Wetted stream channel, fish-food organisms and trout relative to the wetted perimeter inflection point instream flow method
by Samuel Clark Lohr

A thesis submitted In partial fulfillment of the requirements for the degree of Doctor of Philosophy In Biological Sciences
Montana State University

Abstract:
Some biological assumptions of the wetted perimeter instream flow method are that: 1) abundance of aquatic invertebrates is proportional to riffle area, 2) wetted perimeter can be used as an Index of invertebrate abundance, and 3) at flows below the wetted perimeter-discharge inflection point, stream fish may become food limited. To evaluate these assumptions, field and laboratory tests were conducted to investigate the relationships among stream discharge, riffle wetted perimeter, and aquatic invertebrate abundance, cutthroat trout density and growth relative to increased prey abundance, and prey abundance, habitat volume, and cutthroat trout residency in artificial stream channels.

The wetted perimeter method was performed, and benthic and drifting invertebrates were collected from dewatered and unaltered flow reference riffles in two streams during summer. Benthic invertebrate densities were similar between test and reference riffles on most sample dates but invertebrate biomass was usually lower at the test riffle in one stream. This resulted in invertebrate biomass and caloric content being significantly lower on the test riffle when discharge was below the wetted perimeter inflection point. In both streams, invertebrate drift density was typically greater at dewatered riffles. Differences in stream discharge, however, caused drift rates to be substantially lower at dewatered riffles, effectively reducing potential food abundance for drift-feeding fish.

Supplemental feeding of cutthroat trout in experimental stream enclosures increased trout growth rates compared to trout in unfed, control enclosures during late summer. Volitional residency of trout in enclosures was unaffected by supplemental feeding so that no trends in trout density and increased food abundance were observed.

Short-term residency (20 d) of cutthroat trout (51-75 mm TL) in artificial stream channels was influenced more by ration than incremental reductions in water depth. However, larger trout (122-159 mm TL) failed to establish residency, suggesting that unsuitable habitat may be more important than ration for determining residency of larger trout.

Reductions in stream discharge affected abundance of fish-food organisms primarily through declines in riffle area and invertebrate drift rate, with the greatest reduction occurring when stream discharge was below the wetted perimeter inflection point. Such reductions may potentially restrict growth of older trout and abundance of young individuals.

WETTED STREAM CHANNEL, FISH-FOOD ORGANISMS AND TROUT RELATIVE TO THE WETTED PERIMETER INFLECTION POINT INSTREAM FLOW METHOD

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Advisor: Robert G. White, Ph.D.

Montana State University
1993

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APPROVAL

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Samuel Clark Lohr

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Approved for the Major Department

22 April 1993 — Robert E. Moore
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STATEMENT OF PERMISSION TO USE

VITA

Samuel Clark Lohr was born in Lexington, North Carolina on 9 December 1960 to Robert G. Lohr and Maxine W. Lohr. He was graduated from Lexington Senior High School in June 1979. He entered the University of North Carolina at Chapel Hill in August 1979 and graduated with a Bachelor of Science degree in Zoology in June 1983. He began graduate studies at Western Carolina University in August 1983 and received a Master of Science degree in Biology in August 1985. He began studies toward a Doctorate in Biological Sciences through the Montana Cooperative Fishery Research Unit at Montana State University in September 1985. He wed Lynn E. Taylor in June 1991.

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ABSTRACT

Some biological assumptions of the wetted perimeter instream flow method are that: 1) abundance of aquatic invertebrates is proportional to riffle area, 2) wetted perimeter can be used as an index of invertebrate abundance, and 3) at flows below the wetted perimeter-discharge inflection point, stream fish may become food limited. To evaluate these assumptions, field and laboratory tests were conducted to investigate the relationships among stream discharge, riffle wetted perimeter, and aquatic invertebrate abundance, cutthroat trout density and growth relative to increased prey abundance, and prey abundance, habitat volume, and cutthroat trout residency in artificial stream channels.

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GENERAL INTRODUCTION

Water demand for various uses has led to the degradation of stream ecosystems in North America. The recognition of maintaining instream flows to protect stream resources as a beneficial water use has stimulated the development of instream flow programs in practically every state and province of the United States and Canada. Instream flow programs function as an administrative framework to allocate water among users, institute water reservations according to respective policies, and provide instream flow methods which are used to make flow recommendations to protect stream ecosystems. In a survey of 46 states and 12 provinces, Reiser et al. (1989) reported that at least 17 instream flow methods are in use or being reviewed for use.

The diversity of methods used to make instream flow recommendations reflects differences in stream ecosystems to which specific methods are amenable, costs of performing various methods, and objectives of the agency making a recommendation. Objectives may be maintenance of water quality, the preservation of certain aesthetic features of the stream, and, in most cases, the protection of fishery resources. The latter may include maintenance of target species at some acceptable level or enhancement of the aquatic community through negotiations of flows with a water user (Leathe and Nelson 1986).

Methods that identify fish as the primary management target use a carrying capacity concept (Wesche and Rechard 1980). That is, the number or biomass of fish that can be indefinitely supported is positively related to stream flow up to a point where excessive flows become detrimental to fish populations (Anderson and Nehring 1985; Seegrist and Gard 1972). Nelson (1980) analyzed 4 to 13 years of trout standing crop estimates and stream flow records in four rivers in southwest Montana. He concluded that flow regime the preceding year was the most important factor controlling trout abundance. White (1975) concluded that changes in flow regime may account for variations in brown trout abundance and body size in a Wisconsin stream. Wolff et al. (1990) documented a four- to six-fold increase in brown trout standing stock after minimum flows were increased five times in a regulated stream in Wyoming. Schlosser and Ebel (1989) found that cyprinid density increased in years of elevated flow in a small headwater stream of Minnesota. They emphasized that the timing of cyprinid life history events in conjunction with flow variation greatly influences population dynamics of stream fishes.

Although more water typically translates into more fish at a stream site, an understanding of the specific linkages between fish populations and stream characteristics is tenuous. This is evident in the development of instream flow methods. The general strategy has been the construction of models that predict changes in a variable, or set of variables, important to various life stages of fish as a function of stream flow. Although several models adequately predict the variables for which they were designed (White et al. 1981), conflicting conclusions have been reached concerning the linkage between index variables and the response of fish populations (Orth and

Maughan 1982; Annear and Conder 1984; Randolph and White 1984; Mathur et al. 1985; Conder and Annear 1987; Scott and Shirvell 1987). This is due to what Wesche and Rechard (1980) called the "fallacy of the state of the art." That is, most instream flow methods do not address biological consequences, and this is a common criticism of many instream flow methods. There are few methods that directly predict fish abundance or biomass from stream data (Morhardt and Mesick 1988; but see Fausch et al. 1988). Incomplete knowledge of the complex interactions between biotic and abiotic factors that determine the carrying capacity of a stream for fish is the foundation of this criticism. Energy source, water quality, temperature, physical habitat structure, flow regime, and biotic interactions have been identified as primary factors affecting populations of stream fish (Orth 1987).

Elucidating linkages among these factors and their relations to fish population dynamics would be difficult at the present state of knowledge and impractical for most instream flow studies. Most instream flow methods have been developed from large empirical databases, and when sufficient information has been obtained, generalizations concerning the relationships among these factors and fish populations are made. Instream flow methods can then utilize simplifying assumptions that incorporate empirically derived generalizations (Trihey and Stalnaker 1985). Acquisition and incorporation of relationships among flow, habitat, and fish populations into instream flow methods is a continuing process for refinement of present methods and considered a major research need (Mathur et al. 1985; Reiser et al. 1989).

Major considerations in selecting an instream flow method appropriate for use in Montana were a method that: 1) uses site specific field data, 2) is cost-effective in application on a statewide scale, 3) is biologically reliable in maintaining existing fishery resources at an acceptable level, and 4) produces a single flow recommendation which simplifies compliance (Leathe and Nelson 1986). The wetted perimeter inflection point method was deemed suitable to best fulfill these needs compared to the Tennant Method and incremental methodology (Nelson 1980; Leathe and Nelson 1986). The method is used during summer to early autumn when low stream flows typically coincide with the greatest water demands.

The wetted perimeter inflection point method is based solely on stream riffles, which are affected more by flow reductions than are other areas and are an important site for production of invertebrate fish-food organisms (Hynes 1970). The method assumes that the carrying capacity of a stream for fish is proportional to fish-food producing areas and that riffle wetted perimeter (a linear measure of wetted stream bed perpendicular to flow) is a reliable index of this relationship (Leathe and Nelson 1986). Because the physical characteristics of riffles are sensitive to changes in flow, maintenance of acceptable flows in riffles is assumed to preserve other stream habitats for fish.

Recommendations are derived from the relationship between riffle wetted perimeter and stream flow. A computer program (WETP) developed by the Montana Department of Fish, Wildlife and Parks accepts 2-10 sets of water surface elevations at different flows on up to 150 riffle transects (Nelson 1989). Regression analysis is performed on water surface elevations (stage) and stream flows (discharge) to produce a rating curve for each transect. The rating curves are combined with cross-sectional profiles of the transects and averaged to derive a composite wetted perimeter-discharge curve.

From zero flow, wetted perimeter increases rapidly with small increases in flow until water reaches the sides of the channel. An inflection point occurs on the curve where the rate of change between discharge and wetted perimeter decreases. A typical wetted perimeter-discharge curve has either one or two prominent inflection points. Recommendations are made at stream flows equal to or greater than the stream flow at the wetted perimeter inflection point and flows are judged sufficient to maintain existing aquatic communities. When two inflection points occur, the upper inflection point is assumed to represent flows providing optimal stream conditions (Nelson 1989). Ultimate selection of a flow recommendation is based on professional judgment relative to the biological potential of the specific stream (Leathe and Nelson 1986).

In Montana and elsewhere, allocational conflicts exist between people who wish to withdraw water from streams and those who wish to have it left in streams. Questions concerning the validity of the wetted perimeter inflection point method may serve as the basis for legal challenges to instream flow recommendations. In light of the recognized weaknesses in present instream flow methods (i.e. "fallacy of the state of the art"), the objective of this study was to investigate the linkages among several factors influencing fish populations relative to stream flow. Specifically, it was to clarify the linkages among stream flow, wetted perimeter, food and habitat availability, and trout populations. This information was used to evaluate underlying assumptions of the wetted perimeter inflection point method. The following hypotheses were tested:

1. Aquatic macroinvertebrate abundance declines in response to decreases in stream discharge and riffle wetted perimeter.

2. Increased food availability affects trout population density and individual growth rate of fish.

3. Food and habitat availability interact to determine trout residency.

INVERTEBRATE ABUNDANCE AND REDUCTIONS IN STREAM DISCHARGE

Introduction

Abundance and distribution of aquatic invertebrates is related to a suite of interacting factors. Anderson and Wallace (1984) placed these factors into four general categories: 1) physical constraints, 2) trophic considerations, 3) physiological constraints, and 4) biotic interactions. Invertebrate community structure is the response of individual species integrating these factors and their interactions.

Stream discharge has a primary influence on factors affecting aquatic invertebrate communities. Discharge affects dissolved oxygen and water temperature (Ward and Stanford 1980), which sets physiological limits for aquatic invertebrate taxa. Water depth, current velocity, and substrate type are largely determined by discharge and impose physical constraints on invertebrate microdistribution and abundance (Minshall and Minshall 1977; Reice 1980). Also, these variables affect invertebrate trophic relations through their influence on abundance of potential invertebrate prey, transport and retention of detritus (Egglishaw 1969; Culp et al. 1983; Rabeni and Minshall 1977; Egglishaw 1969), and availability of aquatic plant material (Hynes 1970). The role of biotic interactions (predation and competition) in structuring benthic communities tends to vary inversely with the severity of environmental conditions that are largely dependent on stream discharge (Peckarsky 1980).

The diversity of morphological, behavioral, and life history features of aquatic invertebrates is evidence of physical and physiological constraints, and biotic and trophic relations interacting over evolutionary time with the long-term flow regime (Hynes 1970). The influence of stream discharge on invertebrate abundance and distribution is apparent in areas where the natural flow regime has been altered. Major types of human caused flow perturbations range from diel or arrhythmic fluctuations, to flow reduction caused by dams or water diversions (Ward and Stanford 1980).

Benthic invertebrate communities exhibit differential responses to flow perturbations. No consistent relationship between benthic density and natural dewatering of riffles was observed in southern Appalachian streams (Cada et al. 1983). Experimental flow reductions in streams and artificial channels have elicited minimal responses in the benthos (Hafele 1978; White et al. 1981). Benthic communities below dams producing either reduced flow or flow fluctuations have reduced species diversity, reduced biomass, and increased density in comparison to pre-impoundment communities or those in unaltered portions of the drainage basin (Ward and Stanford 1980; Brusven 1984).

Stream discharge influences invertebrate drift through effects on several abiotic factors (Brittain and Eikeland 1988), primarily water velocity (Waters 1972). Changes in water velocity may elicit increased active or passive entry of invertebrates into the water column (Poff and Ward 1991). Abrupt reductions in stream discharge generally cause an increase in drift density (Minshall and Winger 1968; Pearson and Franklin 1968; Radford and Hartland-Rowe 1971; Brusven et al. 74; Gore 1977; White et al. 1981; Corrarino and Brusven 1983; Poff and Ward 1991). Drift density tends to return to pre-reduction levels within a week (White et al. 1981), but drift rate may remain low (Poff and Ward 1991) due to reduced flow and presumably to associated decreases in riffle area (Trotzky and Gregory 1974; Evans 1979).

With increasing demand for water for agricultural, industrial, hydroelectric, and municipal uses, there is a need to protect instream flows. Montana Department of Fish, Wildlife, and Parks selected the wetted perimeter inflection point method for recommending minimum instream flows to protect aquatic resources (Leathe and Nelson 1986). The method is based on the relationship between stream discharge and riffle wetted perimeter, a linear measure of stream bed in contact with water. Wetted perimeter is a function of stream discharge and stream channel profile. From zero flow, wetted perimeter rapidly increases with discharge, but the rate of increase declines as water fills the channel. An inflection point occurs in the wetted perimeter-discharge relationship where further increases in discharge primarily contribute to water depth, with relatively small changes in wetted perimeter. Riffle profiles typically have one or two prominent inflection points, depending on stream channel geometry, and instream flow recommendations are made relative to inflection points (Leathe and Nelson 1986). The proximate goal of the method is to recommend stream flows that maintain riffle wetted perimeter.

Several biological assumptions link the wetted perimeter-discharge relationship to predicted responses of stream biota (Leathe and Nelson 1986). Because riffles provide habitat for aquatic invertebrates, invertebrate abundance is assumed to be proportional to riffle area. Thus, wetted perimeter is used as an index of riffle area and invertebrate abundance. Stream discharges below the inflection point are deemed detrimental to invertebrate communities. Because game fish are either directly dependent on invertebrates as food, or on forage fish that use invertebrates, the wetted perimeter method is based on the assumption that flow reductions below an inflection point may reduce food availability for fish.

The objective of my study was to evaluate assumptions of the wetted perimeter instream flow method relative to stream discharge, wetted perimeter, and invertebrate abundance. I compared benthic and drifting invertebrate abundance between riffles exposed to the natural flow regime and dewatered by diversion during late summer and early fall months when water demands for irrigation are high. The null hypothesis was that there would be no difference in invertebrate abundance between dewatered and unaltered flow riffles.

Methods

Study Sites

Bozeman Creek. Bozeman Creek is a third order stream in Gallatin County, Montana. The stream flows north out of the Gallatin Mountain Range and enters the East Gallatin River near the city of Bozeman (Figure 1). Bozeman Creek has a mean annual flow of 0.8 m^3/s

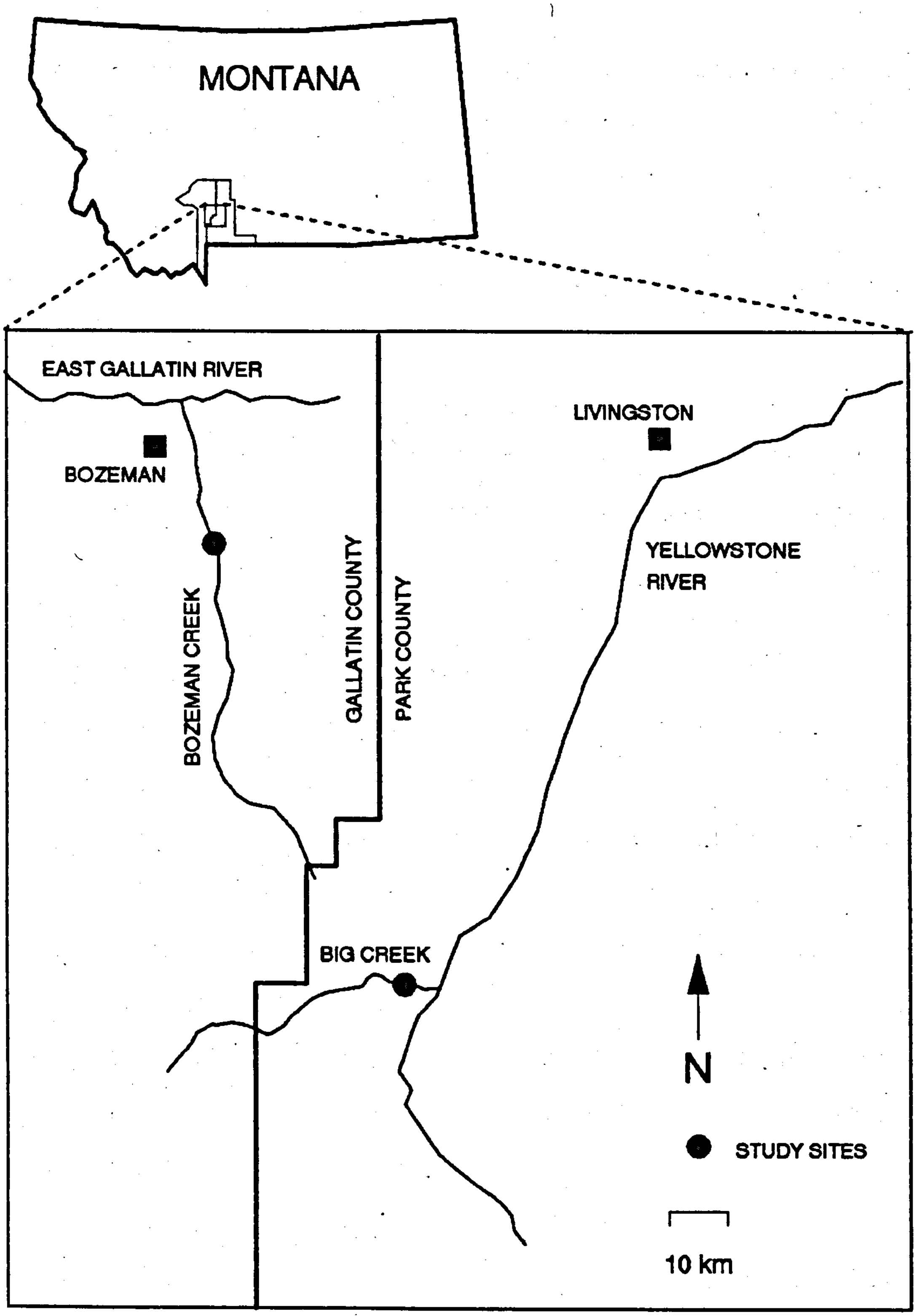

Figure 1.-Location of study sites in Bozeman Creek and Big Creek.

and a 73 km^2 drainage basin (USGS 1992). The riparian community is composed primarily of cottonwood (*Populus* sp.) and willow (*Salix* sp.) stands that provide shading for most of the stream. Brook trout (*Salvelinus fontinalis*) and mottled sculpin (*Cottus bairdi*) are the most abundant fish in the stream.

I selected one riffle above and one below a diversion dam to apply the wetted perimeter instream flow method and to monitor invertebrate abundance associated with natural (reference) and altered (test) flow conditions. The invertebrate sampling station on the test riffle was 77 m below the dam. This riffle extended 61 m upstream to the plunge pool below the dam. The invertebrate sampling station on the reference riffle was 56 m above the dam, at the lower end of a 60 m-long riffle. Sampling stations were separated by 133 m. Water chemistry was similar between riffles in September ranging from 7.9 to 8.1 for pH, 220.0 to 225.8 µmhos for conductivity, 34.7 to 44.4 mg $CaCO_3$/L for alkalinity, and dissolved oxygen was 10.1 mg O_2/L at both riffles. Invertebrate sampling occurred from July to September 1989.

Big Creek. Big Creek is a third order stream that flows from the east slopes of the Gallatin Mountain Range in Park County, Montana (Figure 1). It enters the Yellowstone River about 34 km north of the town of Gardiner. Big Creek has a mean annual flow of 1.8 m^3/s and a 174 km^2 drainage basin (USGS 1992).

Water from the lower reach of Big Creek is diverted for irrigation by three ditches located 1.6, 2.5, and 2.7 km above the mouth. In most years, the lowest 1.6 km is completely dewatered (Byorth 1990). I selected three riffles, two below (test) and one above (reference) diversion structures to apply the wetted perimeter instream flow method and to monitor invertebrate abundance. The lowest invertebrate sampling station (downstream) was 200 m below the most downstream diversion while the other dewatered station (middle) was 100 m above this diversion. Test riffles were in primarily run-riffle areas of Big Creek with narrower stream widths and greater water depths compared to the reference (upstream) riffle. The reference invertebrate sampling station was in a pool-riffle area located 200 m above the highest diversion. In previous summers (1987-1989), dissolved oxygen was 8.8 mg O_2/L, conductivity was 81.0 μmhos, alkalinity was 46.1 mg $CaCO_3$/L, and pH was 7.2 (Byorth 1990). Big Creek was sampled from July to August 1990.

Drift Collections

At each sampling station, three steel bars were driven into the stream bed at the thalweg and left there for the duration of the studies. Pairs of rectangular driftnets (50 x 30 cm openings with a 1-m long net of 0.5 mm mesh) were placed against the steel bars, sampling the entire water column. Sample time was typically 15-60 min, depending on stream discharge. Mean water depth and velocity (0.6 depth) was calculated from three measurements taken at equally spaced locations across the opening of each net. Measurements were made with a top-setting rod and electronic current meter at the midpoint of the sample time. Samples were washed into labeled bottles containing a solution of 4% formalin and rose bengal (to stain invertebrates). Sample time, mean water depth, and velocity were used to calculate water volume sampled by each net.

To determine diel periodicity, drift was sampled at each riffle during four time periods: noon, within one-half-hour after sunset, at midnight, and within one-half-hour before sunrise. During each sample period, water temperature was recorded. Sample dates were: 18-19 July, 2-3 August, 28-29 August, and 14-15 September 1989 for Bozeman Creek and 16-17 July and 30-31 July 1990 for Big Creek.

In the laboratory, each drift sample was washed and separated into two size fractions with sieves (coarse ≥ 1.0 mm; fine ≥ 0.5 mm). For a sample, portions of a coarse fraction were spread in white pans and all invertebrates removed from debris and placed in labeled bottles of 4% formalin. Pan contents were discarded when no invertebrates were found in a 3 min period. The process was repeated until all portions of a coarse fraction were examined. Aquatic invertebrates were identified to the lowest practical taxonomic level using a dissecting scope (0.7-40 X) and various taxonomic sources (Wiggins 1977; Merritt and Cummins 1984; Stewart and Stark 1988; Pennak 1989; D. G. Gustafson, Department of Biology, Montana State University, personal communication). Individuals of terrestrial origin, including those with aquatic immature stages, were assigned to a single terrestrial category. All individuals were counted and total body length (distance from front of head capsule to end of abdomen) was measured with an ocular micrometer. Individuals were then assigned to 1.0 mm size classes.

Portions of fine fractions were spread in a small tray and inspected under a dissecting microscope. Invertebrates were counted, measured, and placed into taxonomic groups similar to those for coarse fractions. While this was repeated for all portions of fine fractions with relatively small amounts of material, some fine fractions were subsampled. The entire fraction was evenly spread in a rectangular, plexiglass chamber (10 cm x 10 cm x 12 cm) and partitions were inserted that divided the fraction into four equal portions. Materials from two of the resulting cells in the chamber were processed. Taxa counts and body length data were combined for both coarse and fine fractions of a sample.

To estimate invertebrate biomass, published regression equations of dry weight on body length (Rogers et al. 1976, 1977; Smock 1980) were used to predict dry weight (mg) of invertebrate size classes of each taxon. Biomass values were converted to caloric equivalents using Coffman (1967), Brocksen et al. (1968), and Cummins and Wuycheck (1971).

Invertebrate counts were scaled to water volume sampled and numeric drift density (no./m^3) was calculated for each taxon and total taxa per driftnet. Drift rates (no./h) were calculated by multiplying drift density by hourly stream discharge. Drift density and rate were also expressed as dry biomass and calories. Mean estimates of all drift measures, during a time period, for the paired nets were used to describe diel periodicity of invertebrate drift. To calculate daily drift measures, invertebrate counts were weighted by day and night length (time between sunrise and sunset) according to sample period, i.e., the mean of sunset, midnight, and sunrise samples represented nocturnal drift whereas noon samples represented diurnal drift. This was done for each net of the paired driftnets. Means for paired nets were used to estimate daily drift at each sampling station.

Benthic Collections

Benthic samples were collected following drift sampling on 19 July, 4 August, 31 August, and 17 September 1989 in Bozeman Creek and 18 July and 1 August 1990 in Big Creek. Five evenly spaced samples were initially taken on a transect 0.5 m upstream of the driftnets using a Hess sampler (sample area 0.08 m^2). Subsequent samples were taken within 0.5 m upstream of the last benthic sample. Water depth, temperature, and mean water velocity (0.6 depth) were measured at each sample location. The Hess sampler was embedded 5 to 10 cm into the stream bed and the substrate was disturbed for 1 min to dislodge invertebrates. Dominant substrate particles (≥ 10 cm) were carefully scrubbed with a brush to remove invertebrates and measured. Samples were preserved and processed in the same manner as drift samples. Benthos was expressed as both numeric (no./m^2) and caloric (cal./m^2) density as well as dry biomass (g/m^2).

Data Analyses

Data for the wetted perimeter inflection point instream flow method were collected at each riffle in Bozeman Creek and Big Creek following procedures of Nelson (1989). Due to abrupt dewatering, only two calibration flows were used in Big Creek.

Comparisons of water depth, water velocity, and substrate diameter associated with benthic samples at each riffle were made with t-tests for Bozeman Creek and analysis of variance for Big Creek (Sokal and Rohlf 1981). I used Mann-Whitney or Kruskal-Wallis tests (Zar 1984; Daniel 1990) to compare numeric and caloric density, biomass, and body length of benthic invertebrates between riffles in Bozeman Creek and in Big Creek. Comparisons for total taxa in both streams were made and for dominant taxa, those consistently comprising over 1% of all taxa in most samples, in Bozeman Creek. Because phenological events for invertebrates probably occurred during the studies, only comparisons between riffles on a sample date were conducted. A 0.05 significance level was used in all tests.

To compare numeric drift density between riffles, I scaled invertebrate densities to the mean volume of water sampled by the four or six driftnets used during a time period. I then performed G-tests (Sokal and Rohlf 1981) on numeric drift density (mean of paired driftnets rounded to nearest integer) weighting expected values equally between riffles. To determine potential influence of physical differences in riffles on drift density, G-tests were performed calculating expected drift densities proportional to stream discharge, wetted perimeter, and mean water velocity for each riffle. Additional tests were conducted for mean daily drift density (no./100 m^3). To describe differences in community structure, I calculated Horn's index of overlap (Horn 1966) between riffles on every sample date using mean numeric proportions of each taxa for drifting and benthic invertebrates.

Results

Bozeman Creek

Calibration stream discharges for applying the wetted perimeter instream flow method ranged from 0.26 to 0.64 m^3/s and from 0.39 to 0.99 m^3/s at the test and reference riffles, respectively (Table 1). Of the five transects used to measure stream channel profiles at each riffle, one typically had wetted perimeter values much larger than the others and was excluded in deriving the wetted perimeter-discharge relationships (Nelson 1989). A single inflection point occurred at 0.23 m^3/s at the test riffle (Figure 2), while two inflection points, at 0.14 and at 0.31 m^3/s, occurred for the reference riffle (Figure 2).

Discharge during invertebrate sampling ranged from 0.17 to 0.41 m^3/s at the test riffle and from 0.32 to 0.51 m^3/s at the reference riffle. On any sampling date, discharge was 20% to 47% lower and riffle wetted perimeter was 6% to 29% less at the test compared to the reference riffle (Table 1). Differences between riffles for stream width and mean water velocity were generally similar to those for wetted perimeter, whereas water depth differed little between the riffles. Stream discharge was considerably below the wetted perimeter inflection point (Figure 2) at the test riffle when the last invertebrate sample was collected. At this time, stream discharge was near the upper wetted perimeter inflection point at the reference riffle.

Seventy-four invertebrate taxa were collected in Bozeman Creek (Appendix A). These included at least 34 insect families represented

Table 1.-Stream discharge, and mean wetted perimeter, stream width, water depth, and water velocity and percent difference for values between the test and reference riffles in Bozeman Creek, June-September 1989. Numbers in parentheses=1 SE, N=4.

Variable	30 June[a]	19 July[b]	26 July[a]	3 August[b]	22 August[a]	29 August[b]	15 September[b]
				Test riffle			
Discharge (m^3/s)	0.64	0.41	0.38	0.33	0.26	0.25	0.17
Wetted perimeter (m)	7.10(0.13)	6.51(0.26)	6.39(0.28)	6.16(0.27)	5.72(0.11)	5.67(0.10)	4.70(0.30)
Stream width (m)	6.88(0.16)	6.31(0.30)	6.19(0.32)	5.97(0.31)	5.54(0.14)	5.49(0.14)	4.53(0.32)
Water depth (m)	0.16(0.01)	0.14(0.01)	0.12(0.01)	0.13(0.01)	0.12(0.01)	0.11(0.01)	0.11(0.01)
Water velocity (m/s)	0.59(0.04)	0.49(0.04)	0.47(0.03)	0.45(0.03)	0.41(0.03)	0.40(0.03)	0.34(0.03)
				Reference riffle			
Discharge (m^3/s)	0.99	0.51	0.53	0.46	0.39	0.37	0.32
Wetted perimeter (m)	7.51(0.35)	6.89(0.28)	6.92(0.29)	6.82(0.26)	6.70(0.25)	6.70(0.25)	6.60(0.25)
Stream width (m)	7.19(0.38)	6.59(0.30)	6.63(0.31)	6.53(0.28)	6.44(0.27)	6.42(0.26)	6.32(0.25)
Water depth (m)	0.17(0.01)	0.13(0.01)	0.14(0.01)	0.13(0.01)	0.12(0.01)	0.12(0.01)	0.11(0.01)
Water velocity (m/s)	0.83(0.05)	0.58(0.03)	0.60(0.03)	0.55(0.03)	0.50(0.03)	0.49(0.03)	0.46(0.03)

Table 1.–Continued.....

Variable	30 June[a]	19 July[b]	26 July[a]	3 August[b]	22 August[a]	29 August[b]	15 September[b]
	Percent difference between test and reference riffles						
Discharge (m^3/s)	-35	-20	-28	-28	-33	-32	-47
Wetted perimeter (m)	-5	-6	-8	-10	-15	-15	-29
Stream width (m)	-4	-4	-7	-9	-14	-14	-28
Water depth (m)	-16	8	-14	0	0	-8	0
Water velocity (m/s)	-29	-16	-22	-18	-18	-18	-26

[a]Wetted perimeter calibration.
[b]Invertebrate samples.

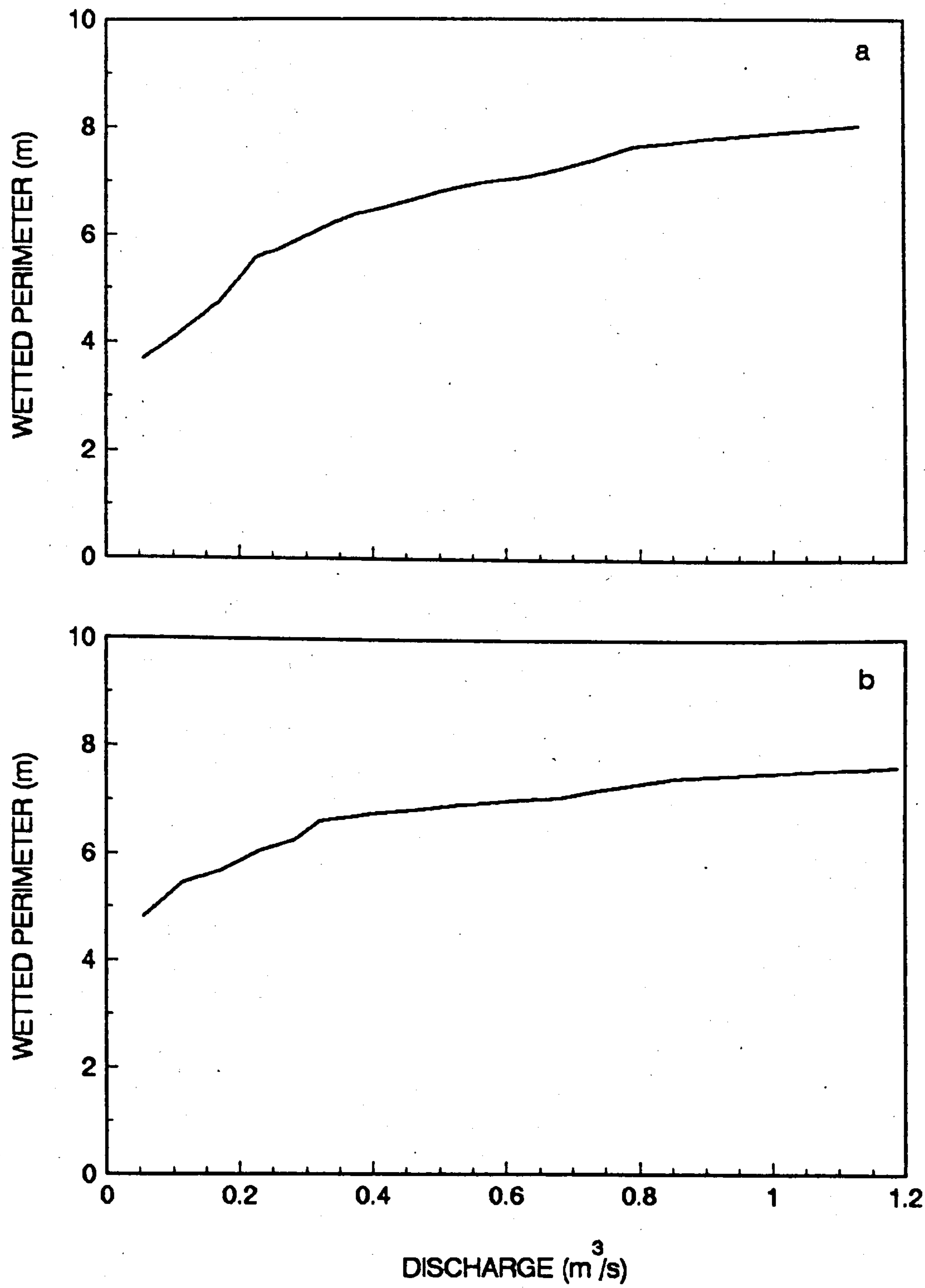

Figure 2.-Mean wetted perimeter-discharge relationships for the test (a) and reference (b) riffles in Bozeman Creek, July-September 1989.

by 48 genera, and early instars which could only be identified to order or family. In addition to the terrestrial category, four non-insect groups, Turbellaria, Nematomorpha, Oligochaeta, and Acarina, were collected. Because these groups were sampled sporadically or in small numbers, they were excluded from analyses. Ephemeroptera was typically the most numerically abundant order (23 to 44% of total organisms) in benthic samples, followed by Coleoptera and Diptera (Appendix A). Coleoptera was the largest contributor to total biomass (30 to 60%). Ephemeroptera dominated drift abundance (58 to 77%) and biomass (43 to 65%; Appendix A).

Stream characteristics were similar between riffles at benthic sample locations on all invertebrate sample dates. Mean water depth and velocity did not significantly differ ($P>0.05$, t-test; Table 2) between riffles on any sample date, though water velocity on the reference riffle was almost twice that on the test riffle on 4 August ($P=0.053$, t-test; Table 2). Substrate diameter was similar between riffles ($P>0.05$; Mann-Whitney test; Table 2) but exhibited greater variability on the test riffle. Water temperature was identical between riffles on every sample date (Table 2).

For total benthic invertebrates, numeric density (no./m^2) increased with decreasing discharge and wetted perimeter (Figure 3) but was not significantly different ($P>0.05$; Mann-Whitney test) between riffles on any sample date. Biomass (g/m^2) and caloric density (cal./m^2) generally increased at the reference riffle and remained relatively constant at the test riffle as discharge declined (Figure 3). Both biomass and caloric density were significantly greater

(P=0.022; Mann-Whitney test) at the reference than the test riffle on 15 September, the final sample date.

Table 2.-Comparison of physical characteristics at benthic sample sites at the test (T) and reference (R) riffles in Bozeman Creek, July-September 1989. Numbers in parentheses=1 SE, N=5.

Date	Site	Temp. (C)	Depth (m)	P[a]	Velocity (m/s)	P[a]	Substrate diameter (cm)	P[b]
19/7	T	13	0.21(0.04)	0.183	0.50(0.05)	0.358	7.31(1.57)	0.835
	R	13	0.15(0.02)		0.60(0.09)		7.97(0.54)	
4/8	T	11	0.17(0.03)	0.327	0.35(0.04)	0.053	6.21(1.22)	0.753
	R	11	0.14(0.00)		0.63(0.12)		7.48(0.32)	
31/8	T	9	0.15(0.02)	0.750	0.45(0.11)	0.548	8.28(1.03)	0.210
	R	9	0.14(0.02)		0.55(0.11)		6.69(0.35)	
17/9	T	8	0.14(0.03)	0.912	0.27(0.07)	0.201	7.28(0.39)	0.402
	R	8	0.14(0.02)		0.42(0.08)		7.61(0.40)	

[a]Results from t-tests.
[b]Results from Mann-Whitney tests.

Differences in body length resulted in significantly lower biomass and caloric densities of invertebrates at the test compared to the reference riffle. Although body length of invertebrates was similar between riffles on the first three sample dates, individuals were significantly smaller (Figure 4; P=0.012; Mann-Whitney test) at the test riffle on the final sample date. Significantly smaller body lengths resulted in predicted dry weights of individuals to be lower at the test compared to the reference riffle. Small trichopteran larvae (<1.0 mm) made a substantial contribution (>20%) to total invertebrates at the test riffle on the final sample date while this

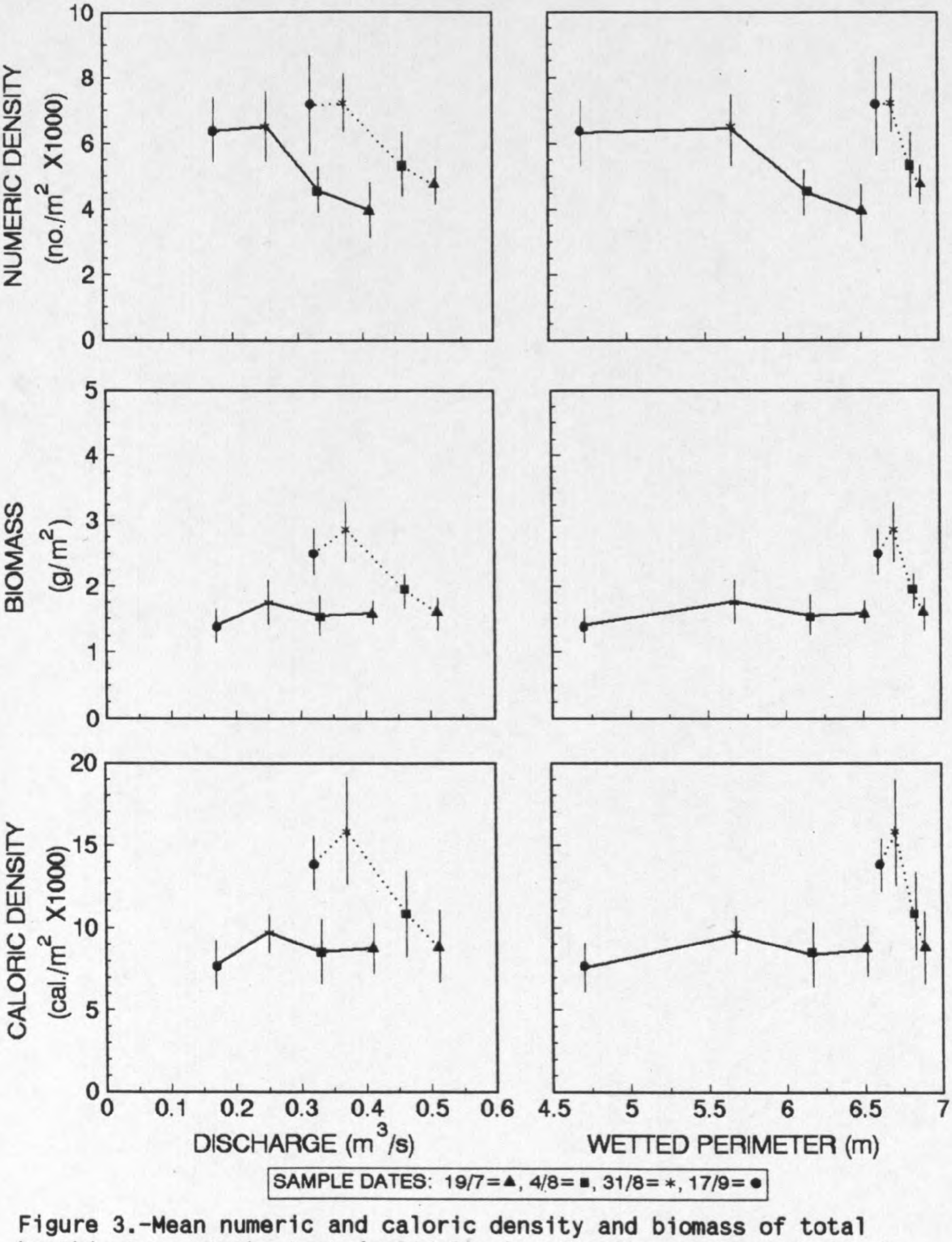

Figure 3.-Mean numeric and caloric density and biomass of total benthic taxa at the test (solid line) and reference (broken line) riffles relative to stream discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

group made up only 2% of total invertebrates at the reference riffle (Appendix A).

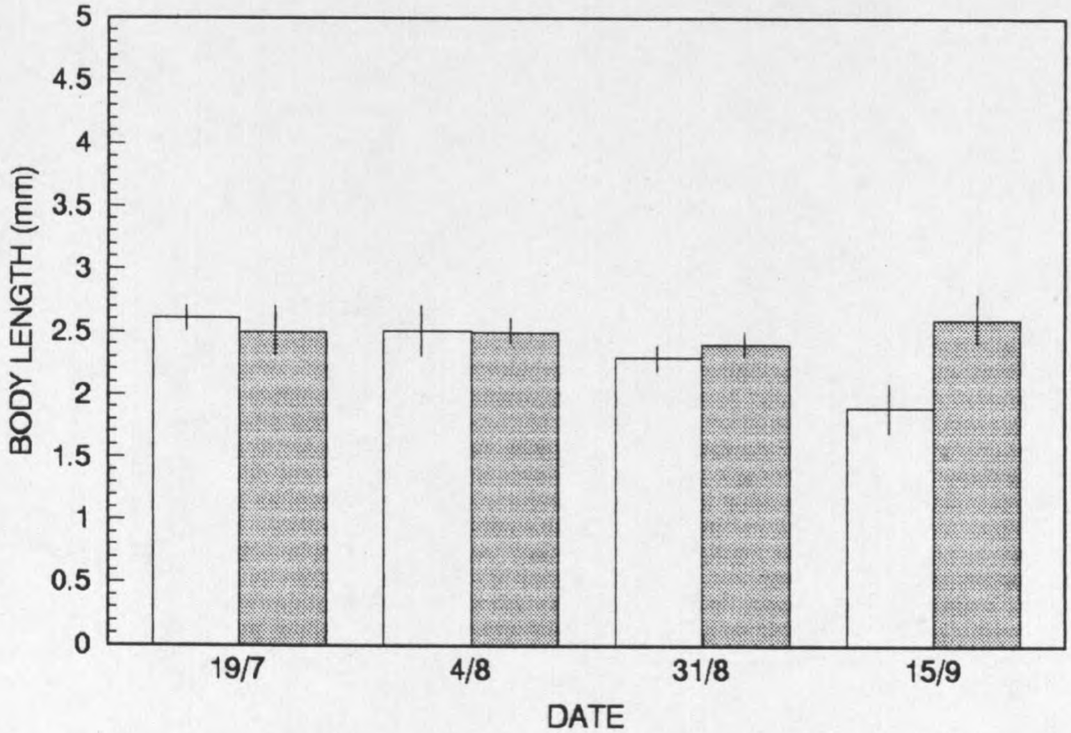

Figure 4.-Mean body length of total benthic taxa at the test (open bars) and reference (shaded bars) riffles on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

Based on proportions that each taxa contributed to total invertebrate abundance, benthic community structure was relatively similar between riffles on all sample dates. Horn's index of overlap ranged from 0.925 to 0.967 on the first three sample dates. Even with high abundance of small trichopterans at the test riffle on the final sample date, community overlap was relatively high between riffles, 0.745.

General trends in numeric and caloric density, and biomass were relatively similar between riffles for the four dominant taxa (*Baetis* spp., *Zapada* spp., elmid larvae, and Chironomidae; Figures 5-8). Although relatively high variation in the abundance of individual taxa occurred on many sample dates (e.g., *Zapada* spp. on the final sample date), numeric density did not significantly differ (P>0.05, Mann-Whitney test) between riffles.

Body lengths of individual taxa were not significantly different between riffles on most sample dates (Figure 9). Exceptions were *Baetis* spp. on the final sample date and elmid larvae on the third sample date (P=0.037 for both taxa; Mann-Whitney test). In both instances, individuals were larger at the reference than the test riffle. For *Baetis* spp., this resulted in substantially higher biomass and caloric density (P=0.060, Mann-Whitney test; Figure 5) at the reference riffle.

Diel drift pattern of total taxa was similar between riffles and declined during the study. Drift density and rate were highest in samples collected at sunset and midnight (Figure 10). Minimum drift typically occurred in noon samples. Patterns for caloric drift rate resembled numeric drift rate. Mean body length of invertebrates was generally smaller in noon samples compared to other time periods (Figure 10); this pattern was less prominent at the reference riffle on 28-29 August and 14-15 September.

Drift density of total taxa was similar between riffles in seven of 16 time periods on four dates (P>0.05, G-test; Table 3; Appendix A). However, drift density was significantly greater at the test than

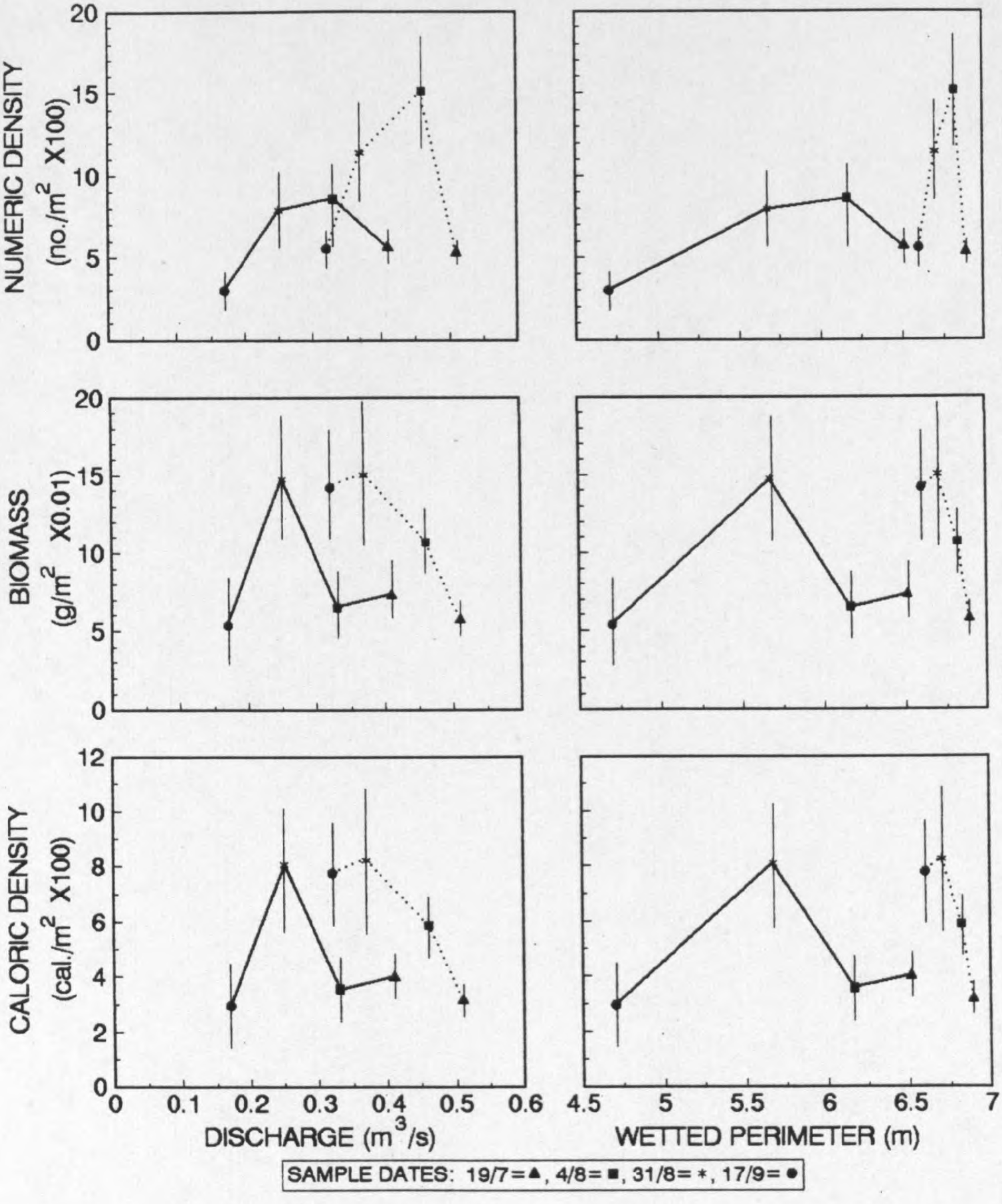

Figure 5.-Mean numeric and caloric density and biomass of *Baetis* spp. in benthic samples at the test (solid line) and reference (broken line) riffles relative to stream discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

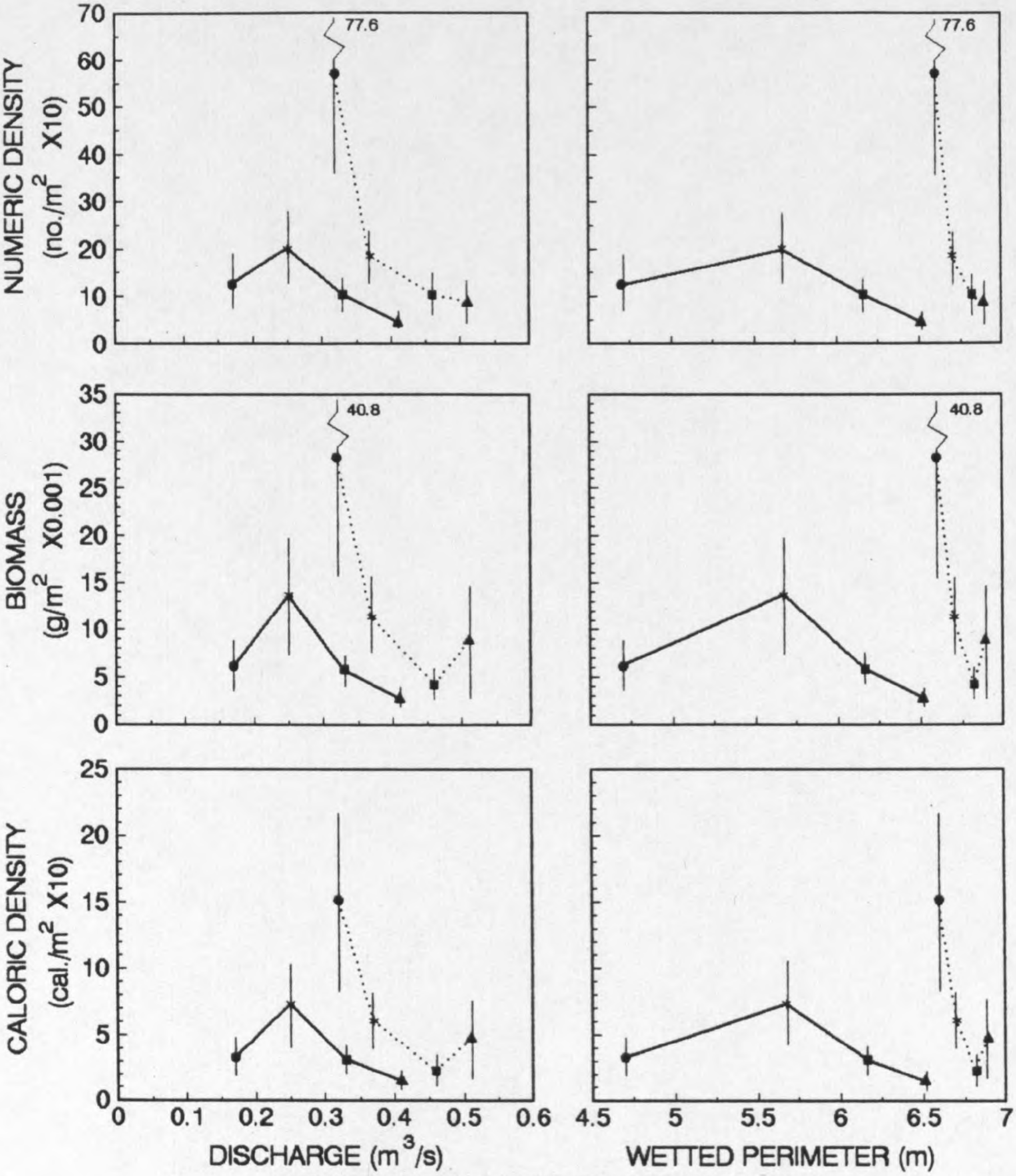

Figure 6.-Mean numeric and caloric density and biomass of *Zapada* spp. in benthic samples at the test (solid line) and reference (broken line) riffles relative to stream discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

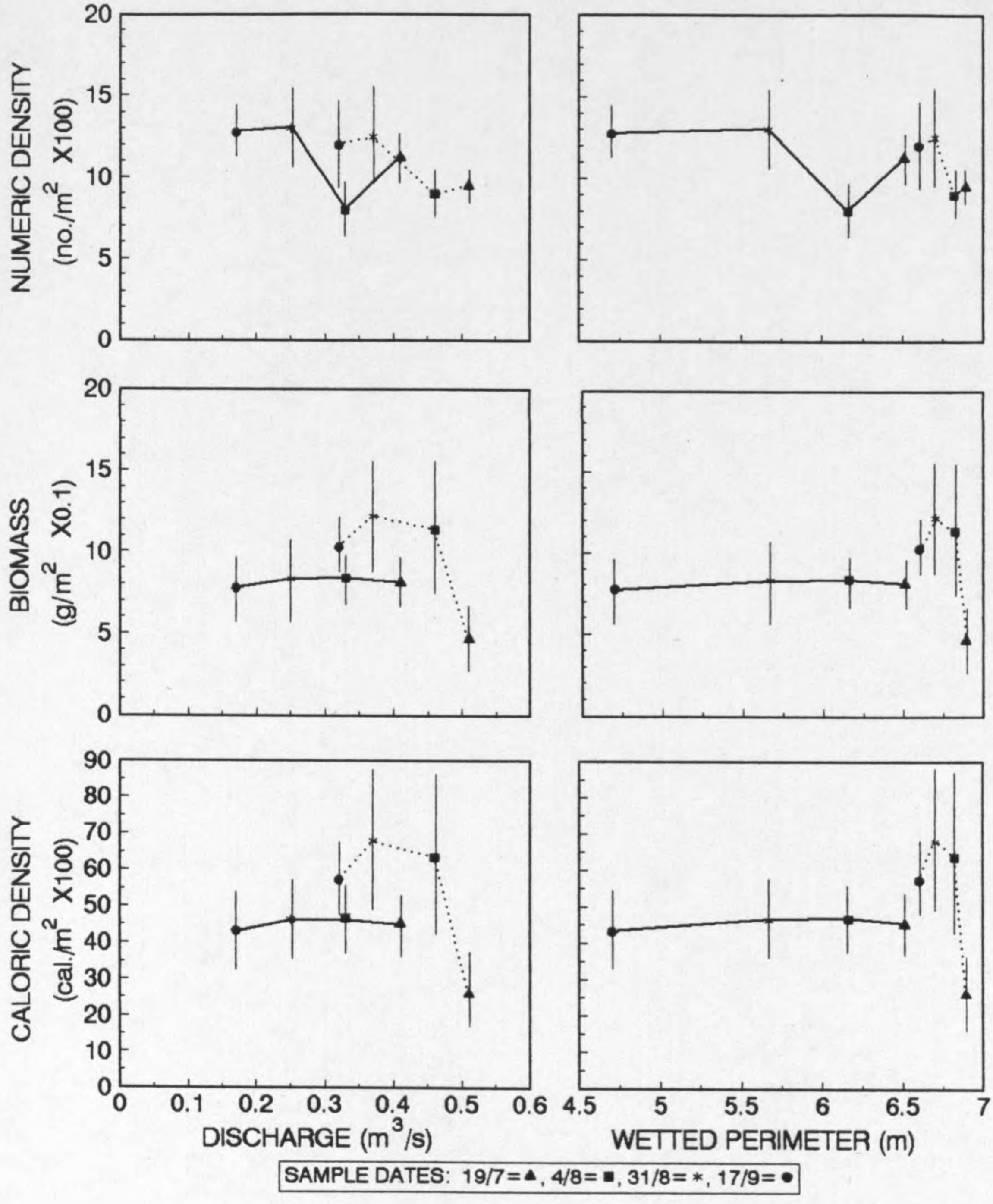

Figure 7.-Mean numeric and caloric density and biomass of elmid larvae in benthic samples at the test (solid line) and reference (broken line) riffles relative to stream discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

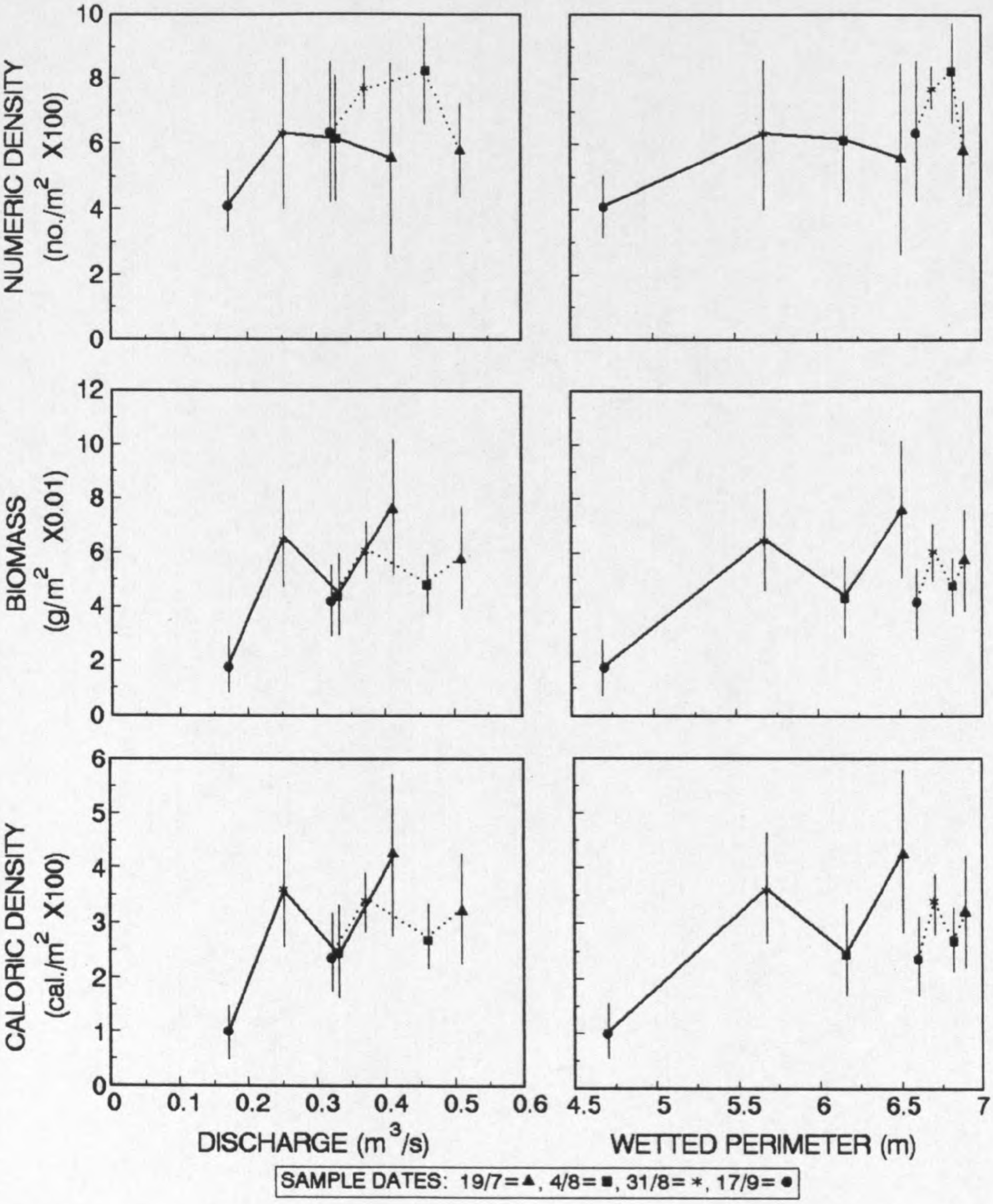

Figure 8.-Mean numeric and caloric density and biomass of Chironomidae in benthic samples at the test (solid line) and reference (broken line) riffles relative to stream discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

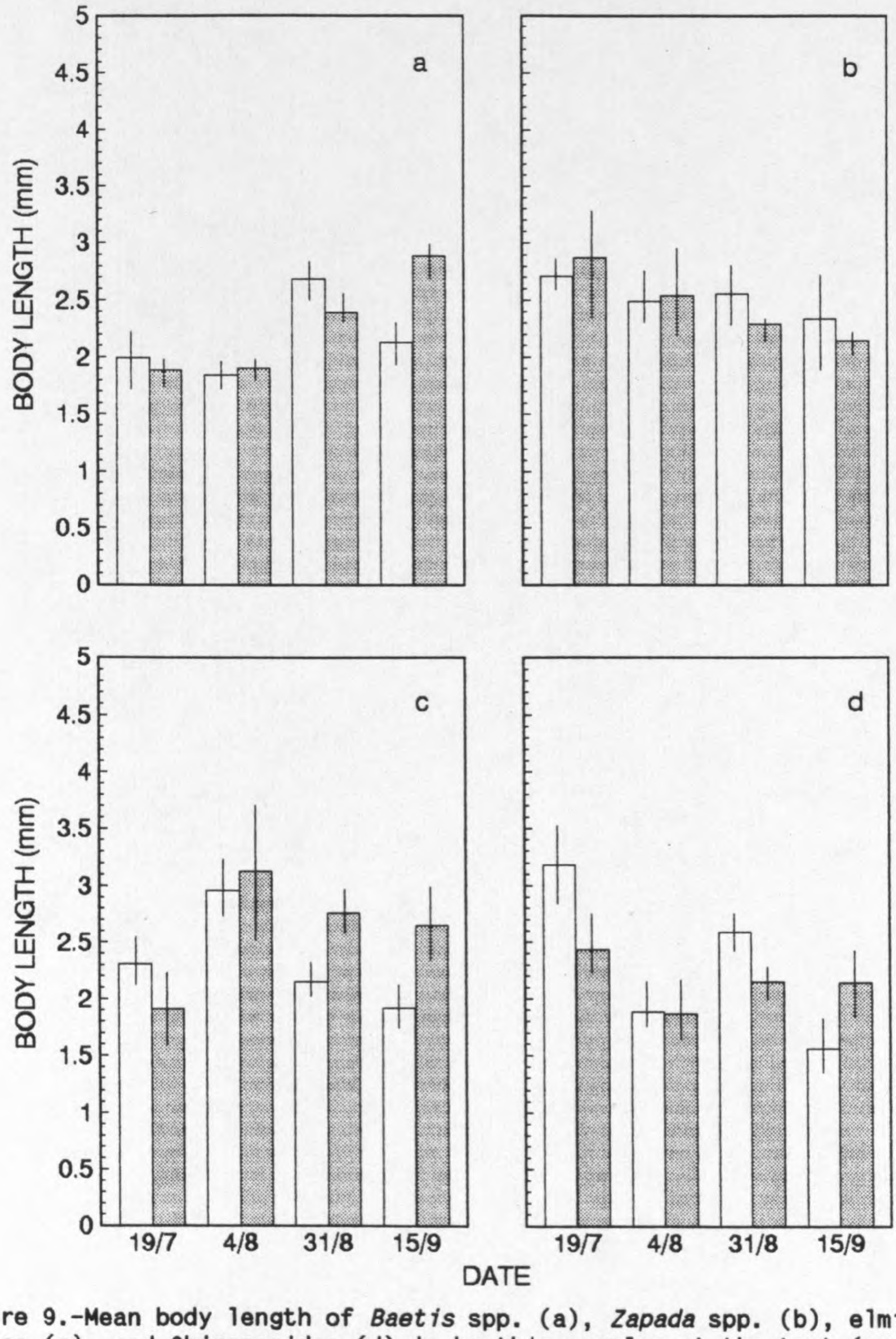

Figure 9.-Mean body length of *Baetis* spp. (a), *Zapada* spp. (b), elmid larvae (c), and Chironomidae (d) in benthic samples at the test (open bars) and reference (shaded bars) riffles on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

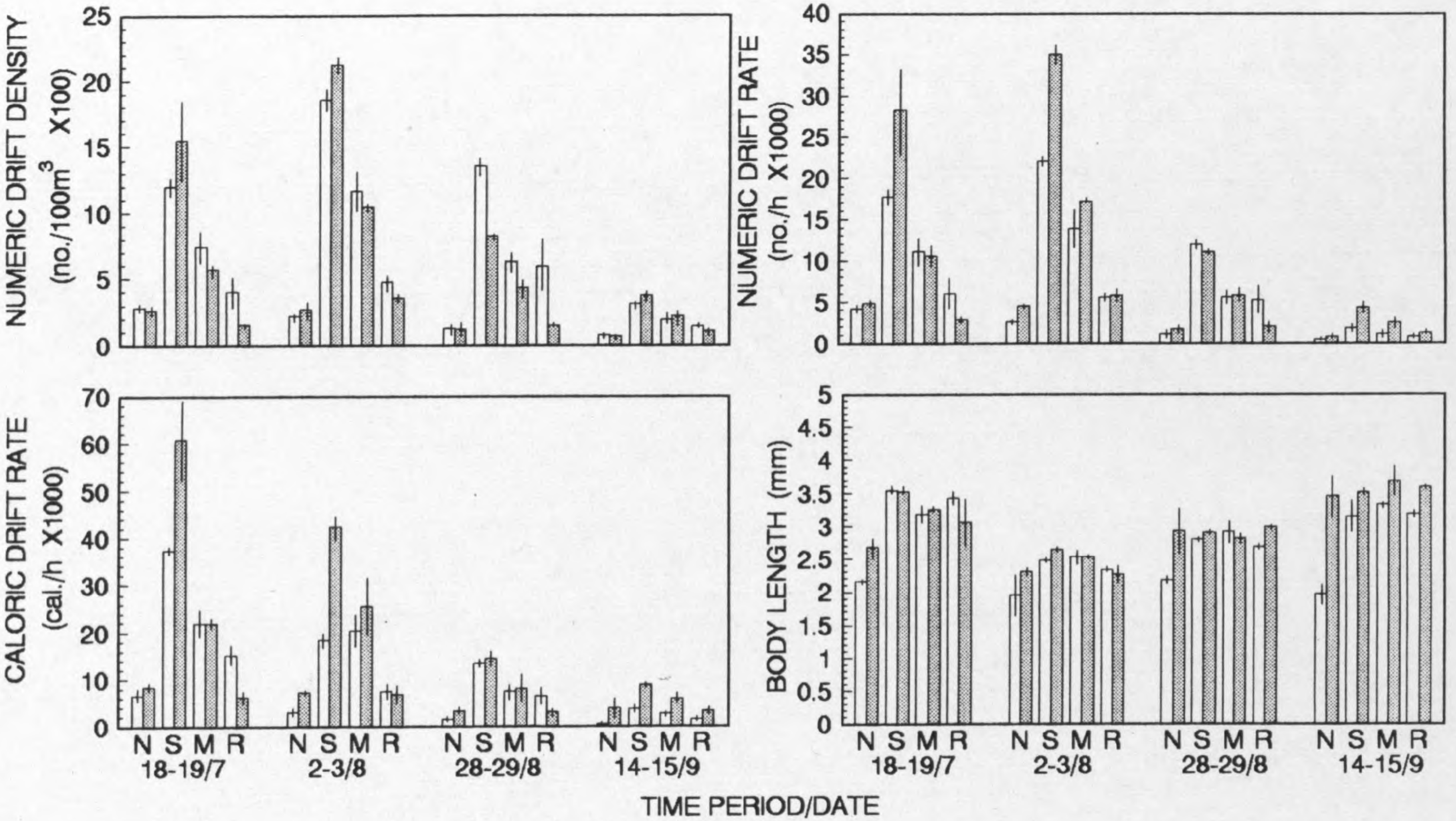

Figure 10.-Mean drift density, numeric and caloric drift rate, and mean body length by time period (N-noon, S-sunset, M-midnight, R-sunrise) on four sample dates for total taxa at the test (open bars) and reference (shaded bars) riffles in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

Table 3.-Results of G-tests for mean drift density between riffles per time period (TP; N-noon, S-sunset, M-midnight, R-sunrise) for total taxa, *Baetis* spp., *Zapada* spp., and Chironomidae weighted equally between riffles (E), and proportional to stream discharge (Q), wetted perimeter (WP), and mean water velocity (VEL) on four sample dates in Bozeman Creek, July-September 1989. Symbols left and right of slash indicate drift density at the test and reference riffles, respectively, relative to expected values, ns=not significant.

		Total taxa				*Baetis* spp.				*Zapada* spp.				Chironomidae			
Date	TP	E	Q	WP	VEL	E	Q	WP	VEL	E	Q	WP	VEL	E	Q	WP	VEL
18-19/7	N	ns	+/-	ns	ns	ns	ns	ns	ns	—[a]	—[a]	—[a]	—[a]	+/-	+/-	+/-	+/-
	S	-/+	ns	-/+	ns	-/+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	M	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-	ns	ns	ns	ns	ns	ns	ns	ns
	R	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-	—[a]	—[a]	—[a]	—[a]	ns	ns	ns	ns
2-3/8	N	ns	ns	ns	ns	-/+	ns	-/+	-/+	—[a]	—[a]	—[a]	—[a]	ns	ns	ns	ns
	S	-/+	+/-	ns	ns	ns	+/-	ns	+/-	—[a]	—[a]	—[a]	—[a]	ns	ns	ns	ns
	M	ns	+/-	+/-	+/-	ns	+/-	+/-	+/-	ns	ns	ns	ns	ns	ns	ns	ns
	R	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-	—[a]	—[a]	—[a]	—[a]	ns	ns	ns	ns
28-29/8	N	ns	+/-	ns	ns	ns	ns	ns	ns	—[a]	—[a]	—[a]	—[a]	—[a]	—[a]	—[a]	—[a]
	S	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-	ns	ns	ns	ns	—[a]	—[a]	—[a]	—[a]
	M	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-	ns	ns	ns	ns	—[a]	—[a]	—[a]	—[a]
	R	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-	—[a]	—[a]	—[a]	—[a]	+/-	+/-	+/-	+/-

Table 3.-Continued....

Date	TP	Total taxa E	Total taxa Q	Total taxa WP	Total taxa VEL	*Baetis* spp. E	*Baetis* spp. Q	*Baetis* spp. WP	*Baetis* spp. VEL	*Zapada* spp. E	*Zapada* spp. Q	*Zapada* spp. WP	*Zapada* spp. VEL	Chironomidae E	Chironomidae Q	Chironomidae WP	Chironomidae VEL
14-15/9	N	ns	+/-	+/-	+/-	-/+	ns	ns	-/+	--[a]	--[a]	--[a]	--[a]	--[a]	--[a]	--[a]	--[a]
	S	-/+	+/-	ns	ns	ns	+/-	+/-	ns	-/+	ns	ns	ns	--[a]	--[a]	--[a]	--[a]
	M	ns	+/-	+/-	ns	ns	+/-	ns	ns	-/+	ns	ns	ns	--[a]	--[a]	--[a]	--[a]
	R	ns	+/-	+/-	+/-	ns	+/-	+/-	+/-	--[a]	--[a]	--[a]	--[a]	--[a]	--[a]	--[a]	--[a]

--[a] Inadequate sample size for tests.

the reference riffle during six time periods, while drift density was significantly lower on the test riffle in three time periods. Therefore, drift density at the test riffle was greater or similar to that at the reference riffle for most time periods. On 28-29 August, drift density was substantially higher at the test than the reference riffle during every time period except noon (Table 3; Figure 10).

Drift density was rarely proportional to stream discharge, wetted perimeter, or mean water velocity at each riffle (Table 3). While drift density was similar between riffles in two and five time periods relative to discharge and wetted perimeter, respectively, drift density at the test riffle was often significantly greater. Relative to mean water velocity, drift density was similar between riffles for seven time periods ($P>0.05$, G-test; Table 3). Weighting values for mean water velocity were intermediate to those for discharge and wetted perimeter for all but the final sample dates (Appendix A), when stream discharge was below the wetted perimeter inflection point at the test riffle.

Drift rate was usually greater on the reference than the test riffle for most time periods (Figure 10). But because drift rate is a function of drift density and discharge, a 32% reduction in stream discharge by the dam was offset by relatively high drift densities resulting in similar drift rates between riffles on 28-29 August (Figure 10). Drift rate at the reference riffle was consistently greater than the test riffle on the final sample date when discharge was below the wetted perimeter inflection point.

In addition to drift density and discharge, caloric drift rate is dependent on biomass of drifting individuals. Mean caloric drift rate was usually greater at the reference than the test riffle due to higher drift rates and larger body lengths of invertebrates (Figure 10).

Diel drift pattern of *Baetis* spp. resembled that of total taxa (Figures 10 and 11). Drift density was similar ($P>0.05$, G-test; Table 3; Appendix A) between riffles in seven of 16 time periods and the number of non-significant results for tests did not increase relative to discharge, wetted perimeter, and mean water velocity at each riffle on the four sample dates. Drift density of *Baetis* spp. was significantly greater at the test than the reference riffle for six of 16 time periods ($P<0.05$, G-test; Table 3). Also, numeric and caloric drift rate was usually greater at the test riffle, except on 28-29 August (Figure 11).

Zapada spp., elmid larvae, and Chironomidae, generally composed between 1% and 5% of total invertebrate drift and were absent during some time periods (Appendix A). Low drift density precluded tests between riffles in some instances and elmid larvae were not considered in any tests due to inadequate numbers in samples.

Zapada spp. drifted primarily at night and were either absent or at greatly reduced densities during noon and sunrise samples (Figure 12). When present in sufficient numbers, *Zapada* spp. drift density was similar between riffles and similar relative to stream discharge, wetted perimeter, and mean water velocity at the riffles ($P>0.05$, G-test; Table 3) on the first three sample dates. On 14-15 September,

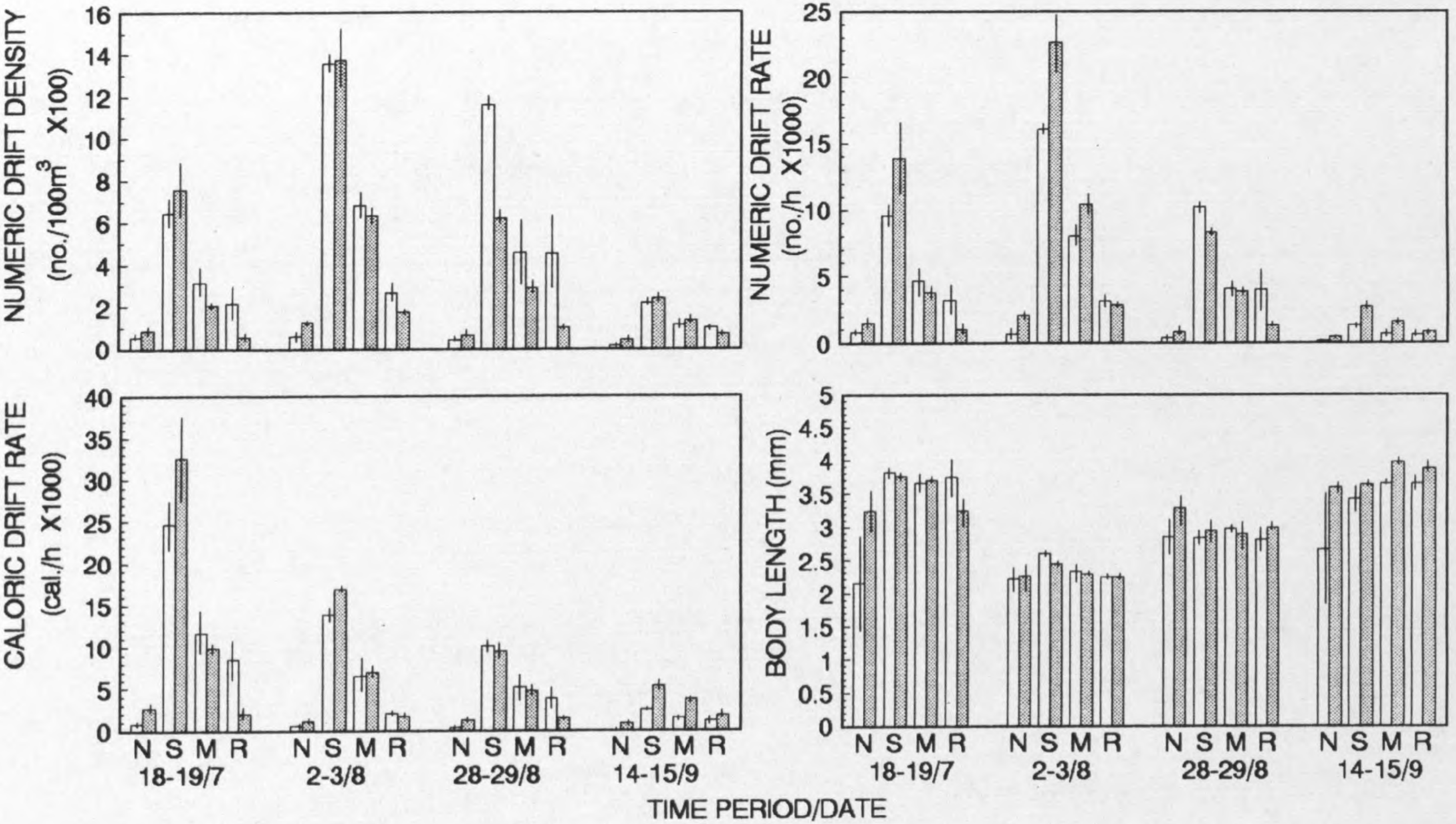

Figure 11.-Mean drift density, numeric and caloric drift rate, and mean body length by time period (N-noon, S-sunset, M-midnight, R-sunrise) on four sample dates for *Baetis* spp. at the test (open bars) and reference (shaded bars) riffles in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

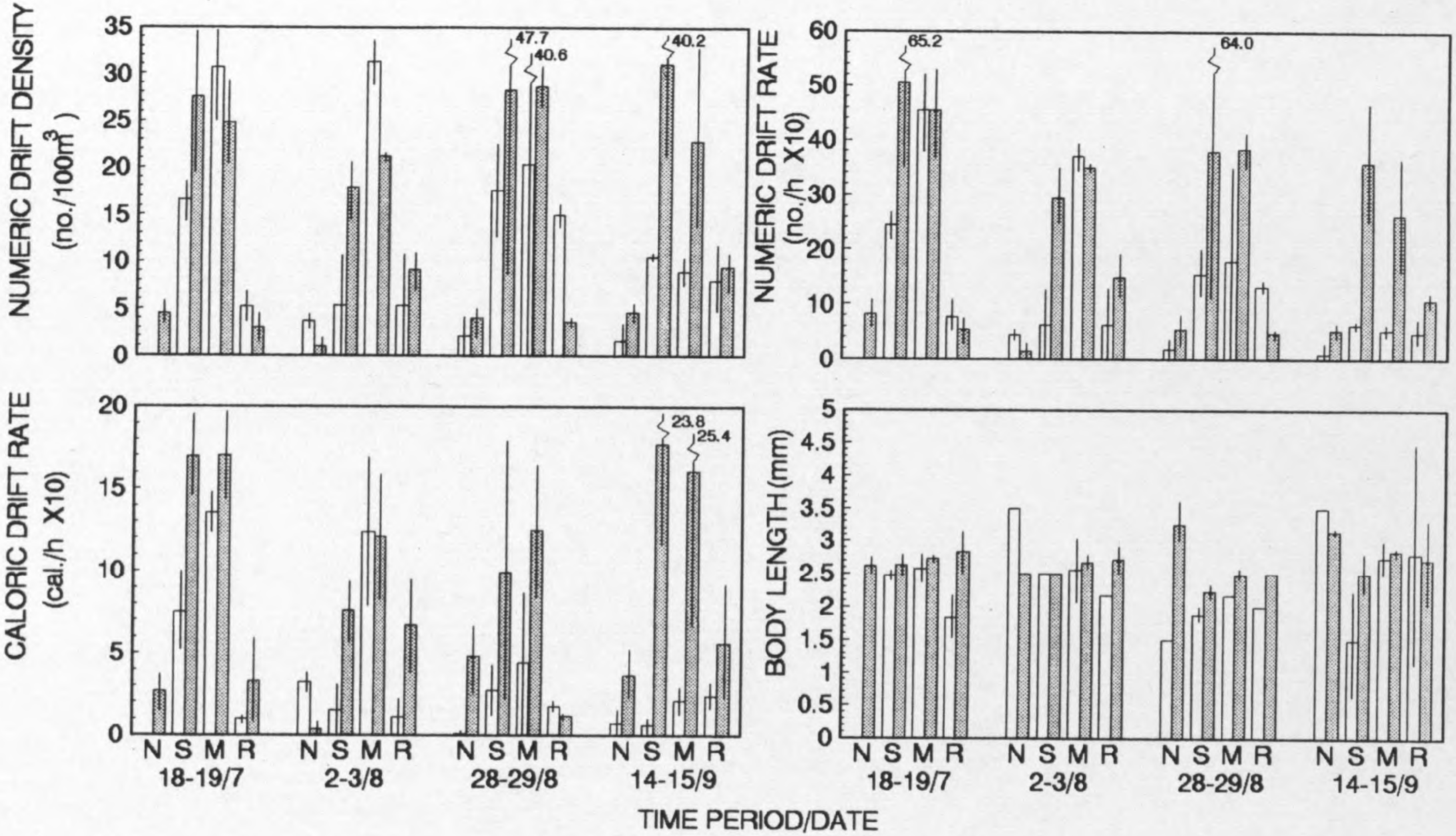

Figure 12.-Mean drift density, numeric and caloric drift rate, and mean body length by time period (N-noon, S-sunset, M-midnight, R-sunrise) on four sample dates for *Zapada* spp. at the test (open bars) and reference (shaded bars) riffles in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

significantly lower densities of *Zapada* spp. were present at the test riffle at sunset and midnight (P<0.05, G-test; Table 3; Figure 12). Relative to discharge, wetted perimeter, and mean water velocity, drift densities were similar (Table 3). Overall, numeric and caloric drift rates were higher at the reference riffle and no consistent trends in body size and time period were apparent (Figure 12).

Drift of Chironomidae greatly decreased on the last two sample dates (Figure 13). Numbers were too small to perform G-tests except for sunrise on 28-29 August. Drift density was similar between riffles and proportional to all physical factors on the first two sample dates, except for noon 18-19 July, when drift at the test riffle was significantly greater than the reference riffle (Table 3; Figure 13; Appendix A). On 28-29 August, sunrise drift density at the test riffle was significantly greater than at the reference riffle (P<0.05, G-test; Table 3). When equally weighted, however, drift density was similar between riffles at this time. Both numeric and caloric drift rate was generally greater at the reference than test riffle.

Trends in mean daily drift density (no./100 m^3) for total taxa at both riffles were similar during the study. Invertebrate drift density increased from the first to the second sample date, and then declined (Figure 14). Drift density was similar (P>0.05, G-test; Table 4) between riffles on all sample dates, except on 28-29 August when it was significantly greater at the test riffle. Because discharge, wetted perimeter, and water velocity were lower below the dam, drift density, relative to these factors, was significantly

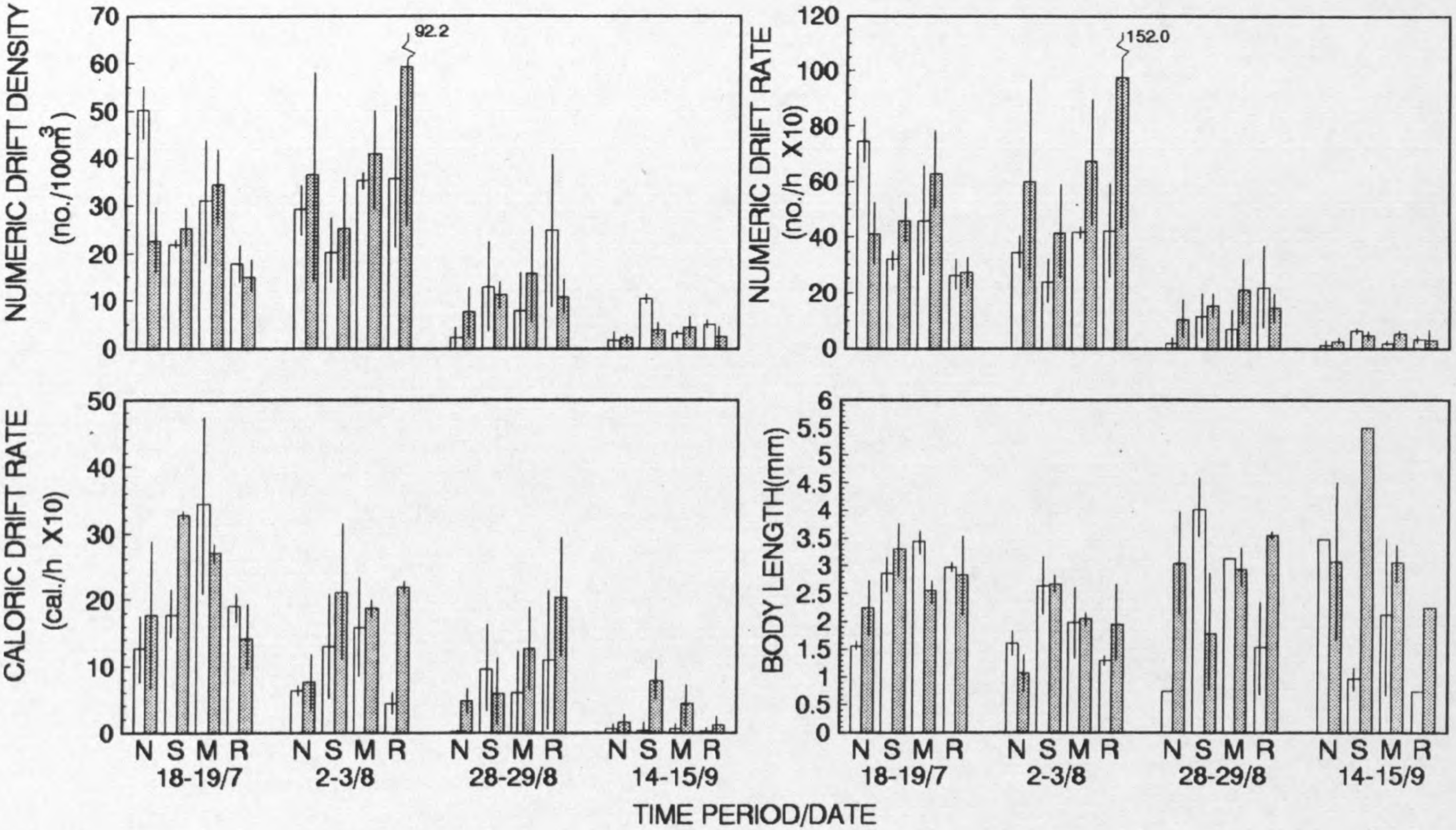

Figure 13.-Mean drift density, numeric and caloric drift rate, and mean body length by time period (N-noon, S-sunset, M-midnight, R-sunrise) on four sample dates for Chironomidae at the test (open bars) and reference (shaded bars) riffles in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

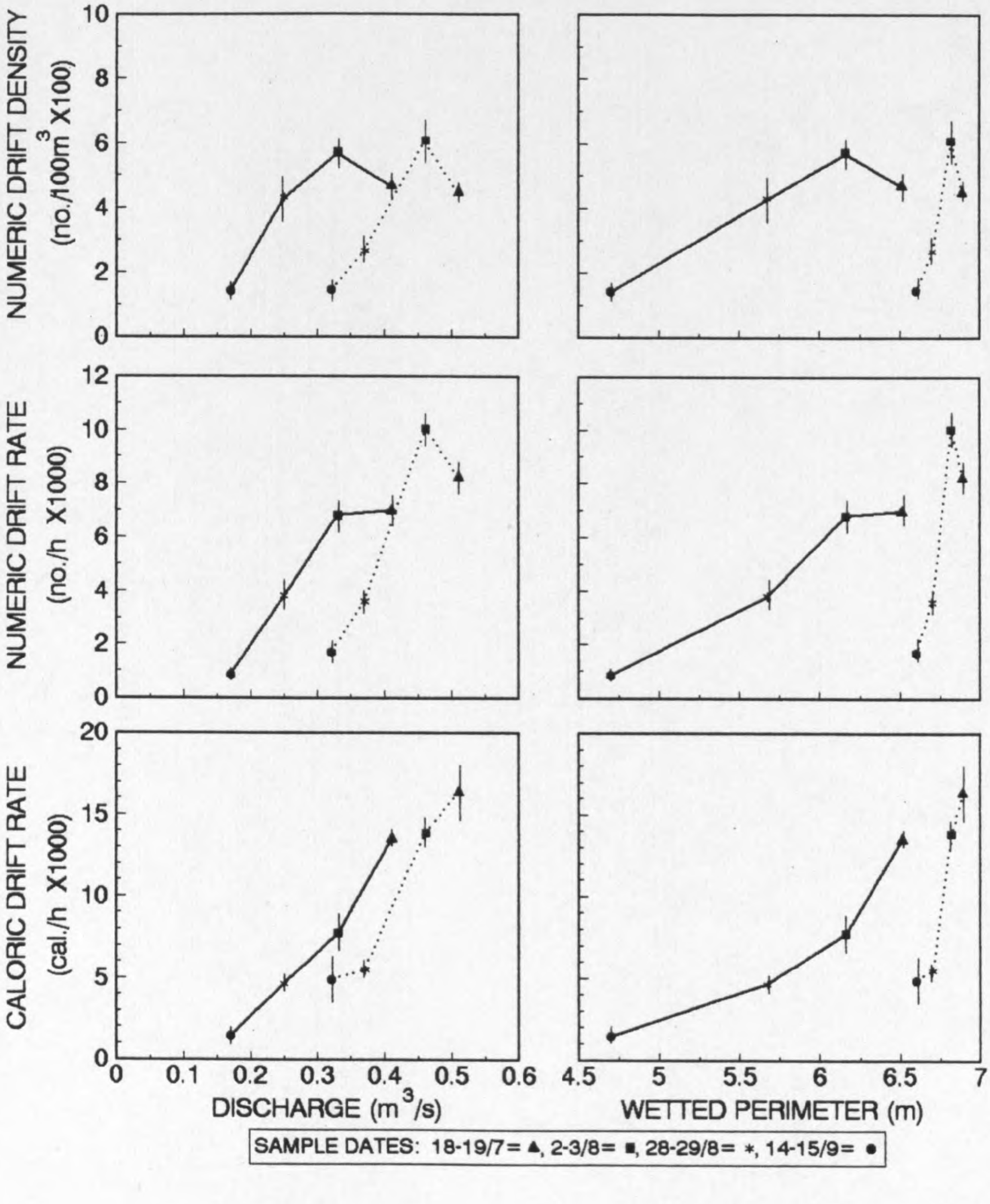

Figure 14.-Mean daily numeric drift density, and numeric and caloric drift rate for total taxa at the test (solid line) and reference (broken line) relative to discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

greater at the test than the reference riffle on most sample dates (Table 4; Appendix A).

Table 4.-Results of G-tests for mean daily drift density between riffles on four sample dates for total taxa, *Baetis* spp., *Zapada* spp., and Chironomidae weighted equally between riffles (E), and proportional to stream discharge (Q), wetted perimeter (WP), and mean water velocity (VEL) in Bozeman Creek, July-September 1989. Symbols left and right of slash indicate drift density at the test and reference riffles, respectively, relative to expected values, ns=not significant.

Date	Drift density			
	E	Q	WP	VEL
	Total taxa			
18-19/7	ns	+/-	ns	+/-
2-3/8	ns	+/-	ns	+/-
28-29/8	+/-	+/-	+/-	+/-
14-15/9	ns	+/-	+/-	+/-
	***Baetis* spp.**			
18-19/7	ns	+/-	ns	ns
2-3/8	ns	+/-	ns	ns
28-29/8	+/-	+/-	+/-	+/-
14-15/9	ns	+/-	ns	ns
	***Zapada* spp.**			
18-19/7	ns	ns	ns	ns
2-3/8	ns	ns	ns	ns
28-29/8	ns	ns	ns	ns
14-15/9	ns	ns	ns	ns
	Chironomidae			
18-19/7	+/-	+/-	+/-	+/-
2-3/8	ns	ns	ns	ns
28-29/8	ns	ns	ns	ns
14-15/9	--[a]	--[a]	--[a]	--[a]

--[a] Inadequate sample size for tests.

With similar drift densities between riffles on three of four sample dates, reductions in stream discharge on the test riffle reduced numeric drift rates 15% and 33% on 18-19 July and 2-3 August, respectively (Figure 14). Although stream discharge had decreased 32% below the dam by 28-29 August, numeric drift rate was 6% higher than the reference riffle. By the final sample date, stream discharge below the dam had decreased 47% and drift rate was 50% less than the reference riffle. Wetted perimeter at the test riffle was 29% of that for the reference riffle on the final sample date. Mean body length of all taxa was greater at the reference than the test riffle (Figure 15). With differences in mean body length and stream discharge between riffles, mean daily caloric drift rate at the test riffle was 15% to 70% less than the reference riffle during the study (Figure 14).

Mean daily drift density of *Baetis* spp. was similar ($P>0.05$, G-test; Figure 16; Table 4) between riffles except on 28-29 August when drift density was significantly greater at the test riffle. Identical patterns occurred for drift density relative to wetted perimeter and mean water velocity (Table 4). However, drift density was significantly lower ($P<0.05$, G-test; Table 4) at the test riffles relative to stream discharge. With decreased discharge on the test riffle, mean daily drift rate was 18% to 57% lower than the reference riffle except on 28-29 August when drift rate was 16% greater (Figure 16). Due to larger size of individuals at the reference riffle (Figure 15), mean daily caloric drift rate was <1% to 61% less at the test riffle (Figure 16).

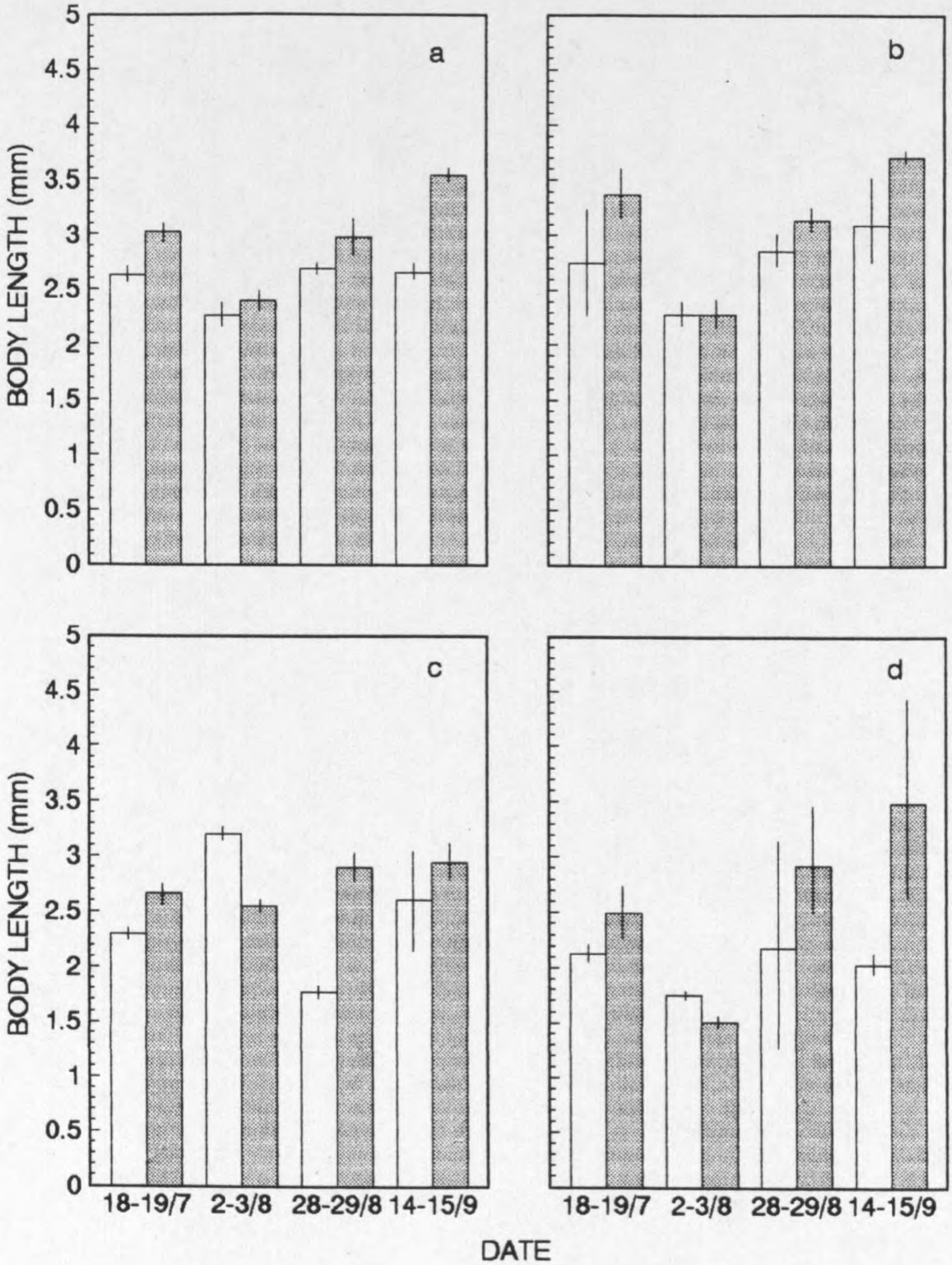

Figure 15.-Mean body length of total taxa (a), *Baetis* spp. (b), *Zapada* spp. (c), and Chironomidae (d) for daily drift at the test (open bars) and reference (shaded bars) riffles on four sample dates in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

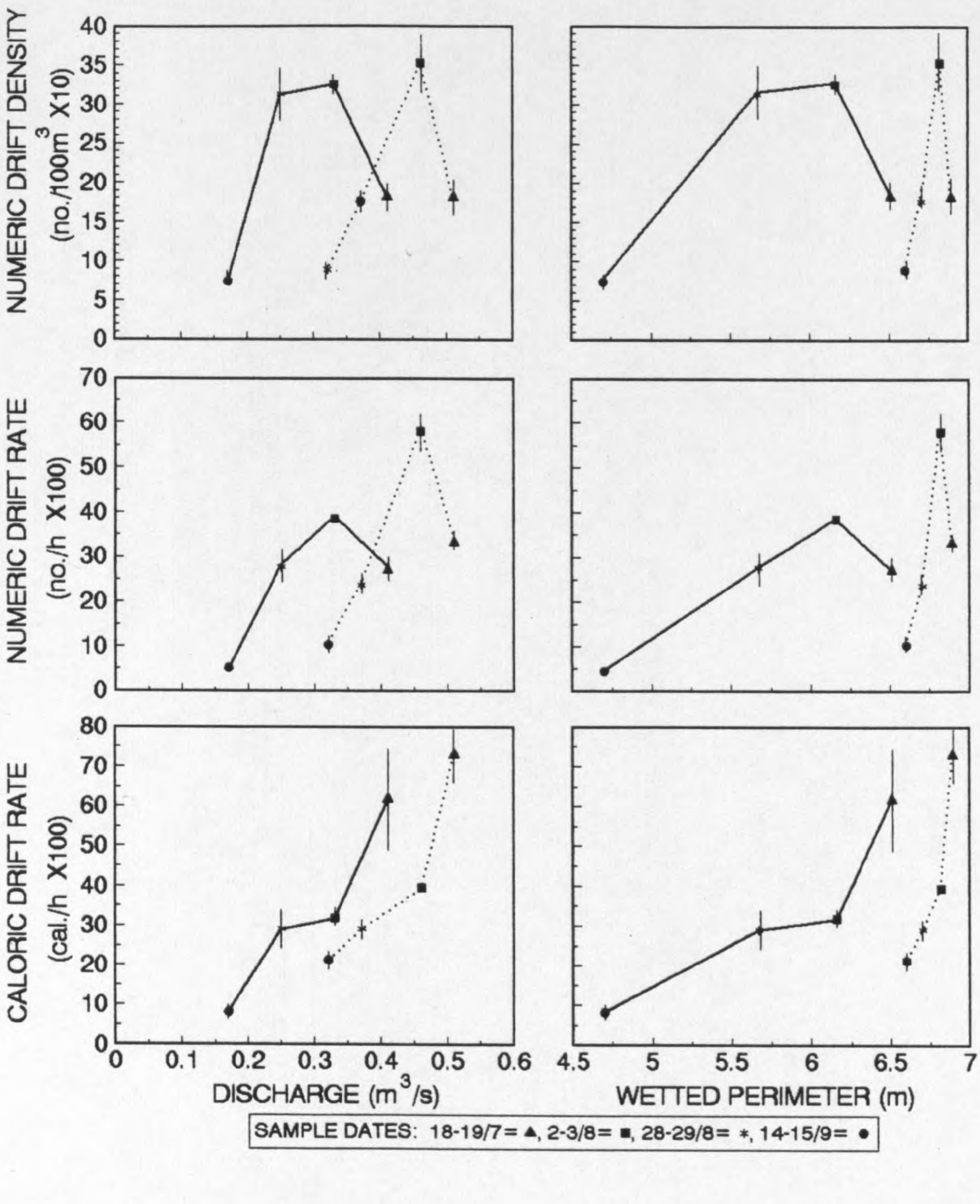

Figure 16.-Mean daily numeric drift density, and numeric and caloric drift rate for *Baetis* spp. at the test (solid line) and reference (broken line) riffles relative to discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

Mean daily drift of *Zapada* spp. exhibited considerable variability (Figure 17). Although mean daily drift density at the test riffle ranged from 14% greater than to 58% less than the reference riffle (Figure 17), drift density was not significantly different between riffles on any sample date, nor did drift density differ between riffles relative to discharge, wetted perimeter, and mean water velocity (Table 4). Numeric drift rate at the test riffle was 18% to 79% lower than the reference riffle on all sample dates (Figure 17). Larger individuals at the test riffle on 2-3 August (Figure 15) resulted in caloric drift rate 11% greater than the reference riffle. On the final sample date, numeric and caloric drift rates at the test riffle were 79% and 86% lower than those at the reference riffle (Figure 17).

Mean daily drift density of chironomids was significantly greater, 72%, at the test riffle on the first sample date ($P<0.05$, G-test; Figure 18; Table 4). Drift density was similar between riffles on following sample dates, although inadequate sample sizes on the last sample date precluded testing. After the first sample date, numeric drift rate was 33% to 49% less at the test riffle (Figure 18). Also, mean body length of individuals was from 25% to 42% smaller at the test riffle on the final two sample dates. Lower numeric drift rate and smaller body size resulted in caloric drift rates at the test riffle which were from 18% to 85% of those at the reference riffle.

Overall, mean daily drift density was minimally affected by differences in discharge and associated physical conditions at the two riffles during the study. An exception was on the third sample date

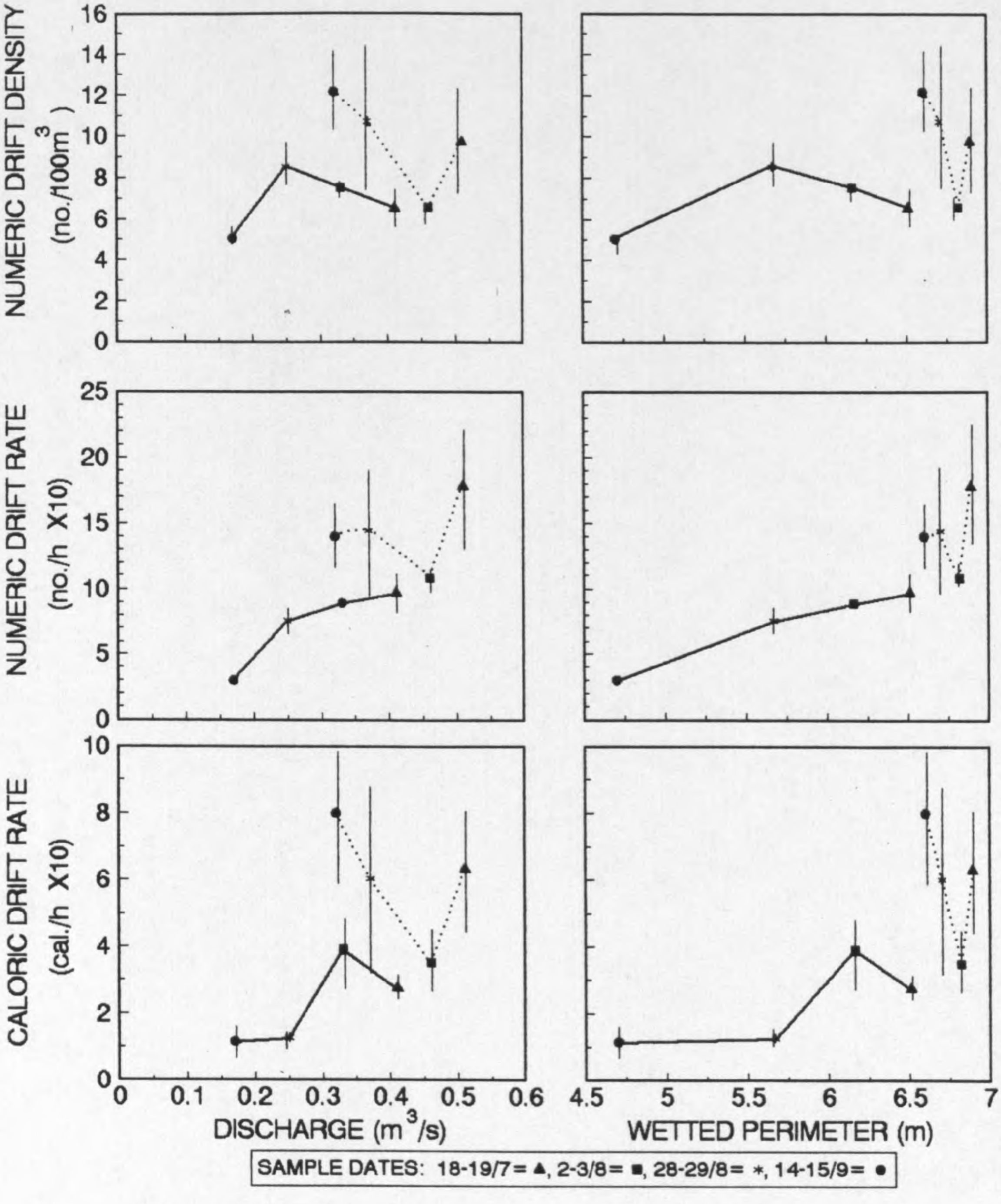

Figure 17.-Mean daily numeric drift density, and numeric and caloric drift rate for *Zapada* spp. at the test (solid line) and reference (broken line)riffles relative to discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

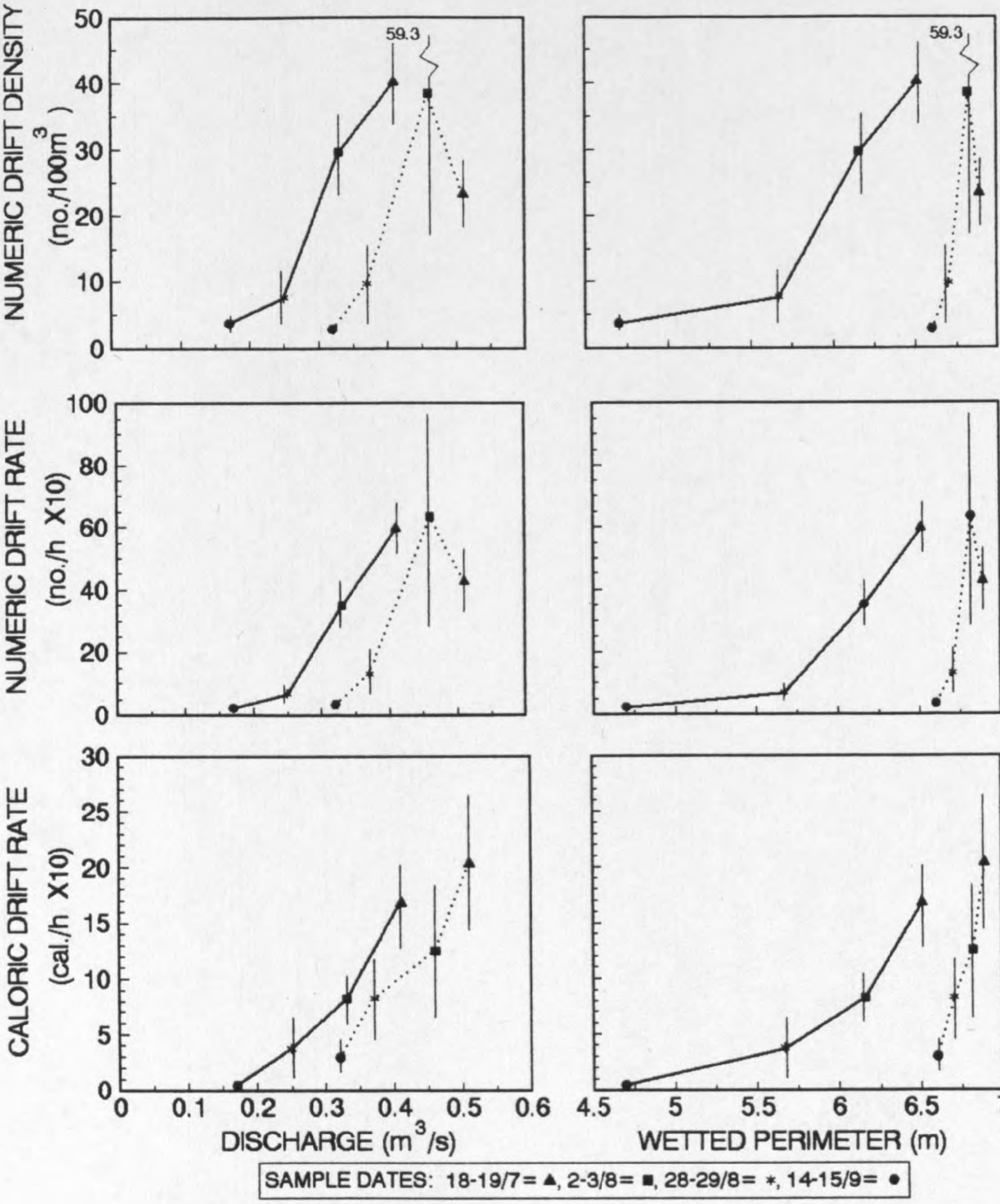

Figure 18.-Mean daily numeric drift density, and numeric and caloric drift rate for Chironomidae at the test (solid line) and reference (broken line)riffles relative to discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

when drift density at the test riffle was about twice that at the reference riffle. As stream discharge declined below the dam, drift rate was most affected. Concomitant with artificial reductions in discharge, mean body length of individuals decreased below the dam. This resulted in larger differences in caloric drift rate between the riffles than the relative reduction in discharge. Values for Horn's index of overlap were relatively high on all sample dates ranging from 0.973 to 0.994 for mean daily drift density.

Big Creek

Stream discharges for calibrating the wetted perimeter instream flow method were 0.31 and 0.01 m^3/s, 0.49 and 0.04 m^3/s, and 1.51 and 0.93 m^3/s for the downstream, middle, and upstream riffles (Table 5) in Big Creek, respectively. Inflection points for wetted perimeter-discharge relationships occurred at about 0.10 m^3/s for the downstream and middle riffles and at 0.20 m^3/s for the upstream riffle (Figure 19). Stream discharges at the downstream and middle riffles were 38% and 27% lower than at the upstream riffle on the first invertebrate sample date and were 94% and 87% lower on the second sample date (Table 5). Thus, stream discharge was well below the wetted perimeter inflection points for the downstream and middle riffles when the second invertebrate samples were collected (Figure 19). At this time, wetted perimeter, stream width, and mean water velocity of the dewatered riffles were considerably less than at the upstream riffle (Table 5).

Table 5.-Stream discharge, and mean wetted perimeter, stream width, water depth, and water velocity and percent difference for values between the downstream and middle riffles compared to the upstream riffle in Big Creek, July-August 1990. Numbers in parentheses=1 SE, N=5.

Variable	17 July[a]	23 July[b]	31 July[a]	9 August[b]
		Downstream riffle		
Discharge (m^3/s)	1.07	0.31	0.07	0.01
Wetted perimeter (m)	6.07(0.33)	5.00(0.27)	3.35(0.44)	1.70(0.43)
Stream width (m)	5.27(0.30)	4.35(0.21)	2.92(0.35)	1.33(0.27)
Water depth (m)	0.30(0.02)	0.17(0.01)	0.09(0.02)	0.04(0.01)
Water velocity (m/s)	0.72(0.10)	0.44(0.04)	0.36(0.10)	0.44(0.31)
		Middle riffle		
Discharge (m^3/s)	1.27	0.49	0.17	0.04
Wetted perimeter (m)	7.35(0.25)	6.86(0.22)	5.66(0.35)	3.12(0.19)
Stream width (m)	6.47(0.21)	6.11(0.17)	5.04(0.31)	2.86(0.20)
Water depth (m)	0.28(0.01)	0.17(0.01)	0.10(0.01)	0.05(0.01)
Water velocity (m/s)	0.71(0.02)	0.48(0.02)	0.34(0.02)	0.27(0.01)
		Upstream riffle		
Discharge (m^3/s)	1.73	1.51	1.28	0.93
Wetted perimeter (m)	14.68(0.46)	14.47(0.43)	14.17(0.45)	13.38(0.51)
Stream width (m)	14.13(0.46)	13.91(0.44)	13.63(0.47)	13.09(0.51)
Water depth (m)	0.13(0.01)	0.13(0.01)	0.13(0.01)	0.12(0.01)
Water velocity (m/s)	0.92(0.05)	0.84(0.04)	0.75(0.03)	0.62(0.04)

Table 5.-Continued.....

Variable	17 July[a]	23 July[b]	31 July[a]	9 August[b]
Percent difference between downstream and upstream riffles				
Discharge (m^3/s)	-38	-80	-95	-99
Wetted perimeter (m)	-59	-65	-76	-87
Stream width (m)	-63	-69	-79	-90
Water depth (m)	131	31	-31	-67
Water velocity (m/s)	-22	-48	-52	-29
Percent difference between middle and upstream riffles				
Discharge (m^3/s)	-27	-68	-88	-96
Wetted perimeter (m)	-50	-58	-60	-77
Stream width (m)	-54	-56	-63	-78
Water depth (m)	115	31	-23	-58
Water velocity (m/s)	-23	-43	-55	-57

[a]Invertebrate samples.
[b]Wetted perimeter calibration.

Taxa collected in Big Creek were similar to those in Bozeman Creek (Appendix A). Ephemeroptera comprised the greatest numeric abundance of all invertebrate orders (43% to 58%) in benthic samples, typically followed by Diptera and Plecoptera (Appendix A). Also, Ephemeroptera consistently comprised the greatest biomass (36% to 56%; Appendix A). Ephemeroptera comprised from 69% to 85% of total taxa and made up 73% to 84% of the biomass in drift samples (Appendix A).

Water depth, velocity, and substrate diameter were similar ($P>0.05$; ANOVA; Table 6) among riffles at benthic sample locations on

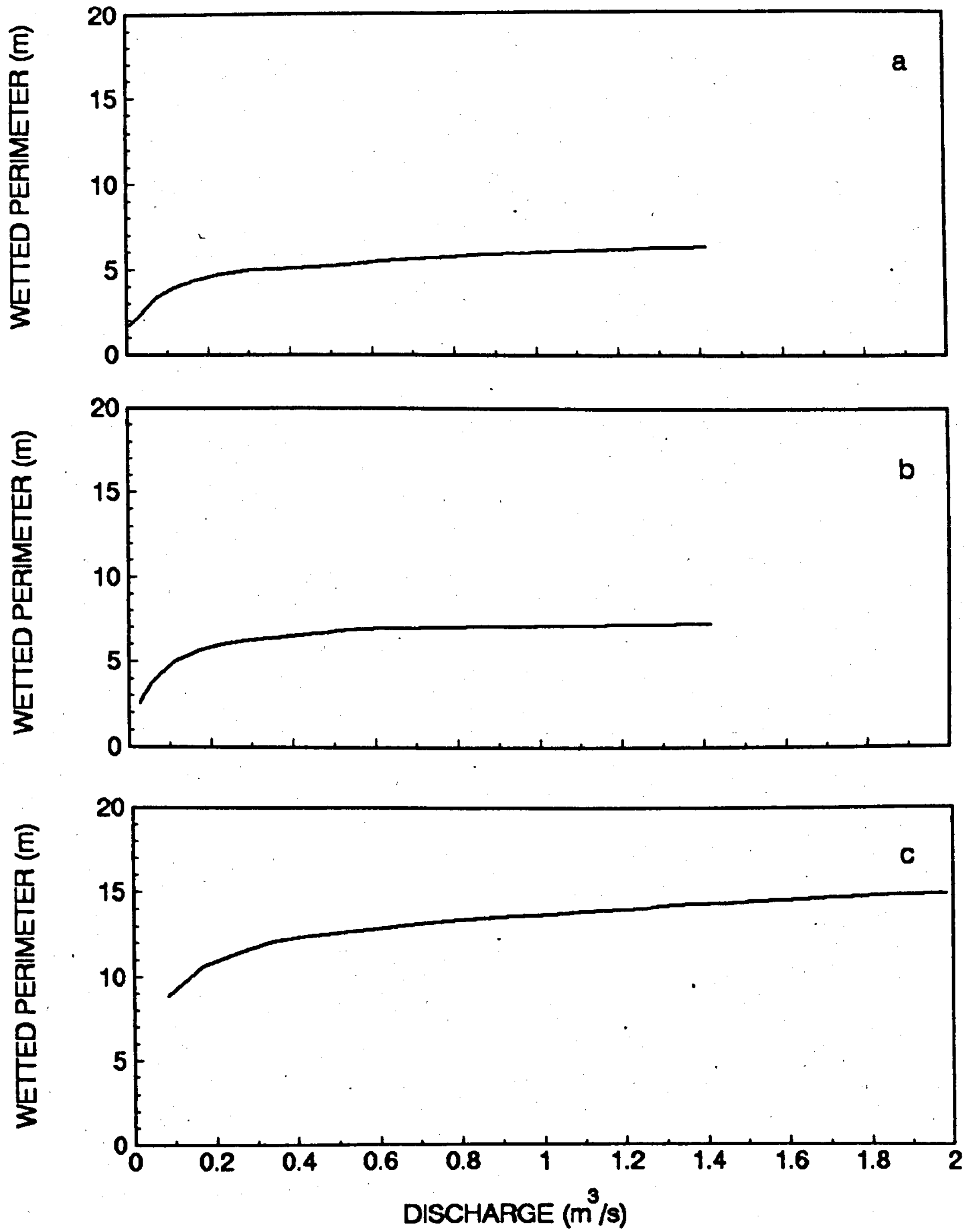

Figure 19.-Mean wetted perimeter-discharge relationships at the downstream (a), middle (b), and upstream (c) riffles in Big Creek, July-August 1990.

the first sample date. Substantial dewatering, prior to the second sample date, resulted in significantly lower water velocities at the dewatered riffles compared to the upstream riffle (P<0.001; ANOVA; Table 6). Substrate diameter and water depth were similar among riffles on both sample dates. Reductions in stream discharge elicited increases in stream temperature of 2 to 3 C at dewatered riffles (Table 6).

Table 6.-Comparison of physical characteristics at benthic sample sites at the downstream (D), middle (M), and upstream (U) riffles in Big Creek, July-August 1990. Numbers in parentheses=1 SE, N=5.

Date	Site	Temp. (C)	Depth (m)	P[a]	Velocity (m/s)	P[a]	Substrate diameter (cm)	P[b]
17/7	D	12	0.27(0.04)		0.44(0.06)		9.31(0.65)	
	M	12	0.30(0.02)		0.59(0.07)		8.33(1.95)	
	U	12	0.25(0.01)		0.59(0.06)		10.33(0.73)	
				0.285		0.288		0.548
1/8	D	15	0.18(0.02)		0.12(0.04)		10.18(0.77)	
	M	14	0.15(0.02)		0.18(0.04)		10.90(0.92)	
	U	12	0.19(0.02)		0.63(0.07)		11.58(0.74)	
				0.373		<0.001[b]		0.500

[a]Results from ANOVA.
[b]Results from Newman-Keuls test: D and M < U.

Numeric density of total benthic taxa at the downstream riffle was significantly lower than at either the middle or upstream riffle on the first sample date (P<0.05, Kruskal-Wallis test; Figure 20) while density was not different among riffles on the second sample date (P>0.05, Kruskal-Wallis test; Figure 20). Even though biomass and caloric density tended to be greater in the upstream riffle than

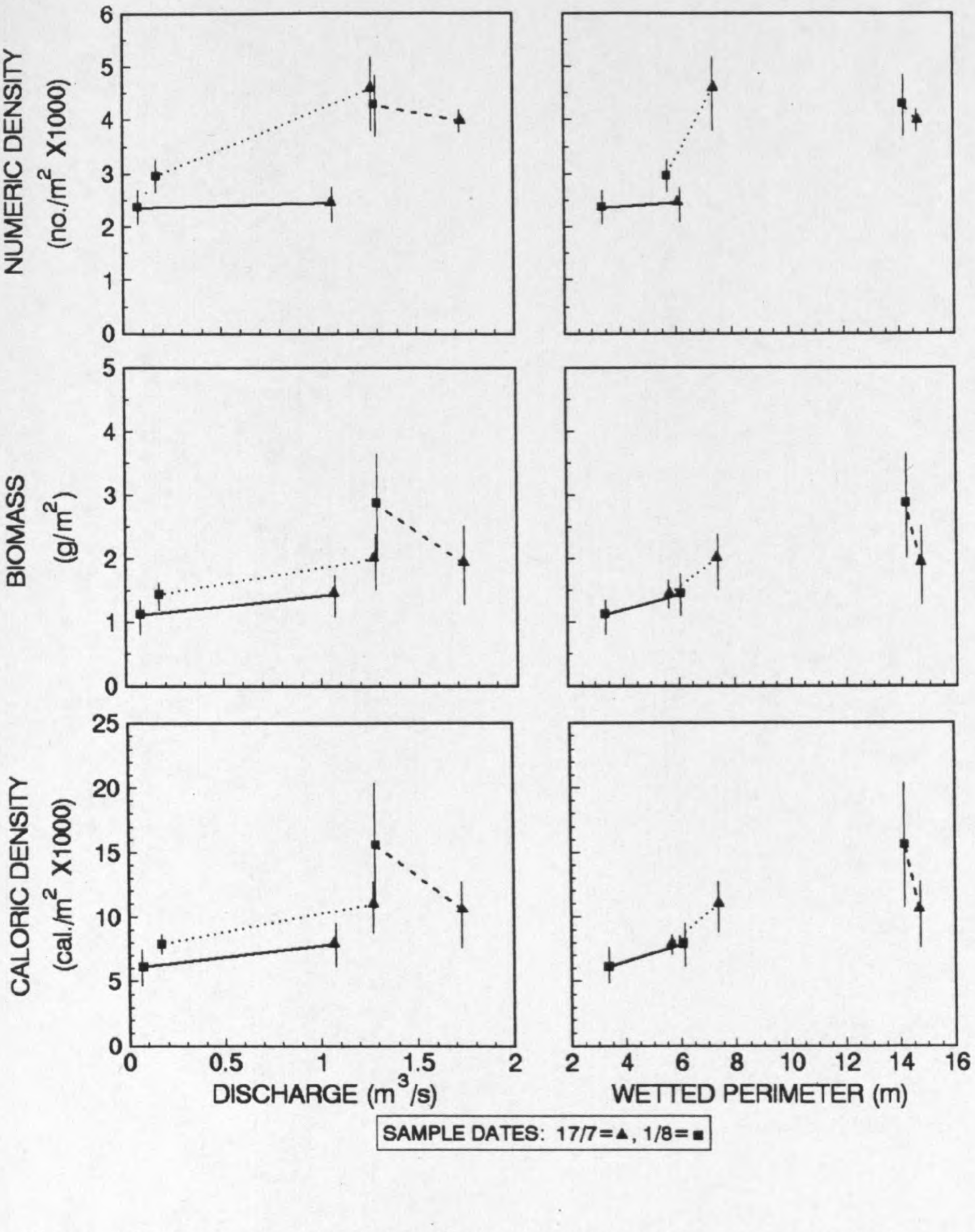

Figure 20.-Mean numeric and caloric density and biomass of total benthic taxa at the downstream (solid line), middle (dotted line), and upstream (dashed line) riffles relative to stream discharge and wetted perimeter on two sample dates in Big Creek, July-September 1990. Vertical bars±1 SE, N=5.

in the dewatered riffles, these measures did not differ among riffles on either sample date (P>0.05, Kruskal-Wallis test). Mean body lengths of all taxa were similar among riffles (P>0.05, Kruskal-Wallis test; Figure 21). Horn's index of overlap ranged from 0.916 to 0.949 on the first sample date and from 0.867 to 0.938 on the second sample date for comparisons between all pairs of riffles.

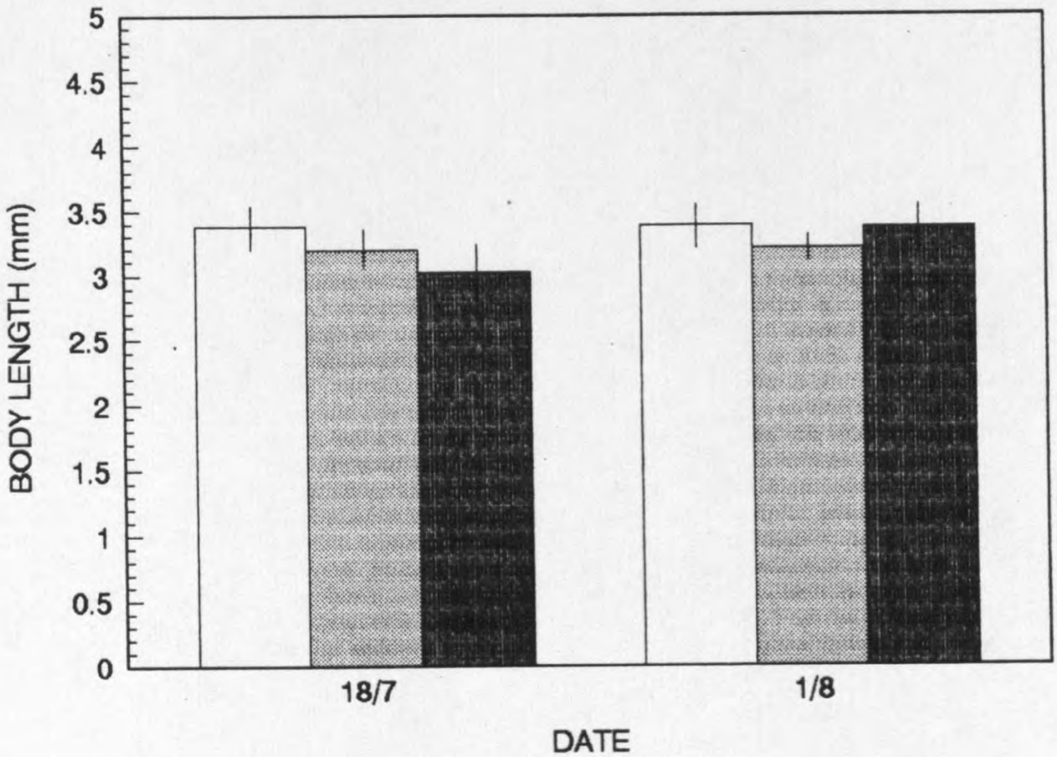

Figure 21.-Mean body length of total benthic taxa at the downstream (open bars), middle (light shaded bars), and upstream (dark shaded bars) riffles on two sample dates in Big Creek, July-August 1990. Vertical bars±1 SE, N=5.

Diel drift pattern was similar and highly nocturnal at all riffles, with greatest drift at sunset (Figure 22). Drift density increased for all time periods on the second sample date. Overall, drift density was usually significantly greater at either the

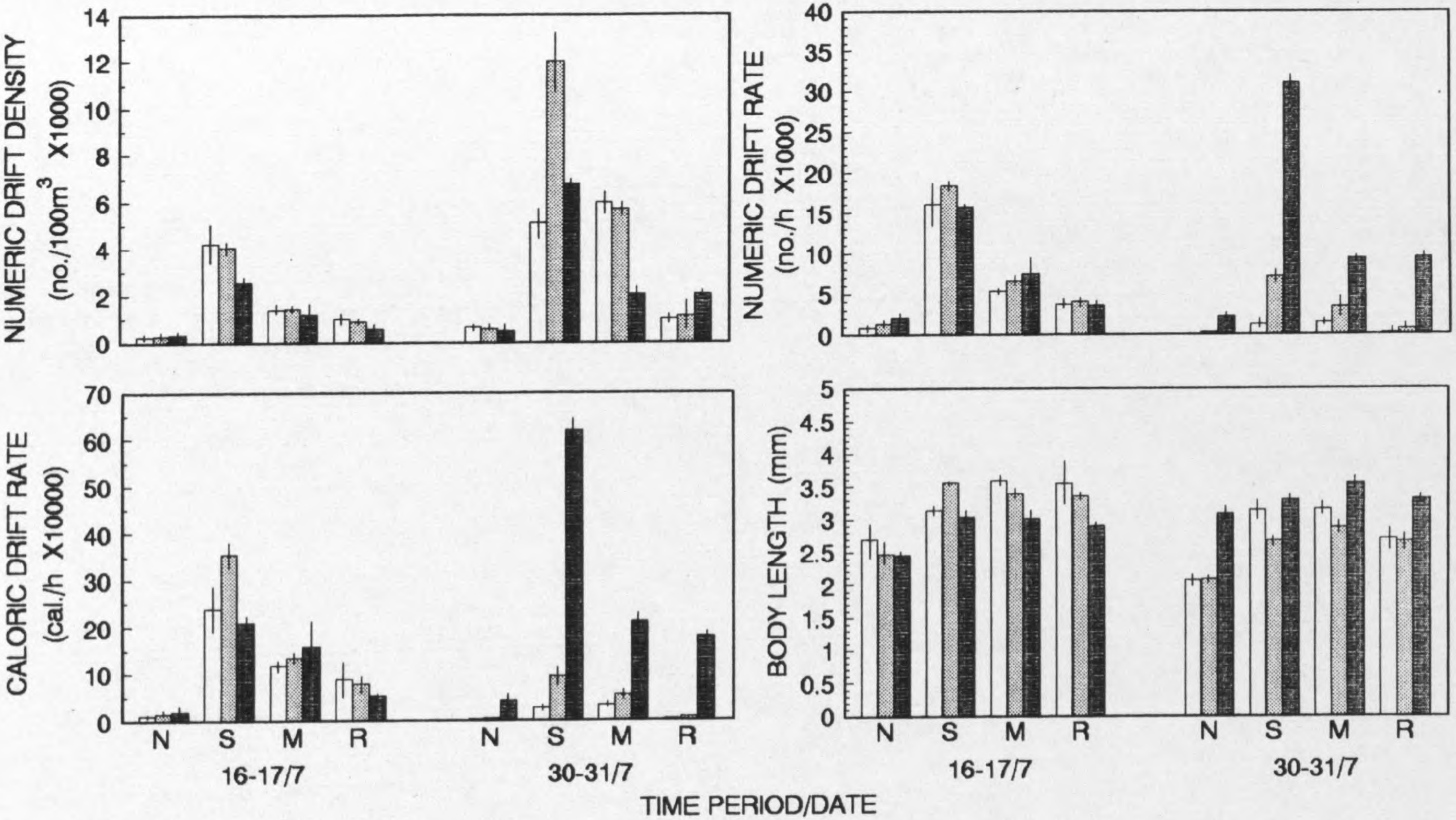

Figure 22.-Mean drift density, numeric and caloric drift rate, and mean body length by time period (N-noon, S-sunset, M-midnight, R-sunrise) on two sample dates for total taxa at the downstream (open bars), middle (light shaded bars), and upstream (dark shaded bars) riffles in Big Creek, July 1990. Vertical bars are ranges for paired driftnets.

downstream, middle or both dewatered riffles than at the upstream riffle ($P<0.05$, G-test; Table 7; Appendix A). Drift density was similar only for the noon time period on the second sample date. This trend was consistent for nearly all times periods relative to discharge, wetted perimeter, and mean water velocity (Table 7).

Table 7.-Results of G-tests for mean drift density among riffles per time period (TP: N-noon, S-sunset, M-midnight, R-sunrise) for total taxa weighted equally between riffles (E), and proportional to stream discharge (Q), wetted perimeter (WP), and mean water velocity (VEL) on two sample dates in Big Creek, July 1990. Symbols left, center, and right of slashes indicate drift density at the downstream, middle, and upstream riffles, respectively, relative to expected values, ns=not significant.

		Drift density			
Date	TP	E	Q	WP	VEL
16-17/7	N	-/+/+	ns	+/+/-	ns
	S	+/+/-	+/+/-	+/+/-	+/+/-
	M	+/+/-	+/+/-	+/+/-	+/+/-
	R	+/+/-	+/+/-	+/+/-	+/+/-
30-31/7	N	ns	+/+/-	+/+/-	+/+/-
	S	-/+/-	+/+/-	+/+/-	-/+/-
	M	+/+/-	+/+/-	+/+/-	+/+/-
	R	-/-/+	+/+/-	+/+/-	+/+/-

Reductions in stream discharge at the downstream (94%) and middle (87%) riffles on the second sample date resulted in much reduced numeric drift rates compared to the upstream riffle (Figure 22). Numeric and caloric drift rates were relatively similar among riffles on the first sample date when stream discharge differed by no more than 38%. Mean body length of individuals drifting was smaller in the downstream and middle riffles on the second sample date (Figure 22). This, as well as reductions in stream discharge, accentuated differences in caloric drift rate among riffles on the second sample date.

Mean daily drift density (no./100 m^3) was comparable among riffles on the first sample date and dramatically increased on the second sample date with the greatest increases at dewatered riffles (Figure 23). Drift density was significantly greater on both dewatered riffles than the upstream riffle on each sample date with equal weightings and relative to discharge, wetted perimeter, and mean water velocity (Table 8; Appendix A). Although drift density was greater at the dewatered riffles, large differences in discharge resulted in drift rates 94% (downstream) to 79% (middle) less than the upstream riffle on the second sample date. Also, mean body length decreased between sample dates on the dewatered riffles and slightly increased on the upstream riffle (Figure 24). This resulted in a 94% (downstream) and 85% (middle) reduction in caloric drift rate compared to the upstream riffle. These differences were not related to changes in invertebrate community composition since Horn's index of overlap ranged from 0.974 to 0.997 between all pairs of riffles on the two sample dates.

Discussion

Reductions in discharge influenced invertebrate drift, had minimal effects on benthic invertebrate density within riffle areas that remained submersed, and caused a decline in absolute invertebrate

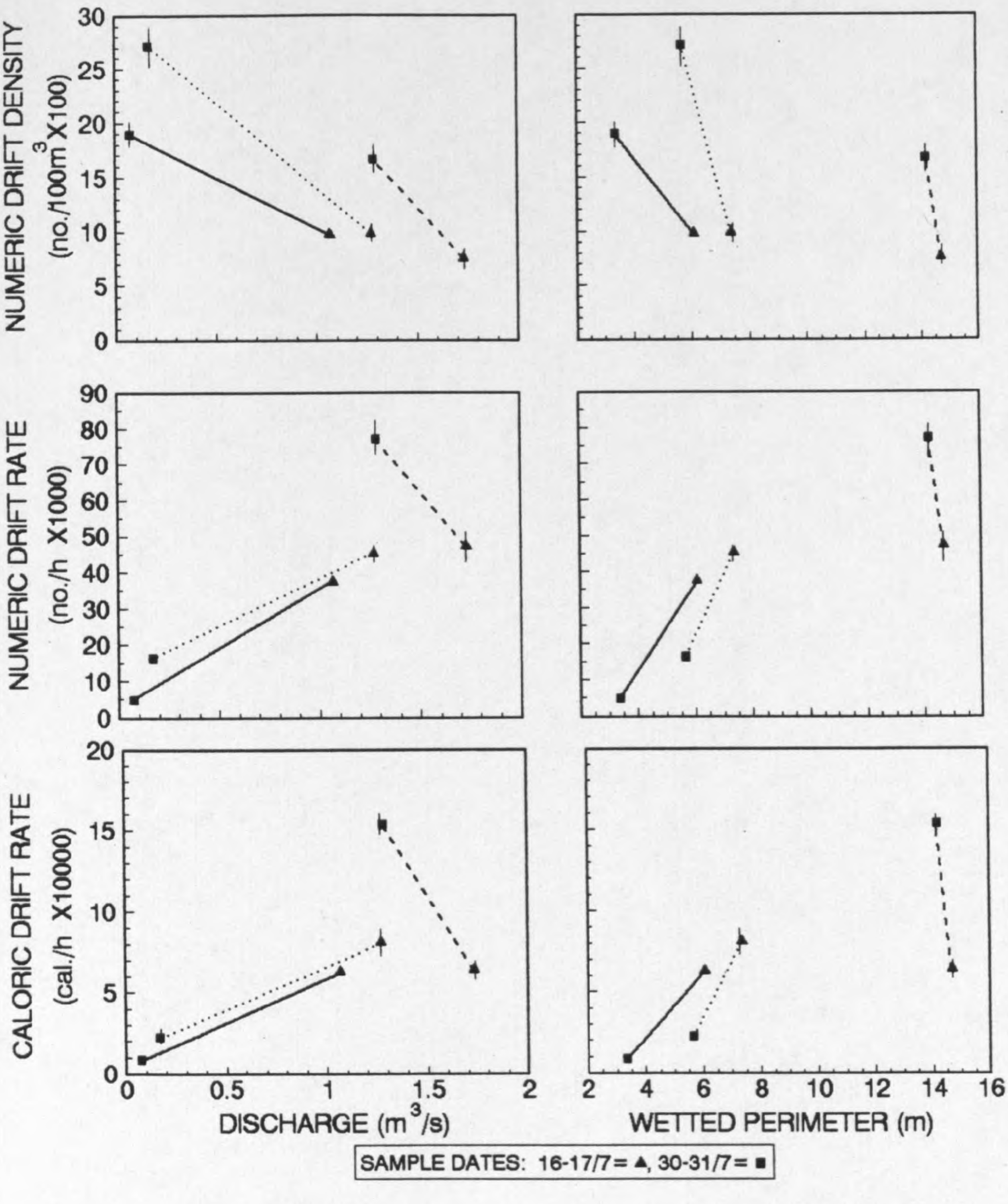

Figure 23.-Mean daily numeric drift density, and numeric and caloric drift rate for total taxa at the downstream (solid line), middle (dotted line), and upstream (dashed line) riffles relative to stream discharge and wetted perimeter on tow sample dates in Big Creek, July 1990. Vertical bars are ranges for paired driftnets.

Table 8.-Results of G-tests for mean daily drift density among riffles for total taxa weighted equally between riffles (E), and proportional to stream discharge (Q), wetted perimeter (WP), and mean water velocity (VEL) on two sample dates in Big Creek, July 1990. Symbols left, center, and right of slashes indicate drift density at the downstream, middle, and upstream riffles, respectively, relative to expected values, ns=not significant.

	Drift density			
Date	E	Q	WP	VEL
16-17/7	+/+/-	+/+/-	+/+/-	+/+/-
30-31/7	+/+/-	+/+/-	+/+/-	+/+/-

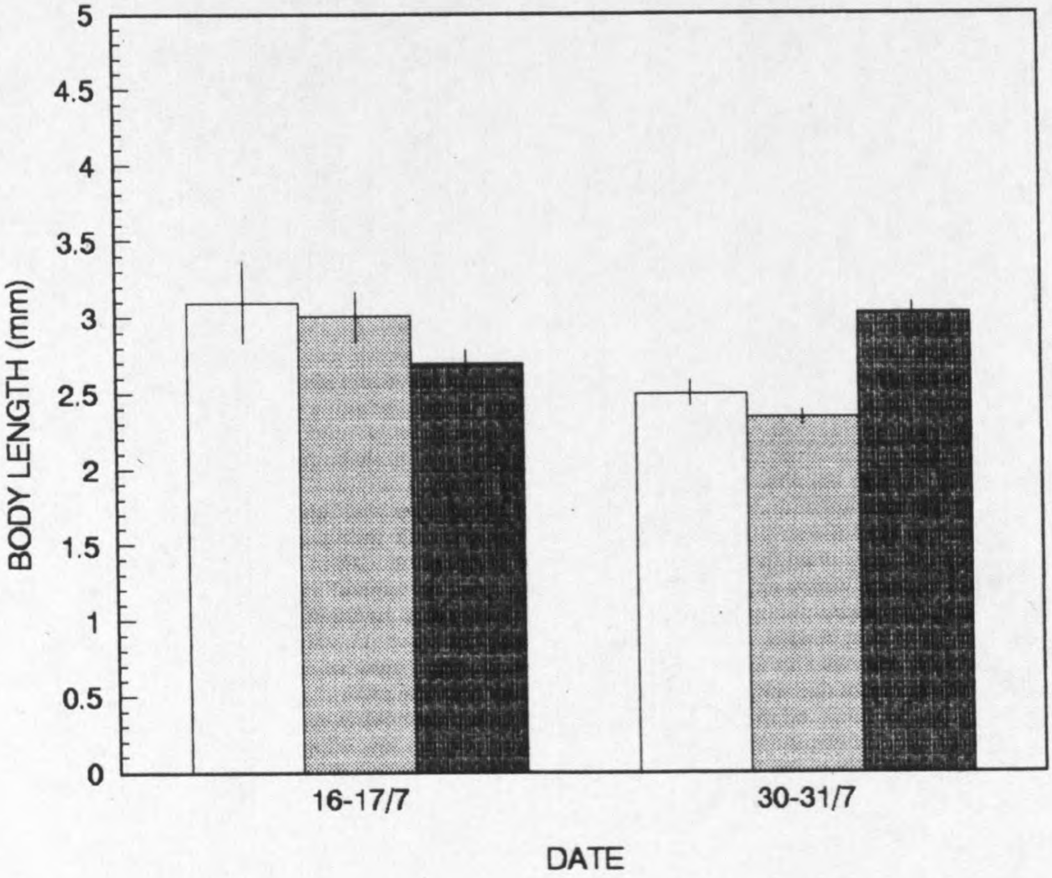

Figure 24.-Mean body length of total taxa for mean daily drift at the downstream (open bars), middle (light shaded bars), and upstream (dark shaded bars) riffles on two sample dates in Big Creek, July 1990. Vertical bars are ranges for paired driftnets.

abundance. Drift densities at dewatered riffles were typically similar to or greater than that at reference riffles. But drift rate was lower in dewatered than reference riffles. Benthic abundance rarely differed between riffles but dewatering may have elicited a reduction in body size of some taxa, reducing benthic biomass and caloric content of benthic and drifting invertebrates. Differences in riffle area, indicated by wetted perimeter, resulted in lower invertebrate abundance, per riffle length, in dewatered than reference riffles.

Density of stream benthos appears to be relatively unmodified by reductions in discharge. In several southern Appalachian Mountain streams, Cada et al. (1983) found no consistent trends in benthic invertebrate abundance between riffles susceptible to drying and riffles that remained completely wetted at various stream discharges. White et al. (1981) found no differences in benthic density of most invertebrate taxa between artificial stream channels with constant discharge and with reductions in discharge of up to 85%; however, at 95% of initial discharge in fall tests, there was a 43% increase in benthic density in the reduced compared to the constant discharge channel. Similarly, McClay (1968) and Hafele (1978) noted increased benthic density in riffles below stream diversions, which reduced discharge by 75% compared to riffles above diversions. Increases in benthic density with discharge reductions have been attributed to declining riffle area and subsequent invertebrate movement toward the thalweg to avoid stranding (Corrarino and Brusven 1983).

Benthic densities increased at test and reference riffles as discharge declined in Bozeman Creek. This trend was consistent with seasonal abundances of invertebrates (Logan 1963; Mackay and Kalff 1969) and probably related to phenology. Benthic insects in temperate streams are typically less abundant in spring and summer than other seasons due to emergence; abundance increases in late summer and fall as eggs hatch (Hynes 1970). In Bozeman Creek, benthic densities were similar between riffles on all sample dates despite relatively large differences in stream discharge and wetted perimeter (up to 47% and 29%, respectively). These similarities were not unexpected since water depth, velocity, and substrate diameter were not significantly different at benthic sample locations, even though mean water velocity on the dewatered riffle was considerably lower than the reference riffle. Gradual declines in stream discharge, allowing invertebrates to adjust positions in response to changes in stream conditions, may have contributed to absence of an increase in density on the dewatered riffle. Also, Corrarino and Brusven (1983) found stranding of nearly all near shore invertebrates in fall tests and attributed this to limited mobility of early instars. Limited ability of early instar individuals at the stream margins of Bozeman Creek to move toward the thalweg would have lessened potential crowding due to reductions in stream discharge.

An apparent effect of dewatering on benthic invertebrates in Bozeman Creek was a significant reduction in mean body length for total taxa, as well as for the most abundant taxon, *Baetis* spp., on the last sample date. At this time, discharge was below the wetted perimeter inflection point at the dewatered riffle and the lowest mean water velocity occurred. It was unlikely that this was the result of phenological differences of invertebrates since water temperatures were identical between riffles on all sample dates. Although numeric densities were similar between riffles, biomass and caloric densities were significantly lower below the diversion than on the reference riffle. Substantial decreases in benthic invertebrate biomass have been noted in dewatered reaches of rivers below dams compared to upstream areas above impoundments (Evans 1979; Ward and Stanford 1980; Brusven 1984). Differences in biomass have been attributed to shifts in benthic community composition; communities in dewatered areas were dominated by relatively small individuals, primarily dipterans. The lowest value for community overlap occurred on the final sample date in Bozeman Creek, but the difference in community composition between riffles was slight given the relatively high value of Horn's index. White et al. (1981) noted virtually no change in benthic community composition at 95% dewatering but biomass was lower in their test channel, even with increased invertebrate density. Similar observations were made by Hafele (1978). Because some invertebrate taxa may have specific habitat requirements for substrate size, water depth and velocity (Gore and Judy 1981; Orth and Maughan 1983) which may vary by developmental stage, I speculate that water velocity may have been below the tolerance ranges for late instars at the test riffle.

No consistent trends were apparent for benthic invertebrates among three riffles in Big Creek. Invertebrate densities were significantly higher at the middle and upstream riffles than the downstream riffle on the first sample date. On the second sample date, benthic density did not differ among riffles despite extremely large differences in stream discharge, wetted perimeter, and mean stream velocity. In contrast to the benthos in Bozeman Creek, body length of invertebrates on dewatered riffles in Big Creek did not decrease relative to the upstream reference riffle. Thus, biomass and caloric density were similar on both sample dates. Undoubtedly, sample variability contributed to these results. It is unknown when, within the 2 week period between sample dates, water withdrawal was increased. It is possible that the short time between the second sample date and increased water withdrawal could have affected the response of the benthos since indices of community overlap were relatively high among all riffles.

Even though benthic densities did not differ between dewatered and reference riffles in Bozeman Creek and Big Creek, a substantial reduction in total invertebrate abundance would exist due to differences in wetted area between riffles. With riffles of equal length and benthic density, absolute invertebrate abundance would be reduced according to differences in wetted perimeter between riffles, 6% to 29% in Bozeman Creek and 50% to 87% in Big Creek. The reduction would be accentuated, relative to caloric content of invertebrates, if flow characteristics on dewatered riffles were amenable to smaller invertebrates.

Abundance of drifting invertebrates can be extremely variable and is influenced by various abiotic and biotic factors, e.g. season, stream discharge, water velocity, photoperiod, food abundance, species, and presence of other species (Brittain and Eikeland 1988). While increases in drift have been associated with specific life-history events such as pre-emergence or pupation activity (Stoneburner and Smock 1979) and periods of rapid growth (Krueger and Cook 1981), seasonally, drift is usually minimal in fall and winter and highest in spring and summer (Elliott 1967; Waringer 1992). Increases in drift density have been reported for both increases (Anderson and Lehmkuhl 1968; Pearson and Franklin 1968; Scullion and Sinton 1983; Irvine 1985; Perry and Perry 1986) and decreases (Minshall and Winger 1968; Pearson and Franklin 1968; Radford and Hartland-Rowe 1971; Gore 1977; White et al. 1981; Corrarino and Brusven 1983) in stream discharge. Poff and Ward (1991) simultaneously diverted water into and away from experimental riffles to investigate relations between invertebrate drift and flow variation relative to an unaltered control riffle in a portion of the upper Colorado River. Most taxa responded more strongly to decreases rather than increases in discharge.

I observed no consistent trend in drift density between riffles during any time period in Bozeman Creek. In most instances, drift density was either similar between riffles or drift density was significantly greater on the dewatered riffle. Differences in physical characteristics of the riffles, discharge, wetted perimeter, and mean water velocity, did not account for differences in drift between riffles, i.e. drift density was not proportional to these features. On a daily basis, mean drift density was similar between riffles except on the third sample date when drift density was significantly higher on the dewatered riffle. Stream discharge was near the inflection point for the wetted perimeter-discharge relationship on this date. Presumably, hydraulic conditions were rapidly changing and may have contributed to elevated drift density on the dewatered riffle.

Drift density was also significantly higher on the dewatered riffles for most time periods in Big Creek. Mean daily drift density was significantly higher on dewatered riffles on both sample dates and drift was not proportional to discharge, wetted perimeter, or mean water velocity. Between sample dates, drift density substantially increased while stream discharge, wetted perimeter, and mean water velocity decreased at all riffles.

Increased drift density on dewatered riffles in Bozeman Creek and Big Creek is consistent with the view that drift is an active process, not merely passive dislodgement from the substrate. Poff and Ward (1991) argued that increased drifting was primarily an active response to dewatering because reductions in discharge lowers water velocity and hence boundary layer sheer stress, effectively reducing the likelihood that invertebrates would be passively dislodged from the substrate. Water velocity was lower on dewatered riffles than upstream riffles in Bozeman Creek and Big Creek, suggesting that greater drift was a behavioral phenomenon.

Possible mechanisms eliciting active invertebrate drift in response to reductions in discharge include: lateral movement toward midstream areas to avoid stranding which results in high benthic densities and subsequent dispersal; and abandonment of stream areas with unsuitable hydraulic characteristics. Corrarino and Brusven (1983) postulated that, because reduced flows caused habitat loss for invertebrates at the margins of their experimental channel, an increase in benthic density may have occurred that elicited increased density dependent interactions resulting in elevated drift (Dimond 1967). Several authors (Pearson and Franklin 1968; Bird and Hynes 1981; Perry and Perry 1986) reported substantial lateral movement of invertebrates to the thalweg during dewatering and greater drift from stream margins. Invertebrates may abandon areas with unsuitable hydraulic conditions, e.g. low water velocity. Minshall and Winger (1968) noted a several-fold increase in diurnal drift with discharge reductions that minimally affected stream width but caused water depth and velocity to decline by more than 50%. Others have acknowledged the contribution of changes in hydraulic conditions from dewatering to increased drift (Gore 1977; White et al. 1981). A behavioral response by invertebrates to avoid unsuitable areas is to remain in the water column (Walton 1980; Allan and Feifarek 1989), thereby prolonging drift time and extending drift distances which may result in enhanced drift density (Poff and Ward 1991).

While both mechanisms would be expected to contribute to the drift response as a stream undergoes reductions in discharge, similarities in benthic densities between riffles in Bozeman Creek and on the second sample date at Big Creek suggests that unsuitable stream conditions were created that elicited greater drift from the dewatered riffles than the reference riffle. At benthic sample locations, mean water velocities on the dewatered riffles were below values reported for velocity preferences for *Baetis* spp. (0.53 and 0.35 m/s; White et al. 1981; Orth and Maughan 1983), the most abundant taxa in the benthos and drift in both streams.

Increases in drift density on dewatered riffles appears to be a temporary response, with drift density returning to previous levels within 1-2 weeks (White et al. 1981; Corrarino and Brusven 1983). But with reductions in discharge, drift rate may be substantially reduced (White et al. 1981; Poff and Ward 1991). In this study, drift rate was consistently lower on dewatered riffles compared to upstream riffles in Bozeman Creek and Big Creek. In Bozeman Creek, numeric drift rate on the dewatered riffle ranged from 6% greater, to 50% less than that for the reference riffle, for differences in discharges from 20% to 47%. The dependency of drift rate on discharge was most evident for the second sample date at Big Creek when drift density was considerably greater on dewatered riffles than the reference riffle, but numeric drift rate was from 79% to 94% lower. Differences in discharge ranged from 27% to 94% between the dewatered and upstream riffles.

Using data from fall tests of White et al. 1981 and Corrarino and Brusven (1983), I calculated mean numeric drift rates for their control channels (constant discharge) and test channels (dewatered for 1 and 2 weeks, for each study). At 50% flow reduction, numeric drift rate was 34% and 41% below control levels in 2 years of tests (Corrarino and Brusven 1983). In White et al. (1981), drift rate was initially 50% higher in the test than the control channel at equal discharges, and drift rate was 10% and 13% greater in the test than the control channel with discharge differences of 50% and 70%, respectively. When discharge was reduced 85% and 95%, numeric drift rate in the test channel was 23% and 62% below that of the control channel, respectively. In both studies, drift rate was more closely related to discharge than wetted perimeter since differences in wetted perimeter between channels were usually less than half the percent difference in discharge. Response of drift rates to reduced flow in Bozeman Creek and Big Creek concur with those observed by White et al. (1981) and Corrarino and Brusven (1983).

White et al. (1981) concluded that the major effect of dewatering on fish feeding was a potential reduction in food availability as evidenced by reduced drift rates. This is a major concern if, as my data suggest, dewatering elicits a reduction in biomass, and hence caloric content of invertebrates in both the benthos and drift in addition to reductions in drift rate. For example, percent difference between riffles was greater for daily caloric drift rate than daily numeric drift rate. In Bozeman Creek, mean caloric drift rate for the dewatered riffle was 18% to 70% below that for the reference riffle and the greatest difference occurred on the final sample date.

Relative to assumptions of the wetted perimeter instream flow method, dewatering did not cause a reduction in benthic or drift density. However, it did result in lower absolute invertebrate abundance, per riffle length, at dewatered than at reference riffles due to loss of riffle area. Dewatering was associated with a reduction in drift rate and caused a reduction in size of individuals in both the benthos and drift, effectively decreasing energetic value of potential food items for fish. The greatest disparity between riffles in biomass and caloric content of invertebrates occurred during the sample dates when discharge was below the wetted perimeter inflection point on dewatered riffles. The potential impacts of reductions in discharge on food availability for drift-feeding fish is underscored by the reliance of drift rate on discharge. This was illustrated by drastic increases in drift density between sample dates at dewatered riffles on Big Creek which suffered equally drastic declines in drift rates at the levels of discharge reductions observed in this study. Without a sustained increase in drift density, any reduction in discharge would cause a reduction in drift rate.

While impacts of reductions in discharge appear greatest for potential fish-food organisms when discharge falls below the wetted perimeter inflection point, the presumption of food limitation in fish can not be made without knowledge of the nature of the fish population. For instance, natural reductions in discharge may diminish food availability in streams with a relatively dense fish population so that modest levels of dewatering, even above the inflection point, could restrict fish growth or abundance. Greater reliance of drift-feeding fish on prey from terrestrial origin during late fall (Hunt 1975), as streams reach low flows, may be an indication of greater abundance of terrestrial prey as well as depressed levels of aquatic food items. Because terrestrial fish-food abundance may be sporadic in nature, abundance of terrestrial organisms were a third to over five times that for aquatic invertebrates in Bozeman Creek and Big Creek, minimum flow recommendations based on wetted perimeter estimates should be conservative, i.e. considerably above the inflection point, in streams with highly valued fish populations to minimize potential impacts on aquatic invertebrate drift rates.

Summary

Some biological assumptions of the wetted perimeter inflection point instream flow method are that: abundance of aquatic invertebrates is proportional to riffle area and wetted perimeter can be used as an index of invertebrate abundance, and therefore, of availability of food for fish. I performed the instream flow method and compared benthic and drifting invertebrate abundance between artificially dewatered and unaltered flow riffles in two streams to evaluate the relation among invertebrate abundance, stream discharge, and riffle wetted perimeter.

In Bozeman Creek, invertebrates were collected from two riffles when discharge and wetted perimeter differed by 20-47% and 6-29% on four sample dates. Density of total benthos and dominant taxa (*Baetis* spp.) did not differ between riffles but body length was usually lower at the dewatered riffle. This resulted in significantly lower biomass and caloric density of invertebrates at the dewatered riffle on the final sample date when discharge was below the wetted perimeter inflection point. Invertebrate drift density (no./m^3) was usually similar between riffles or significantly greater at the dewatered riffle, but differences in stream discharge resulted in numeric drift

rates (no./h) being 6% greater to 50% lower at the dewatered riffle, and caloric drift rates being from 18-71% lower.

Invertebrates were collected from two dewatered, and an unaltered flow upstream riffle on two sample dates at Big Creek. Compared to the upstream riffle, water diversions caused a 27% and 38% reduction in discharge on the first sample date, and a 87% and 95% reduction in discharge on the second date at the dewatered riffles. Wetted perimeter was 50% to 76% lower at dewatered riffles due primarily to differences in channel profiles. While no consistent trends in total benthic density and biomass were observed among the three riffles, severe reductions in stream discharge on the second sample date were associated with increased invertebrate drift density with the greatest increases at the dewatered riffles. Daily numeric drift rate was 79% and 94% lower at the dewatered riffles and caloric drift rate was 87% and 94% lower compared to the upstream reference riffle.

Reductions in stream discharge and riffle wetted perimeter had minimal effects on benthic invertebrate density. This suggests that absolute invertebrate abundance, per riffle length, is proportional to riffle area, and hence riffle wetted perimeter. Discharge reductions, however, may diminish food value of potential invertebrate prey for fish through declines in invertebrate size and biomass. Although invertebrate drift density may increase in response to dewatering, reductions in discharge may elicit a decline in drift rate which would reduce food availability for primarily drift-feeding fish. This effect was accentuated when reduced stream discharges were accompanied by reductions in the size and biomass of drifting invertebrates.

EFFECTS OF SUPPLEMENTAL FEEDING ON CUTTHROAT TROUT IN STREAM ENCLOSURES DURING LATE SUMMER

Introduction

Predator-prey interactions and their relation to growth and abundance of salmonids in streams has long been a controversial issue in salmonid ecology. Allen (1969) proposed that benthic invertebrates available as food for salmonids may control fish growth rates and that fish predation may influence invertebrate density. A positive relationship between invertebrate abundance and salmonid production, abundance, and biomass exists in streams (Ellis and Gowing 1957; Gibson and Galbraith 1975; Murphy et al. 1981; Waters 1982; Wilzbach and Hall 1985). Salmonids receiving higher rations maintained greater densities in artificial stream channels compared to those on lower rations (Symons 1971; Slaney and Northcote 1974; Wilzbach 1985). Mesick (1988), however, found that food availability had little effect on trout residency.

Studies designed to evaluate the effects of salmonid predation on invertebrates have shown little or no change in total benthic abundance (Allan 1982; Culp 1986; Reice and Edwards 1986), but abundance of specific taxa may be affected (Griffiths 1981; Bechara et al. 1992; Power 1992). In contrast, some studies have found greater benthic densities and larger individuals in stream areas without salmonids or with relatively low densities of salmonids compared to areas with abundant salmonids (Pentland 1930; Straskraba 1966; Allan 1975). Wilzbach et al. (1986) found a reduction in drift of large invertebrates in pools containing cutthroat trout compared to pools without trout when habitat complexity (substrate crevices and light levels) was controlled.

For salmonids, food availability is intimately linked to stream space and has presumably led to the evolution of social conventions to partition food and space among individual fish (Chapman 1966). Slaney and Northcote (1974) noted a positive relationship between juvenile rainbow trout abundance and food availability, and observed that territory size and frequency of aggressive encounters varied inversely with the amount of food in artificial stream channels. Bachman (1984) concluded that adult brown trout formed dominance hierarchies where individual fish showed fidelity to specific foraging sites and used sites in an energy conserving manner. He proposed that foraging sites may be a limiting factor at high population densities, but that brown trout growth rates were independent of population density.

Salmonids usually occupy low water velocity foraging sites adjacent to relatively high velocity, invertebrate rich areas, to conserve energy and maximize food intake (Chapman and Bjornn 1969; Jenkins 1969; Griffith 1972; Bachman 1984; Fausch and White 1981, 1986). Using juvenile coho salmon, brown trout, and brook trout in an artificial stream, Fausch (1984) found that coho salmon consistently used sites with high "potential profit" and displaced brown trout and brook trout from such sites. Bachman (1982) proposed a model for brown trout, relating energy expended in swimming and access to invertebrate drift, to predict conditions under which a trout would shift diets or migrate.

Although salmonid abundance and growth rates are ultimately related to overall food availability, relative stability of growth rates within populations has been reported for brook trout (McFadden 1961; Cooper et al. 1962; McFadden et al. 1967) and brown trout (McFadden and Cooper 1964) at different population densities. The relative insensitivity of growth rate to population density in these cases prompted McFadden (1969) to conclude that, in most streams, regulation of salmonid density is affected primarily through changes in fish density as opposed to changes in growth rate. Recently, Newman and Waters (1989) compared brown trout production among eight contiguous sections of a Minnesota stream. Although significant differences in fish densities existed, trout growth rates did not differ among sections. They attributed differences in densities to variation in available habitat. Therefore, trout density may be controlled primarily by habitat features, i.e., adequate foraging and refuge sites, while growth rate is dependent on efficient habitat use (Bachman 1984), stream temperature (Edwards et al. 1979), and food availability (Mason 1976).

The objective of my study was to determine the effects of augmenting food supply on cutthroat trout growth and density in a natural stream during late summer. In determining the response of brown and rainbow trout to habitat features, Morhardt and Mesick (1988) introduced relatively high numbers of trout into stream enclosures and used the number of fish remaining after emigration had ceased as a short term response variable they termed "behavioral carrying capacity". They proposed that this represented the influence of habitat treatments in the enclosures and provided an indication of potential carrying capacity of the streams for trout during the study period. I used a similar approach to test the null hypothesis that cutthroat trout growth and density would not differ between enclosures receiving supplemental feeding and those that did not. An additional objective was to use trout growth, stomach contents, and bioenergetic equations to estimate food consumption rates of cutthroat trout and compare these values to invertebrate drift rates as an estimate of trout foraging efficiency.

Methods

Study Site

The study was conducted on Brackett Creek in Gallatin County, Montana (Figure 25). Brackett Creek arises as three forks in the Bridger Mountain range and flows east for 32 km before entering the Shields River, a tributary of the Yellowstone River, near the community of Clyde Park. The drainage encompasses 150 km^2 and the stream has a mean annual discharge of 0.7 m^3/s (USGS 1992).

The study site was located on the Middle Fork of Brackett Creek 3.2 km above the confluence of the North, South, and Middle Forks (Figure 25). The site represented a second order stream with a 23 km^2 drainage basin at a elevation of 1840 m above msl. It was in a meadow area with relatively low gradient characterized by a high degree of sinuosity (2.7) and numerous pools. Steam width ranged from 0.8 m to

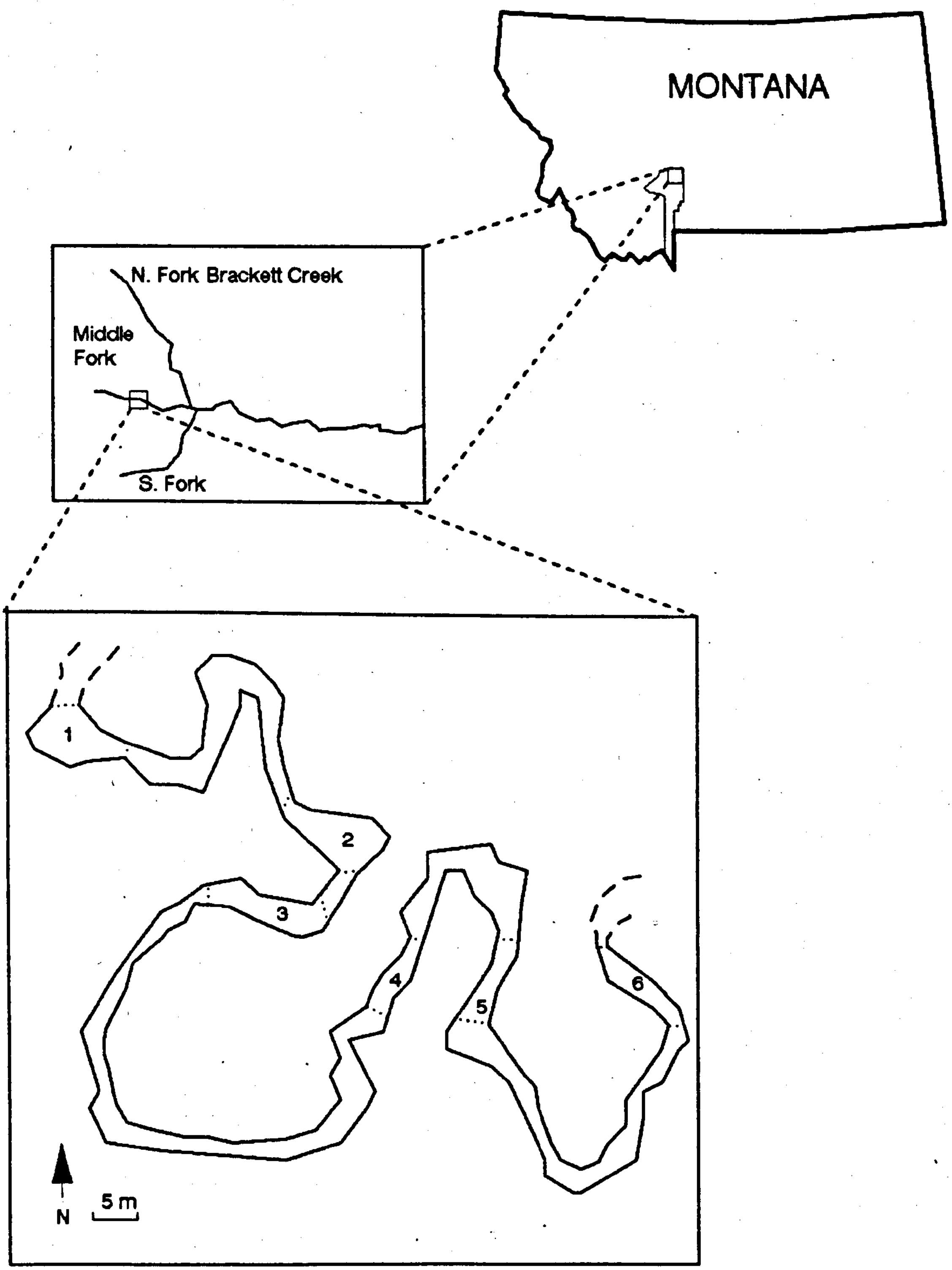

Figure 25.-Location of study site and enclosures (#1-6) in Brackett Creek, July-September 1989 and 1990.

5.5 m (2.6 ± 0.1, mean ± 1 SE) and the dominant substrate size was 4 to 15 cm (8.1 ± 0.4, mean ± 1 SE). During the 2 year study, July-September 1989 and 1990, stream discharge ranged from 0.072 to 0.026 m^3/s and water chemistry was similar between years (8.61-10.13 mg O_2/L for dissolved oxygen, 8.05-8.17 for pH, 338-373 µmhos for conductivity, and 107.3-172.0 mg $CaCO_3/L$ for alkalinity). The riparian community was dominated by willow, *Salix* sp., birch, *Betula* sp., and fir, *Pseudotsuga* sp. The dominant periphyton, primarily the red algae *Boldia* sp. (Prescott 1978; W. Dodds, MSU Department of Biology, personal communication), formed dense growths covering much of the riffle areas. Considerable logging had occurred in upper drainage basin and the area was grazed by sheep during the study. Brook trout (*Salvelinus fontinalis*) and Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) were the only fish species present.

Stream Enclosures and Study Design

I enclosed six pools within the study site to test effects of supplemental feeding on abundance and growth of cutthroat trout. Enclosures consisted of upstream and downstream traps placed in the thalweg. Plastic screen leads (13 mm mesh) angled from the traps to the stream banks. Traps and leads were embedded in the substrate 10 to 15 cm and held in place by steel bars driven into the stream bed. Each enclosure encompassed a single pool and a portion of an upstream riffle. Enclosures were consecutively numbered 1 to 6 starting from the upstream end of the study site (Figure 25).

Habitat was described along a baseline established by extending a measuring tape between each upstream and downstream trap. Transects perpendicular to stream flow were set at 1-m intervals along baselines. Water depth and mean velocity (0.6 depth) were measured with a top-setting rod and electronic current meter at five equally spaced intervals along each transect and the length of each transect was recorded. Surface area of undercut bank, overhanging vegetation (within 0.3 m of the water surface) and instream debris, providing overhead cover to trout, was measured at each transect. Baseline length, mean stream width, and water depth were used to calculate area and volume of each enclosure while riffle areas (<0.15 m deep) were excluded from calculations. Habitat measurements were made at the start (July) and end (September) of the tests in 1990, but because enclosures were used in other tests after September in 1989, habitat was only measured in July. The ratio of percent change in habitat to percent reduction of stream discharge in 1990 was used to estimate habitat in September 1989.

Multiple passes with a backpack electrofishing unit (Coffelt Electronic Company, Inc.) were used to remove fish residing within enclosures. Electrofishing passes proceeded in an upstream direction and were repeated until no fish were captured. Fish were anesthetized with tricane methanesulfonate and their species, total length (mm), and weight (nearest g) were recorded. All brook trout received an adipose fin clip and were released in the stream outside the enclosures. All cutthroat trout (≥ 90 mm) were individually marked with a coded fingerling tag (Floy Tag Co.) placed in the anterior base of the dorsal fin. Trout were held in the stream until they had recovered from anesthesia. To eliminate potential effects of prior residency, cutthroat trout were released into different enclosures than they were originally captured. Additional cutthroat trout were collected from other areas of the Middle Fork and North Fork of Brackett Creek to supplement experimental populations.

Trout were collected on 24, 25, and 30 July, 1989 and released into enclosures. During an acclimation period (25 July to 4 August), trapped trout were returned to the enclosures. Direction of movement and tag codes were recorded. Observed mortality was recorded and subtracted from the number of trout introduced. Each day beginning 5 August, total length, weight, and tag codes were recorded from trapped trout. Stomach contents were then collected by gastric lavage (Light et al. 1983), and the trout were released outside the enclosures. In 1990, cutthroat trout were collected and introduced into enclosures on 9, 10, and 12 July following the same procedure as in 1989. The acclimation period ended on 20 July 1990. The first day that trapped trout were retained was considered day 1 of the test period in each year.

Downstream enclosures (#4-6) were designated experimental and received supplemental feeding once daily while upstream enclosures (#1-3) were controls and did not receive supplemental food. Frozen brine shrimp, *Artemia salina*, and krill, *Euphausia pacifica* (Murex Aqua Foods Inc.), was allowed to thaw in three 100 L containers. A hose attached to the base of each container delivered the mixture to a perforated pipe anchored to the upstream end of each experimental enclosure while a gas powered generator operated a pump to supply stream water to the containers. Experimental enclosures received 250 g wet weight (22.6 g dry weight) of brine shrimp and 65 g wet weight (9.4 g dry weight) of krill daily in 1989. In 1990, 226 g wet weight (20.5 g dry weight) of brine shrimp and 85 g wet weight (12.4 g dry weight) of krill were delivered to each experimental enclosure. Feeding commenced between 1000 and 1300 h and took approximately 1 h.

I used electrofishing to recover trout remaining in enclosures at the end of tests. Trout were anesthetized, their total length, weight, and tag codes were recorded, and stomach contents were collected. Electrofishing began on the mornings of 30 September 1989 and 22 September 1990 after experimental enclosures received supplemental feeding.

I calculated Fulton condition factors (Anderson and Gutreuter 1983) of all trout when they were introduced into enclosures, trapped, and recovered at the end of tests. Condition factors, total lengths, and weights were compared among enclosures with analysis of variance for each year (Sokal and Rohlf 1981). Multiple comparisons were made with Newman-Keuls multiple range test (Zar 1984). Initial and final condition factors, total lengths, and weights of trout collected in traps and recovered at the end of tests were compared with paired t-tests (Sokal and Rohlf 1981). All data were transformed ($\log_e$) to achieve normality and homogeneity of variances when appropriate. To better describe length and weight relationships for trout recovered at the end of tests, I calculated regression equations of transformed ($\log_e$) length and weight values (Cone 1989) for trout in each enclosure. I used a dummy variable (Kleinbaum et al. 1988) to compare slopes for length-weight relationships for trout at the start and end of tests. Also, specific growth rates (Busacker et al. 1990) were calculated for all trout remaining at the end of the tests and values were compared among enclosures with Kruskal-Wallis tests (Daniel 1990) for each year. Multiple comparisons were made according to Zar (1984) for significant ($P<0.05$) results. Degree of association among trout abundance, density, biomass, standing crop, growth rates, drift rates, and habitat characteristics was estimated with Spearman Rank Correlation Coefficients (Daniel 1990).

Invertebrate Drift

Drifting aquatic invertebrates were used as an estimate of food available to trout. Steel bars were driven into the stream bed at the thalweg to support a single driftnet above the upstream trap of each enclosure. Bars remained in place for the duration of the study. Driftnets had a rectangular frame (50 x 30 cm) attached to a 1 m long net made of 0.5 mm mesh cloth. Driftnets were placed against the steel bars and extended from the substrate to above the water surface so that the entire water column was sampled. Sample time typically ranged from 30 to 60 min, depending on stream discharge and severity of net fouling. Mean water depth and velocity (0.6 depth) was calculated from three measurements taken at equally spaced locations across the opening of each driftnet. Measurements were made with a top-setting rod and electronic current meter at the midpoint of the sample time. Nets were removed from the stream and collected material was washed into labeled bottles and preserved with a solution of 4% formalin and rose bengal (to stain invertebrates). Sample time, mean water depth, and velocity were used to calculate volume of water sampled by each net.

Drift was simultaneously sampled at each enclosure at noon, within one-half-hour after sunset and before sunrise, and at midnight. Sample dates were 16-17 August, 5-6 September, and 21-22 September in 1989 and 24-25 July, 9-10 August, 21-22 August, and 12-13 September in 1990. Water temperature was recorded during each sample period and light levels were measured with a photometer. Also, stream discharge was measured after samples were collected on each date.

In the laboratory, each drift sample was washed and separated into two size fractions with sieves (coarse ≥ 1.0 mm; fine ≥ 0.5 mm). Portions of a coarse fraction were spread in white pans and all invertebrates were removed from debris and placed in labeled bottles of 4% formalin. Pan contents were discarded when no invertebrates were found in a 3-min period. The process was repeated until all portions of a coarse fraction were examined. Aquatic invertebrates were identified to the lowest practical taxonomic level using a dissecting scope (0.7-40 X) and various taxonomic sources (Wiggins 1977; Merritt and Cummins 1984; Stewart and Stark 1988; Pennak 1989; D. G. Gustafson, Department of Biology, Montana State University, personal communication). Individuals of terrestrial origin and adults with aquatic immature stages were assigned to a single terrestrial category. All individuals were counted and total body length (distance from front of head capsule to end of abdomen) was measured with an ocular micrometer. Individuals were then assigned to 1.0 mm size classes.

Portions of fine fractions were spread in a small tray and inspected under a dissecting microscope. Invertebrates were counted, measured, and placed into taxonomic groups similar to those for coarse fractions. Taxa count and body length data were combined for both coarse and fine fractions of a sample.

To estimate biomass and caloric equivalents of drifting invertebrates, published regression equations of dry weight on body length (Rogers et al. 1976, 1977; Smock 1980) were used to predict dry weight (mg) of each taxon in the various size classes of invertebrates. These values were converted to caloric equivalents (Coffman 1967; Brocksen et al. 1968; Cummins and Wuycheck 1971) and dry weight and caloric values were multiplied by the number of individuals in each size class for a taxon.

Invertebrate counts were scaled to water volume sampled by a net to calculate numeric drift density (no./m^3) for each taxon and total taxa in a sample. Drift rates (no./h) were calculated by multiplying drift density by hourly stream discharge. Drift density and rate were also expressed as dry biomass and calories. Mean estimates of all drift measures during a time period were used to determine diel periodicity of invertebrate drift. To calculate mean daily drift per enclosure, driftnet estimates were weighted by day and night length (time between sunrise and sunset) according to sample period, i.e., the mean of sunset, midnight, and sunrise samples represented nocturnal drift whereas noon samples represented diurnal drift.

Aquatic insects in the drift were assigned to their respective orders, while remaining taxa were assigned to the categories Acarina, terrestrial, and "worms" (Oligochaeta, Turbellaria and Nematomorpha). I calculated the percentage that each category and order contributed to total invertebrate drift for numbers and dry weight. Also, separate percentages were calculated that included brine shrimp and krill for experimental enclosures.

Diet Analysis

Stomach contents were used to estimate food consumption rates for trout recovered at the end of the tests. Stomach contents were sorted to the lowest practical taxonomic level, enumerated and total body length was measured for intact food items. Individual taxa were placed into preweighed aluminum pans and dried at 105 C for 48 h. After cooling in a desiccator, pans were weighed (nearest 0.001 mg) on a microbalance and dry weights were determined by difference.

Preliminary tests of sampling efficiency for the gastric lavage procedure, using stomachs collected from trapped trout, indicated removal of 86% stomach contents based on dry weight. Also, I assumed loss of 25% dry weight of stomach contents from preservatives (Allan 1981). Dry weights for stomach contents were adjusted to account for these factors. Relative dry weight (mg/g) of food items in each stomach was calculated as milligrams of stomach contents per gram of trout live weight at the end of the tests.

Relative food consumption rates were calculated from stomach contents for individual trout at the end of the tests in both years.

I assumed that fish feeding was continuous and constant (Adams and Breck 1990), and calculated daily consumption rate as:

$$C = 24 \cdot S \cdot K$$

C is daily consumption rate (mg/g/d); S is relative dry weight of stomach contents for an individual trout (mg/g); K is instantaneous rate of gastric evacuation (h).

Elliott (1972) incorporated water temperature and prey type into a set of equations to predict gastric evacuation rates for brown trout. Cunjak and Power (1987) modified these equations by assigning potential prey items to four categories (Plecoptera, Trichoptera, terrestrial prey, and all other prey), and used the modified equations to estimate time required for 99% gastric evacuation for brook trout. I assumed that their equations were applicable to cutthroat trout and estimated gastric evacuation time as:

$$X_{99\%} = \sum_{i=1}^{4} (p_i(4.6052/a_i e^{b_i T}))$$

$X_{99\%}$ is time (h) required for 99% evacuation of stomach contents; p is proportion of the four prey categories; i is prey category, 1...4; a_i and b_i are prey specific constants; and T is water temperature (C). Gastric evacuation time was used to calculate evacuation rate.

Relative caloric consumption rates (cal./g/d) were calculated for each trout using caloric equivalents of each prey category. Means for each enclosure were multiplied by trout biomass to determine total caloric consumption rates (cal./d). To determine prey selection, electivity indices (Ivlev 1961) were calculated for each trout using numeric proportions of prey categories in the diet of each trout and drift collected on the final sample date. Mean body length of intact prey items in dominant prey categories was compared to that of invertebrate drift to investigate potential size selective predation by trout. Relative consumption rates (no./g/d and cal./g/d) were compared among enclosures with Kruskal-Wallis tests (Daniel 1990) for both years.

I used Elliott's bioenergetic equations (Elliott 1975a, b, c, d; 1976a, b, c) developed for brown trout to predict components of the daily energy budget for cutthroat trout (consumption rate (C), respiration (R), proportion of consumption lost as waste (P_F for feces and P_U for excretory products), and growth (B) for trout on maximum and maintenance rations; Appendix B). Maintenance consumption rates (C_{main}) were calculated using weight of individual trout and water temperature at the end of the tests. Maintenance ratio (daily food consumption rate based on stomach contents/C_{main}) was calculated for each trout and used to evaluate estimated feeding rates relative to maintenance energy requirements. Values were compared among enclosures with Kruskal-Wallis tests (Daniel 1990). Also, foraging efficiency was calculated for each enclosure as the ratio of total consumption by all trout to daily caloric drift rate on the last drift sample date for each enclosure.

To predict maximum growth and consumption rates of trout during the study, I converted bioenergetic equations into a simulation model (BIOE1; Appendix B) similar to that employed by Preall and Ringler (1989). I performed simulations for all trout in an enclosure from the first day of introduction until the end of tests or when individual trout emigrated from the enclosures. Ecological growth coefficients (percent of maximum growth rate attained; Preall and Ringler 1989) were compared among all enclosures for trout that remained to the end of the tests each year with Kruskal-Wallis tests (Daniel 1990). Also, foraging efficiency (ratio of predicted consumption rates to daily caloric drift rate for each enclosure and drift sample date) was calculated for total C_{main} and C_{max} to determine the adequacy of available food to meet energetic requirements of trout.

Consumption rates required to produce observed growth for individual trout were estimated with a second model (BIOE2; Appendix B). Estimates were scope of growth (difference between C_{max} and C_{main}; Elliott 1979) scaled by EGC added to C_{main} for individuals that increased in weight and C_{main} scaled by specific growth rate for individuals that experienced negative growth.

Results

Physical Habitat

Stream discharge declined during the tests in both years with the reduction in 1990 about twice as great as in 1989 (Figure 26). While this was largely due to an earlier starting date in 1990, discharge was usually higher on the same dates in 1990 than in 1989. During the study, discharge declined 37% and 61% in 1989 and 1990, respectively. Because of the small size of Brackett Creek, storms caused erratic stream flows but stage typically returned to previous

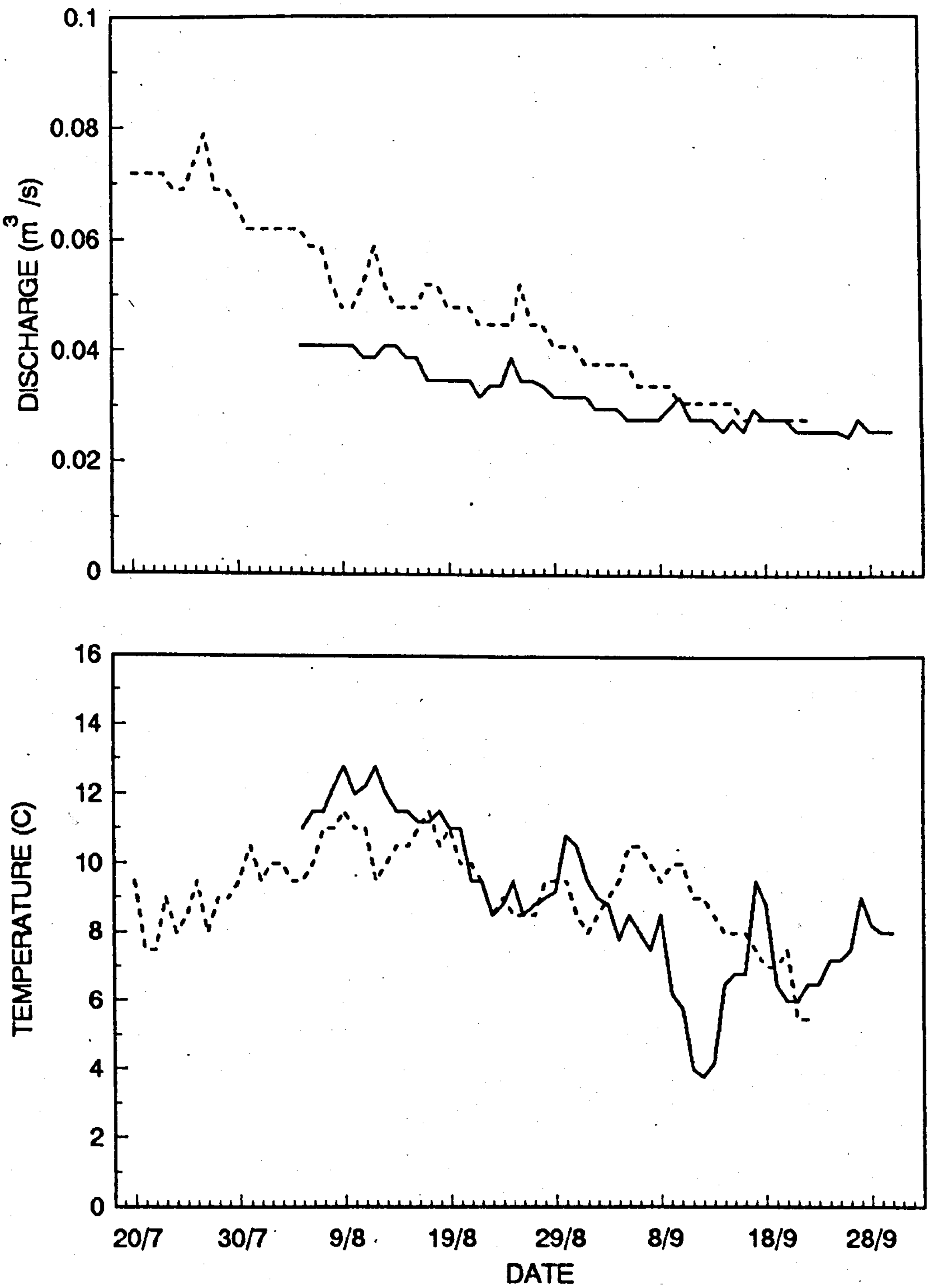

Figure 26.-Stream discharge and mean daily water temperature for Brackett Creek in 1989 (solid lines) and 1990 (broken lines).

levels within a few hours. Enclosure 1 was washed out in 1989 by high flow.

Although mean water temperature for the entire test period was 8.9 C in 1989 and 9.2 C in 1990, temperature varied more in 1989 (3.8 to 12.8 C) than in 1990 (5.5 to 11.0 C; Figure 26). Temperature declined during the tests in both years and, because of a snow storm, extremely low water temperatures occurred from 10 to 15 September 1989.

Physical habitat (i.e. mean stream width, water depth, velocity, overhead cover, pool volume and surface area) varied among enclosures for each year. At the beginning of tests in 1989, enclosure surface areas ranged from 12.5 to 23.4 m^2, while in 1990, areas ranged from 14.5 to 24.5 m^2 (Table 9). With a 61% reduction in discharge in 1990, enclosure areas decreased from 3 to 24% by the end of the tests. Likewise, stream width, water depth, velocity, and pool volume declined. Differences in enclosure area estimates and those made at the beginning of the study in 1989 ranged from 1 to 12% (Table 9).

<u>Invertebrate Drift</u>

Invertebrate drift was composed of 63 taxa represented by aquatic insects, the non-insect groups Oligochaeta, Turbellaria, Nematomorpha, and Acarina, and terrestrial individuals (Appendix C). Individual driftnets sampled from 6 to 49% of stream discharge and light was typically >1000 $\mu E/s/m^2$ for noon samples and <5 $\mu E/s/m^2$ at all other sample times. Water temperature did not vary among driftnets during a sample.

Table 9.-Length, mean stream width, water depth, water velocity, cover, volume, surface area, and percent change (%) in total cover and surface area from the start (S) to end (E) of tests for each enclosure (E) in Brackett Creek, 1989 and 1990. Numbers in parenthesis=1 SE.

					Cover[a]						Area	
E	Length (m)	Width (m)	Depth (m)	Velocity (m/s)	Total (m^2)	UCB (m^2)	OHV (m^2)	ISD (m^2)	%	Volume (m^3)	Surface (m^2)	%
					1989							
2 S	5.0	4.33(0.66)	0.27(0.06)	0.06(0.01)	2.70	0.10	1.60	1.00		5.85	23.4	
2 E[b]	5.0	3.71	0.25	0.06	2.45	0.07	1.38	1.00	-9	4.64	22.7	-3
3 S	5.0	3.18(0.22)	0.28(0.06)	0.10(0.04)	1.40	0.40	0.00	1.00		4.45	15.9	
3 E[b]	5.0	3.09	0.25	0.09	0.87	0.40	0.00	0.47	-38	3.86	14.2	-11
4 S	4.0	3.13(0.08)	0.28(0.05)	0.09(0.03)	4.10	0.80	2.80	0.50		3.51	12.5	
4 E[b]	4.0	3.06	0.24	0.08	3.41	0.80	2.28	0.33	-17	2.94	12.4	-1
5 S	6.0	2.23(0.11)	0.23(0.02)	0.07(0.01)	2.55	0.85	1.00	0.70		3.08	13.9	
5 E[b]	6.0	1.95	0.22	0.07	2.52	0.82	1.00	0.70	-1	2.57	12.2	-12
6 S	6.0	2.39(0.50)	0.26(0.01)	0.06(0.02)	2.20	1.50	0.00	0.70		3.73	14.4	
6 E[b]	6.0	2.17	0.24	0.04	2.07	1.37	0.00	0.70	-6	3.12	13.1	-9
					1990							
1 S	6.0	3.85(0.76)	0.29(0.03)	0.12(0.02)	2.65	1.65	1.00	0.00		6.70	23.1	
1 E	6.0	2.91(0.45)	0.21(0.03)	0.06(0.01)	1.35	1.15	0.20	0.00	-49	3.67	17.5	-24
2 S	5.4	4.53(0.38)	0.35(0.04)	0.10(0.01)	5.50	0.50	3.00	2.00		8.56	24.5	
2 E	5.4	4.32(0.38)	0.31(0.04)	0.06(0.01)	4.55	0.25	2.30	2.00	-17	7.23	23.3	-5

Table 9.-Continued.....

E	Length (m)	Width (m)	Depth (m)	Velocity (m/s)	Cover[a]					Volume (m^3)	Area	
					Total (m^2)	UCB (m^2)	OHV (m^2)	ISD (m^2)	%		Surface (m^2)	%
3 S	5.3	3.32(0.55)	0.36(0.08)	0.08(0.02)	4.35	0.75	0.80	2.80		6.33	17.6	
3 E	5.3	2.71(0.76)	0.30(0.06)	0.05(0.01)	2.15	0.75	0.00	1.40	-50	4.31	14.4	-18
4 S	6.0	2.42(0.53)	0.21(0.04)	0.12(0.03)	3.25	1.00	1.90	0.35		3.05	14.5	
4 E	6.0	2.33(0.48)	0.16(0.04)	0.09(0.01)	2.45	1.00	1.30	0.15	-25	2.24	14.0	-3
5 S	6.3	2.57(0.47)	0.21(0.04)	0.16(0.02)	2.40	0.90	1.00	0.50		3.40	16.2	
5 E	6.3	2.03(0.35)	0.20(0.04)	0.07(0.01)	2.35	0.85	1.00	0.50	-2	2.56	12.8	-21
6 S	7.2	2.48(0.69)	0.20(0.02)	0.16(0.02)	2.95	1.75	0.00	1.20		3.57	17.7	
6 E	7.2	2.10(0.55)	0.18(0.02)	0.07(0.01)	2.70	1.50	0.00	1.20	-8	2.72	15.0	-15

[a]Cover types: UCB=under cut banks, OHV=overhead vegetation, ISD=instream debris.
[b]Estimated values.

The terrestrial category comprised the greatest numeric percentage of all invertebrate groups in the drift (Figure 27), ranging from 38 to 65% of mean drift density on three sample dates in 1989 (Appendix C). Drift rates of aquatic taxa decreased with discharge. The terrestrial group substantially increased on the third sample date and contributed more to total numeric and caloric drift rate than aquatic taxa (Figure 27). Because terrestrial organisms were larger than aquatic taxa (Figure 27), this category comprised 70 to 93% of drift biomass (Appendix C) increasing the terrestrial contribution to caloric drift rate (Figure 27). Mean daily caloric drift rate of five enclosures for all taxa ranged from 69619 to 107874 cal./d during 1989. Drift of aquatic taxa was relatively similar among enclosures compared to total drift, which included terrestrial organisms on each sample date (Appendix D). Among enclosures, the lowest drift for aquatic and all taxa generally occurred in enclosures 3 and 4 and the highest drift in enclosure 2 (Appendix D).

Ephemeropterans and terrestrial organisms composed the greatest numeric percentages of drifting invertebrates in 1990, 35 to 58% and 17 to 49%, respectively (Appendix C). While drift density and numeric drift rate remained relatively constant or slightly increased on four sample dates in 1990, caloric drift rate declined (Figure 27). Mean body length of terrestrial organisms was consistently larger than aquatic taxa on the final three sample dates (Figure 27) which caused terrestrial organisms to contribute proportionally more to total biomass (24 to 66%, Appendix C). Among enclosures, caloric drift rates of aquatic taxa were consistently lower in enclosures 3 and 4

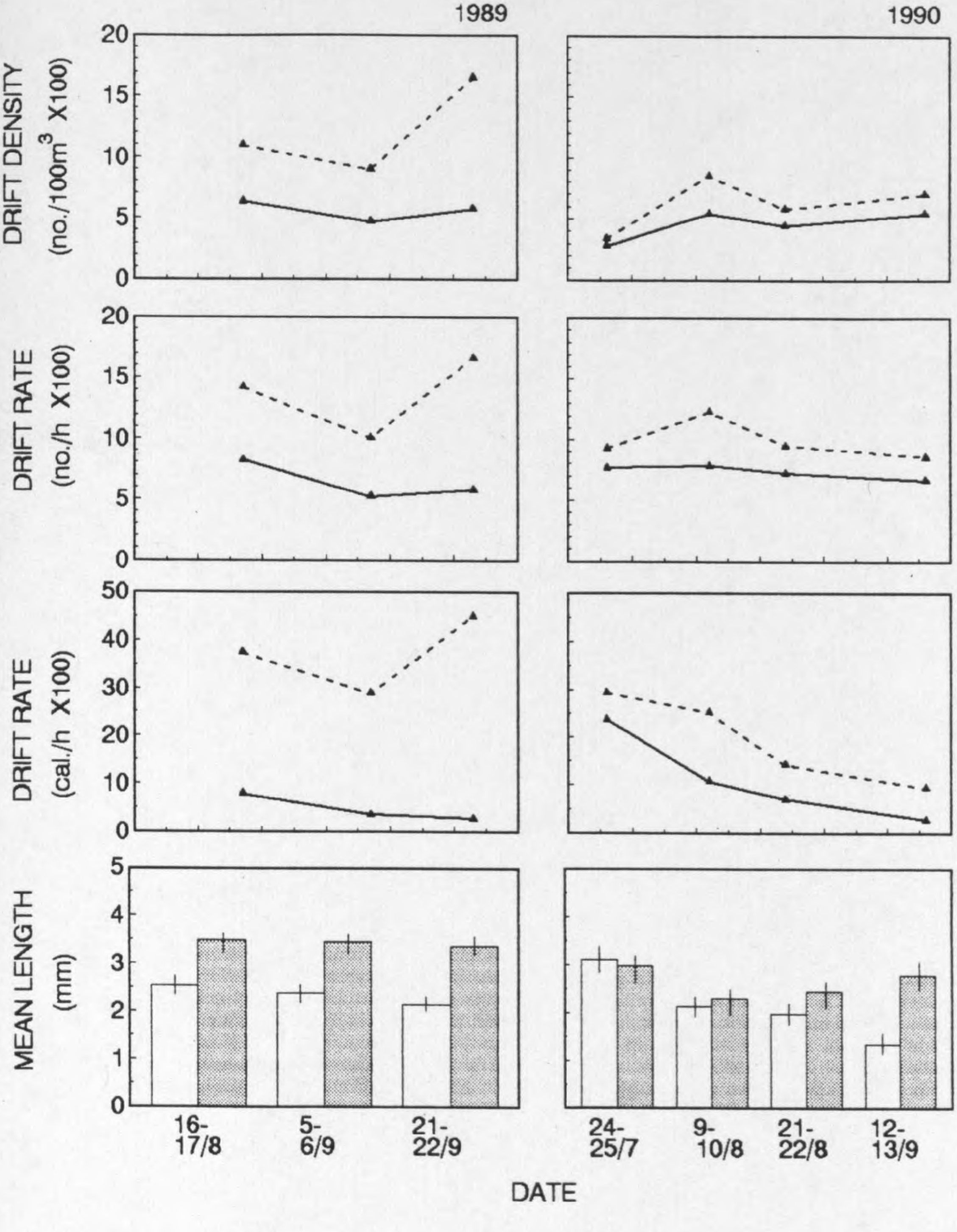

Figure 27.-Mean drift density and rate (numeric and caloric) of aquatic taxa (solid lines) and all taxa (broken lines) and mean body length of aquatic taxa (open bars) and terrestrial taxa (shaded bars) in Brackett Creek, 1989 and 1990. N=5 in 1989, N=6 in 1990. Vertical bars±1 SE.

than other enclosures while caloric drift rate in enclosure 2 was typically higher than the other enclosures (Appendix D). Mean daily caloric drift rate of the six enclosures ranged from 22844 to 70544 cal./d for all taxa.

Addition of brine shrimp and krill to experimental enclosures increased the number and biomass of daily drift by over 50,000 individuals and 32.0 g dry weight per day. Although supplemental feeding occurred as a daily pulse for 1 h, brine shrimp and krill greatly exceeded natural drift and contributed proportionally more than half of total drift (numbers and biomass) to experimental enclosures (Appendix C).

Diel drift patterns were similar between years. Aquatic invertebrate drift density and rate peaked at sunset and was minimal at noon or sunrise (Figure 28). Mean body length of aquatic taxa was smaller for noon samples than other time periods. The terrestrial group was more abundant in either sunset or noon samples and was typically larger than aquatic taxa (Figure 28).

Cutthroat Trout

The number of trout originally residing in enclosures varied (Table 10). Total fish density, brook trout and cutthroat trout combined, ranged from 0.6 to 1.6 fish/m^2. Although mean length and weight of all trout did not significantly differ among enclosures in 1989 (ANOVA, P=0.996 for length; P=0.947 for weight), trout in enclosure 6 were significantly smaller than trout residing in other enclosures in 1990 (ANOVA, P=0.020 for length; P<0.001 for weight;