass in the mainstem of the Colorado River (See Chapter 3 Results: Distribution of biomass). Aerial videotapes at each of these flows were taken with a Panasonic 3/4" format video camera attached to a helicopter with a Tyler mount. The helicopter maintained an elevation of 455 to 548 m above the river during videotaping. Map and Image Processing System (MIPS) software by Microimages, Inc. was used to calculate the area of each cobble bar. Each image was calibrated by measuring the distance between two fixed points in the field that were visible in the video frame. Calculations for potential plant and animal biomass at Lees Ferry for each research flow were derived from the product of the area (m^2) of cobble bar exposed below high water (807m^3/s) at flows of 425 m^3/s, 227 m^3/s, and 141m^3/s and the biomass (gm/m^2) for selected bioa. Calculations for potential plant and animal energy were derived from energy values (joules/mg, Table 5.1) of selected biota multiplied by the biomass for each respective biotic component at selected research flows. These estimates at various research flows must be used with some caution since we assume that biomass of each biotic component is relatively uniform at all stages, which may or may not be true. None-the-less, these initial values provide preliminary estimates of potential biomass for major components of the food base at various research flows at Lees Ferry.

RESULTS

In Situ Simulation Of Regulated Flow Experiments

Results from two separate in situ experiments (Experiment I and II) conducted on a raft in the Colorado River at Lees Ferry, showed significant losses in algal and macroinvertebrate biomass after 5 consecutive days of repeated 12-hr exposures for both day and night treatments. In Experiment I, multivariate analysis

(MANOVA) of ln-transformed data for day and night treatments showed a significant (F = 6.7; df = 3, 44; p = 0.001) overall reduction in biomass between initial and final treatments for Cladophora glomerata, and for Gammarus lacustris and chironomid, two important macroinvertebrates in the Colorado River food web. Only day exposure treatments showed significant downstream export in Cladophora biomass; i.e. 50% was removed after day exposures and 24% removed following night exposures (Table 5.3, Fig. 5.1). These losses in Cladophora biomass result in a loss of 2,214,000 joules/m^2 for day exposed treatments and 939,000 joules/m^2 for night exposed treatments. There was no significant (F = 1.7; df = 3, 20, p = 0.20) overall difference in biomass between initial and final treatments for submerged controls.

Both day and night exposure treatments showed a significant reduction in biomass and derived energy for chironomids and Gammarus (Table 5.3, Fig. 5.1). For example, 85% of the chironomid biomass was removed after day exposures and 49% was removed after night exposures, while 90% of the Gammarus biomass was removed after day exposures and 84% was removed after night exposures. Also, energy loss in larval chironomids and Gammarus during exposure treatments was estimated at 9,508 joules/m^2 and 23,239 joules/m^2, respectively, for day exposed treatments and 6,400 joules/m^2 and 53,500 joules/m^2, respectively, for night exposed treatments (Table 5.3). Although multivariate analysis showed no significant reduction in dry weight biomass for oligochaetes and gastropods after repeated day or night exposures, descriptive statistics suggested a strong trend toward reductions in biomass for these biotic categories as well.

In Experiment II, multivariate analysis (MANOVA) of ln-transformed data showed a significant (F = 23.9; df = 4, 43; p < 0.001) overall reduction in biomass for Cladophora, periphytic diatoms associated with Cladophora, and chironomid larvae after five days of repeated 12-hr exposures. Both day and night treatment exposures showed a significant reduction in Cladophora biomass (Table 5.4, Fig 5.2). For example, 56% of the initial Cladophora dry weight biomass was removed after repeated day exposures, and 65% of the initial biomass was removed after repeated night exposures. These reductions in Cladophora biomass result in a reduction of 1,450,000 joules/m^2 during day exposures and 2,400,000 joules/m^2 during night exposures at Lees Ferry (Fig. 5.2.) There were no significant differences between day and night initials or day and night finals (Fig. 5.2).

There was a significant reduction in ash-free dry mass for periphytic diatoms during day exposures (Fig. 5.2), however, there was no significant reduction in dry weight biomass (inorganic and organic) for periphytic diatoms for either day or night exposures in Experiment II (Table 5.4). This suggests a significant loss in dissolved organic matter (DOM) from epiphytic diatom assemblages during day exposures, but no significant loss in cell number. Diatom cell density estimates for day exposure treatments concur with this observation in that there was no significant difference in diatom cell number between initial and final treatments

Table 5.3. Dry weight biomass (gm/m^2, ± SE) and energy (joules/m^2 x 10^3) for selected biotic components after 12-hr exposures during the day and night for five consecutive days during June 1-5, 1991 (Experiment I) at Lees Ferry, Arizona. n = 12.

BIOTA	DAY Initial	DAY After 5 days	DAY % Change	NIGHT Initial	NIGHT After 5 days	NIGHT % Change
Cladophora (Dry Wt	* 343.1 ± 69.4	153.8 ± 28.1	55.2	341.4 ± 55.0	261.2 ±23.8	23.5
Cladophora (Energy)	* 4032.5 ± 80.8	1818.8 ± 33.4	55.2	3993.9 ± 64.3	3055.0 ± 278.7	23.5
Chironomids (Dry Wt.)	** 0.520 ± 0.109	0.074 ± 0.019	85.8	* 0.622 ± 0.110	0.316 ± 0.085	49.2
Chironomids (Energy)	** 10.96 ± 2.31	1.57 ± 0.40	85.8	* 13.19 ± 2.32	6.70 ± 1.81	49.3
Gammarus (Dry Wt.)	* 1.59 ± 0.57	0.16 ± 0.06	89.9	* 3.16 ± 0.98	0.55 ± 0.29	82.6
Gammarus (Energy)	* 25.96 ± 9.47	2.66 ± 0.93	89.9	* 62.58 ± 17.13	9.15 ± 4.73	82.6
Gastropod (Dry Wt.)	2.82 ± 2.16	0.07 ± 0.05	97.5	0.72 ± 0.34	0.48 ± 0.29	33.3
Oligochaete (Dry Wt.)	1.15 ± 1.06	0.0	100.0	0.05 ± 0.02	0.03 ± 0.01	40.0
Oligochaete (Energy)	23.55 ± 21.87	0.0	100.0	1.03 ± 0.63	0.59 ± 0.27	40.0
Blue-green Crust (Dry Wt.)	1.3 ± 1.23	0.0	100.0	0.0	0.0	0.0

* $p < 0.05$
** $p < 0.01$

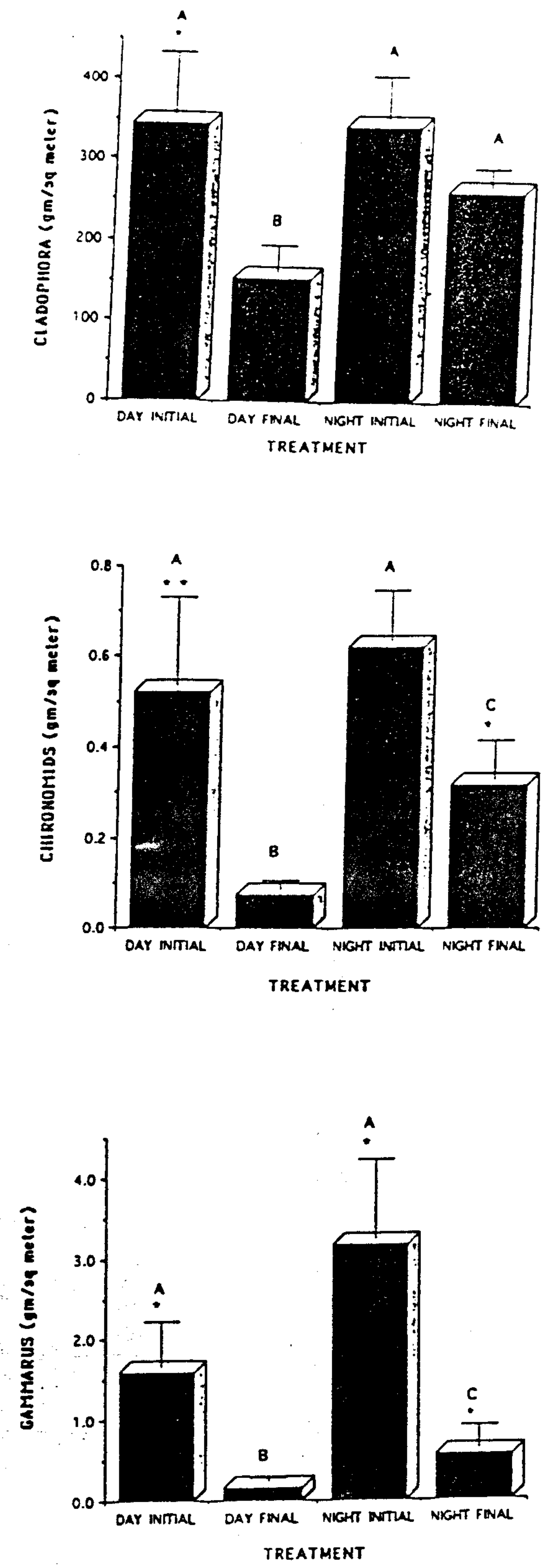


Figure 5.1 Initial and final average dry weight biomass (gm/²; SE) for Cladophora glomerata, chironomids, and Gammarus lacustris after repeated day and night 12-hr experimental exposures for 5 days at Lees Ferry, Arizona, during June 1-5, 1991 (Experiment I). Letters above histograms are significantly different at <0.05 (*) and < 0.01 (**) for univariate contrasts.

Table 5.4 Dry weight biomass (gm/m², ± SE) and energy (joules/m² x 10^3) for selected biotic components after 12-hr exposures during the day and night for five consecutive days during June 12-16, 1991 (Experiment II) at Lees Ferry, Arizona. n = 12.

	DAY			NIGHT		
BIOTA	Initial	After 5 days	% Change	Initial	After 5 days	% Change
Epiphyton (Cell density)	168.63 ± 22.3	194.96 ± 36.0	13.4			
Epiphyton (Dry Wt)	106.1 ± 26.3	75.1 ± 10.5	29.2	162.7 ± 41.6	79.8 ± 16.7	50.5
Epiphyton (Ash-Free)	** 14.74 ± 1.5	7.75 ± 0.4	47.4	14.44 ± 1.9	11.17 ± 1.2	22.6
Epiphyton (Energy)	** 172.45 ± 17.2	88.48 ± 5.7	47.4	* 168.94 ± 22.6	130.57 ± 13.9	22.6
Cladophora (Dry Wt.)	** 221.9 ± 21.4	97.9 ± 9.7	55.9	** 305.9 ± 44.1	107.1 ± 14.2	65.3
Cladophora (Energy)	** 2594.5 ± 250.2	1145.6 ± 112.9	55.9	** 3578.7 ± 515.7	1182.1 ± 190.9	65.3
Chironomid (Dry Wt.)	** 0.996 ± 1.94	0.198 ± 0.044	80.1	** 1.229 ± 0.137	0.181 ± 0.032	85.3
Chironomid (Energy)	** 21.12 ± 11.49	4.20 0.02	80.1	** 26.06 ± 7.44	3.84 ± 0.68	85.3
Gammarus (Dry Wt)	* 4.37 ± 1.49	0.94 0.68	78.5	* 1.20 ± 0.33	0.13 ± 0.09	89.2
Gammarus (Energy)	* 72.06 ± 24.38	15.47 ± 11.23	78.5	* 19.78 ± 5.41	2.08 ± 1.54	89.2

* $p < 0.05$
** $p < 0.01$

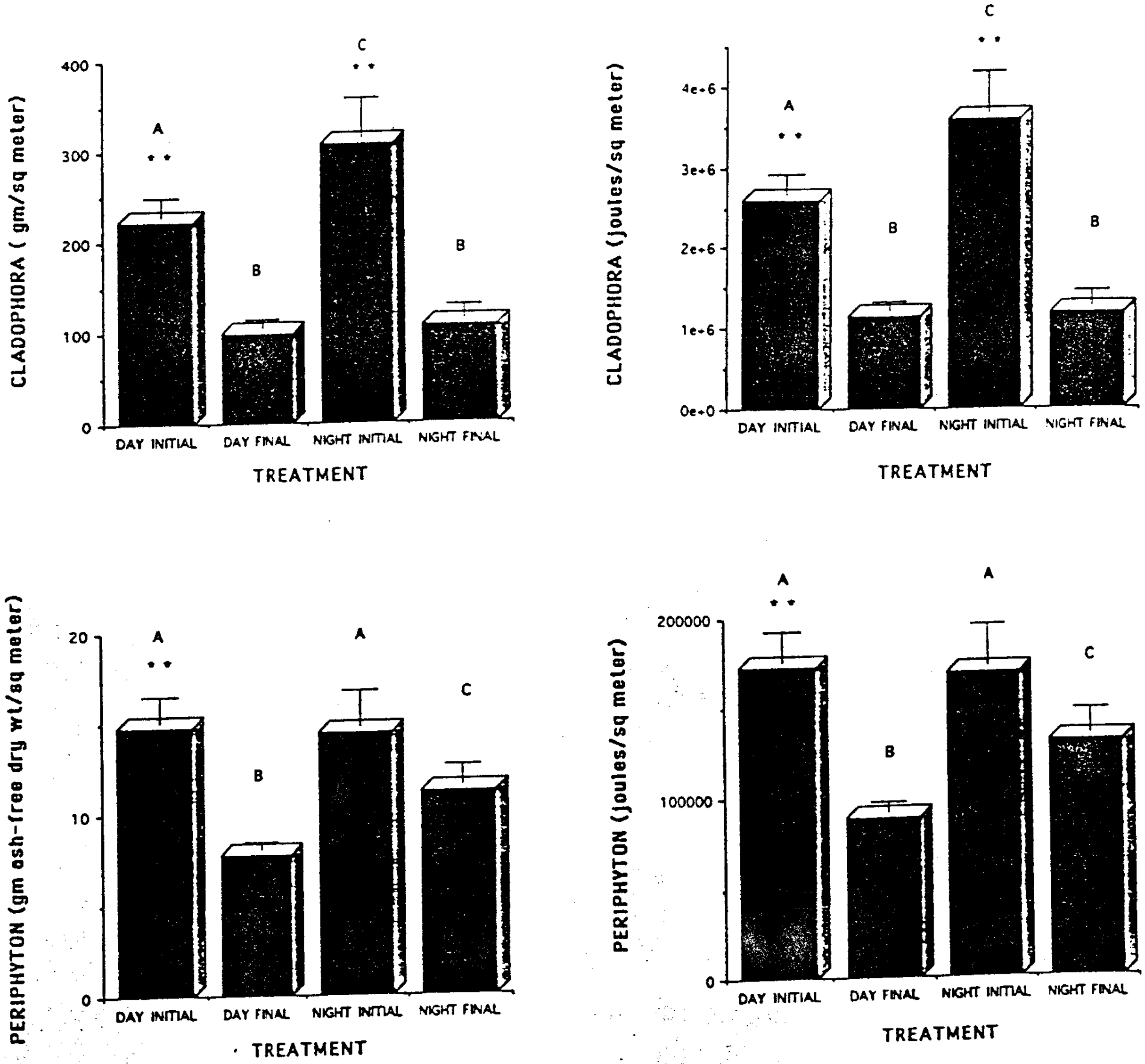


Figure 5.2 Initial and final average dry weight biomass (gm/^{2}; SE) and energy (joules/m^2) for Cladophora glomerata and epiphytic diatoms (periphyton) after repeated day and night 12-hr experimental exposures for 5 days at Lees Ferry, Arizona, during June 12-16, 1991 (Experiment II). Letters above histograms are significantly different at <0.01 (**) for univariate contrasts.

(Table 5.4). Night exposures showed no significant loss in ash-free dry mass for periphytic diatoms, and there was no significant difference between initial day and night treatments (Fig. 5.2). The estimated loss of energy from periphyton assemblages during repeated exposure was 84,000 joules/m^2 during day exposures and 38,000 joules/m^2 during night exposures (Fig. 5.2).

Animals showed an even greater reduction in dry weight biomass than plants following repeated day and night exposures in Experiment II. There was an 80% reduction in dry weight biomass for midge larvae (chironomids) during day exposures and an 85% reduction during night exposures (Fig. 5.3). Based on these reductions in chironomid biomass we estimated 17,000 joules/m^2 were removed following repeated day exposures and 23,000 joules/m^2 were removed after repeated night exposures. Although multivariate analysis showed no significant reduction in dry weight biomass for Gammarus ($F = 0.132$, $df = 1, 66$, $p = 0.717$) for repeated exposures, descriptive statistics and univariate analysis suggested a strong trend toward reduction in biomass after exposure treatments. There was a 78% reduction of Gammarus biomass after day exposures, and an 89% loss after night exposures (Fig. 5.3). The high variance between samples are due to smaller quadrat harvests (4 cm^2) resulting in the lack of significance between initials and finals. Derived energy losses for Gammarus from biomass losses include 57,000 joules/m^2 for day exposures and 18,000 joules/m^2 for night exposures.

Daily observations of aquatic communities subjected to 12-hr experimental exposures at Lees Ferry showed a significant ($p < 0.001$) reduction in macroinvertebrate biomass after the first day and a significant ($p = 0.002$) reduction in Cladophora biomass after the second day in both day and night exposure treatments (Experiment III). After two 12-hr day exposures, 48% of the Cladophora and associated epiphytes were removed, whereas 43% of the biomass was removed after two 12-hr night exposures (Table 5.5, Fig. 5.4). There was a 90% reduction in macroinvertebrate biomass after one 12-hr day exposure and an 85% reduction after one 12-hr night exposure (Table 5.5, Fig. 5.4). In each case, no significant reductions in biomass occurred between consecutive days following day one for animals and day two for plants. After five days of repeated daily exposures, >98% of the initial macroinvertebrate biomass was removed, while an average of 69% of the initial Cladophora assemblage was removed after the same time period (Table 5.5). There were no significant differences in either Cladophora or macroinvertebrate biomass between day and night exposures for any treatment, and no significant difference in either Cladophora or macroinvertebrate communities throughout the experiment in control treatments (Table 5. 5).

Experimental studies at Lees Ferry showed significant ($F = 20.1$, df 2, 420, $p < 0.001$) differences in macroinvertebrate and Cladophora biomass between control channel rocks (continuously exposed) and shore rocks (exposed daily) after 5 and 11 days of regulated flows (141 m^3/s to 850 m^3/s) in the Colorado River

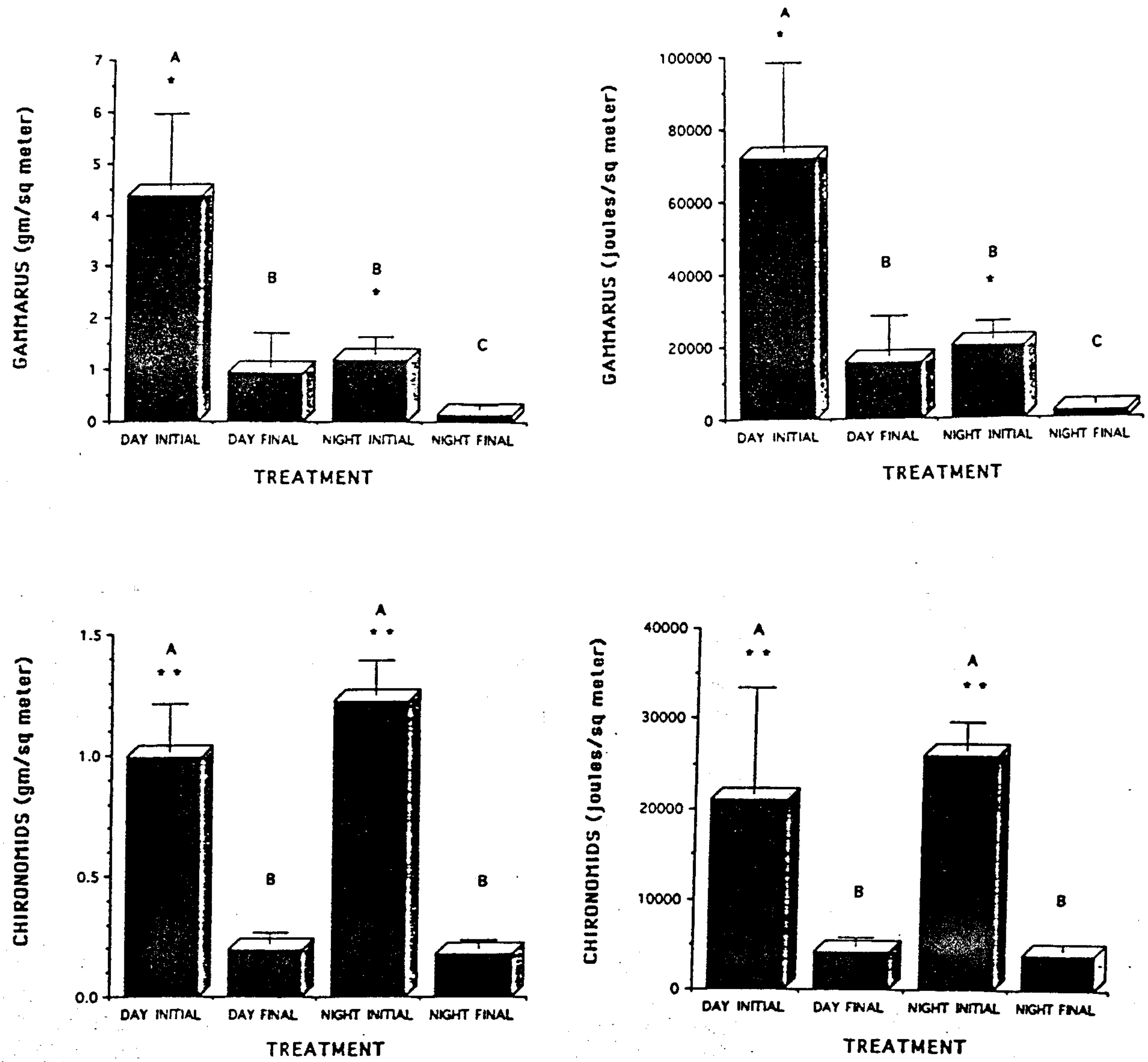


Figure 5.3 Initial and final average dry weight biomass (gm/^{2}; SE) and energy (joules/m^2) for <u>Gammarus lacustris</u> and chironomid larvae after repeated day and night 12-hr experimental exposures for 5 days at Lees Ferry, Arizona, during June 12-16, 1991 (Experiment II). Letters above histograms are significantly different at <0.05 (*) and <0.01 (**) for univariate contrasts.

Table 5.5. Average daily dry weight biomass (gm/m2; ± SE) for algae and macroinvertebrates following 12-hr day and night exposure periods for five consecutive days at Lees Ferry, Arizona during June 29 to July 3, 1991 (Experiment III). n = 12.

PERIOD	ALGAE		MACROINVERTEBRATES		CONTROL	
	DAY	NIGHT	DAY	NIGHT	PLANT	ANIMAL
Initial	118.6 (21.2)	136.3 (17.6)	4.218 (2.08)	5.273 (1.74)	111.6 (8.4)	3.206 (0.89)
1-Day	75.1 (9.9)	93.9 (11.1)	0.431 (0.16)	0.743 (0.41)	103.3 (11.0)	2.570 (0.72)
2-Day	62.4 (11.6)	77.7 (13.1)	0.32 (0.14)	0.25 (0.07)	96.4 (9.91)	2.595 (0.75)
3-Day	60.2 (11.7)	77.0 (13.6)	0.367 (0.18)	0.91 (0.43)	115.9 (22.5)	1.557 (0.53)
4-Day	43.4 (8.3)	60.3 (11.3)	0.223 (0.18)	0.169 (0.12)	114.9 (9.9)	1.754 (0.74)
5-Day	31.0 (8.1)	48.9 (13.5)	0.085 (0.035)	0.010 (0.007)	108.1 (9.4)	1.799 (0.41)

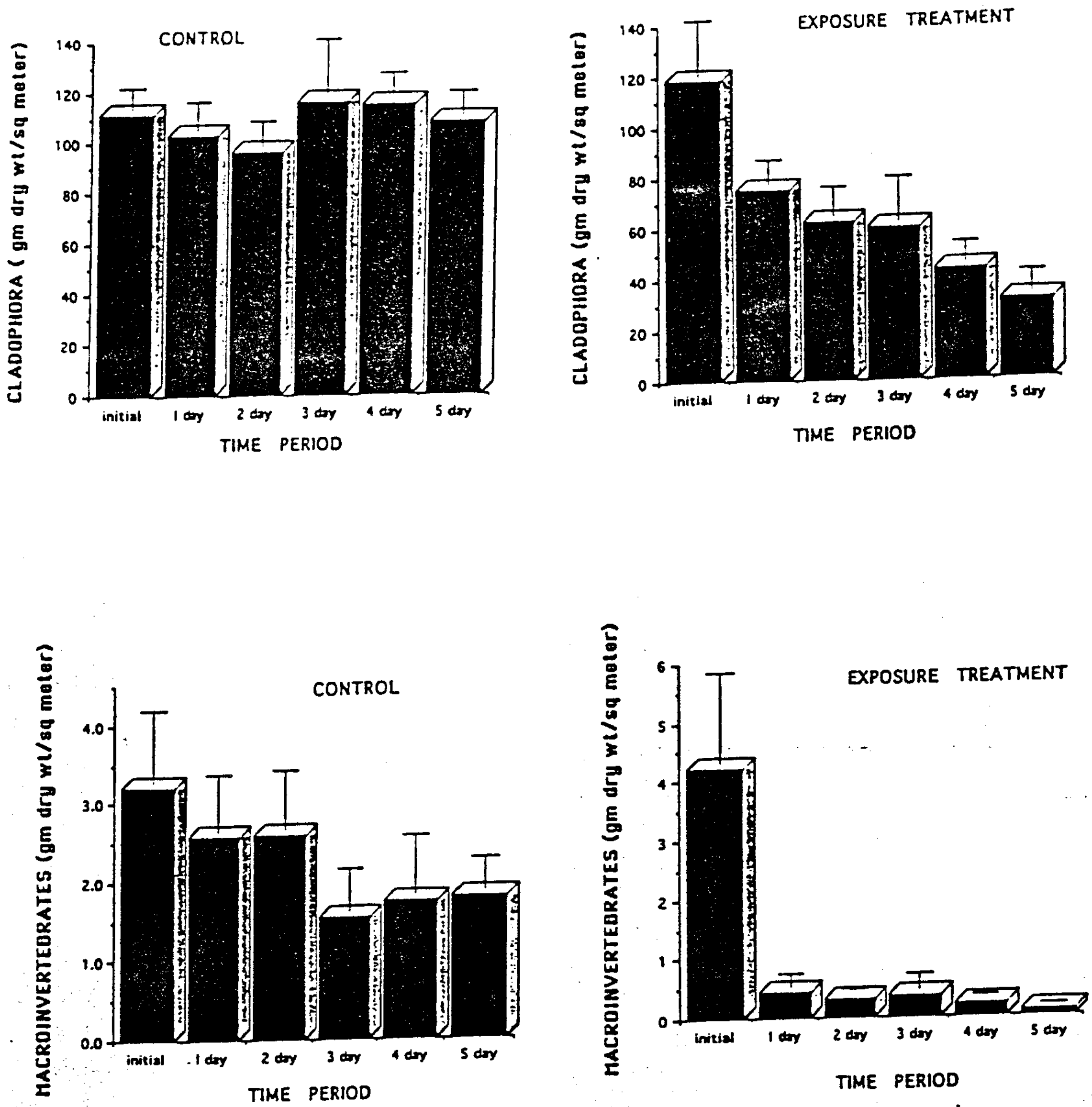


Figure 5.4 Average daily loss (gm/m², SE) of Cladophora glomerata and macroinvertebrate biomass for submerged controls and experimental day exposure treatments over a 5-d period at Lees Ferry, Arizona, during June 29 to July 3, 1991 (Experiment III).

(Experiment IV). Fifty-five percent of the initial Cladophora biomass and nearly 83% of the initial macroinvertebrate biomass were removed from shore rocks that were regularly exposed at daily intervals for 11 days (Table 5.6, Fig. 5.5). There was no significant (F = 1.239, df 3, 284, p = 0.296) difference in either macroinvertebrate or Cladophora biomass between initial rocks and rocks that were continuously submerged in the channel throughout the entire experiment.

The recolonization (recovery) of macroinvertebrates onto rocks that were exposed daily for 11 days was more rapid than the recolonization of Cladophora (Experiment IV, Fig. 5.5). There was no significant (F = 0.032, df 1, 70. p = 0.858) difference between resubmerged shore treatments and control channel treatments for macroinvertebrate biomass following a 5-day resubmergence of shore rocks. However, there was a highly significant (F = 11.28, df 1, 70, p = 0.001) difference in Cladophora biomass on resubmerged shore treatments and continously submerged channel rocks; i.e. resubmerged shore rocks had 40% less Cladophora biomass than control channel rocks (Table 5.6).

Multivariate analysis of variance (MANOVA) for ln-transformed data showed no significant (F = 0.541, df 6, 8, p =0.765) difference in drift of Cladophora, chironomid larvae, and Gammarus between control and treatment channels after colonized rocks were exposed during the day or night for 12-hr periods over a 3-day period (Experiment V). Although multivariate analyses showed no significant difference in drift between control and exposure treatment channels, descriptive statistics suggested strong trends toward an increase in drift for selected biota following exposure periods (Table 5.7). For example, the average biomass of Cladophora collected in drift nets in control channels was 0.05 gm/day (SE± 0.018) compared to 0.14 gm/day (SE± 0.083) and 0.28 gm/day (SE ± 0.20) for day and night exposed treatments, respectively (Table 5.7). Likewise, the average biomass of Gammarus collected in control channels was 0.002 gm/day (SE ± 0.002) compared to 0.004 gm/day (SE ± 0.001) and 0.009 gm/day (SE ± 0.006) for day and night exposed treatment channels, respectively.

Average daily values for air temperature, relative humidity, and cloud cover (measured at 0600 hr, 1200 hr, and 1800 hr) are provided in Table 5.8 for each experiment. Experiment I had the lowest mean air temperature (16.3°C, SE ± 1.1), while Experiments II, III, IV, and V had average daily air temperatures of 20.5°C (SE ± 0.8), 22.2°C (SE ± 0.8), 23.4°C (SE ± 0.5), and 22.8°C (SE ± 1.4), respectively.

Estimates of Energy Loss at Selected Research Flows

Extrapolation from aerial estimates of cobble bar between high water (807 m^3/s, 28,000 cfs) and selected research flows were used to derive potential biomass and/or energy for various biotic components at Lees Ferry. We used the Map and Image Processing System (MIPS), to estimate the area inundated by flows of 142 m^3/s (5,000 cfs), 227 m^3/s (8,000 cfs), 425 m^3/s (15,000 cfs) and approximately 807 m^3/s (28,000 cfs). Approximately 67,981 m^2 of river channel occurs below 142

Table 5.6. Average dry weight biomass (gm/m2; ± SE) for algae and macroinvertebrates from continuously submerged (channel) and exposed (shore) treatments during 30 June to 16 July 1991 at Lees Ferry, AZ (Experiment IV). Samples (n = 36) were taken from each treatment after 5-days and 11-days. Recovery samples (n = 36) were taken from each treatment after a resubmergence period of 5 days.

BIOTA	INITIAL		5-DAY		11-DAY		RECOVERY	
	Channel	Shore	Channel	Shore	Channel	Shore	Channel	Shore
Plant	194.6 (13.7)	220.1 (17.2)	229.5 (21.4)	132.6 (16.1)	200.8 (21.5)	98.4 (9.5)	232.8 (22.1)	141.9 (15.5)
Animal	9.3 (1.7)	14.5 (2.6)	14.2 (2.8)	2.4 (1.0)	7.3 (2.3)	0.01 (0.007)	15.5 (3.4)	14.6 (3.4)

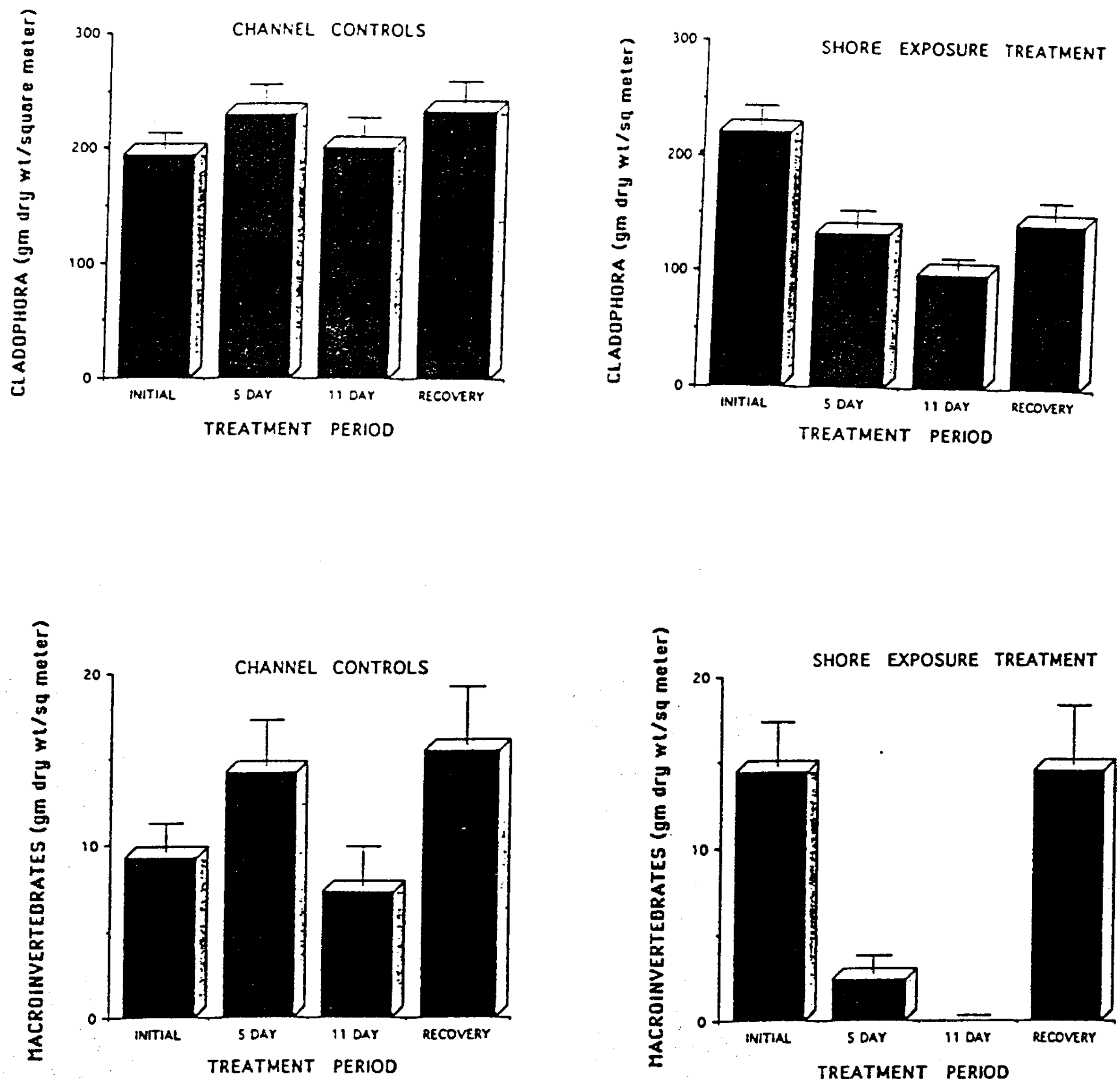


Figure 5.5. Average biomass (gm/m2, SE) for Cladophora glomerata and macroinvertebrates for channel controls (submerged) and shore (exposed) treatments for 5-d, 11-d, and a 5-d recovery at Lees Ferry, Arizona, during June 30 to July 16, 1991 (Experiment IV).

Table 5.7. Average dry weight biomass (gm/day, ± SE) for Cladophora, chironomid larvae, and Gammarus drift in experimental sluice channels at Lees Ferry, AZ during July 12-18, 1991 (Experiment V). Controls were continuously submerged, day treatments were exposed for 12-h during daylight, and night treatments were exposed for 12-hr during the night. n = 3.

BIOTA	CONTROL	DAY	NIGHT
Cladophora	0.052 (± 0.018)	0.144 (± 0.083)	0.257 (± 0.20)
Chironomids	0.000	0.000	0.001 (± 0.001)
Gammarus	0.002 (± 0.002)	0.004 (± 0.001)	0.009 (± 0.006)

Table 5.8. Average daily values (n = 3) for air temperature (°C), cloud cover (%), and relative humidity (%) for the five experiments conducted at Lees Ferry, AZ.

DAY	AIR TEMPERATURE (°C)	% CLOUD COVER	% RELATIVE HUMIDITY
	EXPERIMENT ONE (1-5 JUNE)		
1	13.7	80.0	
2	13.7	43.3	
3	18.3	20.0	
4	17.3	30.0	
5	18.3	10.0	
	x = 16.3; SE ± 1.1	x = 36.7; SE ± 12.2	
1	21.3	46.7	33.7
2	21.3	10.0	28.0
3	19.0	10.0	30.3
4	22.7	0.0	29.7
5	18.3	53.3	38.0
	x = 20.5; SE ± 0.8	x = 24.0; SE ± 10.9	x = 31.9; SE ± 1.8
	EXPERIMENT THREE (29 JUNE-3 JULY)		
1	20.7	13.0	29.0
2	23.0	3.3	27.7
3	21.0	0.0	33.2
4	21.3	0.0	19.8
5	25.0	3.3	19.7
	x = 22.2; SE ± 0.8	x = 6.5 SE ± 2.7	x = 25.9; SE ± 2.7

TABLE 5.7 (Cont.)

DAY	AIR TEMPERATURE (°C)	% CLOUD COVER	% RELATIVE HUMIDITY
		EXPERIMENT FOUR (12-14 JULY)	
1	24.3	23.3	31.2
2	23.3	6.5	34.9
3	22.7	33.3	35.0
	x = 23.4; SE ± 0.5	x = 21.0; SE ± 7.8	x = 33.7; SE ± 1.3
		EXPERIMENT FIVE (30 JUNE-12 JULY)	
1	24.7	3.3	17.8
2	26.7	0.0	19.3
3	27.0	0.0	20.5
4	27.3	26.7	28.0
5	22.7	46.7	33.5
6	22.0	70.0	42.7
7	21.3	32.7	52.7
8	19.0	20.0	57.3
9	15.0	66.7	60.5
	x = 22.8; SE ± 1.4	x = 29.6; SE ± 9.0	x = 36.9; SE ± 5.3

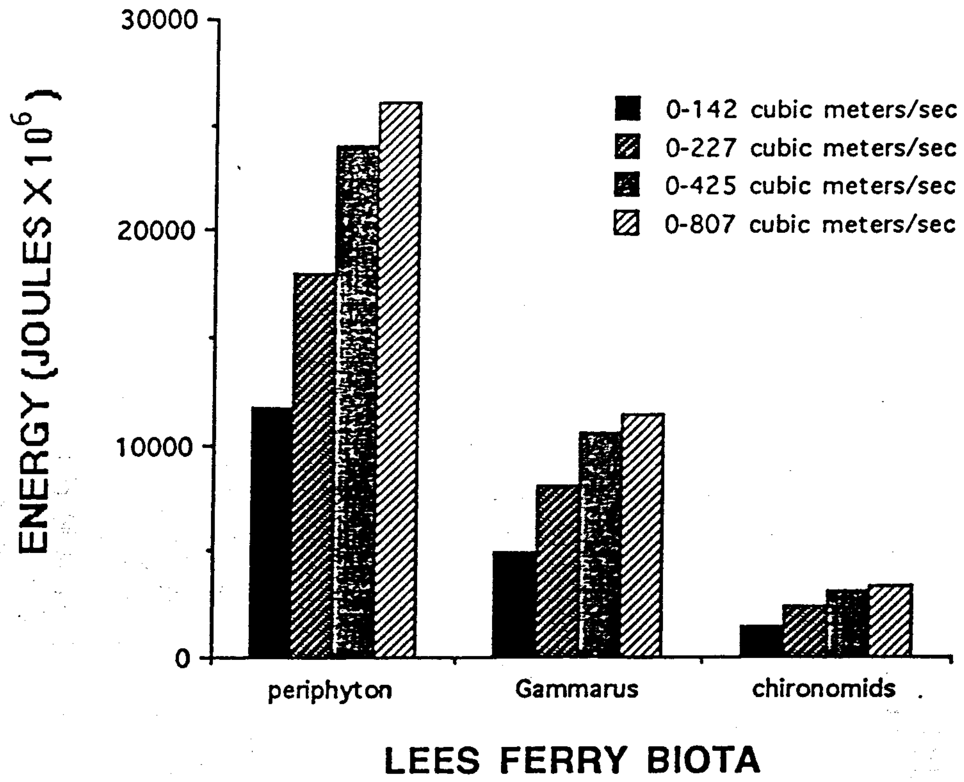


Figure 5.6. Estimated ecosystem energy (joules x 10^6) for epiphytic diatoms (periphyton), Gammarus lacustris, and chironomid larvae in the Colorado River at Lees Ferry, Arizona, at flow stages of 0-142 m^3/s, 0-227 m^3/s, 0-425 m^3/s, and 0-807 m^3/s.

m^3/s at Lees Ferry, while 44,100 m^2, 34,571 m^2, and 12,220 m^2 of cobble bar area is present between 142-227 m^3/s (5,000-8,000 cfs), 227-425 m^3/s (8,000-15,000 cfs), and 425-807 m^3/s (15,000-28,000 cfs), respectively. We used standing crop/m^2 field data and energy/gm ash-free dry mass data (Chapter 5) for food base components (epiphytic diatoms, chironomid larvae, Gammarus) to estimate ecosystem energy/m^2 for this cobble bar. This model assumes that the aquatic habitat below 142 m^3/s (our lowest cobble bar collection state) is uniform.

The projected amount of energy (joules) available as epiphytic diatoms, chironomid larvae, and Gammarus from this wide reach at three different flow stages is illustrated in Figure 5.6. The stage elevation below 142 m^3/s supports an estimated ecosystem energy of 18.1 x 10^9 joules, while a base flow stage of 227 m^3/s supports 28.5 x 10^9 joules, a base flow of 425 m^3/s supports 37.6 x 10^9 joules, and that of 807 m^3/s supports 40.9 x 10^9 joules. Thus the highest potential amount of ecosystem energy (epiphytic diatoms, chironomid larvae, Gammarus) occurs at high water flows (807 m^3/s), i.e., the greatest area of river channel is unundated. There is >2 times more potential ecosystem energy at flows of 807m^3/s than at 142 m^3/s and nearly 1.5-fold and 2-fold more energy at flows of ≤227 m^3/s and ≤425 m^3/s, respectively, for each biotic component at Lees Ferry (Fig. 5.6).

This model provides a preliminary estimate of potential biomass for major components of the food base at various research flows at Lees Ferry. These estimates may serve as a minimum estimate for the cobble bars in the reach from Glen Canyon Dam to Lees Ferry. This model does not apply to reaches downstream of Lees Ferry, where detailed areal analyses have yet to be applied to ecosystem energy estimates. The aquatic food base in downstream reaches is, at present, far less affected by exposure.

DISCUSSION

In situ experiments showed that daily exposures during discharge fluctuations in the Colorado River limit benthic biomass and ecosystem energy. Reductions in plant and animal biomass occurred during both day and night experimental treatments. Daily harvests of treatments at Lees Ferry showed a significant reduction (≥38% loss) in Cladophora biomass after two days of repeated 12-hr exposure periods for both day and night treatments and ≥70% reduction after five days of repeated exposures. Usher and Blinn (1990) reported similar losses of Cladophora biomass after repeated 12-hr exposures in laboratory experiments. The repeated exposures (≤12 hr) during fluctuating flows caused Cladophora tufts to become stranded, holdfast systems to dry and become weakened, and algal filaments to detach from cobble substrates during the rising arm of discharges following low flow periods.

The removal of Cladophora from cobble substrates and subsequent downstream export during regulated flow eliminates potential food and refuge for macroinvertebrates in localized regions in the Colorado River ecosystem. Also, the loss of Cladophora during the rising arm of regulated flows (Leibfried and Blinn

1986) results in the downstream transport of large amounts of potential energy (>2,000 x 10^3 joules/m^2) in tufts of course particulate organic matter (CPOM). Unlike previous reports (Powers 1990), Cladophora tufts in the Colorado River are largely free of macroinvertebrates (personal observations). The low animal densities in Cladophora tufts may be a function of high water turbulence in the series of rapids in the Colorado River and/or perhaps most of the macroinvertebrates have abandoned the stranded Cladophora prior to its detachment. Also, due to relatively low densities of downstream macroinvertebrates (See Results: Distribution and biomass), recruitment into floating Cladophora tufts is low. The fate of these CPOM (Cladophora) tufts in the Colorado River ecosystem is unclear, although, this floating organic matter may be processed by microbes and/or consumed by animals as it is exported downstream. However, based on the composition of downstream macroinvertebrates and their diets it is unlikely that these Cladophora tufts contribute directly to the downstream food web. It is probable that many of these Cladophora tufts collect in quiet backwaters along the way or wrap around emergent objects in flowing waters of the mainstem. It is presumed that microbial processing is faster in warmer back waters (>20°C) than in the thermally constant cold water (ca. 11°C) of the mainstem, which may account for the relatively low densities of downstream macroinvertebrates. The low densities of downstream macroinvertebrates suggest that energy flow uncouples between microbes and Cladophora tufts in the Colorado River ecosystem, or at least is somewhat restricted. The processing rates, destination, and role(s) of drifting Cladophora tufts in the Colorado River ecosystem must be examined.

The microscopic epiphytic diatoms, that are attached to the highly branched filaments of Cladophora, serve as the primary food for several of the dominant macroinvertebrates in the Colorado River food web. The small cell diameter (<0.1 mm), high energy, and great abundance of these microscopic diatoms make them an optimum food for macroinvertebrates. Our studies indicate that >90% of the diet of Gammarus and >60% of the diet of chironomid larvae in the tailwaters of Glen Canyon Dam are comprised of diatoms. In contrast, <1% of the diet of macroinvertebrates consisted of Cladophora and Oscillatoria. However, the importance of diatoms as a food source is greatly reduced in downstream food webs of the Colorado River; i.e. diatoms make up <10% of the diet in chironomid larvae at Diamond Creek (RK 361) while sand and bacteria comprise the balance of the diet. It is likely that high levels of suspended sediment and reduction in diatoms associated with Cladophora contribute to the shift in macroinvertebrate diets at downstream sites. Hardwick et al. (1992) reported four times fewer epiphytic diatoms associated with Cladophora at Diamond Creek (RK 354) than in the tailwaters of Glen Canyon Dam. Also, suspended sediment was over 85 times higher at downstream sites (>1020 mg/l^{-1}) than in the tailwaters (United States Geological Survey, 1985). Thus, the highly branched filaments of Cladophora (some tufts extend over 1.5 m in length) provide large surface areas for the attachment of diatoms, but provide limited value as a direct food source for macroinvertebrates. The dense stands of Cladophora may also provide an important refuge from predators for macroinvertebrates in the Colorado River ecosystem.

Our experiments showed significant reductions in ash-free dry mass (organic) for epiphytic diatoms after repeated day exposures, but no significant reductions in dry weight (inorganic and organic). This suggests the internal organic contents of cells are leached and enter downstream drift during exposure treatments, while empty diatom cells remain attached to Cladophora filaments. Dissolved organic matter (DOM) released from diatom cells during regulated flow may serve as important substrata for bacteria, which in turn may function as food for downstream macroinvertebrate communities. The potential increase in DOM initiated during regulated flows may be instrumental in supplying bacteria to downstream dipteran larvae. The incremental increase in biomass of chironomid larvae below the Paria River (RK 1-90), and subsequent increase in simuliid larvae below the Little Colorado River (RK 90-320), suggests a sequential change in food processing by macroinvertebrates in the Colorado River continuum (Vannote et al. 1980). Chironomids in the Colorado River ecosystem utilize epiphytic diatoms, bacteria and fine detritus, while sestonic bacteria and micro-algae play an important role in the diets of filter-feeding simuliid larvae (Wallace & Merritt 1980). The relatively high densities of downstream simuliid larvae in the Colorado River suggest the presence of smaller food particles (e.g. sestonic bacteria) in these reaches. The loss of DOM from upstream epiphytic communities during regulated flows and the fate of this organic resource need further examination.

Macroinvertebrates quickly abandon stranded Cladophora tufts during low flows and move into isolated pools of stranded water. In fact, experiments showed significant reductions (>85%) in macroinvertebrate biomass in Cladophora tufts after one 12-hr exposure for both day and night treatments. Many of these animals are swept downstream during the rising arm of discharges following low flow periods (Leibfried and Blinn 1986). The importance of this invertebrate drift in the Colorado River ecosystem is unclear and needs further study.

One might expect a high diversity of macroinvertebrates in cold, clear water reaches like Lees Ferry including a variety of mayflies, stoneflies, caddisflies, chironomids, odonates (damselflies and dragonflies), etc. (Ward 1992). However, the macroinvertebrate community at Lees Ferry is rather limited, comprised of several chironomid species (primarily Cricotopus annulator), two snail species, several oligochaetes, and Gammarus lacustris (Fig. 5.7). There have been several hypotheses proposed for the limited macroinvertebrate diversity at Lees Ferry, each of which could be tested in situ and/or in the laboratory. They include: 1) the filtering action of Glen Canyon Dam reduces CPOM (small arrow on Fig. 5.7) and therefore limits species like caddisflies and stoneflies that utilize CPOM and associated microbes as a food source (i.e., shredders), 2) the natural substrata at Lees Ferry have been highly modified with the dense growth of Cladophora therefore restricting many of the aforementioned taxa which prefer hard stable rock substrata, 3) the armoring effect due to high discharge below Glen Canyon Dam has increased the overall median particle size of substrata and therefore has

COLORADO RIVER FOOD WEB

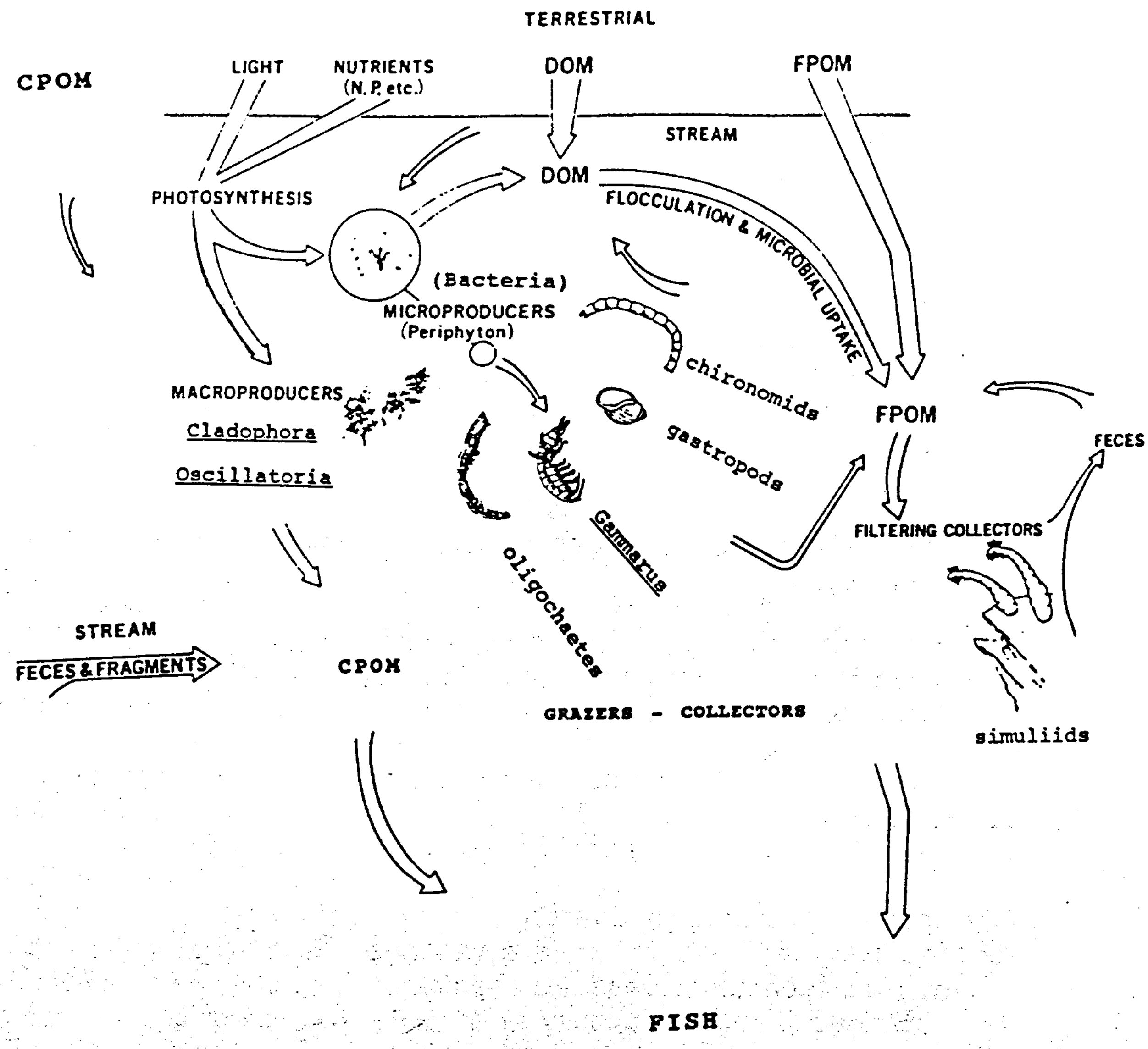


Figure 5.7. Food web for the tailwaters of Glen Canyon Dam in the Colorado River ecosystem. Note that periphytic diatoms on Cladophora comprise the major food base for the relatively low number of grazer taxa (chironomid larvae, gastropods, Gammarus, oligochaetes). Also note the relatively low input of CPOM (small arrow) below Glen Canyon Dam. Filter-feeding simuliids and detrital feeding chironomid larvae become important in the food web below the confluence of the Paria River.

reduced the heterogeneity of substrata and habitat niche space available for macroinvertebrates, 4) lack of suitable substrata (i.e., CPOM) limit case-building caddisfly populations, 5) macroinvertebrates that typically utilize periphytic diatoms as a primary food source (grazers, scrappers) have evolved enzymes suitable for warmer downstream reaches where the canopy is open and water temperatures are warmer and undergo seasonal change. The constant cold water conditions at Lees Ferry lack seasonal variance in water temperature and therefore do not provide critical cues for larval development and reproduction.

CHAPTER SIX: FUTURE MONITORING OF THE AQUATIC FOOD BASE IN THE COLORADO RIVER, GRAND CANYON NATIONAL PARK

INTRODUCTION

The lower trophic levels in the Colorado River below Glen Canyon Dam are recognized by the National Park Service as a management priority. Results from the GCES Phase II studies showed strong negative effects of minimum and fluctuating discharges on benthic biomass, and reduction of tailwaters production may affect the aquatic ecosystem downstream. Interim flows criteria were adopted, in part, to reduce impacts of fluctuating flows on benthic algai (Cladophora glomerata and associated diatoms) and macroinvertebrate (Diptera, Gastropoda, Annelida, and Gammarus) assemblages. Interim flows consist of maximum and minimum flow limits, reduced fluctuation and ramping rates, and monthly variation in flow volume. Further modification of dam operating criteria may result from the Record of Decision on the GCD-EIS by the Secretary of the Interior. Management of the trophic integrity of the Colorado River will require scientifically sound, consistent monitoring and incorporation of monitoring results in management action plans and implementation. Therefore, we offer several suggestions regarding development of monitoring and management strategies in this chapter.

The quantity and rate of benthic production determines the ecological potential of this fluvial ecosystem, and fluctuating discharges negatively affect productivity by reducing the biomass of primary producers. The normal minimum discharge level to which this system is subjected on a regular (e.g. monthly) basis limits potential production. In other words, low flow, even for a single weekend, can result in a die-back of Cladophora and recovery may require several months. Our GCES-II study showed that Cladophora is restricted to discharge stages below 142 m^3/s, and we experimentally demonstrated that fluctuating flows significantly reduced benthic biomass.

MONITORING RECOMMENDATIONS

Monitoring is required to determine whether the interim flows management program is producing the desired effects, or at least not causing further deterioration of the aquatic food base. Several monitoring tasks are recommended:

1) The monitoring program should determine whether or not interim flows are affecting primary and secondary production. This is best accomplished by continuing system-wide sampling on a seasonal basis. For the short term, we recommend continued sampling at the 10 sites from Lees Ferry to Diamond Creek in order to monitor changes on a system-wide basis.

2) The monitoring program should evaluate the rate of production during the low, medium, and high volume interim flow months at Lees Ferry and, at a minimum, below the confluence of the Paria River. The single largest "stair-step" decline in production takes place at the Paria River confluence.

3) The rate of recolonization by benthic algae and macroinvertebrates varies by taxon and season, and should be monitored. Our studies at Lees Ferry indicate that recolonization by benthic algae is a slow process, but macroinvertebrates may recolonize rather rapidly. Recolonization by blue-green algae is considerably slower in the lower reaches, requiring many months. Knowledge of the rate of recovery of the lower aquatic trophic levels following low volume flow months and exceptional low flows is therefore essential to the evaluation of interim and subsequent flows.

4) The rate and volume of organic drift determines the delivery of upstream production to downstream reaches. Allochthonous upstream organic matter may be an important source of energy for downstream reaches. GCES-II synoptic studies suggested that drift (algae, macroinvertebrates, and detritus) is positively correlated with the range of daily discharge fluctuations. Flow criteria that reduce stream power and promotes benthic production should reduce overall drift (at least initially) and reduce the amplitudes of daily fluctuation in drift. The monitoring program should evaluate the amount and continuity of drift as affected by dam operations and in comparison with GCES-II research results. We recommend monitoring drift at the same 10 sites used by the U.S. Geological Survey in GCES-II.

5) The aquatic food base supports not only a unique native fish fauna with several Federally listed species, but also a diverse riparian insectivore fauna. The aquatic lower trophic levels are recognized by the National Park Service as a primary component of this fluvial ecosystem. The monitoring approach recommended here should continue to contribute geographically-based information needed for effective long-term monitoring, information best archived in scientific information management system (GIMS). Several themes of interest include benthic algal and macroinvertebrate biomass and species composition. These elements can be integrated and compared with fisheries and, potentially, terrestrial fauna layers. Monitoring data should therefore be compiled in an appropriate fashion for inclusion into the planned GIMS.

6) Lastly, low constant flows have been used to photograph the system for geomorphic and hydrologic purposes. While low flows are essential to monitoring annual and longer-term changes in this system, such flows will exert significant impacts on benthic production in this system through desiccation and exposure. We therefore recommend that the minimum flow for these constant flow tests be maintained at a level of 200-225 m^3/s, rather than at the 142 m^3/s stage previously used. These somewhat higher levels for constant flow evaluations are consistent with the low flow release levels associated with interim flows, and will not have a detrimental effect on the system production.

CHAPTER SEVEN: CONCLUSIONS AND MANAGEMENT CONSIDERATIONS.

INTRODUCTION

In this chapter we present a synthesis of our results and our conclusions regarding dam effects on the lower aquatic trophic relationships in the Colorado River corridor downstream from Glen Canyon Dam. We then examine the overall consequences of flow fluctuation to the aquatic ecosystem and examine the potential consequences of the EIS alternatives to this system.

The purpose of this study was to provide seasonal baseline data on the aquatic food base in the Colorado River ecosystem in Grand Canyon downstream from Glen Canyon Dam. We examined the taxonomy, distribution, phenology, biomass, dietary requirements, and ecological roles of aquatic algal and macroinvertebrate species to assess the impacts of dam operations on this fluvial ecosystem. This study will serve as a key element for the Glen Canyon Environmental Study (GCES) Interim Flow Aquatic Food Base Monitoring Program for the Colorado River ecosystem.

Our results indicate the following: 1) The overriding factors affecting primary producers and consumers are dam operations and tributary influence (increased turbidity) which results in a stair-step decrease in biomass below the confluence of the Paria River. 2) The filamentous green alga, Cladophora glomerata, was dominant above the Paria River and Oscillatoria spp., crustose blue-green algae (Cyanobacteria), was dominant below the Little Colorado River. 3) Macroinvertebrate biomass and abundance are strongly negatively correlated with distance from the dam, and are positively correlated with Cladophora. 4) Wide reaches had higher standing stocks of macroinvertebrates than narrow reaches for both pool and riffle habitats. 5) The aquatic Diptera assemblage was dominated by chironomids (8 common species) and Simuliium arcticum, the principal simuliid species. 6) Aquatic Diptera diversity is influenced by channel geomorphology. 7) Gammarus lacustris (Amphipoda) is largely replaced by chironomid larvae below the Paria River, and by simuliid larvae below the Little Colorado River. 8) Cladophora serves as a substratum for epiphytic diatoms which make up a major portion of the diet of chironomid larvae and Gammarus. 9) Over 50% of the algal biomass and at least 75% of macroinvertebrate biomass were removed after repeated 12-hr exposures over a five-day period in both day and night experimental treatments at Lees Ferry. 10) Daily observations revealed a significant reduction in macroinvertebrate biomass after the first day and a significant loss in algal biomass after the second day of experimental treatments. 11) After five days of recovery, there was no significant difference in macroinvertebrate biomass on control rocks and re-submerged treatment rocks, however, there was significantly lower Cladophora biomass on re-submerged treatments compared to controls. 12) Potential ecosystem energy for epiphytic diatoms, Gammarus, and chironomid larvae were estimated for the Lees Ferry reach for low, medium, and high flows.

To evaluate the impacts of the EIS flow alternatives on the lower aquatic trophic levels, we developed a stage to area model of ecosystem energy for the Lees Ferry cobble bar (RK 0.6). We used the Map and Image Processing System (MIPS), to estimate the area inundated by flows of 142 m^3/s (5,000 cfs), 227 m^3/s (8,000 cfs), 425 m^3/s (15,000 cfs) and approximate 807 m^3/s (28,000 cfs). Approximately 67,981 m^2 of river channel occurs below 142 m^3/s at Lees Ferry, while 44,100 m^2, 34,571 m^2, and 12,220 m^2 of cobble bar area occurs between 142-227 m^3/s, 227-425 m^3/s, and 425-807 m^3/s, respectively. We used standing crop/m^2 field data and energy/gm ash-free dry mass data (Chapter 5) for food base components (epiphytic diatoms, chironomid larvae, Gammarus) to estimate ecosystem energy/m^2 for this cobble bar. This model assumes that the aquatic habitat below 142 m^3/s (our lowest cobble bar collection stage) is uniform.

The projected amount of energy (joules) available as epiphytic diatoms, chironomid larvae, and Gammarus from this wide reach at three different flow stages is illustrated in Figure 5.6. The stage elevation below 142 m^3/s supports an estimated ecosystem energy of 18.1 x 10^9 joules, while a base flow stage of 227 m^3/s supports 28.5 x 10^9 joules, a base flow of 425 m^3/s supports 37.6 x 10^9 joules, and that of 807 m^3/s supports 40.9 x 10^9 joules. Thus the highest potential amount of ecosystem energy (epiphytic diatoms, chironomid larvae, Gammarus) occurs at high water flows (807 m^3/s), i.e., the greatest area of river channel is unundated. There is >2 times more potential ecosystem energy at flows of 807m^3/s than at 142 m^3/s and nearly 1.5-fold and 2-fold more energy at flows of $\leq$227 m^3/s and $\leq$425 m^3/s, respectively, for each biotic component at Lees Ferry (Fig. 5.6).

This model provides a preliminary estimate of potential biomass for major components of the food base at various research flows at Lees Ferry. These estimates may serve as a minimum estimate for the cobble bars in the reach from Glen Canyon Dam to Lees Ferry. This model does not apply to reaches downstream of Lees Ferry, where detailed areal analyses have yet to be applied to ecosystem energy estimates. The aquatic food base in downstream reaches is, at present, far less affected by exposure

The protocol used in this study is recommended for implementation as part of the interim and long-term monitoring program in the Colorado River ecosystem through Grand Canyon. This study will assist the National Park Service and the Bureau of Reclamation develop a comprehensive understanding of aquatic ecosystem dynamics under alternative flow regimes for the Glen Canyon Environmental Studies Phase II Environmental Impact Statement.

I. The overriding factors affecting primary producers and consumers are dam operations and tributary influences (increased turbidity) which result in a "stair-step" decrease in biomass below the confluence of the Paria River. The minimum discharge elevation reached on approximately a monthly basis determines the maximum stage at which benthic Cladophora and macroinvertebrates can persist. Higher minimum flows increase Cladophora cover and aquatic production. biomass is positively correlated with channel width and increases from low velocity/pool habitats to high velocity/riffle habitats. In 1991, the composition of primary producers changed from a Cladophora-diatom periphyton community in the tailwater reach above the Paria River to an Oscillatoria-detritus association with increasing dominance of simuliids in the lower reaches. The trophic significance and long term patterns of distribution of Oscillatoria require further research.

II. The aquatic Diptera assemblage is dominated by chironomids (8 common species) and Simuliium arcticum, the principal simuliid species. Distance from dam, channel geometry, season, and long-term changes influenced dominance patterns of macroinvertebrates.

III. Wide reaches comprise nearly 50% of the river corridor, and occur from Glen Canyon Dam to Mile 11, Mile 40 to Mile 76, and Mile 160 to Mile 214. Wide reaches are characterized by lower current velocity, and contain broad, cobble bar riffles and relatively shallow pools floored with fine (silt/fine sand) sediments. In contrast, narrow reaches have higher current velocity, more large-boulder rapids, and deeper pools. biomass estimates and species composition of macroinvertebrates and primary producers are related to reach width. Wide reaches account for 98% and 70% of the total biomass in pool and riffle habitats, respectively. The growth of Cladophora is profuse between Glen Canyon Dam and the Paria River confluence, but decreases 15-fold downstream from Mile 1.0. Macroinvertebrate densities and biomasss follow the same pattern.

IV. Cladophora serves as a substratum for epiphytic diatoms, which comprise >45% and >90% of the diet of chironomids and Gammarus, respectively. Cladophora provides refuge for macroinvertebrates, but not direct food resources. Oscillatoria provides cover for burrowing chironomids and lumbricid worms, but may have little food value to macroinvertebrates.

V. Experimental exposures to daily discharge fluctuations removed >50% of the algal and at least 75% of the macroinvertebrate biomass after repeated 12-hr exposures over a five day period in both day and night experimental treatments. Daily observations revealed a significant reduction in macroinvertebrate biomass after the first day and a significant loss in algal biomass after the second day of experimental treatments. After five days of recovery, there was no significant difference in macroinvertebrate biomass on control rocks and re-submerged treatment rocks. There is a significant loss in soluble organics compared to particulate cell constituents for the diatom periphyton association.

VI. Hypsographic (area inundated by different stages) relationships under different discharges coupled with energy values for each trophic component will allow predictions of ecosystem energy losses under different discharges. If the minimum flow of the river were raised from the present low flow of 28.3 m^3/s (1,000 cfs) to 227 m^3/s (8,000 cfs), the energy of this site would be increased by an estimated 1.5

x 10^9 joules, a threefold increase in ecosystem energy in the fluctuating zone. Similarly large increases in ecosystem energy are expected in other wide reaches of the river, and ecosystem energy levels would increase modestly in narrow reaches as well. If energy (food) limitations exist for any of the life stages of native or valued non-native fish, increasing the base flow may result in an important increase in biomass and ecosystem energy.

VII. Additional research on the role(s) of regulated flow on primary and secondary productivity, the importance of Cladophora drift to downstream communities, the importance of Oscillatoria in the aquatic food base and sediment stability, and the rate of recolonization by algae and macroinvertebrates at different interim flows are recommended to refine management of the Colorado River ecosystem.

Aquatic production is maximized under constant flows and benthic biomass and ecosystem energy are negatively correlated with the range of discharge fluctuation. The more frequent the fluctuation, the lower the benthic biomass and ecosystem energy in the "intertidal" zone. Our experiments suggest that even a single weekend period of low flow will significantly reduce benthic biomass. We predict the following positive and negative consequences of fluctuating flows.

POTENTIAL POSITIVE CONSEQUENCES OF FLUCTUATING FLOWS

1. Increased light penetration over depth may increase epiphyton biomass.
2. Increased dissolved organic matter (DOM) released from epiphyton (downstream export).
3. Increased drift as a food base for fish.
4. Increased availability of hard substrata.

POTENTIAL NEGATIVE CONSEQUENCES OF FLUCTUATING FLOWS

PRIMARY CONSEQUENCES:

1. Limit biomass and productivity to permanently wetted zones.

SECONDARY CONSEQUENCES:

1. Increased light penetration over depth may affect Cladophora biomass.
2. Light limitation through increased turbidity at higher flows.
3. Intensify predator-prey interactions due to restricted space under low flows.
4. Intensify loss in localized reaches through drift.
5. Change in epiphyton species assemblage may affect macroinvertebrate populations.
6. Increased loss of detritus.
7. Increased competitive advantage of blue-green algae over Cladophora.
8. Decreased system-wide production because some reaches (e.g. lower Marble Canyon, lower Grand Canyon) typically experience drawdown during the day.

Of the seven EIS alternatives the "no change", high, and medium fluctuations would result in no change or decreased aquatic production (Table 7.1). The monthly constant fluctuations would result in modest increases in aquatic production. The low fluctuations, seasonally adjusted constant, and annual constant flows would result in significant increases in aquatic production.

Table 7.1. Expected impacts of Glen Canyon Dam Environmental Impact Statement alternatives on the lower aquatic trophic levels in the downstream reaches of the Colorado River, Arizona.

EIS ALTERNATIVE	CONSEQUENCES ON LOWER AQUATIC TROPHIC LEVELS
FLUCTUATING FLOWS	
No Action	Benthic algal and macroinvertebrate production restricted by exposure to below the normal minimum flow of 28.3 cm^3/s (1,000 cfs). Maximum drift.
Maximum Flux	Benthic algal and macroinvertebrate production restricted by exposure to below the normal minimum flow of 28.3 cm^3/s (1,000 cfs). Maximum drift.
High Flux	Benthic algal and macroinvertebrate production restricted by exposure to below the normal minimum flow of 84.9 cm^3/s (3,000 cfs). Maximum drift.
Moderate Flux	Benthic algal and macroinvertebrate production restricted by exposure to below the normal minimum flow of 141.5 cm^3/s (5,000 cfs). Moderate drift.
Low Flux	Benthic algal and macroinvertebrate production restricted by exposure to below the normal minimum flow of 141.5 cm^3/s (5,000 cfs). Moderate drift and low velocities may mean increases in other aquatic plants. Aggredation of silt in channel and accumulation of detritus and detritivores. Possible overgrowth of <u>Cladophora</u> on hard substrata or coating of hard substrata by <u>Oscillatoria</u> thereby reducing available habitat for simuliids. Steady flows may enhance populations of semi-aquatic biting flies, particularly Ceratopogonidae.

Table 7.1 (Cont.)

EIS ALTERNATIVE	CONSEQUENCES ON LOWER AQUATIC TROPHIC LEVELS
STEADY FLOWS	
Steady Existing Monthly Volumes	Of the three steady flow alternatives, this alternative would have the greatest impact on the aquatic food base. Benthic algal and macroinvertebrate production restricted by exposure to below the existing monthly volumes of 226.4 cm^3/s (ca 8,000 cfs). Lower drift and low velocities may mean increases in other aquatic plants. Aggredation of silt in channel and accumulation of detritus and detritivores. Possible overgrowth by Cladophora on hard substrata or coating of hard substrata by Oscillatoria thereby reducing available habitat for simuliids. Steady flows may enhance populations of semi-aquatic biting flies, particularly Ceratopogonidae.
Seasonally Adjusted	Benthic algal and macroinvertebrate production restricted by exposure to below the bi-seasonal normal minimum volume of 226.4 cm^3/s (ca. 8,000 cfs). Lower drift and low velocities may mean increases in other aquatic plants. Aggredation of silt in channel and accumulation of detritus and detritivores. Possible overgrowth of Cladophora on hard substrata or coating of hard substrata by Oscillatoria thereby reducing available habitat for simuliids. Steady flows may enhance populations of semi-aquatic biting flies, particularly Ceratopogonidae.
Year-'Round	Benthic algal and macroinvertebrate production restricted by exposure to below the annual minimum volume of 322 cm^3/s (ca 11,5000 cfs). Minimum drift and low velocities may mean increases in other aquatic plants. Aggredation of silt in channel and accumulation of detritus and detritivores. Possible overgrowth of Cladophora on hard substrata or coating of hard substrata by Oscillatoria thereby reducing available habitat for simuliids. Steady flows may enhance populations of semi-aquatic biting flies, particularly Ceratopogonidae.

Table 7.1 (Cont.)

EIS ALTERNATIVE	CONSEQUENCES ON LOWER AQUATIC TROPHIC LEVELS
LIMITED DYNAMICS	
"Ninth" Alternative	Benthic algal and macroinvertebrate production restricted by (Ecosystem Dynamics) exposure to below the seasonal normal minimum flow. Moderate drift in most seasons, with maximum drift and development of fresh bare substrata for simuliid colonization during annual "flood" peaks. Low velocities may mean increases in other aquatic plants. Patterns of detrital accumulation would more closely resemble the pre-dam condition.

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