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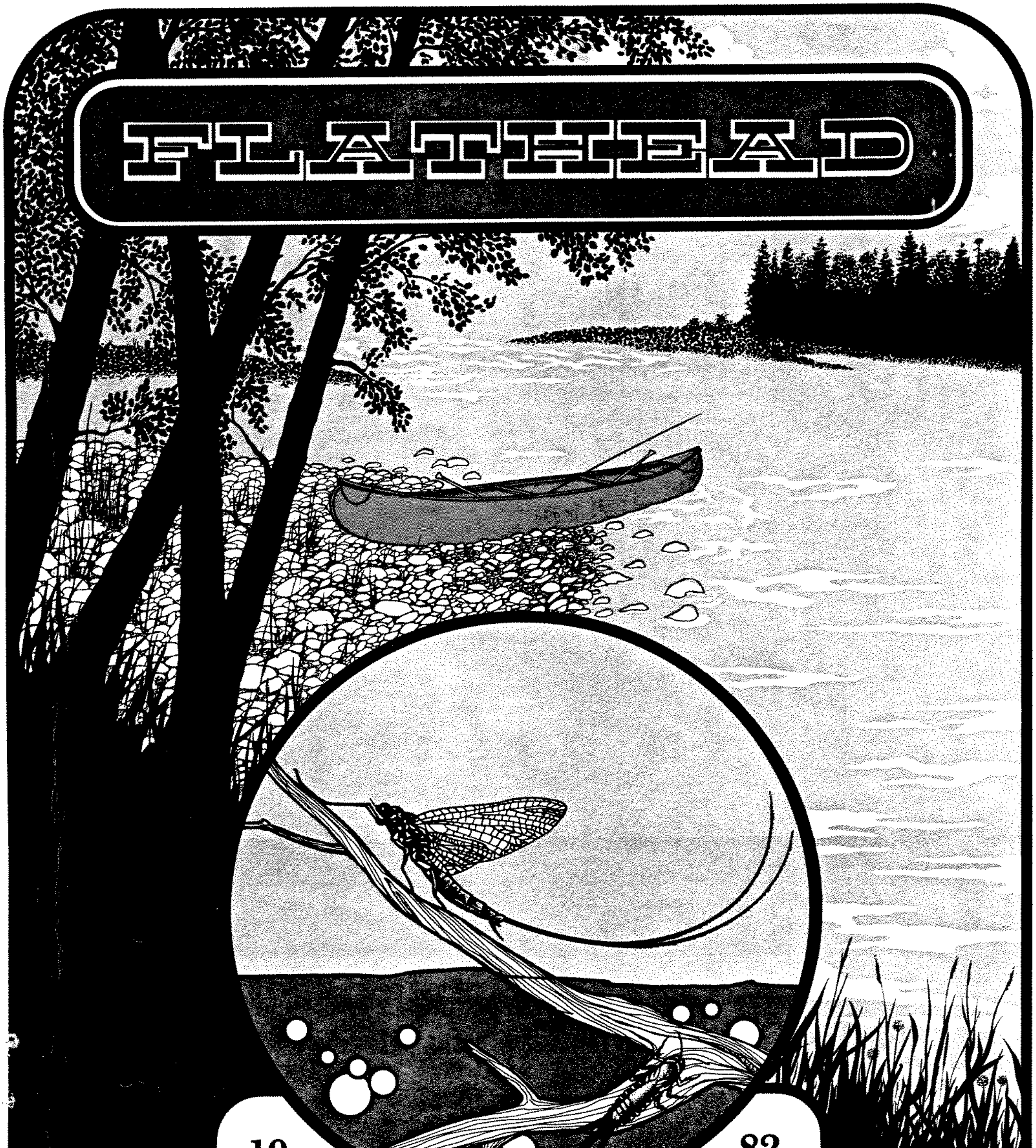

IMPACTS OF HUNGRY HORSE DAM ON THE INVERTEBRATES IN THE FLATHEAD RIVER—FINAL REPORT

Research Conducted by: MONTANA DEPARTMENT OF FISH, WILDLIFE AND PARKS
Sponsored by: BUREAU OF RECLAMATION

IMPACTS OF HUNGRY HORSE DAM ON THE INVERTEBRATES IN THE FLATHEAD RIVER

FINAL REPORT

by

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Montana Department of Fish, Wildlife and Parks
Kalispell, Montana

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EXECUTIVE SUMMARY

An aquatic macroinvertebrate study was begun in June, 1979 as part of a larger study which was funded by the U.S. Bureau of Reclamation. A fisheries study was designed to assess the probable impacts of several proposed power alternatives in the areas of the Flathead River affected by discharges from Hungry Horse Dam. The benthic invertebrate study was undertaken to provide baseline information on density and biomass, community composition, and species diversity of macroinvertebrates in the South Fork of the Flathead River downstream from Hungry Horse Dam and in the mainstem Flathead River above and below the confluence with the South Fork. Other areas of study included a seasonal study of the food habits of whitefish and trout in regulated and control areas, an experimental study on the effects of different rates of increase in discharge and times of shutdown at Hungry Horse Dam on insect drift, an evaluation of the effects of different discharge regimes on selected insect life histories, and measurement of the effects of river discharges on seston, periphyton, and Aufwuchs productivity.

Biotic diversity is severely reduced and community composition is grossly altered in the regulated South Fork of the Flathead River. The mean of the Shannon diversity indices for the four months which were used to calculate seasonal values was 0.8 at the South Fork station and generally in the range of 3.1 to 3.3 at the main river sites. The fauna in the South Fork was dominated by the dipteran family Chironomidae, which represented 85 percent of invertebrates by mean annual density. The mayflies, stoneflies, and caddisflies represented only four percent of the invertebrate density in the South Fork as compared to 75 percent at the control site. The combined effects of flow fluctuations, the severe changes in the temperature regime (varying from only 3° to 7° C annually and thus providing much colder summer temperatures and warmer winter temperatures), and the consequent changes in the food base for invertebrates are responsible for the marked changes in zoobenthic composition.

In contrast to the South Fork, both main river sites (above and below the confluence with the South Fork) had diverse insect faunas. No significant differences in overall diversity were shown between the control and partially regulated (downstream from the confluence with the South Fork) sites using Shannon diversity indices. The increase in biotic diversity which generally occurs with increasing distance downstream from a dam, occurs abruptly in the Flathead River where the South Fork joins the unregulated North and Middle Forks. The mainstem Flathead River is affected by the addition of waters from the regulated South Fork, but the adverse effects on the macroinvertebrates are greatly tempered due to dilution by the North and Middle Forks. This can be attributed to factors such as temperature modification, the flushing and redeposition of sediments which occurs during spring runoff, the import of particulate organic carbon and drifting insects from usptream areas and other factors.

Although no significant differences were shown in species diversity, there were compositional changes in the partially regulated portion of

the river. Mayflies were far more abundant in the control area (54 percent versus 27 percent), while stoneflies and dipterans showed higher densities in the partially regulated area (Plecoptera - 21 percent versus 15 percent; Diptera - 38 percent versus 24 percent). The composition of caddisflies was markedly different at the two sites, which is probably related to differences in periphyton and particulate organic carbon particle sizes of the seston. The timing of events in the life cycles of a number of species was different at the two main river sites; this can be correlated with seasonal temperature differences in the control and partially regulated areas of the river, which are due to discharges of hypolimnetic water from Hungry Horse Dam.

Annual means of individual counts (no/m²) and biomass (cc/m²) data indicate that densities of zoobenthos are higher in the South Fork (10,472 ± 6,372) than at the control (6,666 ± 6,144) and partially regulated (6,412 ± 7,078) sites. Overall, biomass is not significantly different at the three sites (control - 12.1 ± 4.2; partially regulated - 14.4 ± 9.0; regulated - 12.3 ± 5.8).

Three ordination techniques; polar ordination, principal components analysis, and detrended correspondence analysis, were applied to the macroinvertebrate data from the months of October, December, March, and July to assess differences in community composition between sampling stations. Each of the ordination techniques produced a spatial gradient between regulated and control sites. All ordination methods in all four seasons ordered well along an axis corresponding to disturbances due to river regulation.

The values for each sampling station obtained using the ordinations, as well as the diversity values, were used in correlation analyses to assess the importance of various environmental factors in determining macroinvertebrate community associations. Generally, ash free dry weight and chlorophyll a in the periphyton, particulate organic carbon in the seston, substrate heterogeneity, and rates of change in velocity showed significant correlations with Shannon diversity and the values obtained using polar ordination and detrended correspondence analysis.

Seasonal measurements of ash free dry weight and chlorophyll a in the periphyton showed a much higher biomass at the South Fork than at the other two stations. Mean fall ash free dry weight values (g/m²) were 140-200 at the regulated South Fork compared to 4.0 to 4.5 at the unregulated station. However, productivity measurements at the South Fork station during the fall were not in proportion to the high biomass measured at that site. The productivity/respiration ratio was highest at the partially regulated station (2.69), but was not significantly different between any of the three stations. Productivity is low in the Flathead River system when compared to the Kootenai River in northwestern Montana.

Mean annual values of particulate organic carbon (POC) in the seston (mg/l) were lowest in the South Fork (.07 ± .06), highest at the reference station (.14 ± .18), and intermediate at the partially regulated station

(.11 ± .10). This is largely a function of higher levels of suspended materials during periods of runoff in unregulated areas. The relative percentage of POC in each of four size fractions of seston was altered by the fact that larger particles settled out in Hungry Horse Reservoir. The larger size fractions contained a smaller percentage of the POC below the dam. The two largest size fractions (165-1000 μm) increased 15 to 20 times just after water elevations rose at the partially regulated site. This was due to the fact that the initiation of hydropower generation resulted in the sloughing of periphyton and resuspension of materials.

The washing out of finer materials from the substrate due to fluctuating flows downstream from dams was reflected in our substrate measurements. The mean size of surface rocks was largest and the heterogeneity of particle sizes was lowest at the South Fork station where the substrate is severely armored.

Invertebrate drift densities were studied in relation to rates of increase in discharge caused by hydropower generation and in relation to time of shutdown at Hungry Horse Dam with regard to time of day. Significantly more insects were recorded in the drift in the partially regulated section of the river near Columbia Falls just after flows started to increase, but no major differences were found between the two rates of increase in discharge. The effect of decreasing flows on insect drift in the mainstem river was not marked at the sampling station, either when shutdown occurred during the day or at night. This may be due to the fact that rates of velocity change are damped in the partially regulated section due to the entry of the free-flowing North and Middle Forks of the Flathead River. Also, there is little recolonization of shoreline zones where flows fluctuate due to the frequency of changes in discharge.

A food habits study of mountain whitefish and trout was done in April, July, and October, 1980. An Index of Relative Importance (IRI) of items in the diet (the arithmetic mean of the percent composition by density, volume, and frequency of occurrence) was calculated to compare stations, seasons, age classes, and species. Caddisflies and dipterans had the highest IRI's in the stomachs of mountain whitefish in all age classes at all stations. Terrestrial invertebrates were of major importance in the fall. Trout fed more heavily on mayflies, stoneflies, and terrestrial invertebrates. No consistent differences were found in the food preferences of whitefish in the partially regulated as compared with the free-flowing section of the mainstem Flathead River.

ACKNOWLEDGEMENTS

Robert Schumacher, Regional Fisheries Manager, was instrumental in developing the initial study proposal. Dr. Jack Stanford, University of Montana Biological Station, provided work space for invertebrate sorting and enumeration, the use of a stonefly reference collection, and equipment and materials for periphyton and particulate organic carbon analyses. U.S. Bureau of Reclamation personnel, especially Rich Clark and Nick Anderson, assisted in obtaining the flows required for invertebrate sampling. The U.S. Geological Survey provided flow and temperature data (special thanks to Shirley Mickelson). The U.S. Forest Service and U.S. Fish and Wildlife Service provided additional microscopes for our use.

William Perry assisted with macroinvertebrate enumeration, supervised the volumetric analyses for invertebrate biomass estimates, and did the periphyton and particulate organic carbon analyses. Paul Leonard, Ken Fraser, and William Perry assisted with field work, data calculations, and graphics. We are indebted to employees of the CETA and YACC programs for their assistance in the collection and sorting of aquatic insects. Among the people who spent many tedious hours sorting insects were: Dave Arland, Dennis Barrow, John Bender, Nita Davis, Debbie deGennaro, Laurie Dollan, Dave Donaldson, Buddy Drake, Sandy Entzel, Kirk Fallon, Mark Gaub, Wanda Jamieson, Rick Johnson, Susan Kraft, Emmy Keller, Cathy Leddy, Robert Post, Chuck Richardson, Cathy Schloeder, Better Schrader, Terry Seliger, Wendy Senger, Arlene Sinclair, John Squires, Jill Stanley, Ron Tate, Cora Torpin, and Ande Wood. Dave Donaldson and Rick Johnson did the bulk of the volumetric measurements for biomass estimates. Robert McFarland provided computer programming assistance. Burwell Gooch ran the computer program for the diversity indices. Loren Bahls identified the algal species and did the periphyton community structure analyses. Bill Shepard verified the Coleoptera identifications. Cathy Turley and Mary Chubb typed the manuscript.

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INTRODUCTION

The benthic invertebrate study was begun in June 1979, as part of a larger fisheries study to assess the impacts of various proposed power alternatives and operating regimes on the aquatic biota in the Flathead River. Hungry Horse Dam, which is located 8 km upstream from the mouth of the South Fork of the Flathead River, was completed in 1953. It is operated for flood control and power production by the Bureau of Reclamation. The crest of the dam is 1087 m above sea level. Four penstocks are located 75 m below the crest.

The present minimum flow from Hungry Horse Dam is 4.2 m^3/sec (150 cfs) and peak discharge is approximately 323 m^3/sec (11,417 cfs). The Bureau of Reclamation is assessing several alternatives which would increase peaking capacity and total annual power production. These include uprating the existing generators, a powerhouse addition, and the construction of a reregulating dam which would have an estimated storage capacity of 2.4×10^6 m^3. Maximum discharge from the existing dam could be increased to 390 m^3/sec.

The aquatic invertebrate study was undertaken to provide baseline information on community composition, species diversity, biomass, and life history characteristics of macroinvertebrates in the Flathead River above and below the confluence of the South Fork and in the South Fork of the Flathead River downstream from Hungry Horse Dam. The impact of operating regimes which have been proposed to enhance the fishery are being assessed with regard to their effect on the fish food organisms. The objectives of the invertebrate study are:

1. To sample the benthos at monthly intervals over a two-year period in order to compare invertebrate densities and biomass in control and regulated areas of the Flathead River.

2. To assess differences in community composition in control and regulated areas with the use of diversity indices and ordinations techniques.

3. To (seasonally) study the food habits of whitefish and trout in regulated and control areas of the river and to ascertain whether certain species are feeding selectively on the drift or on the bottom.

4. To determine experimentally whether different rates of increases in discharge and times of shutdown at Hungry Horse Dam differentially affect invertebrate drift.

5. To assess the effect of regulation and of different discharge regimes on the rates of growth and times of emergence of selected aquatic insect species.

The construction of Hungry Horse Dam has resulted in a number of downstream modifications which are of significance to river zoobenthos.

Dams can exert profound perturbative influences on the downstream riverine environment, and rapid, short-term fluctuations due to hydropower production have profoundly altered biological processes in the South Fork. Unpredictable and fluctuating flow conditions below dams with operational schedules based primarily on power needs have a detrimental effect on the benthos by inducing catastrophic drift, causing stranding, and altering the habitat. The manipulation of discharge affects the total lotic ecosystem. Certain changes in the discharge regime from dams can benefit invertebrate populations (high minimum flows, predictable flows, selective withdrawal systems, etc.). Water discharge is a factor of key importance to the benthos, especially due to its influence on temperature, current velocity, composition of the substrate, and the availability of food (Henricson and Müller 1979).

Temperature is an important environmental factor affecting the benthos in the regulated areas of the Flathead River. The hypolimnial releases from Hungry Horse Dam have stabilized temperatures in the South Fork; the yearly thermal regime is severely altered, varying only from 3°C to 7°C. The marked reduction in thermal amplitude in the South Fork as compared to the unregulated North and Middle Forks during the course of our study is shown in Figures 1, 2 and 3. The lack of appropriate thermal criteria for hatching, growth and emergence may be the major factor contributing to the absence of many species of insects in the South Fork (Stanford 1975).

In general, environmental heterogeneity and biotic diversity will be reduced near an upstream impoundment, but will show a progressive recovery with increasing distance downstream (Ward and Stanford 1979). This recovery occurs abruptly in the Flathead River where the South Fork joins the unregulated North and Middle Forks. Because the ameliorative effect imposed by unregulated segments is much greater than in many regulated rivers, the mainstem Flathead River will be referred to as <u>partially regulated</u>. The mainstem Flathead River is affected by the addition of waters from the regulated South Fork, but the adverse effects on the macroinvertebrates are greatly tempered due to dilution by the North and Middle Forks.

The partially regulated Flathead River also shows the late fall and winter elevation (Figure 4) and summer depression (Figures 5 and 6) in river temperatures, although to a lesser extent than the South Fork. In the partially regulated areas of the river, severe thermal fluctuations over short periods of time may occur as power releases peak and wane. In the summer during periods when there is no generation, river temperatures warm quickly, since most of the flow is from the North and Middle Forks.

Discharges from Hungry Horse Dam also affect the availability of food for macroinvertebrates. The lack of trophic diversity contributes to the severely altered invertebrate composition in the South Fork. The South Fork supports a dense growth of periphytic algae in the permanently wetted area of the river. Inorganic sediments settle out in the reservoir,

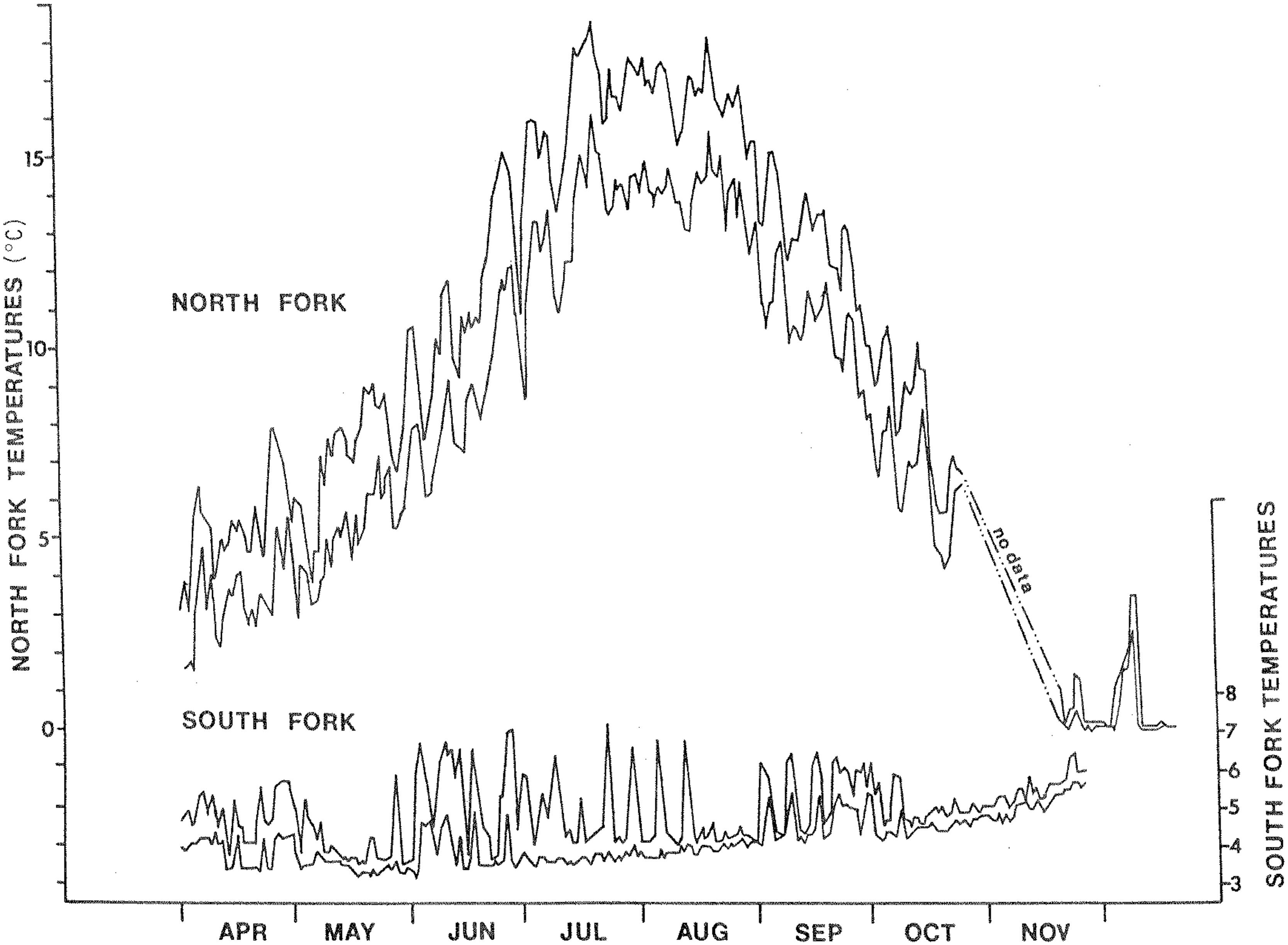

Figure 1. Daily maximum and minimum temperatures recorded at USGS stations on the North (unregulated) and South (regulated) Forks of the Flathead River from April, 1979 through November 1979.

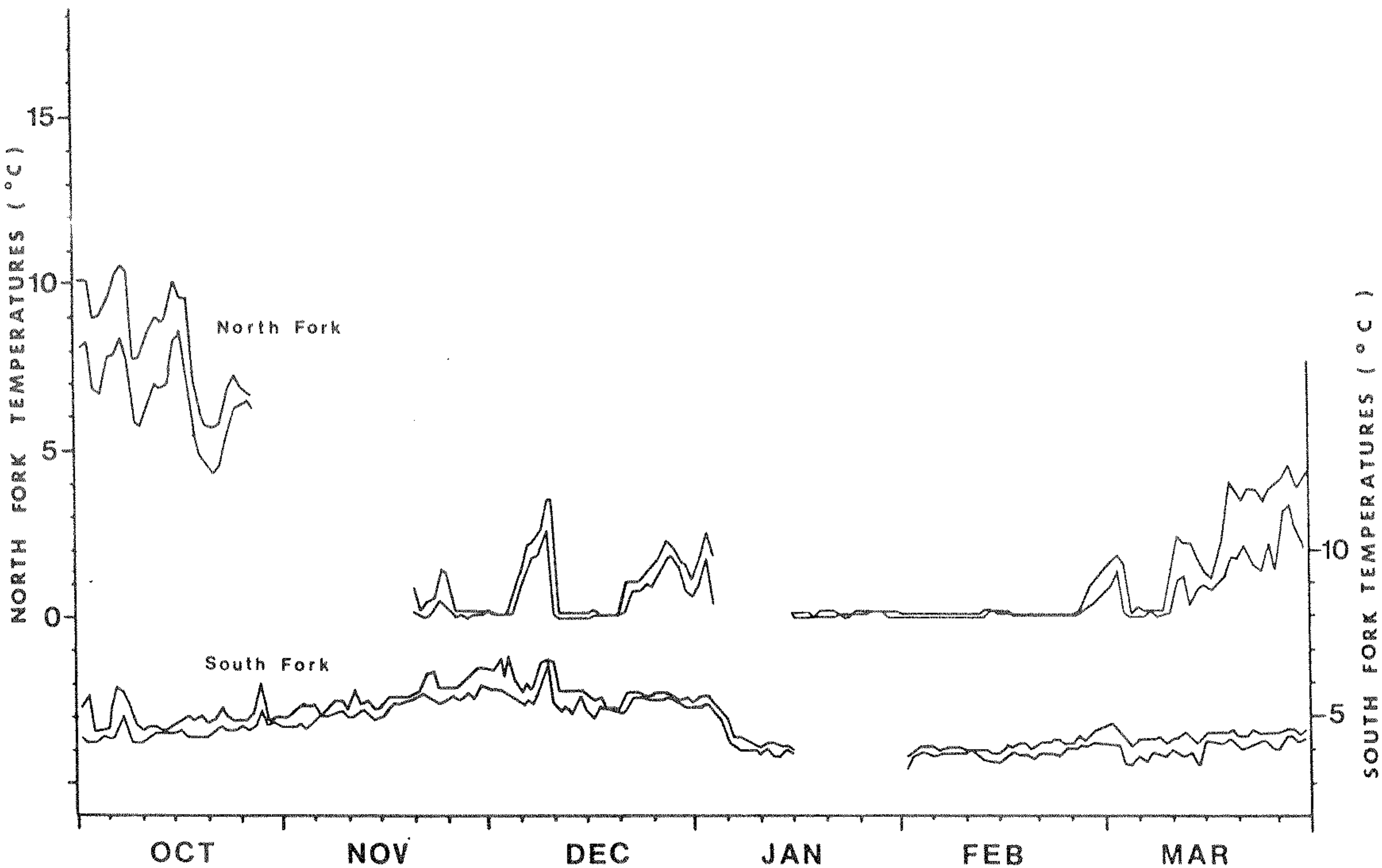

Figure 2. Daily maximum and minimum temperatures recorded at USGS stations on the North (unregulated) and South (regulated) Forks of the Flathead River from October, 1979 through March, 1980.

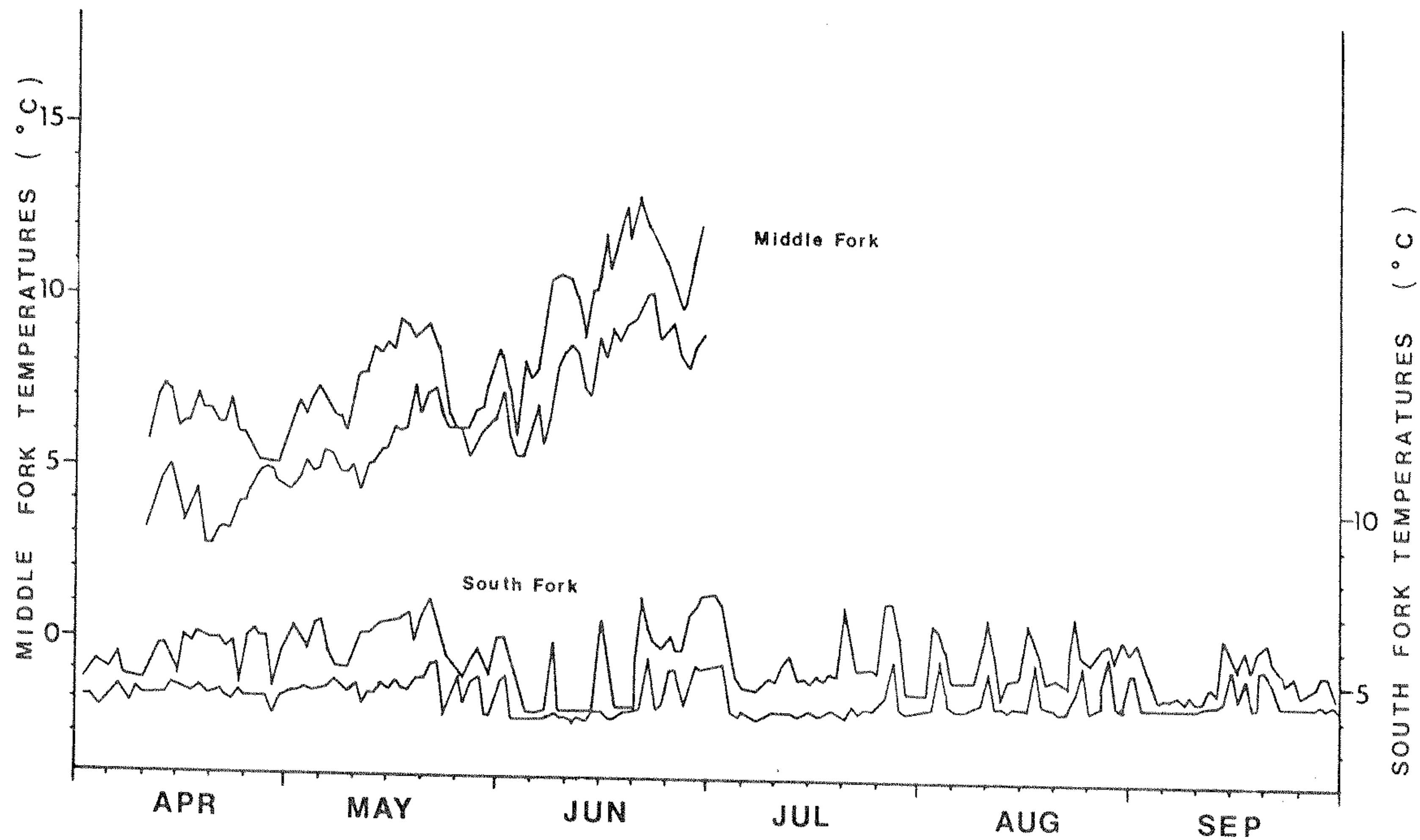

Figure 3. Daily maximum and minimum temperatures recorded at USGS stations on the Middle (unregulated) and South (regulated). Forks of the Flathead River from April through September, 1980.

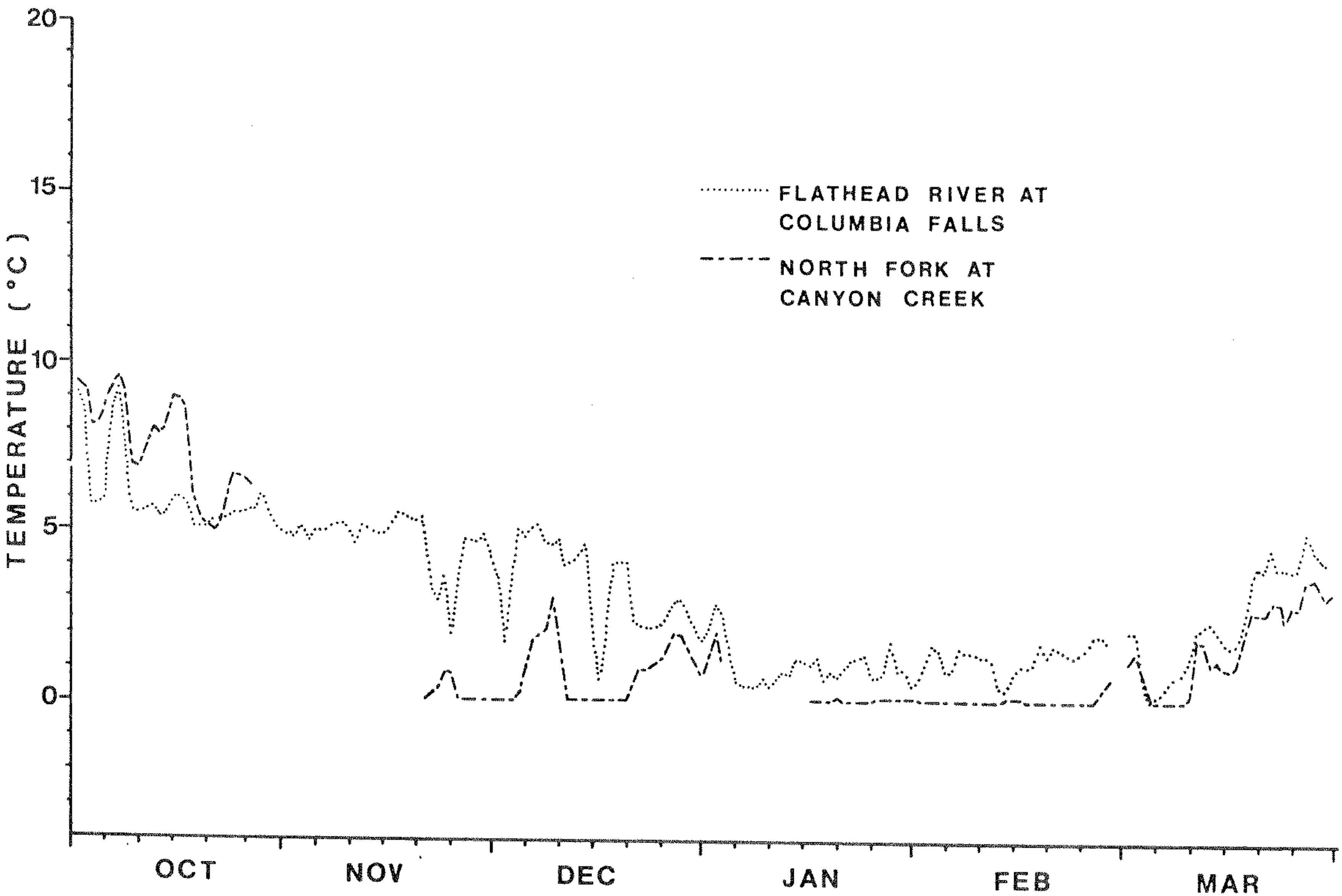

Figure 4. Mean daily temperatures recorded in the unregulated (North Fork) and partially regulated (Columbia Falls) areas of the Flathead River, October, 1979 through March, 1980.

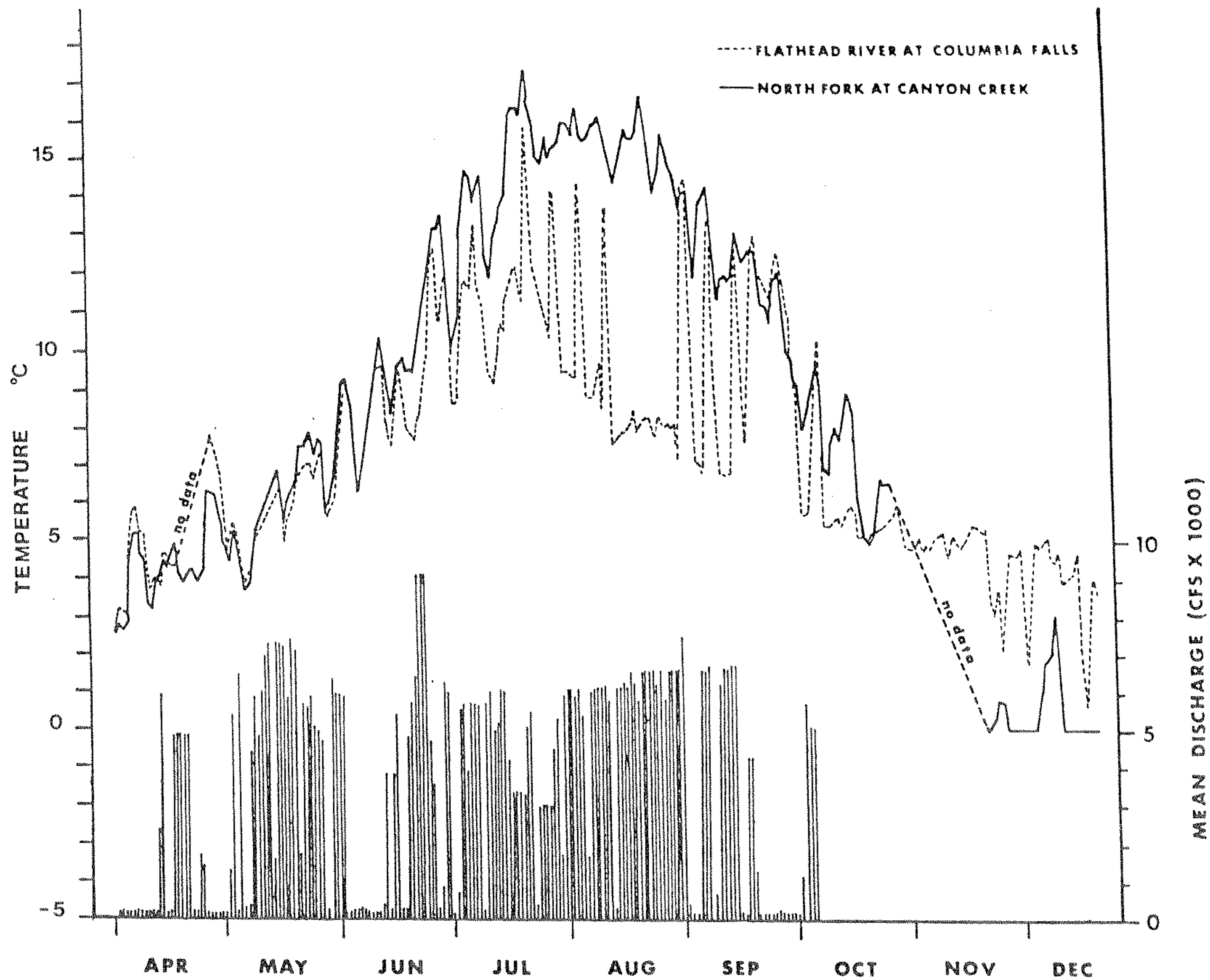

Figure 5. Mean daily temperatures recorded at USGS stations on the unregulated North Fork and partially regulated mainstem Flathead River from April, 1979 through December, 1979.

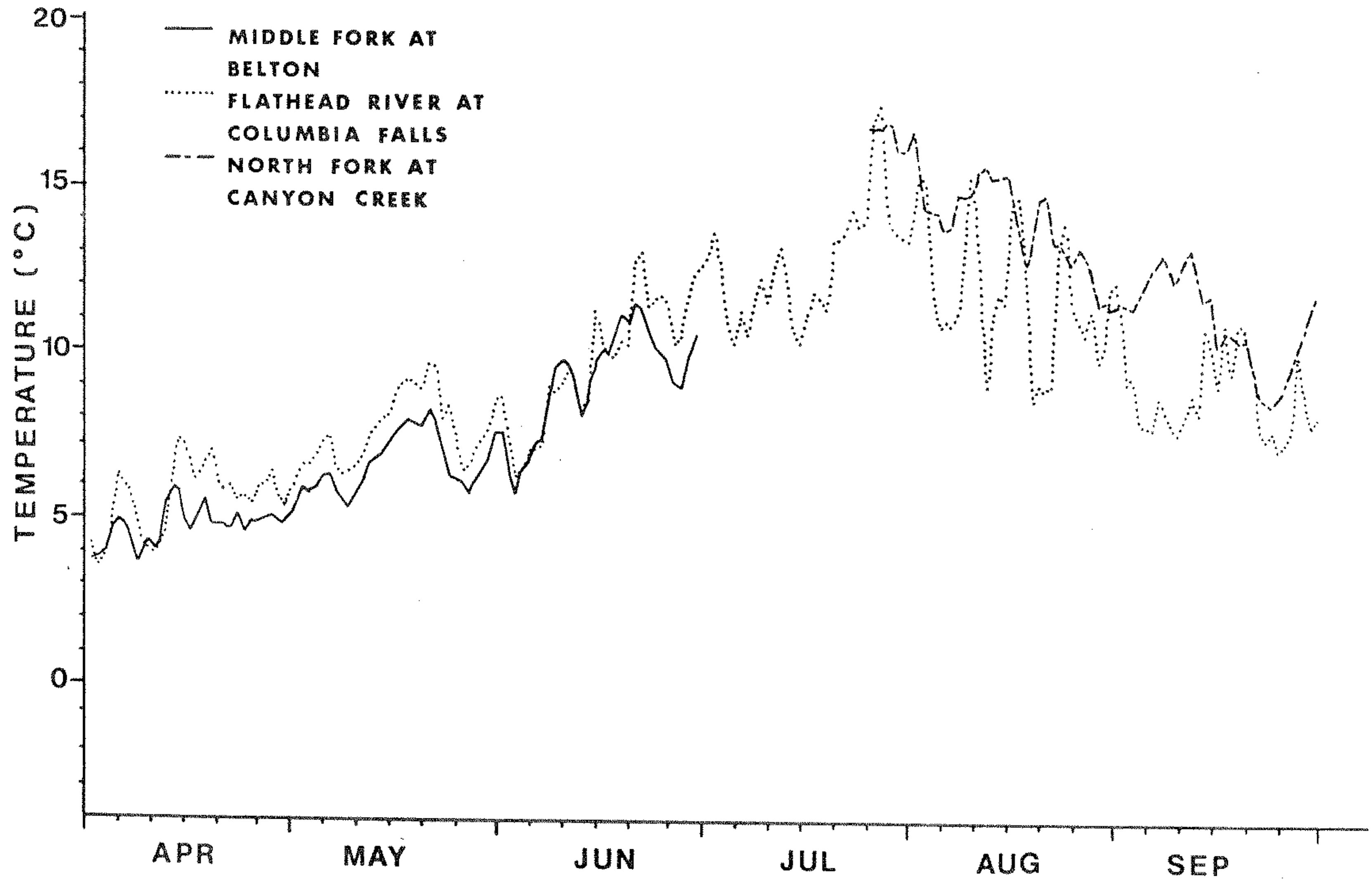

Figure 6. Mean daily temperatures recorded in the unregulated (North and Middle Forks) and partially regulated (Columbia Falls) areas of the Flathead River, April through September, 1980.

reducing turbidity and sediment scour in the South Fork and mainstem Flathead River, thus allowing increased periphyton growth. Seston from the reservoir is not abundant in the South Fork, since water is withdrawn only from the unproductive hypolimnion of the reservoir. Organic carbon is more abundant in the partially regulated areas of the Flathead River due to input from the unregulated forks and recruitment of debris from shoreline areas and sloughing of periphyton during generation.

Regulation also affects the composition of streambed materials and thus reduces habitat diversity. Natural areas of the Flathead River are characterized by loosely compacted flood plain materials composed of large cobble interspersed with smaller gravels and sand. In the South Fork, the smaller materials have been removed from the surface layer of rocks by the clearwater discharges from Hungry Horse Dam. The reservoir acts as a settling basin for inorganic material, so there is no redeposition of the finer gravels and sand in the tailwater area. Substrate particle size has been shown to have an important effect on community structure (Cummins 1966; de March 1976; Minshall and Minshall 1977; Williams 1980).

DESCRIPTION OF STUDY AREA

The Flathead River drains 21,876 km^2 of southeast British Columbia and northwest Montana. It is the northeastern most drainage in the Columbia River Basin. Three forks of approximately equal size drain the west slope of the Continental Divide. The South Fork flows out of the Bob Marshall Wilderness area to Hungry Horse Reservoir, a deep-storage impoundment approximately 66 km long with a storage capacity of $4,268 \times 10^6$ m^3. Discharge from Hungry Horse Dam varies from a minimum flow of 4.2 m^3/sec to a peak discharge of 323 m^3/sec, and vertical water level fluctuations in the South Fork downstream from the dam can vary as much as 2.5 m daily. The South Fork is grossly altered for its entire course (8 km) before it joins with the North and Middle Forks of the Flathead River. The hydrograph of the mainstem Flathead River below the confluence with the South Fork is determined by the sum of the discharge from the three forks. Peak flows in the mainstem normally occur in May and June, coinciding with peak runoff in the North and Middle Fork drainages. Except for peak runoff periods, the hydrograph of the mainstem parallels that of the South Fork (Figures 7 and 8).

The macroinvertebrate work has been concentrated in riffle areas at three study sites: 1) South Fork of the Flathead River - 7.4 km from Hungry Horse Dam near the mouth of the South Fork; 2) Glacier Bible Camp (Control Site) - 1.2 km north of the mouth of the South Fork; and 3) Kokanee Bend Fishing Access Site - 12 km south of the mouth of the South Fork in the partially regulated mainstem Flathead River (Figure 9).

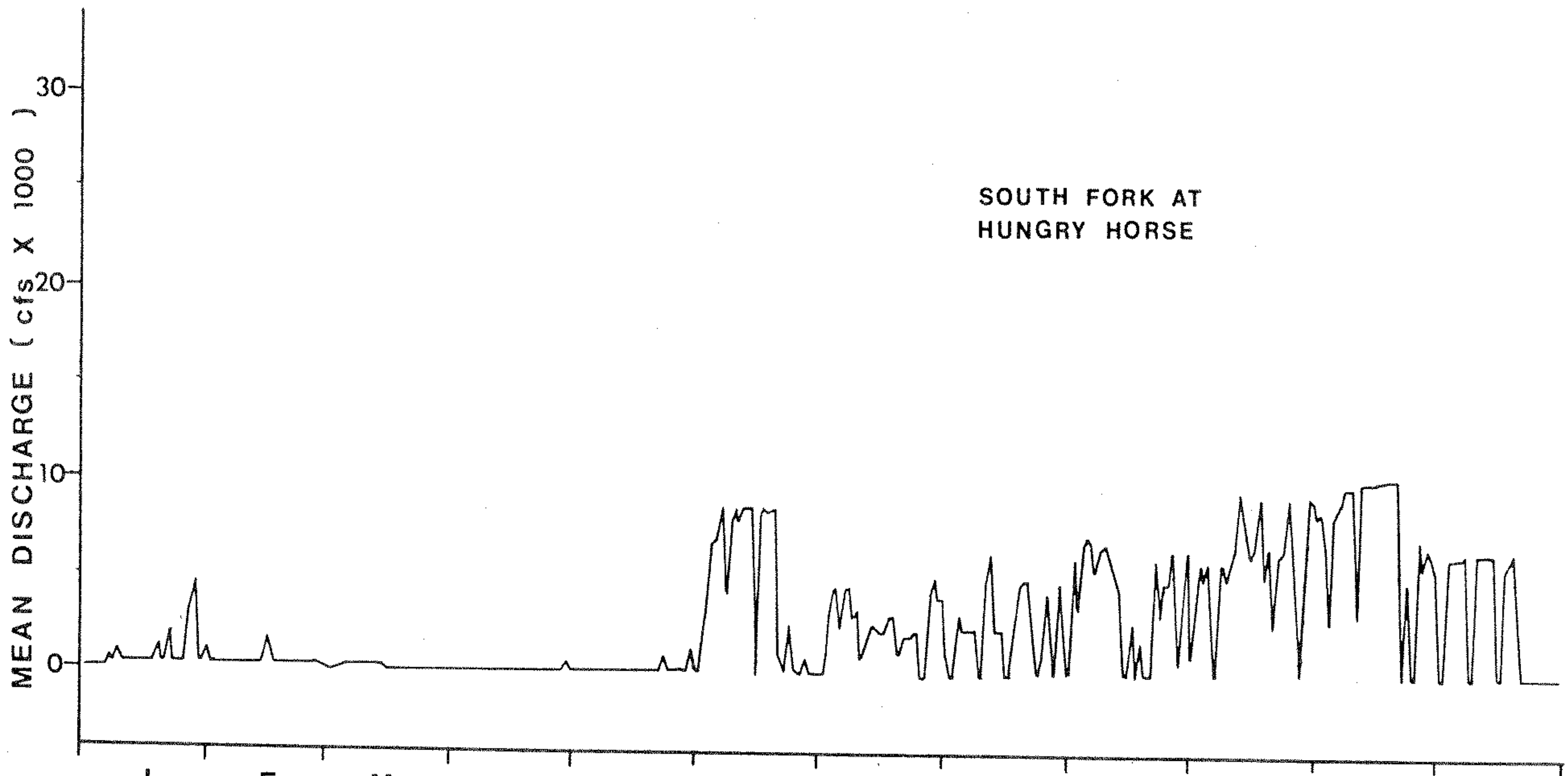

Figure 7. Mean daily discharge recorded in the South Fork of the Flathead River during the 1980 water year.

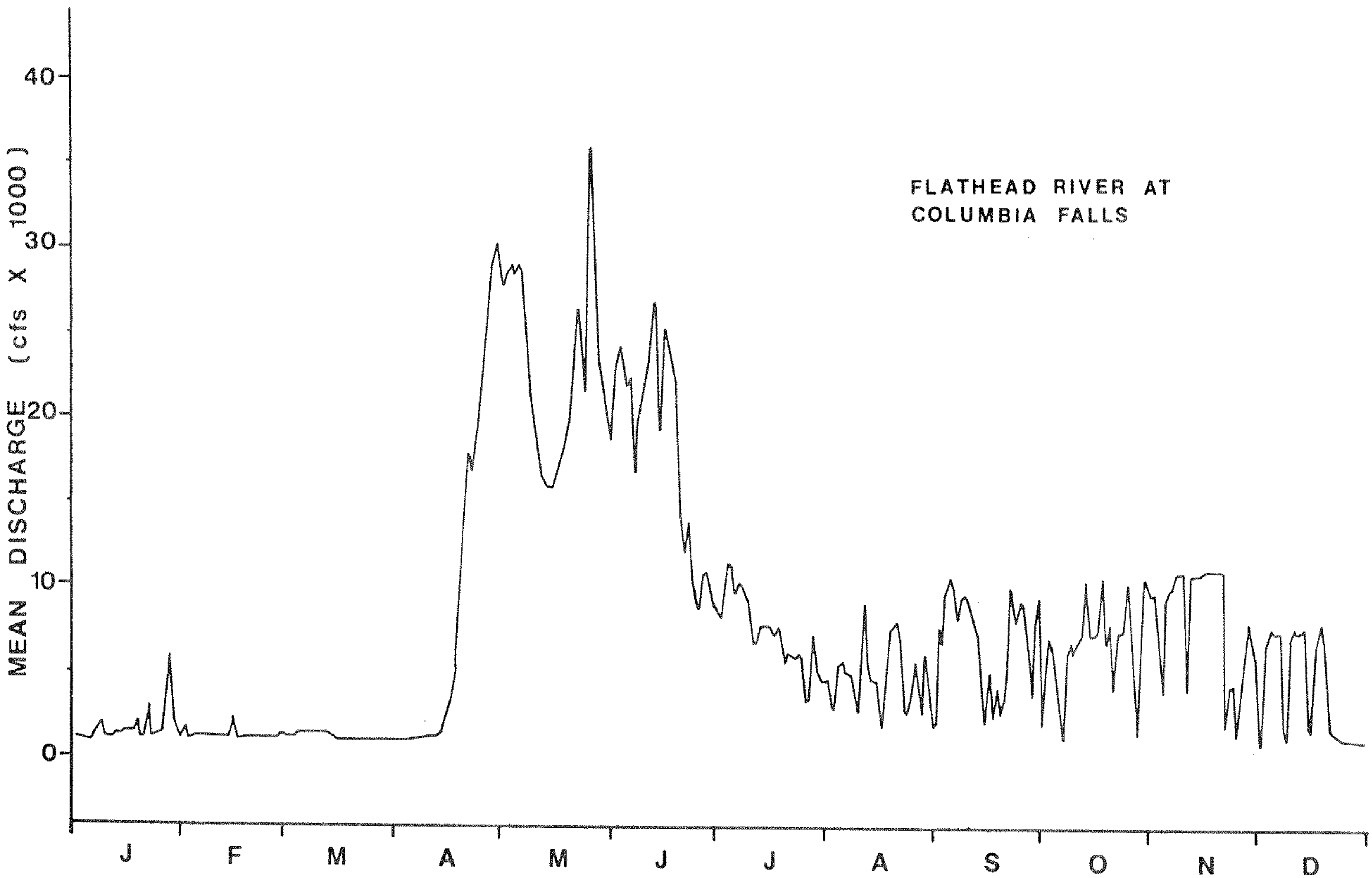

Figure 8. Mean daily discharge recorded in the partially regulated Flathead River (Columbia Falls) during the 1980 water year.

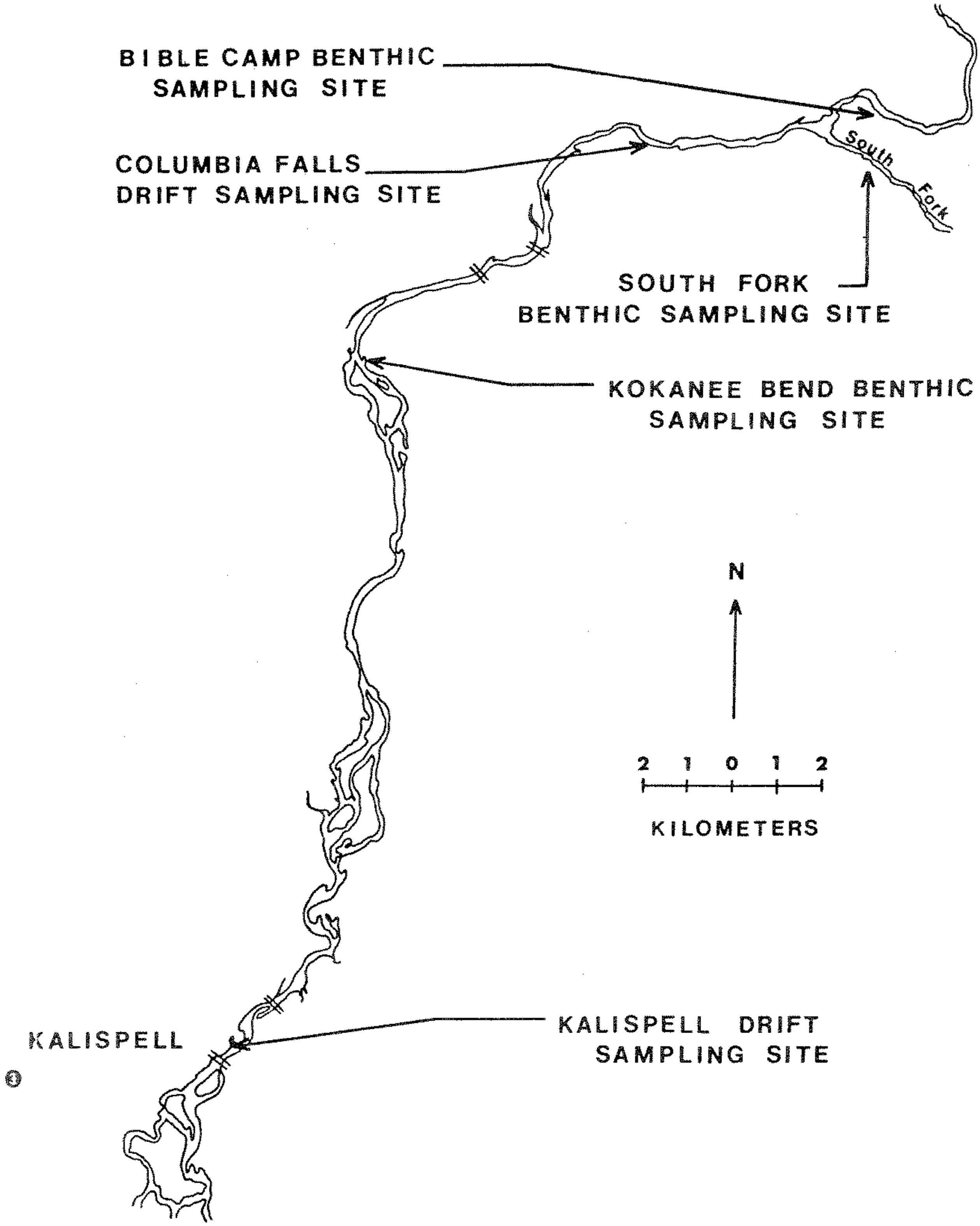

Figure 9. Macroinvertebrate sampling sites in the main stem and South Fork Flathead Rivers, 1979-1980.

METHODS

MACROINVERTEBRATE DATA

Monthly sampling of benthic invertebrates at the three established sites was begun in July, 1979. Eight to ten samples were taken at each site each month through September, 1980 by a combination of systematic sampling (the transect method) and stratified random sampling (selection of habitat types). Starting in October, 1980, the sample number was reduced to three samples per month at each of the three sites until sampling was terminated in April, 1981.

All samples were taken at conditions of minimum discharge from Hungry Horse Dam (4.2 m^3/sec. in all months but January and February, 1980, when minimum flows were 12.7 m^3/sec). The maximum depth which was generally sampled was about 25 cm, which excluded animals living deeper in the substrate. Mean current velocity (taken with a Price AA current meter at the 0.6 depth) and water depths were taken just upstream from each benthic sample.

Two different samplers were used in an effort to reduce biases associated with any one sampling device. Sampling in the Flathead River was difficult due to the large substrate sizes, so conventional samplers had to be modified. Both samplers enclose a sample area of one-third m^2 and have a small mesh size (150 μm) for retaining small instars of insects.

The modified kick net consisted of an outer rectangle 97 cm wide and 89 cm high made of Nitex with a 355 μm mesh and bordered with canvas. A bag (72 cm long, 150 μm mesh) with an opening 44 cm by 42 cm extended from the rectangular portion of the net. The net was held downstream from the sampling area which was delineated by a square made of one-quarter inch strap iron and encompassed one-third m^2. The net was curved around the square with the bottom taut during sampling. Rocks in the sample area were individually lifted inside the bag and brushed clean by hand. After all of the larger rocks were removed, the collection area was disturbed by kicking for 15 seconds. Organisms were retained in a clear acrylic bucket (with a drain made of Nitex with a 150 μm mesh) at the cod end of the net.

The other sampler employed in this study was a circular depletion sampler described by Carle (1976). It functioned more efficiently at faster current velocities. The height of our sampler was 54 cm and the inside circumference and diameter were 205 and 65 cm, respectively. The collecting net was made of Nitex with 150 μm mesh. Our sampler was made of aluminum, which was flexible and allowed the sampler to be wedged in around large rocks. Heavy rubber was riveted to the bottom of the sampler to provide a seal. An exact sample site was chosen by attempting to find a location where large rocks did not intersect the sampler edge. The sampler was then rapidly thrust down and turned into the substrate. If the sampler could not be stabilized and sealed within a few seconds by moving rocks, the site was abandoned. The procedure was the same as with the kick net, brushing all the large rocks and removing them and then kicking the substrate within the sampler for 15 seconds.

Organisms were preserved in 10 percent formalin to which Rose Bengal stain had been added. Macroinvertebrates were handpicked from the algae, detritus, and inorganic material, sorted to order and placed in vials containing 75 percent alcohol. The larger insects were removed (greater than 2 mm in length) and then a one-quarter or one-eighth subsample was taken. The subsample was completely picked with the aid of a microscope. All insects were identified to the lowest taxonomic level possible and enumerated using a laboratory counter. A number of workers were employed to sort samples, so quality control procedures were adopted to insure consistency. All samples were checked by a supervisor and subsampling methods were standardized.

Biomass was measured by volume displacement, with any volume less than 0.1 ml assigned a trace value of 0.05. Volumetric measurements were made with the use of a 50 milliliter burette and a graduated centrifuge tube.

Three drift nets were constructed of heavy materials to accommodate changes in discharge and large enough to adequately sample when drift rates were low. These nets had a rectangular opening measuring 45.7 by 30.5 cm and a Nitex bag with 355 μm opening which was 1.5 meters long. The frame was made of angle iron with holes for steel rods which were driven into the substrate. Rubber flanges projecting backward from the edge of the net prevented large insects from walking out of the net.

Two nets were set parallel to each other and to the shoreline to collect duplicate samples. In drift experiments at the Columbia Falls bridge, drift nets were set at the water's surface off either side of a jet boat, which was tied to the bridge. This enabled us to take samples at the same location as discharge was increased or decreased. Flow rates through the nets were monitored with a current meter. Generally, nets were set for a period of one hour. Invertebrate drift was studied in relation to rates of increase in discharge (normal start-up - 145→3,400→10,000 cfs and emergency start-up 145→10,000 cfs). Drift was also studied in relation to time of shutdown with regard to time of day (shutdown before and after dark).

Adult insects were collected by hand, with sweep nets, in pit traps (buried cans containing formalin covered with a thin film of diesel fuel), and with light traps (containing uv fluorescent lights used with 110 volt A.C.). Six pit traps were in position at the three sites from March to August, 1980. Light traps were operated nightly from June to October, 1980 at the control and partially regulated sites.

ENVIRONMENTAL VARIABLES

Water samples were collected on a monthly basis from November, 1979 to November, 1980. Chemical parameters measured on water samples from the South Fork included total suspended solids (gravimetric), particulate and dissolved organic carbon (International Oceanography Total Organic Carbon Analyzer), Na^+, K^+, Ca^{++}, Mg^{++}, NO_3^-, $SO_4^=$ (ion exchange chromatography Dionex Corporation), and total P (Standard Methods). The analyses were conducted by the Analytical Services Group of the Freshwater Research Laboratory at the University of Montana Biological Station.

Flow data and continuous recording thermograph data collected by the U.S. Geological Survey were obtained for the South Fork, North Fork, Middle Fork and mainstem Flathead River at Columbia Falls.

The periphyton standing crop was quantified at the sampling station on a seasonal basis (August, October and January) by measuring ash-free dry weights and chlorophyll *a* on material collected from the streambed. For ash-free dry weight analyses the Aufwuchs layer was removed from a randomly selected rock and the surface area was measured. Replicate samples were taken at two depths. Chlorophyll *a* samples were taken by using a flexible template with a known area (e.g. 6 cm^2) and scraping the periphyton within that area. The sample for analysis of chlorophyll was placed in an opaque, screw-cap centrifuge tube, and frozen until it was extracted. Methanol was used in the extraction process (Holm-Hansen and Rieman 1978); calculations were made according to Lorenzen (1967) using experimentally determined absorption coefficients (Rieman 1978).

Benthic community metobolism was measured by placing rocks from a circumscribed area of the riverbed in recirculating chambers used *in situ* and recording changes in oxygen evolution. Calculations were made of gross productivity, net community productivity, 24-hour respiration, net daily metabolism, and the productivity-respiration ratio.

Organic carbon in the seston was quantified as particulate (POC) and dissolved (DOC) on a monthly basis for the first year of the study. Analyses were conducted according to Vacarro and Menzel (1964) in which organic carbon is oxidized and quantified in an infrared detector (Oceanography International, Inc.). In order to determine how the particle sizes which are available to insect filter feeders are altered by river regulation, the particulate component of the seston was size-fractionated on a seasonal basis (September, November, and February) at the control and regulated sites. A wet filtration method was used to size fractionate samples of the seston, and the organic carbon content of each size class was determined with the use of a carbon analyzer. Particulates were sized into fractions (0.45-10 μm, 10-165 μm, 165-355 μm and 355-1000 μm) by passing known volumes of water sequentially through the different mesh sizes. Particulate organic carbon greater than 355 μm (but less than 2 cm) was collected using the insect drift nets. They were set in place for a timed interval at conditions of minimum discharge, and the flow rate was monitored so that the volume filtered could be quantified. All insects and any debris larger than 1 cm was removed prior to analysis for ash-free dry weight.

Periphyton species identifications were made by Loren Bahls (Montana Department of Environmental Sciences); he also analyzed periphyton community structure using methods described in Bahls, et al. (1979).

The substrate was characterized at each of the four sampling stations. The intermediate axis (the widest width) was measured on all surface rocks in an area encompassing 0.33 m^2. Six replicate samples were taken at random from the zone of fluctuating flows during minimum discharge from Hungry Horse Dam. Replicate samples were taken of the subsurface rocks, which were then fractionated into six size classes (>50, 50-19 19-16, 16-2, 2-.063, and <.063 mm) using soil sieving techniques. A heterogeneity index (Schwoerbel 1961) was calculated for the subsurface samples. Heterogeneity (degree of particle size diversity) was calculated by making a plot of the cumulative percentage by weight against the particle size (mm); heterogeneity = particle size 60%/particle size 10%.

Species diversity was compared at six sites on the Flathead River using Shannon and Brillouin diversity indices. They were calculated using data collected during the months of October and December, 1979 and March and July, 1980 at the South Fork, Kokanee Bend and Bible Camp samples sites. Data collected for the fish food habits study (three kick samples per site per month taken at Columbia Falls and Kalispell during March, July and October, 1980) as well as six kick samples collected in October, 1980 at Spotted Bear (above Hungry Horse Reservoir) were also used to calculated diversity indices. Samples were pooled by sampler type at each sample location and date. Values obtained by using the two indices were almost identical, so only the Shannon Index will be discussed.

The formula used for the Shannon function was $H' = \sum_{i}^{s} \left(\frac{N_i}{N}\right) \log_2 \left(\frac{N_i}{N}\right)$

where s = number of taxa in sample, N_i = number of individuals in taxon i, and $N = \sum_{i}^{s} N_i$. A value of zero is obtained when all individuals belong to the same species. The maximum value of H' depends on the number of individuals counted and is obtained when all individuals belong to different species. H' usually varies between three and four in natural stream areas and is usually less than one in polluted or stressed stream areas.

Evenness (E_v), as measured by Margalef (1957) is a ratio of the observed H' to a maximum theoretical diversity (H'_{max}) computed with all individuals equally distributed among the species. Maximum diversity (H'_{max}) was computed as $\log_2 s$; therefore evenness = $\frac{H'}{\log_2 s}$. Evenness generally ranges between 0 and 1. Perturbation reduces E_v below 0.5 and generally to a range of 0.0 to 0.3.

CORRELATION ANALYSIS OF ENVIRONMENTAL VARIABLES AND MACROINVERTEBRATE DATA

Ordination techniques were applied to the data with the use of two computer programs from the Cornell Ecology Program series - DECORANA, a Fortran program which was used for detrended correspondence analysis

(Hill 1979) and ORDIFLEX, which was utilized for polar ordination and principal components analysis (Gauch 1977). DECORANA was performed with no transformation of the data and no downweighting of rare species. Polar ordination was run with both automatic and user selected samples used as endpoints. Percentage distance was the measure used for the computation of similarity of species composition among the various samples, which is required for polar ordination. A major function of ordination was identification of groups of similar samples. The equation for the percentage distance (PD) similarity measure is:

$$PD_{jk} = IA - PS_{jk}, \text{ where } PS_{jk} = \frac{200 \cdot \sum_{i=1}^{I} \min (D_{ij}, D_{ik})}{\sum_{i=1}^{I} (D_{ij} + D_{ik})}$$

where IA is the internal association, PS is the percentage similarity, where the summations are over all species (I), D_{ij} and D_{ik} are the abundances of species i in samples j and k, and S_j and S_k are the numbers of species in samples j and k. The data was log transformed before principal components analysis was applied. The output from PCA was centered and standardized.

The reduced biological data was then related to environmental predictor variables using multiple regression and correlation analysis. These statistical methods were utilized to assess the importance of such factors as rates of flow change, temperature, substrate heterogeneity, and altered autochthonous (periphyton) and allochthonous (seston) carbon resources in determining the composition of benthic communities downstream from dams.

Correlation analyses included data from the three seasons in which environmental parameters were measured (summer, fall, and winter). Ash-free dry weight (AFDW) and chlorophyll *a* (chl *a*) measurements of periphyton biomass were included, as were particulate organic carbon (POC) measurements of the seston. The carbon fractions were lumped into two groups; the two size fractions less than 165 μm (which included most of the POC) were combined. The substrate heterogeneity index was used as the measure of substrate. The sum of the mean daily temperatures for the three months in each season was used as the measure of temperature. The rate of increase of the water level on gauges was used as the indicator of rates of change in flows at the Flathead River sites. These factors were used as the independent variables in the correlation analyses.

The dependent variables included the seasonal values obtained with the use of diversity indices and the three ordinations, detrended correspondence analysis (DECORANA), polar ordination (PO), and principal components analysis (PCA), on data collected during July, October and January. The mean monthly values for density (no/m²) and biomass (cc/m²) were averaged for the three months in each season.

Environmental data for temperature (degree days summed by season), flow (velocity rates of change), substrate heterogeneity, coarse (165-

1000 μm) and fine (.45-165 μm) POC in the seston, ash-free dry weight (AFDW) and Chl *a* in the periphyton, and gross community productivity were ordinated for three seasons using detrended correspondence analysis (DECORANA).

RESULTS AND DISCUSSION

A total of 432 quantitative benthic samples were picked and analyzed numerically and volumetrically during this study.

SPECIES DIVERSITY AND COMMUNITY ORDINATIONS

The benthic invertebrate composition was grossly different in the South Fork than at the mainstem stations. Species diversity was low in the South Fork. Reductions in species diversity in the tailwater areas downstream from hypolimnial release reservoirs have been found by a number of researchers (e.g. Pearson et al. 1968, Hilsenhoff 1971, Hoffman and Kilambi 1971, Spence and Hynes 1971, Fisher and Lavoy 1972, Lehmkuhl 1972, Ward 1974 and 1976, and Young et al. 1976). The fauna in the South Fork was dominated by the dipteran family Chironomidae (Appendix A). Reproducing populations of turbellarians, nematodes, oligochaetes, and water mites were also present. A few other insect species may complete their life cycles under the constant temperature conditions that exist in the South Fork, although their populations were very small. These included the stoneflies, *Zapada columbiana*, *Zapada cinctipes*, *Capnia spp.*, *Utacapnia spp.*, *Taenionema pacificum*, *Sweltsa sp.*, and *Kogotus modestus*, the mayflies *Baetis tricaudatus*, *Baetis bicaudatus*, *Rhithrogena robusta*, *Cinygmula sp.* and *Epeorus grandis*, the caddisfly *Rhyacophila verrula*, and the dipteran *Simulium arcticum*.

A total of 46 species of insects have been collected in the South Fork. Because only one or a few individuals of many of these species were collected, it is unlikely that they have reproducing populations in the South Fork. Many of these probably drifted downstream from Fawn Creek, a tributary of the South Fork. In September, 1979, five qualitative samples were taken in Fawn Creek. All but two of the species found in the South Fork during the fall season were collected in the Fawn Creek samples, providing circumstantial evidence that these species could be drifting from Fawn Creek. Some of the species collected in the South Fork were characteristic of smaller streams like Fawn Creek and have not generally been reported in rivers as large as the Flathead River. Many of these species may exist for a time in the South Fork because they are adapted to the colder, more constant temperatures found in headwater streams.

In contrast to the South Fork, both the control and partially regulated stations on the mainstem Flathead River had diverse insect faunas. A total of 97 species have been identified at the control site and 95 species at the partially regulated site.

A species list was compiled which included all of the species collected during the course of the study (Table 1). The relative abundance of species is indicated: rare = 1 or 2 specimens collected during the entire study; infrequent = an average of less than $10/m^2/year$; abundant = $>1000/m^2/year$. The common category is by far the most inclusive. The Chironomidae, some other dipteran groups, and certain species of the Coleoptera and Hemiptera were identified only to family, so the species

Table 1. Species list (R = rare, I = infrequent, C = common, A = abundant)

	Unregulated	Partially Regulated	Regulated
EPHEMEROPTERA	27	25	14
Siphlonuridae			
Siphlonurus sp.	R		
Ameletus cooki	C	C	
Ameletus sparsatus	C	C	
Ameletus oregonensis	I	I	
Ameletus connectus	R		
Parameletus sp.		R	
Baetidae			
Baetis tricaudatus	A	C	C
Baetis bicaudatus	R	R	C
Baetis hageni	C	C	
Baetis propinquus	I	I	
Pseudocleon sp.	C	C	
Callibaetis sp.		R	
Heptogeniidae			
Rhithrogena hageni	A	C	R
Rhithrogena robusta	I	I	R
Epeorus albertae	C	I	
Epeorus longimanus	C	C	R
Epeorus grandis			I
Epeorus (Iron) sp.	R	R	R
Epeorus deceptivus			R
Cinygmula tarda	C	C	I
Ephemerellidae			
Ephemerella inermis	C	C	R
Drunella doddsi	C	C	R
Drunella flavilinea	C	C	R
Drunella spinifera	I	I	
Caudatella heterocaudata	I	I	R
Caudatella hystrix	R		
Serratella tibialis	C	C	R
Timpanoga hecuba	R		
Leptophlebiidae			
Paraleptophlebia heteronea	C	I	
Paraleptophlebia bicornuta	I	I	
PLECOPTERA	35	29	19
Pteronarcidae			
Pteronarcys californica	I	I	
Pteronarcella badia	C	C	R

Table 1. (Continued)

	Unregulated	Partially Regulated	Regulated
Plecoptera - continued			
Peltoperlidae			
Peltoperla brevis			R
Taeniopterygidae			
Taenionema pacificum	C	C	I
Doddsia occidentalis	I	I	
Nemouridae			
Zapada cinctipes	C	C	I
Zapada columbiana	R	R	I
Prostoia besametsa	C	C	R
Amphinemura sp.	R		R
Visoka cataractae			R
Leuctridae			
Despaxia augusta			R
Capniidae			
Capnia confusa	C	C	I
Utacapnia poda	C	C	
Utacapnia distincta	C	C	
Utacapnia columbiana	C		
Utacapnia trava	C		
Isocapnia sp.			R
Isocapnia crinita	C	C	
Isocapnia missourii	C	C	
Isocapnia grandis	I	C	
Isocapnia vedderensis	I	I	
Eucapnopsis brevicauda	I	I	
Perlidae			
Classenia sabulosa	C	C	
Hesperaperla pacifica	C	C	
Calineuria californica	R		R
Doroneuria theodora			R
Perlodidae			
Skwala parallela	C	C	
Diura knowltoni	C	C	
Isogenoides colubrinus	C	C	
Cultus pilatus		I	
Setvena bradleyi			R
Megarcys watertoni	R		R
Kogotus modestus	R		R

Table 1. (Continued)

	Unregulated	Partially Regulated	Regulated
Plecoptera - Perlodidae (Continued)			
Isoperla fulva	C	C	
Isoperla patricia	I	I	
Chloroperlidae			
Sweltsa coloradensis	C	C	R
Suwallia pallidula	C	C	R
Suwallia autumna	C	C	
Trisnaka diversa	C	C	
Utaperla sopladora	R		
Alloperla severa	I	I	
Paraperla frontalis	R	R	
TRICHOPTERA	19	23	10
Philopotamidae			
Wormaldia sp.		R	
Hydropsychidae			
Arctopsyche grandis	I	C	
Parapsyche elsis			R
Hydropsyche oslari	C	I	
Hydropsyche cockerelli	C	I	R
Hydropsyche occidentalis	C	I	R
Rhyacophilidae			
Rhyacophila angelita	C	C	R
Rhyacophila bifila	C	C	R
Rhyacophila coloradensis	I	I	R
Rhyacophila vaccua	I	I	
Rhyacophila vagrita			R
Rhyacophila vao	I	I	
Rhyacophila vepulsa		I	R
Rhyacophila verrula			I
Glossosomatidae			
Glossosoma alascense	C	C	
Glossosoma excitum	C	C	
Glossosoma pterna	C	C	
Glossosoma velona	R	R	
Glossosoma sp.			R
Agapetus sp.		R	

Table 1. (Continued)

	Unregulated	Partially Regulated	Regulated
Trichoptera - Continued			
Hydroptilidae			
Hydroptila ajax	I	I	
Brachycentridae			
Brachycentrus americanus	I	C	
Brachycentrus occidentalis	I	C	
Lepidostomatidae			
Lepidostoma pluviale	I	I	
Limnephilidae			
Apatania sp.		I	
Neophylax rickeri	I	I	
Onocosmoecus unicolor	I	I	
HEMIPTERA			
Corixidae	I	I	
COLEOPTERA			
Haliplidae			
Brychius sp.	I	I	
Dytiscidae		I	
Elmidae			
Heterlimnius sp.		R	
Narpus sp.	R		
Optioservus quadrimaculatus	C	C	
Zaitzevia parvula	C	C	
DIPTERA	11	12	3
Deuterophlebiidae		R	
Blephariceridae	I	I	
Tipulidae			
Antocha sp.	R	R	
Hexatoma sp.	C	I	
Tipula sp.	R	R	
Ceratopogonidae	I	I	

Table 1. (Continued)

	Unregulated	Partially Regulated	Regulated
Diptera - continued			
Simuliidae			
Simulium arcticum	C	C	C
Chironomidae	C	A	A
Tanyderidae			
Protanyderus sp.	I	C	
Athericidae			
Atherix variegata	I	C	
Empidiae			
Chelifera sp.	I	I	
Hemerodromia sp.	I	I	R
TOTAL	97	95	46

list is an underestimate of the total population. Species lists for the control and partially regulated sites were similar, but there were a number of differences in the abundance of species at the two sites.

Species diversity was compared at six sites on the Flathead River using the Shannon diversity index. The mean of the diversity indices for the four seasons for which they were calculated was 0.8 at the South Fork station and generally 3.1 to 3.3 at the main river sites (Table 2). Thus no significant differences in overall diversity were shown between the control and partially regulated sites. Differences in composition were found between the main river sites, but diversity indices do not take into account the species involved.

Although diversity has been considered an intrinsic property of communities, the more recent view is that it is too vague (Hurlbert 1971) and that the two components (species richness and equitability) often vary independently (Moore 1975). Ordination and clustering methods are currently considered to be more informative methods for reducing biological data and arraying it spatially. Ordination techniques were applied to the data using two computer programs from the Cornell Ecology Program series. DECORANA was used for detrended correspondence analysis (Hill 1979), and ORDIFLEX was used for polar ordination and principal components analysis (Gauch 1977).

Ordination values are based on the similarity of the quantitative species composition at the various sites. The various ordination techniques use different mathematical methods to determine the compositional similarities between samples. Each of the samples (8-10 samples at each station for each of the four months these techniques were applied to the data) was ordinated separately in each season, and then the output values for each sample were averaged to give a mean for each sample station. Mean values for the primary axis are presented for each of the ordination techniques (Table 3). The values for each site should not be viewed as absolutes, rather the relative distance between sites is the important parameter. All of the ordination techniques produced a spatial gradient between regulated and control sites. Values of the subsequent axes (not presented in Table 3) can be used to array the samples in multi-dimentional space. The relationship between stations is best seen by arraying the values for the axes in two or three-dimensional space. Two examples of the spatial relationships are presented: DECORANA for the spring season (Figure 10) and polar ordination applied to fall data (Figure 11); values from the regulated Kootenai River system are included for comparative purposes. All ordination techniques in all four seasons ordered well along an axis corresponding to disturbances due to river regulation.

ABUNDANCE AND DISTRIBUTION

The 1980 water year (October 1979 to September 1980) was used for detailed comparisons of numbers (no./m^2) and biomass (cc/m^3) at the three sample stations. Accurate quantification of numbers and biomass was

Table 2. Shannon Diversity Indices

		October		December		March		July			
		Kick	Circular	Kick	Circular	Kick	Circular	Kick	Circular	$\bar{x}$	s.d.
South Fork	H'	0.22	0.17	0.6	0.22	0.97	1.0	1.79	1.15	0.8	(0.6)
	Ev	0.06	0.06	0.14	0.05	0.22	0.24	0.37	0.26	0.18	(0.12)
Columbia Falls	H'	3.32				2.65	2.33	3.3		2.9	(0.5)
	Ev	0.63				0.57	0.45	0.61		0.57	(0.08)
Kokanee Bend	H'	3.05	3.17	3.18	3.26	2.99	3.08	3.7	3.64	3.3	(0.3)
	Ev	0.59	0.59	0.62	0.61	0.59	0.61	0.67	0.72	0.63	(0.05)
Kalispell	H'	3.33				2.93		3.51		3.3	(0.3)
	Ev	0.64				0.60		0.72		0.65	(0.06)
Bible Camp	H'	3.07	2.81	3.16		2.79	2.96	3.42	3.4	3.1	(0.3)
	Ev	0.57	0.57	0.59		0.53	0.57	0.64	0.65	0.59	(0.04)
Spotted Bear	H'	3.23								3.25	
	Ev	0.57								0.57	

Table 3. Values (mean and standard deviations of eight samples) obtained for the primary axis using three community ordination techniques - detrended correspondence analysis (DECORANA), polar ordination (P.O.) and principal components analysis (P.C.A.). Eigenvalues (Eig = amount of the variation explained by the first axis = % EV).

	Fall - October, 1979			Winter - December, 1979		
	DECORANA Eig. .507	P.O.	P.C.A. % EV 55.0	DECORANA Eig. .704	P.O.	P.C.A. % EV 21.8
South Fork (regulated)	268.7(1.8)	91.2(9.0)	85.0(9.4)	0.6(0.9)	82.5(7.5)	23.1(10.6)
Kokanee Bend (partially regulated)	17.9(13.1)	43.3(1.3)	4.5(0.9)	75.4(20.6)	51.3(4.9)	7.0(5.5)
Bible Camp (reference)	57.0(16.5)	36.8(4.2)	3.2(1.6)	72.1(13.6)	42.4(4.5)	5.5(3.6)
Columbia Falls (partially regulated)	132.7(9.0)	45.2(2.5)	7.6(2.1)	N.S.	N.S.	N.S.
Kalispell (partially regulated)	133.7(14.6)	44.3(2.7)	7.3(2.2)	N.S.	N.S.	N.S.
Spotted Bear (reference)	193.3(8.7)	38.9(4.5)	6.2(1.3)	N.S.	N.S.	N.S.

	Spring - March, 1980			Summer - July, 1980		
	DECORANA Eig. .503	P.O.	P.C.A. % EV 24.3	DECORANA Eig. .454	P.O.	P.C.A. % EV 26.5
South Fork (regulated)	12.1(6.5)	87.7(9.7)	71.6(14.5)	12.0(7.9)	91.0(6.5)	83.8(12.1)
Kokanee Bend (partially regulated)	103.6(15.1)	52.7(7.6)	6.3(5.1)	140.8(27.3)	50.5(5.0)	8.0(5.9)
Bible Camp (reference)	173.9(31.7)	41.7(2.4)	7.4(4.9)	135.4(17.1)	52.4(3.4)	8.0(4.6)
Columbia Falls (partially regulated)	83.5(21.7)	59.7(4.6)	11.5(4.4)	186.3(26.5)	45.6(6.0)	4.8(2.8)
Kalispell (partially regulated)	146.0(11.4)	47.0(2.9)	8.8(1.0)	139.7(16.5)	41.9(6.1)	7.4(3.8)

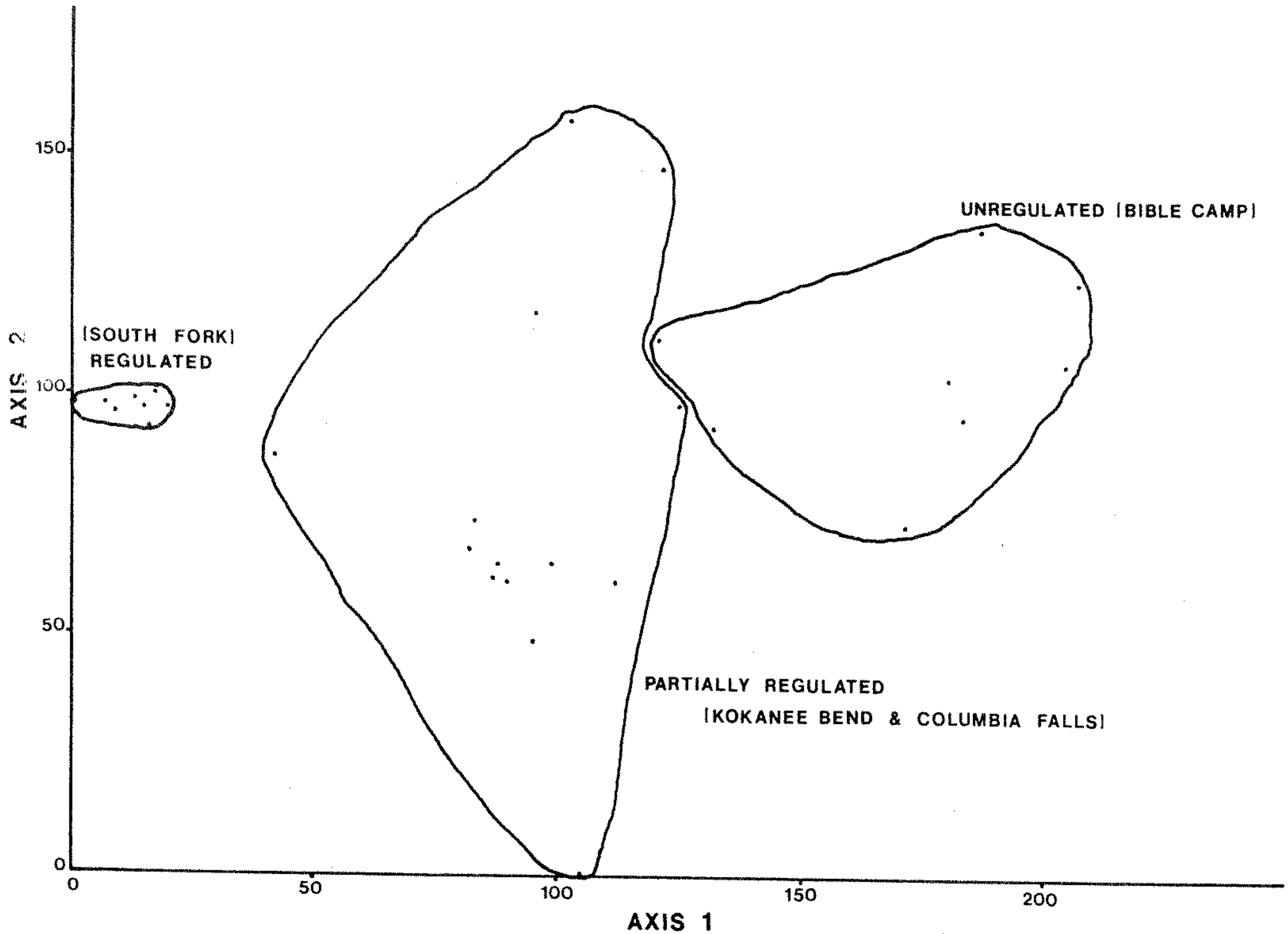

Figure 10. Values for the first and second axes of the detrended correspondence analysis (DECORANA) which was run on data from March, 1980. Points represent individual samples and all samples from one sample station are circumscribed.

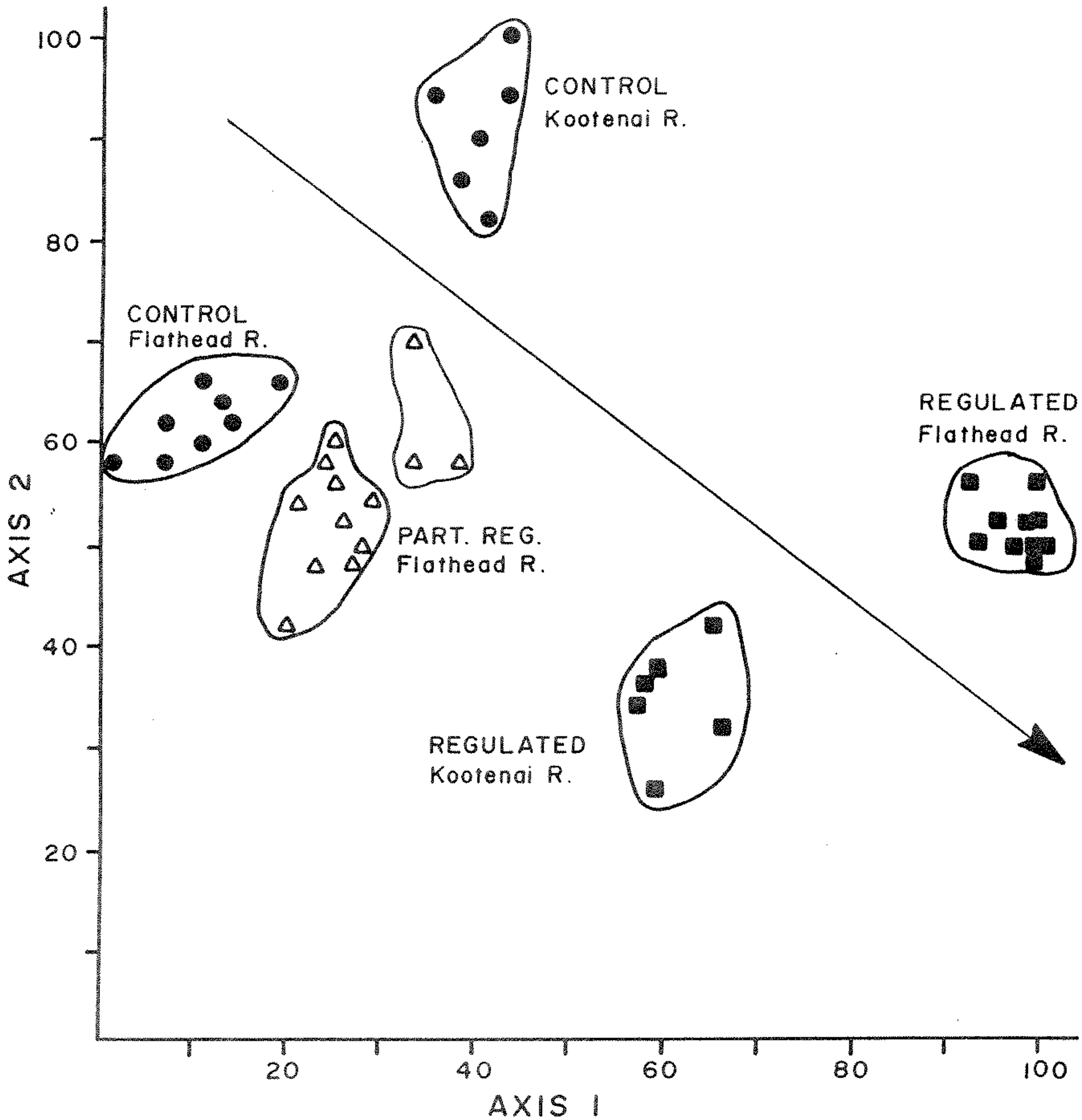

Figure 11. Values for the first and second axes of a polar ordination which was run on data from the Flathead and Kootenai River samples collected in October 1979. Points represent individual samples and all samples from one study station are circumscribed.

difficult in a large, regulated river. With our sampling gear, it was possible to sample only at minimum flows near the shore in riffle areas. The highest densities were found near waters edge where current speeds were slower than those near the middle of the river. The Flathead River had an extensive hyporheic zone which could not be sampled. The channel and adjacent substrata were composed of loosely compacted flood-plain gravels. Water circulated deep within the substrate and laterally from the river channel (Stanford and Gaufin 1974). This subterranean habitat was colonized by certain species of macrobenthos, in particular, a few species of stoneflies which were collected only when they were near emergence (e.g. Isocapnia spp.).

The Bible Camp site was frozen during the winter and could not be sampled during January and February. Densities were low at the Kokanee Bend site during the winter months, suggesting that some species may have moved deeper into the substrate. It was also difficult to sample during the runoff period, although reasonably good samples were obtained at waters edge during June after the shoreline areas were recolonized. It was not possible to sample during May when the runoff began, because insects had not colonized recently wetted areas.

Mean numbers per square meter were calculated for each insect order at each site by month (Appendix B - Tables and Figures). The Chironomidae were treated separately due to the large numbers represented by this family of dipterans in regulated areas. The monthly means were averaged to give an annual mean (Table 4, Figure 12). The chironomids and oligochaetes dominated in the South Fork and the mayflies, stoneflies, and caddisflies were much reduced. The annual mean for the mayflies was much higher at the control site, but the annual mean numbers of the other orders were larger at the partially regulated site.

The annual mean number/m² of total macroinvertebrates was highest in the South Fork (10,472). This was significantly different from the Bible Camp (6,666) and Kokanee Bend (6,412) sites (based on an analysis of variance (ANOVA) test run on log transformed monthly mean densities). The total number of invertebrates was most affected by the numerically dominant groups - the midges, blackflies, certain mayflies and large numbers of small instars of any of the common species. During most months the total number of invertebrates per square meter was highest in the South Fork (Figure 13). Differences between the Bible Camp and Kokanee Bend sites were due to compositional shifts and differences in the timing of life cycles at the two sites.

Density and Biomass Estimates

The mean monthly densities of the three insect orders most sensitive to perturbation were graphed for the South Fork (Figure 14), Kokanee Bend (Figure 15), and Bible Camp (Figure 16) study sites. Small densities of Plecoptera and especially the Trichoptera were found in the South Fork. The Ephemeroptera showed an increase from January to May. This may have been due in part to the lack of generation at Hungry Horse Dam

Table 4. Densities ($\bar{x}$ no./m^2) (Kick + Circular Samples)
Annual Mean of Monthly Means (October 1979 - September 1980)

	Bible Camp n=9 $\bar{\bar{x}}$(s.d.)	Kokanee Bend n=9 $\bar{\bar{x}}$(s.d.)	South Fork n=11 $\bar{\bar{x}}$(s.d.)
Ephemeroptera	3,608(1,789)	1,738(899)	330(193)
Plecoptera	990(1,201)	1,335(1,753)	76(37)
Trichoptera	374(332)	522(483)	8(7)
Chironomidae	1,427(534)	1,739(992)	8,931(3,078)
Other Diptera	194(359)	708(1,465)	148(313)
Other Invertebrates	74(56)	370(269)	979(344)
TOTAL	6,666(3,072)	6,412(3,539)	10,472(3,186)
Percent Composition	%	%	%
Ephemeroptera	54.1	27.1	3.2
Plecoptera	14.9	20.8	0.7
Trichoptera	5.6	8.1	0.08
Chironomidae	21.4	27.1	85.3
Other Diptera	2.9	11.0	1.4
Other Invertebrates	1.1	5.8	9.3

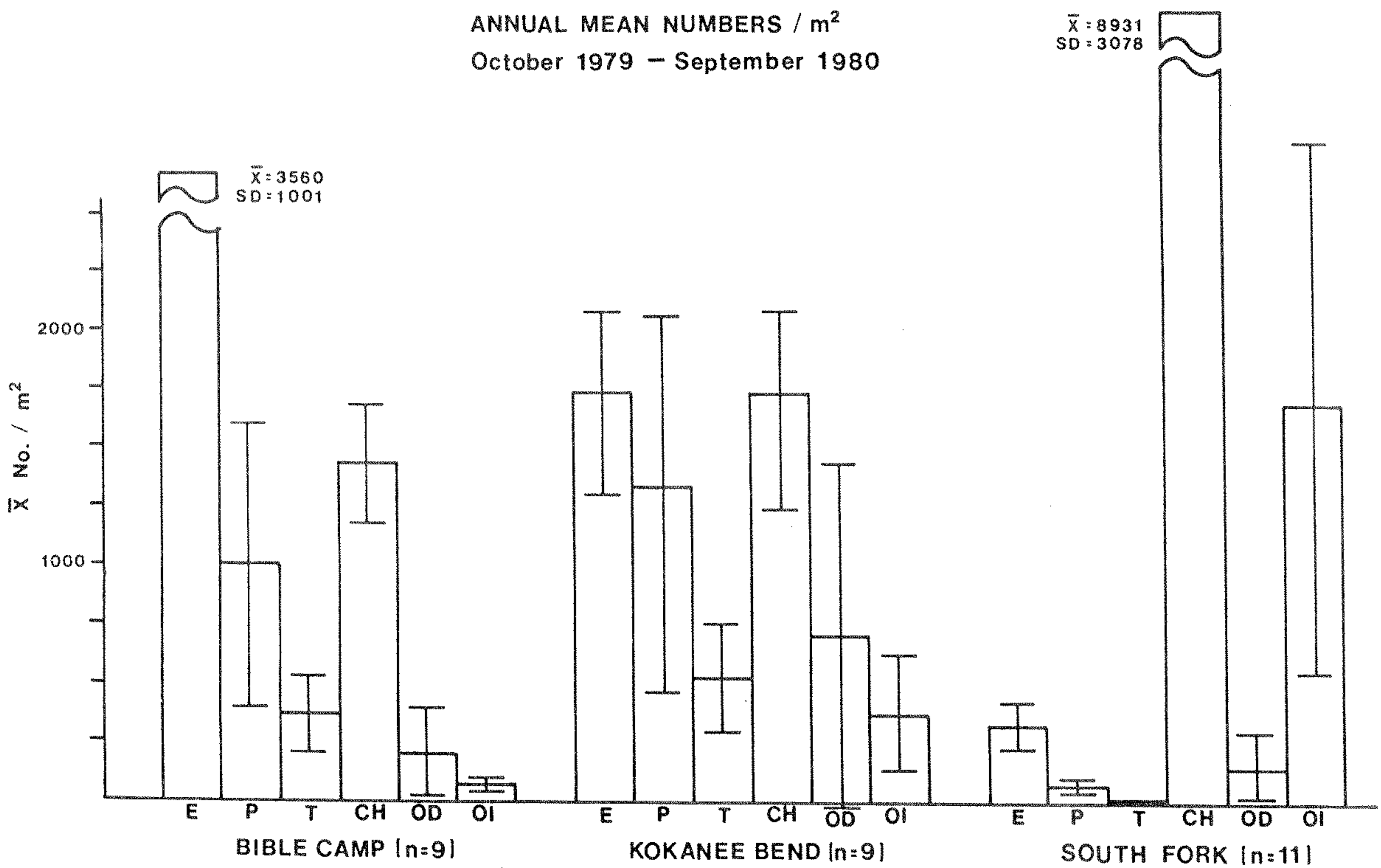

Figure 12. Mean number of invertebrates per square meter; annual means of monthly means. Bars represent means, I represents standard deviations. E = Ephemeroptera; P = Plecoptera; T = Trichoptera; Ch = Chironomidae; OD = Other Diptera; OI = Other Invertebrates.

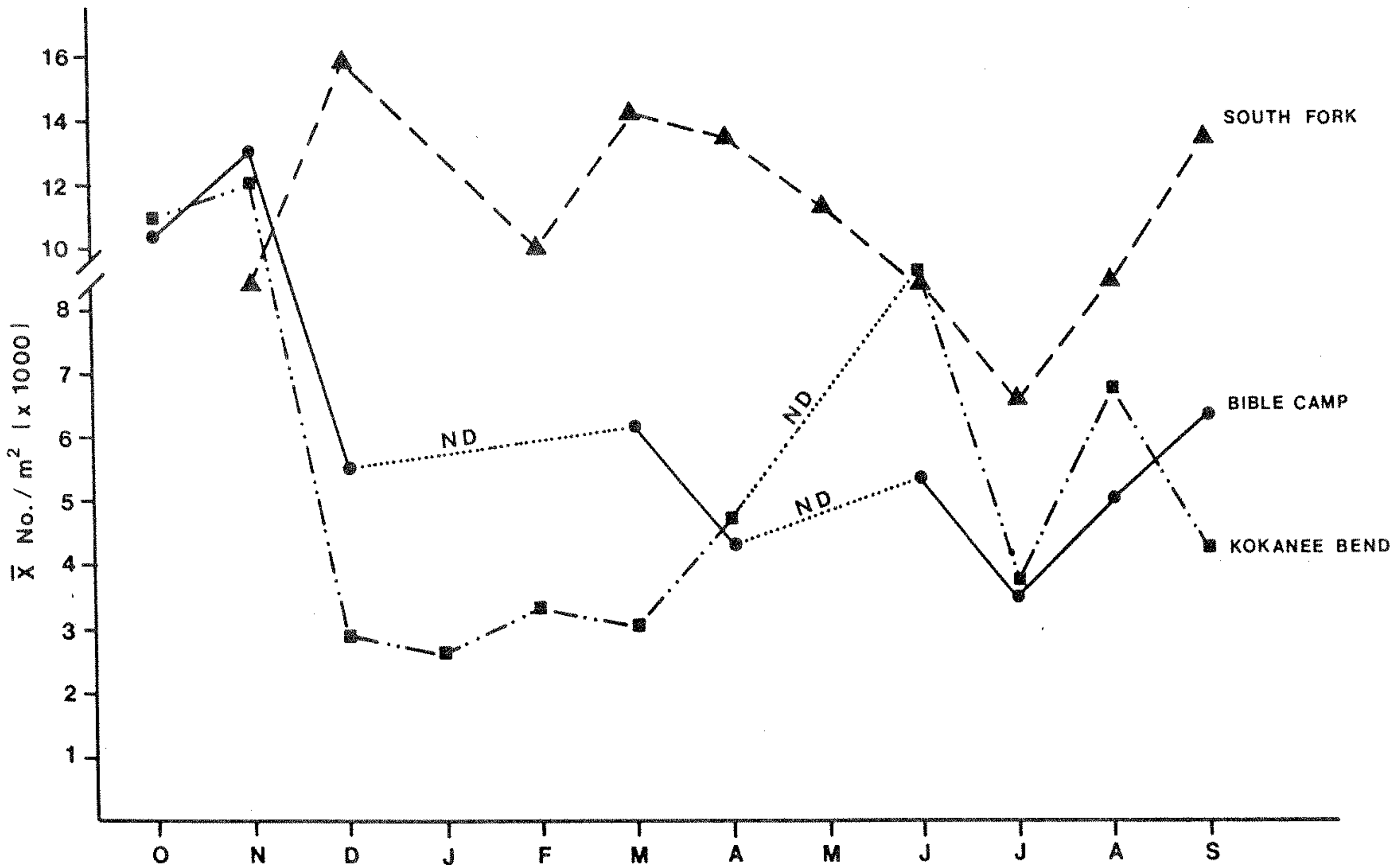

Figure 13. Mean numbers of total invertebrates per square meter, October, 1979 through September, 1980.

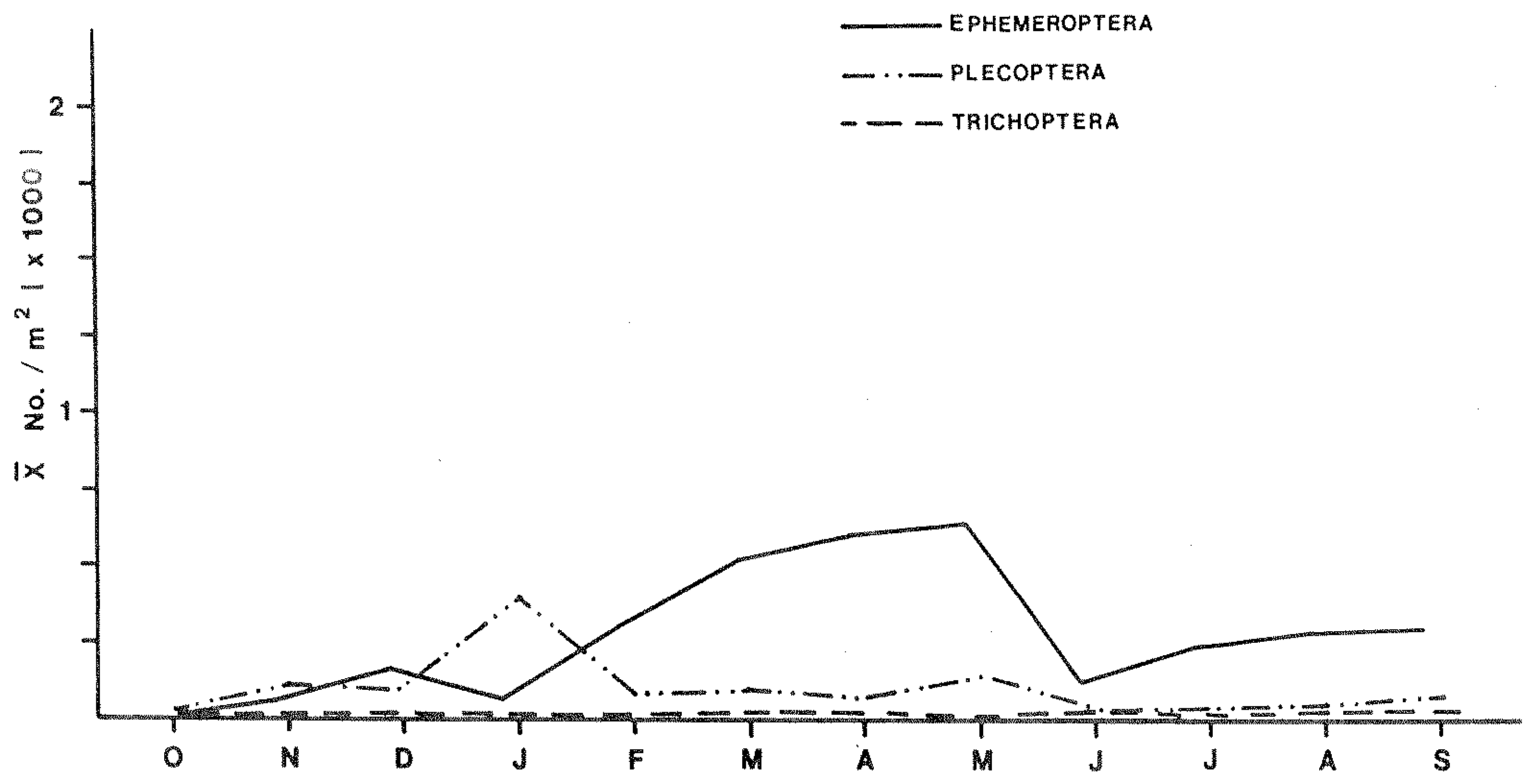

Figure 14. Mean number/m^2 of the insect orders Ephemeroptera, Plecoptera, and Trichoptera at the South Fork (regulated) sampling site, October 1979 - September 1980.

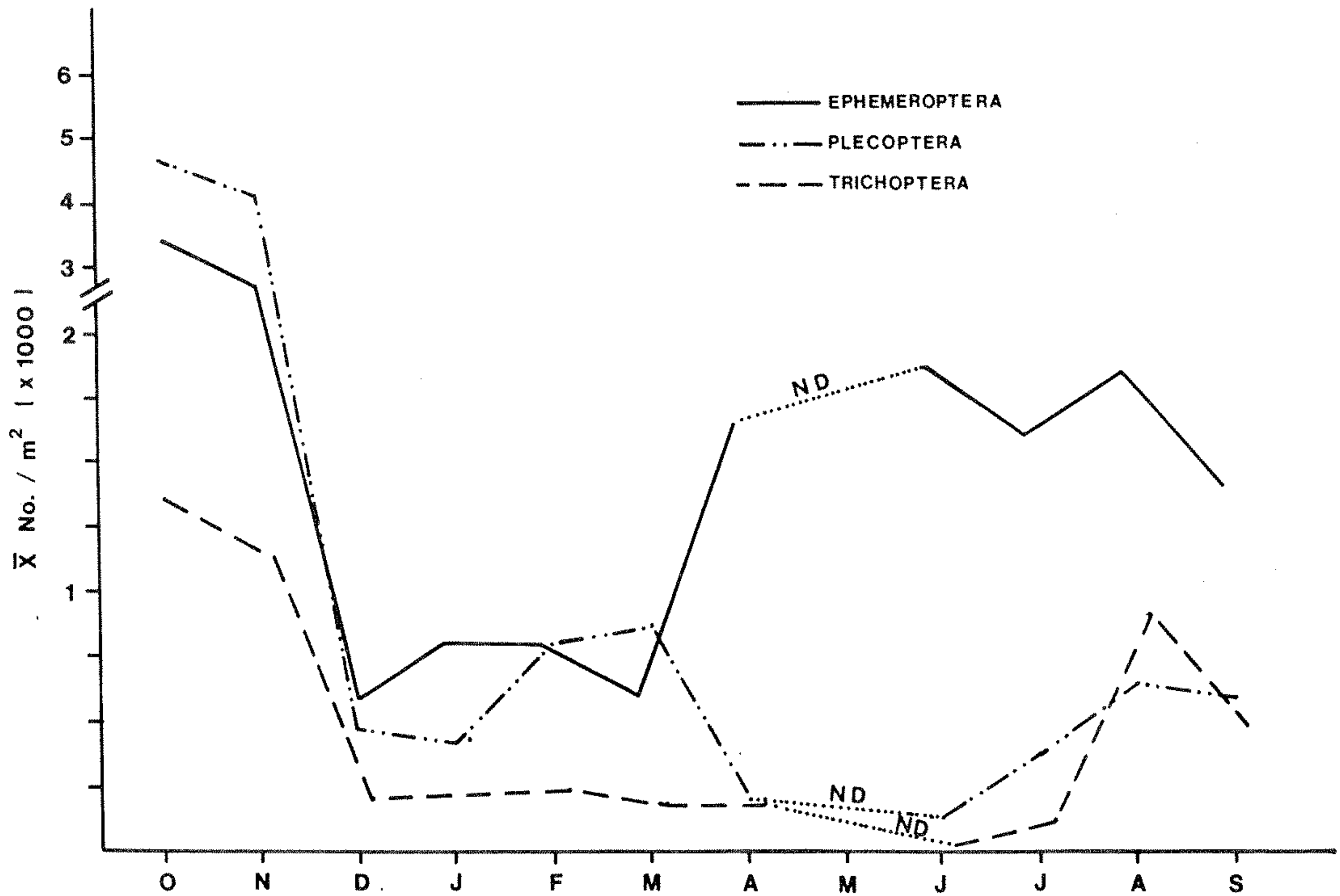

Figure 15. Mean number/m² of the insect orders Ephemeroptera, Plecoptera and Trichoptera at the Kokanee Bend (partially regulated) sampling site, October 1979 - September 1980; N.D. = no sample taken.

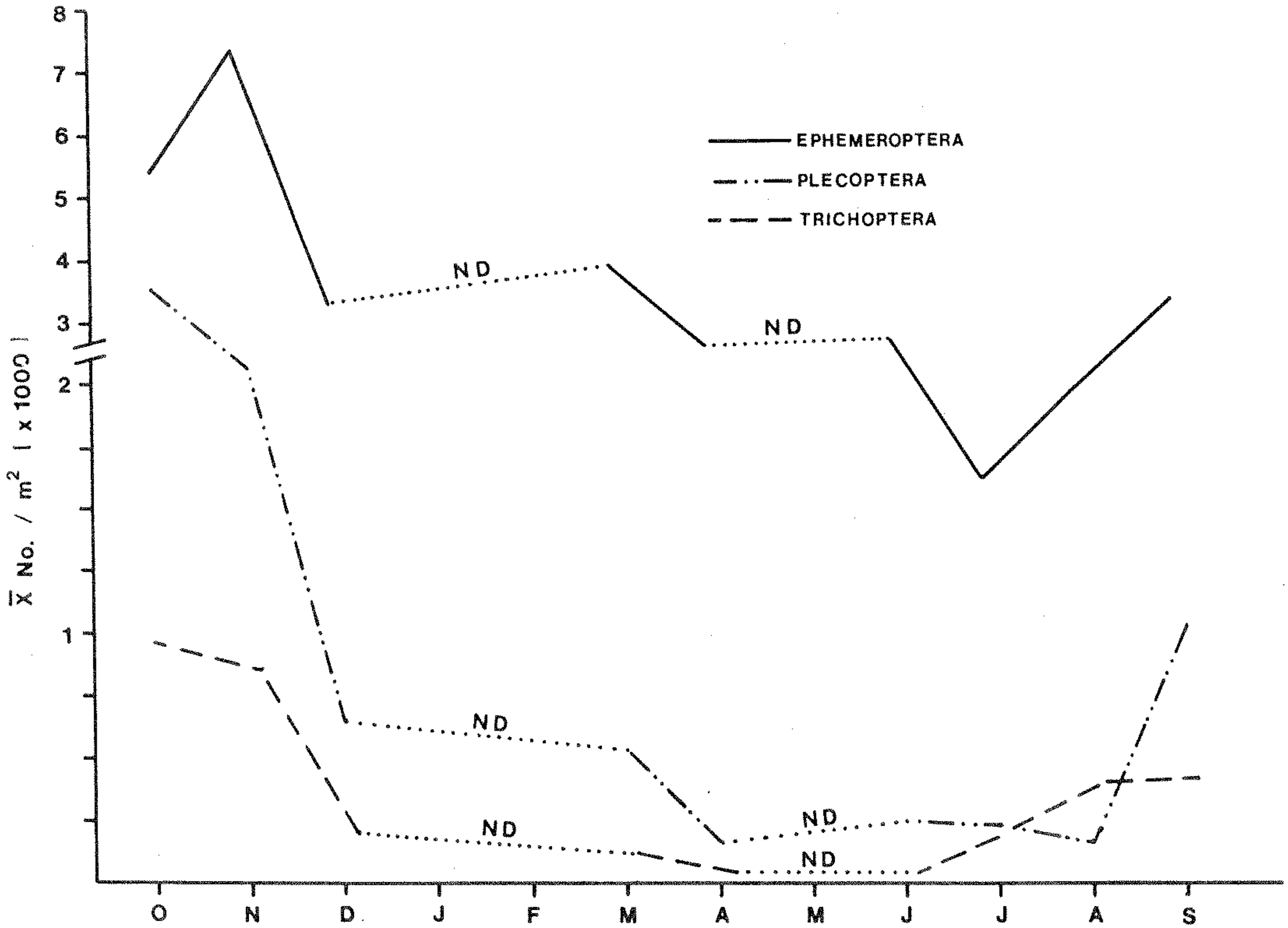

Figure 16. Mean number/m² of the insect orders Ephemeroptera, Plecoptera and Trichoptera at the Bible Camp (control) sampling site, October 1979 - September 1980; N.D. = no sample taken.

during the winter months (Figure 7), which may have allowed thermally tolerant species to build up populations through drift from Fawn Creek. This winter maximum in mayfly numbers is shifted from the population maximum of Ephemeroptera in October and November at the other two sites (Figure 17). In part, it may reflect differences in the life cycles of the different species of mayflies which inhabit the South Fork and main river sites.

Numbers of Plecoptera and Trichoptera generally paralleled each other through time at the mainstem sites (Figures 15 and 16). Numbers of these two orders of insects were generally higher at Kokanee Bend than at the Bible Camp. Ephemeroptera were collected in larger numbers at the Bible Camp than at the Kokanee Bend site (Figure 17). This trend was especially marked in December and March. The fall increase in these three orders at both sites reflected the life cycle patterns of the most abundant species. Many mayflies and caddisflies and some stoneflies emerged in the late spring, summer and early fall months. Numbers of these orders of insects tended to peak in October, then started to decrease as normal demographic events led to fewer, larger insects of many species.

Mayflies

The species lists were similar for the Bible Camp and Kokanee Bend sites (Table 1), but a number of species showed marked changes in density at these sites (Tables 5 and 6). Most mayfly species were more abundant at the control site. The reduction in mayflies at Kokanee Bend could indicate a reduction in fine particulate organic matter in the substrate. The clearwater discharges from the dam would remove the finer organic sediments on which some species of mayflies feed. Webster et al. (1979) developed a model of the effects of impoundment on organic matter transport which predicted no deposition of benthic particulate organic matter below the resevoir due to the fact that repeated rising discharges suspend smaller and lighter particles and transport them downstream. Many mayflies are found in the shallow water along water's edge during their early developmental stages. These shoreline areas were particularly affected by fluctuating flows.

Two of the common heptageniid species, *Rhithrogena hageni* and *Epeorus longimanus*, have their gills arranged to form a suction cup which assists in maintaining their position on rock surfaces. Rapid water fluctuations and increased algal growths probably impaired the efficiency with which they could maintain their positions in the boundary layer on the surfaces of rocks. Henricson and Müller (1979) suggested that those species of mayflies which overwinter as eggs or small quiescent nymphs deep in the substrate may be better pre-adapted to regulated conditions, since they are exposed to flow fluctuations for only a short time as active, full-grown nymphs. *Serratella tibialis* and *Pseudocleon sp.* fall into this category and are the only mayfly species which were found in greater numbers at the Kokanee Bend site.

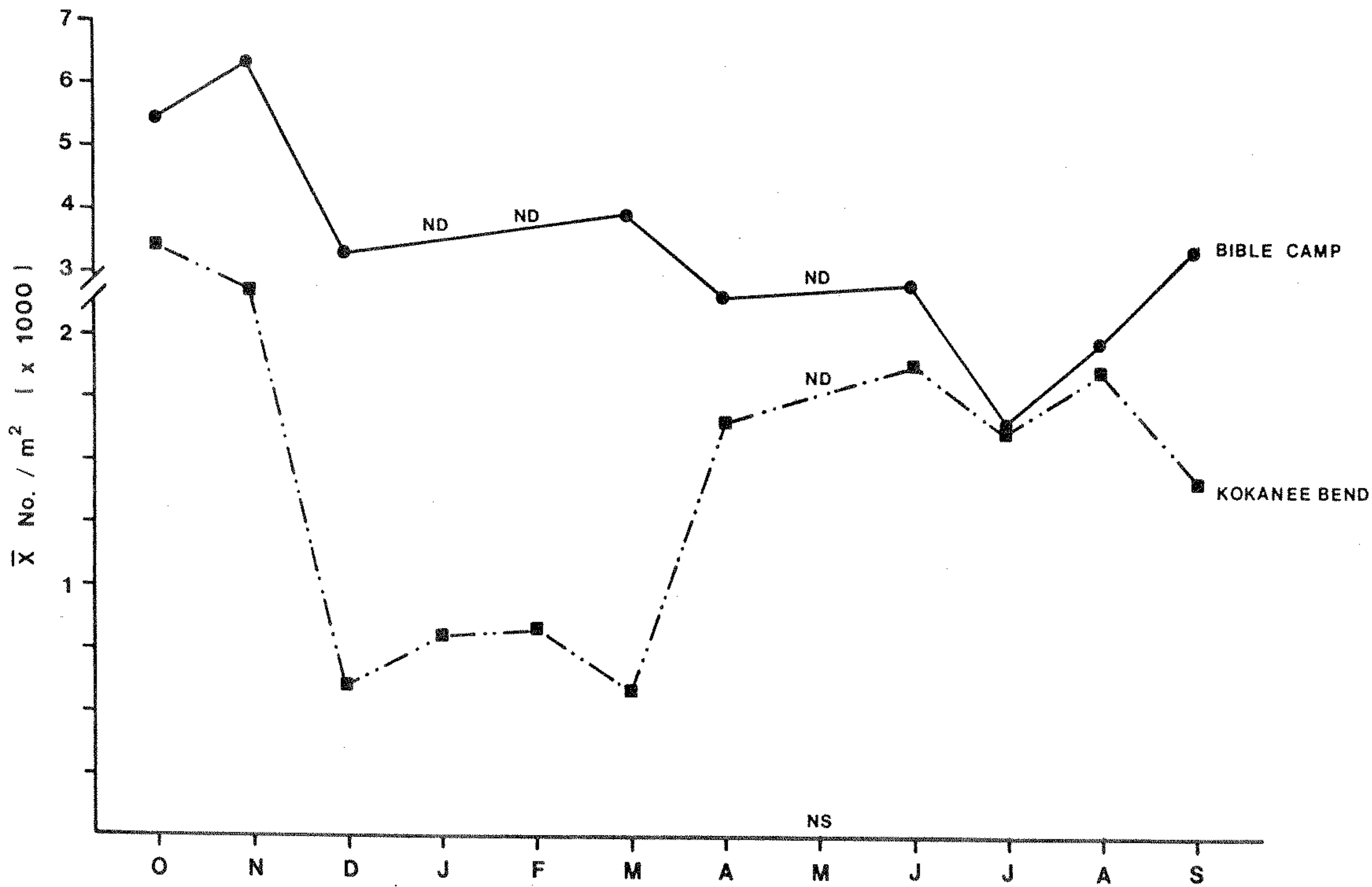

Figure 17. Mean number/m² of the insect order Ephemeroptera at the control (Bible Camp) and partially regulated (Kokanee Bend) sampling site, October 1979 - September 1980; N.D. = no sample taken.

Table 5. Macroinvertebrates with higher densities in the free-flowing Flathead River (Bible Camp sampling site). Annual mean number/m² (October 1979 - September 1980).

	Bible Camp $\bar{x}$(s.d.)	Kokanee Bend $\bar{x}$(s.d.)
EPHEMEROPTERA		
Baetis hageni	247(277)	43(75)
Rhithrogena hageni	1,079(910)	258(179)
Epeorus sp.	116(78)	37(85)
Ephemerella doddsi	59(58)	28(30)
Ephemerella inermis	198(188)	111(138)
Paraleptophlebia heteronea	36(36)	3(4)
TRICHOPTERA		
Symphitopsyche oslari	130(183)	20(36)
Symphitopsyche cockerelli	35(40)	11(15)
Hydropsyche occidentalis	33(42)	4(6)
DIPTERA		
Hexatoma sp.	7(9)	3(3)

Table 6. Macroinvertebrates with higher densities in the partially regulated Flathead River (Kokanee Bend sampling site). Annual mean number/m² (October 1979 - September 1980).

	Bible Camp $\bar{x}$(s.d.)	Kokanee Bend $\bar{x}$(s.d.)
EPHEMEROPTERA		
Ephemerella tibialis	80(96)	204(253)
PLECOPTERA		
Pteronarcella badia	27(56)	63(61)
Capniidae	174(144)	341(264)
Chloroperlidae	38(34)	104(84)
TRICHOPTERA		
Arctopsyche grandis	21(31)	190(248)
Glossosoma sp.	43(120)	234(385)
DIPTERA		
Atherix variegata	3(5)	7(9)
Simulium arcticum	196(449)	706(1,447)

Stoneflies

A number of stonefly species do not show significantly different densities at the two main river sites. The families Capniidae and Chloroperlidae were found in larger numbers at the Kokanee Bend site. *Pteronarcella badia* also occurred in consistently larger densities at the Kokanee Bend site. It is a shredder which is often found in depositional areas. Wood and large particulate matter were collected much more frequently in our sample nets at Kokanee Bend and there are indications that course particulate organic matter was more abundant in the substrate in the regulated areas. This may be related to the fact that fluctuating flows can collect more debris from shoreline areas. After the spring runoff the river channel is removed from shoreline vegetation in unregulated areas.

Caddisflies

Caddisflies often show compositional changes in regulated areas (Henricson and Müller 1979). In the Flathead River, *Arctopsyche grandis* was much more abundant at the partially regulated site, and the other hydropsychid species (*Hydropsyche oslari, H. cockerelli, H. occidentalis*) were more abundant at the control site (Tables 4 and 5). Hauer (1980) found the same relative abundances of these species in the free-flowing North and Middle Forks and further downstream in the partially regulated mainstem river. *Arctopsyche* is a large particle feeder (mesh net openings generally vary from 400-500 μm, Wallace et al. 1979). Carbon fractionation work has shown differences in available particle sizes at the two sites. It may also be that *Arctopsyche* is more resistant to current fluctuations (perhaps because their nets are stronger). *Glossosoma sp.* showed a marked increase in density at the partially regulated site. It is an algal scraper and is probably more abundant due to increased periphytic growth in the regulated areas. The saddle cases it constructs and firmly affixes to rock surfaces would also make it more resistant to displacement or desiccation due to flow changes. *Brachycentrus spp.* is another grazer which was found in higher numbers at the partially regulated site.

Dipterans

Most dipterans were collected in greater numbers at the Kokanee Bend site (e.g. Blephariceridae, Deuterophlebiidae, *Antocha sp.*, *Atherix variegata, Protanyderus sp., Simulium arcticum,* and the Chironomidae). The first two families have suckers which would enable them to hold on during velocity changes; they also are algal scrapers and periphyton was more abundant in regulated areas. *Atherix, Protanyderus* and many Chironomidae are burrowers which would not be as subject to catastrophic drift during the quick velocity changes due to regulation. *Simulium arcticum* abundances may be related to larger amounts of the smaller size fractions of particulate organic matter in the seston at Kokanee Bend.

The annual mean of mean monthly estimates of biomass (cc/m^2) indicated that the total biomass of macroinvertebrates was not significantly different at the three sites (based on an ANOVA test). Kokanee Bend data showed slightly higher values on an annual basis (13.9) than the Bible Camp (11.9) and South Fork (11.9) data (Table 7, Figure 18). The Chironomidae and oligochaetes still dominated the fauna in the South Fork, but not by the overwhelming proportion that was characteristic of the density estimates.

The biomass data from the Bible Camp and Kokanee Bend stations showed the same general trend on an annual basis as the numerical data. Biomass of mayflies was higher at the Bible Camp, biomass of stoneflies and caddisflies was higher at Kokanee Bend, and the Chironomidae and Other Invertebrate categories were not significantly different. Other Invertebrate category included dipterans other than the chironomids, as well as non-insect invertebrates.

Percent composition was calculated from the means of annual density and biomass (Tables 3 and 7). Annual percentages by numbers and volumes were averaged in the Density-Biomass Index (Table 8) to give an overall mean comparison of the sampling stations. Numerical and volumetric data were compared at the three sites by converting the actual mean monthly values to percent composition (Tables 9 and 10).

A one-way ANOVA test was run on transformed data of the percent composition by insect order at the three stations (arcsin $\sqrt{\%\ \text{composition}}$). Densities by insect order were significantly different ($p<.05$) for the following pairwise comparisons between sites:

Ephemeroptera	-	All were significantly different
Plecoptera	-	All were significantly different
Trichoptera	-	South Fork and Bible Camp, South Fork and Kokanee Bend
Chironomidae	-	All were significantly different
Other Diptera	-	South Fork and Kokanee Bend
Other Invertebrates	-	All were significantly different

An ANOVA test was also run on transformed data of percent composition by biomass for each insect order. All pairwise comparisons between sites were significantly different with the exception of the South Fork and Kokanee Bend for the Ephemeroptera and the Bible Camp and Kokanee Bend for the Trichoptera.

In the South Fork, percent composition was much higher on a biomass than on a numerical basis for the Ephemeroptera, Plecoptera, Trichoptera, and Other Invertebrates. In comparisons of the other two sites (Appendices B & C), the mayflies showed both higher numbers and biomass at the control site in every month. Both numbers and biomass of stoneflies were generally higher at Kokanee Bend (with the exception of December, June and September when numbers were higher at the Bible Camp). Numbers and biomass of caddisflies were also generally higher at Kokanee Bend (with the exception of the months of June and July when numbers and biomass were higher at the Bible Camp, and the months of August and September when volumes were higher at the Bible Camp). The Chironomidae showed higher numbers and volumes at Kokanee Bend in the months of October, November, April, June

Table 7. Biomass (cc/m²) (Kick + Circular Samples)
Annual Mean of Monthly Means (October 1979 - September 1980)

	Bible Camp n=9 $\bar{\bar{x}}$(s.d.)	Kokanee Bend n=9 $\bar{\bar{x}}$(s.d.)	South Fork n=11 $\bar{\bar{x}}$(s.d.)
Ephemeroptera	3.9(1.2)	2.9(0.7)	1.9(0.8)
Plecoptera	2.6(1.2)	4.8(1.5)	0.7(0.4)
Trichoptera	2.5(1.0)	3.2(2.4)	0.2(0.2)
Chironomidae	1.4(0.4)	1.3(0.2)	5.9(1.7)
Other Invertebrates	1.7(0.6)	2.2(2.5)	3.6(1.3)
TOTAL	12.1(2.1)	14.4(4.5)	12.3(2.9)
Percent Composition	%	%	%
Ephemeroptera	32.2	20.1	15.4
Plecoptera	21.5	33.3	5.7
Trichoptera	20.7	22.2	1.6
Chironomidae	11.6	9.0	48.0
Other Invertebrates	14.0	15.3	29.3

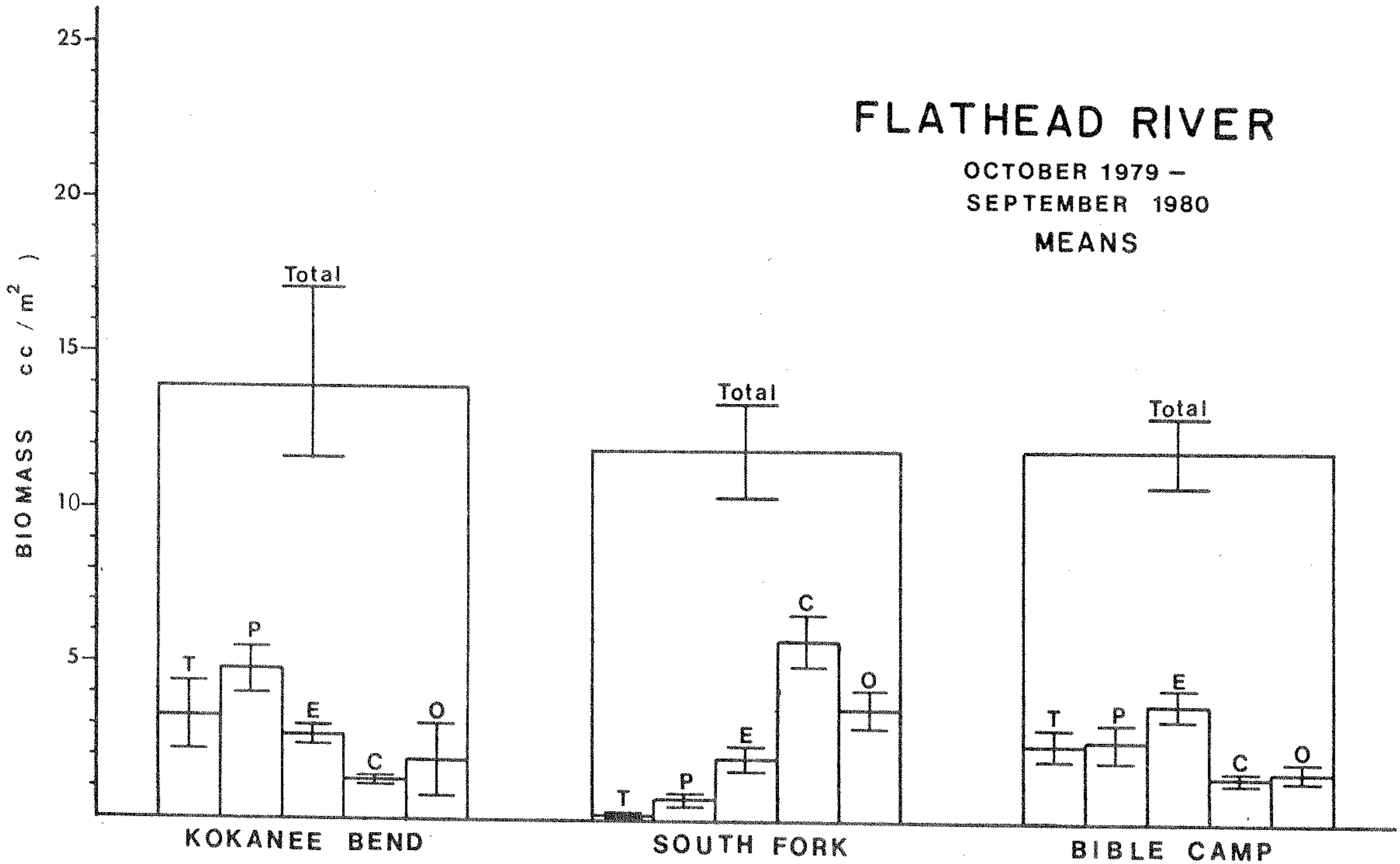

Figure 18. Biomass (cc/m²) of invertebrates; annual means of monthly means. Bars represent means; I represents standard deviations, means of total invertebrate biomass are represented by the large blocks. T = Trichoptera; P = Plecoptera; E = Ephemeroptera; C = Chironomidae; O = Other Diptera and Other Invertebrates.

Table 8. Density-Biomass Index calculated as the mean of annual percent composition of numbers and annual percent composition of volumes.

	Bible Camp n=9 $\bar{x}$ %	Kokanee Bend n=9 $\bar{x}$ %	South Fork n=9 $\bar{x}$ %
Ephemeroptera	43.2	23.6	9.3
Plecoptera	18.2	27.1	3.2
Trichoptera	13.2	15.2	0.8
Chironomidae	16.5	18.1	66.7
Other	9.0	16.1	20.0

Table 9. Percent of total number (no./m^2) of invertebrates represented by insect order (Kick and Circular samples combined).

	Ephemeroptera	Plecoptera	Trichoptera	Chironomidae	Other Diptera	Other Invertebrates
Bible Camp						
October	52.0	34.0	9.3	3.4	0.2	1.2
November	56.3	18.8	6.5	16.9	0.5	1.0
December	59.8	11.7	3.8	23.8	0.3	0.5
January	----	----	----	----	----	----
February	----	----	----	----	----	----
March	62.6	8.6	2.1	25.7	0.3	0.8
April	63.1	3.5	1.3	29.4	2.2	0.4
May	----	----	----	----	----	----
June	50.7	4.7	1.3	38.6	4.1	0.6
July	46.4	6.8	6.5	34.8	3.4	2.1
August	39.0	3.2	7.9	26.7	22.6	0.6
September	51.1	14.7	7.4	22.1	0.9	2.8
Kokanee Bend						
October	30.6	42.7	12.2	6.9	0.6	7.0
November	22.4	33.6	9.4	33.5	0.3	0.8
December	20.8	16.4	11.7	35.0	0.5	15.6
January	30.4	16.1	16.3	34.3	1.0	1.9
February	25.1	24.6	7.3	40.1	1.0	1.9
March	19.4	27.8	5.9	43.1	1.7	2.3
April	34.6	4.1	3.9	37.2	16.0	4.1
May	----	----	----	----	----	----
June	20.2	1.4	0.3	25.9	49.2	3.0
July	43.4	10.3	3.0	30.6	4.1	8.4
August	27.2	9.5	13.3	28.2	9.8	12.0
September	33.2	13.7	11.2	31.9	2.1	7.9

Table 9. (Continued)

	Ephemeroptera	Plecoptera	Trichoptera	Chironomidae	Other Diptera	Other Invertebrates
South Fork						
October 1979	0.2	0.7	0.01	97.7	0	2.5
November	0.7	1.3	0.05	93.5	0	4.4
December	1.0	0.7	0.006	95.3	0	3.0
January 1980	3.3	0.6	0	87.4	0	8.7
February	3.0	0.8	0.1	88.4	0.4	7.4
March	3.7	0.8	0.1	85.8	0.4	9.3
April	4.5	0.5	0.2	78.8	7.4	8.6
May	5.8	1.2	0.1	79.3	4.4	9.2
June	1.4	0.2	0.06	80.5	0.3	17.5
July	3.6	0.5	0.03	79.6	0.08	16.2
August	3.2	0.5	0.06	82.6	0.1	13.6
September	5.3	0.9	0.05	78.5	0.02	15.0

Table 10. Percent of total biomass (cc/m^2) of invertebrates represented by insect order (Kick and Circular samples combined).

	Ephemeroptera	Plecoptera	Trichoptera	Chironomidae	Other
Bible Camp					
October	25.5	31.2	25.5	6.4	11.5
November	24.3	25.7	27.8	11.1	11.1
December	30.5	26.7	17.1	11.4	14.3
January	----	----	----	----	----
February	----	----	----	----	----
March	39.7	24.4	16.0	11.5	8.4
April	43.4	20.2	13.2	11.6	11.6
May	----	----	----	----	----
June	42.1	11.4	11.4	13.2	21.9
July	35.2	14.8	22.1	18.0	9.8
August	22.2	17.6	21.3	11.1	27.8
September	26.1	16.3	29.3	14.1	14.1
Kokanee Bend					
October	16.9	41.6	26.0	7.1	8.4
November	14.0	32.3	38.9	7.4	7.4
December	16.4	38.2	26.4	10.0	9.1
January	17.4	33.0	38.3	6.1	5.2
February	17.2	41.8	21.6	11.2	8.2
March	18.1	44.9	22.0	7.9	7.1
April	23.9	26.8	29.7	10.1	9.4
May	----	----	----	----	----
June	17.6	26.0	4.9	7.8	43.6
July	30.8	30.8	12.5	11.7	14.2
August	22.7	29.9	18.6	11.3	17.5
September	26.5	35.4	16.8	11.5	9.7

Table 10. (Continued)

	Ephemeroptera	Plecoptera	Trichoptera	Chironomidae	Other
South Fork					
October	5.3	2.7	0	73.3	18.7
November	19.8	0	0	54.2	26.0
December	13.1	0.8	0	59.0	27.0
January	10.5	7.6	1.2	55.6	25.1
February	14.2	6.2	1.8	57.5	20.4
March	15.8	6.5	1.4	51.1	25.2
April	18.2	3.1	3.8	34.0	40.9
May	22.7	7.2	1.0	36.6	32.5
June	15.2	6.5	0.2	32.6	45.6
July	22.2	7.1	0.8	37.3	32.5
August	23.4	6.6	2.2	39.4	28.5
September	9.3	11.1	0.9	50.0	28.7

and August and at the Bible Camp in December, March, July and September.

Ephemeroptera were the numerically dominant order at the Bible Camp in all months (Appendix B, Table and Figures). Plecoptera were dominant numerically at Kokanee Bend in October and November, Diptera dominated from December through June, and Ephemeroptera dominated July through September.

When biomass was considered, the dominant order in any month could change (Appendix C, Table and Figures). To some extent, dominance volumetrically was a matter of chance, because if more large stoneflies or caddisflies were captured in the samples for a particular month, the balance was shifted. At the Bible Camp, mayflies were dominant volumetrically in all months but October when stoneflies were dominant, and November and September when caddisflies were dominant. The stoneflies were dominant volumetrically at Kokanee Bend, except in November, January and April when caddisflies were dominant, and June when large numbers of blackflies changed the dominant category to Other.

Life History

Temperature is an important regulator of the sequencing of insect life histories. Insect growth and emergence can be greatly influenced by temperature patterns. Various researchers have documented the importance of temperature on larval development (Macon 1960, Becker 1973, Nebeker 1973, Stanford 1975, Corkum 1978) and on emergence (Macon 1958, Rupprecht 1975, Illies and Masteller 1977). Our data indicated changes occurred in growth rates and emergence times of some insects due to regulation.

Many insects have strict temperature requirements, and minor alterations in temperature can have drastic effects. Life histories are often dimensioned by temperature summation criteria (Lehmkuhl 1972, Stanford 1975). The degree day is an example of a summation criterion used in the study of insect life histories. Mean daily temperatures are summed for a given period of time (week, month, season) to give a comparison of the cumulative heat load in different areas. Species for which the number of degree days is inadequate for larval maturation may be eliminated. The emergence portion of the life history of some stoneflies may be affected by the dampening of maximum temperature cues in regulated streams. Stanford (1975) reported the emergence of *Pteronarcella badia* was cued by maximum temperatures. Fraley (1979) reported no emergence of *Pteronarcys californica* in a regulated portion of the Madison River because the altered thermal regime lacked proper maximum temperature cues.

Colder summer temperatures at Kokanee Bend slowed summer growth rates. The total number of degree days (graphed as mean daily temperatures summed by the month) was less in the partially regulated sections of the river from June through September due to cold water discharges from Hungry Horse Dam (Figure 19). Mean daily temperatures were summed by the month, season, and year for the three study areas of the river during the period of study (Table 11).

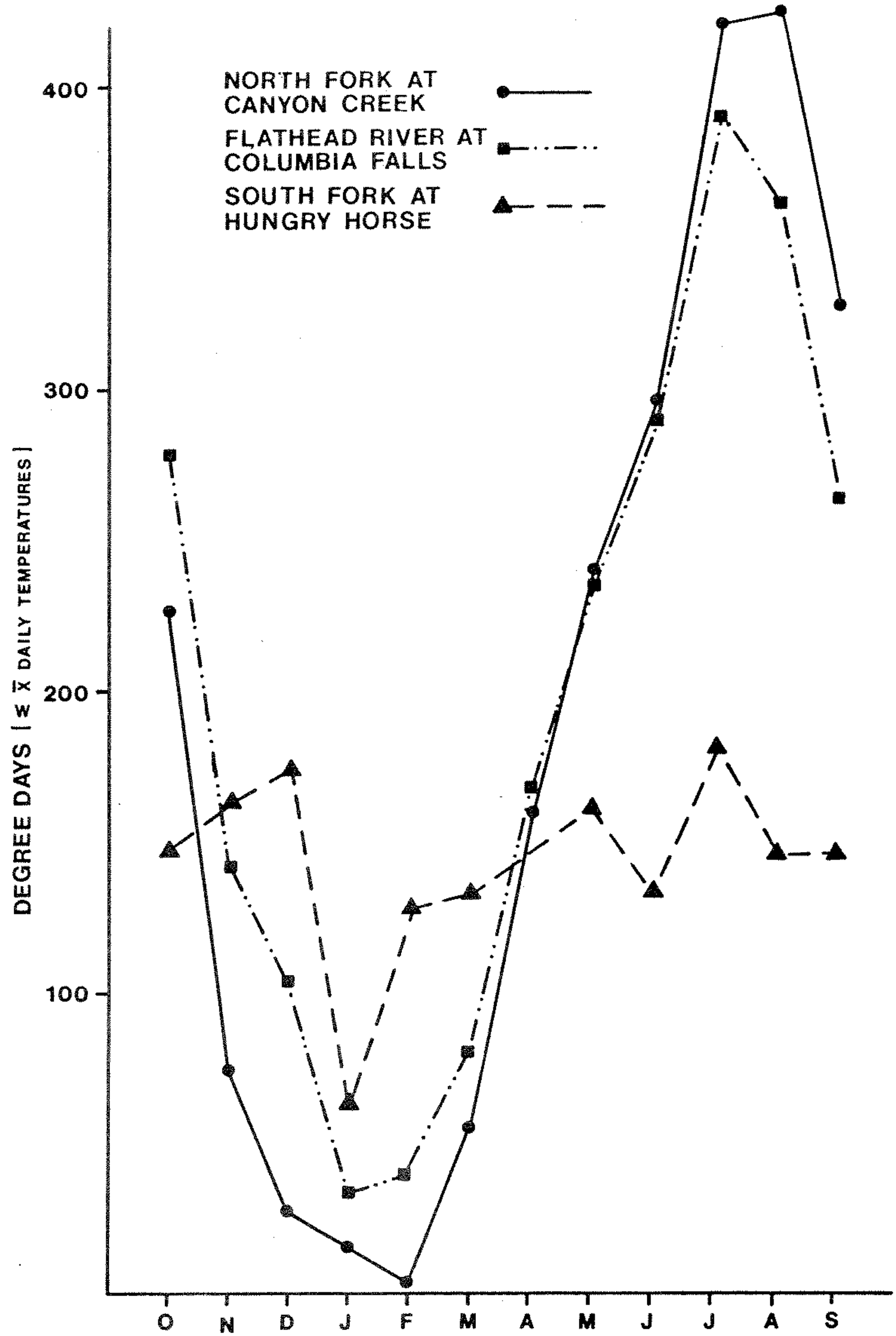

Figure 19. Degree days (mean daily temperatures) summed by the month for control (North Fork), partially regulated (Columbia Falls), and regulated (South Fork) areas of the Flathead River for the 1980 water year.

Table 11. Mean daily temperatures (degree days) summed by the month, season, and year for the three segments of the Flathead River.

	Month	1979		1980		1981	
		Season	Month	Season	Month	Season	Month
Columbia Falls (partially regulated)	Oct.				188.5		209
	Nov.			432	141.5	431	130
	Dec.				102.0		92
	Jan.				34.5		74
	Feb.			153.5	38.5	277	73
	Mar.				80.5		130
	April		135		168.5		
	May	591	186	693.5	234.5		
	June		270		291.0		
	July		356.5		389.0		
	Aug.	950.5	279	1,012	361.5		
	Sept.		315		261.5		
				TOTAL	2,290.5		
South Fork (regulated)	Oct.				148.5		155.5
	Nov.			484	162.5	452	143.5
	Dec.				173.0		153
	Jan.				62.5		144
	Feb.			311	115.5	391	121.6
	Mar.				133.0		125.4
	April		135		145.0		
	May	378.5	108.5	443.5	160.0		
	June		135		138.5		
	July		120		141.5		
	Aug.	394	124	436	152.0		
	Sept.		150		142.5		
				TOTAL	1,674.5		
North Fork (unregulated)	Oct.				225.0		217
	Nov.			251	n.d.	309.5	82.6
	Dec.				26.0		9 9
	Jan.				5.5		10.8
	Feb.			62	2.0	14	26.8
	Mar.				54.5		102.7
	April		135				
	May	621	186		n.d.		
	June		300				
	July		449.5		452.5		
	Aug.	1,305	480.5	1,202.5	422.5		
	Sept.		375		327.5		
				TOTAL	2,220.0		

A number of species which were in early instars during the summer and early fall, when temperatures were warmer at the control site, obtained maximum numbers one month later at Kokanee Bend than at the control site (e.g. *Drunella doddsi, Serratella tibialis, Drunella flavilinea, Epeorus sp., Paraleptophlebia heteronea, Classenia sabulosa, Isoperla fulva, Pteronarcella badia, Arctopsyche grandis, Hydropsyche oslari, Hydropsyche cockerelli, Brachycentrus occidentalis, and Atherix variegata*). This was apparently due to the fact that the heat accumulation was greater during the summer and early fall months in unregulated areas of the river. Elliott (1972) found that the time between oviposition and hatching and the length of the hatching period may be greatly extended by low summer temperatures. The reverse situation appears to have occurred in species which were growing later in the fall when temperatures were warmer in the partially regulated areas. Small capniid and chloroperlid stoneflies reached their maximum abundance one month later at the cooler Bible Camp section.

In order to assess the effects of regulation on insect growth rates, the head capsules of two species of mayflies, (*Drunella flavilinea, Serratella tibialis*), two species of stoneflies (*Pteronarcella badia, Taenionema pacificum*), and one caddisfly (*Hydropsyche oslari*) were measured each month from July 1979 through September 1980 (the growth of the two stoneflies was also measured during the second winter). The total head capsule width through the eyes was measured for the mayfly and stonefly species, while the interocular distance (through the eyes) was used for the hydropsychid caddisfly.

The mayfly, *Drunella flavilinea*, emerged in July and August and laid its eggs, which did not hatch until the following winter or spring (small instars were first collected in January in the Kootenai River, but generally not until after runoff in the Flathead River). *Serratella tibialis* also had an egg diapause; it emerged in August and September and small nymphs were first collected in April. There were no consistent differences in head capsule measurements at the two sites for these two species, but both species emerged about a month earlier in the unregulated than in the partially regulated section of the Flathead River (Table 12). This was presumably due to the fact that colder temperatures in the partially regulated area in the summer delayed maturation.

The stoneflies, on the other hand, emerged in the spring and tended to emerge sooner in the partially regulated areas. Their head capsule widths were generally somewhat larger in the partially regulated areas during the winter when temperatures were warmer than in unregulated areas (Table 13). *Taenionema pacificum* emerged much earlier in 1981 (February and March) than in 1980 (March, April and May). Water temperatures were much warmer during the second winter due to warmer weather conditions and more frequent generation at Hungry Horse Dam. The head capsules of *Hydropsyche oslari* were measured only through the first fall at the Kokanee Bend site, due to a small sample number in the partially regulated area. They appeared to emerge somewhat later at Kokanee Bend (their emergence period extended into August), and hatching appeared to be later (September and October as opposed to August and September at the Bible

Table 12. Ephemeroptera Head Capsule Widths (mm).

	Drunella flavilinea		*Serratella tibialis*	
	Bible Camp $\bar{x}$ (d) n	Kokanee Bend	Bible Camp	Kokanee Bend
July 19, 1979	1.45(.17) 22	1.52(.15) 11	.74(.13) 61	.86(.24) 31
August 20, 1979	none	1.59(.12) 6	1.18(.14) 29	1.20(.17) 105
September 17, 1979	none	none	none	1.36(.09) 20
April 15, 1980	none	.67(.00) 1	none	.24(.01) 4
May	runoff	runoff	runoff	runoff
June 8, 1980	.94(.34) 32	1.07(.09) 12	.89(.44) 26	.37(.09) 123
July 11, 1980	1.62(.07) 20	1.55(.16) 57	.81(.11) 112	.70(.11) 128
August 11, 1980	1.78(.00) 1	1.63(.00) 2	1.19(.16) 50	1.17(.18) 123
September 11, 1980	none	1.93(.00) 1	none	1.37(.14) 33

Table 13. Plecoptera head capsule widths (mm).

	Pteronarcella badia		*Taenionema pacificum*	
	Bible Camp	Kokanee Bend	Bible Camp	Kokanee Bend
7/19/79	.53(.07) 56	.55(.12) 65	none collected	.21(.06) 155
8/20/79	.70(.06) 29	.71(.10) 99	.22(0) 9	.25(.06) 69
9/17/79	1.04(.31) 13	.96(.14) 120	none collected	.25(.10) 117
10/10/79	1.16(.32) 22	1.10(.18) 101	.27(.07) 133	.32(.11) 154
11/13/79	.82(.34) 28	1.41(.19) 110	.43(.10) 192	.54(.10) 154
12/18/79	none collected	1.51(.21) 108	.51(.11) 110	.69(.11) 61
1/15/80	frozen	1.62(.18) 96	frozen	.96(.40) 134
2/11/80	frozen	1.67(.16) 85	frozen	.93(.10) 112
3/14/80	1.62(.13) 6	1.67(.16) 73	.88(.10) 149	1.02(.12) 100
4/14/80	1.75(.05) 3	1.81(.23) 53	1.10(.12) 92	1.18(.07) 10
5/80	runoff	runoff	runoff	runoff
6/8/80	.51(.38) 52(7 mature)	.76(.68) 16(5 mature)	none	none
7/11/80	.53(.05) 50	.53(.06) 102	.18(.04) 14	.18(.03) 83
8/11/80	.90(.28) 6	.67(.11) 44	.31(.05) 7	.29(.05) 25
9/11/80	none collected	.89(.12) 70	.24(.05) 104	.27(.11) 67
12/31/80	1.56(.18) 6	none collected	.76(.10) 95	none collected
2/4/81	1.48(.22) 28	1.64(.17) 20	1.19(.42) 168	.97(.12) 111
3/30/81	1.53(.14) 13	1.79(.29) 15	1.23(.04) 4	1.23(.05) 2

Camp) and growth slower at first. However, growth was faster in the regulated Kootenai River in the winter than in the unregulated Flathead River, where temperatures were colder.

Some insect species show flexibility in the timing of life cycles, and growth rates and emergence times are adjusted according to the prevailing temperatures, whereas the tolerance limits of other species may be exceeded or competitive disadvantages may result in species replacements.

Sweeney and Vannote (1978) found that small adult aquatic insects with reduced fecundity resulted when temperatures were either warmed or cooled with respect to more optimal thermal conditions. Temperature apparently affected adult size by altering the larval growth rate and the timing and rate of adult tissue development. Monitoring adult size and fecundity of aquatic insects was suggested as a tool for assessing the impact of sublethal alteration of natural temperature patterns. Warming the seasonal cycles of a river by 2° to 3° C might eliminate species by affecting body size and fecundity.

This should be considered when planning prolonged winter discharges from Hungry Horse Dam. It is possible that sustained winter discharges from Hungry Horse Dam could increase the winter heat load in the river enough to eliminate certain species of stoneflies. During the winter of 1981, a number of species emerged earlier in the partially regulated areas of the river (starting in January). This was probably due to the combined effects of sustained winter discharge and warmer weather conditions. In a colder winter, higher winter water temperatures may induce emergence into lethally cold air or during periods when mating was impossible. The raising of river temperatures may disrupt mating behavior in some species by widening any time lag between emergence of males and females (Nebeker 1971a).

Coutant (1967) has shown that a slight temperature increase (1°C) will cause hydropsychid caddisflies to emerge two weeks earlier downstream from the Hanford (Washington) reactors than in upstream areas. In experimental situations, it has been demonstrated that exposure of aquatic insect larvae to artificially high temperatures and stable flow conditions can cause advances in the onset of adult emergence of up to five months in some species (Nebeker 1971b).

Stoneflies have been almost eliminated from the Kootenai River (Montana) since impoundment (Huston et al. 1980). This may be due in part to warmer winter temperatures. However, in the Kootenai River, winter discharges are generally continuous (no weekend shutdown) for a period of several months, which allows a greater heat accumulation. It is probable that night and weekened shutdowns at Hungry Horse Dam will prevent deleteriously high heat accumulations, although higher daily maximum temperatures than in control areas may eliminate certain species. Preliminary data indicates that stoneflies are a food source for cutthroat trout during the winter in the partially regulated area of the Flathead River. The impact of discharge changes on what appears to be an important food resource should be considered in management decisions.

Environmental Variables

In an attempt to explain the differences in macroinvertebrate community structure in regulated and control areas, various environmental factors were also measured. It has been found that other biotic factors better explain the variation in macroinvertebrate communities, than do factors such as the chemical composition of the rivers, so the most emphasis was placed on quantifying these.

The altered food regime in regulated rivers leads to changes in the biota. Given suitable flow conditions, reduced turbidity and increased light penetration below dams often allow increased development of algae and macrophytes (Ward 1976c). Warmer winter water temperatures and the absence of ice may allow a high year-round production of periphyton in the comparatively nutrient-rich water below most deep-release dams. This may lead to increased numbers of scraper organisms which utilize the periphyton as a food source.

Periphyton biomass was much higher at the South Fork regulated site than at the other two sites (Table 14, Figure 20). An analysis of variance test (ANOVA) showed significant biomass differences between all sites in all seasons. The only pairwise comparisons between sites which were not significantly different were all pairwise comparisons for Chl *a* in the summer and between the Bible Camp and Kokanee Bend for Chl *a* in the fall. Maximum biomass was measured during the fall (September and October).

Periphyton productivity was measured in September, 1981 with the use of *in situ* recirculating chambers (Table 15, Figure 21). ANOVA tests showed that gross productivity was significantly different only between the South Fork and Bible Camp sites. Productivity measurements at the South Fork station were not in proportion to the very high biomass measured at that site. Due to differences in photoperiod respiration, net community productivity was significantly different between all sites. The P/R ratio was highest at the Kokanee Bend site, but was not significantly different between any of the stations. All stations were autotrophic during the fall season. Stanford et al. (1981) measured lower productivity and higher respiration in the partially regulated portion of the Flathead River in March, 1981 resulting in a very slightly heterotrophic P/R ratio (0.97). At that time, they obtained P/R values of 1.41 and 1.23 for the unregulated North and Middle Forks of the Flathead River. Values obtained from the Kootenai River system are included in Table 15 and Figure 21 for comparative purposes. The Kootenai River is generally much more productive. The Fisher River is a tributary of the regulated Kootenai River and was used as a reference station.

Analysis of the species composition of periphyton samples from the three sample stations in September, 1981 indicated *Chaetophora pisiformis* was an abundant soft-bodied algae at the Bible Camp and Kokanee Bend stations, while *Ulothrix zonata* was abundant in the South Fork (Appendix D). *Ulothrix* was also found to be a common genus in the regulated South Platte River (Ward 1976) and in the regulated Grand River, Ontario (Spence and Hynes 1971). Shannon diversity of diatom species was highest at

Table 14. Periphyton Biomass as measured by ash free dry weight (AFDW) and chlorophyll *a* (Chl *a*).

	$\bar{x}$ AFDW (s.d.) g/m^2	$\bar{x}$ Chl a (s.d.) g/m^2
August 21, 1980		
South Fork	38.0(25.0)	0.121 (.06)
Kokanee Bend	7.3(4.5)	0.0323(.012)
Bible Camp	1.9(0.5)	0.0270(.016)
October 12, 1980		
South Fork	140.0(91.0)	0.383 (.21)
Kokanee Bend	13.0(4.0)	0.0222(.005)
Bible Camp	4.5(5.0)	0.019 (.007)
December 3, 1980		
South Fork	17.0(10.0)	0.1954(.068)
Kokanee Bend	4.5(3.1)	0.0149(.007)
Bible Camp	9.3(6.4)	0.0391(.019)
September 1981		
South Fork	201.5(47.2)	0.234 (.127)
Kokanee Bend	2.01(.90)	0.009 (.007)
Bible Camp	3.99(1.11)	0.026 (.008)

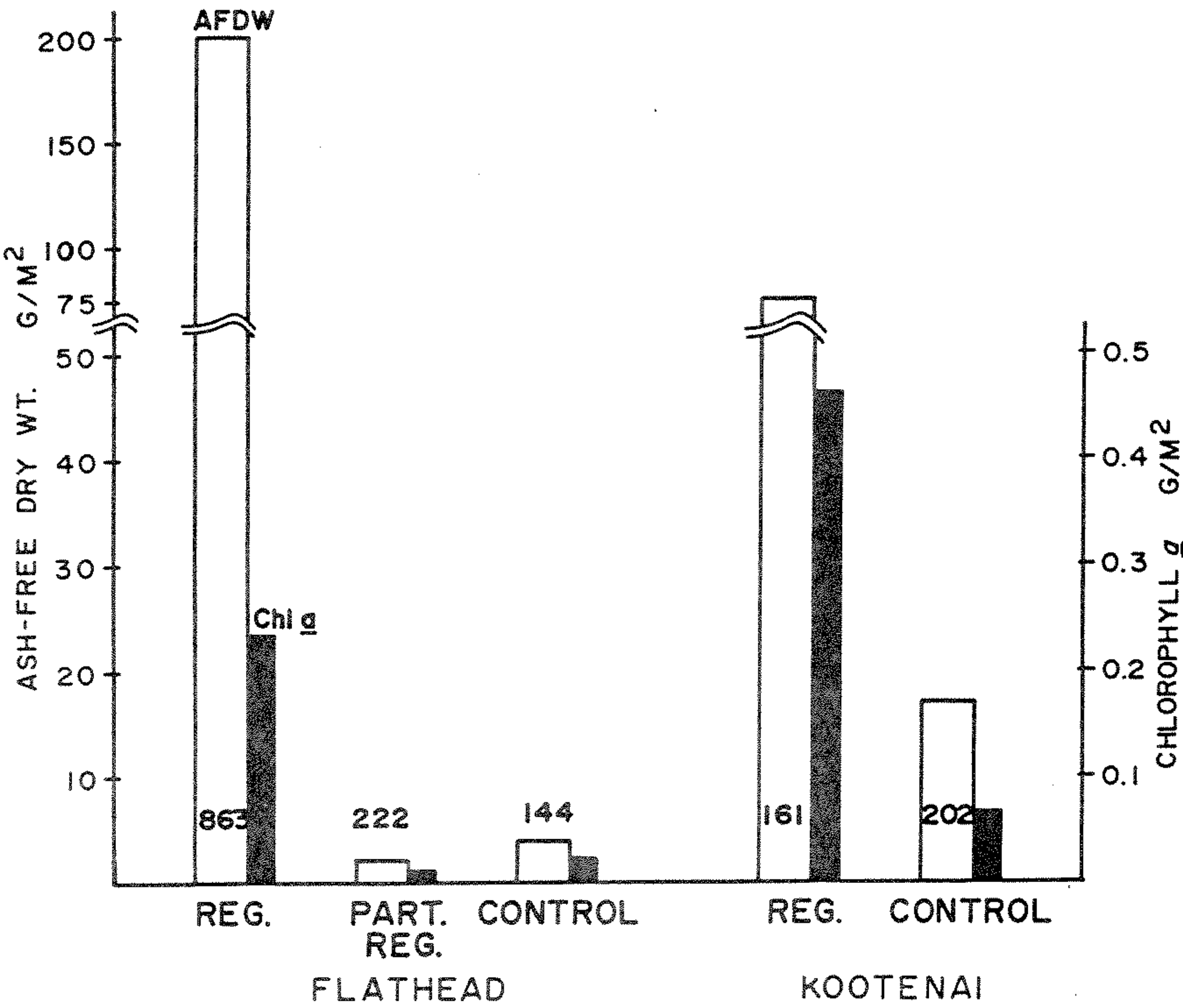

Figure 20. Ash free dry weight (g/m^2) and chlorophyll a (g/m^2) measured in periphyton scraped from natural substrate in September 1981.

Table 15. Parameters of periphyton community metabolism in regulated and free-flowing segments of the Flathead and Kootenai River systems. Data are means and standard deviations of measurements in three recirculating respiratory chambers used *in situ*. September, 1981.

	Units in mg O_2/m^2/day				
	GP	NCP	R_{24}	NDM	P/R
Flathead River					
South Fork	1,428(418)	1,326(294)	618(168)	810(336)	2.36(0.58)
Kokanee Bend	664(94)	519(73)	269(116)	396(93)	2.69(0.84)
Bible Camp	493(30)	362(23)	242(27)	252(24)	2.05(0.18)
Kootenai River					
Dunn Creek (regulated)	3,273(283)	2,307(108)	1,792(363)	1,481(143)	1.86(0.26)
Fisher River (reference)	1,277(119)	1,086(140)	372(75)	895(166)	3.53(0.85)

GP = gross productivity = $\Sigma O_2 + R_{24}$
NCP = net community productivity = GP - photoperiod respiration
R_{24} = respiration, 24 hour, as measured
NDM = net daily metabolism = GP - R_{24}
P/R = productivity - respiration ratio

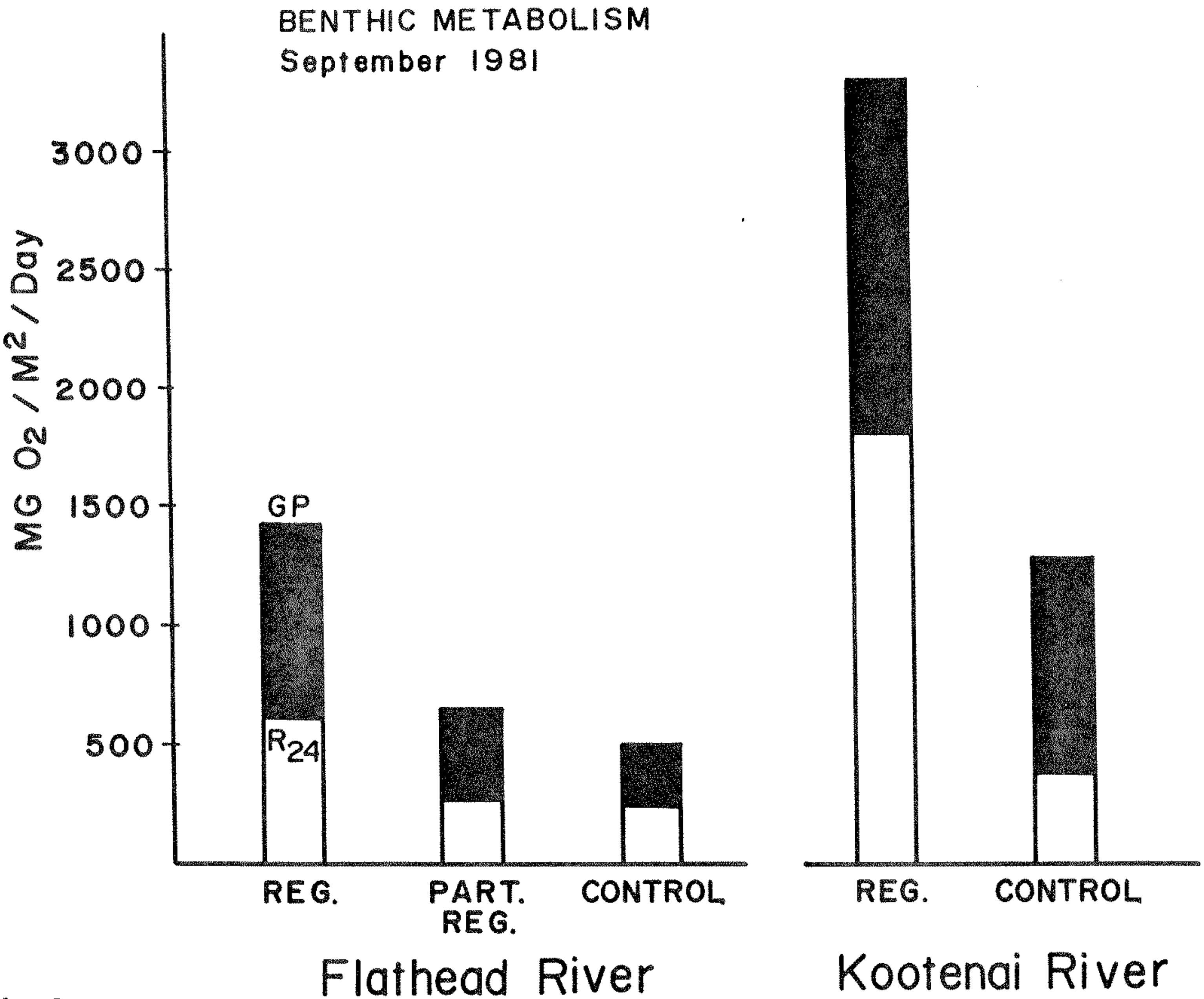

Figure 21. Parameters of periphyton community metabolism in regulated and free-flowing segments of the Flathead and Kootenai River systems. The total bar represents gross productivity, the black area is net daily metabolism, and the white area is 24-hour respiration.

the reference station (3.23), lowest in the regulated South Fork (2.06) and intermediate in the partially regulated section (2.56). Monoraphidae, which are sessile and attached, composed a larger percentage of the periphyton at the Bible Camp (57.8%) and Kokanee Bend stations (67.5%), while Araphidae, which are planktonic diatoms, made up a larger percentage in the South Fork (74.0%). *Fragilaria vaucheriae*, *Achnanthes minutissima*, and *Diatoma tenue* were common diatom species in the South Fork; *Achnanthes minutissima*, *Cymbella microcephala*, and *Fragilaria vaucheriae* were the most common at Kokanee Bend, and *Achnanthes minutissima*, *Synedra ulna*, and *Cymbella microcephala* were common at the Bible Camp during September.

The downstream transport of particulate organic matter (POM) in the seston is altered by reservoirs and dams. Dams act as barriers which prevent the transport of certain categories of organic matter; their effect is partly dependent upon release depths. There have been many recent investigations of particulate organic matter (POM) dynamics in natural streams, when water is withdrawn from surface layers. Filter-feeding insects are usually not found below reservoirs in the concentrations found in the outlets of many natural lakes, unless they are supplied with plankton-rich surface water from above the dam (Müller 1962).

Particulate organic matter is also affected by the type of flow regime. Size distribution of drifting seston is a function of flow intensity. Algae and other POM may be sloughed and transported during high flows, and deposited during low flows. Studies done at the partially regulated station as discharge was increased for hydropower generation showed large amounts of POM were put into suspension as flows increased. This included sloughed algae and resuspended organic matter, as well as debris collected from shoreline areas which were not wetted at lower discharges.

Mean annual values of total particulate organic carbon (mg/l) were lowest in the South Fork (.07 ± .06), highest at the Bible Camp (.14 ± .18), and intermediate at Kokanee Bend (.11 ± .10). The South Fork values reflect mainly the composition of POC in water discharged from the dam, plus a minimal component from sloughing of periphyton, which increases with discharge. The partially regulated, and particularly the free-flowing sections of the river, had high POC during spring runoff, which increased the overall mean at these sites.

Particulate organic carbon was fractionated into four size classes during conditions of full generation from Hungry Horse Dam (Table 16, Figure 22), reflecting a larger component from sloughing of algae in the regulated sections and maximizing differences between the Bible Camp and Kokanee Bend stations. Samples were taken in September before leaf fall, in November after leaf fall, and during March. Samples were not taken during the period of natural runoff. Total POC values were highest at Kokanee Bend (due primarily to the cumulative effects of the sloughing of periphyton at that site) and lowest at the South Fork. March values were highest, as spring runoff was beginning.

The percentage of POC in each of the four size fractions was altered by the dam. The three larger size classes tended to be smaller below

Table 16. Four size fractions of particulate organic carbon (POC) as measured at the three sample stations in three seasons. Numbers and percentages are based on the means of three replicate samples.

	Total POC (mg/l)	A 355-1,000μm (%)	B 165-355μm (%)	C 10-165μm (%)	D .45-10μm (%)
September 10, 1980					
South Fork	.0656	2	5	43	50
Kokanee Bend	.0810	2	5	32	62
Bible Camp	.0745	1	4	48	47
November 18, 1980					
South Fork	.0557	1	3	30	66
Kokanee Bend	.0923	1	4	40	55
Bible Camp	.0694	1	1	36	62
March 17, 1981					
South Fork	.0952	1	3	10	86
Kokanee Bend	.1441	1	5	46	48
Bible Camp	.1110	1	1	26	72

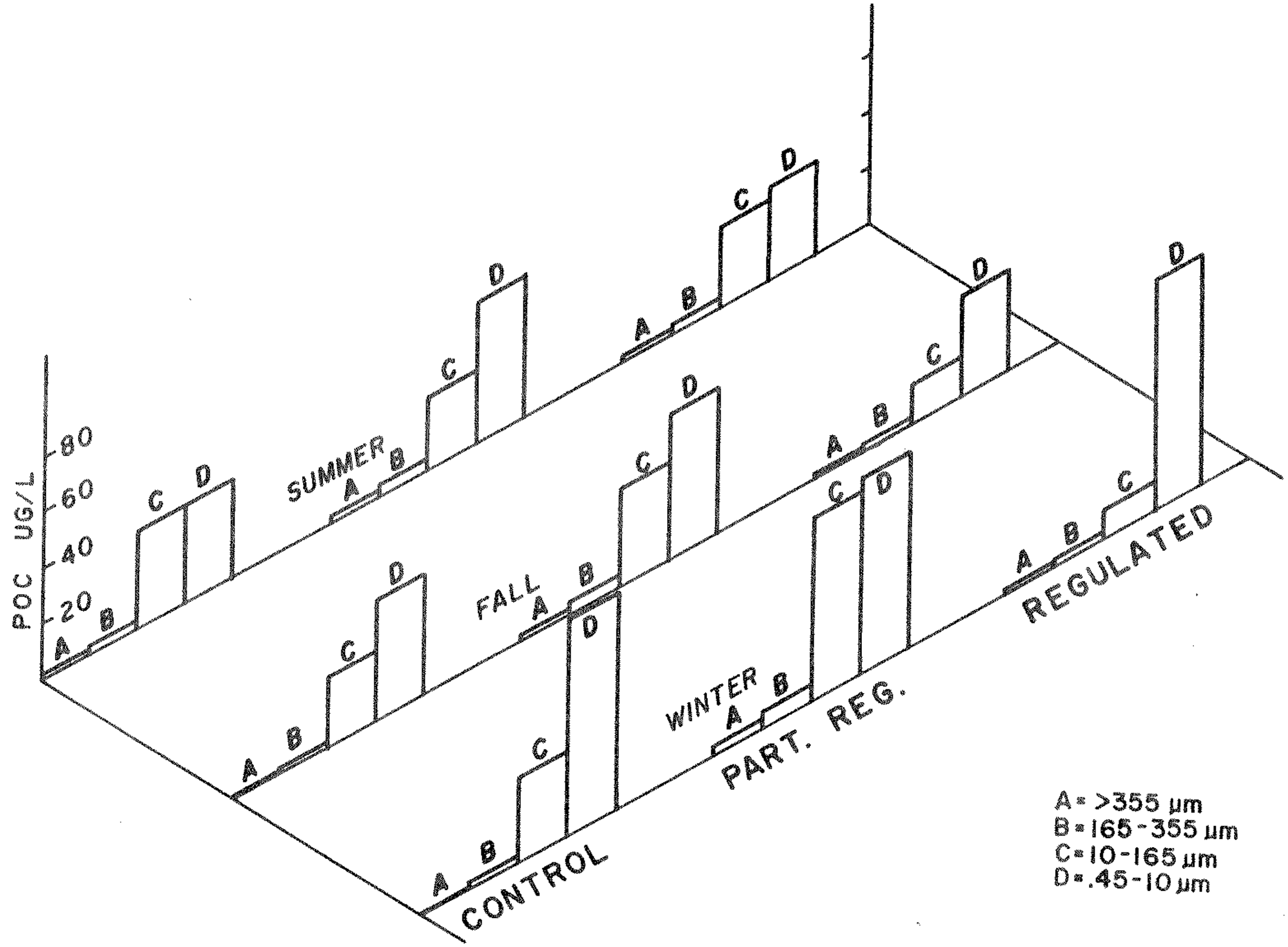

Figure 22. Four size fractions of particulate organic carbon (POC) measured during September and November 1980, and March 1981 at the Bible Camp, Kokanee Bend, and South Fork sample stations.

the dam during periods of high turbidity in unregulated sections, due to sedimentation in Hungry Horse Reservoir. The A, B, and C size fractions were significantly different between the South Fork and the other two sites during the slight runoff conditions that occurred in March. Sloughing of periphyton in the South Fork increased the amount in these larger size classes at the regulated study site, especially during September and November when periphyton biomass was higher. The three largest size classes tended to represent a greater proportion of the POC in the partially regulated area due to sloughing. In particular, the 165-355 μm fraction was significantly different (ANOVA test) at the Kokanee Bend and Bible Camp in all seasons.

To measure the effect of sloughing and resuspension of material, seston was fractionated and net seston (particles larger than 355 μm were collected in the insect drift nets) was measured as the initiation of hydropower generation at Hungry Horse Dam caused water levels to rise at the Kokanee Bend site on September 9, 1981. With the increase in flows the two largest size fractions (A and B) increased 15 to 20 times. The C and D fractions increased threefold (Table 17, Figure 23). All size fractions were significantly different (ANOVA) before and after changes in water elevation. Net seston increased dramatically from 2.5 mg/m^3 to 1,430 mg/m^3 two hours later and 3,600 mg/m^3 three hours after water levels began to rise (Figure 24). Net seston did not include the sticks and logs which were recruited from shoreline areas as flows rose, as we excluded these from the net.

Particulate organic carbon greater than 355 μm was also measured seasonally at conditions of minimum flow with the use of the insect drift nets. The drift nets were used because larger volumes of water needed to be filtered in order to adequately quantify the largest size class. Values for net seston were three to six times higher in the partially regulated areas of the river than at the Bible Camp station in the summer and fall.

The size of food particles is important to the filter feeding insects, as well as to those that gather detritus. Blackflies are filter feeders which had an annual mean density of $700/m^2$ at the Kokanee Bend site as compared with $200/m^2$ at the Bible Camp. *Arctopsyche grandis*, a filter feeding caddisfly which spins nets with a relatively large mesh, had an annual mean density of $190/m^2$ at Kokanee Bend and $20/m^2$ at the Bible Camp. The correlation coefficient for *Arctopsyche* densities at six sites on the Flathead and Kootenai Rivers and POC >165 μm was .834 ($p<.05$, 4 d.f.). Thus, certain of the macroinvertebrate compositional changes between the partially regulated and control sites can probably be explained on the basis of the distribution of the size particles of POC.

Other environmental factors which are known to have important effects on aquatic insect distributions are flow, temperature, and substrate. Flow and temperature data were obtained from the U.S. Geological Survey for the three sections of the Flathead River. Rates of flow change were calculated from gauge height readings taken as discharge was increased (Graham et al. 1980).

Table 17. Size fractions of organic carbon in the seston during a flow change experiment on September 9, 1981, at the Kokanee Bend station. Fractionations were begun before and approximately 1, 2 and 4 hours after the river elevation began rising. Data given are means of three fractionations.

	Total POC (mg/l)	A 355-1000μm	B 165-355μm	C 10-165μm	D .45-10μm
Run 1	89.1	.45(.08)	1.07(.13)	55.9	31.7(.50)
Run 2	182.0	5.44(1.8)	9.88(2.3)	84.4	82.3(7.1)
Run 3	257.9	6.03(.99)	16.8 (1.1)	154.0	81.1(.64)
Run 4	266.6	8.82(.21)	16.2 (.62)	164.0	77.6(1.5)

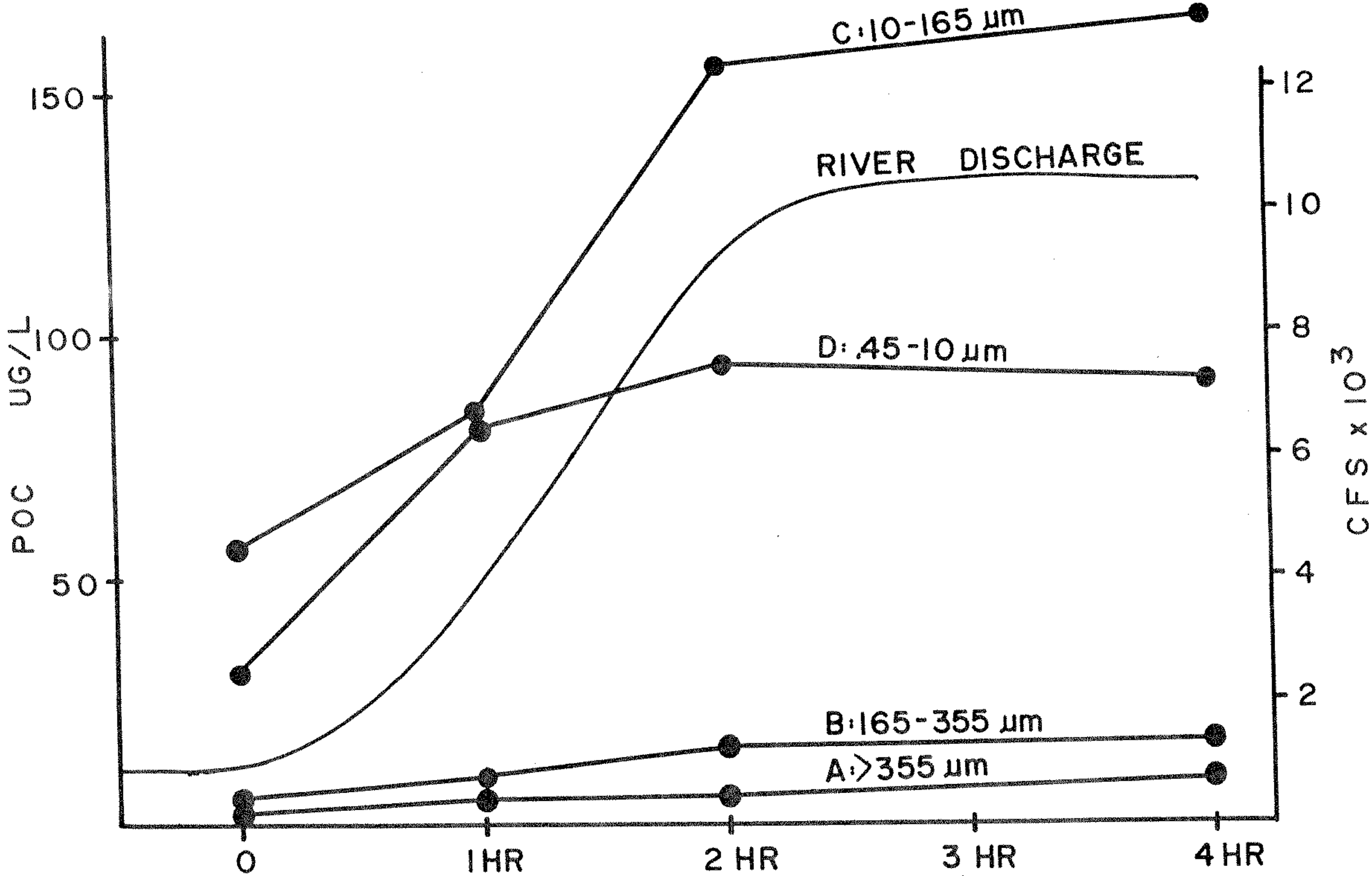

Figure 23. Increase in four size fractions of particulate organic carbon (POC) with an increase in river discharge in September, 1981, at the Kokanee Bend station in the partially regulated Flathead River.

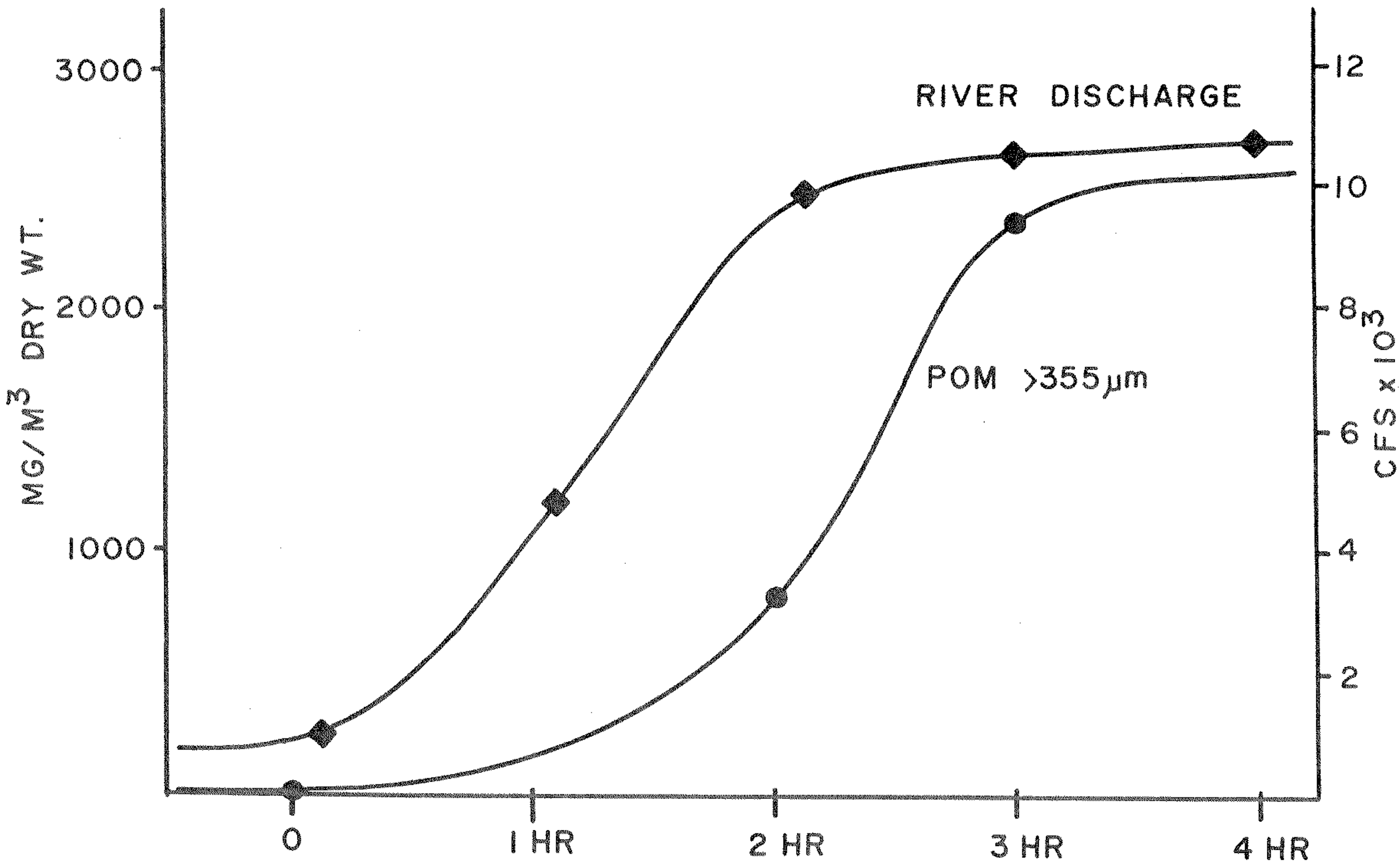

Figure 24. Increase in net seston (>355μm) with increase in river discharge at the Kokanee Bend station of the mainstem Flathead River in September 1981.

The surface substrate material was largest at the South Fork and smallest at Kokanee Bend; all pairwise comparisons were significantly different (Table 18). The heterogeneity index for the subsurface substrate indicates that the heterogeneity of particle sizes in the South Fork is reduced (13.3) when compared to the partially regulated area (28.6).

Generally, downstream from a dam the small particles are washed out by fluctuating flows and are not replaced during runoff periods because the sediments settle out in the reservoir. The partially regulated area receives sediments from the two free-flowing forks during periods of runoff. The amount of material in the smallest size class (<.063 mm) was significantly different (based on an ANOVA test) at the South Fork as compared to the Bible Camp and Kokanee Bend sites. The 2-.063 mm size class was significantly different at the South Fork and Kokanee Bend sites and the 2-16 mm class was significantly different at the South Fork and Bible Camp sites. The mean subsurface particle size of 24 mm at the South Fork was much larger than the mean size of 10.5 mm at the Bible Camp.

Correlation Analyses of Environmental and Macroinvertebrate Data

The composition of benthic communities downstream from dams may be largely due to the flow regime, resultant temperature patterns, substrate and altered autochthonous (periphyton) and allochthonous (POC in the seston) resources. To assess the importance of these factors in determining community associations, multiple regressions and correlations were performed.

A correlation matrix between biological measurements and measurement of environmental variables was obtained for the three Flathead River stations (Table 19), and another correlation analysis was run which included three stations from the Kootenai River (one control, two regulated) as well as the Flathead River stations (Table 20). A number of correlations between two independent variables and between independent and dependent variables were significant* ($p<.05$) or highly significant** ($p<.01$). The measurement of temperature did not give many correlations, presumably because insects respond to temperature on an annual rather than a seasonal basis (also in the Kootenai River temperatures do not change much between the two regulated sites, while invertebrate composition showed a considerable change).

Among the dependent variables, numbers and biomass did not show many significant correlations. Although diversity indices have been somewhat out of favor for invertebrate analyses in recent years, their use appears quite adequate to elucidate differences in these regulated river environments. Principal components analysis was the least successful ordination technique used. It was one of the earlier ordination techniques developed and has since been shown to have problems with the mathematical assumptions not conforming to actual environmental differences.

Another correlation analysis (Table 21) was performed which included annual means for total POC, gross productivity, degree days summed for

Table 18. Measurements taken of surface substrate by measuring the intermediate axis and of the subsurface substrate using sieving techniques in September, 1981, at the three sample stations.

	SURFACE SUBSTRATE				SUBSURFACE SUBSTRATE						
	N	$\bar{x}$(cm)	s.d.	Heterogeneity Index	Size $\bar{x}$ grain (mm)		50-19	19-16	mm 16-2 %	2-.063	<.063
South Fork	169 (84.5/m²)	10.60	(5.11)	13.3	24.0	#1	44.4	7.5	38.0	10.0	0.3
						#2	52.5	7.8	28.6	10.8	0.2
Kokanee Bend	242 (121/m²)	7.43	(2.51)	28.6	14.0	#1	45.7	6.2	28.3	19.0	0.8
						#2	39.0	4.0	36.5	19.6	0.9
Bible Camp	223 (111/m²)	8.44	(3.73)	14.3	10.5	#1	35.8	8.8	43.0	11.5	0.9
						#2	22.5	7.0	49.7	19.8	1.0

Table 19. Flathead River Stations only - Pearson correlation matrix for seasonal data - see text for explanation of data entered. n= 9 (3 seasons at 3 stations) d.f.= 7

		Veloc.	Temp.	Subst.	POC >165	POC <165	AFDW	Chla
				Independent Variables				
Independent Variables	Velocity	1.0						
	Temperature		1.0					
	Substrate			1.0				
	POC >165			.752*	1.0			
	POC <165		-.639			1.0		
	AFDW	.747*					1.0	
	Chl a	.677*		-.616			.848**	1.0
Dependent Variables	Numbers							
	Biomass							
	Diversity	-.689*		.623			-.798**	-.932**
	DECORANA	-.623					-.633	-.783*
	PO	.807**					.782*	.911**
	PCA			.669			.747*	.677*

* - p= .05 = .666*
** - P= .01 = .798**

Table 20. Pearson correlation matrix for seasonal data. See text for explanation of data entered. (n=18 (3 seasons at 6 stations - Flathead River + 3 Kootenai River sites) d.f. = 16).

		Independent Variables												
		Veloc.	Temp.	Subst.	POC >165	POC <165	AFDW	Chl a	No's.	Biomass	Diversity	DECOR.	PO	PCA
Independent	Velocity	1.0												
	Temperature		1.0											
	Substrate			1.0										
	POC >165μm			.727**	1.0									
	POC <165μm	.492*		.734**		1.0								
	AFDW	.741**			-.484*	.544*	1.0							
	Chl a	.701**		-.626**	-.608**		.908**	1.0						
Dependent	Numbers								1.0					
	Biomass								.593**	1.0				
	Diversity	-.775**		.672**		.492*	-.720**	-.755**	-.489*		1.0			
	DECORANA	-.656**					-.698**	-.753**			.670**	1.0		
	P.O.	.767**		-.677*		-.486		.480*			-.780**	-.567*	1.0	
	P.C.A.	.598**					.529*							1.0

* p .05 = .468*
** p .01 = .590**

Table 21. Pearson correlation matrix for annual means + fall data. See text for explanation of data entered (n=6 (3 Kootenai River Stations + 3 Flathead River stations) d.f. = 4).

		Independent Variables								
		Veloc.	Temp.	Subst.	$\bar{x}$POC	POC >165	POC <165	AFDW	Chl a	GP
Independent Variables	Velocity	1.0								
	Annual Temperature		1.0							
	Substrate			1.0						
	$\bar{x}$ Annual POC		.760	.811*	1.0					
	Fall POC>165μm					1.0				
	Fall POC<165μm						1.0			
	Fall AFDW							1.0		
	Fall Chl *a*					-.707		.749	1.0	
	Fall GP								.907*	1.0
Dependent Variables	$\bar{x}$ Numbers								.890*	.969**
	$\bar{x}$ Biomass		.834*							.784
	$\bar{x}$ Diversity	-.821*						-.809	-.744	
	Fall DECORANA							-.872*	-.934**	-.853**
	Fall PO	.842*	-.745	-.761	-.879*		-.818*			
	Fall PCA	.783						.902*	.854*	.757

* p<.05 = .811*
** p<.01 = .917**

the entire year, and annual mean numbers, biomass, and diversity. Fall values were used for periphyton, the two seston size fractions, and the ordinations. Yearly mean biomass was significantly correlated with temperature when daily mean temperatures were summed for the year. Gross productivity was significantly correlated with annual mean densities of invertebrates and with DECORANA.

Generally, velocity rates of change, substrate heterogeneity, POC in the seston, and AFDW and Chl *a* in the periphyton were environmental variables which were well correlated with measures of invertebrate diversity and composition. The characteristics of the seston and periphyton, as well as the invertebrate composition, appear to be determined by the type of regulation and vary together.

Environmental variables can also be ordinated to ascertain relationships between sites. Ordination of environmental variables at the sampling stations showed a gradient of values similar to that obtained from the macroinvertebrate ordinations. First axis values ranged from 52-61 at the South Fork, from 25-32 at Kokanee Bend, and from 4-23 at the Bible Camp station.

Experimental Drift Studies

The normal rate of increase drift studies were done on September 16, 1980, the control (minimum flows) was run on September 17, and the emergency start-up rate was tested on September 18. A one-hour sample was taken before flows changed and then at half-hour or hour samples as flows increased.

There had been no discharge at Hungry Horse Dam for two days before experimental insect drift studies were begun on September 16. Recruitment of leaves from shoreline areas quickly clogged the nets as flows began to rise and one sample was lost. Generally, algae which had been sloughed from the bottom as flows increased caused some problems with the clogging of nets. Velocity was monitored at the mouth of the nets as flows changed and the flow information was used to convert numbers of insects per net to number/100m^3. Values for each insect order are given for each of the experimental conditions in Appendix E.

Four samples were taken between 8:00 and 12:00 a.m. for the rate of increase tests on September 16-18 (Figure 25). No significant differences were measured between hourly samples during the control test. Significant differences were recorded between the first and second hours of the test (before and after flows started to increase) for all groups (which included Ephemeroptera, Plecoptera, Trichoptera, Diptera, adults of aquatic insects, terrestrial insects, and total invertebrates) except Trichoptera during the normal rate of increase tests; they were significant for all but Trichoptera and Diptera during the fast rate of increase test. Trichoptera do not often enter the drift during non-emergence times and when they do, they tend to drift along the bottom (especially those with cases) and would not be caught in our surface nets. There were a number of other pairwise comparisons between hours which showed significant differences. Drift densities tended to increase as flows started to change and then

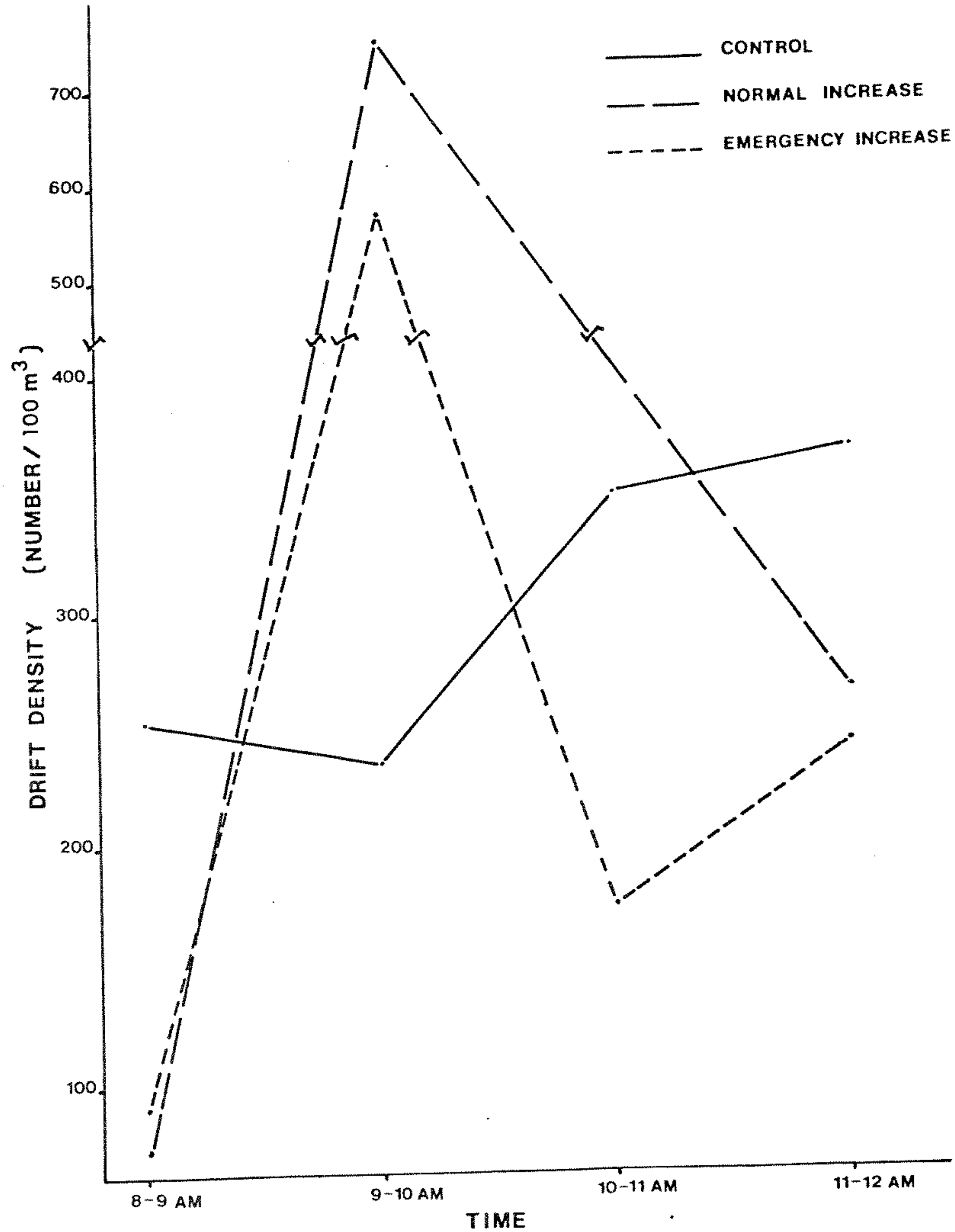

Figure 25. Drift densities (no/100m^3) of all invertebrates sampled over a four hour period on September 16-18, 1980, as discharge was increased at two different rates.

dropped off again after the first hour or two. The fast rate of increase did not appear to cause substantially more drift than the normal rate of increase, although there was a greater rate of drift in some groups (such as terrestrial insects which were swept from shoreline areas). The difference in the two rates of increase is somewhat dampened by the time the water reaches the Columbia Falls bridge due to resistance from the river channel. More adult stoneflies (mainly *Suwallia autumna*) were emerging during the normal rate of increase test, so their numbers increased more than during the emergency rate test.

The effect of decreasing flows on insect drift did not appear to be marked either when shutdown occurred during the day or at night (Appendix F). Since insects generally drift more after dark, it was thought that the effect of changing flows might be more pronounced after dark, but the effect was minimal. Discharge was continued at full generation levels during the control test on September 24. Total drift densities were not significantly different for pairwise comparisons between hours for any of the shutdown times or between shutdown tests within any hourly period. There were temporal differences in drift densities within specific insect orders, but the number of significant differences was the same for the day shutdown and control and there were only a few more significant differences during the night shutdown.

Normally certain species drift more at a particular time of day and differences caused by a decrease in discharge would have to be marked to be significant. In any case, the effect of decreased flows is not marked by the time the water reaches the Columbia Falls bridge. Faster decreases in velocity would be measured in the South Fork near the dam. Dramatic increases in insect drift were measured two miles downstream from Libby Dam on the Kootenai River after flows were decreased from 20,000 to 4,000 cfs. Drift rates also change seasonally and September is not normally a period of high insect drift in the Flathead River.

Insects in the Flathead River may be adapted to flow changes to the point where catastrophic drift due to increases or decreases in discharge is not a common event. There appears to be little recolonization of shoreline areas during periods of full generation and little stranding when flows are reduced. This is mainly due to the frequency of changes in discharge and the fact that flows are seldom high for long enough periods to allow periphyton (in which the insects find protection and on which certain species feed) to colonize the rocks in zones of fluctuating flows. Stranding of large numbers of insects has been recorded in the Kootenai River during the winter months when flows are maintained at high levels for periods of weeks. Insects in the Flathead River are largely confined to the areas which are wetted at minimum flows from Hungry Horse Dam.

Fish Food Habits

The gut contents of the sport fish in the Flathead River were examined to determine if there were differences in their feeding preferences in the partially regulated section of the river as compared with the reference station (Bible Camp) above the mouth of the South Fork in the free-flowing reach of the river. Kokanee salmon were not studied, since they do not feed when in transit to their spawning grounds. Trout were not collected in high numbers by electrofishing, so only a few stomachs were examined, and only an indication of their feeding preferences was determined. Most of the data presented concerns the food habits of the mountain whitefish, *Prosopium williamsoni*.

Fish were collected by electrofishing just after dark in April, July and October, 1980 at the Bible Camp control station and from reaches of the river near Columbia Falls and Kalispell in the partially regulated section of the river. Benthic samples were collected in the kick net, and drift samples were taken before and after dark at the time the fish were sampled. Drift densities were calculated (Waters 1972) and the mean value of all samples taken was used to calculate the percent composition of each insect order in the drift.

The most abundant insect orders in the benthos were the mayflies and dipterans (Appendix G). Dipterans and stoneflies were most abundant at the Columbia Falls station (most influenced by regulation) during April and July, but not during October. Mayflies and dipterans also dominated the drift, (Appendix H) with the dipterans showing much higher drift densities in regulated areas in October when midges were emerging in large numbers. Stoneflies were very abundant in the drift in April when capniids and taeniopterygids were emerging, particularly at the Columbia Falls station, where they composed 83 percent of the drift (Table 22).

Lengths and weights were measured on the captured fish. Mountain whitefish were placed into age categories based on the back-calculated lengths and growth increments determined from scales taken from whitefish in the mainstem Flathead River in 1979-1980 (McMullin and Graham 1981). The percent composition of each insect order in the fish stomachs was calculated using numbers, volumes, and frequency of occurrence for each station during each season (Appendix I). The arithmetic mean of these three percentages was calculated and used as an Index of Relative Importance (IRI) to compare stations, seasons, age classes and species (Appendix I, Table 23 and 24).

Caddisflies and dipterans had the highest IRI's in the stomachs of mountain whitefish in all age classes at all stations (Table 23). Terrestrial invertebrates were of zero importance in the spring, of minor importance in July, but of major importance at all stations in October. No consistent trends between stations were observed, which might be expected, since compositional differences between sites were not major. One would expect to see larger differences in a fully regulated river. There is also the possibility that some fish may move between sites.

Records from trout stomachs are sketchy, but there is an indication that mayflies, stoneflies, and terrestrial insects may be more important in the diets of westslope cutthroat and rainbow trout (Table 24). Terrestrial

Table 22. Percent composition of benthic samples (n=3), drift samples (n=8), and stomach contents of age 2 and age >2 mountain whitefish based on density estimates at three sample stations in the Flathead River in April, 1980. Electivity indices based on benthos and drift are given for each age class.

	Benthos	Drift	Stomachs age 2	Stomachs age >2	Electivity (Benthos) age 2	Electivity (Benthos) age >2	Electivity (Drift) age 2	Electivity (Drift) age >2
Bible Camp			n=6	n=14				
Ephemeroptera	68	50	9	21	-.77	-.53	-.69	-.41
Plecoptera	5	21	2	9	-.43	-.29	-.83	-.40
Trichoptera	2	0.4	3	24	+.20	+.85	+.76	+.97
Diptera	25	29	86	45	+.55	+.29	+.50	+.22
Other Aquatic	0.2	0.01	0	0.3	-1.0	+.20	-1.0	+.93
Terrestrial	0	0	0	0	---	---	---	---
Columbia Falls			n=11	n=15				
Ephemeroptera	20	8	0.7	4	-.93	-.67	-.84	-.33
Plecoptera	21	83	0.2	0.4	-.98	-.96	-1.0	0.99
Trichoptera	2	0.01	0.4	1	-.67	-.33	+.95	+.98
Diptera	57	8	99	94	+.27	+.25	+.85	+.84
Other Aquatic	0.01	0.2	0.04	0	+.60	-1.0	-.67	-1.0
Terrestrial	0	0	0	0	---	---	---	---
Kalispell			n=9	n=16				
Ephemeroptera	52	20	7	18	-.76	-.49	-.48	-.05
Plecoptera	12	62	12	11	0	-.04	-.68	-.70
Trichoptera	0.3	0.2	1	24	+.54	+.98	+.67	+.98
Diptera	32	17	80	46	+.43	+.18	+.65	+.46
Other Aquatic	3	0.01	0	0.6	-1.0	-.67	-1.0	+.97
Terrestrial	0	0.01	0	0	---	---	-1.0	-1.0

Table 23. Index of Relative Importance (IRI) of aquatic and terrestrial invertebrates in the diet of various age classes of mountain whitefish during three seasons in the Flathead River.

	April, 1980			July, 1980			October, 1980		
	Bible Camp	Columbia Falls	Kalispell	Bible Camp	Columbia Falls	Kalispell	Bible Camp	Columbia Falls	Kalispell
Ephemeroptera									
Age 1							(n=10)10	(n=9)22	(n=10) 4
Age 2	(n=6)33	(n=11)20	(n=9)24				(n=9)20	(n=12)21	(n=7) 0
Age 1 & 2				(n=12)35	(n=9)35	(n=12)12			
Age >2	(n=14)45	(n=15)35	(n=16)35	(n=5)33	(n=12)47	(n-12)40	(n=9)20	(n=10)18	(n=12) 8
Plecoptera									
Age 1							4	0	4
Age 2	29	12	31				18	8	0
Age 1 & 2				10	5	6			
Age >2	30	16	33	23	11	13	37	25	4
Trichoptera									
Age 1							32	34	57
Age 2	44	16	11				11	35	44
Age 1 & 2				44	36	41			
Age >2	54	31	58	10	37	51	39	31	38
Diptera									
Age 1							46	60	52
Age 2	49	60	75				19	57	56
Age 1 & 2				59	53	50			
Age >2	49	75	53	68	47	54	9	47	13
Other Aquatic									
Age 1							15	5	0
Age 2	0	4	0				5	4	0
Age 1 & 2				21	5	23			
Age >2	6	0	5	17	9	14	5	4	4
Terrestrial									
Age 1							42	35	9
Age 2	0	0	0				80	51	24
Age 1 & 2				0	19	0			
Age >2	0	0	0	0	11	3	24	36	44

Table 24. Index of Relative Importance (IRI) of aquatic and terrestrial invertebrates in the diets of four species of trout in the Flathead River.

	April, 1980	July, 1980			October, 1980	
	Columbia Falls	Bible Camp	Columbia Falls	Kalispell	Bible Camp	Kalispell
Westslope Cutthroat	n=2	n=5	n=3			n=4
Ephemeroptera	61	76	31			10
Plecoptera	47	30	24			9
Trichoptera	45	42	49			22
Diptera	41	37	13			0
Other Aquatic	0	7	12			21
Terrestrial	22	41	72			88
Rainbow Trout	n=3	n=7			n=7	
Ephemeroptera	28	83			25	
Plecoptera	30	15			32	
Trichoptera	13	37			20	
Diptera	64	35			40	
Other Aquatic	55	5			0	
Terrestrial	0	39			89	
Bull Trout				n=5		
Ephemeroptera				10		
Plecoptera				16		
Trichoptera				19		
Diptera				22		
Other Aquatic				0		
Terrestrial				55		
				10		
Eastern Brook Trout	n=2					
Ephemeroptera	49					
Plecoptera	65					
Trichoptera	0					
Diptera	36					
Other Aquatic	0					
Terrestrial	0					

insects assume more importance to the trout earlier in the year. Bull trout feed primarily on other fish (Leathe and Graham 1982) although they feed on immature aquatic insects as juveniles (Fraley et al. 1981). Leathe and Graham (1982) analyzed cutthroat trout stomachs from the Flathead River below Kalispell in January and September-October, 1981. They calculated very high IRI's for stoneflies in the winter diet, and also found high IRI's for terrestrial insects during the fall.

Differences were found in the feeding habits of the younger versus the older mountain whitefish. The younger age classes tended to feed less on terrestrial insects and heavily on caddisflies and dipterans. The composition of insect species within insect orders which were found in the stomachs changed with age class. For example, the smaller whitefish fed more on small species of caddisflies, such as *Hydroptila*, while the older fish shifted to larger caddis, such as *Glossosoma* and *Brachycentrus*.

The extent to which the whitefish feed on the benthos and on the drift was compared with the use of Ivlev's (1961) Electivity Index (E):

$$E = (r_i - p_i)/(r_i + p_i)$$

which was calculated separately for benthos and drift (r_i is the relative percentage by numbers of an order in the stomach and p_i is the relative percentage by number of an order in the environment (benthos or drift). The index has a possible range of -1 to +1 with negative values indicating avoidance or inaccessibility of the prey item, zero indicating random selection from the environment, and positive values indicating active selection.

Whitefish showed positive selection for caddisflies and dipterans from both the drift and benthos at all stations in all seasons (Table 22, 25 and 26). In the fall there was active selection for terrestrials in the drift. Stoneflies and mayflies showed negative electivity indices at all stations in all months.

Other researchers (e.g. Pontius and Parker 1973) have found that mountain whitefish tend to be bottom feeders. This is not apparent from our electivity indices, which were calculated by insect order. However, when the species composition within orders is considered, our data supports the idea that whitefish are predominantly bottom feeders during much of the year (an exception might be in the fall, when they feed more on terrestrial insects, although they may be catching them after they sink to the bottom). Stomach contents show that whitefish feed heavily on midge larvae, which do not drift readily (midge adults make up the largest component of dipterans in the drift). Caddisflies generally do not drift readily, particularly the heavier cased caddisflies which the whitefish prefer.

We did not estimate stomach fullness; however, many of the whitefish stomachs had relatively little in them compared to the trout stomachs. This may indicate that whitefish feed primarily during the day. This

Table 25. Percent composition of benthic samples (n=3), drift samples (n=4), and stomach contents of age 1 and 2 and age >2 mountain whitefish based on density estimates at three sample stations in the Flathead River in July, 1980. Electivity indices based on benthos and drift are given for each age class.

	Benthos	Drift	Stomachs age 1 & 2	Stomachs age >2	Electivity (benthos) age 1 & 2	Electivity (benthos) age >2	Electivity (drift) age 1 & 2	Electivity (drift) age >2
Bible Camp			n=12	n=5				
Ephemeroptera	48	29	7	2	-.75	-.92	-.61	-.87
Plecoptera	6	2	0.4	0.2	-.88	-.94	-.67	-.82
Trichoptera	8	4	10	6	+.11	-.14	+.43	+.20
Diptera	37	64	79	86	+.36	+.40	+.10	+.15
Other Aquatic	1	0.5	4	6	+.60	+.71	+.78	+.85
Terrestrial	0	0.3	0	0	---	---	-1.0	-1.0
Columbia Falls			n=9	n=12				
Ephemeroptera	45	18	19	21	-.41	-.36	+.03	+.08
Plecoptera	13	2	0.3	9	-.95	-.18	-.74	+.64
Trichoptera	2	4	15	7	+.76	+.56	+.58	+.27
Diptera	39	68	64	61	+.24	+.22	-.03	-.05
Other Aquatic	1	1	0.3	0.5	-.54	-.33	-.54	-.33
Terrestrial	0	7	2	2	---	---	-.56	-.56
Kalispell			n=12	n=12				
Ephemeroptera	31	28	1	7	-.94	-.63	-.93	-.60
Plecoptera	24	5	0.2	0.7	-.98	-.94	-.92	-.75
Trichoptera	5	12	11	13	+.38	+.44	-.04	+.04
Diptera	36	53	74	75	+.35	+.35	+.17	+.17
Other Aquatic	4	0.9	15	4	+.58	0	+.89	+.63
Terrestrial	0	0.7	0	0.1	---	---	-1.0	-.75

Table 26. Percent composition of benthic samples (n=3), drift samples (n=4) and stomach contents of age 1, age 2 and age >2 mountain whitefish based on density estimates at three sample stations in the Flathead River in October, 1980. Electivity indices based on benthos and drift are given for each age class.

	Benthos	Drift	Stomachs Age 1	Stomachs Age 2	Stomachs Age >2	Electivity (benthos) Age 1	Electivity (benthos) Age 2	Electivity (benthos) Age >2	Electivity (drift) Age 1	Electivity (drift) Age 2	Electivity (drift) Age >2
Bible Camp			n=10	n=9	n=9						
Ephemeroptera	53	36	2	3	40	-.93	-.89	-.14	-.89	-.85	+.05
Plecoptera	19	9	0.4	5	20	-.96	-.58	+.03	-.91	-.29	+.38
Trichoptera	6	2	15	4	26	+.43	-.20	+.63	+.76	+.33	+.86
Diptera	22	34	47	6	2	+.36	-.57	-.83	+.16	-.70	-.89
Other Aquatic	0	1	1	0.4	0.4	---	---	---	0	-.43	-.43
Terrestrial	0	18	35	82	12	---	---	---	+.32	+.64	-.20
Columbia Falls			n=9	n=12	n=10						
Ephemeroptera	45	5	5	4	5	-.80	-.84	-.80	0	-.11	0
Plecoptera	23	3	0	2	9	-1.0	-.84	-.44	-1.0	-.20	+.50
Trichoptera	4	0.4	11	5	14	+.47	+.11	+.56	+.93	+.85	+.94
Diptera	24	89	70	52	42	+.49	+.37	+.27	-.12	-.26	-.36
Other Aquatic	4	0.2	0.9	0.7	0.7	-.63	-.70	-.70	+.64	+.56	+.56
Terrestrial	0	3	14	36	29	---	---	---	+.65	+.85	+.81
Kalispell			n=10	n=7	n=12						
Ephemeroptera	36	4	0.1	0	2	-.99	-1.0	-.89	-.95	-1.0	-.33
Plecoptera	34	12	0.1	0	1	-.99	-1.0	-.94	-.98	-1.0	-.85
Trichoptera	1	1	78	10	37	+.97	+.82	+.95	+.97	+.82	+.95
Diptera	26	59	21	87	15	-.11	+.54	-.27	-.48	+.19	-.59
Other Aquatic	3	5	0	0	1	-1.0	-1.0	-.50	-1.0	-1.0	-.67
Terrestrial	0	18	0.6	2	43	---	---	---	-.94	-.80	+.41

provides circumstantial evidence that they feed mostly on the bottom, since most drift occurs at night. This may mean that the insects caught in our night drift samples were not, in actuality, available to them. It is also possible that our benthic samples, which were taken in riffle areas were not representative of the invertebrates in pools where the whitefish more often feed. One would expect the dipterans and cased caddisflies to be more abundant in pool areas of the river.

The fact that whitefish prefer dipterans and grazing species of caddisflies may give them a competitive edge over trout in full regulated rivers, where dipterans and caddisflies tend to dominate. This is probably not the case in the partially regulated Flathead River where composition differences are not as marked as in most regulated rivers.

CONCLUSIONS

Annual means of numbers (no/m^2) and biomass (cc/m^2) data indicate that densities of zoobenthos are higher in the South Fork than at the control and partially regulated sites, but the overall biomass is not significantly different at the three sites. Species diversity is much reduced in the South Fork, but Shannon indices showed no significant differences between the control and partially regulated sites.

The faunal composition was markedly changed (consisting primarily of midges and oligochaetes) and the number of species was decreased in the South Fork, mainly due to the extreme modification of the temperature regime. Due to the addition of water from the North and Middle Forks of the Flathead River, the changes were much less marked in the partially regulated areas of the river. This can be attributed to factors such as temperature modification, the flushing and redeposition of sediments which occurs during spring runoff, the import of particulate organic carbon and drifting insects from upstream areas, etc.

However, there were compositional changes in the partially regulated portion of the river. Mayflies were far more abundant in the control area, while stoneflies and dipterans showed increased abundances in the partially regulated area. The composition of caddisflies was markedly different at the two sites due to differences in periphyton growth and particulate organic carbon particle sizes. The timing of events in the life cycle of a number of species was different at the two sites due to seasonal temperature differences.

Three ordination techniques, which were applied to the macroinvertebrate data to assess differences in community structure between sampling stations, all showed definite spatial differences between regulated, partially regulated and reference stations. Various environmental parameters were quantified in an attempt to explain the differences in macroinvertebrate community structure in regulated and control areas. Seasonal measurements of ash free dry weight and chlorophyll *a* in the periphyton showed a much higher biomass at the South Fork regulated site than at the other two stations. However, productivity was not proportionately higher at the South Fork station. Productivity is comparatively low in the Flathead River system.

The relative percentage of particulate organic carbon (POC) in each of four size fractions of seston was altered by the presence of Hungry Horse Dam. The larger size fractions contained a smaller percentage of the POC below the dam, due to the fact that larger particles settle out in the reservoir. The larger-sized particles were increased dramatically just after water elevations rose due to the initiation of hydropower, which resulted in the sloughing of periphyton and resuspension of materials.

Substrate measurements showed that the mean size of surface rocks was largest at the South Fork station. The heterogeneity of particle sizes was lowest at the South Fork station where the finer materials have been washed out by fluctuating flows.

Correlation analyses were used to assess the importance of various environmental factors in determining macroinvertebrate community associations. Generally ash free dry weight and chlorophyll *a* in the periphyton, particulate organic carbon in the seston, substrate heterogeneity, and rates of change in velocity showed significant correlations with measures of invertebrate diversity and community composition (ordinations).

Invertebrate drift densities were studied in relation to rates of increase in discharge caused by hydropower generation and in relation to time of shutdown at Hungry Horse Dam with regard to time of day. Significantly more insects were recorded in the drift just after flows started to increase, but no major differences were found between the two rates of increase in discharge. The effect of decreasing flows on insect drift in the mainstem river was not marked, either when shutdown occurred during the day or at night.

Food habits studies of mountain whitefish showed that they feed predominantly on caddisflies and dipterans, as well as on terrestrial invertebrates during the fall. Trout fed more heavily on mayflies, stoneflies, and terrestrial invertebrates. No consistent differences were found in the food preferences of whitefish in the partially regulated as compared with the free-flowing section of the mainstem Flathead River.

The ameliorative effects of the North and Middle Forks are limited during seasons of lower flows from natural areas. Major changes in the discharge regime from Hungry Horse Dam during certain times of the year could substantially alter the composition of invertebrates in the mainstem river. Marked increases in discharge during certain seasons (e.g. during the winter) could cause species elimination in the regulated mainstem. The partially regulated section of the Flathead River is a rather unique area, which under the current discharge regime, seems to combine advantages of both free flowing rivers and regulation. This area currently supports a diverse fauna despite perturbations, but is not resistant to species deletion (see Pimm 1979). Until more information is available on what environmental factors are important for the maintenance of a habitat suitable for specific groups of species, caution should be exercised in altering discharge regimes.

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