ZOOPLANKTON OF THE COLORADO RIVER: GLEN CANYON DAM TO DIAMOND CREEK

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ABSTRACT -- Zooplankton were sampled in the Colorado River and terminal portions of its major tributaries from Glen Canyon Dam to Diamond Creek between June 1980 and November 1985. Sixteen of the 33 species of crustaceans found in the river were true plankton; the remainder occasionally occurred as drift. Lake Powell appeared to be the source of most of the zooplankton below the dam. River zooplankton was dominated by copepods; cladocerans were always much less abundant except when spillway releases occurred. Abundance did not decrease significantly over the 241 miles (388 km) between the dam and Diamond Creek, although the percentage of organisms in poor condition increased with distance below the dam. Females carrying eggs, male copepods with internal spermatophores ready for extrusion, and naupliar stages were present in most samples, indicating the potential for active reproduction throughout the river. At high flows, exchange rates between the mainstream and potential refuges for zooplankton appeared to be high. At low flows, populations may be able to persist in terminal pools and backwaters.

In unregulated rivers, true plankton are found only in the lower reaches or for short distances below natural lakes (Ward and Stanford, 1983). With impoundment, reservoirs contribute lentic plankton to the river below the dam. Three factors regulate this contribution (Petts, 1984): 1) the retention time of waters in the reservoir, 2) the seasonal cycle of the lentic plankton, and 3) the nature of the discharge (e.g., depth of release intakes and the rate of discharge). Thus the plankton found in regulated rivers will be "composed of both true lentic plankton, derived from the reservoir, and plankton supplied by the bed, backwaters, and tributaries, of the river below the dam" (Petts, 1984). These factors result in each impoundment/regulated river reach being a unique system.

From the standpoint of zooplankton ecology, the Colorado River below Glen Canyon Dam is unique in other respects. Most of the river's tributaries, dry except during heavy summer rains, contribute little to its flow and would not be expected to supply zooplankton to the mainstem. The number and severity of the rapids along the course of the river to Lake Mead produce an environment ill-suited for plankton. Natural mortality, the filtering of plankton from the flow by the periphyton, especially the dense stands of *Cladophora glomerata* (Usher and Blinn, 1990), and predation by other invertebrates and fish, also suggest that zooplankton surviving discharge should persist only a short distance below the dam. Some results in the literature, however, suggest that areas of retarded flow (e.g., backeddies, terminal pools of tributaries) can serve as loci for endemic populations or as temporary refuges for populations persisting between flooding events (e.g., Shiel and Walker, 1984).

Glen Canyon Dam is a hypolimnial release reservoir with a mean water retention time of 1.23 years (Gloss et al., 1980). Water for the generators is drawn from 4.6 m diameter penstock intakes centered at the 1058 m level (a full pool depth of 70 m). This depth is well below the euphotic zone and mixed layer under most conditions. Other release modes are from the jet tube intakes (about 30 m below the penstocks) and the spillways (surface to about 5 m). Sollberger et al. (1989) found that most of the zooplankton in Lake Powell occur in the upper 10 to 20 m during all seasons, and show little or no diel vertical migration (DVM). This epilimnetic fauna would be particularly susceptible to loss from the lake by spillway discharge. A small fraction of the plankton occurs as deep as 70-100 m, however, and would be continually lost through penstock releases. The amount of this loss will be strongly affected by the lake level, as well as the discharge magnitude, which affects both the withdrawal pattern from the lake (Merritt and Johnson, 1977) and the survival of the plankton in the tailwater and below through interactions of river flow with refuges, severity of rapids, and the frequency and structure of backeddies.

I report here on the distribution and abundance of crustacean zooplankton in the Colorado River from below Glen Canyon Dam to Diamond Creek 241 miles (388 km) below the dam). The research was done before and during the first phase of the GCES (Glen Canyon Environmental Studies; National Research Council, 1987; 1991), a program designed to evaluate the impact on the Grand Canyon ecosystem of fluctuating flows of the Colorado River caused by varying release rates from the dam to meet power demands. The only other study I know of dealing with the zooplankton of this part of the Colorado River (Cole and Kubly, 1976) did not report quantitative data, mainstream sampling locations, or dates of collections.

MATERIALS AND METHODS -- Samples were collected on the dates and between the river miles listed in Table 1. Plankton nets of several diameters and net mesh sizes (Table 1) were deployed using various techniques. River main channel and backeddy samples were taken from boats using surface or repetitive oblique tows; depth control was difficult, so depth of sampling was uncertain and is not reported here. Some collections were made in shallow water from the river bank. Tributary pool collections (e.g., at Kanab Creek and the Little Colorado River) were made by casting and retrieving the net across the pools. A flow meter was used whenever possible to derive volume of water filtered. During heavy sediment load conditions, the flow meter sometimes jammed; this and occasional times when tow/flow conditions were less than the flow meter threshold resulted in an underestimation of volume filtered. Some volumes were calculated from stream flow velocity and the length of time the net was in the water or from the length of tow alone. Some samples were non-quantitative and were used for relative abundance estimates only.

Entire or aliquoted samples were counted under a dissecting microscope. When sediments formed a large fraction of the sample volume, organisms and detritus were elutriated from the sediment and collected in a 102 µm mesh funnel. Adult crustaceans were identified to species whenever possible using Pennak (1978) and Ward and Whipple (1959). Confirmation of identification and updating of taxonomic names used Balcer et al. (1984) and Robertson and Gannon (1981). All copepod nauplii were enumerated as one category in samples collected with 80 µm mesh nets (Table 1). Immature (copepodid) stages of calanoid, cyclopoid, and harpacticoid copepods were counted separately. The number of egg-bearing female copepods were counted, as was the numbers of males with visible internal spermatophores. Copepods in poor condition (parasitized by fungus or protists; internal body structures partially or completely lacking; damaged due to decay) were counted. Cladocerans in poor condition were not enumerated because of difficulties in distinguishing between "natural" deterioration and damage caused by collection, preservation, and analysis.

Because of the diversity in sampling gear and methods used, the restricted number of collection sites and samples taken, and the inherent high variability of planktonic systems, no extensive statistical analysis of the data was undertaken. The data on which this report is based are available in the appendices of Haury (1986).

RESULTS -- Taxonomic Composition - Table 2 summarizes the species of crustaceans known or expected to be present in the plankton of the Colorado River below Glen Canyon Dam. Figure 1 presents the data on taxonomic composition from four series of samples expressed as percentages of total abundance for each of three broad taxa. In terms of individual species, dominant among the calanoids were *Skistodiaptomus pallidus* and *Leptodiaptomus ashlandi*; *Diacyclops thomasi* was always dominant among the cyclopoids, and *Daphnia galeata* among the cladocerans.

In general, calanoid copepods occurred in the highest percentage in all samples except the November 1985 collections, when cyclopoids were dominant in 12 of the 14 samples. Cladocerans were always the least abundant of the taxa except during the summer of 1980. The samples taken then appear to be related to the times of spillway releases.

No relationship between distance down river and proportions of taxa is apparent in the data. Selective removal of taxa has been shown in certain systems (Petts, 1984), with body characteristics (size, shape, and strength) and swimming ability being the critical factors; the data reported here do not show these effects.

Abundance - In none of the individual sample sets is there any clear evidence of a decrease in abundance of any taxonomic category or species with distance down river below Glen Canyon Dam. Figure 2 summarizes this result by plotting total abundance from all collections as a function of river mile.

The greatest flow variations during any sampling period occurred in June 1980 (Figure 3a) when spillways were tested for the first time after the filling of Lake Powell. Figure 3b shows the abundances of the three important taxonomic categories as a function of river mile, which approximates a time series equivalent to the discharge figure. Except for the high abundances of copepods at Mile 64 (Km 103), the high numbers from Mile 144 (Km 232) and beyond are concordant with the high releases following 23 June. With all other factors constant, an increase in discharge should not change the abundance of plankton in terms of density (numbers per unit volume of water); increases in density can occur only through release of waters with a higher density of organisms. This probably occurred with the spillway releases which removed water from the surface layers containing the highest abundances (Stone and Rathbun, 1968; 1969; Sollberger et al., 1989).

Condition - The same factors which suggest that abundance should decrease markedly with distance down river from the dam would also be expected to have an effect on the condition of the organisms captured. While no decrease in abundance was apparent (see above), there was a significant ($p < 0.01$) increase in numbers in poor condition with river mile. As much as 25% of total copepod numbers near Diamond Creek were in poor condition (see Methods for definition).

Endemic and refuge populations - Terminal pools and backeddies are locations where populations of zooplankton could persist, either as quasi-permanent endemics or as refuge populations that gradually decline between recharging of zooplankton from flood events. Table 3 presents the June 1980 comparative abundance data from a) a mainstem bypass channel and the isolated terminal pool at Kanab Creek (Mile 144 [Km 231]); and b) the mainstem and a sheltered (by a sand bar) backeddy at National Canyon (Mile 166 [Km 268]). The exchange rate appears to be high, at least under the release conditions preceding and during sampling (>40,000 ft^3s^{-1} [1,135 m^3 s^{-1}]). This inference is also supported by the agreement in percent of animals in poor condition between the mainstream and possible refuges (not shown).

Reproduction - Egg-bearing female copepods and males with spermatophores ready for extrusion were found throughout the river below the dam on all sampling occasions. The percent of egg-bearing females decreased slightly with distance down river.

Most samples from all distances along the river had relatively high percentages of naupliar stages making up the combined copepod fraction. The average percent of nauplii in all data combined was 33.3% (n=28, sd=20.8, range 0 - 86%). This indicates the importance of survival of these stages from Lake Powell, the possible hatching of eggs from river populations, or losses from endemic or refuge populations. Reproduction occurs throughout the year in Lake Powell in most of the numerically important species, with a minimum of activity in the winter (Sollberger et al., 1989; Haury, unpub. data), so nauplii and reproductively active adult zooplankton could be released to the river any time during the year.

The fraction of mainstream reproductive activity due to Lake Powell-discharged plankton or to endemic or refuge populations in the river is not known. The June 1980 collections provided the only samples where direct comparisons between main channel and potential refuges (backeddies, terminal pools) could be made. There was remarkable agreement between the percent of egg-carrying female copepods in the mainstream and three refuges (mouth of Kanab Creek, National Rapids camp, and Mile 222 Canyon).

Zooplankton and fish - Some data suggest that selective mortality, presumably predation by fish, can alter the relative abundance and size of taxa categories in some parts of the river. Table 3 data shows that there are reduced numbers of cladocerans in the refuges relative to the mainstem; these cladocerans were also of much smaller size than in the mainstem (not shown). This indicates that size-selective predation due to fish may be the cause.

DISCUSSION -- Lake Powell appears to be the source of much of the plankton found in the mainstream of the Colorado River. All the planktonic species listed in Table 2 have been found in the plankton of Lake Powell. The species most important in the river (*S. pallidus*, *L. ashlandi*; *D. thomasi*, *D. galeata*) were usually numerically important as well in Lake Powell (Haury, unpub. data). The one occasion when cladocerans dominated the river plankton was during spillway release. Their dominance would be expected, since cladocerans occur in the greatest abundance near the surface (upper 10-20 m) (Sollberger et al., 1989) and would be most susceptible to release by the spillways.

The data cannot demonstrate whether or not refuge or endemic populations persist for significant periods in the river ecosystem (presumably terminal pools, backeddies, marshes). High releases appear to effectively reduce the residence time of water (and organisms not able to counter the flow) to a point where no difference in copepod community structure can be detected. At lower flows, barriers to exchange (e.g., sand bars, boulder fields) or longer residence times in backeddies may permit persistent populations or at least divergent populations characteristics to emerge.

The lack of relationship between abundance and distance below the dam was not expected. Hynes (1970) provides an extensive discussion of the decrease of plankton abundance usually found with distance below reservoirs. More recent specific examples of distance effects are Armitage and Capper (1976) and Ward (1975). Why the Colorado is different is not clear.

The evidence presented above suggests that Lake Powell plankton can survive the passage down the 240 miles (386 km) to Diamond Creek with only small mortality. If this result is true, then the lake's zooplankton discharges, as modified by the river, have the potential of interacting with endemic resources (e.g., benthic invertebrates, fish spawning and nursery areas) throughout the length of the river to Lake Mead.

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Table 1. Summary of zooplankton collections from the Colorado River. River mile measured from Lee's Ferry, 15 miles (24 km) below Glen Canyon Dam; Diamond Creek is located at Mile 226 (Km 364).

Date	Number of Samples	River Mile	Nets Used Diam (cm)	Mesh (µm)
06/19/80-07/01/80	19	20 to 223	30 30	212 363
12/30/80-01/01/81	5	-15 to -12	30	363
08/02/84	2	43	13	80
12/19/84-01/17/85	10	-15 to 185	13 13	80 243
10/07/85-10/14/85	6	28 to 194	13	80
11/10/85-11/22/85	14	0 to 132	13	80

Table 2. Species of crustaceans found in the Colorado River and terminal portions of its tributaries between Glen Canyon Dam and Diamond Creek. Species or categories marked with an asterisk are true plankton, all occur in Lake Powell; the remainder are normally benthic and are only occasionally found in the plankton of the river as drift. Compiled from Glen Canyon Environmental Studies collections, Haury (1981), and Cole and Kubly (1976).

Copepods

Calanoids*

Aglaodiaptomus clavipes
Aglaodiaptomus forbesi
Leptodiaptomus ashlandi
Leptodiaptomus sicilis
Skistodiaptomus pallidus
Skistodiaptomus reighardi

Cyclopoids

Acanthocyclops vernalis*
Diacyclops thomasi*
Eucyclops agilis
Eucyclops speratus
Mesocyclops edax*
Paracyclops fimbriatus poppei
Tropocyclops prasinus mexicanus*

Cladocerans

Alona affinis
Alona guttata
Bosmina longirostris*
Chydorius sphaericus*
Daphnia galeata mendotae*
Daphnia parvula*
Daphnia pulex*
Diaphanosoma birgei*
Leydigia quadrangularis
Pleuroxis aduncus
Pleuroxis denticulatus

Amphipods

Gammarus lacustris

Ostracods

Cypridopsis vidua
Cyprinotus incongruens
Cyprinotus pellucidus
Cyprinotus salinus
Herpetocypris reptans
Ilyocypris bradyii
Paracandona euplectella
Potamocypris sp.

Table 3. Copepod, cladoceran, and total organism abundance ($\#/m^3$): comparison between backeddies/tributary terminal pools and mainstream. Data from summer 1980.

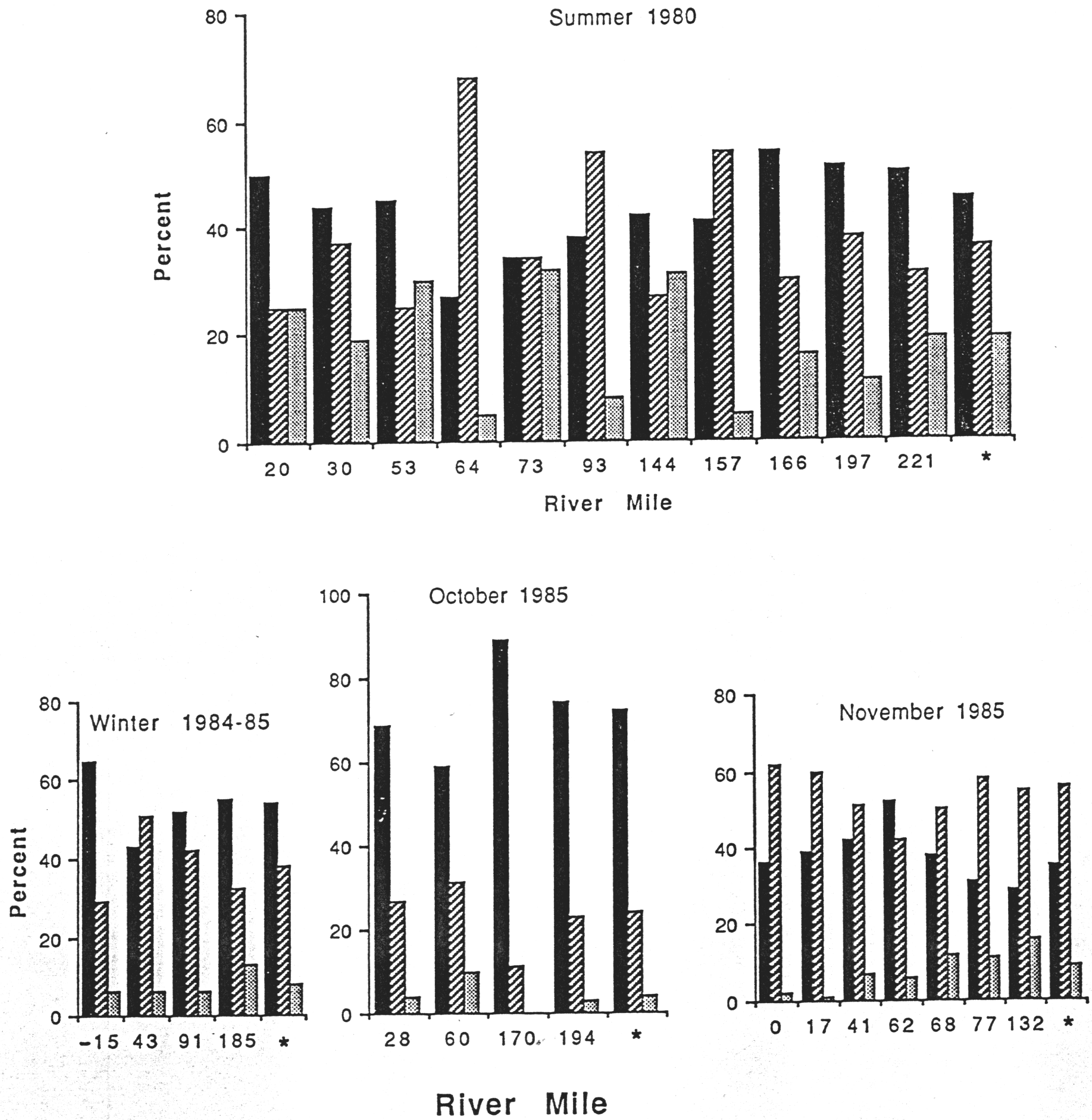
	Copepods Calanoid	Copepods Cyclopoid	Cladocerans	Total Organisms
Kanab Creek				
Mainstream	30.1	22.7	28.1	80.9
Mainstream	48.8	27.5	28.4	104.7
Terminal Pool	127.3	103.4	1.3	232.0
Terminal Pool	39.7	31.2	1.1	72.0
National Canyon				
Mainstream	54.8	36.3	27.5	118.6
Backeddy	46.3	21.6	6.3	74.2

FIGURE LEGENDS

Figure 1. Percent composition of crustacean zooplankton from the Colorado River mainstream as a function of river mile between Glen Canyon Dam and Diamond Creek during four periods: Summer 1980, Winter 1984-1985, October 1985, and November 1985 (see Table 1 for exact dates). Solid bars - calanoid copepods; hatched bars - cyclopoid copepods; shaded bars - cladocerans. Last set of data for each period marked by asterisks is the average for that period.

Figure 2. Abundance of all organisms caught in the plankton of the mainstream Colorado River between Glen Canyon Dam and Diamond Creek as a function of river mile. Data from all collections; note log scale of abundance. There is no significant relationship between abundance and river mile ($r^2 = 0.095$).

Figure 3. a) Average daily discharge from Glen Canyon Dam from 13 to 30 June 1980 (1 cfs [$ft^3\ s^{-1}$] = 0.0283 $m^3\ s^{-1}$). Diamonds - spillway releases; open squares - penstock releases; solid squares - total discharge. b) Abundance of three taxonomic categories plotted against river mile for the June 1980 mainstream Colorado River collections. Sampling began at Mile 20 on 19 June and conluded at Mile 223 on 1 July.



Summer 1980
Percent
80
60
40
20
0
20 30 53 64 73 93 144 157 166 197 221 *
River Mile
October 1985
100
80
60
40
20
0
28 60 170 194 *
Winter 1984-85
Percent
80
60
40
20
0
-15 43 91 185 *
November 1985
80
60
40
20
0
0 17 41 62 68 77 132 *
River Mile

Figure 1

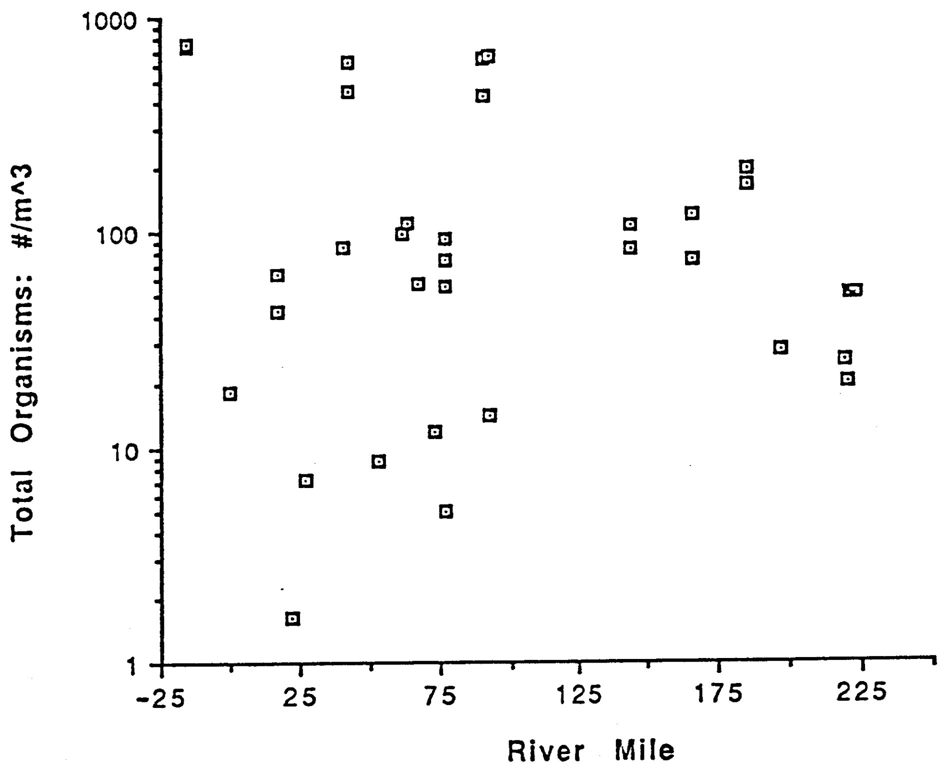
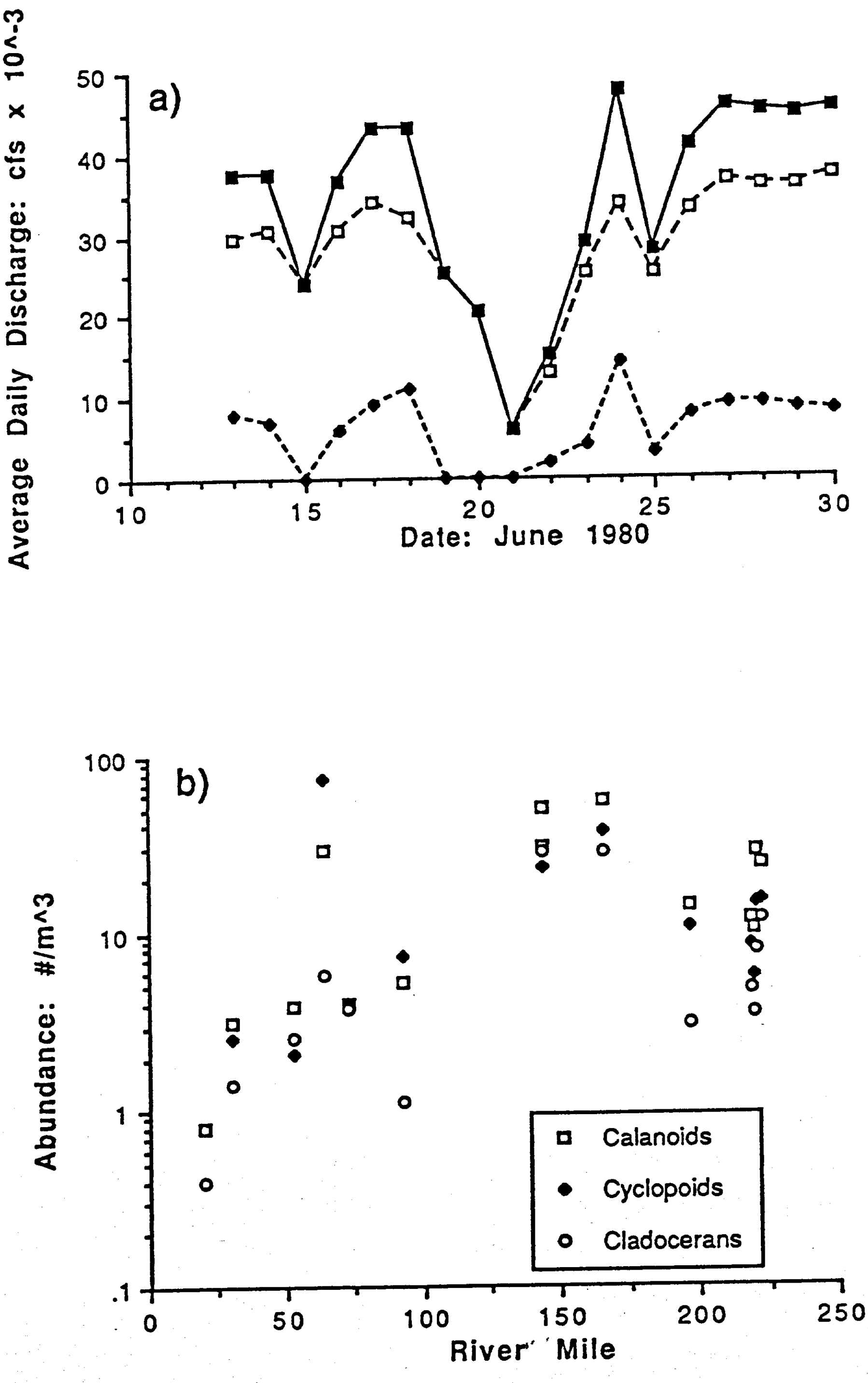

1000
100
10
1
Total Organisms: #/m^3
-25
25
75
125
175
225
River Mile

Figure 2



a)
Average Daily Discharge: cfs x 10^-3
50
40
30
20
10
0
10
15
20
25
30
Date: June 1980
b)
Abundance: #/m^3
100
10
1
.1
0
50
100
150
200
250
River Mile
Calanoids
Cyclopoids
Cladocerans

Figure 3