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EFFECTS OF STEADY VERSUS FLUCTUATING FLOWS ON AQUATIC MACROINVERTEBRATES IN THE COLORADO RIVER BELOW GLEN CANYON DAM, ARIZONA

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THE EFFECTS OF STEADY VERSUS FLUCTUATING FLOWS ON AQUATIC MACROINVERTEBRATES IN THE COLORADO RIVER BELOW GLEN CANYON DAM, ARIZONA

Contract No.: 6400042 Extension

BY

William C. Leibfried and Dean W. Blinn

Department of Biological Sciences
Northern Arizona University
Flagstaff, Arizona
86011

Submitted to:

James deVos and Henry Maddux
Arizona Game and Fish Department
Phoenix, Arizona
85023

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This report determines the impacts of steady versus fluctuating discharges on aquatic macroinvertebrates. Specific objectives include: identify impacts on invertebrate drift, specifically the amphipod Gammarus lacustris; determine standing crop and distribution of aquatic macroinvertebrates under various flow regimes; and quantify the relationship between biomass of Cladophora glomerata, a filamentous green alga, and the standing crop of Gammarus lacustris. Mean drift rates and densities for Gammarus increased during periods of fluctuating flows. Drift was regulated by the rising of discharges after periods of low flows and by the rate that discharges rose and fell. Standing crop of Gammarus was significantly greater from Glen Canyon Dam to Little Colorado River (75 miles below). Standing crop decreased significantly below Little Colorado River. Dramatic reductions in benthic macroinvertebrates was found in the zone of fluctuation along the Colorado River margins. A significant positive correlation exists between Cladophora biomass and standing crop of Gammarus.

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ABSTRACT

The impacts of fluctuating versus steady discharges from Glen Canyon Dam on aquatic macroinvertebrate drift, distribution and standing crop in the Colorado River were studied during 1985 and 1986. A significant positive correlation exisits between Gammarus drift and increasing flows. Mean drift rates and densities of Gammarus lacustris, increased during months of fluctuating discharges. Increased drift only occurred during the rising arm of discharge after periods of low flows below 5,000 cubic feet per second. The most abundant invertebrates in the Colorado River above the confluence of the Little Colorado River were chironomids, amphipods and oligochaetes. Total standing crop of macrobenthos declined significantly at sites below the confluence of the Little Colorado River. Below the confluence of the Little Colorado River, chironomids dominated the main river sites while Gammarus density declined. At the mouths of tributaries and within approximately 200 meters below tributaries chironomids dominated with Ephemeroptera occurring in large numbers. Total benthic standing crop in the Colorado River decreased significantly under fluctuating discharges. On two occasions benthic samples were collected simultaneously in the zone of fluctuation soon after rewetting and in a non-exposed area. Macroinvertebrate density and biomass of Cladophora glomerata was reduced dramatically in substrates exposed to fluctuations. A signifcant positive correlation between standing crop of Gammarus lacustris and Cladophora glomerata biomass was observed for July and October 1985. Pooled data for all four months showed a significant positive correlation between Gammarus abundance and Cladophora biomass.

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CHAPTER ONE: INTRODUCTION AND OBJECTIVES

The aquatic ecosystem below Glen Canyon Dam has been the subject of concern for resource managers since the closing of the floodgates in 1963. Although the regulated, cold, clear water flowing from the dam creates ideal conditions for introduced trout, the constant water temperatures and diurnal discharge fluctuations proved detrimental to river invertebrates (Stone 1964, 1972). The majority of benthic organisms that occur in the river today were introduced to enhance the food base for the trout fishery (Stone 1972).

In order to increase production of introduced trout species Arizona Game and Fish Department (AGFD) introduced snails, midges, several other invertebrate taxa and an amhipod, *Gammarus lacustris* in 1967 and 1968. *Gammarus* adapted to the constant cold water temperatures and quickly became an abundant part of the food chain. Chironomids, and to a lesser extent oligochaetes and gastropods also became established (Carothers and Minckley 1981, Persons et al. 1985). Following these introductions the fishery developed into one of the top trout waters in the West. The invertebrate fauna now found in the Colorado River is a critical component of the food base for the trout fishery throughout the Grand Canyon.

The post dam river environment probably has increased the productivity of algae and invertebrates. Ward (1976a) determined that hypolimnetic release dams alter natural seasonal and diurnal temperature regimes that regulate invertebrate life cycles and developmental patterns. Ward concluded that deep release dams produce low diversity and high standing crop of invertebrates that can adapt to thermal constancy. The aquatic ecosystem below Glen Canyon Dam shows the same trends, i.e. few invertebrate species (*Gammarus* and chironomids) dominate with high standing crops (Carothers and Minckley 1981, Hofknecht 1981). The proliferation of the filamentous, green alga *Cladophora glomerata* and its associated epiphytic diatoms in the regulated Colorado River has increased the habitat and food base for invertebrate species. The importance of increased vegetation for aquatic invertebrate production is well established for European and North American rivers (Hynes 1970, Ward 1976b). Gosse (1981) established a relationship between algal beds and invertebrates specifically for the Colorado River below Glen Canyon Dam.

The operations of Glen Canyon Dam are primarily in response to power demands within the Colorado River Storage Project system. In past years this demand resulted in a peaking power operation that would cause river discharges to fluctuate daily. It was not uncommon to have ranges of 3,000 to 15,000 cubic feet per second (cfs). The effect of these fluctuations was the creation of an "intertidal" zone along the margins of the Colorado River. Due to the filling of Lake Powell in 1980, the range of fluctuating discharges since that time has decreased (BUREC unpublished flow data). Proposed peaking power operations might possibly increase the range of fluctuations and increase

the duration of low flows. This proposed operation would increase the size of the "intertidal" zone possibly decreasing available habitat for algae and invertebrate species.

The impact of these flow regimes on the aquatic biota of the Colorado River in Glen and Grand Canyons is poorly known. The reduction of benthic macroinvertebrate standing crop due to discharge fluctuations has been documented for other systems (Radford and Hartland-Rowe 1971, Fisher and LaVoy 1972, Trotsky and Gregory 1974). The effect of fluctuating flows on invertebrate drift in the Colorado River below Glen Canyon Dam is an important phenomenon, since drifting organisms may provide a substantial food source for salmonids (Chapman 1966). Little data exists on the effects of fluctuating discharges on invertebrate drift in large rivers (Pearson et al. 1968).

Previous research on invertebrates in the Colorado River system is limited. Pearson et al. (1968) and Holden and Crist (1981) described the changes in macroinvertebrates in the Green River below Flaming Gorge Dam. In the Colorado River through Grand Canyon recent studies by Cole and Kubly (1976), Carothers and Minckley (1981), Gosse (1981) and Hofknecht (1981) have attempted to describe the aquatic invertebrate fauna. Unfortunately these studies were unable to quantify invertebrate distribution or the impacts of regulated discharges. Persons et al. (1985) provide limited data on invertebrate densities in the Colorado River near Lees Ferry, Arizona.

OBJECTIVES

The objective of this study was to determine the impact of steady versus fluctuating discharges on aquatic macroinvertebrates. The specific objectives are:

1. To quantify the impacts of steady versus fluctuating flows on invertebrate drift, specifically *Gammarus lacustris* in the Colorado River at Lees Ferry, Arizona.

2. To determine standing crop of aquatic macroinvertebrates, under steady and fluctuating flows, along designated reaches of the Colorado River from Glen Canyon Dam to Diamond Creek.

3. To quantify the relationship between biomass of *Cladophora glomerata* and standing crop of *Gammarus lacustris*.

CHAPTER TWO: METHODS AND MATERIALS

The sampling of benthic macroinvertebrates in large river systems presents problems unique to lotic ecosystems. High discharges, substrate size and channel configuration of these systems require flexible and innovative sampling methodologies (Gosse 1981). In addition, regulated flows from hydroelectric dams can be sporadic and unpredictable. The methods that follow were specially adapted to the Colorado River below Glen Canyon Dam and regulated flow regimes that were available at the time of sampling.

Due to restraints of power production and lake level maintenance, discharges from Glen Canyon Dam were variable during the course of this study. Prior to initiating the field collections, it was agreed that the Bureau of Reclamation would provide steady releases from the Dam from May through September 1985 and would fluctuate flows from October through December 1985. The actual flows that were observed all fluctuated to some degree. May through September steady flows fluctuated less than 8,000 cfs at one time and usually had no drastic rising or falling of water level. October through December flows fluctuated far more drastically with discharges rising from 2-3,000 cfs to greater than 20,000 cfs in less than two hours (USBUREC 1985).

Prior to any sampling, three depth zones were surveyed during an October 1984 experimental drawdown at Glen Canyon Dam. The Bureau of Reclamation conducted a three day decrease in discharges from Glen Canyon Dam allowing researchers an opportunity to examine the effects of reducing flows from 25,000 to 3-5,000 cfs. This low discharge enabled the measurement of three depth zones between the 25,000 and 3-5,000 cfs river stage. Using the 25,000 cfs river level as a standard marker (this level left a debris and bank erosion line visible along the river), these depth cells allowed for a standard reference for sites downriver. Cell I was measured from approximately the 25,000 cubic feet per second (cfs) stage to a depth of 1.0 feet (0.31 meters). Cell II extended from the bottom of Cell I to 4.0 feet (1.3 meters) and Cell III was greater than four feet (1.3 meters) in depth.

OBJECTIVE 1: INVERTEBRATE DRIFT

Invertebrate drift was sampled at one site 10.5 miles above Lees Ferry. Collections were made over a 24 hour period in each of the months of steady flow (May, June, July, August and September 1985) and in each month of fluctuating flow (October, November and December 1985). During each 24 hour period drifting invertebrates were sampled at four hour intervals insuring that steady, increasing and decreasing discharges were represented. Flow releases for at least two weeks prior to any drift samples reflected the conditions of study for that period, i.e. fluctuating or steady discharges.

Five standard invertebrate drift nets with mesh size of 363 microns were employed to collect drifting organisms. Nets had a mouth opening of 1.0 ft x 1.5 ft (30.48x45.72 cm) tapering to a base where a cannister was attached to collect drifting material. Two vertically stacked sets of 2 nets each were established in current approximately 0.5 meter in depth and approximately 5 to 10 meters from shore. One single net was set in shallow water about 0.5 to 1.0 meters from shore. These stacked nets were set to collect surface drifting organisms as well as organisms drifting lower in the water column. Duration of net sets ranged from 15 to 30 minutes depending on detrital accumulation. Discharge through each net was calculated from velocity and surface area measurements at the mouth of each net. These measurements were taken at the beginning of each drift period and repeated when river level changed. If several velocity measurements were taken, the average was used to represent that sample period. Current velocity was always taken at the beginning and end of each net set. Samples from each net were placed in Whirl-pacs and preserved in AFA and returned to the lab for analysis.

Discharge estimates were made for each net during every interval. Three velocity measurements, using a Price AA current meter were taken at six-tenths of the depth in front of the stacked nets. The wetted area of each net was determined and used with velocity estimates to determine discharge through the nets. The equation: discharge = velocity x width x height, was used to determine water volume passing through the drift nets.

Collections were sorted by taxon and enumerated, with identification of invertebrates aided by Merrit and Cummins (1970) and Pennak (1978). Four stacked nets and two shallow nets were analyzed for each four hour period. Gammarus lacustris were sorted by size class; less than 7mm = juvenile and greater or equal to 7mm = mature and dry weights estimated from average weights of amphipods from Objective Three.

Analysis of variance (ANOVA) and correlation tests were utilized (Zar 1984). One way ANOVA was used to compare drift rates and densities by month. Correlations were run to examine the ralationship between Gammarus drift and discharge. The significance level for the study was set at $P<.05$, however print-out probabilities are included in the text.

OBJECTIVE 2: INVERTEBRATE DISTRIBUTION AND STANDING CROP

Benthic macroinvertebrates were sampled at selected sites that coincided with the Arizona Game and Fish Department's (AGF) five study reaches from Glen Canyon Dam to Diamond Creek on the Colorado River (Figure 1). Sites were chosen to include the Colorado River mainstream, selected tributary mouths and the zone of influence in the main river below the mouths. Lees Ferry,

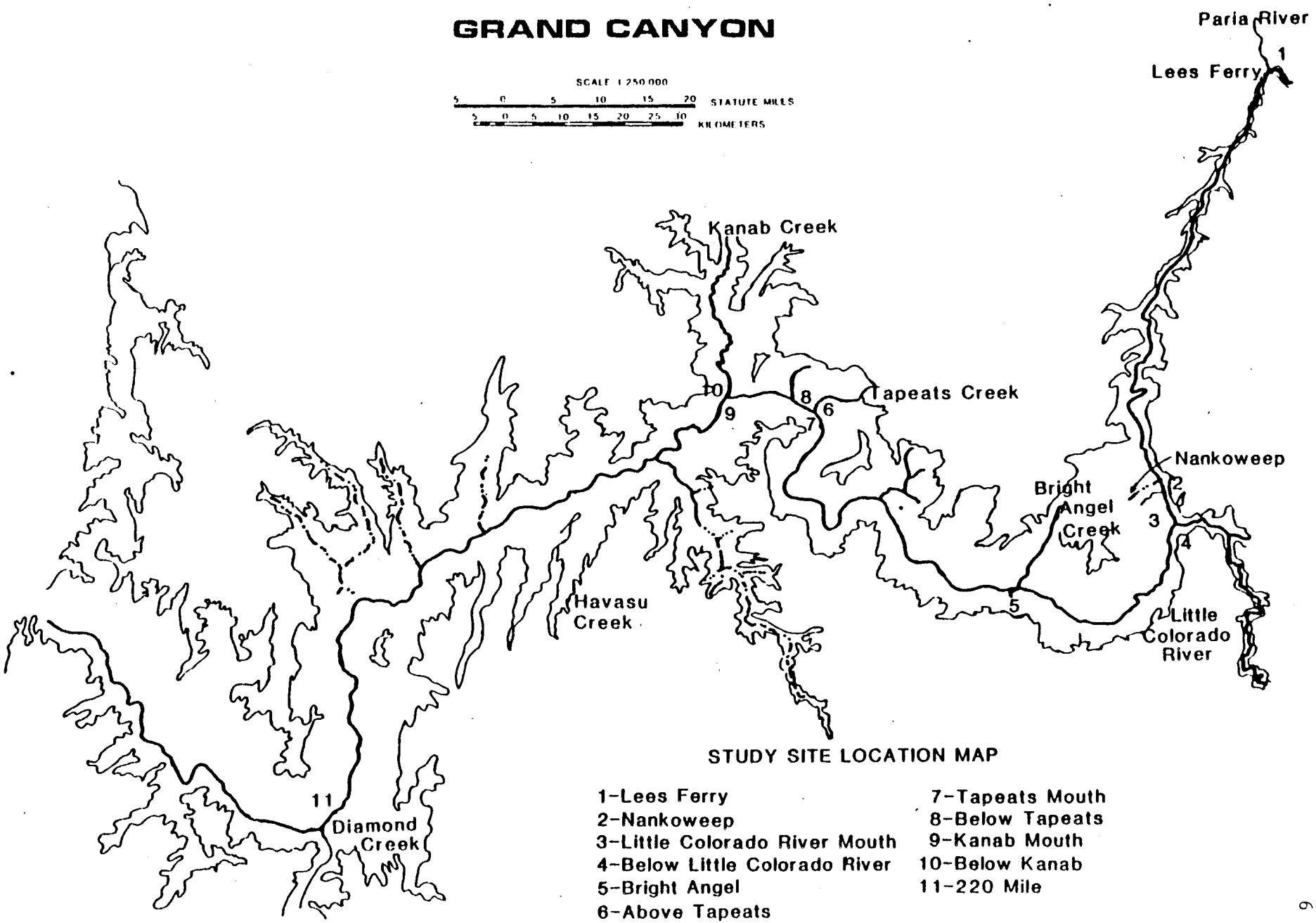


FIGURE 1. Study sites (1-11) for invertebrate distribution and standing crop in the Colorado River through Grand Canyon National Park.

Nankoweap, Bright Angel, Above Tapeats, and 220 mile were mainstream sites. The Little Colorado River, Tapeats Creek and Kanab Creek were sampled for organisms in the mouths and zone of influence below each.

Collections were made using a modified Hess Bottom sampler, with a sampling area of 0.0855 square meter (Hess 1941). Five randomly selected points were located at each site, in the margins of the river at a depth of less than 0.5 meter. The Hess sampler was then placed on a point and pushed into the substrate to insure that organisms were not lost. Where the substrate did not allow a proper seal, the sampler was moved to the closest area where proper placement could be achieved. In some areas where substrate did not afford a tight seal, samples were taken while minimizing loss of sample material. Collections were made in depth cells I, II and III depending on discharges from Glen Canyon Dam at the time of sampling. During July, samples were taken from Cell I only due to inaccessability of Cell II and III because of steady high discharges ranging from 25 - 30,000 cfs. October samples were taken in both Cell II and III depending on the level and timing of fluctuating flows. December's fluctuating flow regime and trip itinerary allowed for more complete sampling of both Cell II and III at the Nankoweep site. During October and December samples were obtained from Cell III and from Cell II after the river had risen and covered the previously exposed substrate. These were the only times that a comparison of Cells was obtained. Substrate type was recorded with each sample according to Cummins (1962).

Sample material was placed in Whirl Pacs and preserved with Alcohol-Formalin-Acetic Acid (AFA) solution. Collections were taken to the lab to be sorted, and enumerated. The amphipod, Gammarus lacustris, was sorted by size class. Animals smaller than 7 millimeters (mm) were considered juvenile and those greater than or equal to 7 mm were of reproductive size. These estimates of sexual maturity were taken from current literature dealing with other aquatic systems and may be slightly different than the Colorado River (Hynes and Harper 1972, Marchant 1981). Dry weights of other invertebrates were obtained from averages calculated in Objective 3. Cladophora glomerata from each sample was dried at 100 centigrade (C) for 24 hours and weighed to the nearest thousandth of a gram (EPA 1973). All samples were weighed on a Mettler electronic balance (Model NO. H20T).

Two way and one way ANOVA were used to compare benthic invertebrate standing crop between sites, months and depth cells (Zar 1984). The significance level for this objective was set at $P<.05$, however print-out probabilities are included in the text.

OBJECTIVE 3: GAMMARUS - CLADOPHORA CORRELATION

A study site for this objective was established at 13.5 miles above Lees Ferry. Using SCUBA (Self Contained Underwater Breathing Apparatus) collections were made during July and

October 1985 and January and March 1986. The study site was chosen to allow a diver safe access to Cladophora covered rocks easily removed from the substrate in moderate current. Depth of collections varied from 2.5 to 4 meters depending on river stage at time of sampling. This collection area was never exposed during periods of fluctuating discharges, with the possible exception of several extreme low discharges of less than 2000 cfs in December 1985.

Using a net to minimize loss of invertebrates the diver would choose rocks of various algal densities and while holding the net downstream of the rock would quickly remove the rock and place it in the net and swim to the surface where a tender would process the sample. All algae and associated invertebrates were scraped from each rock, placed in Whirl-pacs and preserved in AFA. Bare rocks were measured for approximate surface area and recorded on the respective bag. Twenty samples were collected for each season.

In the laboratory, invertebrates were removed from the Cladophora sample and sorted. Gammarus were enumerated and dry weights determined for each size class (<7mm = juvenile and > or equal to 7mm = mature). Cladophora from each sample was dried and dry weight standing crop determined. All samples were dried in an oven at 100 C for 24 hours (EPA 1973). Dry weights for all samples were measured using a Mettler electronic balance (Model H20T).

Biomass of Cladophora and density and biomass of Gammarus were analyzed using correlation statistics to determine the relationship between the two (Zar 1984).

CHAPTER THREE: RESULTS

INVERTEBRATE DRIFT

Five months of steady (approximately 8,000 cfs or less fluctuations) and three months of fluctuating flows (1,500 to 22,000 cfs) were monitored to determine the impact of steady versus fluctuating discharges on aquatic macroinvertebrate drift below Glen Canyon Dam. May through September flows were considered steady and contained no drastic fluctuations. October through December exhibited fluctuations between 1,500 and 22,000 cfs. Due to high flows (>38,000 cfs) in June 1985 this month might be considered anomolous when compared against the other steady flow months whose flows did not exceed 26,000 cfs.

The invertebrate taxa encountered in drift samples were represented by three major groups of riverine organisms and two lacustrine groups from Lake Powell. The amphipod, Gammarus lacustris; Chironomidae and Oligocheatae were found in drift samples and were common in benthic river samples. Cladocerans and copepods, from Lake Powell, were found in drift samples after they had passed through the turbines of Glen Canyon Dam. Neither oligochaetes nor cladocerans and copepods were considered in the analysis of drift samples. The size of these organisms were considered below that of macroinvertebrate classification (Whitton 1975). No oligocheates greater than three millimeters were observed in any drift samples.

A significant positive correlation exists between increasing range of discharges and drift of Gammarus lacustris ($P<0.01$, $n=66$, $r=0.48$; Figure 2). There was no correlation between Gammarus drift and absolute volume of flow from Glen Canyon Dam ($r=0.05$, $n=333$). These correlation data are supported graphically as well (Figures 3-10). Only during October, November and December do drifting Gammarus increase as discharge increases. It is also only during these months that flows fluctuated more than 10,000 cfs.

During months of fluctuating discharges from Glen Canyon Dam mean monthly drift of the amphipod, Gammarus lacustris increased while the drift of chironomids (midges) and the filamentous green alga, Cladophora glomerata declined slightly. Mean drift rates of Gammarus increased from 10.7 organisms per hour for the 5 months of steady flows to 42.3 organisms per hour for the 3 months (October, November and December) of fluctuating flows (Table 1). Mean drift densities (number of organisms per 100 cubic feet of water) for Gammarus and chironomids followed mean drift rates (Tables 2-4). Cladophora mean drift densities (grams per 100 cubic feet of water) remained constant (Table 1).

Total drifting biomass of macroinvertebrates appears to have been influenced by fluctuating discharges. Drift biomass increased from 4.56 grams per hour under steady flows to 5.79

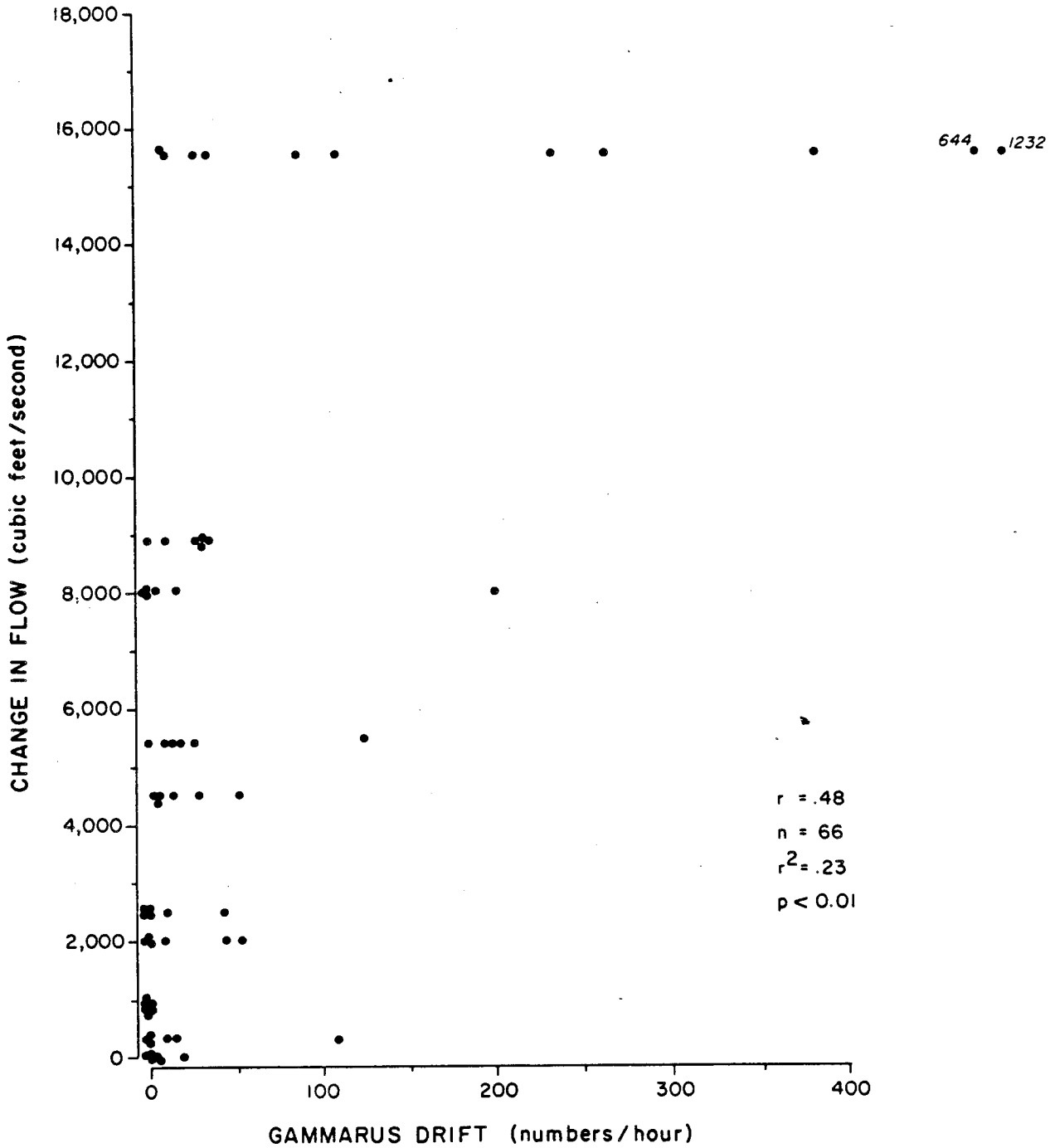


FIGURE 2. Correlation between change in flow and Gammarus drift rate for May-December 1985. Flows are given as increase in flow prior to drift collections.

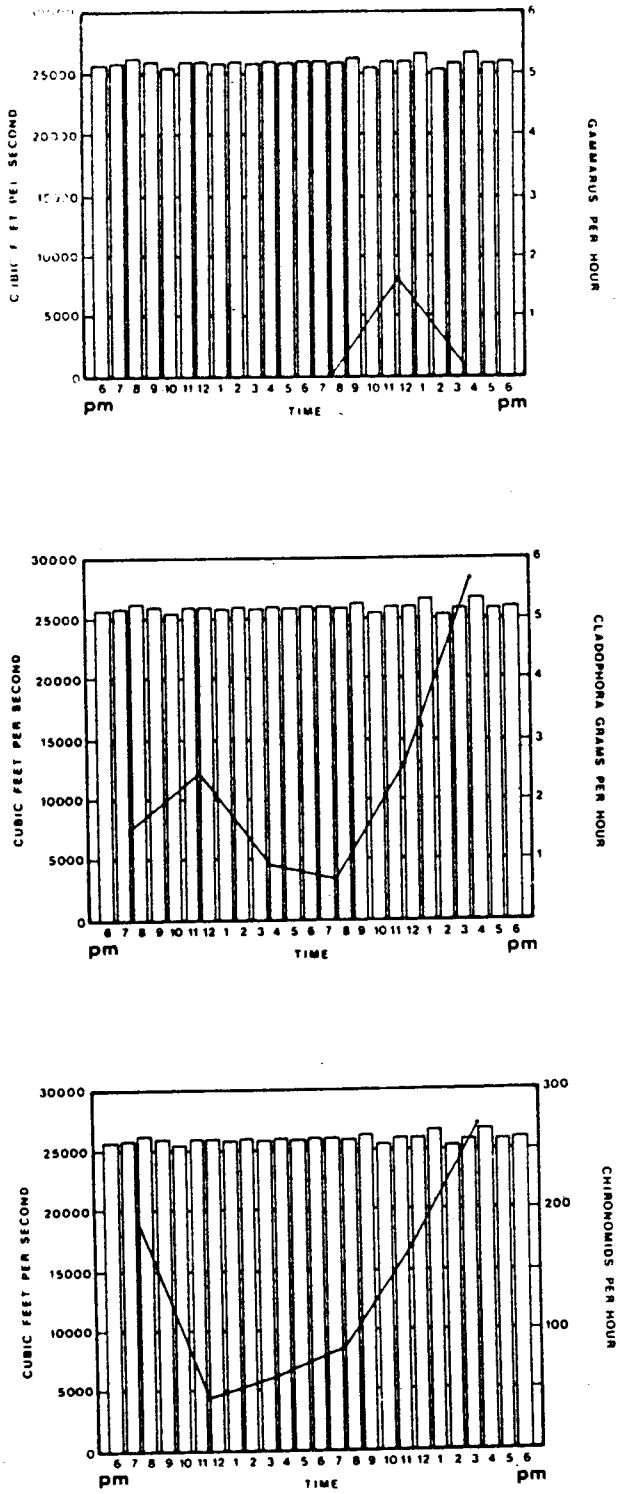
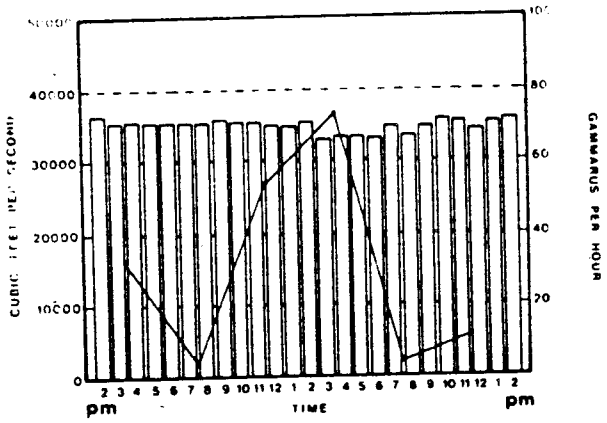
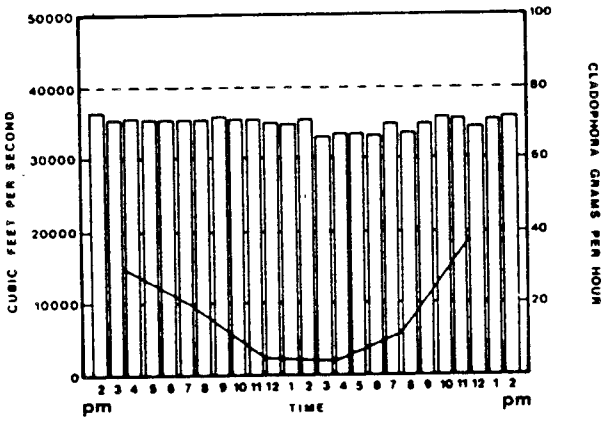


FIGURE 3. Drift rates and hourly flow releases (during steady flows) from Glen Canyon Dam for May 4-5, 1985 over a 24 hr period. (Time is in hours).





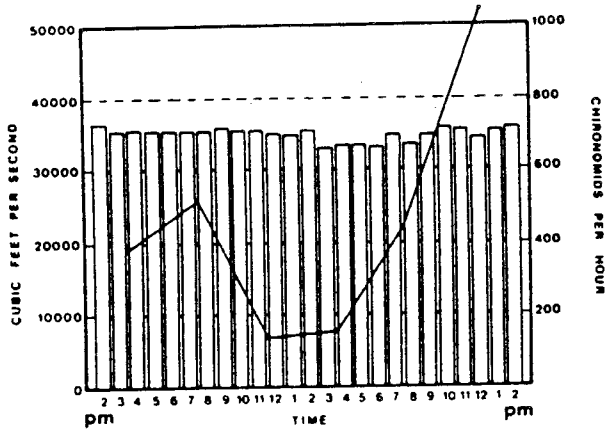


FIGURE 4. Drift rates and hourly flow releases (during steady flows) from Glen Canyon Dam for June 26-27, 1985 over a 24 hr period. (Time is in hours).

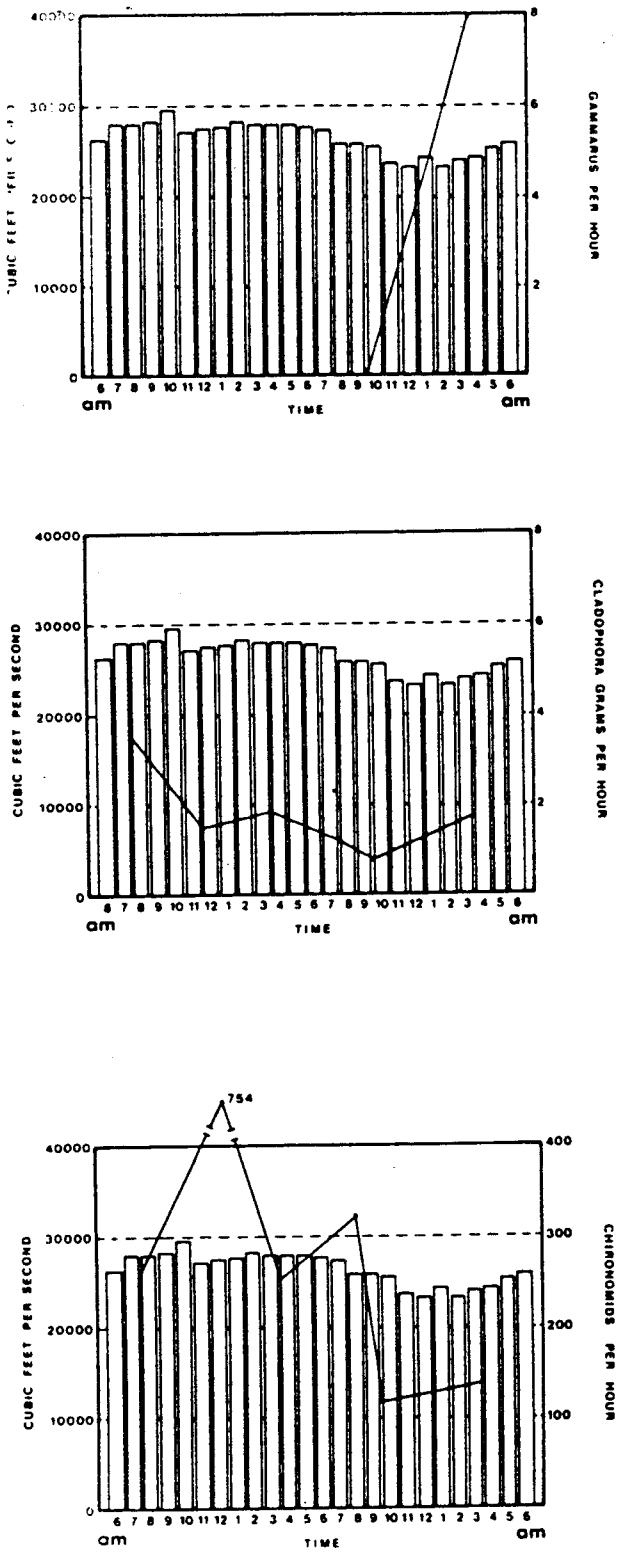


FIGURE 5. Drift rates and hourly flow releases (during steady flows) from Glen Canyon Dam for July 29-30, 1985 over a 24 hr period. (Time is in hours).

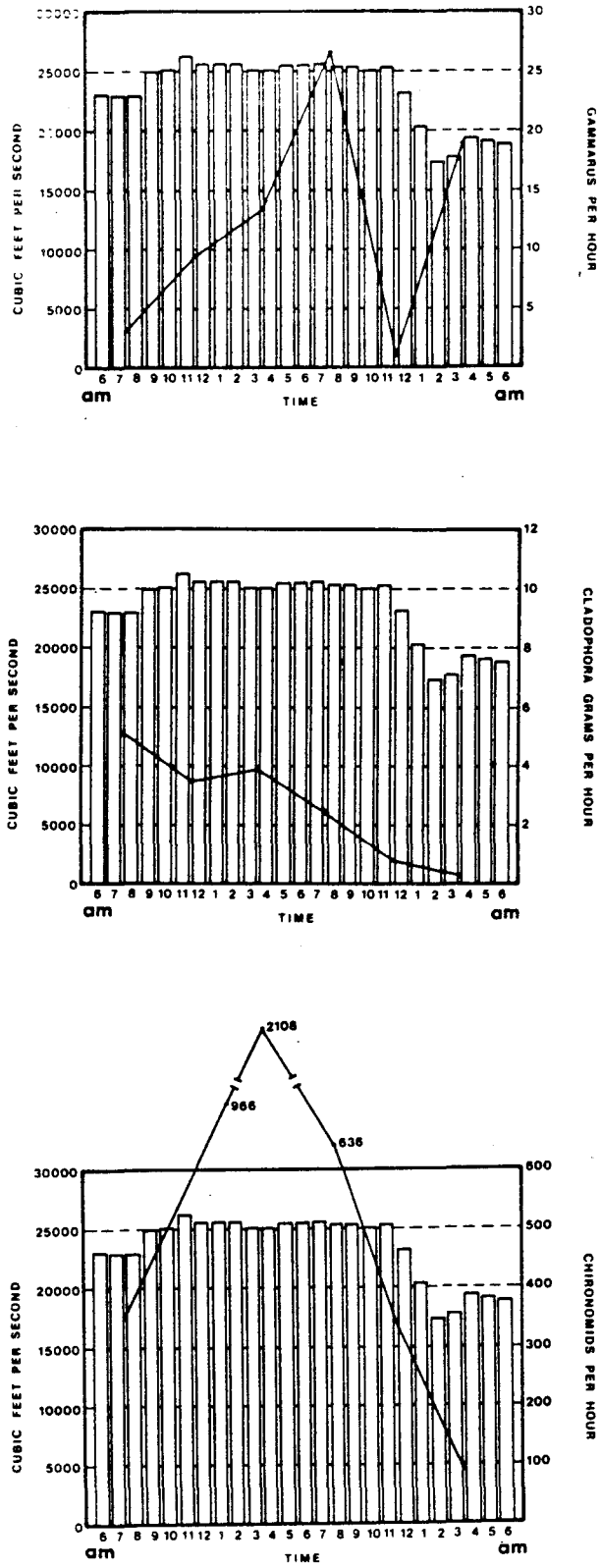


FIGURE 6. Drift rates and hourly flow releases (during steady flows) from Glen Canyon Dam for August 22-23, 1985 over a 24 hr period. (Time is in hours).

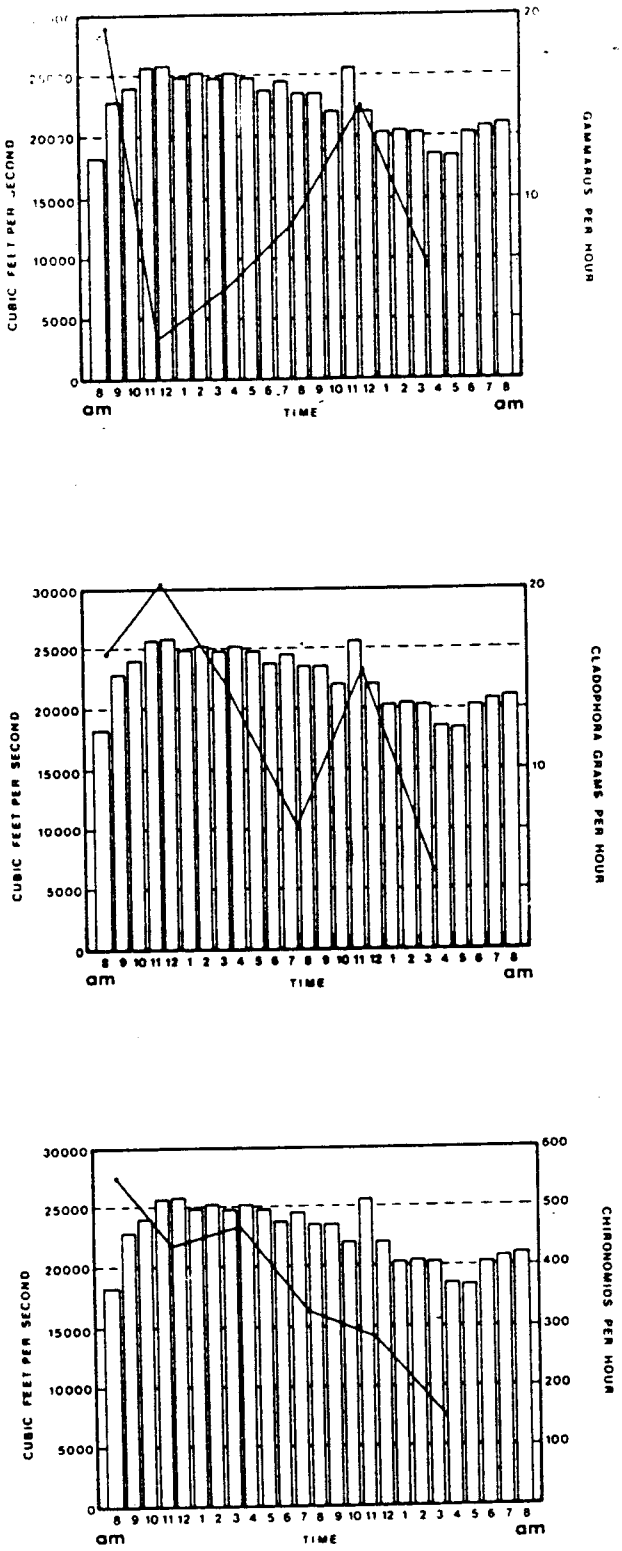


FIGURE 7. Drift rates and hourly flow releases (during steady flows) from Glen Canyon Dam for September 20-21, 1985 over a 24 hr period. (Time is in hours).

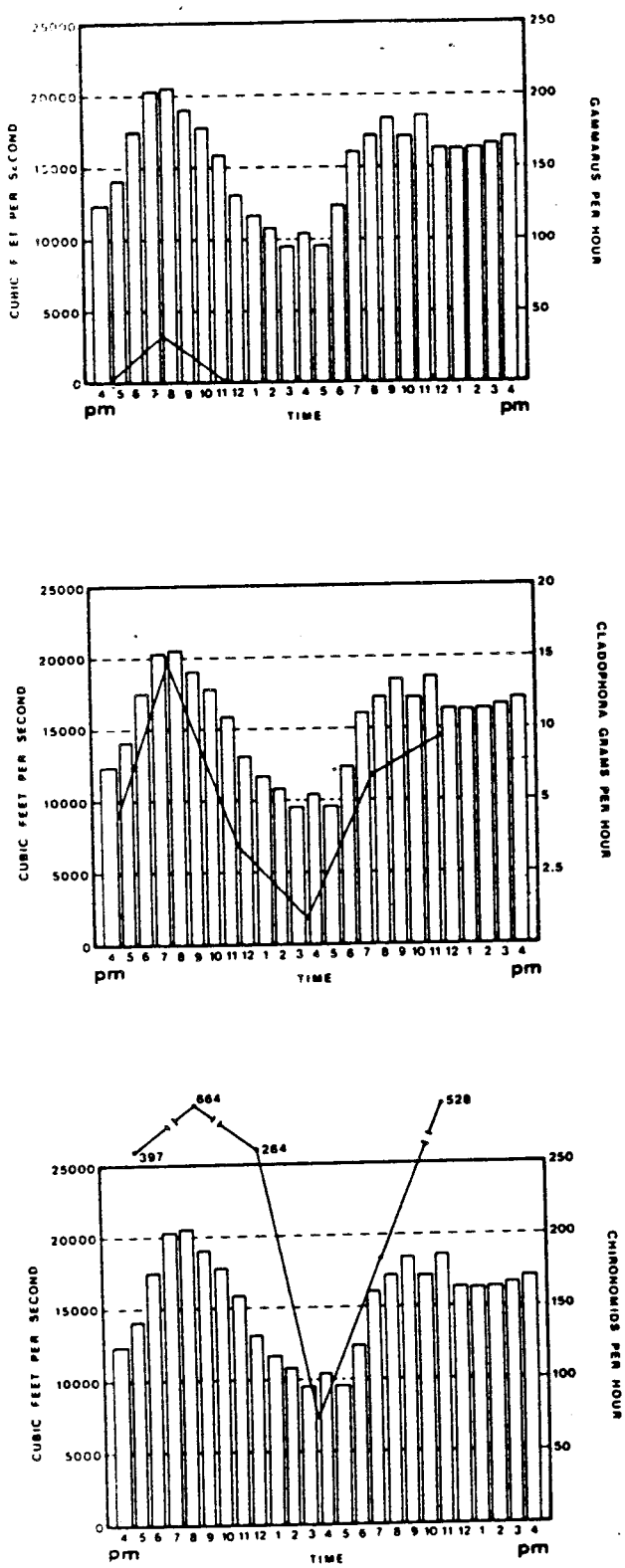


FIGURE 8. Drift rates and hourly flow releases (during fluctuating flows) from Glen Canyon Dam for October 27-28, 1985 over a 24 hr period. (Time is in hours).

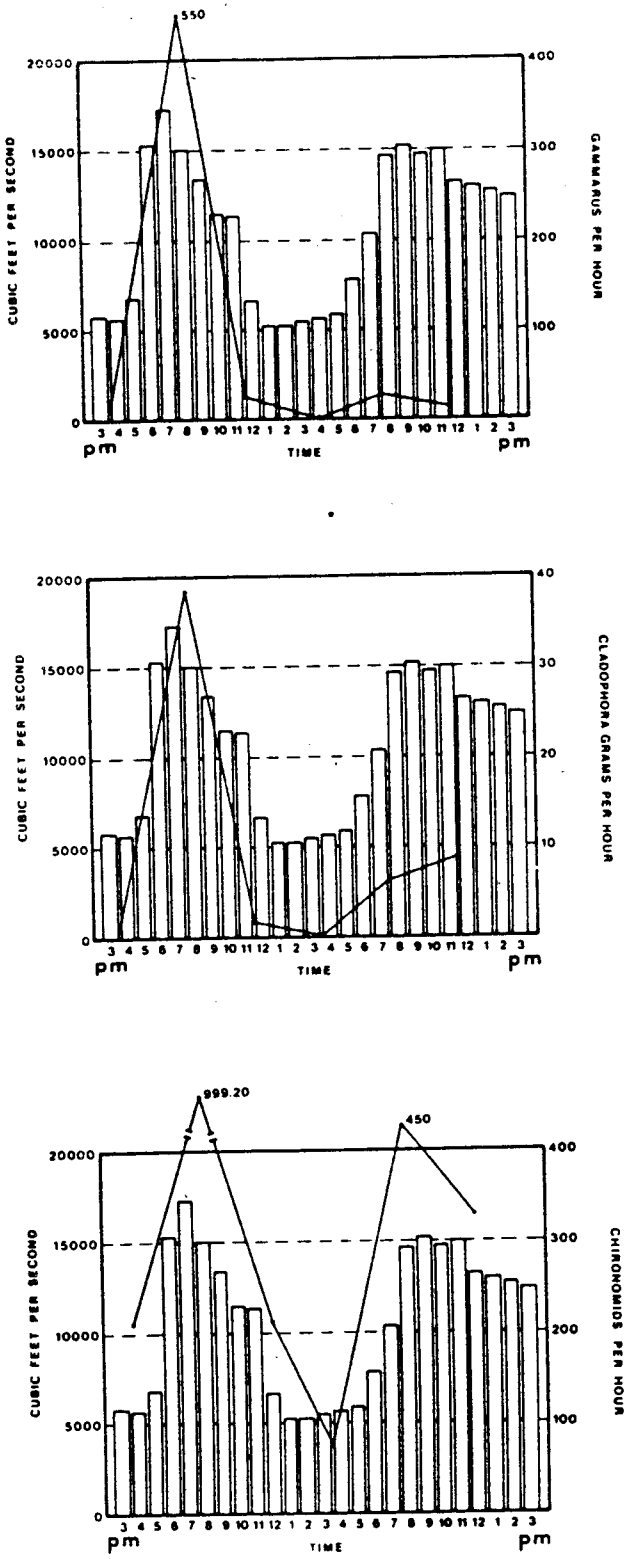


FIGURE 9. Drift rates and hourly flow releases (during fluctuating flows) from Glen Canyon Dam for November 24-25, 1985 over a 24 hr period. (Time is in hours).

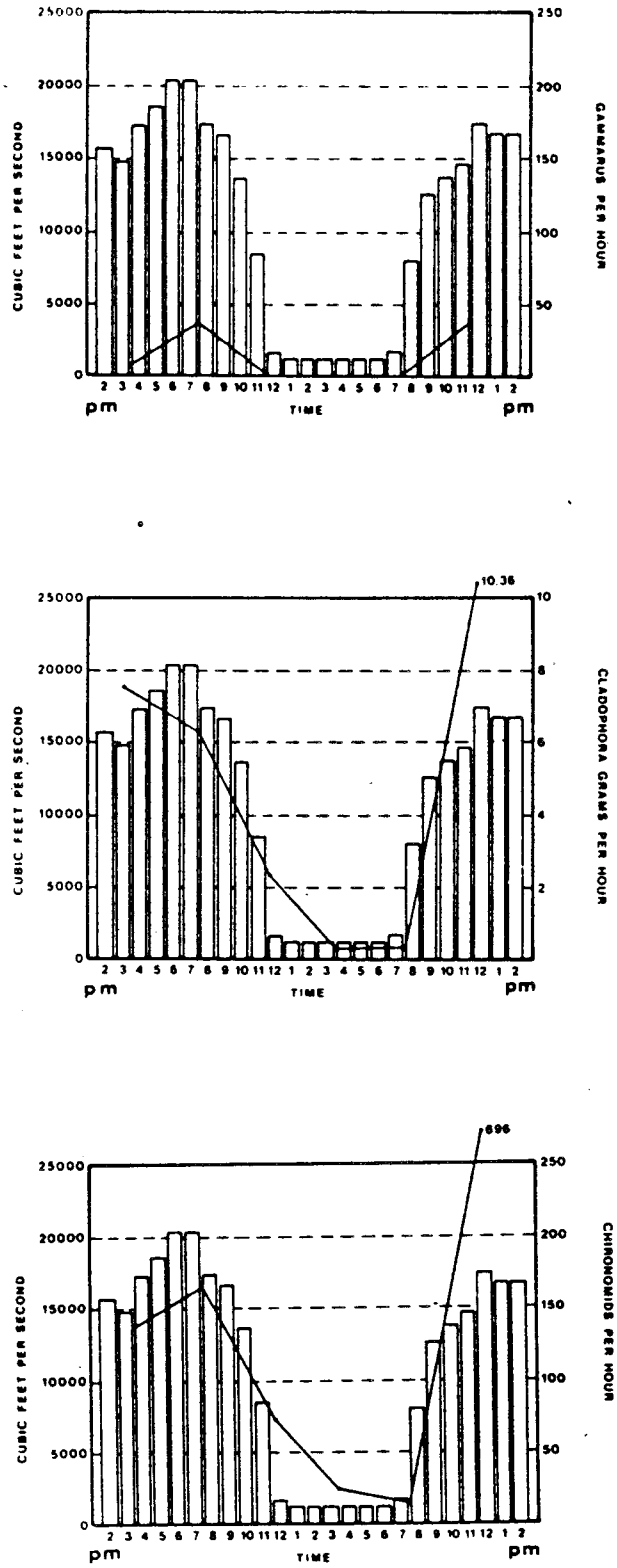


FIGURE 10. Drift rates and hourly flow releases (during fluctuating flows) from Glen Canyon Dam for December 20-21, 1985 over a 24 hr period. (Time is in hours).

TABLE 1. Comparison of mean drift rates and densities in the Colorado River at Lees Ferry, Arizona, for months of steady vs. fluctuating discharges during 1985. (Densities are per 100 cubic feet of water.)

	STEADY (MAY - SEPT.)	FLUCTUATING (OCT.,NOV.,DEC.)
# GAMMARUS	10.7/HR 0.14/100 ft^3	42.3/HR 0.41/100 ft^3
# CHIRONOMIDS	402.5/hr 5.27/100 ft^3	306.1/hr 3.74/100 ft^3
CLADOPHORA (grams dry wt.)	8.29/hr 0.10/100 ft^3	6.85/hr 0.10/100 ft^3
TOTAL BIOMASS (grams dry wt.) per day	0.70 GAMMARUS (15.4%) 3.86 CHIRONOMID (84.6%) 4.56	2.85 GAMMARUS (49.2%) 2.94 CHIROMONID (50.8%) 5.79

TABLE 2. Drift densities for *Gammarus lacustris* (in organisms per 100 cubic feet of water filtered through drift nets) during May through December 1985 in the Colorado River at Lees Ferry, Arizona. (* indicates beginning of 24 hour drift sample period.)

Time	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
6A-10A	0.00	0.05	*0.02	*0.06	*0.20	0.02	0.25	0.02
10A-2P	0.02	0.09	0.00	0.13	0.03	0.01	0.96	0.58
2P-6P	0.00	*0.33	0.00	0.16	0.05	*0.05	*0.23	*0.04
6P-10P	*0.00	0.06	0.00	0.36	0.11	0.42	4.73	0.36
10P-2A	0.00	0.63	0.00	0.02	0.18	0.00	0.27	0.03
2A-6A	0.00	1.11	0.20	0.38	0.07	0.00	0.10	0.08
mean	0.003	0.38	0.04	0.19	0.11	0.08	0.96	0.19
sd	0.008	0.42	0.08	0.15	0.07	0.17	1.85	0.23

TABLE 3. Drift densities of Cladophora glomerata (in grams per 100 cubic feet of water filtered through drift nets) during May through December 1985 in the Colorado River at Lees Ferry, Arizona. (* indicates beginning of 24 hour drift sample period.)

Time	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
6A-10A	0.01	0.10	*0.04	*0.26	*0.18	0.06	0.06	0.00
10A-2P	0.02	0.38	0.03	0.12	0.24	0.09	0.09	0.13
2P-6P	0.03	*0.29	0.02	0.12	0.17	*0.06	*0.02	*0.07
6P-10P	*0.01	0.29	0.02	0.09	0.08	0.17	0.33	0.07
10P-2A	0.03	0.07	0.01	0.03	0.20	0.07	0.03	0.04
2A-6A	0.01	0.07	0.05	0.03	0.05	0.04	0.01	0.002
mean	0.02	0.20	0.03	0.11	0.15	0.16	0.09	0.05
sd	0.01	0.13	0.01	0.08	0.07	0.17	0.12	0.05

TABLE 4. Drift densities for Chironomidae (in organisms per 100 cubic feet of water filtered through drift nets) for May through December 1985 in the Colorado River at Lees Ferry, Arizona. (* indicates beginning of 24 hour drift sample period.)

Time	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
6A-10A	0.90	4.05	*3.14	*7.32	*5.84	1.70	4.93	0.17
10A-2P	1.69	11.19	14.66	12.97	4.76	4.72	3.62	8.79
2P-6P	2.75	*3.86	3.66	25.57	5.74	*5.66	*3.27	*1.28
6P-10P	*1.41	7.46	4.91	8.66	4.25	7.68	8.57	1.71
10P-2A	0.58	1.55	2.07	4.86	3.85	5.09	2.74	2.94
2A-6A	0.84	2.21	3.52	1.96	1.80	1.13	2.24	1.12
mean	1.36	5.05	5.33	10.23	4.37	4.33	4.23	2.67
sd	0.79	3.64	4.66	8.38	1.49	2.49	2.32	3.13

grams per hour under fluctuating flows. The percent contribution to the biomass drift rate from Gammarus lacustris increased from 15.4% under steady flows to 49.2% under fluctuating flows (Table 1).

The most influential factor controlling Gammarus drift below Glen Canyon Dam was the cycle of flow releases. During rising flows, after periods of low flow (<5,000 cfs), amphipod drift rates (Figures 3-10) and densities (Figures 11-14) increased substantially. The periods of highest drift densities of Gammarus occurred during October, November and December with the exception of June where flood conditions were encountered (Table 2). In November drift rates of Gammarus increased to over 500 organisms per hour, the highest of any month surveyed (Figure 9). Although Bureau of Reclamation flow data reported discharges of 5 - 6,000 cfs prior to the increases in flow and consequent rise in drift, discharges were closer to 1,500 (David L. Wegner, personal communication) (See flow regime in Figure 9). A similar trend was observed in December samples when flows rose from 2,000 to 18,000 cfs (Figures 10 and 14). October data reinforces the hypothesis that the range of flows may control drifting organisms. During this sample period flows of less than 5,000 cfs were not encountered and drift rates and densities remained low (Figure 8).

Significant differences were found between date and Cladophora drift rates ($F,7,47=3.05$, $P<0.01$) and chironomid drift density ($F,7,47=2.48$, $P<0.03$) using one way ANOVA. Cladophora drift rates were greatest during June (18.08 g/hr) and September (12.91 g/hr) followed by November (9.49 g/hr). Chiromomid drift densities were highest during July and August (10.22 and 5.33/100 cubic feet of water, respectively; Table 4). No significant differences were found between steady (May - September) and fluctuating flow months (October - December) for either Gammarus, Cladophora or chironomids.

The ratio of mature (> or equal to 7mm) to juvenile (<7mm) Gammarus lacustris encountered in drift collections decreased under fluctuating discharges, ie., the proportion of juveniles was lower with steady flows. Ratios of mature:juvenile under fluctuating flows during October, November and December were 1:5, 1:8.3, 1:8.3, respectively. For steady flow months ratios were; 7:1, 1:18.2, 1:.75, 1:1.3 and 1:2.3 for May through September, respectively. This trend may be the result of seasonal life cycle patterns or may suggest a behavioral response to fluctuating flows that favor stronger swimming, mature amphipods.

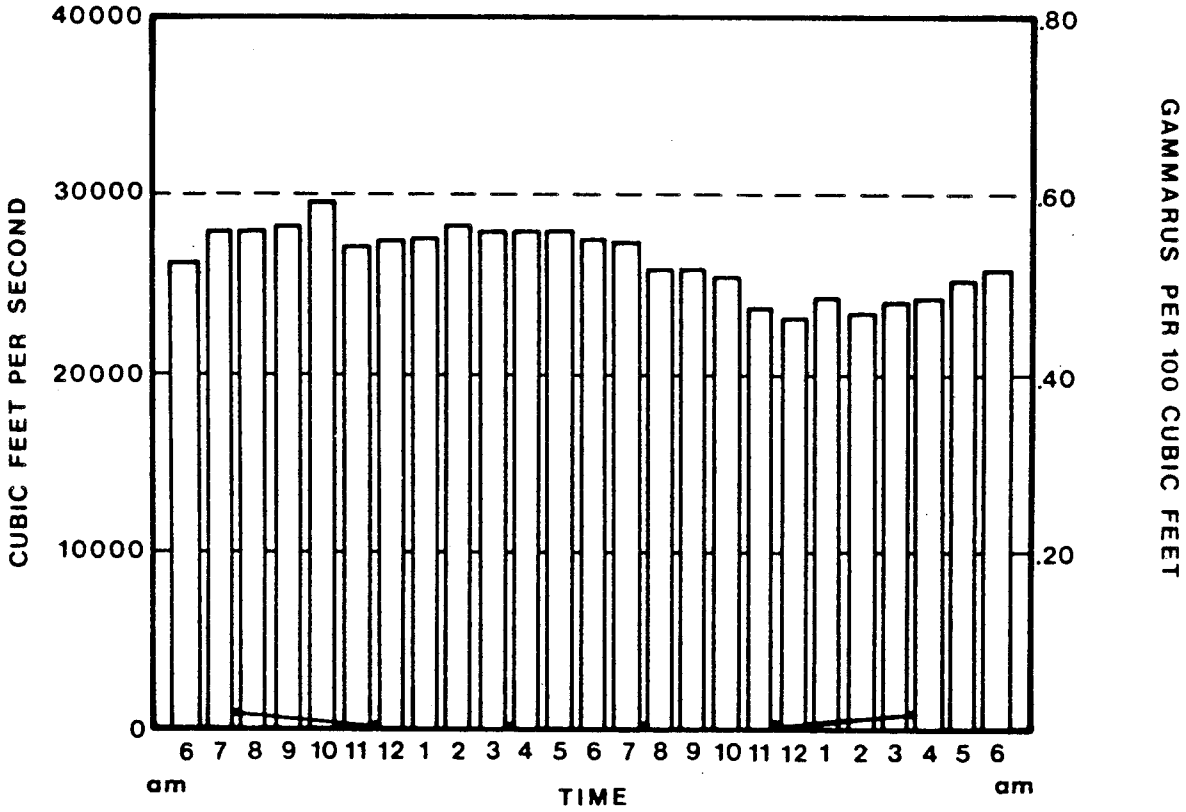


FIGURE 11. Gammarus drift density (number of individuals/100 cubic feet of water) and hourly flow releases (during steady flows) from Glen Canyon Dam for July 29-30, 1985 over a 24 hr period. (Time is in hours).

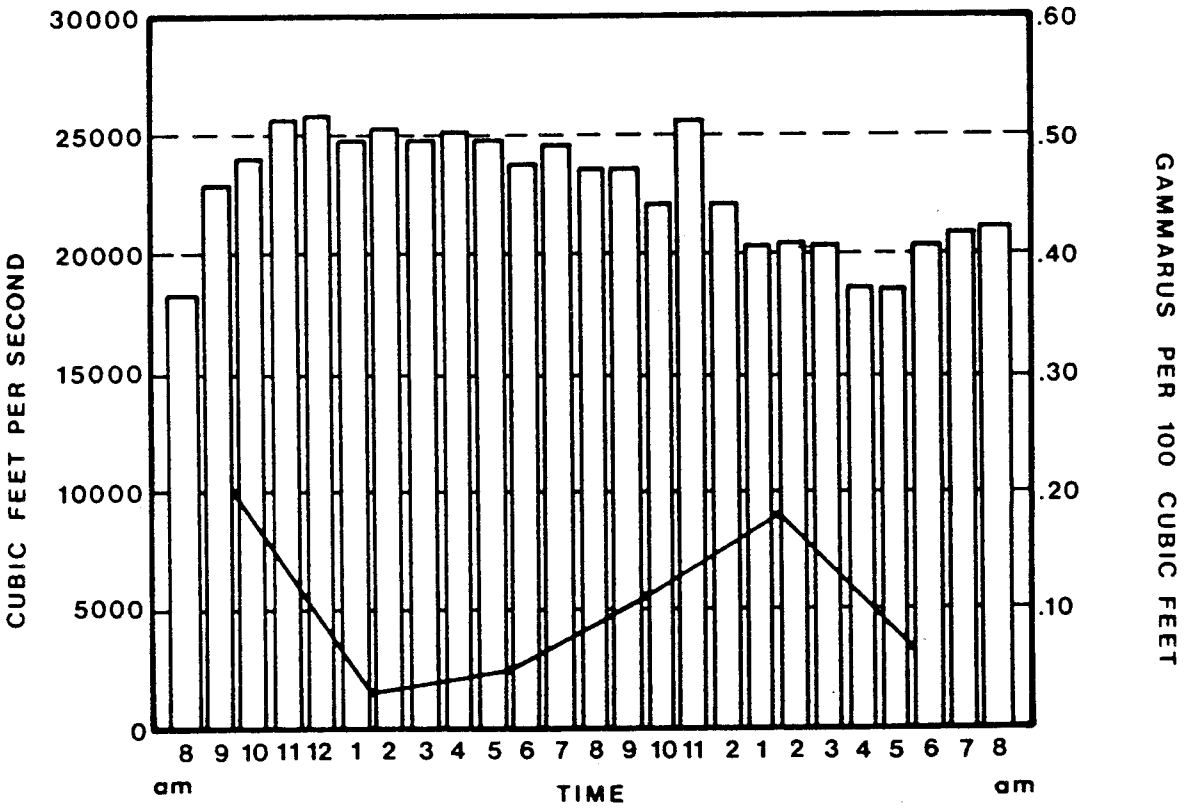


FIGURE 12. Gammarus drift density (number of individuals/100 cubic feet of water) and hourly flow releases (during steady flows) from Glen Canyon Dam for September 20-21 1985 over a 24 hr period. (Time is in hours).

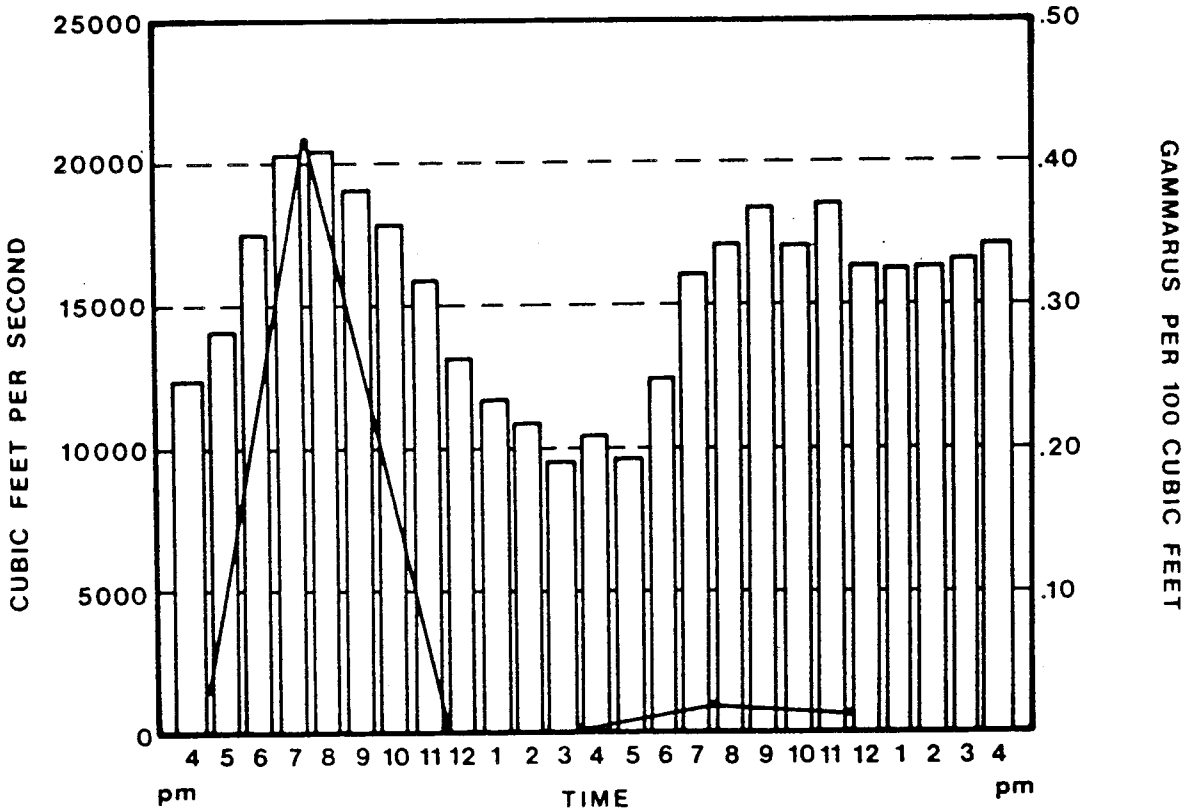
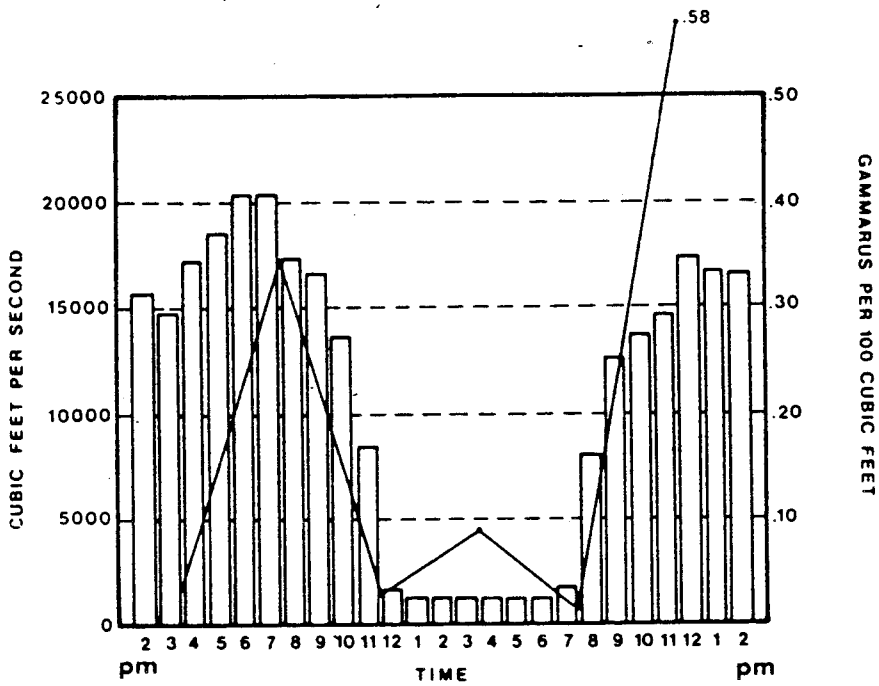


FIGURE 13. Gammarus drift density (number of individuals/100 cubic feet of water) and hourly flow releases (during fluctuating flows) from Glen Canyon Dam for October 27-28, 1985 over a 24 hr period. (Time is in hours).



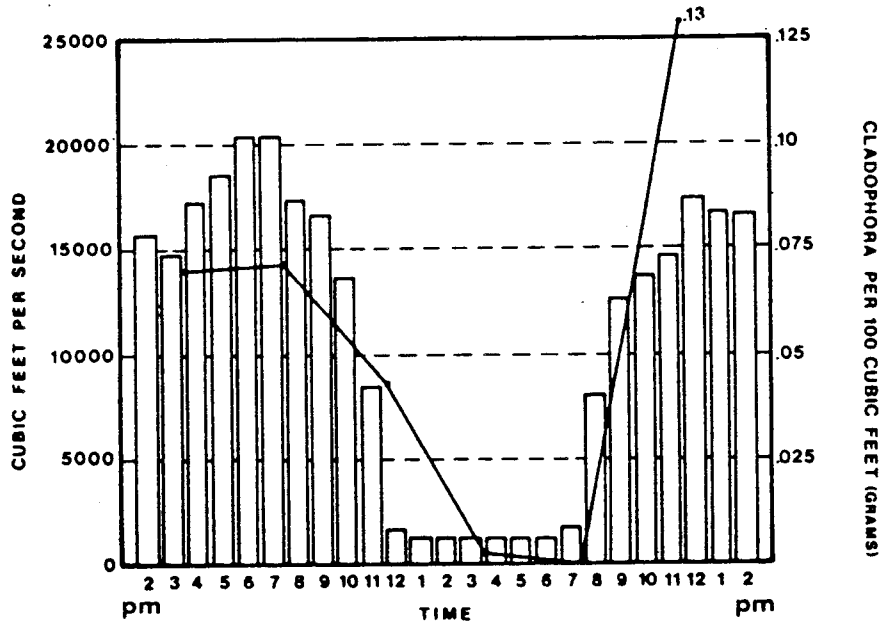


FIGURE 14. Gammarus drift density (number of individuals/100 cubic feet of water) and hourly flow releases (during fluctuating flows) from Glen Canyon Dam for December 20-21, 1985 over a 24 hr period. (Time is in hours).

INVERTEBRATE DISTRIBUTION AND STANDING CROP

Benthic samples were collected in 1985 under flow regimes that varied from a somewhat steady state (18,000 to 26,000 cfs) to daily fluctuations of 1,500 to 25,000 cfs. July samples represent benthos that were not exposed to any flow depletion for approximately 6 months, except for a one week period of flow fluctuations in late April-early May 1985 (USBUREC 1985). October samples were collected after 10 to 14 days of fluctuating flows and December collections represent a benthic community that had experienced three months of fluctuating discharges.

Invertebrate taxa encountered during this study included forms that predominated in the mainstream of the Colorado River and those forms that are characteristic of tributary streams (Table 5). Predominant mainstream taxa included; the amphipod, Gammarus lacustris, Chironomidae (midges), Gastropoda (snails) Oligochaeta (freshwater earthworms) and Simuliidae (black flies). Tributary taxa include; Trichoptera (caddis flies), Ephemeroptera (mayflies), Plecoptera (stoneflies), Simuliidae (black flies), Acarina (mites), Coleoptera (beetles) and Lepidoptera (moths).

Using one way ANOVA we found a significant effect on Colorado River macroinvertebrate standing crop was the location of sample sites either above or below the confluence with the Little Colorado River (LCR). Total organisms declined significantly, ($F_{1,180}=56.6$, $P<.001$), from 1153 individuals per square meter at all sites above the LCR to 287 individuals per square meter at all sites below. This trend was consistent for all taxa collected except the category of "other", which represents mainly invertebrate species associated with tributary sources (Table 6).

The greatest invertebrate standing crops were observed where biomass of Cladophora glomerata and densities of epiphytic diatoms were also high. Mainstream Colorado River sites above the Little Colorado River averaged 1153 total organisms per square meter while mainstream sites below the confluence had a mean of 329 organisms per square meter. Gammarus standing crop was 95 individuals per square meter in the mainstream above the Little Colorado River and 39 individuals per square meter below the confluence ($F_{1,180}=11.73$, $P<.001$).

After pooling sites below side-streams and combining mouth sites, more Gammarus were found at sites below the mouth of tributaries (26 individuals per square meter), than in the mouths themselves (12 individuals per square meter). Generally mainstream sites had a higher standing crop than at the the mouths or below mouth sites (Table 7).

Two way ANOVA using date and kind of site (mainstream, mouth or below mouth) for total organism standing crop showed that mainstream sites declined significantly ($F_{2,173}=3.01$, $P<.05$), from 776 organisms per square meter in October and declined to 429 organism per square meter after 3 months of fluctuating flows

TABLE 5. Invertebrate occurrence in the Colorado River below Glen Canyon Dam, Arizona. Collections for July, October and December 1985 combined.

(Key: GA=Gammarus, CH= chironomid, GS= Gastropoda, OL= Oligochaete SI= Simuliidae, TR= Trichoptera, PL= Plecoptera, AC= Acarina, CO= Coleoptera, LE= Lepidoptera, EP= Ephemeroptera.)

	TAXA										
SITES	GA	CH	GS	OL	SI	TR	PL	AC	CO	LE	EP
LEES FERRY	X	X	X	X	X						
NANKOWEEP	X	X	X	X	X	X					
LCR MOUTH	X	X		X							
BELOW LCR	X	X		X	X						
BRIGHT ANGEL	X	X		X	X						X
ABOVE TAPEATS	X	X		X	X	X		X		X	
TAPEATS MOUTH	X	X		X	X	X	X	X	X		X
BELOW TAPEATS	X	X		X	X	X				X	X
KANAB MOUTH	X	X		X							X
BELOW KANAB	X	X		X	X						X
220	X	X		X	X				X		X

TABLE 6. Average invertebrate standing crop in the Colorado River below Glen Canyon Dam, Arizona for all sites by location during July, October and December 1985. (Organisms per square meter with standard deviations in parenthesis. Location: Above confluence of Little Colorado River or Below the confluence of the Little Colorado River)

TAXA	ABOVE LCR	BELOW LCR
Total Organisms	1153 (1088)	287 (458)
Gammarus lacustris	95 (165)	26 (98)
Chironomid	824 (929)	217 (384)
Gastropoda	18 (49)	0 (0)
Oligochaeta	199 (365)	7 (15)
Other	12 (34)	37 (83)

TABLE 7. Average invertebrate standing crop in the Colorado River below Glen Canyon Dam, Arizona for all sites by kind of site during July, October and December 1985. (Organisms per square meter with standard deviations in parenthesis)

(KIND : 1 = MAINSTREAM, 2= TRIBUTARY MOUTH, 3= BELOW MOUTH)

TAXA	MAINSTREAM	MOUTH	BELOW MOUTH
Total Organisms	732 (919)	253 (436)	278 (497)
Gammarus lacustris	67 (149)	12 (28)	26 (106)
Chironomid	535 (755)	185 (347)	205 (429)
Gastropoda	9 (34)	0 (0)	0 (0)
Oligochaeta	103 (271)	8 (15)	2 (7)
Other	17 (43)	48 (97)	43 (95)

in December. Sites below tributary mouths also decreased significanty from July to October (454 to 133, respectively). These reductions were mainly due to the loss of chironomid standing crop during fluctuating flows. These midges were commonly the most abundant organisms collected (Figures 15,16,17). Cladophora biomass decreased as the frequency of fluctuating flows increased. (Usher et al. 1986).

The effect of fluctuating discharges on macroinvertebrate standing crop appears to be related to the loss of Cladophora biomass that occurs with increased fluctuations. Average Cladophora biomass decreased from Cell III to Cell II, where it was subject to desiccation (Table 8). These data support Usher et al. (1986), who showed decreases in algal biomass from 303.9 to 113.7 grams per square meter as discharges from Glen Canyon Dam went from steady to fluctuating flow regimes. Two way ANOVA showed significant decreases in standing crop occurring for total organisms ($F_{2,140}=5.9$, $P<.003$; Figure 18; Table 9) from July to December. Site variation was also significant for total organism ($F_{11,140}=13.41$, $P<.001$) with significant interactions between site and date ($F_{22,140}=6.93$, $P<.001$). Chironomids ($F_{2,179}=6.891$, $P<.001$) and oligochaetes ($F_{2,179}=6.003$, $P<.003$) also declined significantly from steady to fluctuating flows (Table 9). Gammarus density declined only slightly under flow fluctuation with gastropods and "others" increasing as flows fluctuated (Table 9). Standing crop of invertebrates reacted differently to fluctuating periods depending on the site location. The majority of sites showed a decrease in density with fluctuating discharges (Figures 18-23). In dividing Gammarus into populations from all sites above and populations from all sites below the Little Colorado River, large reductions in standing crop occurred from October to December at sites above the Little Colorado River (Figure 24). Below the confluence amphipod density declined from July to October but rose sharply after three months of flow fluctuations in December. This phenomenon will be discussed in detail in another section of this report.

Due to restrictions in trip logistics and timing of fluctuating discharges while on collection trips, sampling of the "intertidal" zone (depth cell II) while wetted was limited. In October and December 1985 at Nankoweap, samples were obtained in both Cell II and Cell III. On both trips Cell II had been frequently exposed for periods of 7 - 12 hours (USBUREC 1985). Cladophora biomass decreased from 133 grams per square meter in Cell III to 21 in Cell II during December and from 83 to 9 grams per square meter in October. Personal observations (Plate 1) indicated healthy algal growth in Cell III and data by Usher et al. (1986) support these observations. All invertebrate standing crops decreased from Cell III to Cell II (Table 8). Mean December and October total invertebrate density dropped significantly, ($F_{1,7}=9.58$, $P<.017$ and $F_{1,5}=36.13$, $P<.002$, respectively) from 992 to 44 individuals per square meter for December and from 2517 to 772 individuals per square meter for October.

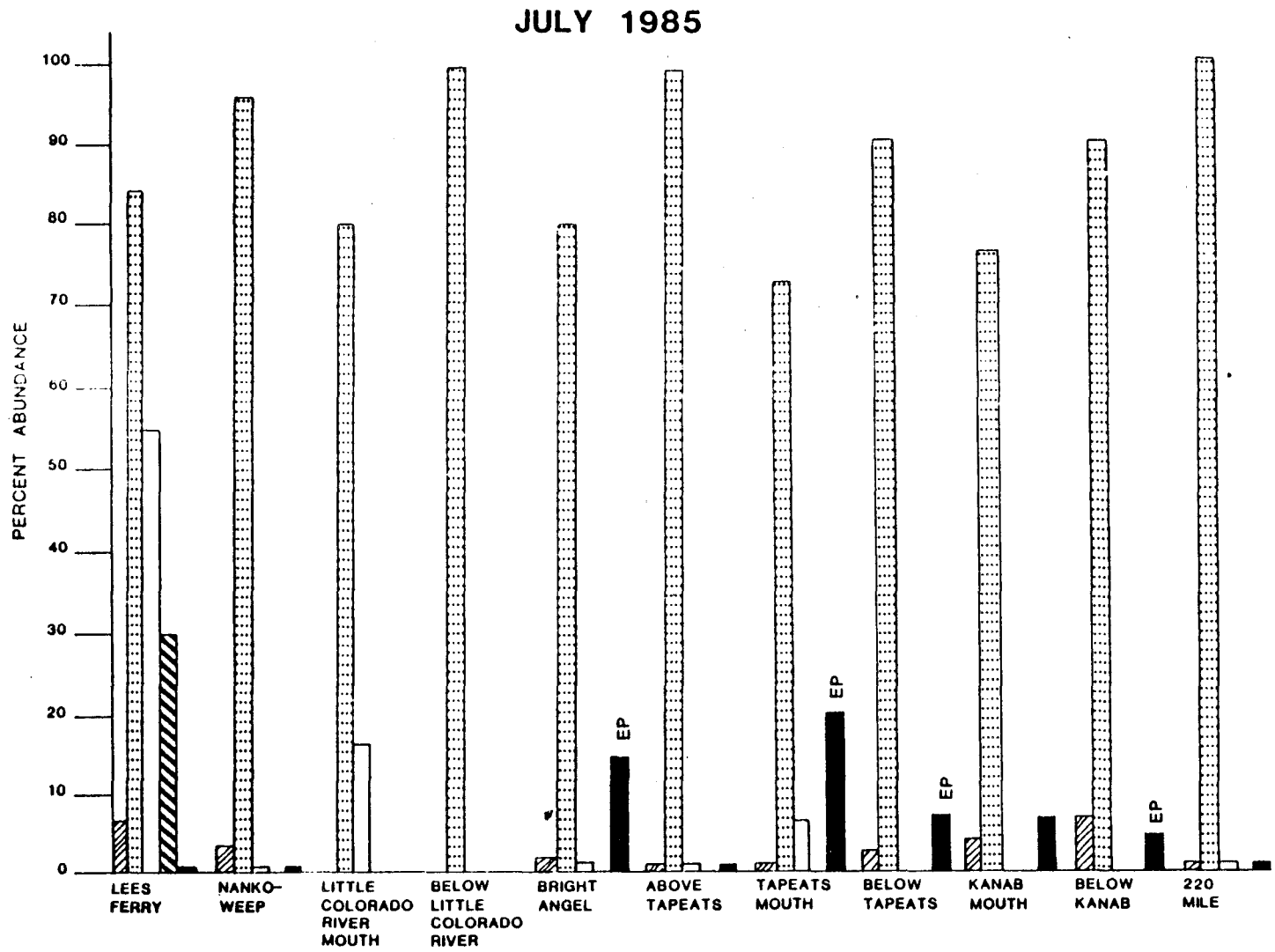


FIGURE 15. Percent relative abundance for macroinvertebrates collected at selected sites in the Colorado River through Grand Canyon National Park during July, 1985. ▨ = Gammarus lacustris, ▥ = Chironomidae, □ = oligochaetes, ▨ = Gastropoda, ■ = other dominant taxa (EP = Ephemeroptera). N = 5 samples for each site.

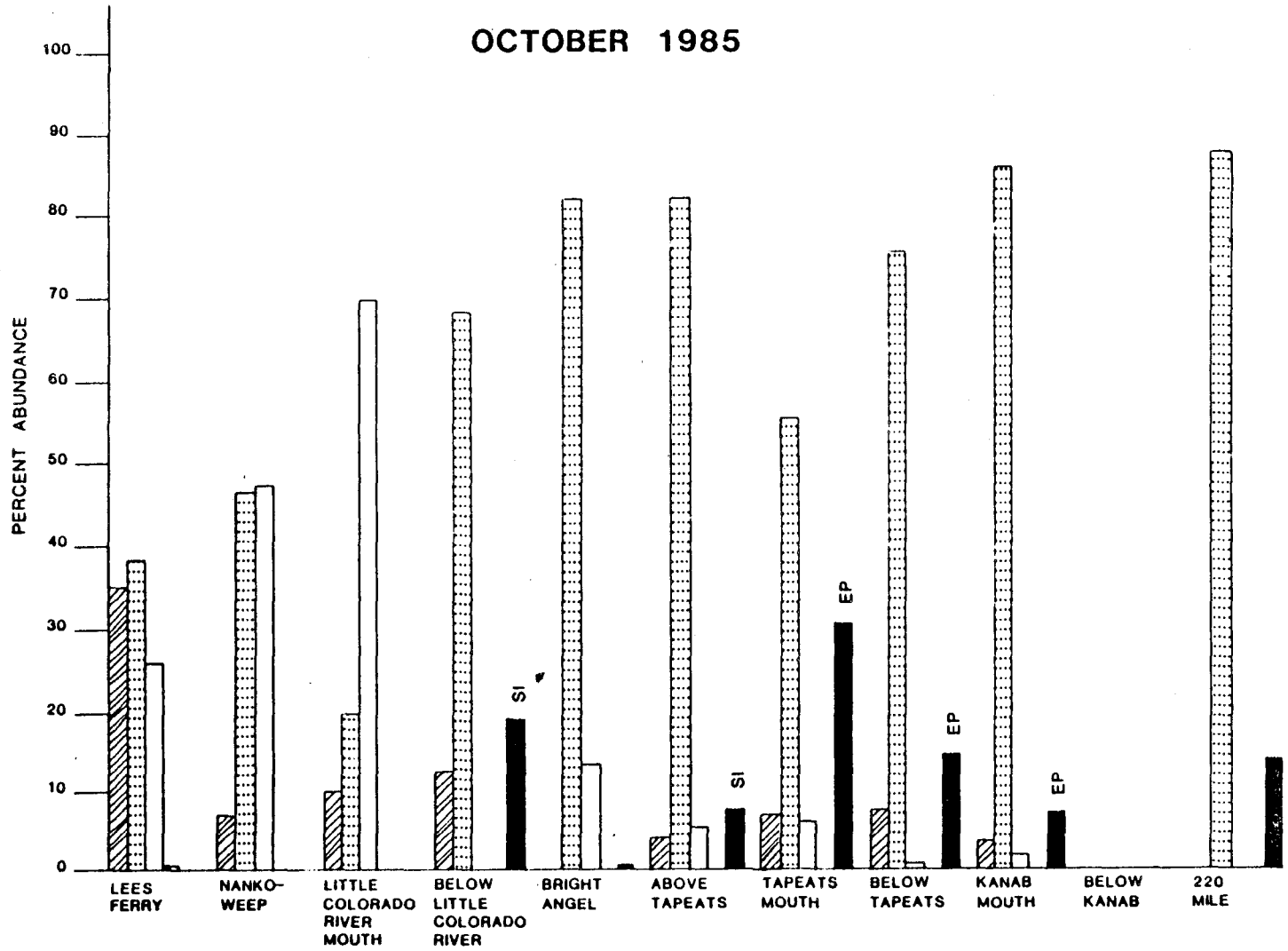


FIGURE 16. Percent relative abundance for macroinvertebrates collected at selected sites in the Colorado River through Grand Canyon National Park during October, 1985. ▧ = Gammarus lacustris, ⬚ = Chironomidae, ⬚ = oligochaetes, ▨ = Gastropoda, ■ = other dominant taxa (EP = Ephemeroptera, SI = Simuliidae). N = 5 samples for each site.

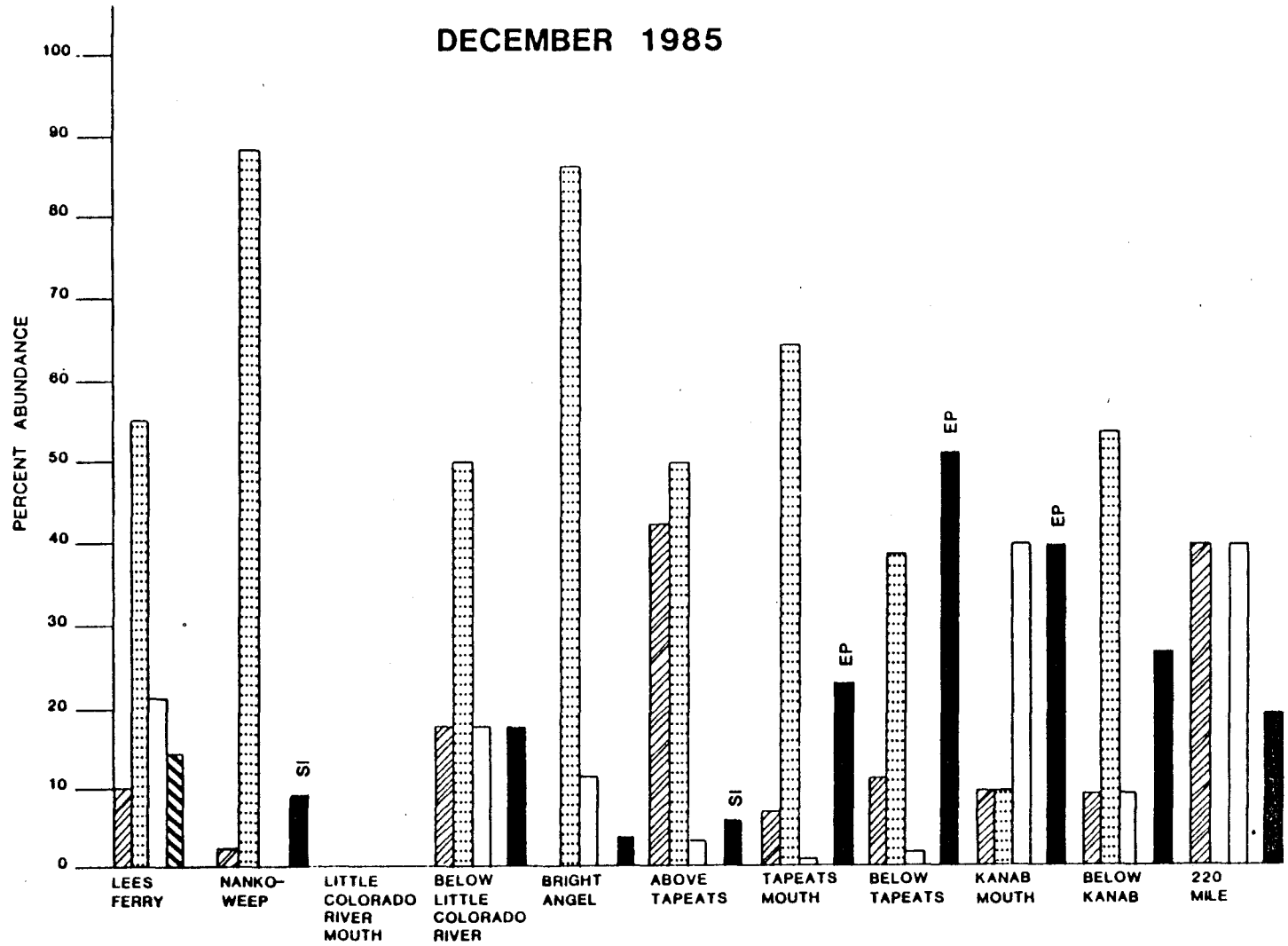


FIGURE 17. Percent relative abundance for macroinvertebrates collected at selected sites in the Colorado River through Grand Canyon National Park during December 1985. ▨ = Gammarus lacustris, ▦ = Chironomidae, □ = oligochaetes, ▨ = Gastropoda, ■ = Other dominant taxa (EP = Ephemeroptera, SI = Simuliidae). N = 5 samples for each site.

TABLE 8. Invertebrate standing crop and *Cladophora glomerata* biomass sampled in Cell II and Cell III at the Nankoweep site. (Cell II subjected to exposure for 7-12 hours daily, Cell III rarely exposed. Standard deviations in parenthesis.)

OCTOBER 1985		
TAXA	CELL II (n=2)	CELL III (n=5)
Total Organisms	772 (529)	2517 (284)
Gammarus lacustris	99 (91)	189 (110)
Chironomid	673 (438)	1160 (210)
Oligochaeta	0	1158 (0)
Gastropoda	0	9 (21)
Cladophora glomerata	9.37 g/m^2	82.81 g/m^2

DECEMBER 1985		
	Cell II (n=4)	Cell III (n=5)
Total Organisms	44 (31)	992 (603)
Gammarus lacustris	3 (6)	19 (20)
Chironomid	12 (17)	884 (562)
Other	23 (19)	89 (55)
Cladophora glomerata	21.35 g/m^2	133.24 g/m^2

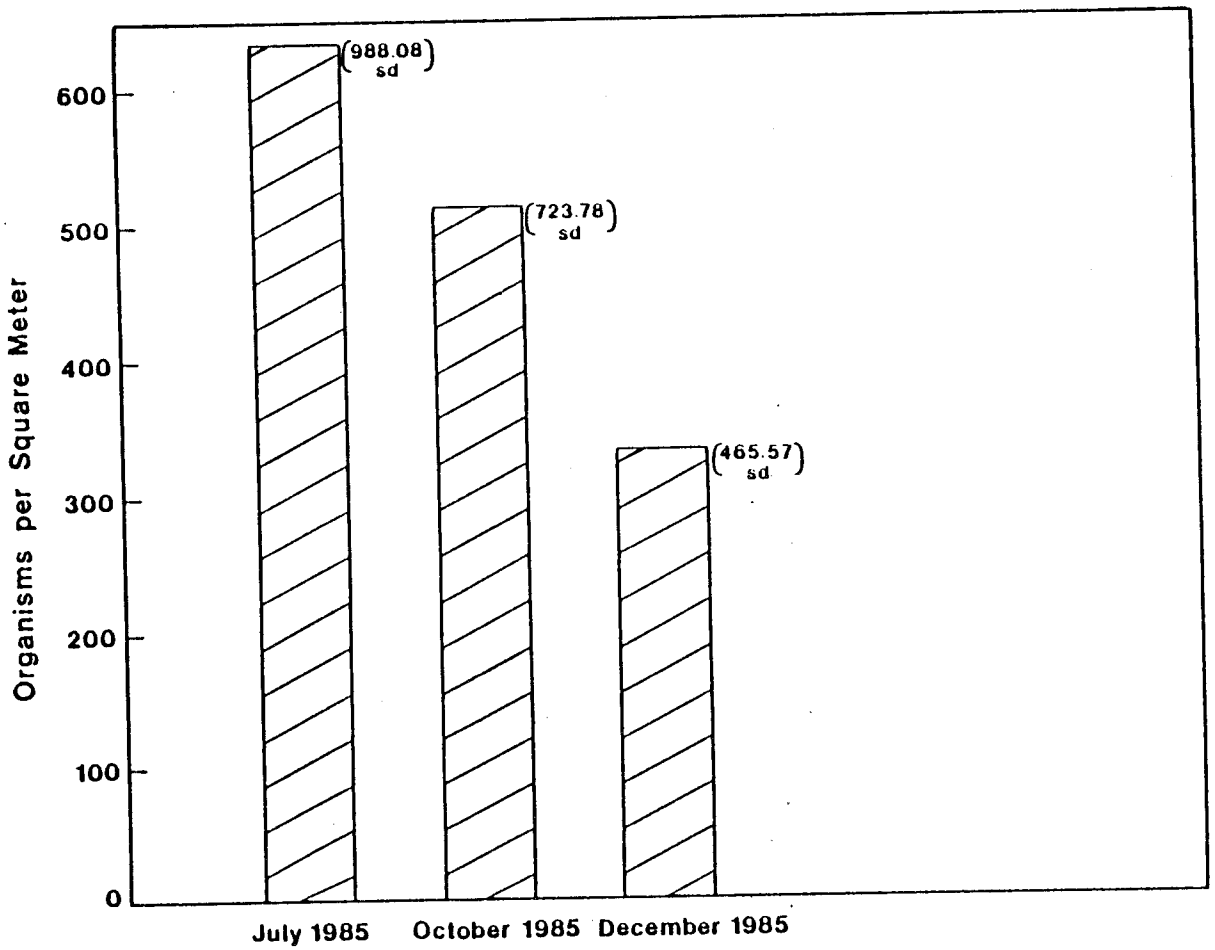


FIGURE 18. Total invertebrate density for all taxa collected from the Colorado River at all sites below Glen Canyon Dam, Arizona. July collections represent steady flows, October collections represent 2 weeks of fluctuating flows and December collections were after 3 months of fluctuating flows. Standard deviations are shown in parentheses at top of histograms.

TABLE 9. Invertebrate standing crop for all sites in the Colorado River below Glen Canyon Dam, Arizona during July, October and December 1985. (Organisms per square meter with standard deviations in parenthesis.)

TAXA	JULY	OCTOBER	DECEMBER
Total Organisms	660 (988)	508 (724)	333 (466)
Gammarus lacustris	23 (50)	54 (142)	52 (146)
Chironomid	594 (915)	300 (377)	203 (339)
Gastropoda	6 (33)	1 (6)	7 (28)
Oligochaeta	14 (46)	124 (323)	24 (75)
Other	21 (48)	26 (68)	47 (99)

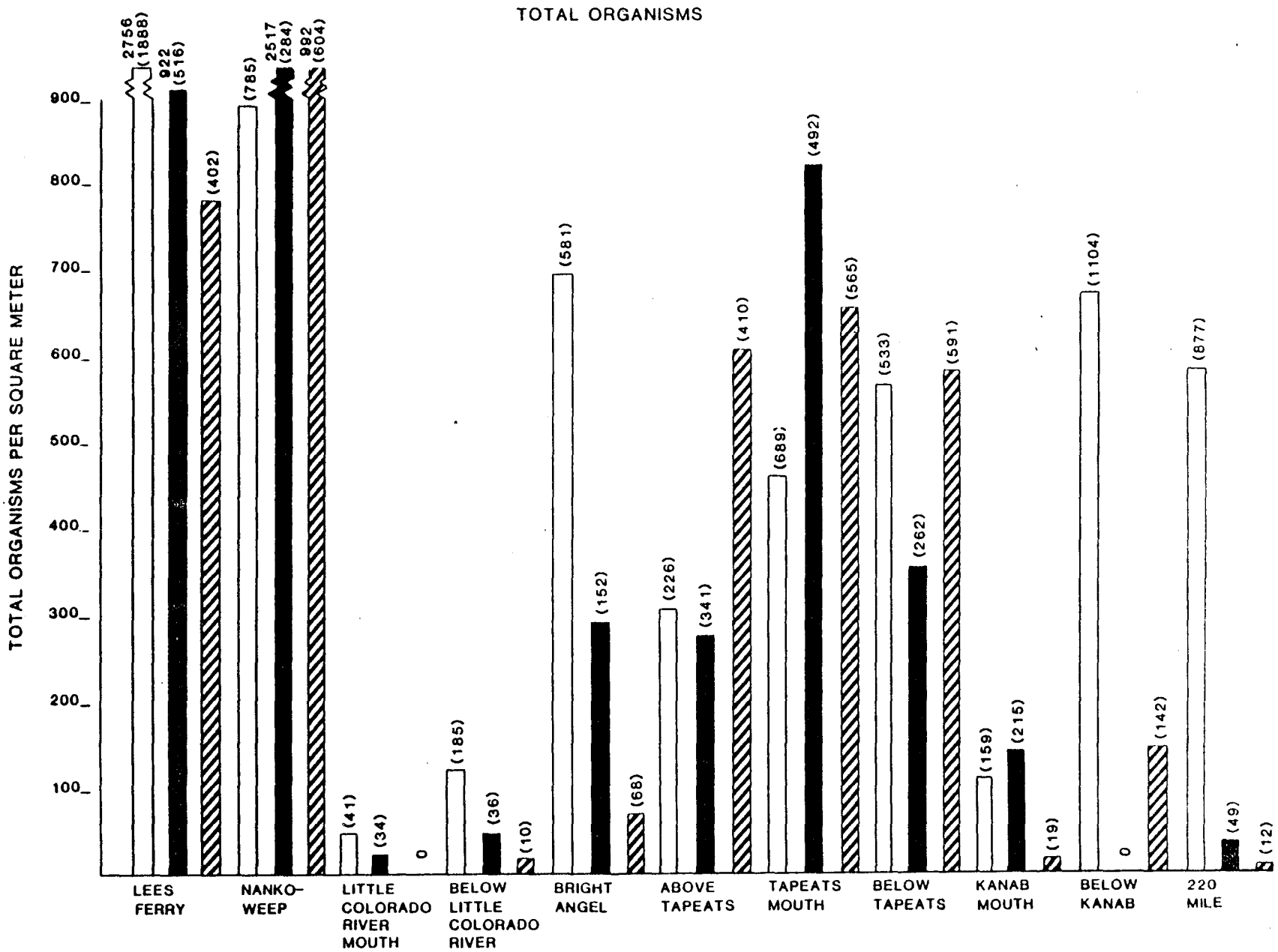


FIGURE 19. Density of all invertebrates collected at selected sites in the Colorado River in Grand Canyon National Park during July, October, and December 1985. (White histograms = July, black histograms = October, hatched histograms = December).

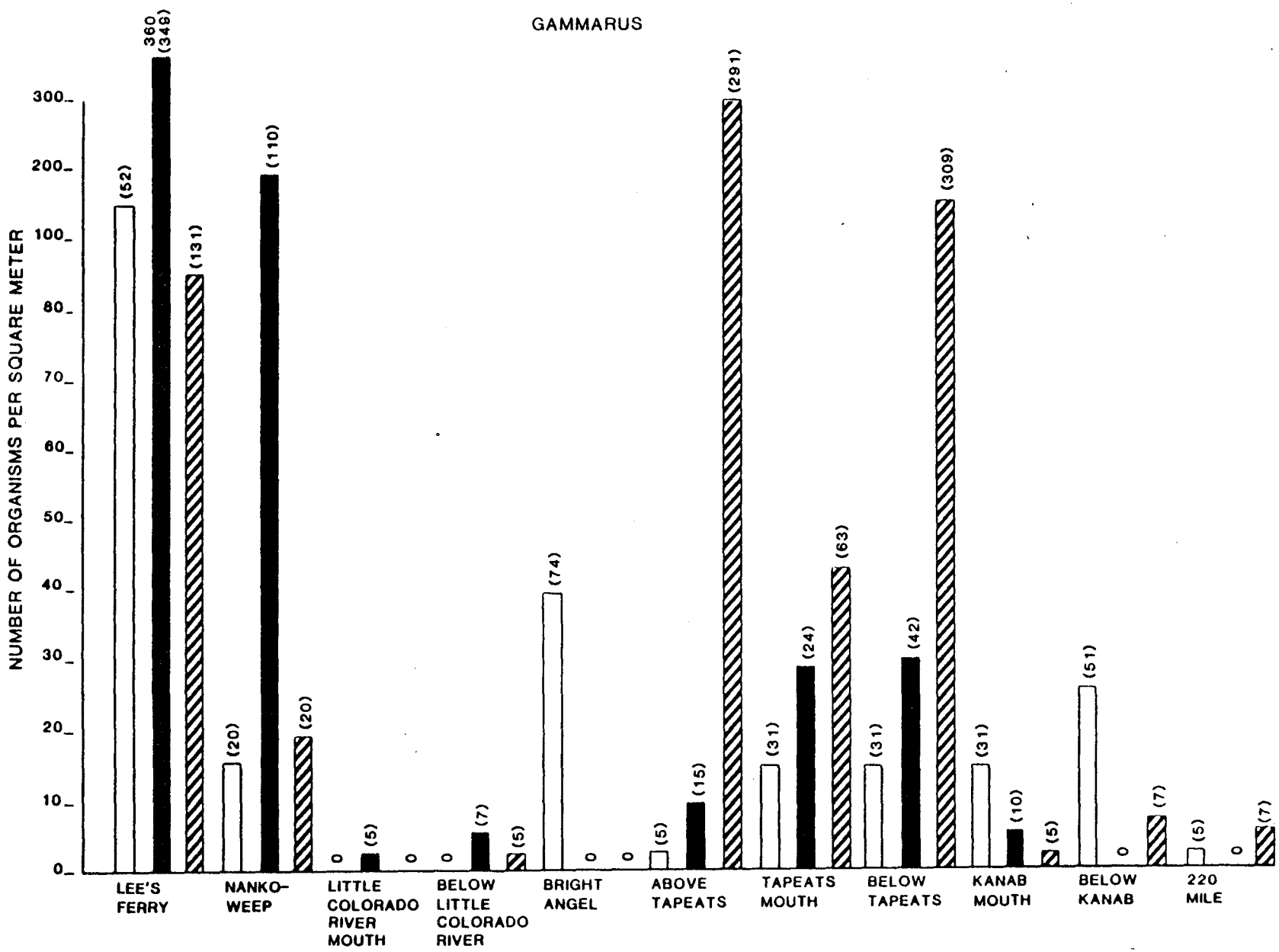


FIGURE 20. Density of Gammarus lacustris collected at selected sites in the Colorado River in Grand Canyon National Park during July, October, and December 1985. (White histograms = July, black histograms = October, hatched histograms = December).

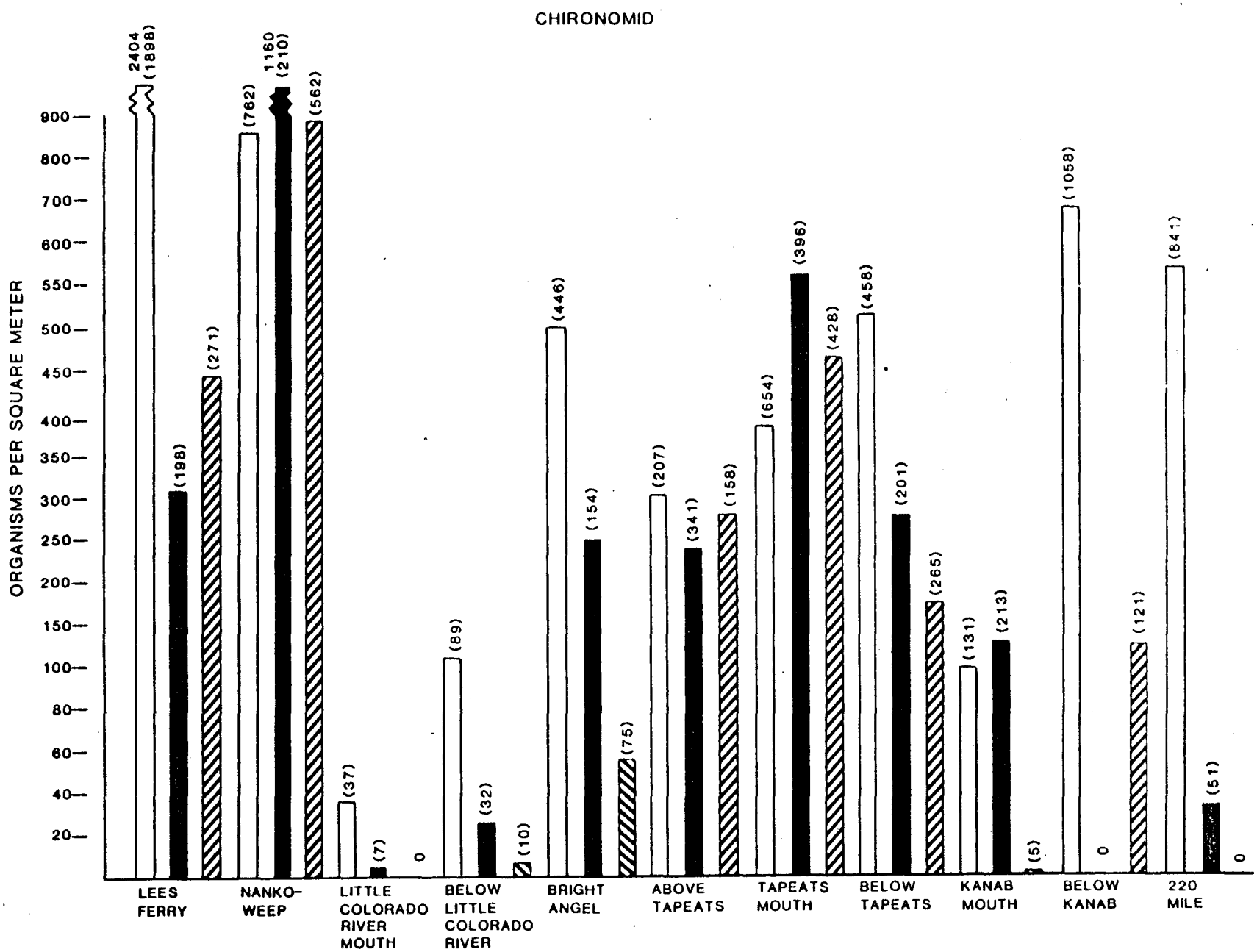


FIGURE 21. Density of chironomids collected at selected sites in the Colorado River in Grand Canyon National Park during July, October, and December 1985. (White histograms = July, black histograms = October, hatched histograms = December).

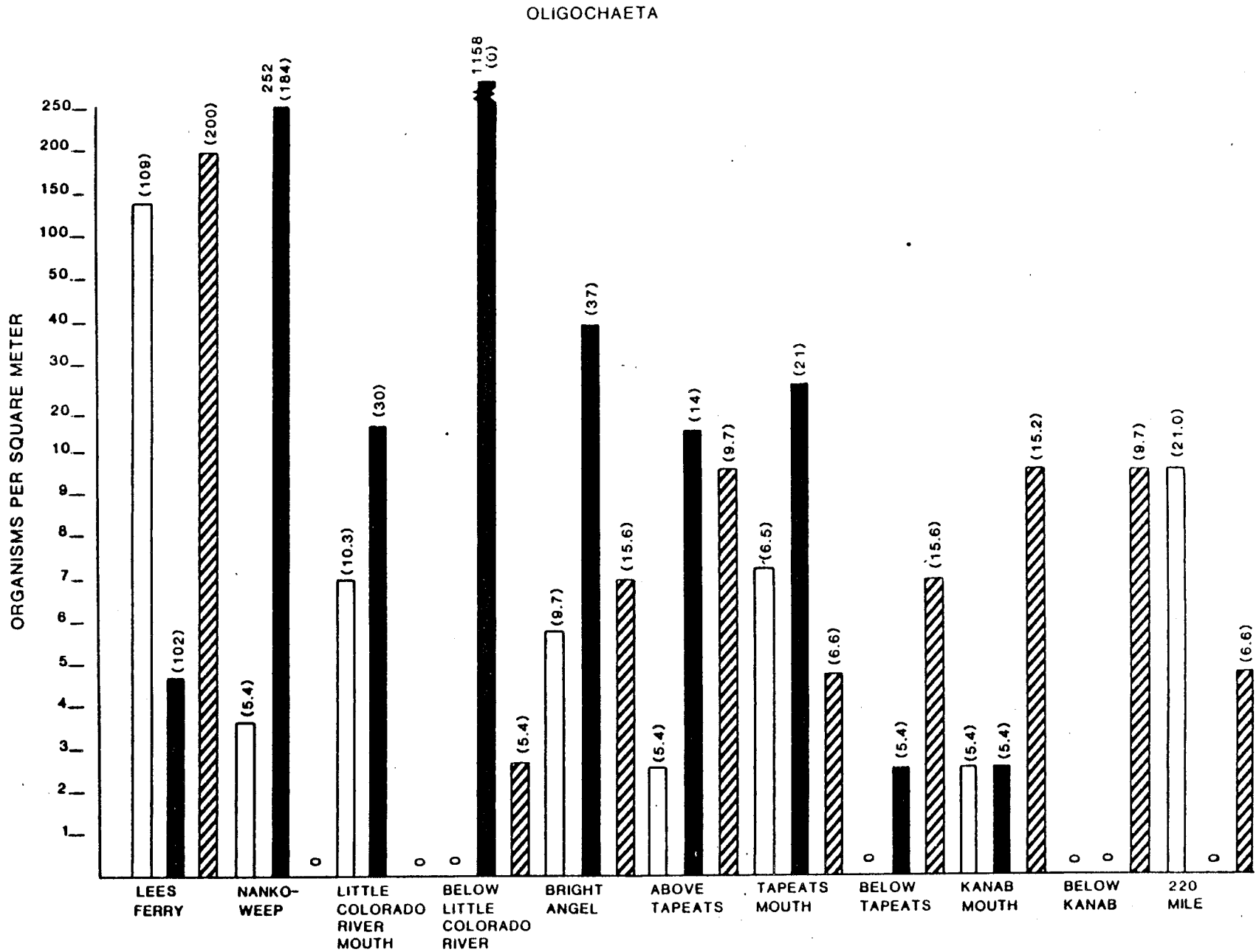


FIGURE 22. Density of oligochaetes collected at selected sites in the Colorado River in Grand Canyon National Park during July, October, and December 1985. (White histograms = July, black histograms = October, hatched histograms = December).

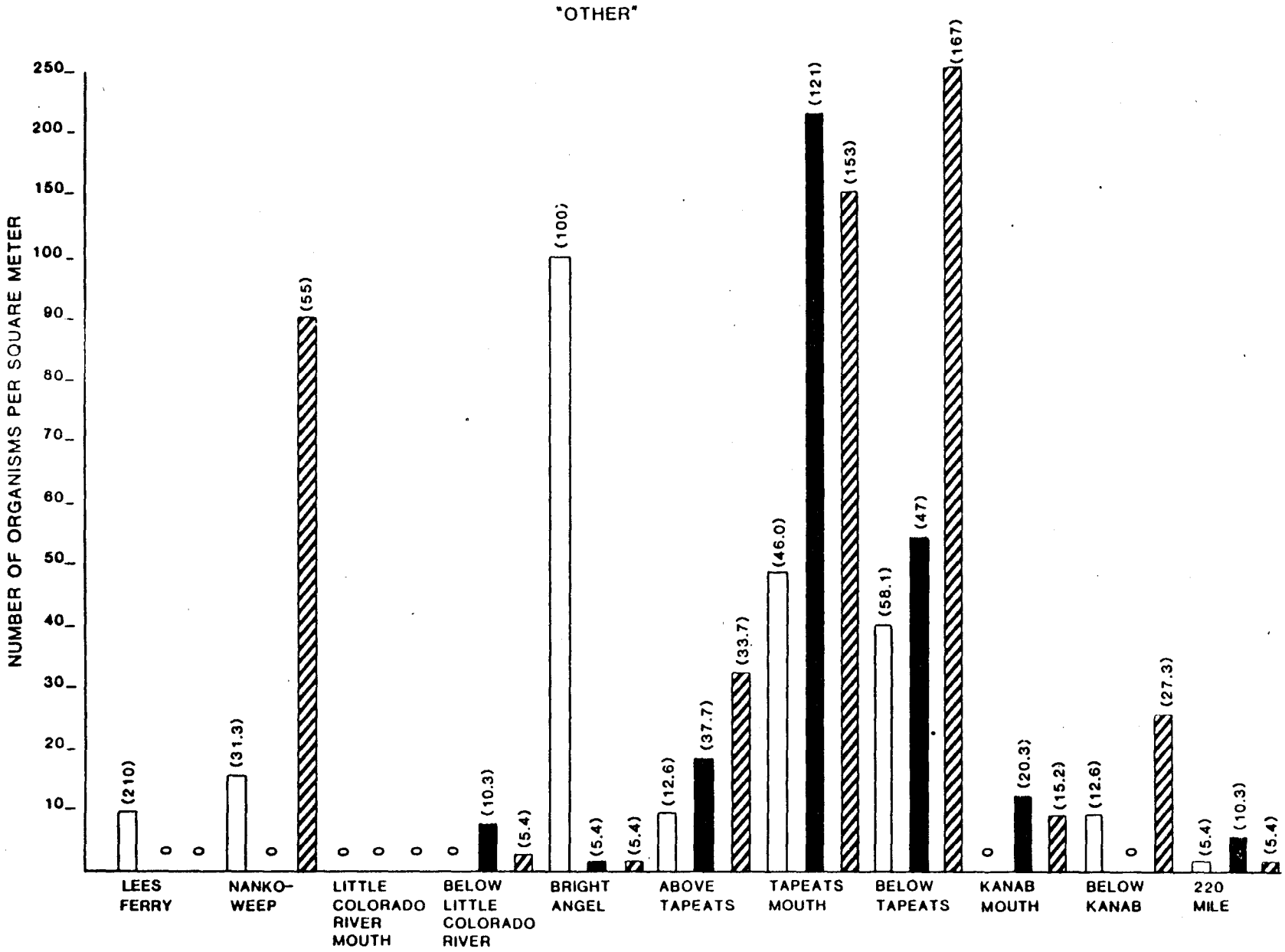


FIGURE 23. Density of "other" invertebrates (Ephemeroptera, Simuliidae, Plecoptera, Trichoptera) collected at selected sites in the Colorado River in Grand Canyon National Park during July, October, and December 1985. (White histograms = July, black histograms = October, hatched histograms = December)

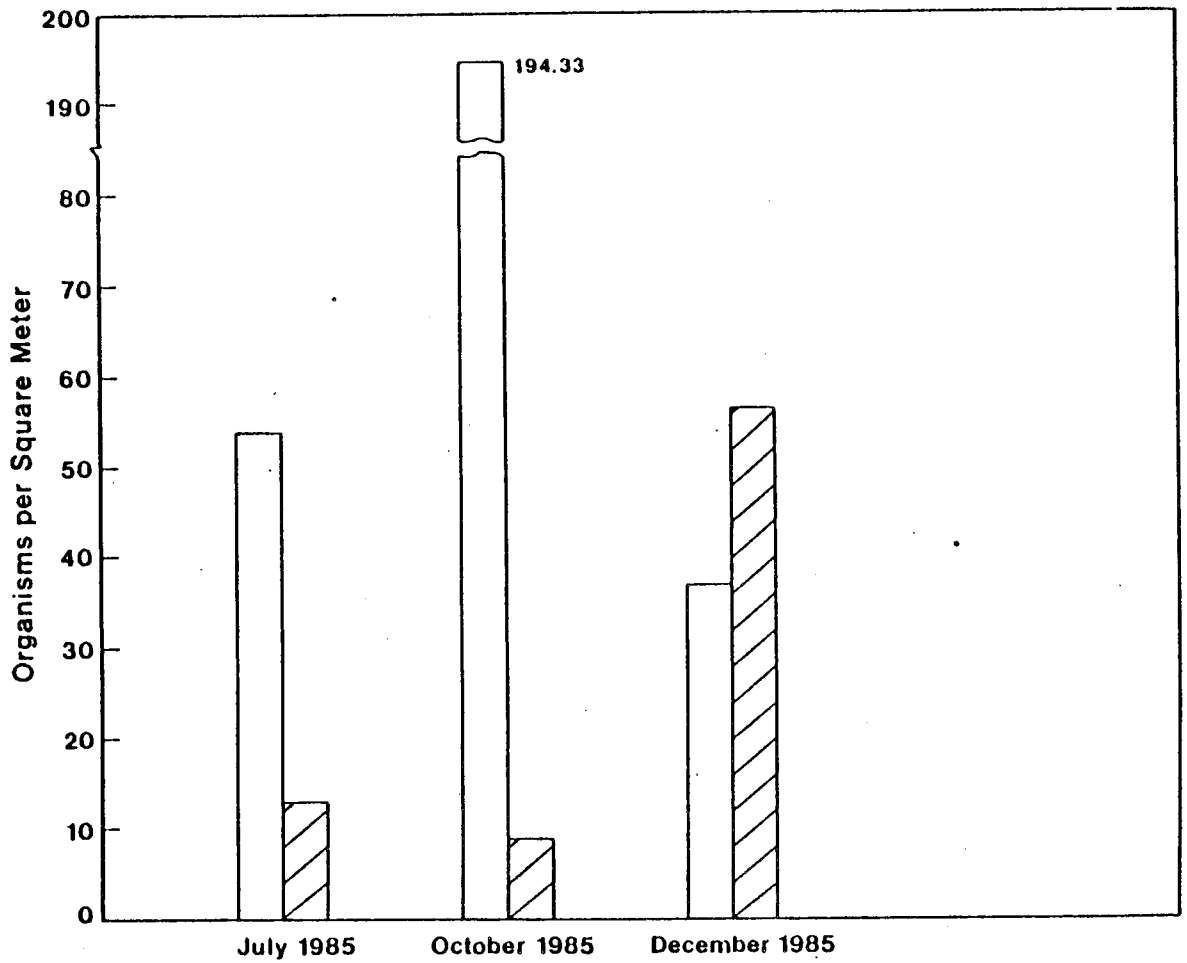


FIGURE 24. Combined density of Gammarus lacustris at all sites in the Colorado River in Grand Canyon National Park during July, October, and December 1985 collection periods. Open histograms represent density for all sites above the Little Colorado River and hatched histograms represent density for all sites below the Little Colorado River.

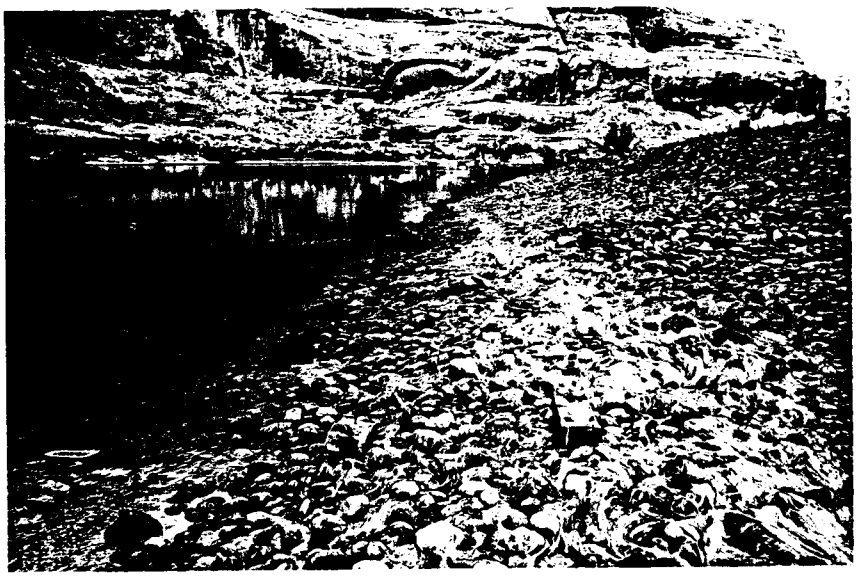


Plate 1. Effect of fluctuating discharges along the margins of the Colorado River below Glen Canyon Dam. (Note bleached Cladophora tufts. This zone corresponds to Cell II).

CLADOPHORA-GAMMARUS CORRELATION

The relationship between the amphipod, Gammarus lacustris, and the filamentous, green alga, Cladophora glomerata was determined using correlation analysis for four different seasons. Significant positive correlations were determined for July 1985 ($r=.51$, $P<0.05$, $n=13$; Figure 25) and October 1985 ($r=.92$, $P<0.01$, $n=20$; Figure 26) between Gammarus density (numbers per square meter) and Cladophora biomass (grams per square meter). Collections sampled in January and March 1986 had no significant correlation between Gammarus and Cladophora. Only during the October 1985 sample did Gammarus biomass (grams per square meter) show a significant positive correlation ($r=.73$, $P<0.01$, $n=20$) with Cladophora biomass. Pooled data for all four months had a significant positive correlation ($r=.84$, $P<0.01$, $n=73$; Figure 27) for Gammarus density and Cladophora biomass.

Density and biomass of Gammarus lacustris and Cladophora biomass changed substantially from July to October 1985 (Table 10). Gammarus density and biomass increased with the onset of fluctuating flows in October 1985, while Cladophora biomass decreased. Reductions in Gammarus density and biomass as well as Cladophora biomass occurred in January 1986. A further decline in biomass and density of amphipods continued in March 1986, with Cladophora biomass increasing during this period (Table 10).

Ratios of mature to juvenile Gammarus changed only slightly between collection periods. These ratios ranged from a low of 1:1.5 in March 1986 to a high of 1:3.3 in October 1985. These benthic collection ratios are generally lower than drift ratios (1:5 to 1:8.3 during fluctuating months) and may suggest that drift affects these proportions. Average weight of individuals was 26 times greater for mature amphipods than juveniles in July 1985. October, January and March individual weights averaged between five and seven times greater for mature amphipods.

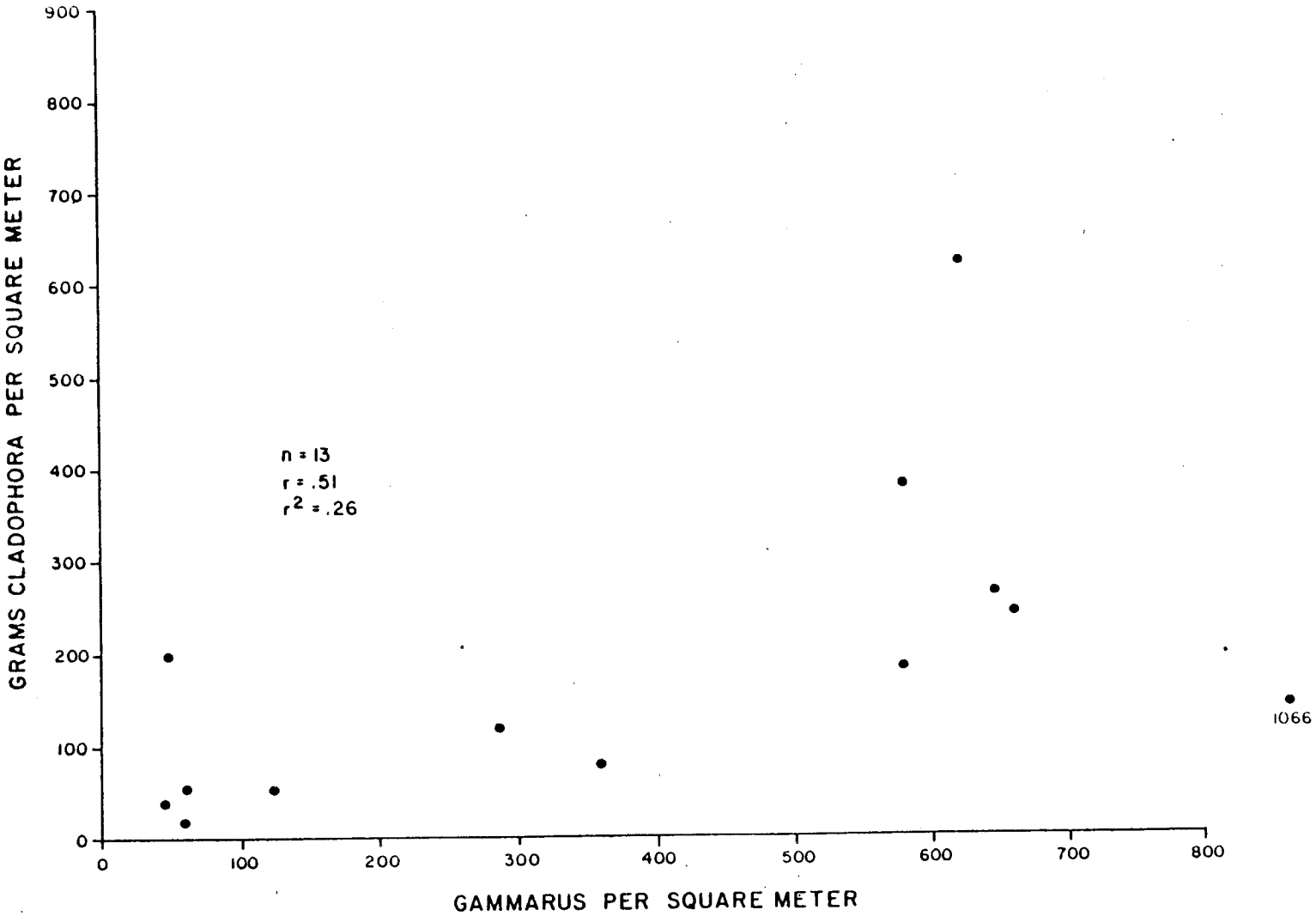


FIGURE 25. Correlation for Cladophora biomass and Gammarus standing crop for July 1985.

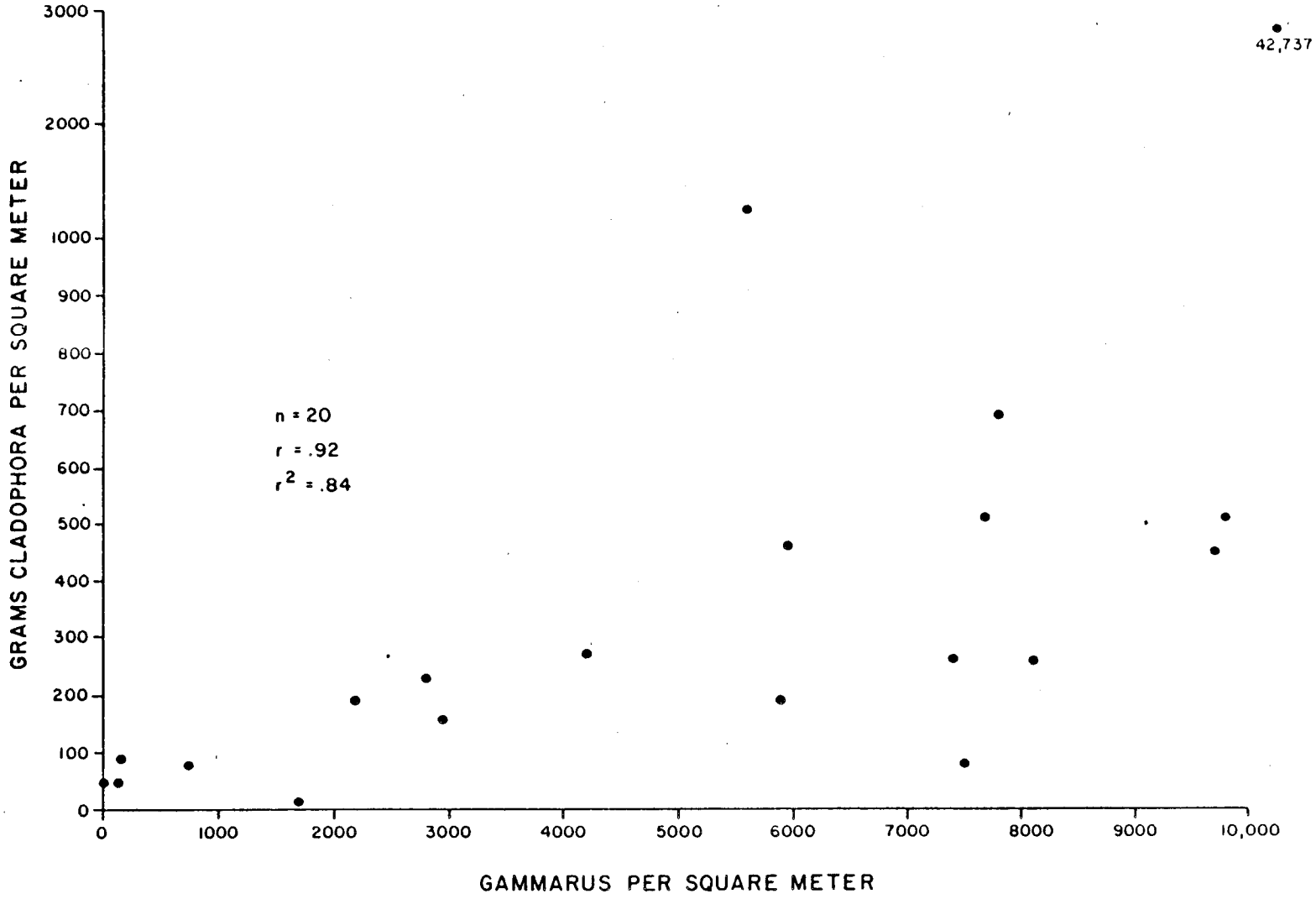


FIGURE 26. Correlation for Cladophora biomass and Gammarus standing crop for October 1985.

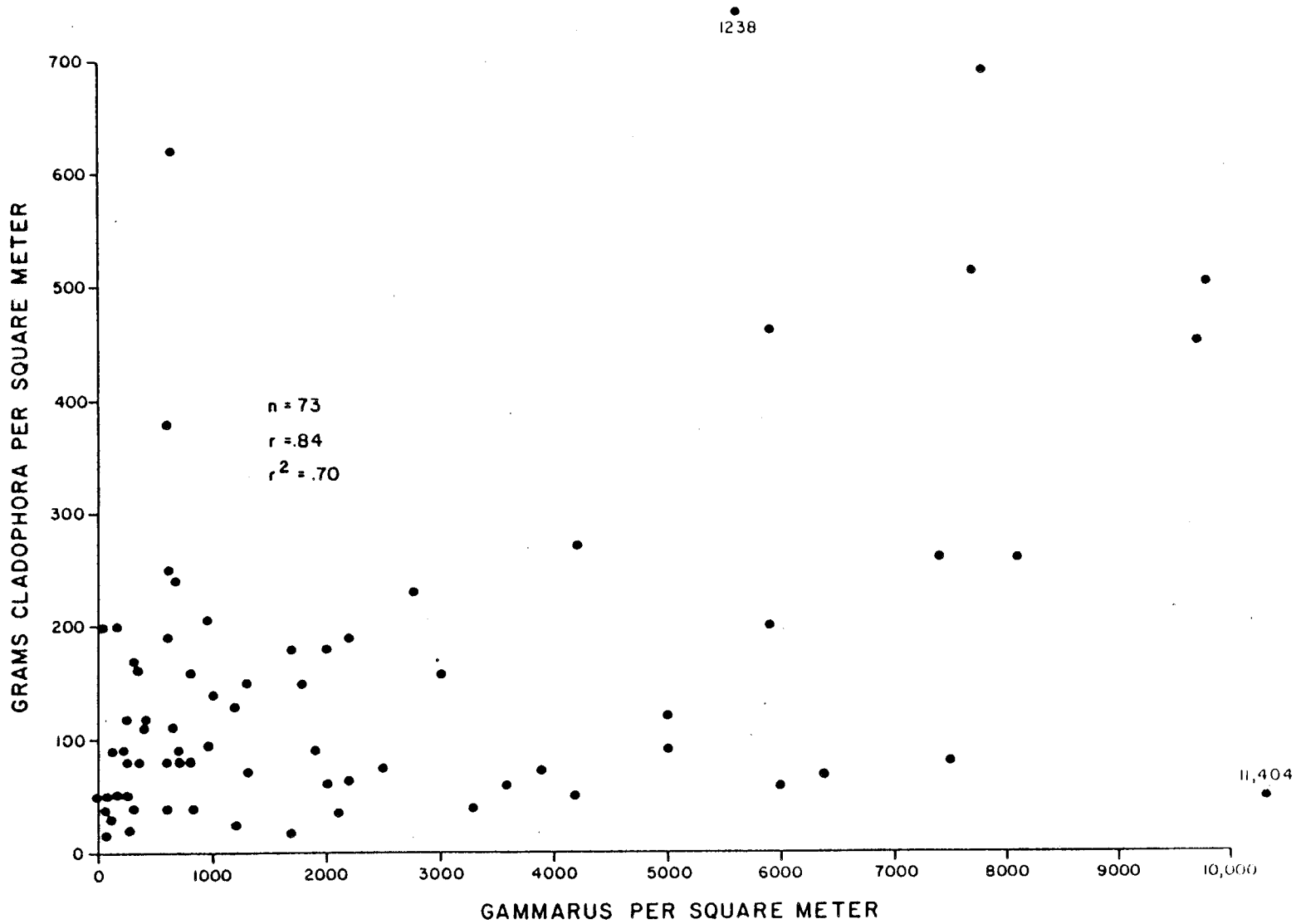


FIGURE 27. Correlation for Cladophora biomass and Gammarus standing crop for pooled data from July and October 1985 and January and March 1986.

TABLE 10. Mean density (animals per meter squared) and biomass (grams per meter squared) of *Gammarus lacustris* and *Cladophora glomerata* collected from depths greater than Cell III in the Colorado River 13.5 miles above Lees Ferry, Arizona.

	Gammarus Density (Biomass)	*Cladophora* Biomass
July 1985 (n=13)	393 animals/m^2 (1.19 grams/m^2)	1688.5 grams/m^2
October 1985 (n=20)	6653 animals/m^2 (4.40 gram/m^2)	427.1 grams/m^2
January 1986 (n=20)	3041 animals/m^2 (3.70 grams/m^2)	60.9 grams/m^2
March 1986 (n=20)	936 animals/m^2 (0.82 grams/m^2)	114.0 grams/m^2

CHAPTER FOUR: DISCUSSION

INVERTEBRATE DRIFT

Drift of invertebrates in natural streams is a common occurrence and has been well documented (Muller 1954, Waters 1961, 1964). Waters (1965a, 1972) classified drift into three catagories: catastrophic, behavioral and constant. In natural stream systems invertebrates are exposed to a myriad of chemical, physical and behavioral factors that can induce any combination of these types of drift. Factors like predation, density, light and flow reduction have been documented as causes for invertebrate drift (Waters 1965 a&b, Minshall and Winger 1968, Hughes 1970, Muller 1974 and Walton et al. 1977). Only recently has the effect of artificial flow increases and reductions on drifting organisms been addressed.

With the increasing demand for water resources in the western United States more rivers are becoming regulated by hydroelectric generating facilities. The effect of controlling the flow of these rivers has resulted in dramatic water level fluctuations that impact aquatic invertebrates. Increased invertebrate drift, stranding of organisms during drawdowns and decrease of near-shore densities have been documented (Brooker and Hemsworth 1978, Covich et al. 1978, Corrarino and Brusven 1983 and Matter et al. 1983).

In the Colorado River below Glen Canyon Dam the effect of regulated discharges on invertebrate drift has never been fully documented. It is possible that if invertebrate drift increases under fluctuating discharges this easily accessible food resource may allow for greater growth of fish species. The objectives of this study were to quantify the drift of aquatic invertebrates under steady and fluctuating flow regimes. The results indicate a significant positive relationship between amphipod drift and the rising arm of fluctuating flows. Gammarus drift increases as discharges increase. Our data suggest that it is the rising discharges and not the absolute flow that cause greater drift. Only during extreme periods of fluctuating discharges, 2,000 to 18,000 cfs, does drift of the amphipod, increase over levels found under more steady discharges. During the month of October 1985 fluctuations from Glen Canyon Dam ranged from 9,000 to 21,000 cfs but drift did not increase from levels found under steady conditions.

The importance of algae as a food source and refugium for aquatic invertebrates is well known (Hynes 1970, Minshall 1984). Once Gammarus are established in the thick Cladophora beds below Glen Canyon Dam, large standing crops may result. When these beds are exposed, the amphipods, being highly mobile, try to crawl towards the water (Personal observation, WCL). At this time they are extremely vulnerable and should the flow of the river increase quickly, large numbers of Gammarus would be forced into the drift. The rate of flow reductions and increases will

affect the numbers of drifting amphipods. If the decrease is slow the organisms will be able to reach the water before the rising current will take them into the drift. A fast decrease followed by a fast increase in flow may result in higher drift rates than a gradual fluctuation.

Mean chironomid drift had no significant change from steady to fluctuating discharge periods although drift density was significantly different between months. The increased standing crop during the warmer months and increased flow fluctuations in November may have contributed to these differences. For the months of fluctuating flows and some steady flow months there is an observed trend between chironomid and Cladophora drift. As more Cladophora is observed during the rising flows, more chironomids are also present. This could be the result of the lack of mobility of larval chironomids that are trapped within the Cladophora filaments as it is torn from the substrate and put into the drift.

Proportions of drifting mature to juvenile Gammarus decreased from steady to fluctuating flow periods. This may be a seasonal life cycle pattern (Hynes and Harper 1972) or possibly a behavioral response that may result from stronger mature forms withstanding current stresses or forcing smaller juveniles to occupy habitats that may be less protected. Size ratios from benthic samples in Objective Three are more similar to ratios from months of steady discharges. This may suggest a constant or behavioral drift occurring during steady flow periods that would have the similar percentages of mature to juvenile amphipods in the drift as in the benthos.

The extent to which Colorado River fishes utilize drifting invertebrates is poorly known. Given that there seems to be a size difference in Gammarus from benthic samples and Gammarus from drift samples taken during fluctuating flow periods, analyzing fish stomachs for these size differences may give an indication of fish preference for benthic or drifting organisms.

Due to the short duration of fluctuating discharges for this study, drift data for November and December should only be taken as short term affects. Longer periods of fluctuating flows should be studied to determine if a net loss of invertebrate standing crop will occur with continuous fluctuations. Drift studies by Iversen and Jessen (1977) indicate a significant net loss of invertebrates downstream. Walburg et al.(1983) reported that benthic production more than compensated for catastrophic drift resulting from discharge fluctuations in a southeastern U.S. river. It is possible that benthic production in the Colorado River below Glen Canyon Dam may not compensate for downstream drift losses.

INVERTEBRATE DISTRIBUTION AND STANDING CROP

The distribution and standing crop of benthic macroinvertebrates in the Colorado River has been altered extensively by regulated flows from Glen Canyon Dam (Carothers and Minckley 1981). The hypolimnetic releases from Glen Canyon Dam produce clear and consistently cold (9-11 centigrade) releases. Pre-dam seasonal floods that scoured the river bottom are now regulated and replaced by daily fluctuations in response to energy needs. These fluctuations create an "intertidal" zone along the margins of the Colorado River below the Dam.

The lack of pre-dam scouring floods and new clear, cold discharges has allowed for dense growths of the filamentous green alga, Cladophora glomerata. It is in those areas of most productive algal growth that the highest standing crop of benthic invertebrates occur. The significant decrease in density of organisms below the confluence with the Little Colorado River parallels the significant decrease of Cladophora glomerata found by Usher et al. (1986). During December at the Above Tapeats and Below Tapeats sites, as well as in July at Below Kanab, Gammarus densities were high (Figure 19). This corresponds to increases in Cladophora biomass during these times (Usher et al. 1986). This trend is similar for total organisms collected at these sites. At sites that had limited algal production, LCR Mouth, Below LCR, Kanab Mouth, 220 Mile and Below Kanab during October and December, invertebrate standing crop was usually lower than sites with higher Cladophora biomass.

The decline in total organisms collected may be directly related to increased fluctuating flow patterns. Although only three collections were made for this study, the influence of seasonality could be concealed by the stronger effects of fluctuating flows. With the lack of seasonal temperature changes it is unlikely that invertebrate life cycle patterns would be as important in the mainstream Colorado River (Ward 1974, Ward and Stanford 1979, Ward 1976b). After three months of fluctuating flows Gammarus density decreased above the confluence of the Little Colorado River but increased at those sites below the confluence. It is possible that the fluctuating discharges during December allowed Cladophora to receive more light and yet did not lower algal biomass, therefore enhancing the habitat for these invertebrates.

Invertebrate standing crop in the "intertidal" zone created by fluctuating discharges was lower than substrates not dewatered. Though the sample size is small and limited to only the Nankoweep site, this trend should apply to the entire zone of fluctuation throughout the Colorado River. Kroeger (1973), Fisher and LaVoy (1972) and Trotsky and Gregory (1974) have shown that fluctuating flow patterns can destroy algal beds necessary for aquatic invertebrates and render them unsuitable even after rewetting. They also state that with longer exposure periods

only more tolerant organisms such as chironomids remain. Cladophora mats may provide short term protection from deccication for some organisms (Brusven et al. 1974).

CLADOPHORA-GAMMARUS CORRELATION

A significant correlation exists between density of Gammarus lacustris and biomass of Cladophora glomerata. These data support previous works that established the importance of vegetation for amphipod species (Pennak and Rosine 1976, Marchant 1981). Data from the months of July and October 1985 each have significant correlations between amphipod standing crop and Cladophora biomass. January and March 1986 data did not show this relationship. Since samples were made at depths of four to five.meters it is unlikely that Cladophora beds were exposed to ambient temperatures. It is possible, however that during the fluctuating flow period from October to January 15 these beds were exposed to greater light intensity as water depth above them decreased. Usher et al. (1986) showed a decline in Cladophora biomass in shallower depths of the Colorado River below Glen Canyon Dam. This correlation between Gammarus and Cladophora may only exist once a critical minimum biomass of algae is surpassed.

The dramatic increase in density of Gammarus lacustris during October 1985 may be attributed to a concentration of amphipods under decreased flows. Prior to this fluctuating flow period, available habitat (ie. Cladophora beds) for amphipods was much greater. As this available habitat decreased, Gammarus were forced to occupy a smaller area and their standing crop increased. The density of amphipods in March 1986 were more similar to those found under July steady flow conditions and may reflect "normal" densities. With the various flow regimes that occurred during this study it is difficult to determine whether changes in amphipod density were the result of natural seasonal life cycle patterns or the influence of discharge fluctuations from Glen Canyon Dam.

Fewer juvenile (< 7mm) Gammarus lacustris were observed in benthic grab samples than were observed in drift samples for the same sample periods. Gammarus frequently are found in streams with greater numbers of juveniles present (Hynes and Harper 1972). The proportion of mature to juvenile amphipods varies with seasonal reproductive cycles that are primarily controlled by temperature (Smith 1973) and light (de March 1982). These differences from benthic to drift samples may indicate that smaller Gammarus are more susceptible to drift induced by fluctuating discharges.

CHAPTER FIVE: CONCLUSIONS AND OPERATING CRITERIA

CONCLUSIONS

1) A significant relationship exists between *Gammarus* drift and increasing discharges. When flows increase more than 10,000 cfs at one time, there appears to be a threshold at which drift increases. Mean drift rates (number of organisms per hour) and drift densities (number of organism per 100 cubic feet of water) for *Gammarus lacustris* increased during periods of fluctuating discharges.

2) The most important factor regulating drift was the rising of discharges after periods of low flows. The rate at which discharges rose and fell and the duration of low flows are also important.

3) Standing crop of *Gammarus lacustris* in the Colorado River was significantly greater from Glen Canyon Dam to the confluence of the Little Colorado River than below the Little Colorado River.

4) Standing crop of benthic macroinvertebrates in the Colorado River below Glen Canyon Dam decreases significantly at sites below the confluence with the Little Colorado River.

5) Dramatic reductions in benthic macroinvertebrates were found in the zone of fluctuation along the margins of the Colorado River.

6) A significant positive correlation exists for pooled seasonal data between biomass of *Cladophora glomerata* and standing crop of *Gammarus lacustris*.

OPERATING CRITERIA

1) Extreme daily fluctuations from 5,000 to 25,000 cfs, with exposure periods of 12 hours or more should be avoided. Loss of algal substrate due to desiccation decreases available habitat for benthic macroinvertebrates, thereby reducing fish food base.

2) Glen Canyon Dam should be operated is such a manner as to approach a seasonal inflow-outflow system with minimal daily fluctuations. This operating criteria should prevent extreme discharge fluctuations and promote algal growth which is important for maintaining invertebrate productivity.

3) Results of the drift study indicate an increase in drifting *Gammarus* with rising discharge levels. However, the data is based on limited data and should not be considered conclusive. Additional long-term drift studies should be initiated to determine the impacts of fluctuating discharges over longer periods.

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