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

by

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APPROVAL

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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.

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.

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 state-wide 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

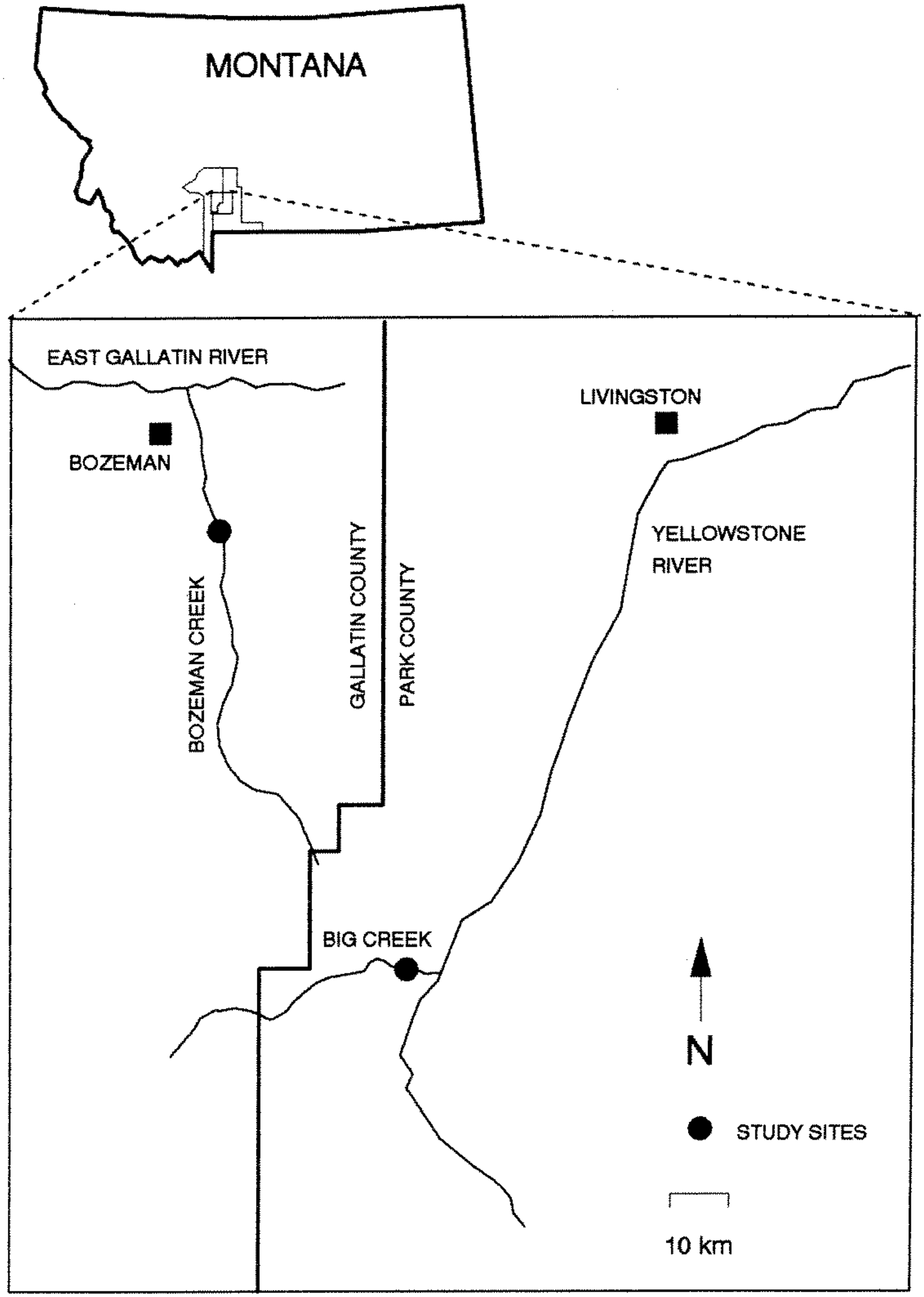

Figure 1.-Location of study sites in Bozeman Creek and Big Creek.

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.

<u>Big Creek</u>. 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 ($\geq$ 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.

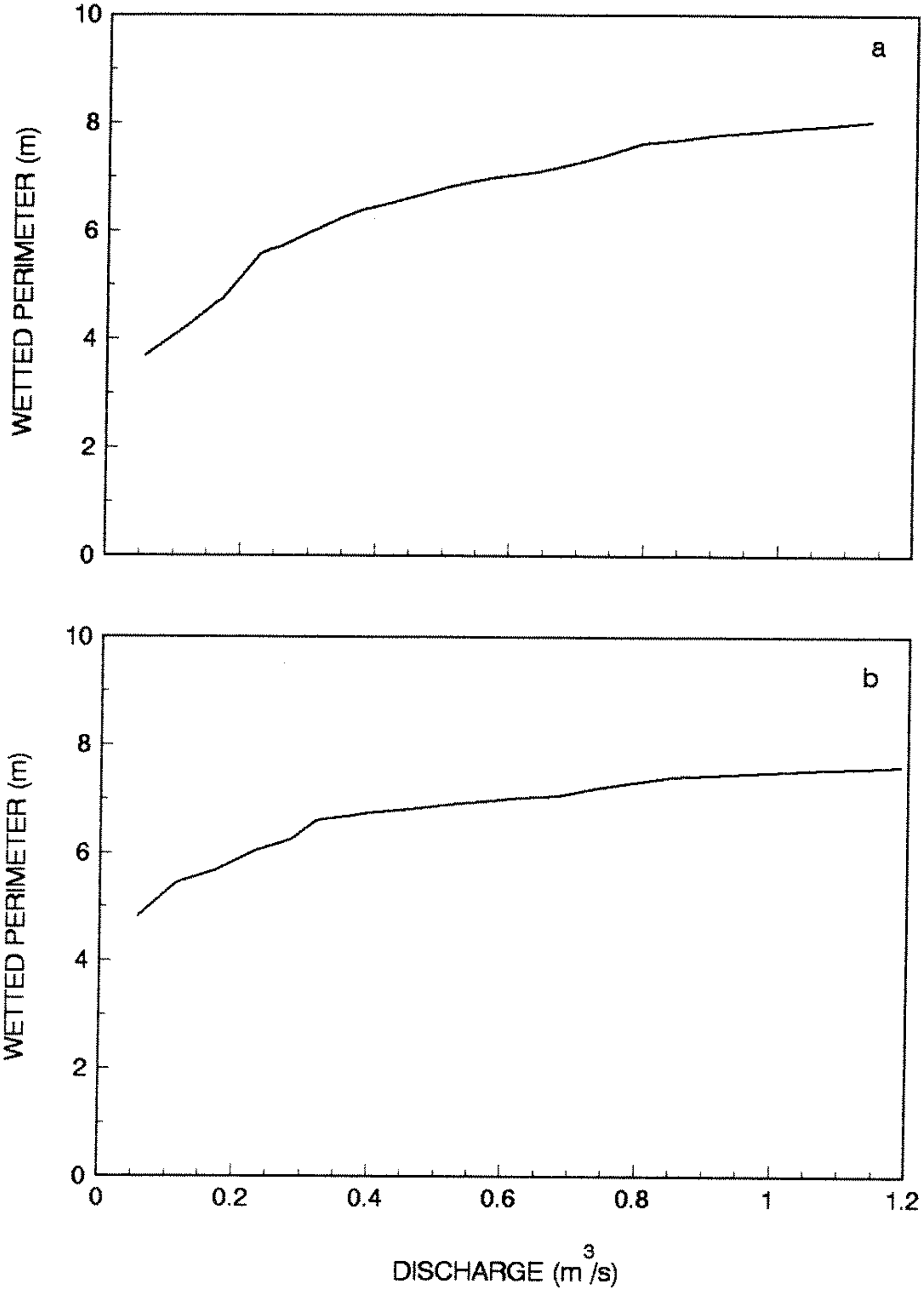

Figure 2.-Mean wetted perimeter-discharge relationships for the test (a) and reference (b) riffles in Bozeman Creek, July-September 1989.

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

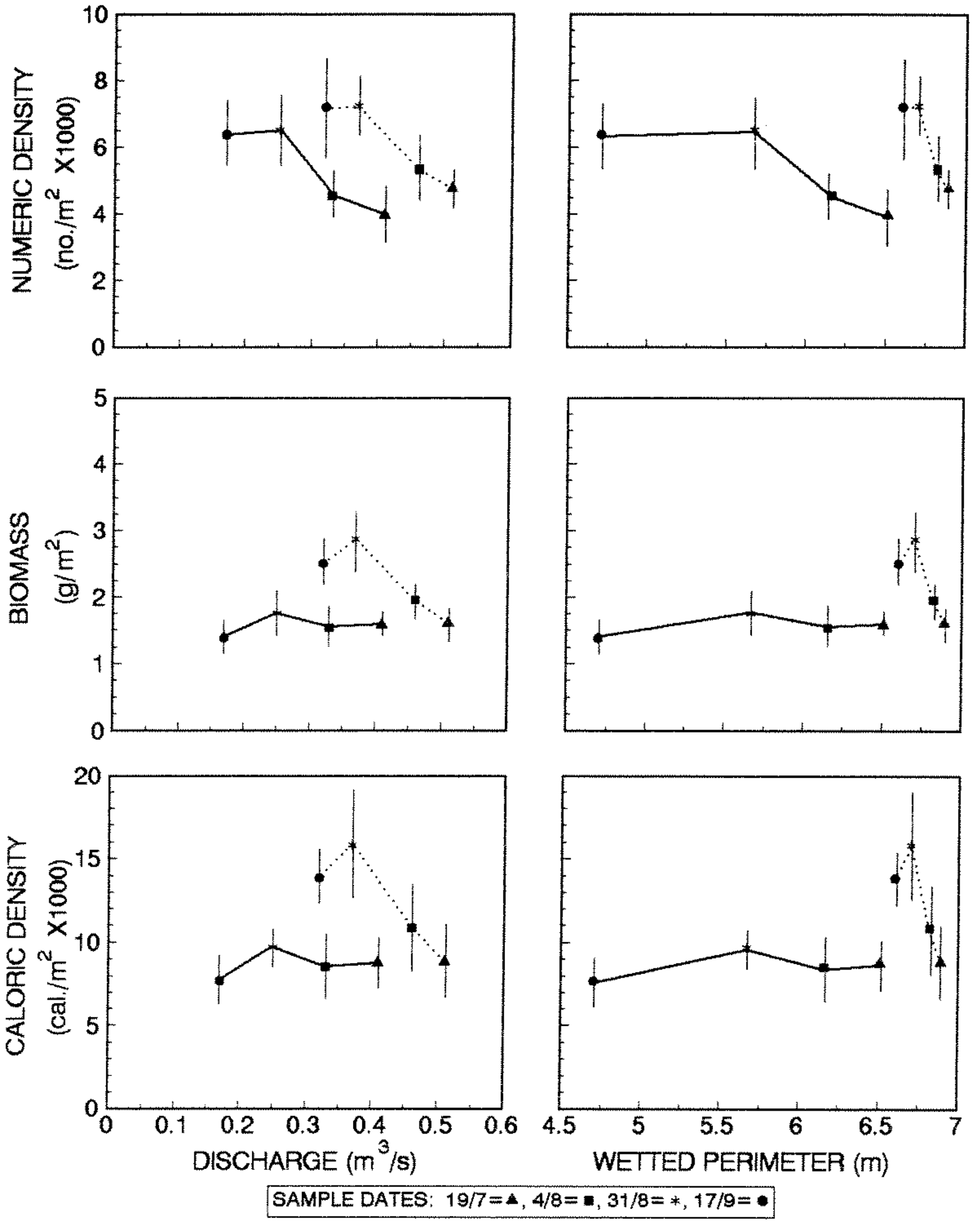

Figure 3.-Mean numeric and caloric density and biomass of total benthic taxa at the test (solid line) and reference (broken line) riffles relative to stream discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

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

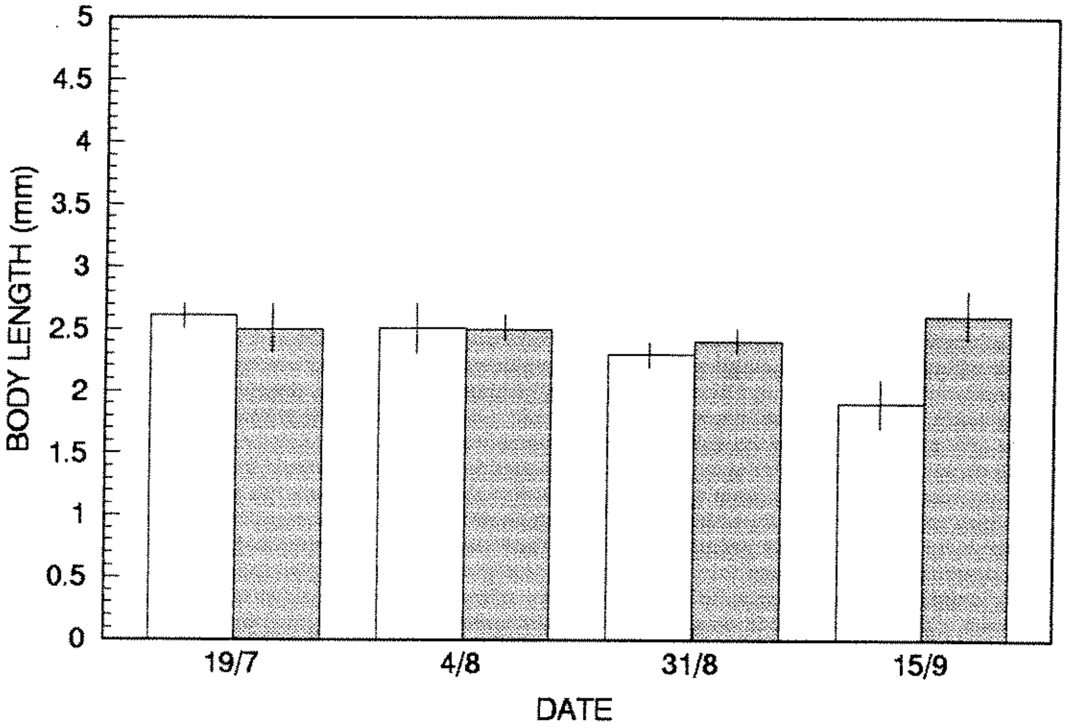

Figure 4.-Mean body length of total benthic taxa at the test (open bars) and reference (shaded bars) riffles on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

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

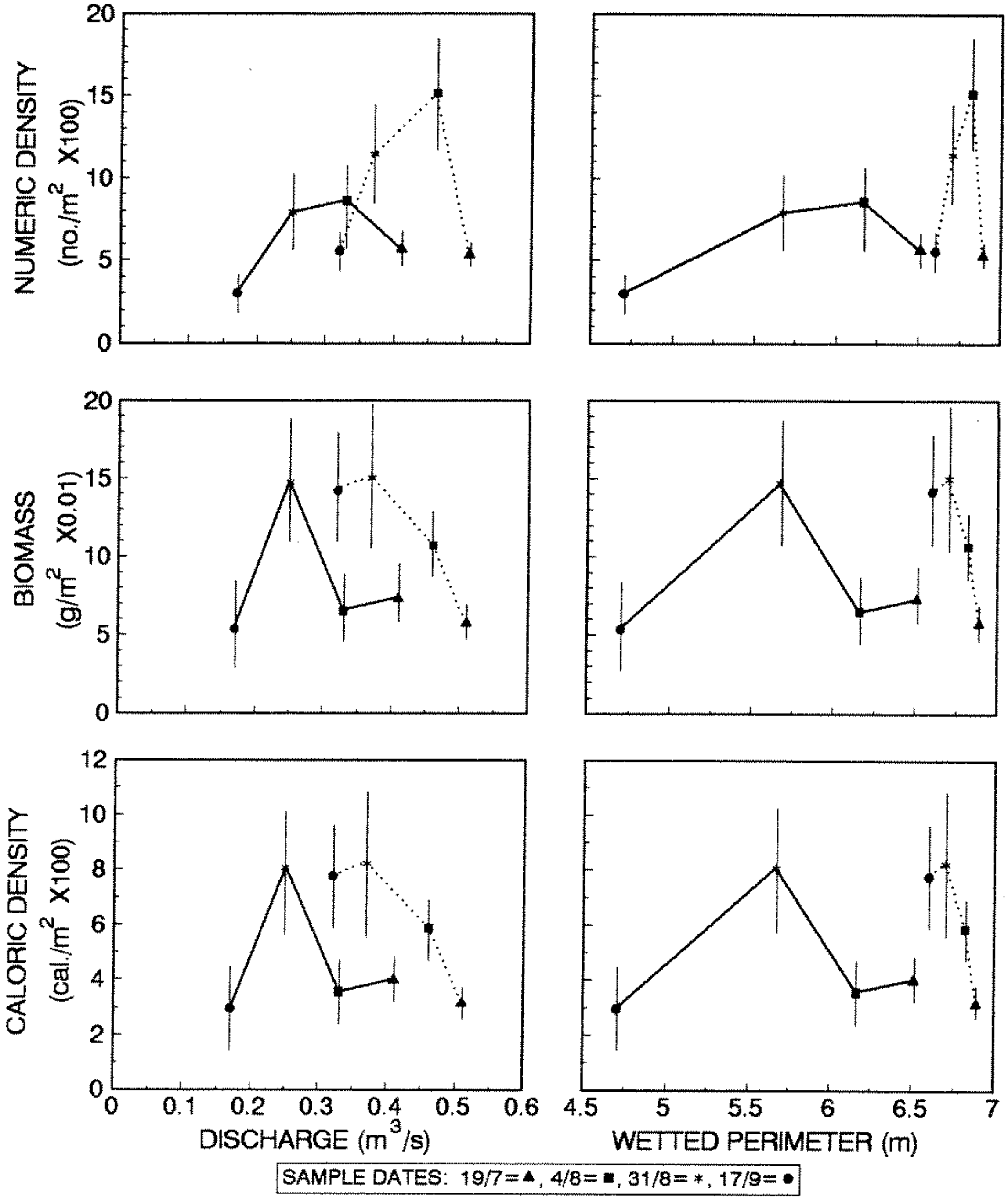

Figure 5.-Mean numeric and caloric density and biomass of *Baetis* spp. in benthic samples at the test (solid line) and reference (broken line) riffles relative to stream discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

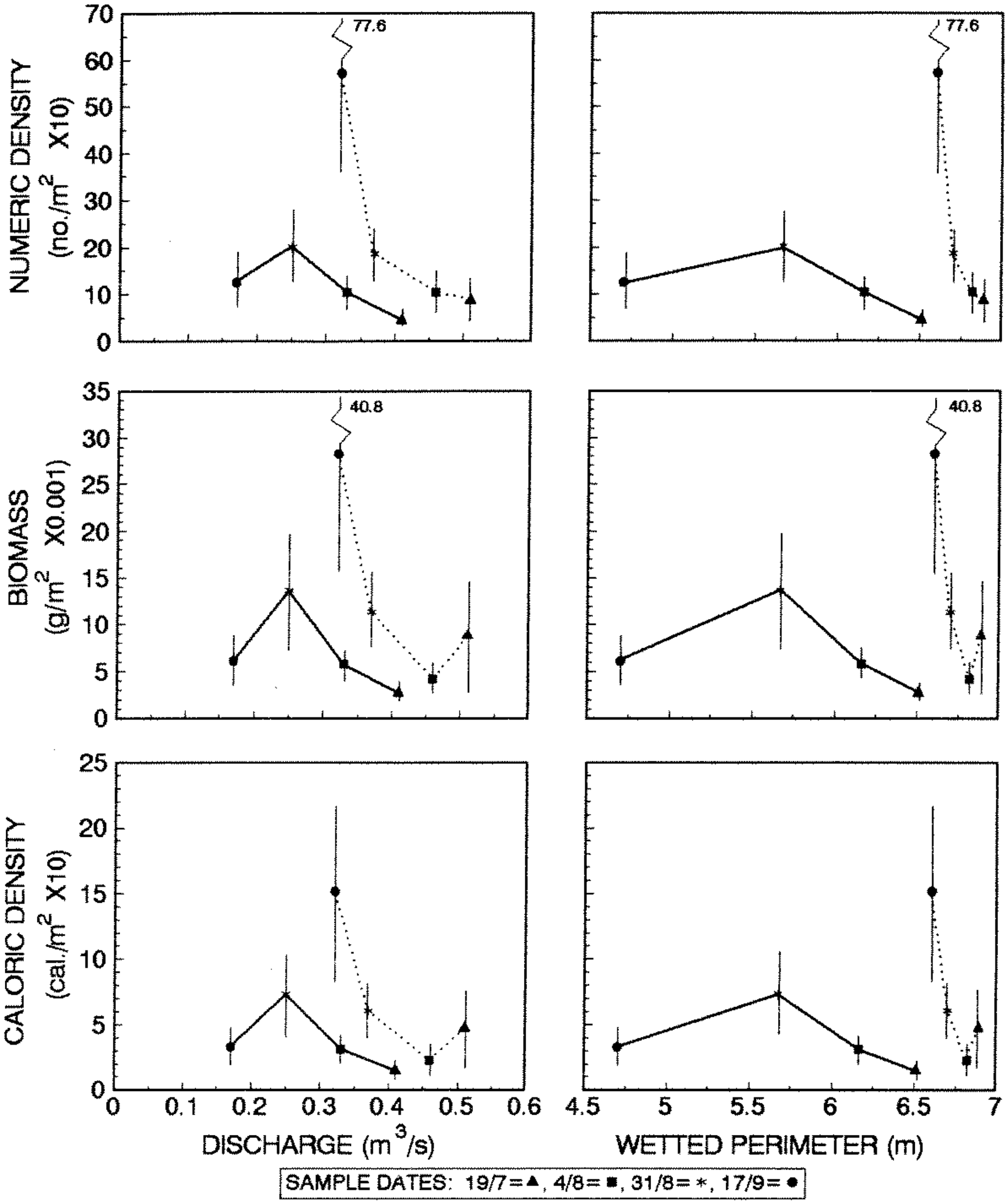

Figure 6.-Mean numeric and caloric density and biomass of *Zapada* spp. in benthic samples at the test (solid line) and reference (broken line) riffles relative to stream discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

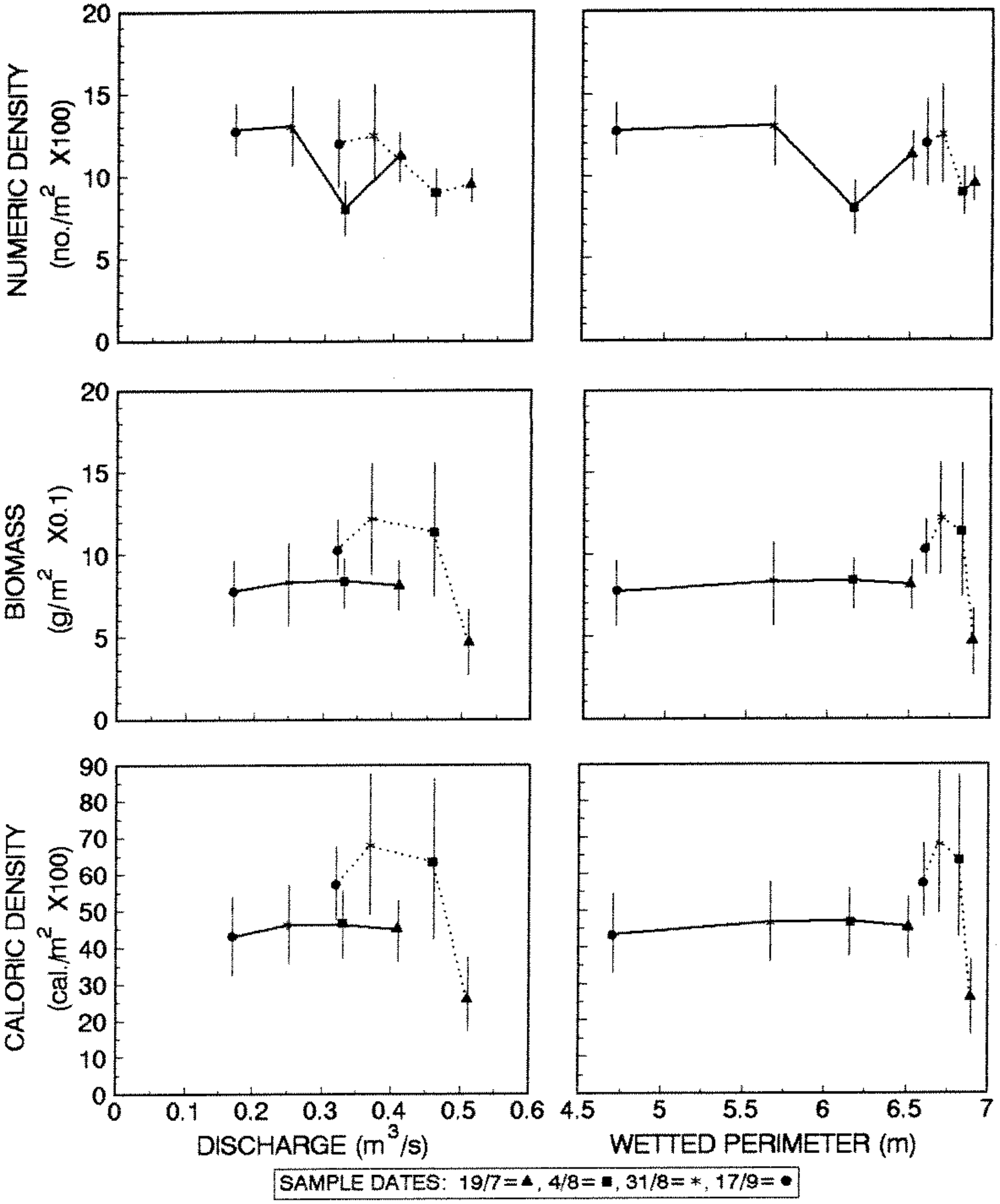

Figure 7.-Mean numeric and caloric density and biomass of elmid larvae in benthic samples at the test (solid line) and reference (broken line) riffles relative to stream discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

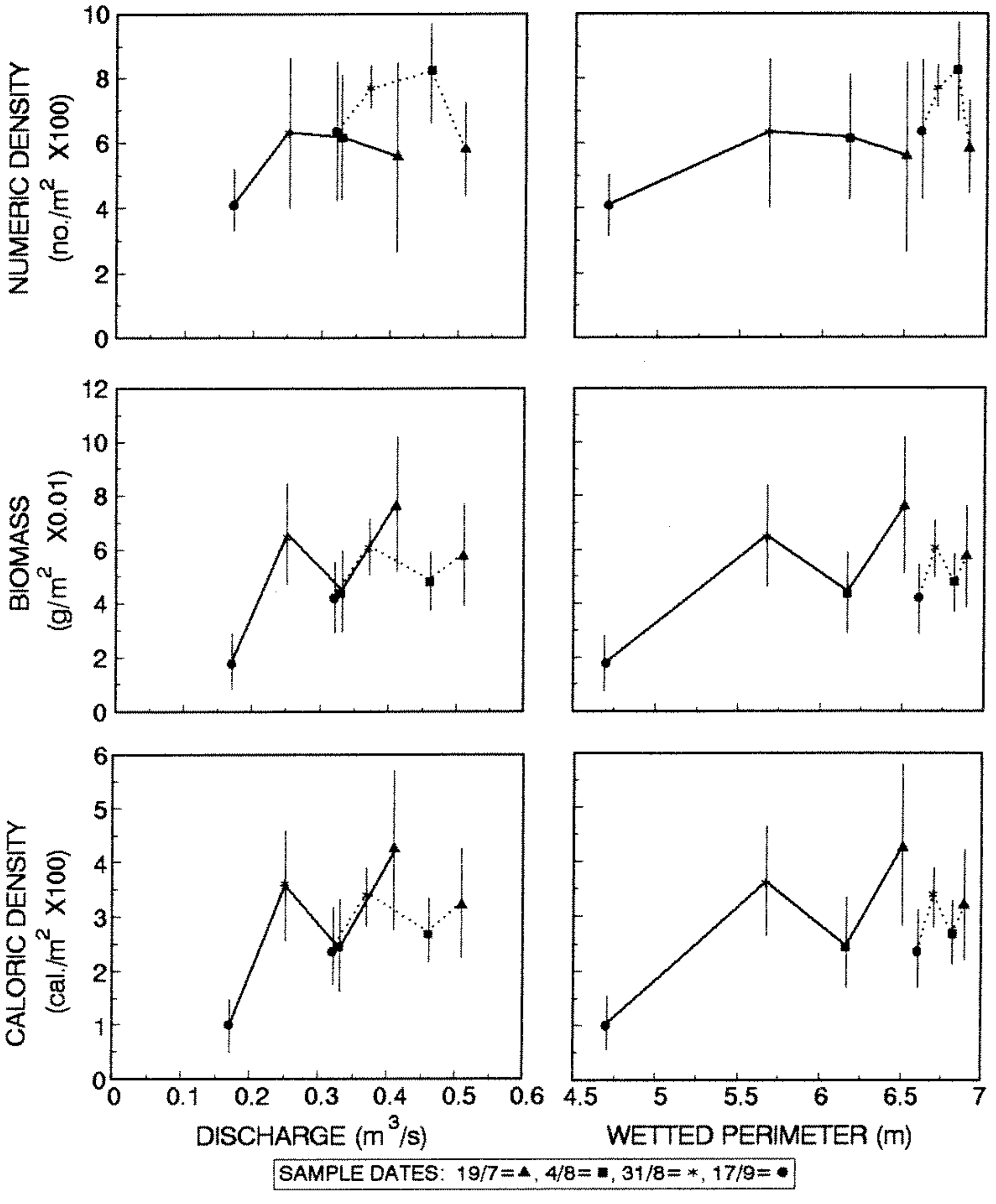

Figure 8.-Mean numeric and caloric density and biomass of Chironomidae in benthic samples at the test (solid line) and reference (broken line) riffles relative to stream discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

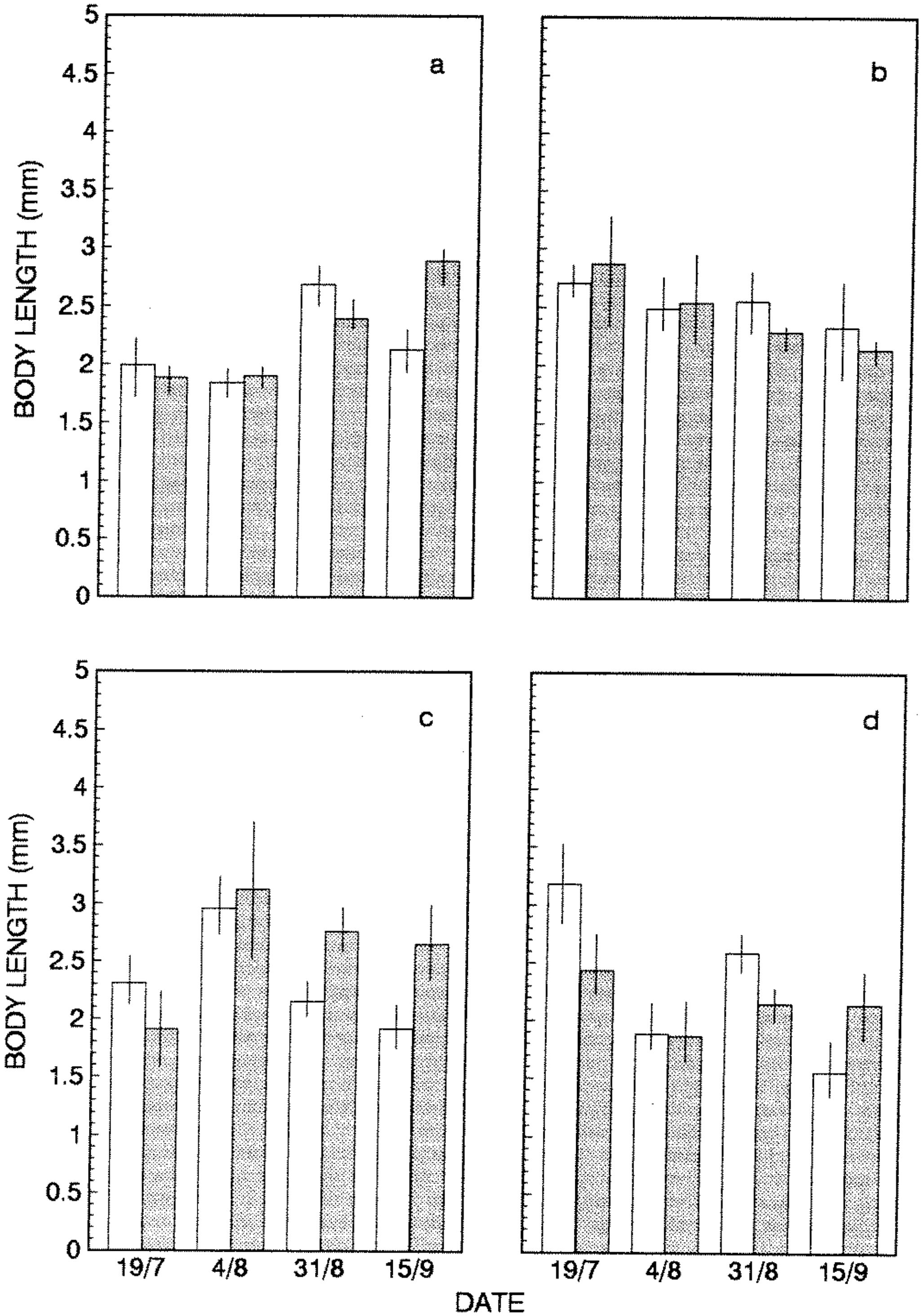

Figure 9.-Mean body length of *Baetis* spp. (a), *Zapada* spp. (b), elmid larvae (c), and Chironomidae (d) in benthic samples at the test (open bars) and reference (shaded bars) riffles on four sample dates in Bozeman Creek, July-September 1989. Vertical bars±1 SE, N=5.

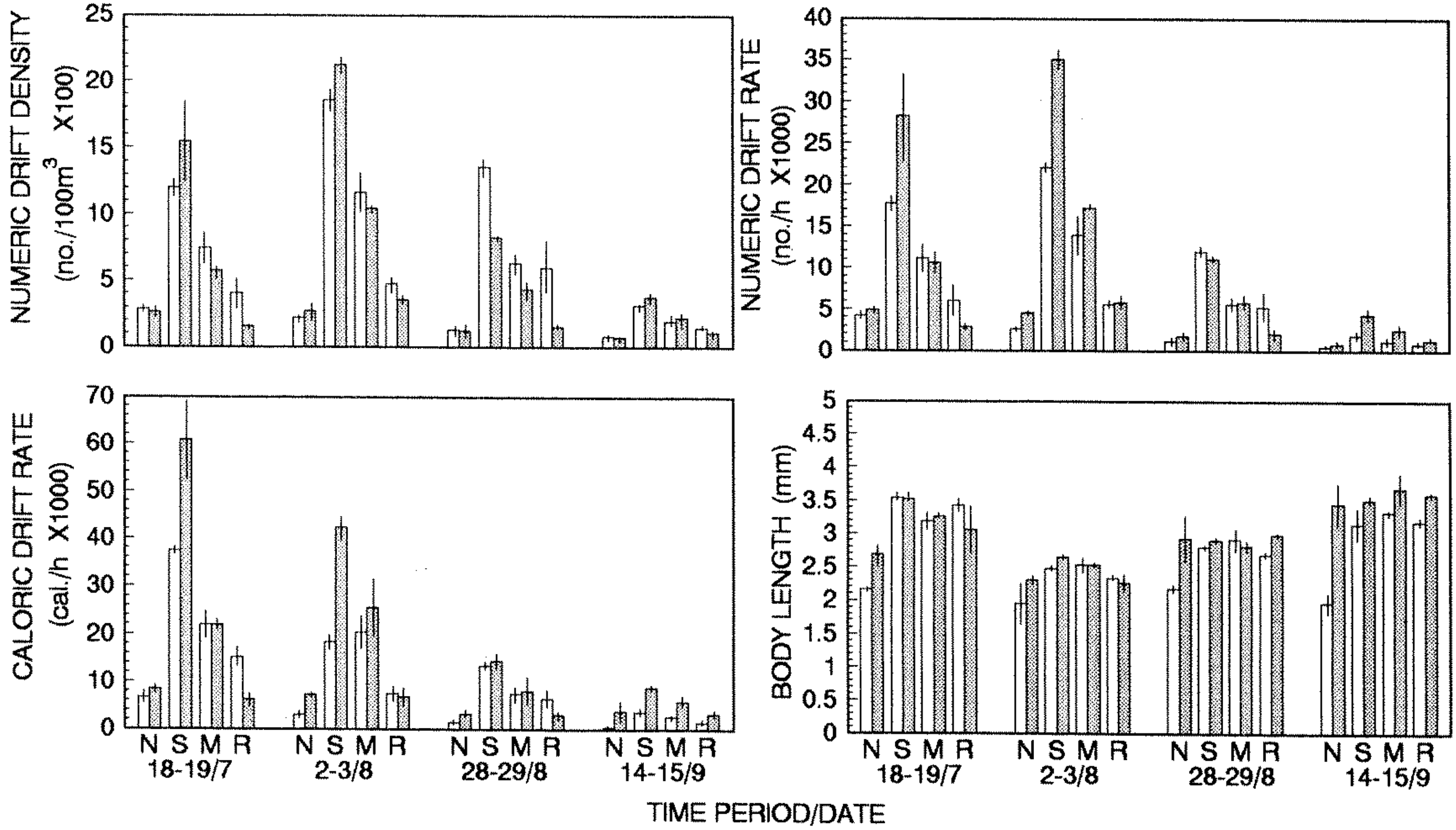

Figure 10.-Mean drift density, numeric and caloric drift rate, and mean body length by time period (N-noon, S-sunset, M-midnight, R-sunrise) on four sample dates for total taxa at the test (open bars) and reference (shaded bars) riffles in Bozeman Creek, July-September 1989. Vertical bars are ranges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

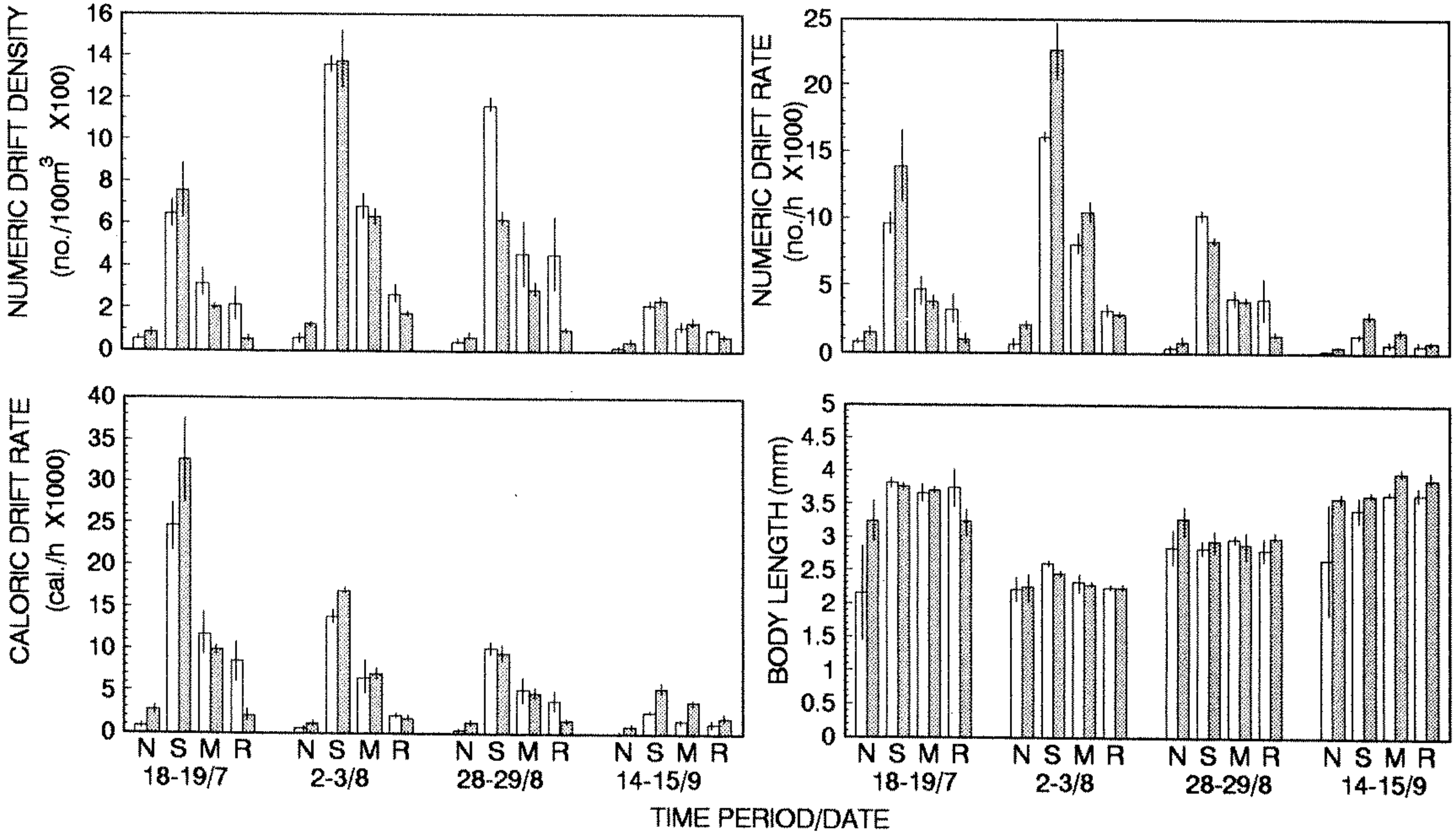

Figure 11.-Mean drift density, numeric and caloric drift rate, and mean body length by time period (N-noon, S-sunset, M-midnight, R-sunrise) on four sample dates for *Baetis* spp. at the test (open bars) and reference (shaded bars) riffles in Bozeman Creek, July-September 1989. Vertical bars are ranges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

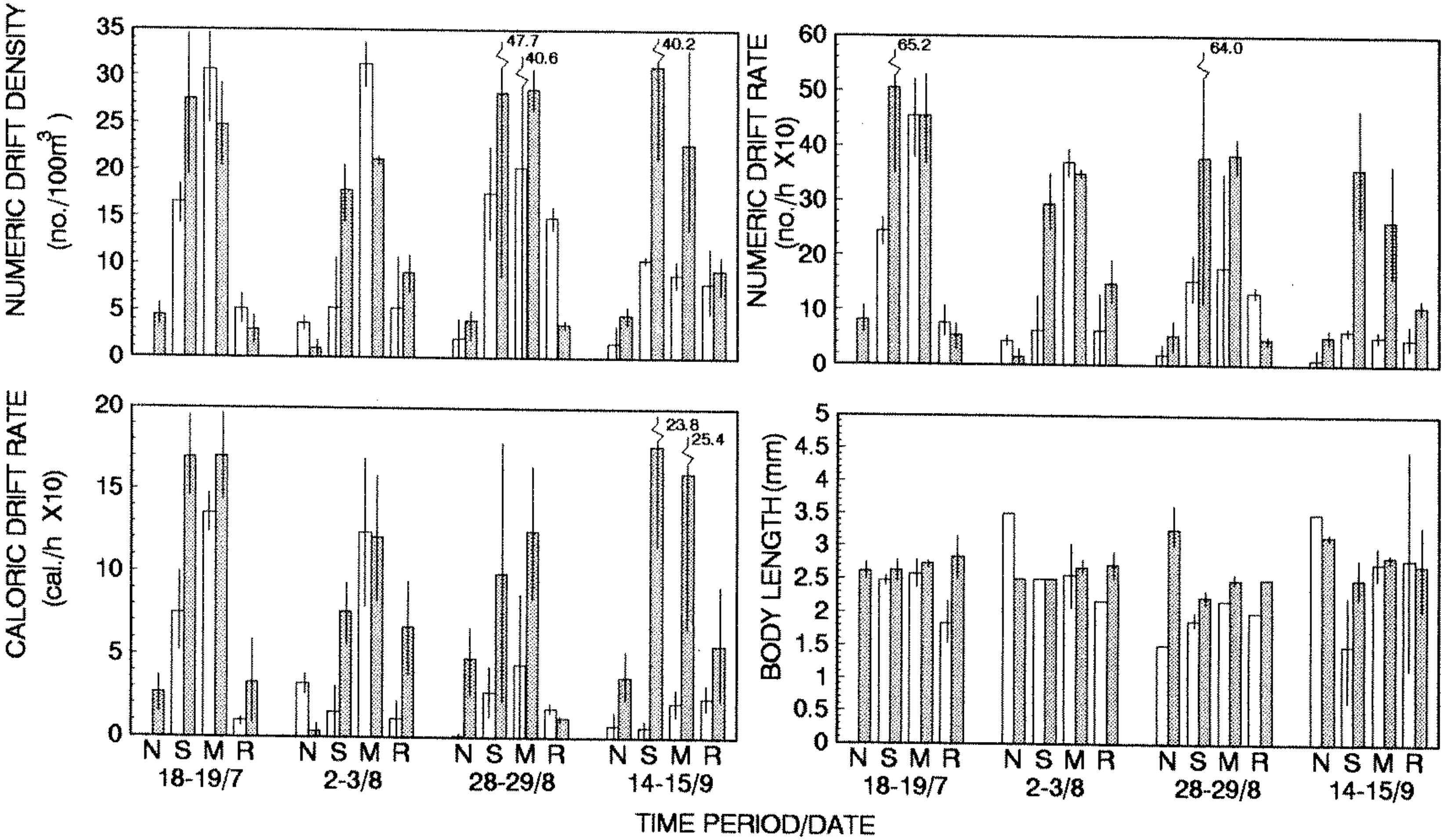

Figure 12.-Mean drift density, numeric and caloric drift rate, and mean body length by time period (N-noon, S-sunset, M-midnight, R-sunrise) on four sample dates for *Zapada* spp. at the test (open bars) and reference (shaded bars) riffles in Bozeman Creek, July-September 1989. Vertical bars are ranges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

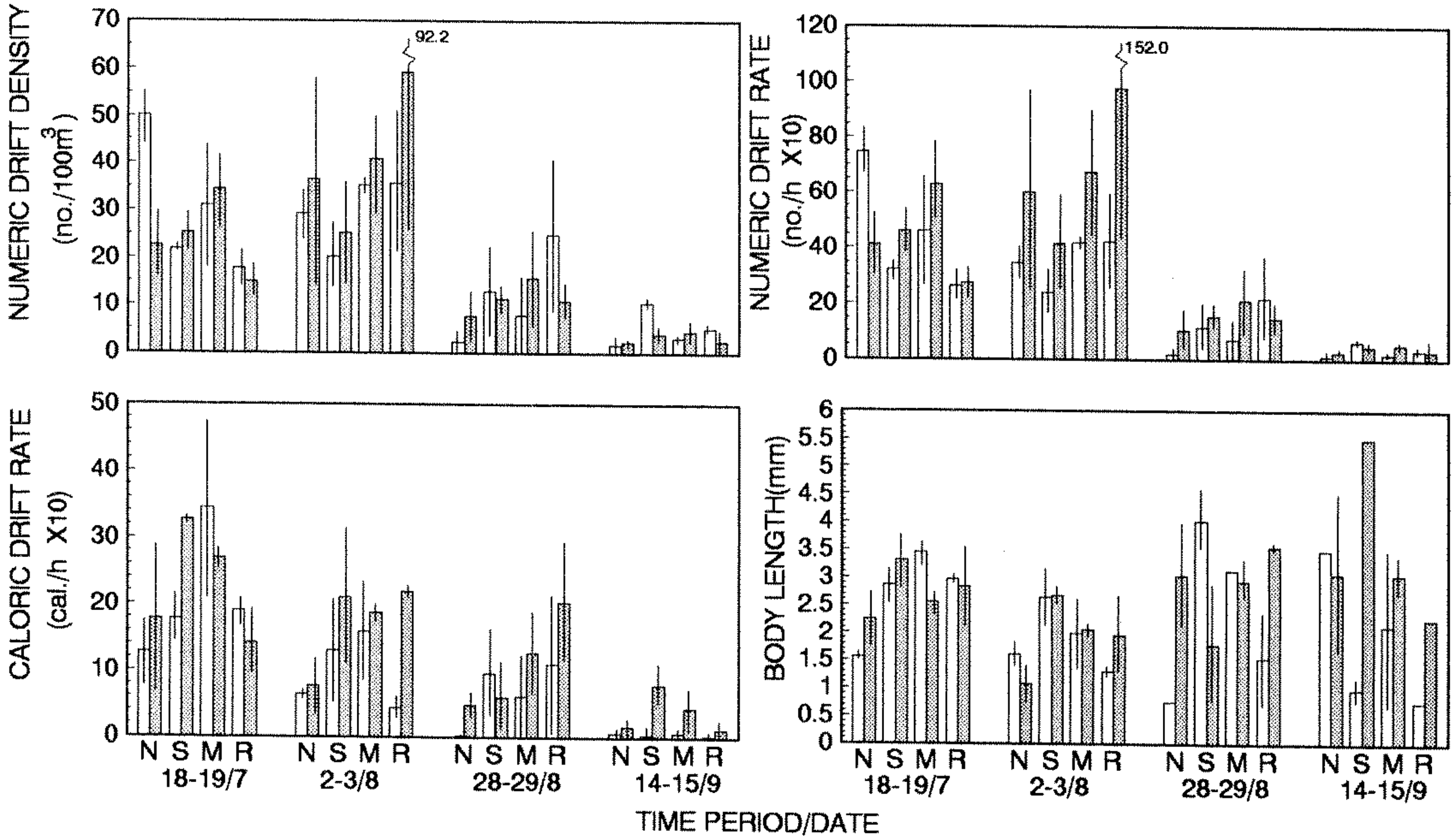

Figure 13.-Mean drift density, numeric and caloric drift rate, and mean body length by time period (N-noon, S-sunset, M-midnight, R-sunrise) on four sample dates for Chironomidae at the test (open bars) and reference (shaded bars) riffles in Bozeman Creek, July-September 1989. Vertical bars are ranges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

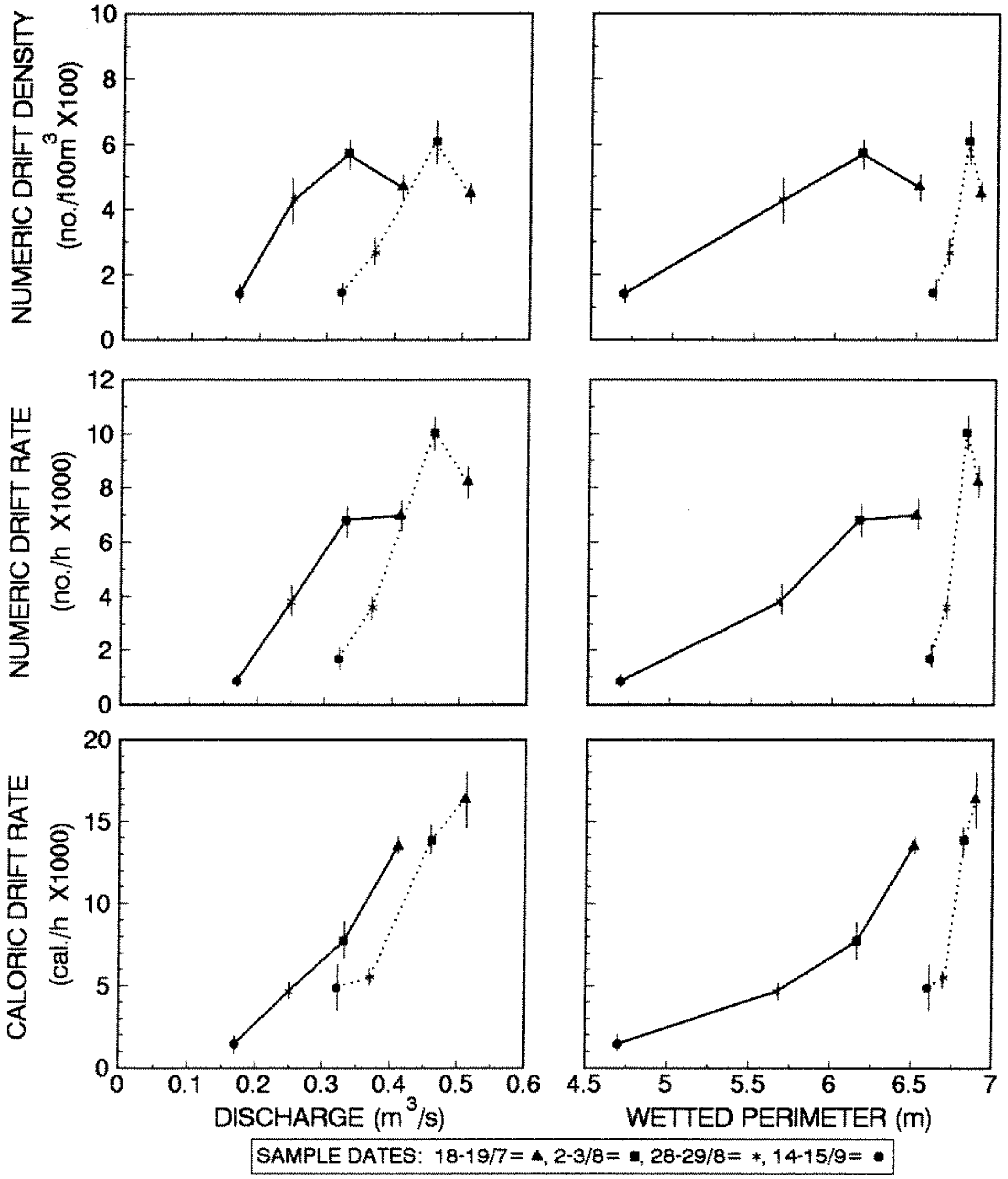

Figure 14.-Mean daily numeric drift density, and numeric and caloric drift rate for total taxa at the test (solid line) and reference (broken line) relative to discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

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).

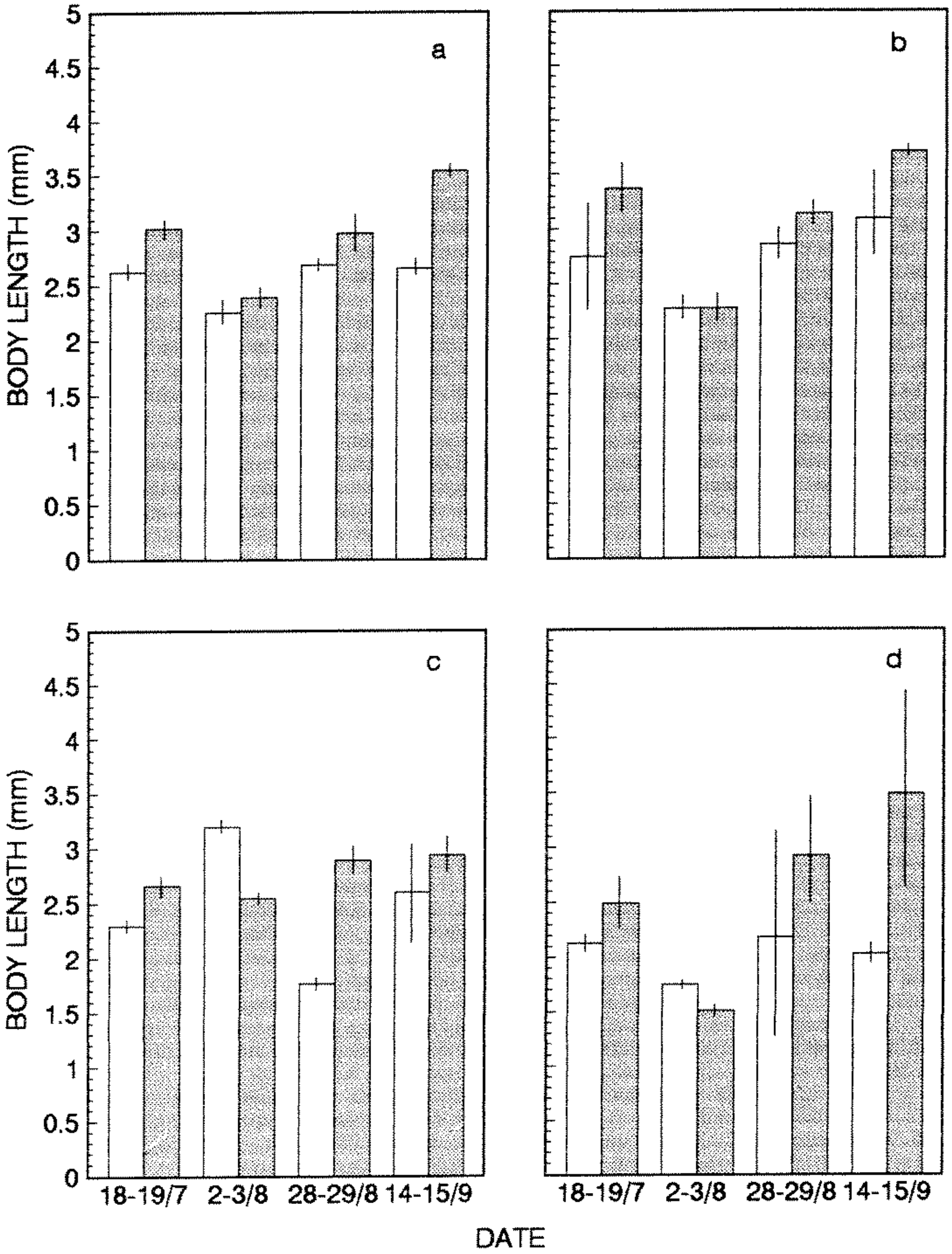

Figure 15.-Mean body length of total taxa (a), *Baetis* spp. (b), *Zapada* spp. (c), and Chironomidae (d) for daily drift at the test (open bars) and reference (shaded bars) riffles on four sample dates in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

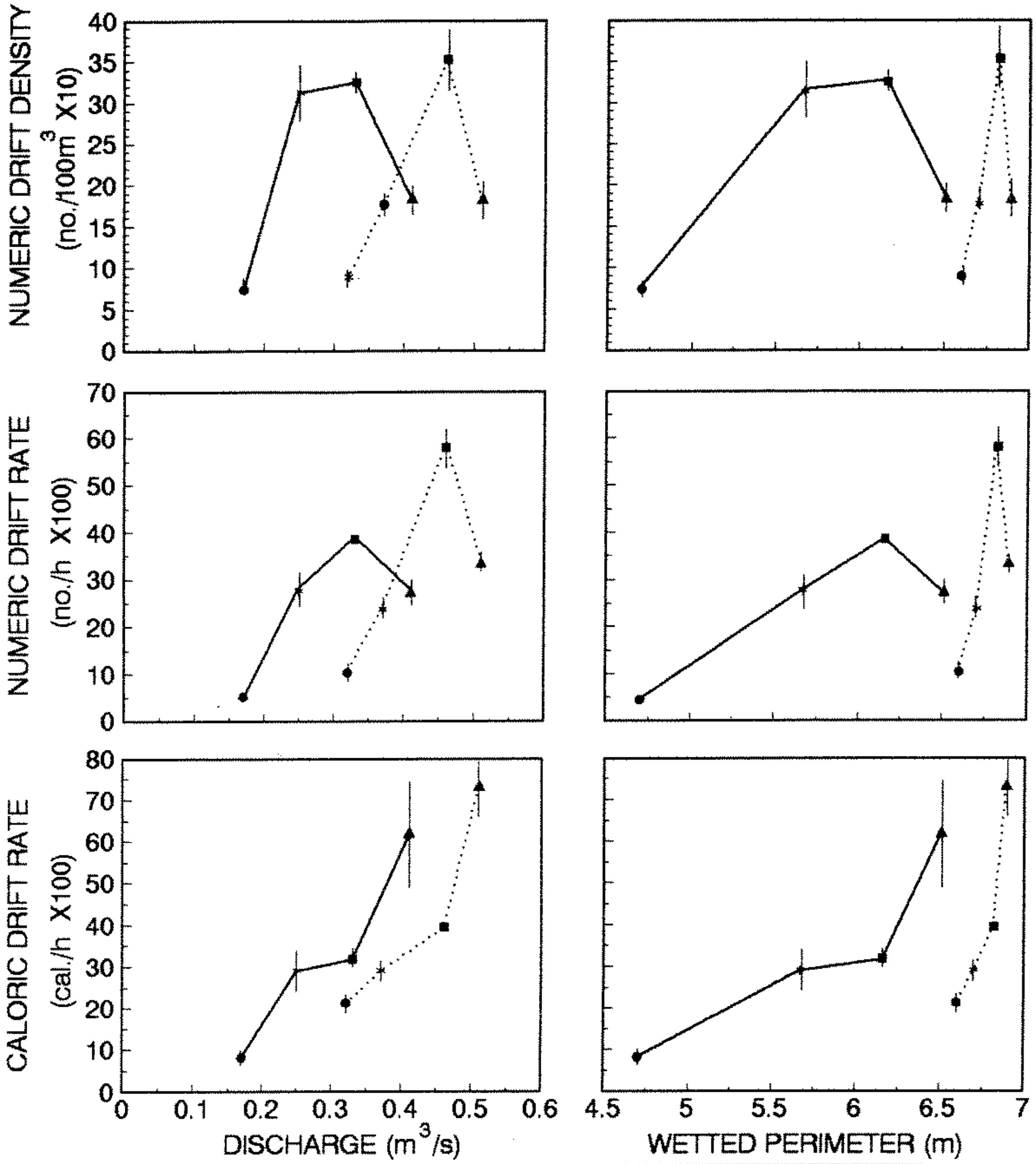

Figure 16.-Mean daily numeric drift density, and numeric and caloric drift rate for *Baetis* spp. at the test (solid line) and reference (broken line) riffles relative to discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

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

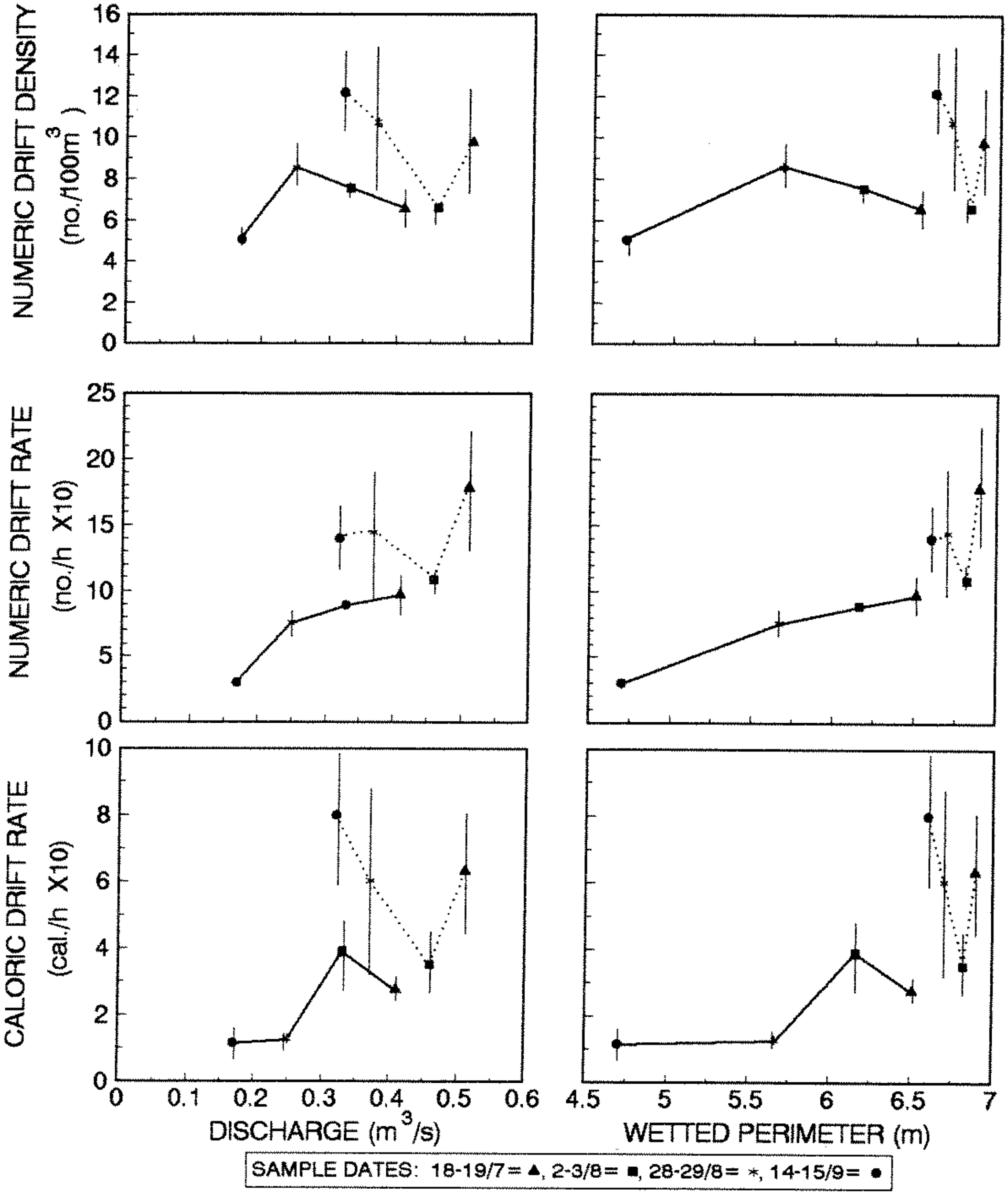

Figure 17.-Mean daily numeric drift density, and numeric and caloric drift rate for *Zapada* spp. at the test (solid line) and reference (broken line)riffles relative to discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

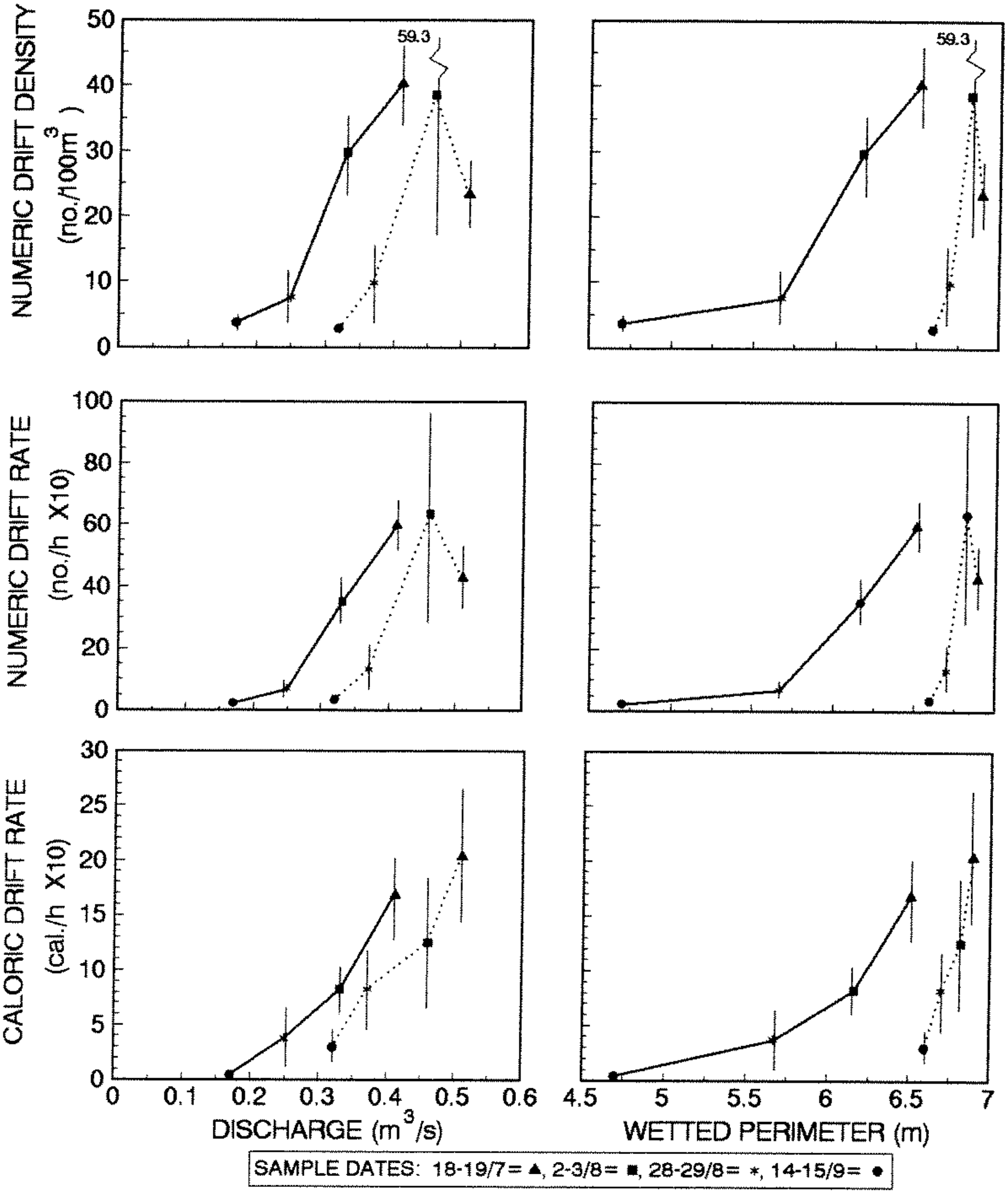

Figure 18.-Mean daily numeric drift density, and numeric and caloric drift rate for Chironomidae at the test (solid line) and reference (broken line)riffles relative to discharge and wetted perimeter on four sample dates in Bozeman Creek, July-September 1989. Vertical bars are ranges for paired driftnets.

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

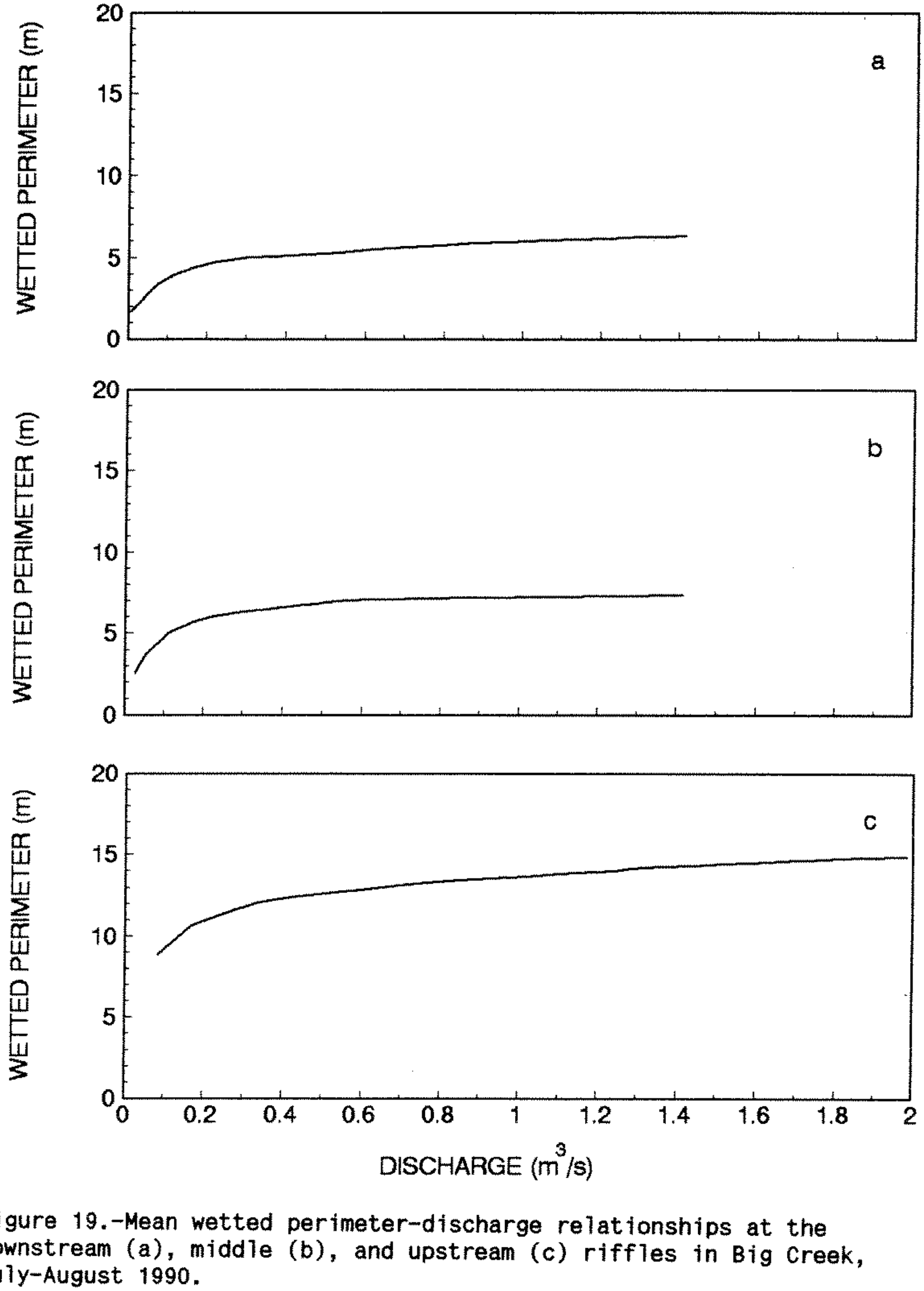

Figure 19.-Mean wetted perimeter-discharge relationships at the downstream (a), middle (b), and upstream (c) riffles in Big Creek, July-August 1990.

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

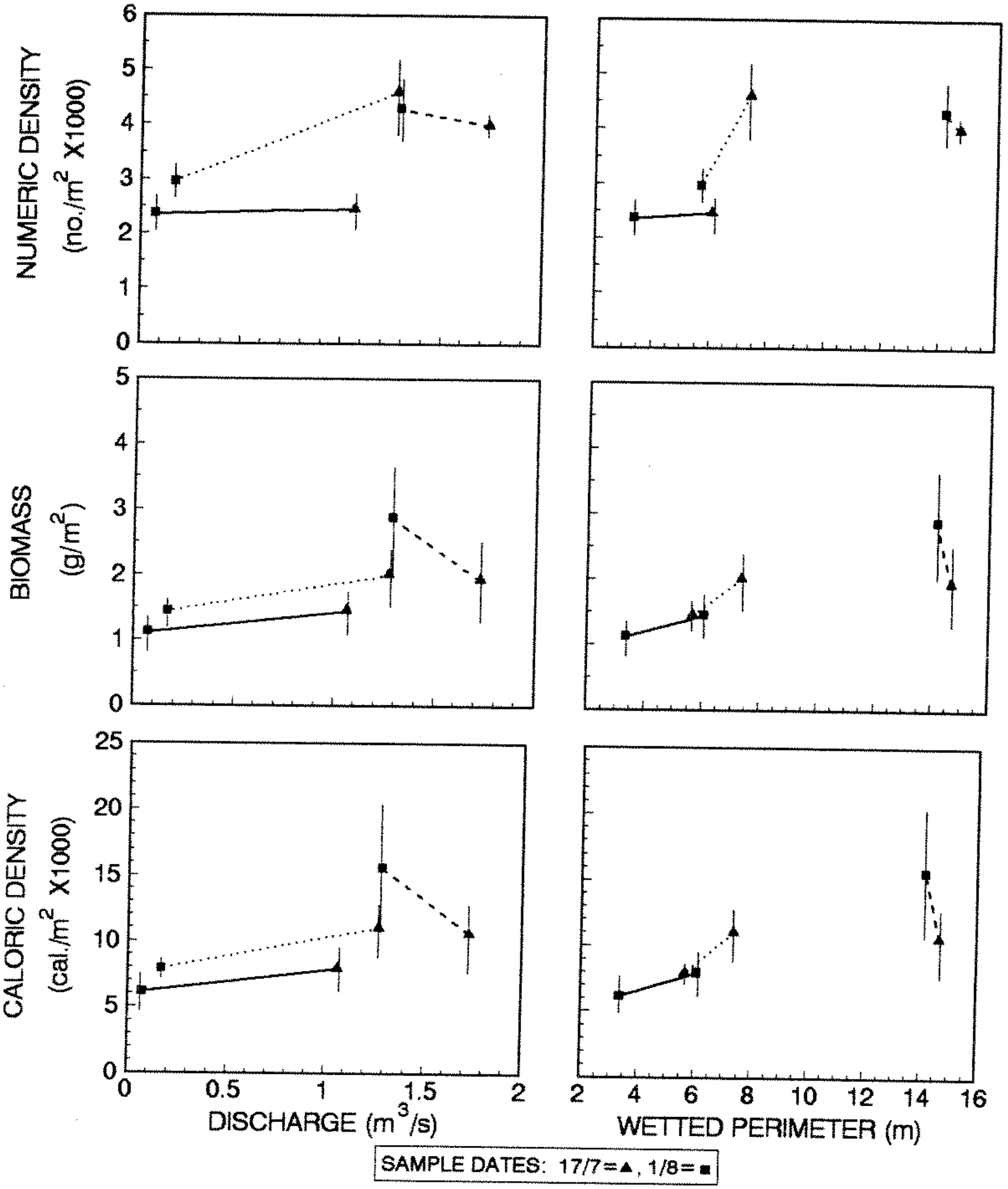

Figure 20.-Mean numeric and caloric density and biomass of total benthic taxa at the downstream (solid line), middle (dotted line), and upstream (dashed line) riffles relative to stream discharge and wetted perimeter on two sample dates in Big Creek, July-September 1990. Vertical bars±1 SE, N=5.

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.

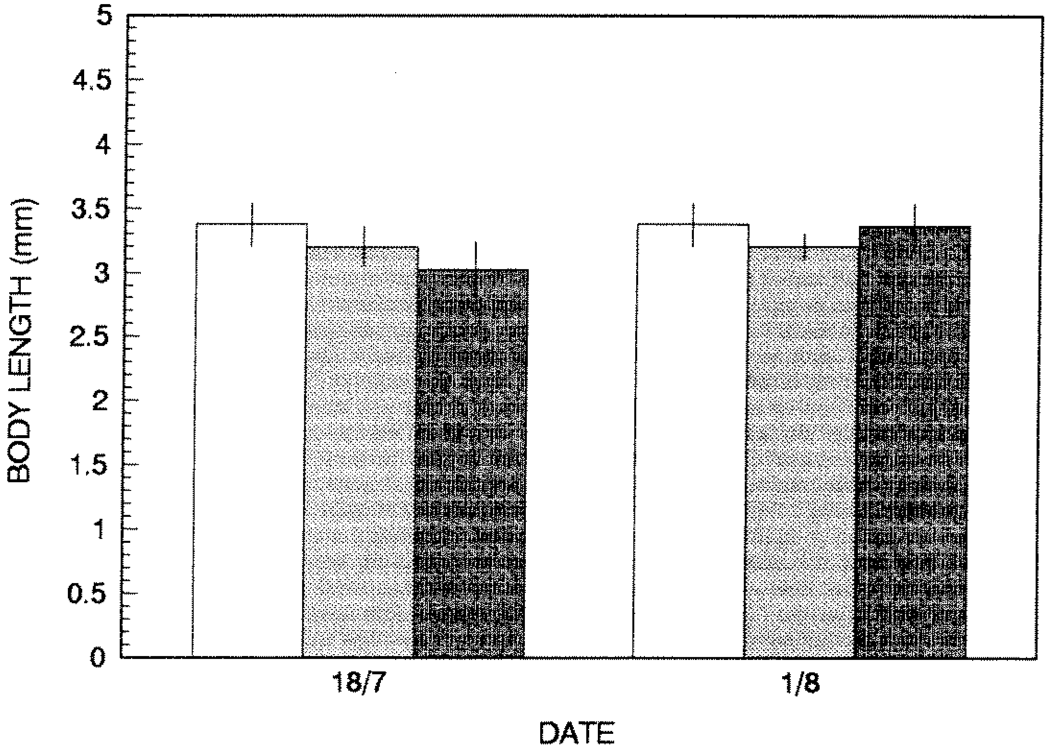

Figure 21.-Mean body length of total benthic taxa at the downstream (open bars), middle (light shaded bars), and upstream (dark shaded bars) riffles on two sample dates in Big Creek, July-August 1990. Vertical bars±1 SE, N=5.

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

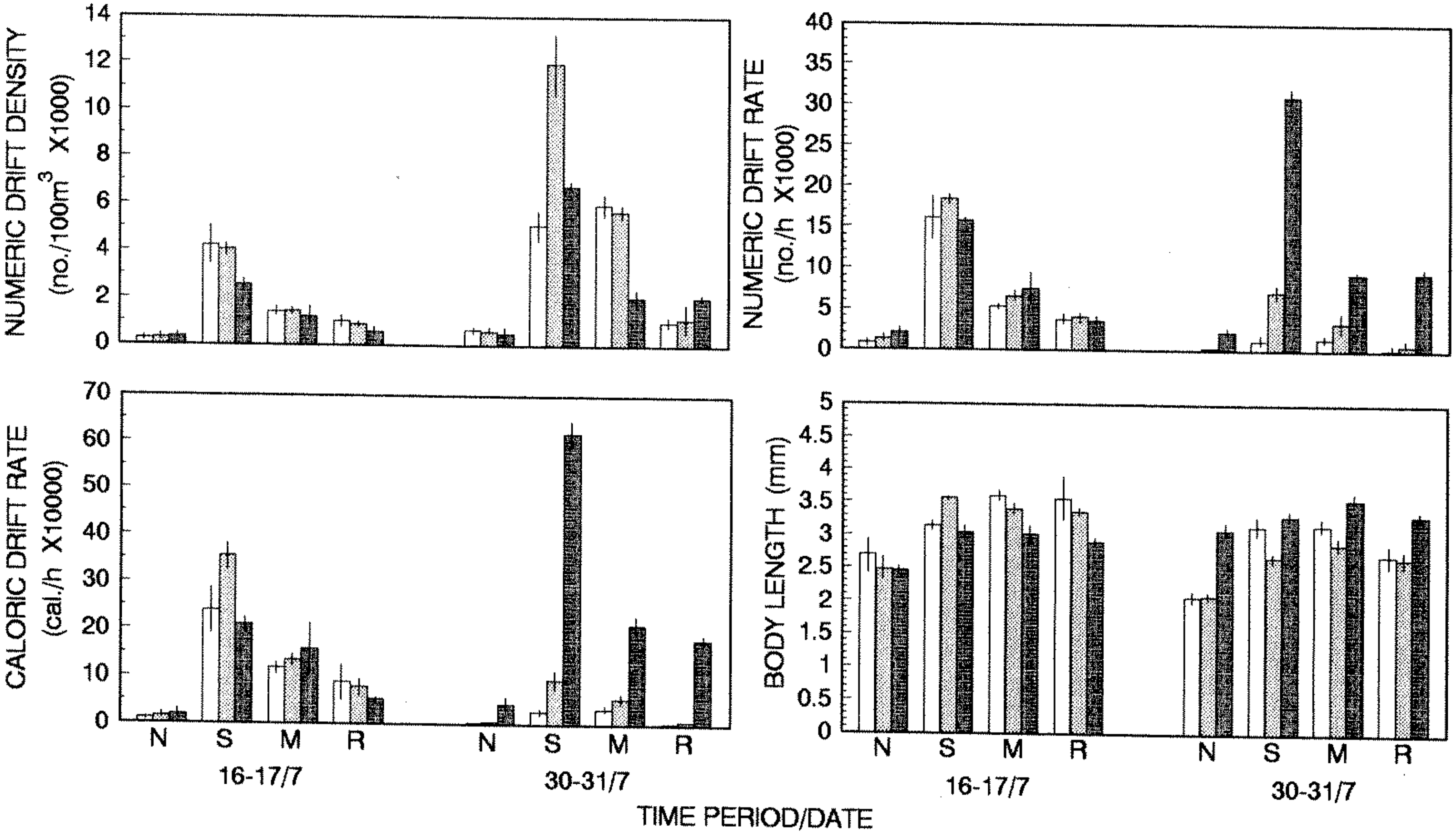

Figure 22.-Mean drift density, numeric and caloric drift rate, and mean body length by time period (N-noon, S-sunset, M-midnight, R-sunrise) on two sample dates for total taxa at the downstream (open bars), middle (light shaded bars), and upstream (dark shaded bars) riffles in Big Creek, July 1990. Vertical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

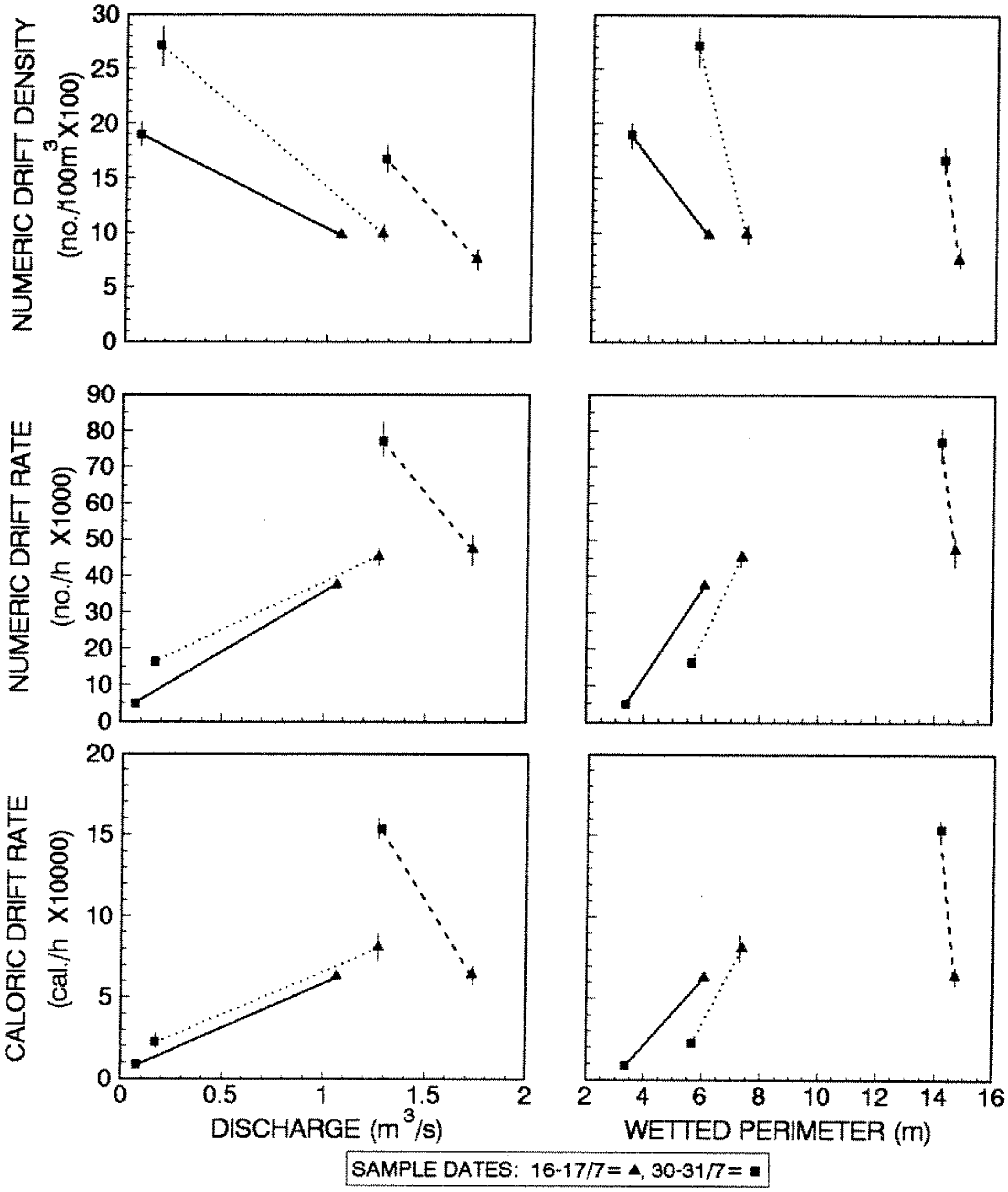

Figure 23.-Mean daily numeric drift density, and numeric and caloric drift rate for total taxa at the downstream (solid line), middle (dotted line), and upstream (dashed line) riffles relative to stream discharge and wetted perimeter on tow sample dates in Big Creek, July 1990. Vertical bars are ranges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

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

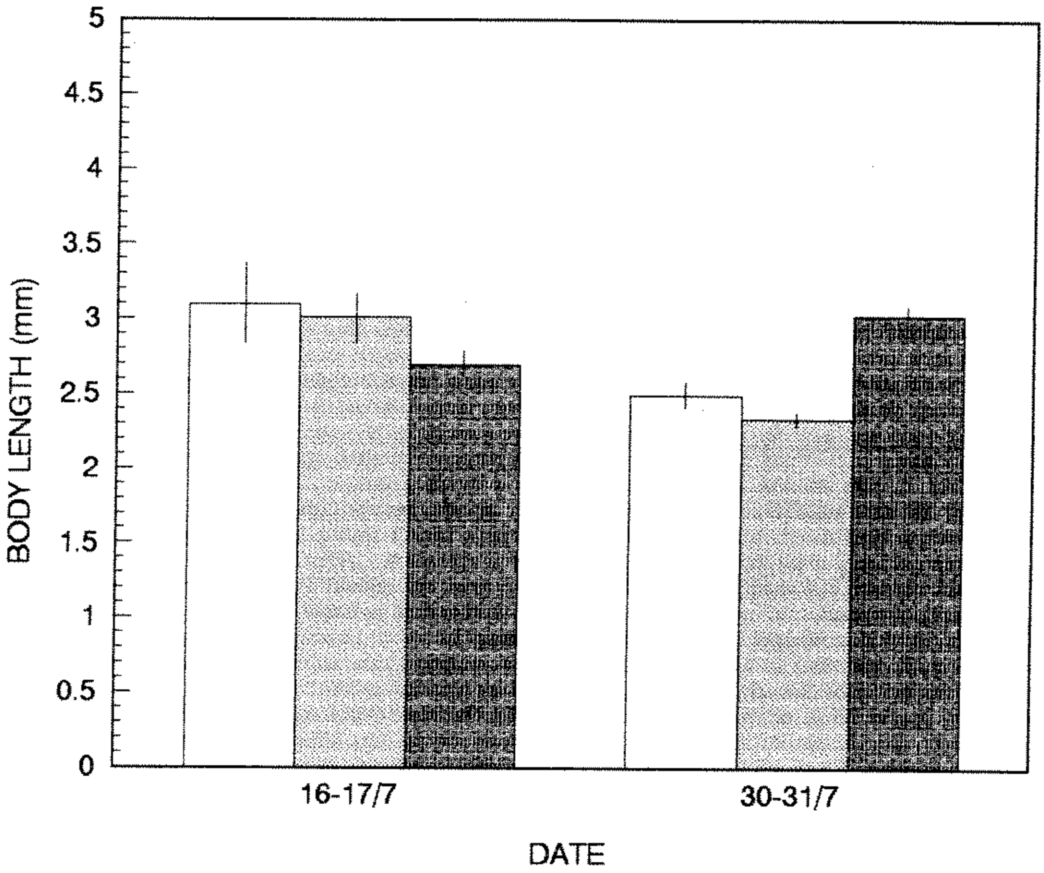

Figure 24.-Mean body length of total taxa for mean daily drift at the downstream (open bars), middle (light shaded bars), and upstream (dark shaded bars) riffles on two sample dates in Big Creek, July 1990. Vertical bars are ranges for paired driftnets.

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

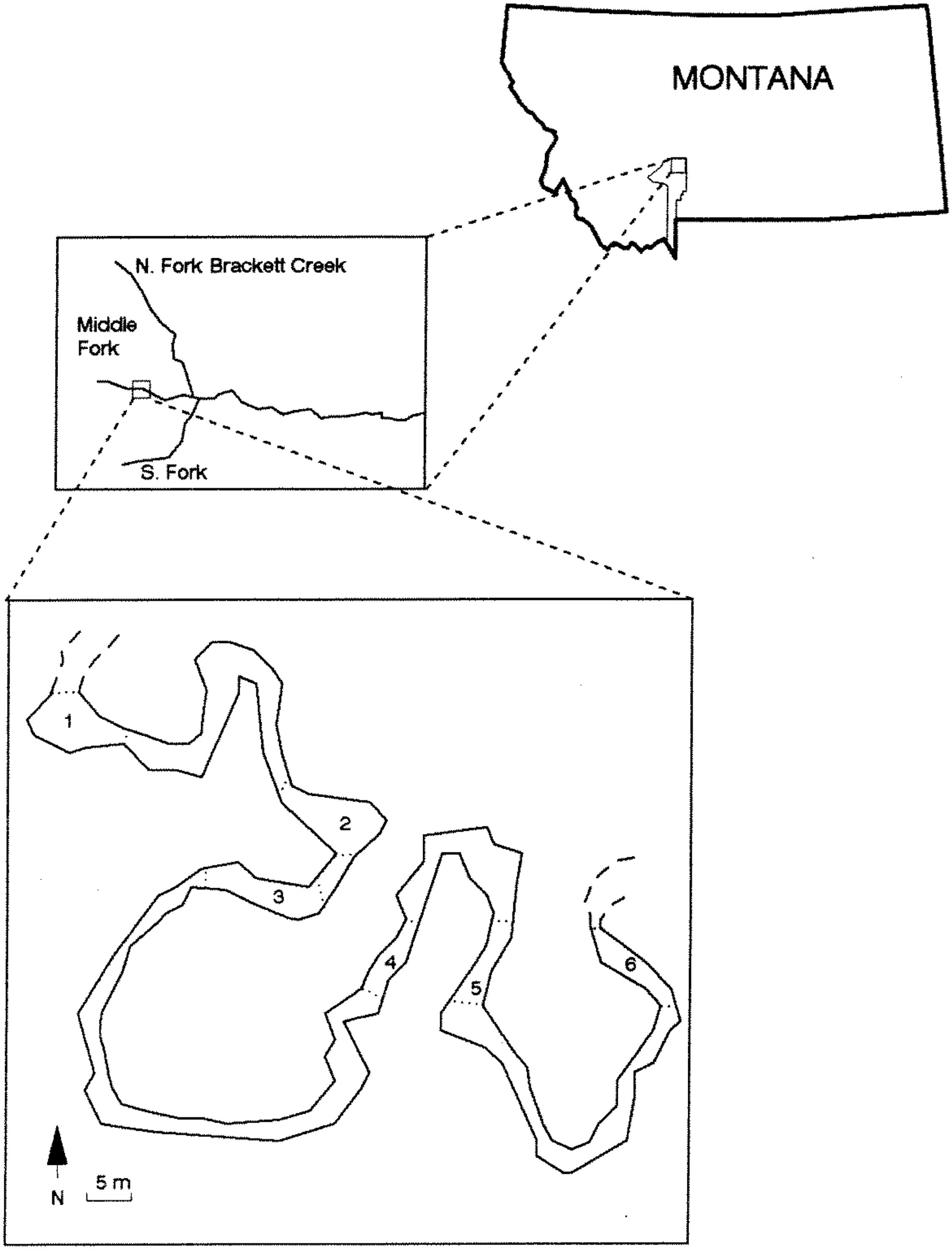

Figure 25.-Location of study site and enclosures (#1-6) in Brackett Creek, July-September 1989 and 1990.

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

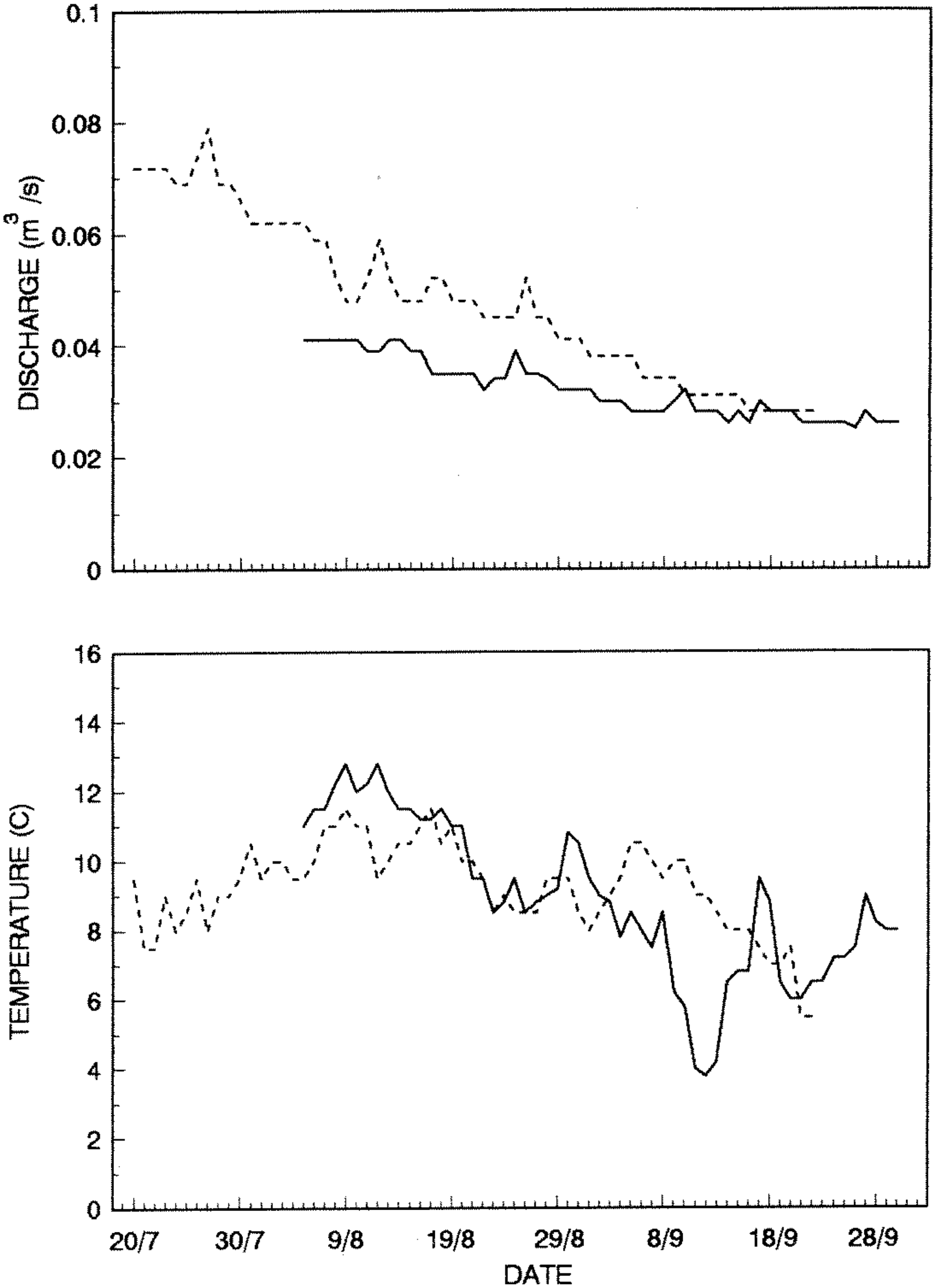

Figure 26.-Stream discharge and mean daily water temperature for Brackett Creek in 1989 (solid lines) and 1990 (broken lines).

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).

Invertebrate Drift

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] Total (m^2)	UCB (m^2)	OHV (m^2)	ISD (m^2)	%	Volume (m^3)	Area 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

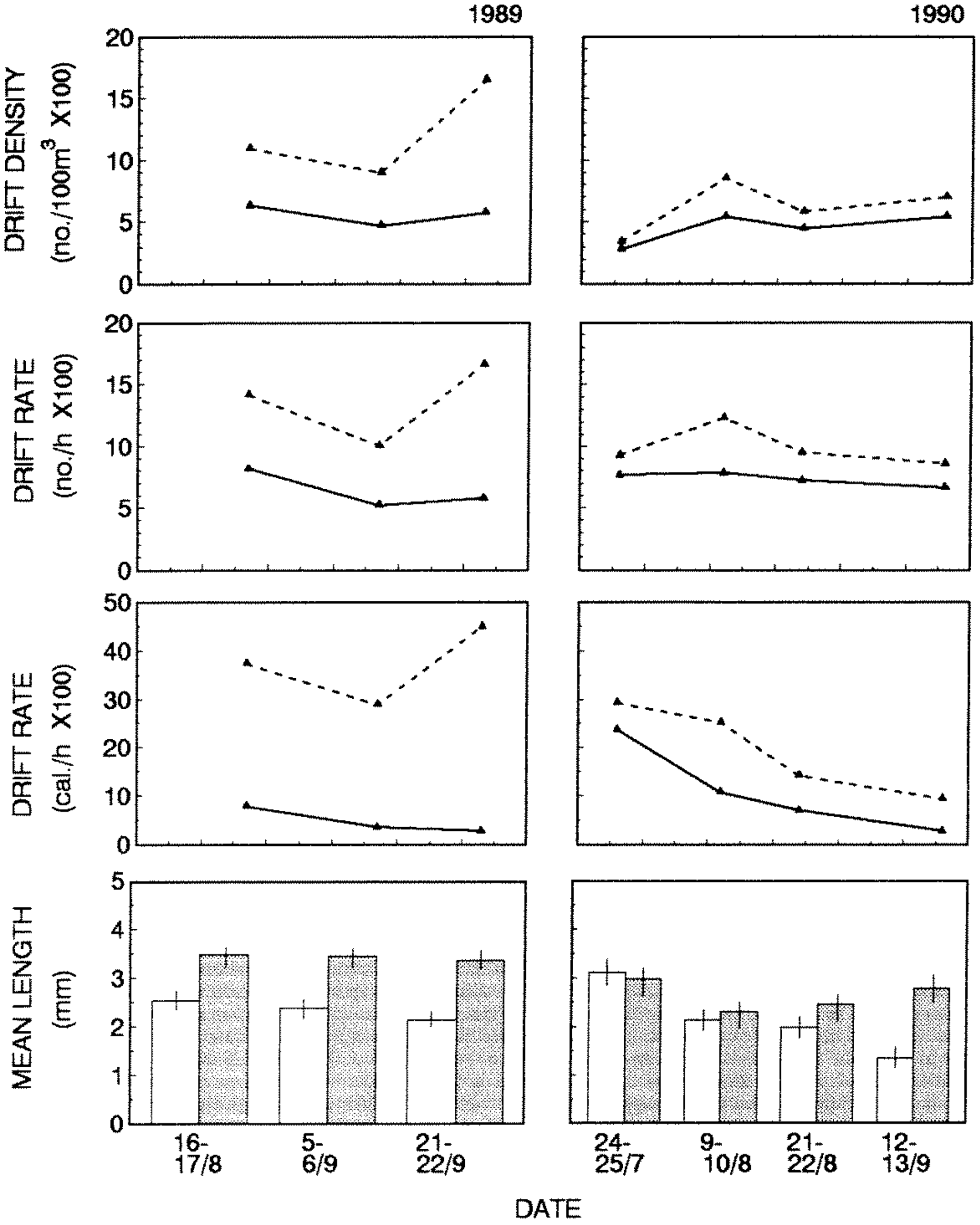

Figure 27.-Mean drift density and rate (numeric and caloric) of aquatic taxa (solid lines) and all taxa (broken lines) and mean body length of aquatic taxa (open bars) and terrestrial taxa (shaded bars) in Brackett Creek, 1989 and 1990. N=5 in 1989, N=6 in 1990. Vertical bars±1 SE.

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;

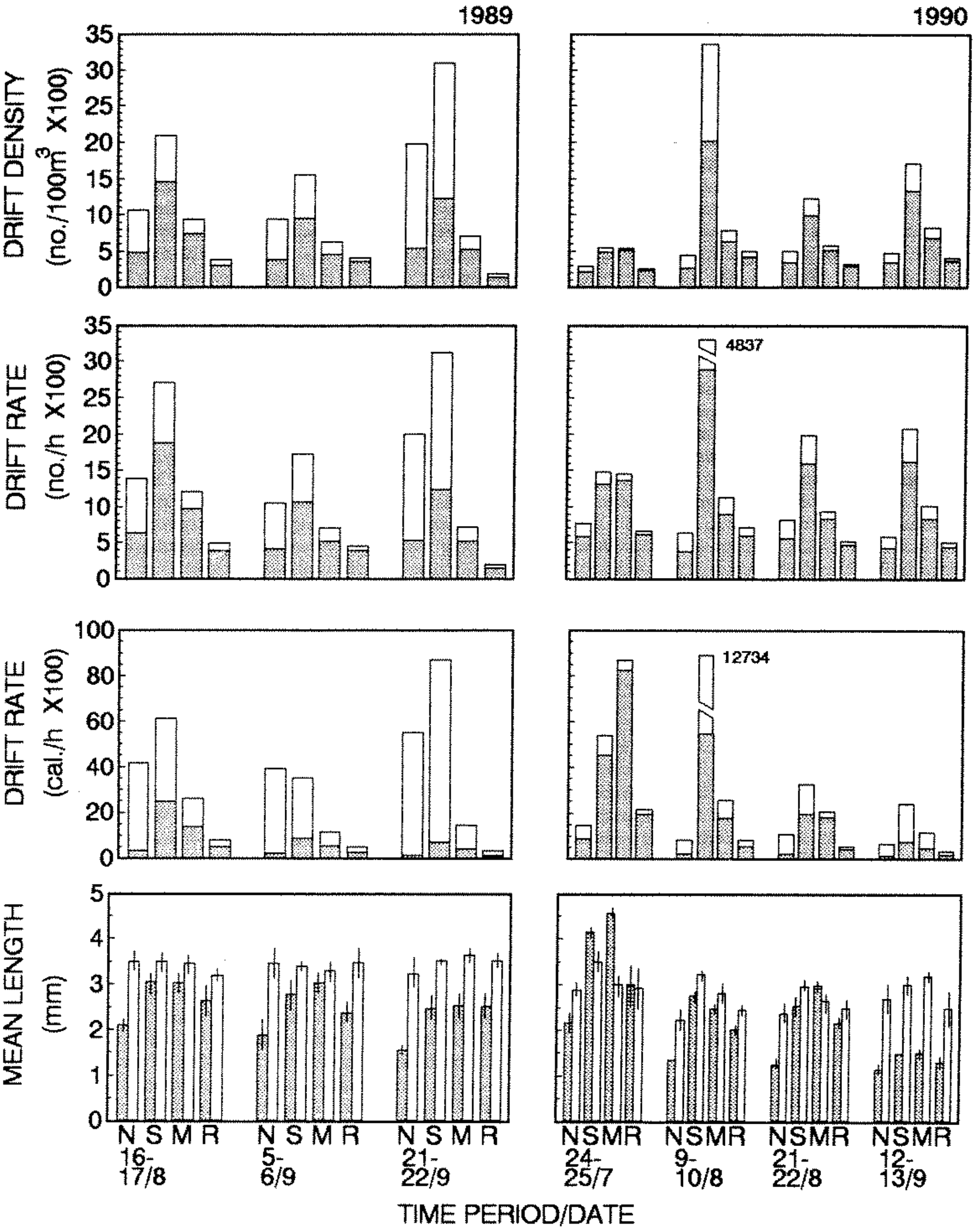

Figure 28.-Mean drift density, rate (numeric and caloric), and body length of aquatic taxa (shaded bars) and terrestrial taxa (open bars) by time period (N-noon, S-sunset, M-midnight, R-sunrise) and date in Brackett Creek, 1989 and 1990. N=5 in 1989, N=6 in 1990. Vertical bars±1 SE.

Table 10). Cutthroat trout typically composed about a third to slightly over half of total trout numbers in each enclosure (Table 10).

Table 10.-Number of total trout and cutthroat trout, mean length, weight, biomass, and density of total trout residing in enclosures (E) at the start of tests in Brackett Creek, 1989 and 1990. Numbers in parenthesis=1 SE.

E	Total Trout	Cutthroat trout	Length (mm)	Weight (g)	Biomass (g)	Density (fish/m^2)
			1989			
2	31	16	116.2(6.7)	24.1(4.9)	747	1.3
3	19	12	113.8(6.2)	18.7(3.7)	355	1.2
4	10	4	112.7(13.7)	22.9(6.7)	229	0.8
5	9	6	113.3(14.8)	24.9(10.5)	224	0.6
6	23	9	117.3(8.7)	24.9(6.3)	573	1.6
			1990			
1	19	7	133.3(11.2)	43.6(10.9)	828	0.8
2	18	6	128.0(7.9)	29.5(5.1)	531	0.7
3	18	8	130.9(9.0)	35.6(10.1)	641	1.0
4	15	7	118.7(10.7)	25.0(7.3)	375	1.0
5	17	8	125.6(8.6)	28.5(5.9)	485	1.0
6	23	13	94.7(7.8)	13.7(3.6)	315	1.3

The numbers and biomass of cutthroat trout in the enclosures at the outset of tests exceeded that of trout that had originally resided in enclosures before experimental manipulations of the populations by 1.2 to 3.5 for numbers and 1.4 to 4.1 for biomass (Table 11). Mean length and weight of cutthroat trout in the test populations did not differ (P>0.05, ANOVA; Appendix E) among enclosures in either year.

Table 11.-Number of introduced cutthroat trout (N), mean length, weight, biomass, and ratios of number (N), biomass (B), and density (D) of introduced cutthroat trout to that of all trout initially residing in enclosures (E) at the start of tests in Brackett Creek, 1989 and 1990. Numbers in parenthesis=1 SE.

E	N	Length (mm)	Weight (g)	Biomass (g)	Ratios N	Ratios B	Ratios D
			1989				
2	36	132.0(4.7)	29.4(4.2)	1058	1.2	1.4	1.5
3	35	130.7(5.0)	29.9(4.5)	1047	1.8	2.9	2.2
4	35	123.6(4.1)	24.1(3.4)	844	3.5	3.7	2.8
5	29	124.3(4.8)	24.7(3.3)	716	3.2	3.2	2.1
6	33	127.0(4.5)	26.8(4.1)	884	1.4	1.5	2.3
			1990				
1	45	138.7(6.1)	39.0(6.7)	1755	2.4	2.1	1.9
2	45	134.5(5.3)	34.0(4.5)	1530	2.5	2.9	1.8
3	43	133.5(5.4)	33.4(4.6)	1436	2.4	2.2	2.4
4	36	138.6(6.2)	36.8(5.5)	1325	2.4	3.5	2.5
5	40	126.0(4.4)	26.0(2.9)	1040	2.4	2.1	2.5
6	43	132.4(5.1)	30.4(3.9)	1307	1.9	4.1	2.4

There was no consistent trend in cutthroat trout emigration and supplemental feeding. About 20% to 60% of cutthroat trout present at the outset of tests emigrated from enclosures in both years (Figure 29). Trout emigrated throughout the study, but most movement occurred within the first 2 to 3 weeks (Figure 29). Regardless of when emigration occurred, trout significantly increased in length before entering traps ($P<0.05$, Paired t-test; Figure 30) while trout weight was typically unchanged or significantly decreased in most enclosures. The inverse relation between change in length and weight resulted in a significant reduction in condition factors ($P<0.05$, Paired t-test; Figure 30). Comparison of initial lengths and weights between cutthroat trout that emigrated and remained in enclosures showed no relation between fish size and emigration in 1989, however smaller individuals emigrated from enclosures 2 and 4 in 1990 while larger individuals emigrated from enclosures 1 and 6. Trout emigration was predominately upstream (≥ 80%) in all enclosures.

Some introduced trout were not recovered. Unaccounted trout ranged from 1 to 9 individuals per enclosure (mean 5.8 in 1989 and 4.0 in 1990) and missing fish were not considered in the analyses. Tag retention for trapped and recovered trout was 64% and 84% in 1989 and 1990, respectively. I used regression equations of final fish length on initial fish length to estimate initial lengths of fish that had lost tags. These estimates were compared to unaccounted fish and a tag code assigned for nearest matches.

There was no consistent trend in numbers of trout remaining in enclosures with and without supplemental feeding. Final cutthroat

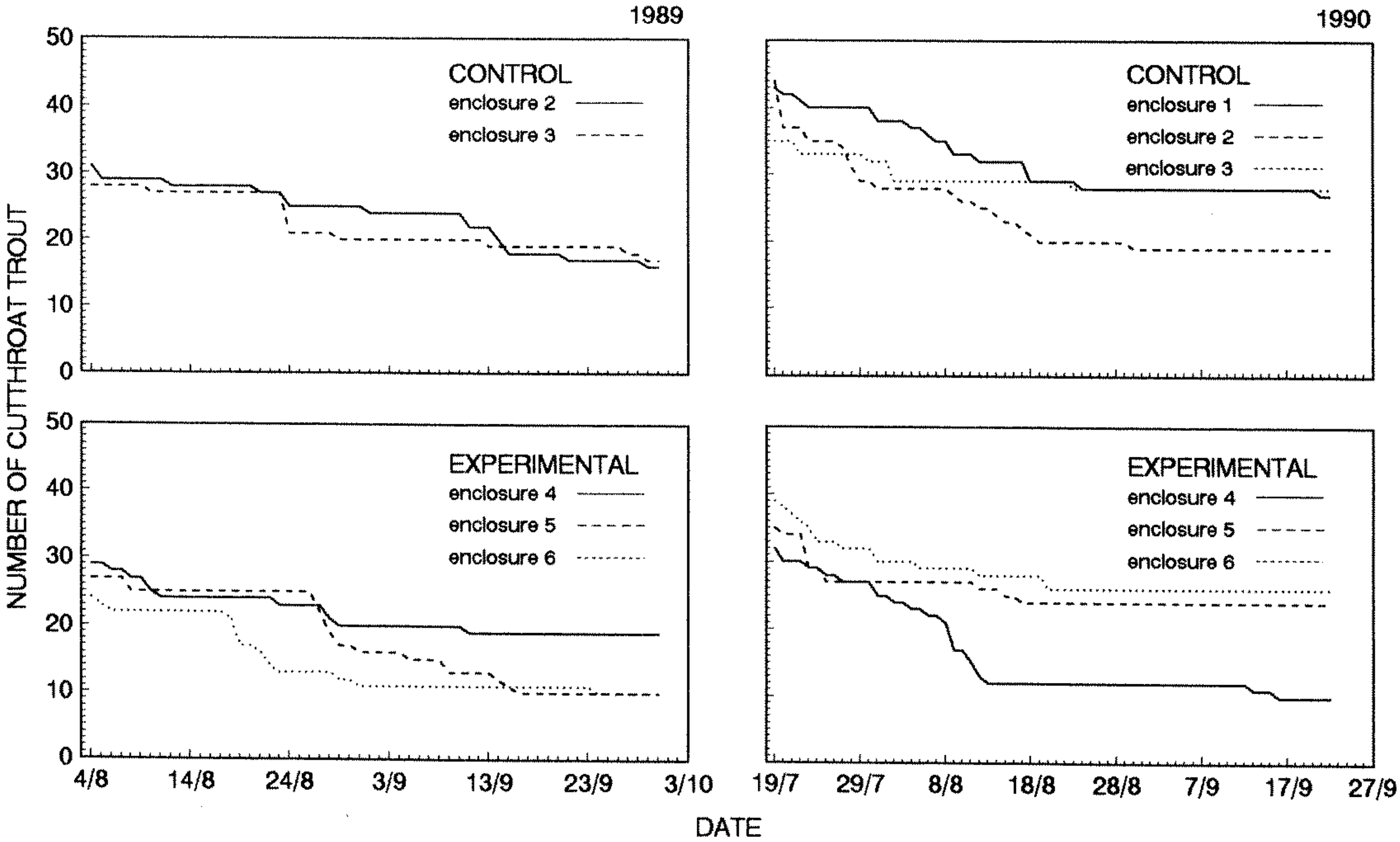

Figure 29.-Number of cutthroat trout remaining in control and experimental enclosures by day in Brackett Creek, 1989 and 1990.

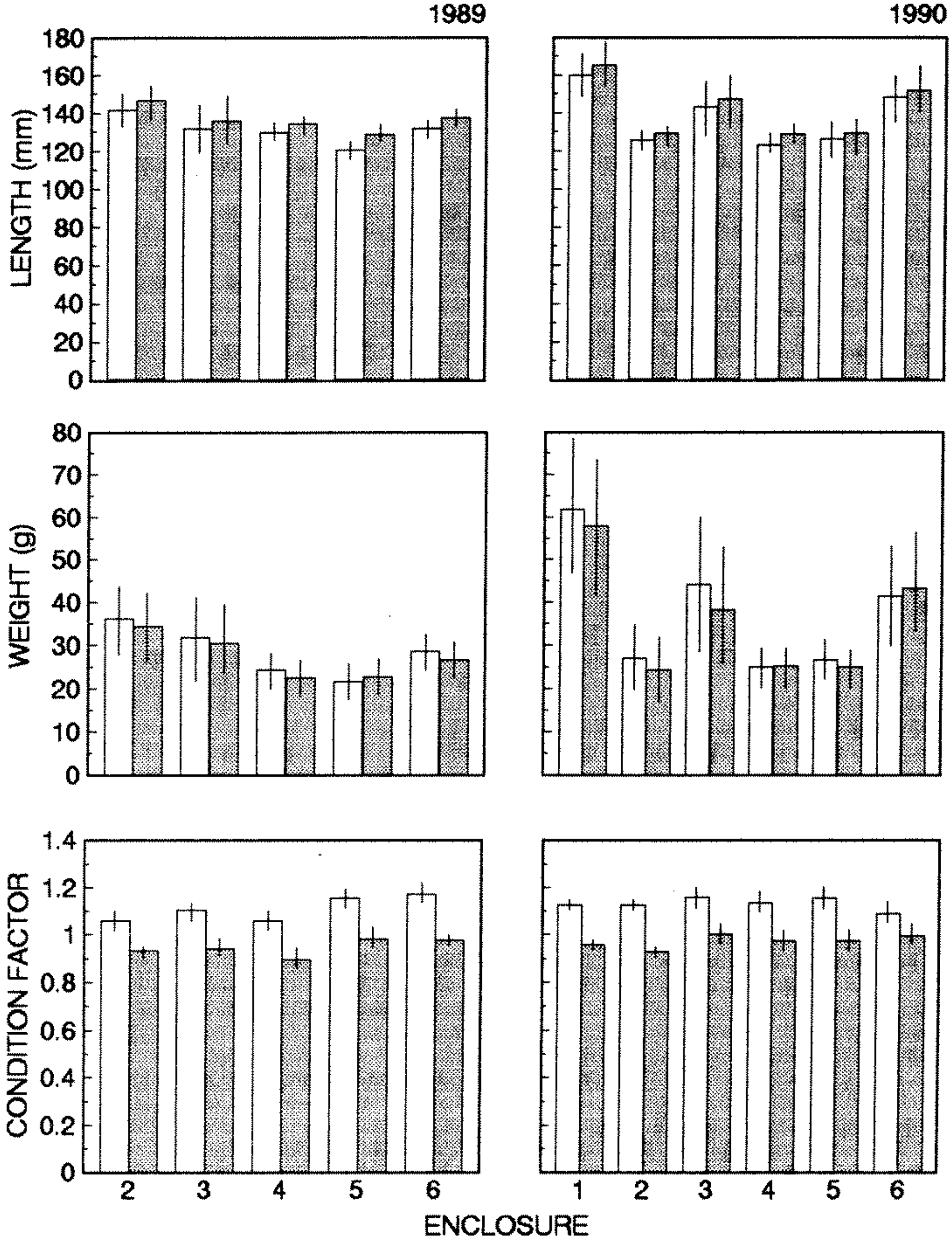

Figure 30.-Mean length, weight, and condition factor for cutthroat trout at the start of the study (open bars) and when collected in traps (shaded bars) for each enclosure in Brackett Creek, 1989 and 1990. N for enclosures: 2=15, 3=10, 4=10, 5=17, 6=14; 1=16, 2=26, 3=7, 4=22, 5=11, 6=13, in 1990. Vertical bars±1 SE. Control enclosures #1-3, experimental enclosures #4-6.

trout densities ranged from 0.7 to 1.9 trout/m^2 in control enclosures and from 0.8 to 1.9 trout/m^2 in experimental enclosures (Figure 31). At the end of tests, trout numbers, density, biomass, and standing crop were rarely correlated with physical features of the enclosures nor with mean caloric drift rates for each enclosure (P>0.05, Spearman Rank Correlation; Appendix F).

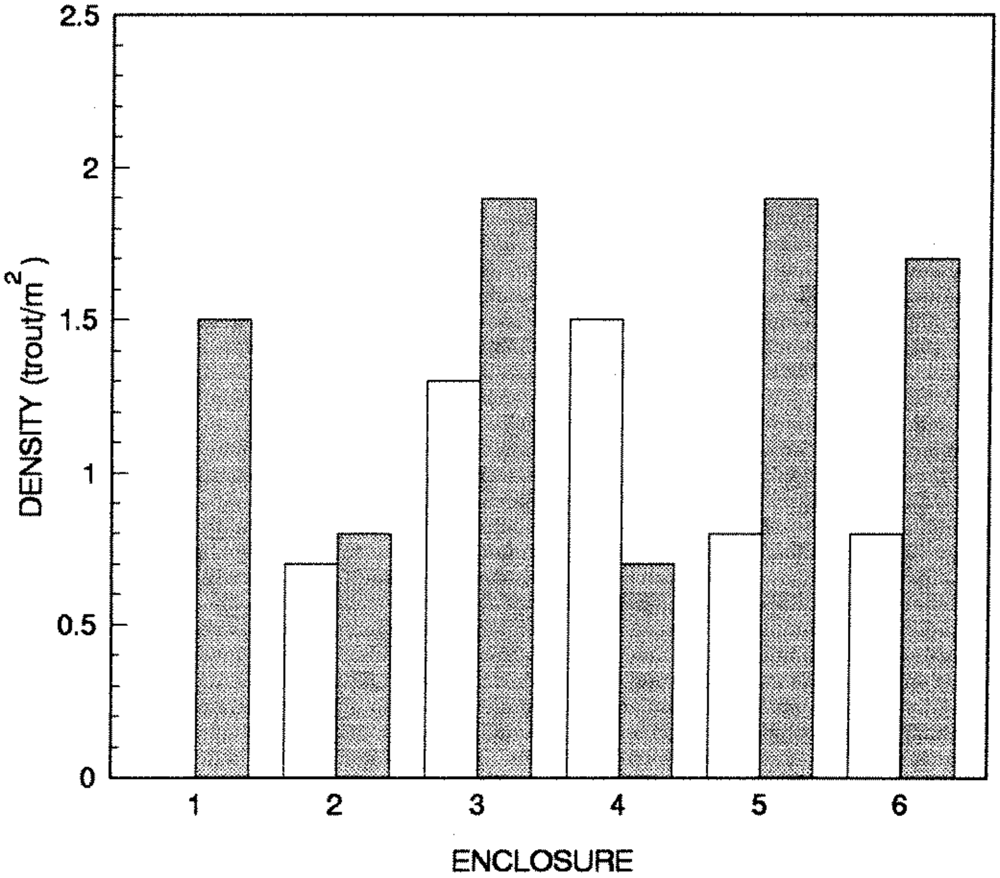

Figure 31.-Density of cutthroat trout at the end of tests for each enclosure in Brackett Creek, 1989 (open bars) and 1990 (shaded bars). Control enclosures #1-3, experimental enclosures #4-6.

Trout remaining at the end of the tests in control enclosures significantly increased in length while weight significantly decreased or was unchanged compared to initial length and weight in both years (Paired t-tests; Figure 32; Appendix E). For experimental enclosures, trout length and weight significantly increased during the study with the exception of enclosure 4 (unchanged) in 1989. Condition factors of trout significantly decreased (paired t-tests; Figure 32) in all control enclosures in both years and in experimental enclosures 4 and 5 in 1989. Initial and final condition factors were not significantly different in enclosure 6 in 1989 and all experimental enclosures in 1990. However, slopes for length and weight regression equations did not differ between trout at the start and end of the tests for all enclosures in 1989 and control enclosures in 1990 ($P>0.05$, Partial F-test; Table 12). In experimental enclosures in 1990, slopes were significantly greater for trout at the end of tests than at the start of tests ($P<0.05$, Partial F-test; Table 12).

Patterns for mean specific growth rates of cutthroat trout were similar among enclosures between 1989 and 1990 (Figure 33). In both years, specific growth rates in enclosure 3, a control, were negative and significantly lower than other enclosures ($P<0.001$, Kruskal-Wallis test). While growth rates of trout in other enclosures were similar in 1989, specific growth rates were significantly greater in experimental than control enclosures in 1990 ($P<0.001$, Kruskal-Wallis test; Figure 33). Mean specific growth rate was rarely correlated with measured habitat features and final trout abundance among enclosures in both years ($P>0.05$, Spearman Rank Correlation; Appendix F). Growth rate, however, was positively related to mean caloric drift rate during the study ($0.05<P<0.11$, Spearman Rank Correlation;

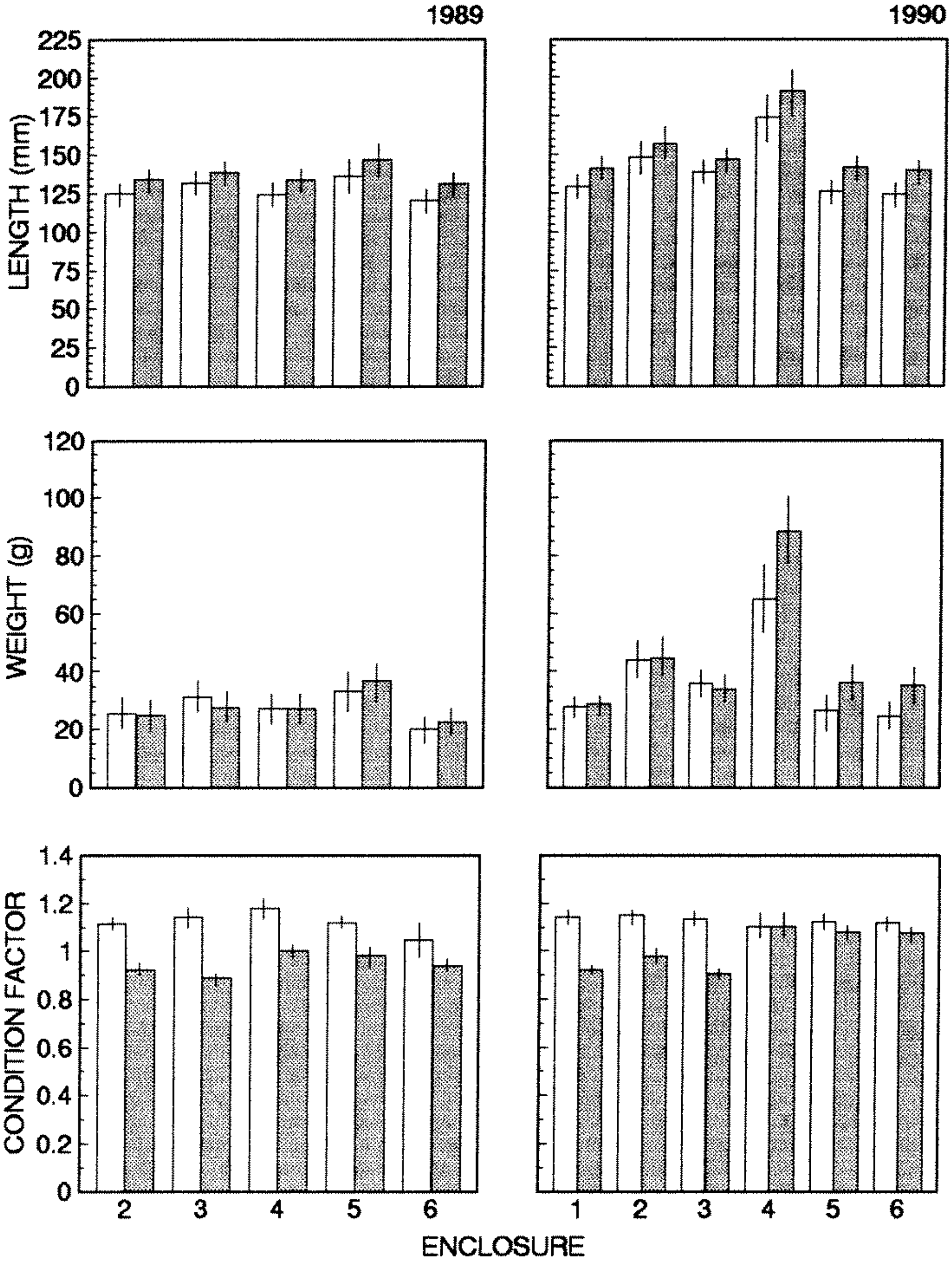

Figure 32.-Mean length, weight, and condition factor for cutthroat trout at the start (open bars) and end of the study (shaded bars) for each enclosure in Brackett Creek, 1989 and 1990. N for enclosures; 2=16, 3=18, 4=19, 5=10, 6=10 in 1989; 1=27, 2=19, 3=28, 4=10, 5=24, 6=26 in 1990. Vertical bars±1 SE. Control enclosures #1-3, experimental enclosures #4-6.

Appendix F). Combining years, growth was significantly correlated with mean caloric drift rate (P=0.045, Spearman Rank Correlation). Additionally, more trout lost weight or did not increase in weight in control (58% both years) compared to experimental enclosures (16% both years; P=0.005, Chi-square goodness-of-fit, in 1989 and P<0.001 in 1990).

Table 12.-Comparison of slopes for length and weight regression equations for cutthroat trout that remained in each enclosure at the start (b_{1I}) and end (b_{1F}) of tests in Brackett Creek, 1989 and 1990. Numbers in parentheses=1 SE. P=results of Partial F-test.

Enclosure	b_{1I}	b_{1F}	df	P
		1989		
2	3.12(0.11)	3.09(0.12)	1,28	0.821
3	3.17(0.16)	3.03(0.08)	1,32	0.457
4	3.16(0.13)	2.98(0.12)	1,34	0.312
5	3.13(0.15)	3.38(0.16)	1,16	0.060
6	3.02(0.37)	2.78(0.12)	1,16	0.583
		1990		
1	2.93(0.11)	3.10(0.06)	1,50	0.221
2	3.06(0.08)	3.22(0.09)	1,34	0.199
3	3.05(0.08)	3.08(0.06)	1,52	0.766
4	2.85(0.13)	3.33(0.09)	1,16	0.007
5	2.98(0.08)	3.27(0.08)	1,44	0.015
6	2.75(0.06)	3.07(0.10)	1,48	0.009

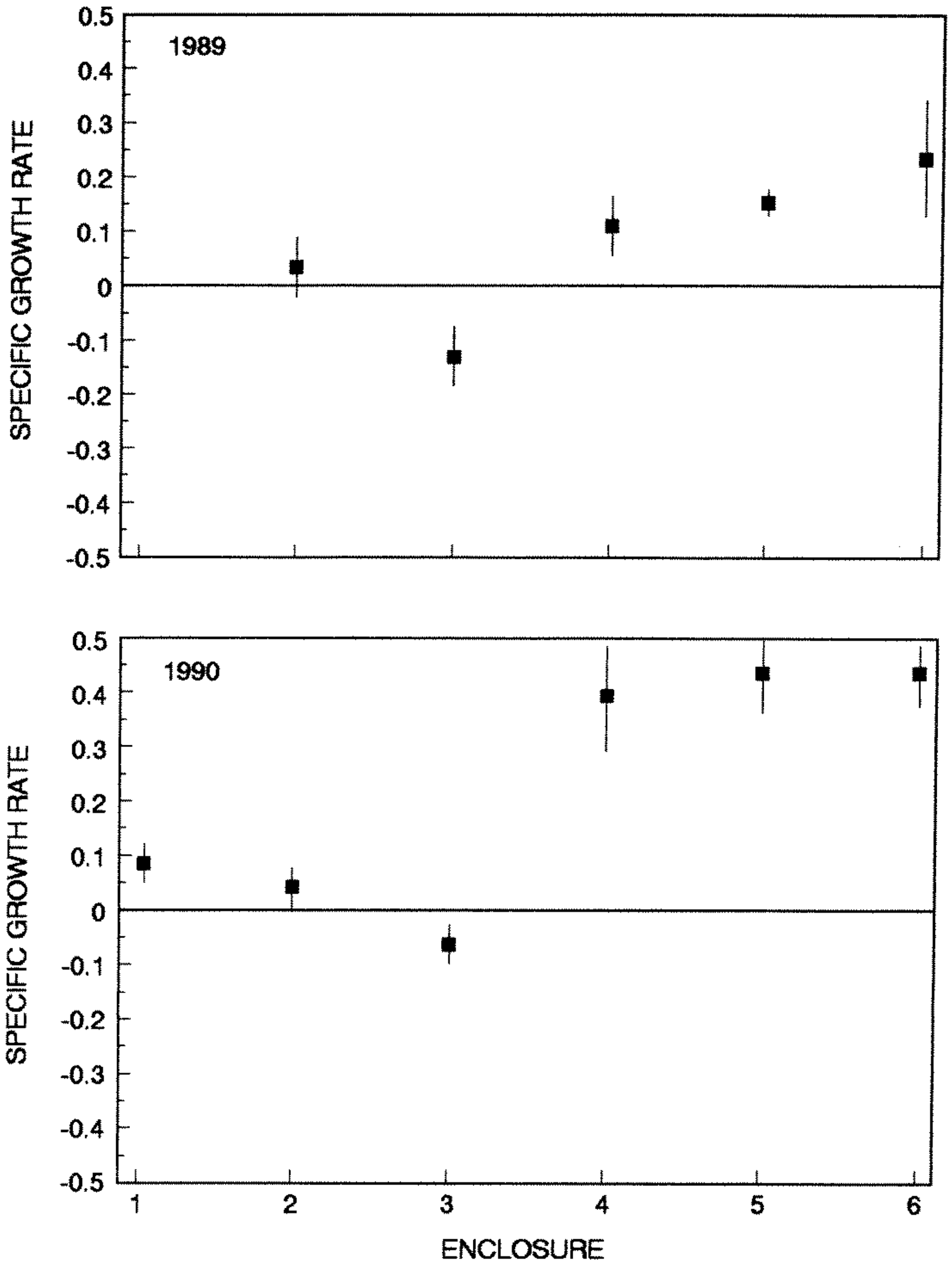

Figure 33.-Mean specific growth rate for cutthroat trout remaining in each enclosure in Brackett Creek, 1989 and 1990. N for enclosures: 2=16, 3=18, 4=19, 5=10, 6=10 in 1989; 1=27, 2=19, 3=28, 4=10, 5=24, 6=26 in 1990. Vertical bars±1 SE. Control enclosures #1-3, experimental enclosures #4-6.

A factor potentially affecting the behavior of cutthroat trout was the presence of brook trout and unmarked cutthroat trout in the enclosures. In both years, 1 to 11 untagged cutthroat trout or brook trout were recovered from each enclosure. Over half of these fish were small (≤ 90 mm) and I assumed they evaded initial electrofishing efforts or were able to pass through the mesh leads of the enclosures. Also, several ripe brook trout, that presumably entered under the downstream leads, probably near the end of the tests, were recovered from enclosure 6 in both years.

Cutthroat Trout Diets

Stomach contents were obtained from 80% to 100% of the cutthroat trout recovered from enclosures at the end of the tests. Amount and composition of material in trout stomachs varied among individuals, but dipterans typically comprised the greatest proportion of total dry weight of prey items in both control and experimental enclosures in 1989 (Figure 34); ephemeropterans typically made up the largest proportion of stomach contents for trout in control enclosures in 1990. Brine shrimp and krill were the most abundant prey categories for trout in experimental enclosures in 1990. Discounting unidentified material, numeric proportions of prey items in trout stomachs were similar to those for dry weight (Figure 35).

Cutthroat trout rarely selected prey items in proportion to their availability in mean daily drift on the final drift sample date. Dipterans were consistently selected (electivity indices > 0) in control and experimental enclosures, both years (Figure 36). While

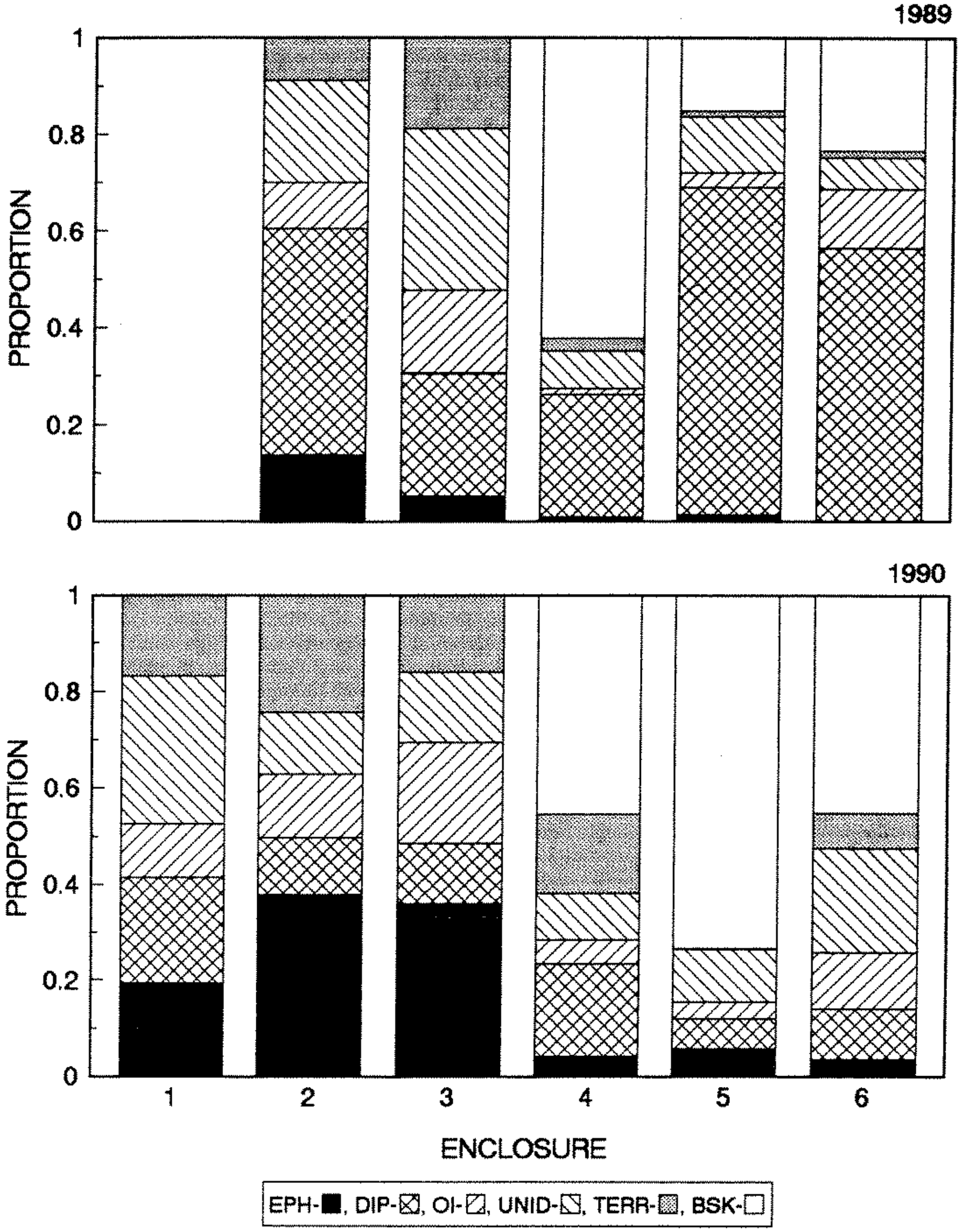

Figure 34.-Relative contribution of prey categories (Ephemeroptera-EPH, Diptera-DIP, other invertebrates-IO, unidentified-UNID, terrestrial-TERR, and brine shrimp and krill-BSK) to mean dry weight of stomach contents for cutthroat trout in each enclosure at the end of tests in Brackett Creek, 1989 and 1990. N for enclosures: 2=13, 3=17, 4=17, 5=9, 6=8 in 1989; 1=26, 2=15, 3=23, 4=10, 5=23, 6=26 in 1990. Control enclosures #1-3, experimental enclosures #4-6.

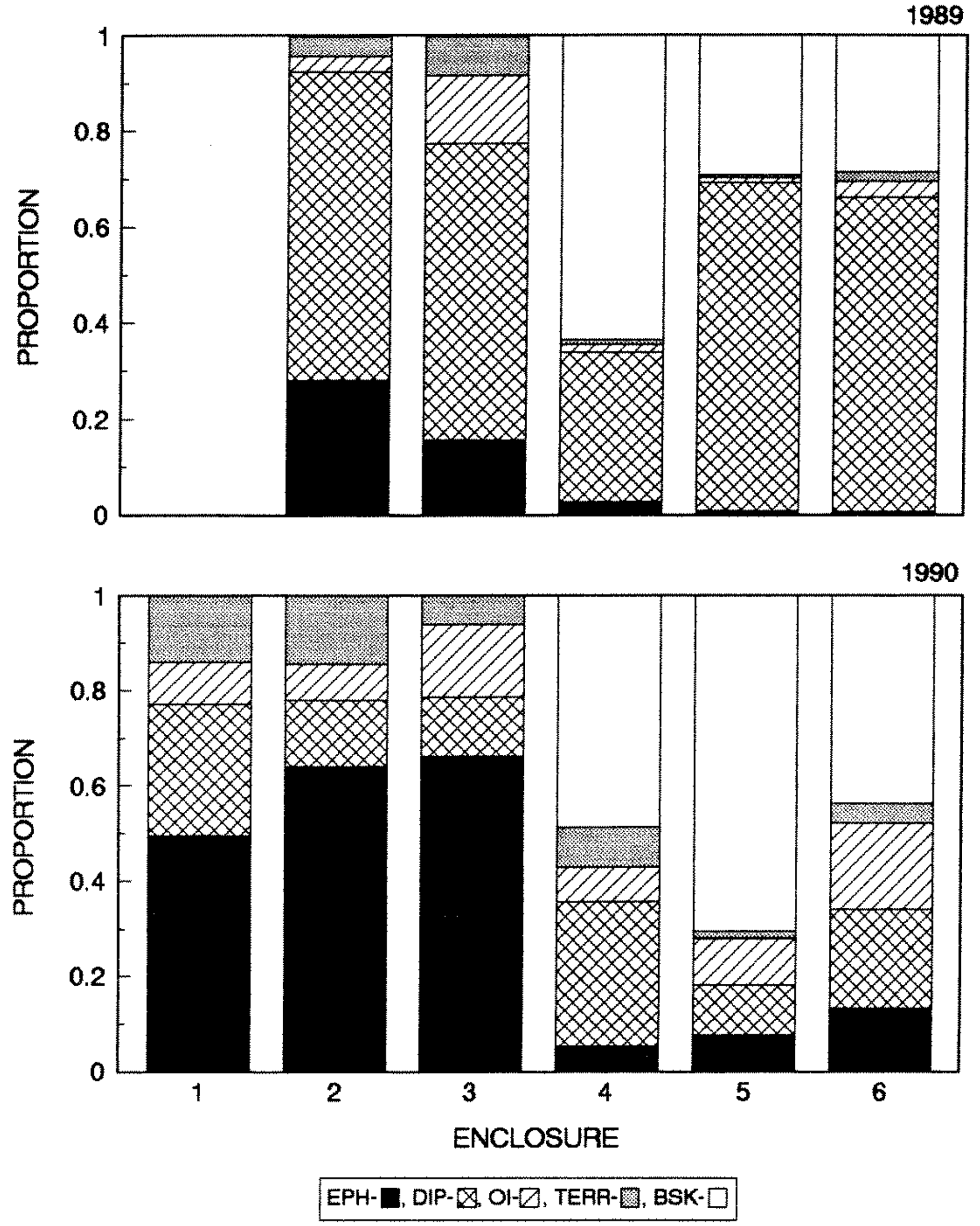

Figure 35.-Relative contribution of prey categories (Ephemeroptera-EPH, Diptera-DIP, other invertebrates-IO, terrestrial-TERR, and brine shrimp and krill-BSK) to numeric abundance of stomach contents for cutthroat trout in each enclosure at the end of tests in Brackett Creek, 1989 and 1990. N for enclosures: 2=13, 3=17, 4=17, 5=9, 6=8 in 1989; 1=26, 2=15, 3=23, 4=10, 5=23, 6=26 in 1990. Control enclosures #1-3, experimental enclosures #4-6.

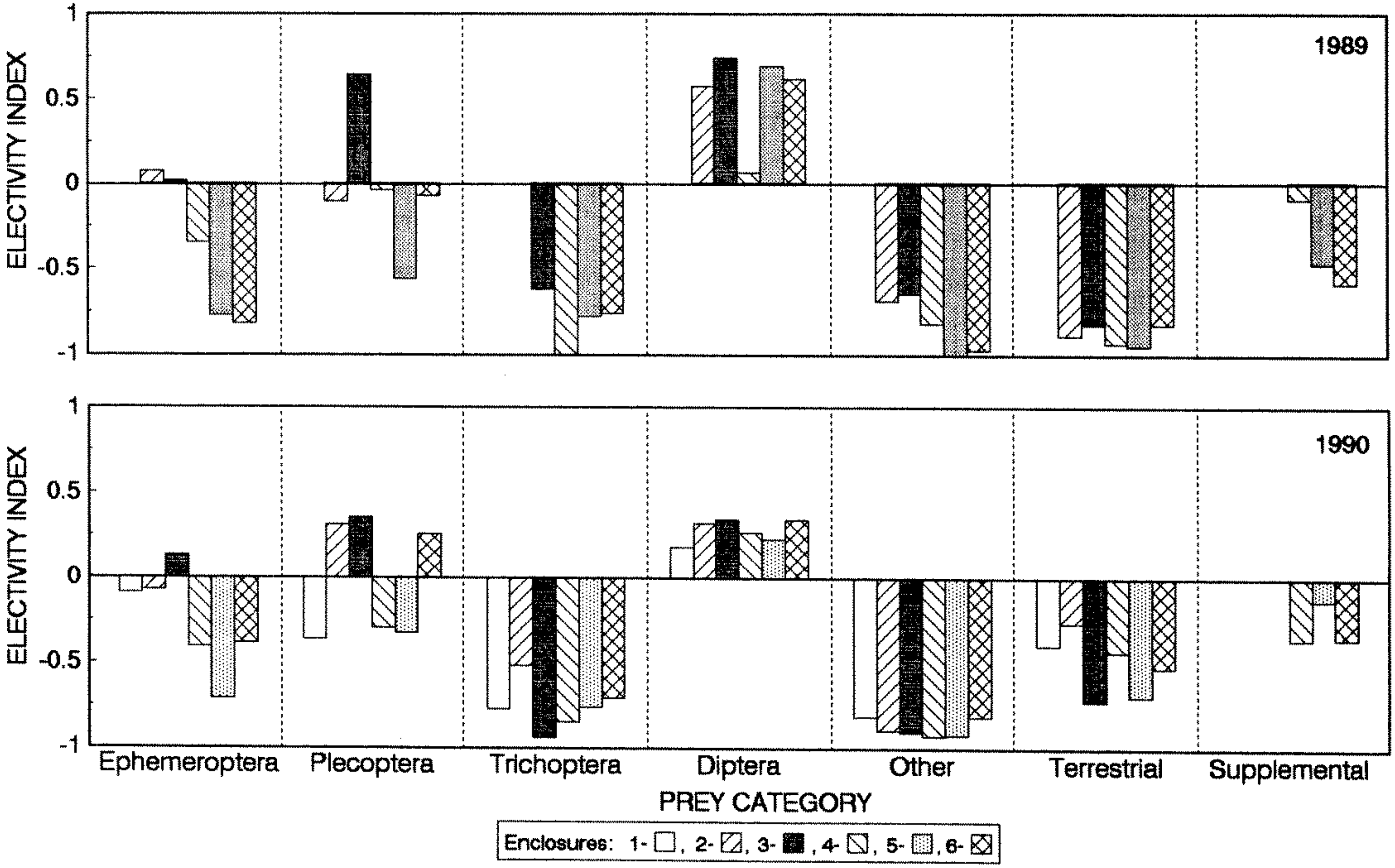

Figure 36.-Mean electivity index of prey categories (Ephemeroptera, Plecoptera, Diptera, other invertebrates, terrestrial taxa, and supplemental brine shrimp and krill) for cutthroat trout in each enclosure in Brackett Creek, 1989 and 1990

ephemeropterans and plecopterans were selected by trout in some enclosures, most remaining prey categories were consumed in lower proportions than their availability (Figure 36). Mean lengths of predominant prey were generally larger than those collected in driftnets, especially in 1990 (Figure 37).

Trout stomachs contained more prey items in 1989 than in 1990. Relative number of prey items per stomach was not significantly different among enclosures in 1989 (P=0.098, Kruskal-Wallis test; Table 13), but trout in enclosure 4 contained significantly fewer prey than trout in other enclosures in 1990 (P=0.001,Kruskal-Wallis test; Table 13). Although stomach contents were highly variable, trout in experimental enclosures generally had higher food consumption rates, based on caloric intake, than trout in control enclosures (Table 13). Relative caloric consumption rates were significantly higher for experimental enclosures than control enclosures in 1989 (P=0.001, Kruskal-Wallis test) while in 1990, consumption rates were significantly lower in enclosure 3 than other enclosures (P=0.011, Kruskal-Wallis test).

Maintenance ratio, the ratio of estimated consumption rate for individual trout to predicted maintenance consumption rate, was used to indicate the degree that a trout met basic metabolic requirements. Based on median maintenance ratio for trout in each enclosure, estimated consumption rates surpassed those needed for maintenance (ratio > 1) in all but one enclosure in 1989 while median maintenance ratio were low (<1) for all enclosures in 1990.

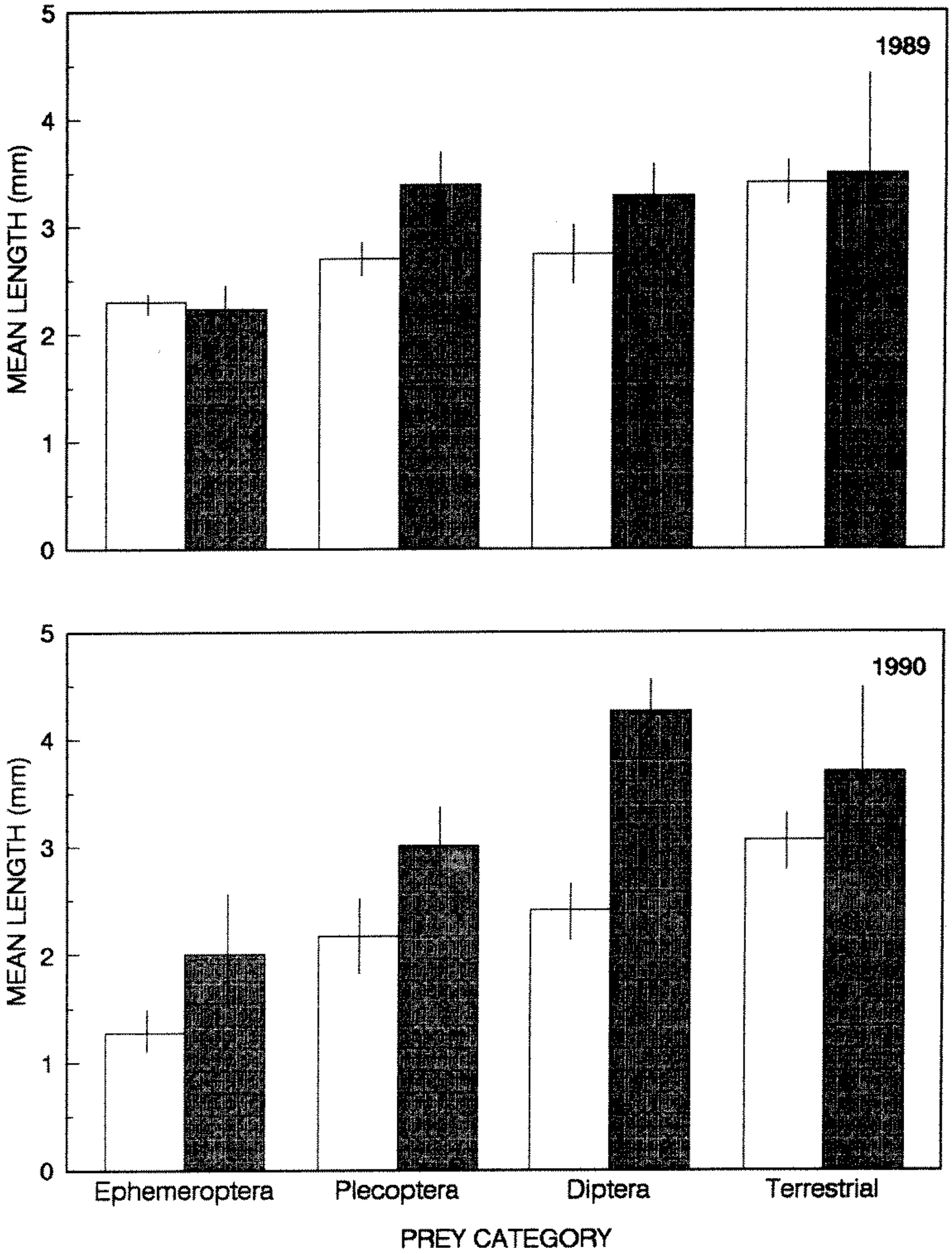

Figure 37.-Mean body length of major prey categories in the drift on the final sample date (open bars) and in the diets of cutthroat trout shaded bars) in Brackett Creek, 1989 and 1990. Vertical bars±1 SE.

Foraging efficiency of all trout in an enclosure (total consumption rate/daily drift rate) ranged from 0.026 to 0.063 in 1989 and from 0.027 to 0.436 in 1990 (Table 13). Artificially increased drift in experimental enclosures resulted in foraging efficiencies considerably lower than in control enclosures. Foraging efficiency was influenced not only by invertebrate drift rates, but estimated food consumption rates and number of trout in an enclosure.

Table 13.-Stomach content analyses for cutthroat trout collected from each enclosure (E) at the end of tests in Brackett Creek, 1989 and 1990, showing number of cutthroat trout recovered (N), median relative number of prey items per trout, median relative calories per trout, total daily consumption rate by all trout (C_{24}), median ratio of daily consumption rate to predicted maintenance ration per trout (CF_{24}/C_{main}), and ratio of daily food consumption rate of all trout in an enclosure to mean daily drift rate in the final invertebrate samples (C_{24}/D_{24}).

E	N[a]	Relative number[b] (no./g)	Relative calories[b] (cal./g)	C_{24} (cal./d)	CF_{24}/C_{main}	C_{24}/D_{24}
			1989			
2	16(13)	4.1 (0.4-14.6)	7.6 (1.6-41.8)	5229	0.64 (0.16-4.07)	0.035
3	18(17)	1.9 (0.4-7.2)	8.1 (1.2-42.7)	6156	1.13 (0.12-5.10)	0.063
4	19(17)	4.5 (0.5-15.0)	24.5 (3.0-58.7)	13569	2.41 (0.35-4.01)	0.052
5	10(9)	1.5 (0.4-5.1)	16.6 (7.0-30.8)	6293	1.58 (0.74-3.31)	0.026
6	10(8)	2.3 (1.3-9.3)	33.8 (4.6-82.5)	8182	3.15 (0.37-10.01)	0.040

Table 13.-Continued.....

E	N[a]	Relative number[b] (no./g)	Relative calories[b] (cal./g)	C_{24} (cal./d)	CF_{24}/C_{main}	C_{24}/D_{24}
			1990			
1	27(26)	0.5 (0.2-3.1)	3.4 (0.1-24.9)	5344	0.27 (0.01-2.47)	0.178
2	19(15)	1.9 (0.5-3.8)	3.9 (1.1-61.1)	6221	0.35 (0.01-5.20)	0.328
3	28(23)	1.6 (0.2-3.9)	2.5 (0.3-82.2)	9381	0.23 (0.03-7.51)	0.436
4	10(10)	0.3 (0.1-1.5)	3.5 (0.9-24.7)	4929	0.39 (0.10-1.98)	0.027
5	24(23)	0.6 (0.2-6.1)	9.8 (0.3-52.2)	12616	0.72 (0.03-4.14)	0.079
6	26(26)	0.6 (0.1-3.9)	7.2 (0.1-112.3)	14465	0.58 (0.03-9.20)	0.088

[a] Numbers in parentheses=trout stomachs analyzed.
[b] Numbers in parentheses=range.

Bioenergetic Equations

Trends in mean ecological growth coefficients (percent of maximum growth rate attained by individual trout, EGC) among enclosures (Figure 38) were similar to patterns observed for specific growth rates (Figure 33). Mean EGC was negative in enclosure 3 in both years. Ecological growth coefficients were significantly lower in enclosure 3 than for other enclosures in 1989 ($P<0.001$, Kruskal-Wallis test). In 1990, mean EGC ranged from 57.2 to 70.2 in

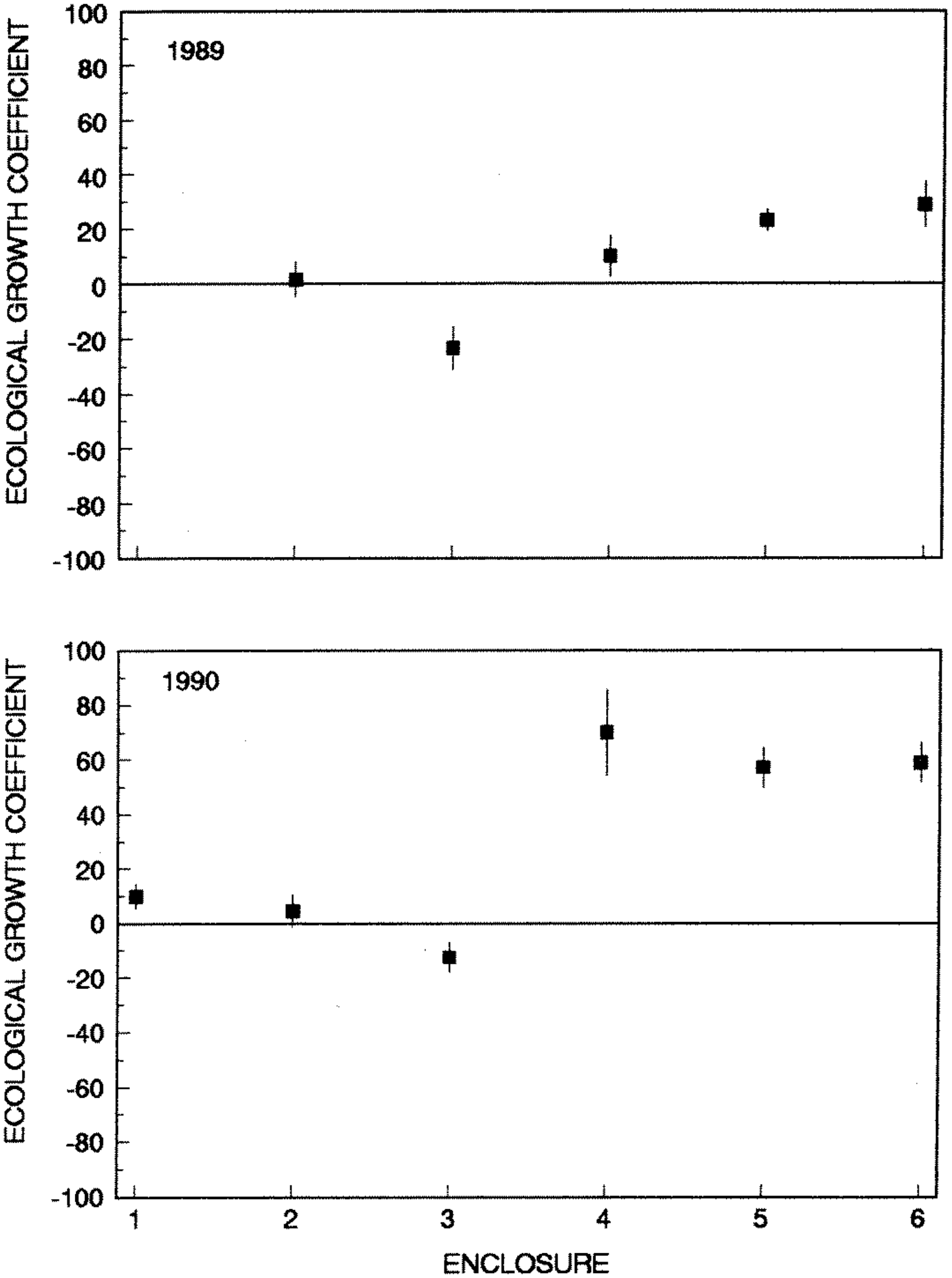

Figure 38.-Mean ecological growth coefficients (percent of maximum growth attained) for cutthroat trout remaining in each enclosure in Brackett Creek, 1989 and 1990. N for enclosures; 2=16, 3=18, 4=19, 5=10, 6=10 in 1989; 1=27, 2=19, 3=28, 4=10, 5=24, 6=26 in 1990. Vertical bars±1 SE. Control enclosures #1-3, experimental enclosures #4-6.

experimental enclosures and these values were significantly greater than those for control enclosures ($P<0.001$, Kruskal-Wallis test; Figure 38).

Model predictions for daily maximum (C_{max}) and maintenance (C_{main}) rations for all trout in an enclosure (Figures 39 and 40) demonstrated the dependence of consumption rates on water temperature, trout number, and trout weight. Negative trends in predicted values were primarily influenced by decreases in water temperature (Figure 25) and the number of trout remaining in enclosures (Figure 29). In 1989, an abrupt drop in water temperature resulted in a dramatic decrease in predictions for C_{max} and to a lesser extent, C_{main} (Figure 39).

After the third week of the tests in 1990, the number of trout in experimental enclosure 4 was about half that in other experimental enclosures. Despite this, C_{max}, C_{main}, and C_{obs} (estimated consumption rates producing observed growth) were relatively similar among the three experimental enclosures (Figure 40). Because trout remaining in enclosure 4 were significantly larger than trout in other enclosures, greater trout weight compensated for differences in trout numbers. Relative differences in C_{obs} and C_{main} among enclosures demonstrated greater growth, hence higher consumption rates, by trout in experimental compared to control enclosures.

Addition of supplemental food caused foraging efficiencies to be consistently lower in experimental than control enclosures (Tables 14 and 15). Drift was sufficient for cutthroat trout to potentially attain C_{max} (ratios < 1) on all drift sample dates in both control and experimental enclosures in 1989 (Table 14). However, in 1990, drift

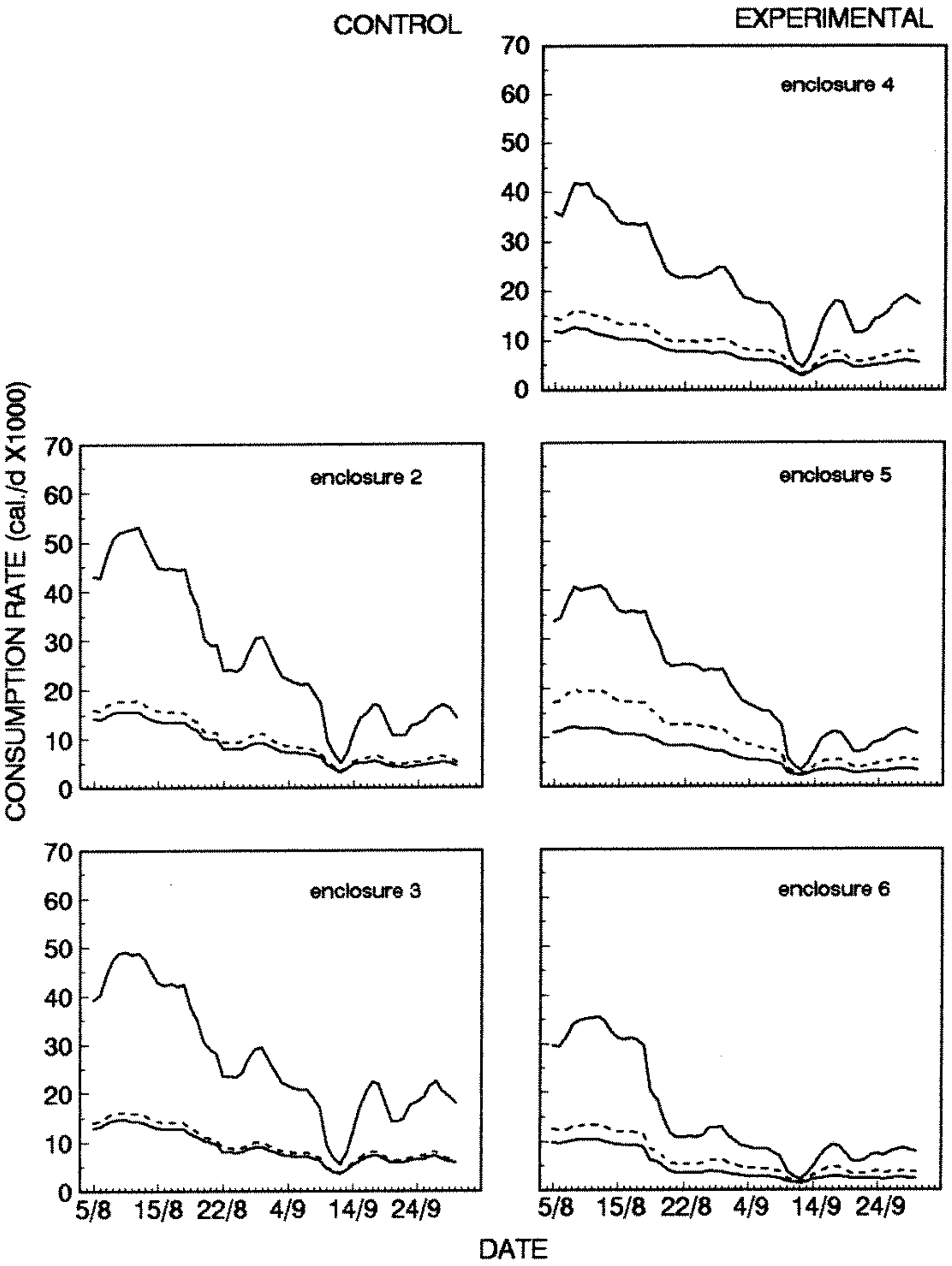

Figure 39.-Observed (broken line) and predicted daily consumption rates for maximum (upper solid line) and maintenance (lower solid line) rations for all cutthroat in each enclosure per day in Brackett Creek, 1989.

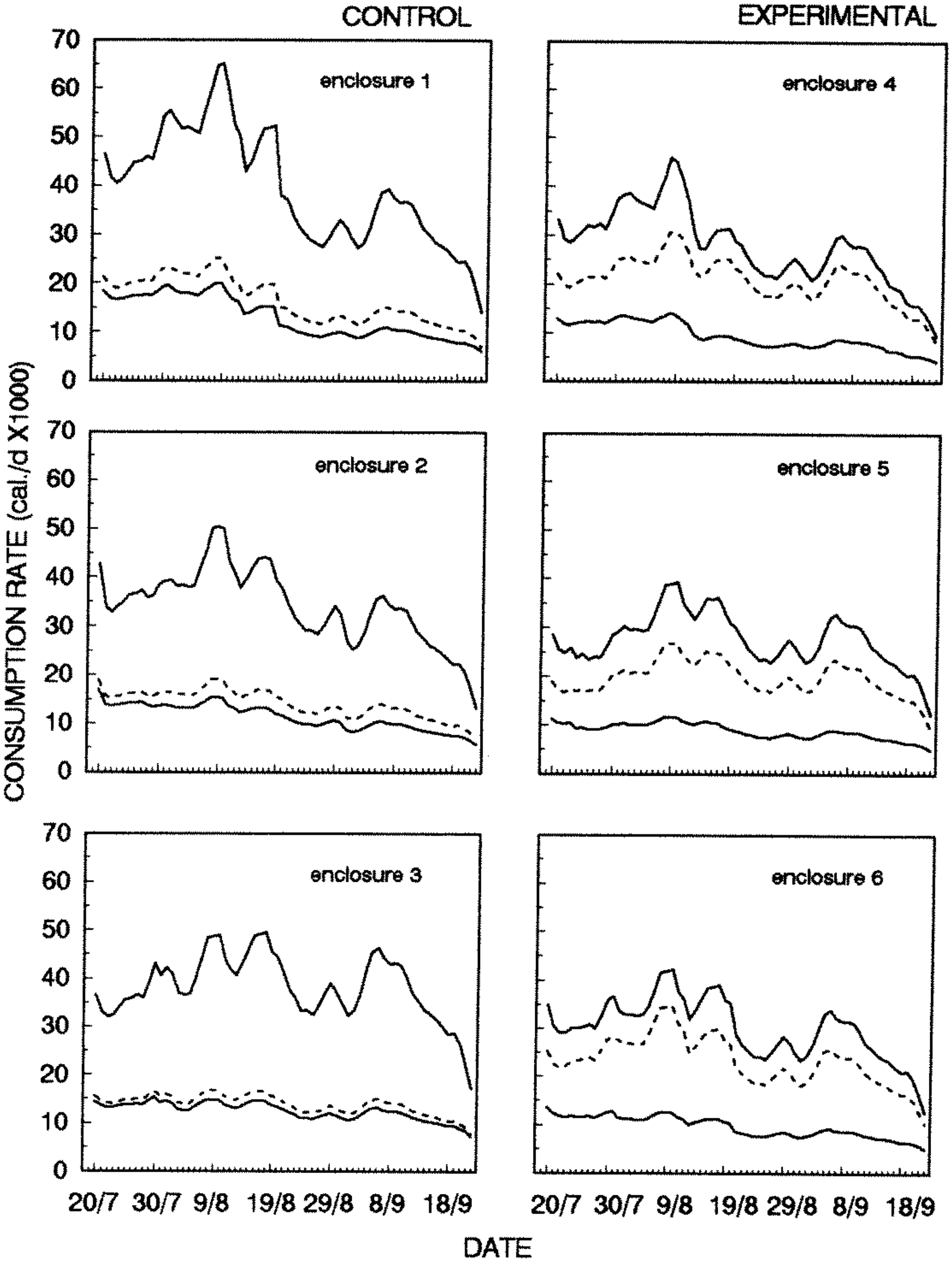

Figure 40.-Observed (broken line) and predicted daily consumption rates for maximum (upper solid line) and maintenance (lower solid line) rations for all cutthroat in each enclosure per day in Brackett Creek, 1990.

in control enclosures was not adequate for trout to meet C_{max} on the final drift sample date, and a third to half of daily drift would be required for C_{main} (Table 15). In both years, drift was adequate for trout to potentially acquire C_{main} and, as most trout had emigrated from enclosures by the final drift sample date, C_{obs} surpassed C_{main} in all enclosures.

Table 14.-Foraging efficiency (food consumption rate (cal./d)/mean daily drift rate per enclosure (cal./d)) for predicted maximum (C_{max}) and maintenance (C_{main}) rations and estimates for observed consumption rate (C_{obs}) for all cutthroat in an enclosure (E) on invertebrate sample dates in Brackett Creek, 1989.

	16-17 August			5-6 September			21-22 September		
E	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}
2	0.46	0.14	0.16	0.22	0.07	0.09	0.07	0.03	0.03
3	0.51	0.16	0.17	0.28	0.10	0.11	0.15	0.06	0.07
4	0.21	0.06	0.08	0.10	0.03	0.04	0.05	0.02	0.02
5	0.13	0.04	0.06	0.08	0.03	0.04	0.03	0.01	0.02
6	0.12	0.04	0.05	0.04	0.01	0.02	0.03	0.01	0.02

Discussion

Abundance and growth of stream dwelling salmonids is dependent on complex interactions between suitable habitat and availability of food resources. I found that supplemental feeding of cutthroat trout in stream enclosures, open to emigration, generally increased trout growth rates in late summer. However, I found no consistent trends in trout density related to supplemental feeding.

Table 15.-Foraging efficiency (food consumption rate (cal./d)/mean daily drift rate per enclosure (cal./d)) for predicted maximum (C_{max}) and maintenance (C_{main}) rations and estimates for observed consumption rate (C_{obs}) for all cutthroat in an enclosure (E) on invertebrate sample dates in Brackett Creek, 1990.

	24-25 July			8-9 August			21-22 August			12-13 September		
E	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}
1	0.60	0.24	0.28	1.72	0.53	0.67	1.33	0.42	0.55	1.03	0.31	0.42
2	0.43	0.17	0.19	0.66	0.20	0.25	0.59	0.19	0.24	1.48	0.46	0.61
3	0.65	0.26	0.27	0.93	0.29	0.32	0.87	0.28	0.31	1.68	0.52	0.58
4	0.16	0.06	0.11	0.20	0.06	0.14	0.15	0.05	0.12	0.13	0.04	0.10
5	0.11	0.04	0.08	0.21	0.06	0.14	0.16	0.05	0.12	0.16	0.05	0.11
6	0.13	0.05	0.11	0.18	0.06	0.15	0.15	0.05	0.12	0.16	0.05	0.12

Studies conducted in both field and laboratory settings have found salmonid densities directly associated with invertebrate abundance. Gibson and Galbraith (1975) found greater abundance of brook trout and Atlantic salmon, *Salmo solar*, at a site immediately below a lake outlet with greater amounts of invertebrate drift than at a site several kilometers downstream. Higher densities of cutthroat trout were associated with recently logged areas of Cascade mountain streams compared to unlogged or secondary growth areas (Murphy et al. 1981; Wilzbach and Hall 1985) where opening the forest canopy increased stream primary production and abundance of invertebrate taxa with a high propensity to drift. Mason (1976) was able to delay emigration of juvenile coho salmon by providing supplemental food in a natural stream. Densities of juvenile rainbow trout (Slaney and Northcote 1974), Atlantic salmon (Symons 1971), and cutthroat trout (Wilzbach 1985) were greater in artificial stream channels that received high as opposed to low rations. In contrast to these studies, cutthroat trout densities at the end of my tests were not related to mean caloric drift rate for individual enclosures, nor were densities consistently higher in experimental versus control enclosures. Furthermore, the fact that trout densities were generally lower at the end of the tests in 1989 than in 1990, when invertebrate drift was generally lower in the latter year, suggests that factors other than food abundance (e.g. stream discharge, habitat quality, and actual food availability) influenced trout density more than supplemental feeding and abundance of drifting invertebrates.

While positive relationships between density of several salmonid species and habitat features (i.e. overhead cover, water depth, velocity, and pool area) are well established (Boussu 1954; Elser 1968; Hunt 1969; Lewis 1969; Wesche 1974; O'Connor and Power 1976; Binns and Eiserman 1979; Bowlby and Roff 1986; Newman and Waters 1989), I found no relation between trout density and the habitat features measured. For coastal cutthroat trout in a small stream, Heggenes et al. (1991b) found strong preferences for depth (>25 cm), water velocity (<20 cm/s), and cover (>40% surface area) and concluded that depth and cover were the most important factors influencing habitat selection. Larger trout (>17 cm total length) selected deeper areas (26 cm) than smaller individuals (<11 cm total length; Heggenes et al. 1991b). Although my enclosures differed primarily with respect to surface area and cover, and to a lesser extent water depth and velocity, they were pool habitats. Mean water depths in enclosures were similar to those preferred by small cutthroat trout (18 cm; Heggenes et al. 1991b). Given the relatively sedentary habits of cutthroat trout in small streams (Heggenes 1991a; Miller 1957), my inability to discern a relation between trout density and habitat features suggests that available habitat was adequate for the remaining trout.

The apparent lack of a relationship between trout density and habitat may have been related to the 37% and 61% decrease in discharge in 1989 and 1990, respectively. Reductions in discharge, and presumably associated changes in habitat, caused brook trout to shift from run to pool habitats (Kraft 1972) and rainbow trout to emigrate from enclosures (Randolph and White 1984) and experimental channels (White et al. 1981). Fish did not exhibit an immediate response to flow reductions in these studies. Kraft (1972) observed that brook trout emigration peaked 10 d after a 90% reduction in discharge. Randolph and White (1984) reported a 10 to 15 d time lag substantially increased correlations between number of trout remaining in stream enclosures and habitat characteristics after discharge was artificially reduced.

Because stream discharge was not stable during the tests in Brackett Creek, simultaneous measures of cutthroat trout density and habitat at the end of the tests may not have adequately described the relationship. Trout densities were greater in 1990 than 1989 in all but one enclosure. Although stream discharge was similar at the end of the tests in both years, discharge was higher during the test in 1990 than 1989. Also, potential errors in results from 1989 when habitat features were estimated rather than measured at the end of tests may have influenced my results.

Although no consistent trends in cutthroat trout density were observed among enclosures, trout grew more in experimental compared to control enclosures. Supplemental feeding increased daily caloric drift rates by at least two-fold in experimental enclosures. Direct relationships between salmonid growth and abundance of potential food organisms are well established and have been shown to vary spatially (Ellis and Gowing 1957; Gibson and Galbraith 1975) and temporally (Waters 1982). In a natural stream, growth of juvenile coho salmon was increased by augmenting food supply (Mason 1976). Juvenile steelhead trout and coho salmon (Johnston et al. 1990) and juvenile and adult Arctic grayling (Deegan and Peterson 1992) had greater growth rates in stream sections enriched with inorganic nutrients compared to control sections. Nutrients increased periphyton which elicited an increase in benthic invertebrate abundance. Also, production of juvenile cutthroat trout was significantly increased in stream areas enriched with sucrose compared to control areas (Warren et al. 1964). In Brackett Creek, mean specific growth rates of cutthroat trout were directly associated with mean caloric drift rates among enclosures each year.

There was considerable variation in cutthroat trout growth rates within enclosures. Most studies relating salmonid growth to abundance of potential food organisms have concentrated on juvenile salmonids (Warren et al. 1964; Mason 1976; Johnston et al. 1990), but when older fish are considered, they typically exhibited greater variability in growth rates than young-of-the-year individuals (Deegan and Peterson 1992). I used older trout (r1) in my tests, and trout that experienced negative or no change in weight during the tests were present in all enclosures, with the exception of one experimental enclosure in 1990 (enclosure 4) where all trout grew. However, the numbers of trout that did not increase in weight were significantly greater in control than experimental enclosures indicating the effects of supplemental feeding.

Differential growth rates among trout within an enclosure may have been related to social status. In salmonid populations, dominance is usually conferred to large individuals that occupy stream sites affording greater net energy intake (Hughes 1992a, b) and potential growth than sites used by subordinate individuals (Symons 1971; Li and Brocksen 1977; Abbott and Dill 1989). In Brackett Creek, correlations between specific growth rate and final trout length and weight were predominantly negative and not significant. Exceptions were some experimental enclosures with nonsignificant, but positive correlations. This suggests that, at levels of food abundance in Brackett Creek, no great differences existed for potential profit (Fausch 1984) among sites occupied by trout if dominance hierarchies were established within the enclosures.

Changes in length and weight were not isometric for trout collected in traps and those recovered at the end of the tests. Because fish on deficit rations initially utilize lipid reserves for metabolic requirements (Weatherley and Gill 1987), reductions in length would not be expected with weight loss, but observed increases in length for cutthroat trout, even those that lost considerable weight, were unanticipated. Comparing growth of Arctic grayling between fertilized and control river sections over 4 years, Deegan and Peterson (1992) noted increases in fish total length even when there was a negative change in weight. While measurement errors probably contributed somewhat to changes in length of cutthroat trout in Brackett Creek, the preponderance of trout with increased length suggests that trout were allocating energy reserves to structural tissues at the expense of other tissue. The adaptive nature of this growth pattern is unknown, but the overall effect was a decline in condition factors during the tests. While the use of condition factors has been criticized, inspection of regression coefficients has been suggested as a more accurate means to depict length-weight relationships (Cone 1989). In Brackett Creek, slopes of length-weight regressions were greater for trout in experimental enclosures at the end of the tests than at the start in 1990, while slopes were similar for trout in control enclosures in 1990 and all enclosures in 1989 (Table 12).

Among enclosures, trends in mean specific growth rates for cutthroat trout were similar between years. Absolute growth, however, was considerably greater in 1990 than in 1989, especially in experimental enclosures. This would be unexpected if growth was solely dependent on food abundance since invertebrate drift rates were generally higher in most enclosures in 1989. In fact, trout stomachs contained more prey in 1989 than 1990, even in enclosures with lower drift rates in the former year. Therefore, factors other than food abundance must have influenced salmonid growth.

Newman and Waters (1989) concluded that factors affecting an entire stream (e.g. temperature and discharge) influenced brown trout growth rates more than habitat differences between stream sections. A major difference in test conditions between years in Brackett Creek were that tests began and ended later in 1989 than 1990. Hence, stream discharge and perhaps quality of trout habitat were at lower levels in the former year. Also, water temperature varied more in 1989 than in 1990, which would have reduced trout growth rates, particularly during the period of low water temperatures in 1989. But between years, temperature does not adequately explain differences in growth rates of trout in experimental enclosures. Trout in experimental enclosures attained an average of 11 to 29% and 57 to 70% of predicted maximum growth rates (based on ecological growth coefficients) in 1989 and 1990, respectively. Mean ecological growth coefficients were similar between years in control enclosures, ranging from negative values for trout that lost weight to a maximum of 1% and 10% in 1989 and 1990, respectively. While bioenergetic equations accounted for differences in water temperature and trout size, their use did not resolve growth differences between years.

I believe that the variability in water temperature, lower stream discharge, and perhaps the later dates of the tests in 1989 than in 1990 may have interacted in influencing cutthroat trout growth. Allen (1969) noted unexplained reductions in fish growth during late summer and early fall when water temperature and food abundance appeared to be adequate for higher growth rates than observed. Low growth of fish in 1989 may have been related to a seasonal growth cycle accentuated by fluctuations in water temperature. Swift (1955) and Brown (1957) noted growth patterns in brown trout, presumably related to maturation of gonads, in which growth rates were depressed for up to two months during the post-spawning period. If a similar pattern exists in cutthroat trout, using greater numbers of trout that had spawned in 1989 than in 1990 may have potentially contributed to differences in growth rates between years. Furthermore, Cunjak (1988) noted a period of rapid lipid loss in early winter as brook trout acclimatized to winter conditions in Ontario streams. This may occur earlier for cutthroat trout in a headwater stream such as Brackett Creek and contribute to differences in cutthroat trout growth rates.

My estimates of food consumption rates based on stomach contents (as well as bioenergetic equations) should be interpreted with caution. Estimates were based on equations derived for brown trout under laboratory conditions and were not verified for their use with cutthroat trout. Stomach contents were collected at one point in time so that possible temporal feeding patterns and food consumption during the tests could not be addressed. With these limitations aside, after supplemental feeding, trout in most experimental enclosures generally achieved greater consumption rates (calories) than those in control enclosures. These results concur with the growth rate data. Also, consumption rates were greater in 1989 than 1990. This was contrary to growth results but consistent with relative drift abundance between years.

With the exception of dipterans, trout used most prey categories in lower proportion than their abundance in the drift. Within dominant prey categories, trout tended to select individuals with greater average body length (Bisson 1978; Ringler 1979; Allan 1981). Brine shrimp and krill were under-represented in trout stomachs compared to their relative abundance in the drift. This was probably influenced by the large quantity and pulsed availability of this prey category. Supplemental food was well represented in the diets of trout and it should be noted that mean body length of brine shrimp and krill (4 and 16 mm, respectively) was considerably greater than that of naturally drifting stream taxa (typically 2-4 mm).

Shortcomings of the consumption rate estimates from stomach contents can also be applied to my use of bioenergetic equations. I assumed that equations were applicable to cutthroat trout and that predicted values approximated those potentially incurred by trout in Brackett Creek. Of all trout recovered from enclosures at the end of the tests, eight (<4%) had observed growth rates exceeding their predicted maxima. Therefore, the energetic models were useful for identifying potential ranges in metabolic requirements and consumption rates as well as providing a means to account for effects of trout size and temperature (Preall and Ringler 1989).

Bioenergetic models also allowed me to compare predicted consumption rates of trout to potential food abundance. In this respect, foraging efficiencies indicated that more than adequate food was present for all trout in enclosures to exceed maintenance consumption rates and, in most instances, maximum consumption rates. Since trout growth was below the predicted maximum, differences between observed and predicted growth rates may have resulted from inadequacies in the bioenergetic equations, other factors affecting individual trout (e.g. higher than predicted energy expenditures), and discrepancies between food abundance and actual availability. Wilzbach et al. (1986) explained differences in relative growth rates of confined cutthroat trout in enclosed pools by differences in drift abundance and habitat. They proposed that habitat features (substrate crevices and shading) controlled availability of drift as potential prey, i.e., likelihood of a drifting individual would be detected and preyed on by a trout. Also, Power (1992) found that invertebrate prey vulnerability varied with substrate refuges so that capture success by fish was greater on bedrock-boulder substrates than cobbles. Therefore, trout foraging behavior (prey selection, capture and handling time, and time of feeding) and habitat variables mediates actual prey availability which is related to prey abundance (Brocksen et al. 1968). Measures of drift abundance in Brackett Creek may not have been an adequate indicator of prey availability to cutthroat trout.

The behavior of cutthroat trout to the augmented food supply in Brackett Creek partially corroborates current ideas of population dynamics in stream-dwelling salmonids. These ideas hold that salmonid abundance is primarily influenced by availability of suitable habitat, recruitment, mortality, and emigration (McFadden 1969; Allan 1969; Newman and Waters 1989). But salmoid growth is primarily dependent on food availability (Mason 1976; Waters 1982; Johnston et al. 1990; Deegan and Peterson 1992) and independent of population density (McFadden 1969; Bachman 1984; Newman and Waters 1989). While cutthroat trout density was not related to habitat features I measured in Brackett Creek, growth rate was independent of population density but varied directly with abundance of potential food items in late summer. Tests conducted throughout the year or in other seasons may reveal other relationships.

Activities that augment abundance of potential fish-food organisms in streams can be expected to increase trout growth rates. If stream habitat is not degraded by such activities, elevated growth rates may elicit increases in trout survival (Martin et al. 1981) and fecundity (Wootton 1985), potentially leading to greater long-term population density.

Summary

Six single pool-riffle complexes were enclosed with fish traps to investigate effects of supplemental feeding on cutthroat trout (≥ 90 mm TL) density and growth rates in a small stream during late summer. Cutthroat trout density was increased in all enclosures and half of the enclosures received daily feeding of frozen brine shrimp and krill.

No consistent trends were observed in final trout density between fed, experimental enclosures and unfed, control enclosures at the end of 65-75 d tests over 2 years. Also, no association was observed between trout density and habitat features measured in each enclosure. Most emigrating trout lost weight during the study in both control and experimental enclosures. However, mean specific growth rates of trout remaining in enclosures at the end of the tests were greater in experimental than control enclosures and the number of trout exhibiting positive growth was significantly greater in experimental than control enclosures.

Based on bioenergetic equations, trout in experimental enclosures attained 11 to 70% of their potential maximum growth rate while trout in control enclosures either lost weight, did not grow, or attained 1 to 10% of predicted maximum growth rate. Comparisons of predicted food consumption rates of trout to periodically sampled invertebrate drift rates indicated that drift was more than adequate to allow trout to achieve growth rates in excess of those observed.

I conclude that, for relatively short periods during summer months, food abundance primarily affects cutthroat trout by influencing growth rates but not density of trout inhabiting principally pool habitats. Trout growth rates and predicted food consumption rates suggest that food abundance, measured as invertebrate drift rate, may not adequately describe actual food availability to trout.

RELATIVE INFLUENCE OF FOOD AND WATER DEPTH ON JUVENILE CUTTHROAT TROUT RESIDENCY IN ARTIFICIAL STREAM CHANNELS

Introduction

Several approaches for recommending stream flows to protect fishery resources are based on the assumption that habitat is the primary factor affecting fish populations (Wesche and Rechard 1980; Orth 1987). Larger numbers of rainbow and steelhead trout, *Oncorhynchus mykiss*, (White et al. 1981), rainbow trout (Randolph and White 1984), brook trout, *Salvelinus fontinalis*, (Kraft 1972) and chinook salmon, *O. tshawytscha*, (Krueger 1979) emigrated from controlled flow channels or streams subjected to discharge reductions than did fish exposed to constant flow or the natural flow regime. Free ranging salmonids in streams have been found associated with specific habitat features such as water velocity, depth, pool volume, and quantity of overhead cover (Boussu 1954; Elser 1968; Hunt 1969; Lewis 1969; Stewart 1970; Wesche 1974; Binns and Eiserman 1979; Bowlby and Roff 1986), all of which are related to stream discharge.

The instream flow incremental methodology (IFIM) defines fish habitat primarily by water depth, velocity, and substrate (Bovee and Cochauner 1977). The method predicts amount of usable stream area (weighted usable area, WUA) at various discharges for fish by using species specific preference ratings for the three habitat components as weighting factors. Although the IFIM is widely used in North America (Resier et al. 1989), attempts to relate WUA to fish populations have generally been inconclusive (Orth and Maughan 1982; Mathur et al. 1985; Scott and Shirvell 1987). Orth (1987) warned that measures of habitat availability may not be consistent predictors of fish abundance since the IFIM does not consider other factors affecting fish population dynamics and the functioning of stream ecosystems, e.g., the roles of predation, competition, and energetics.

In contrast to the IFIM, the wetted perimeter inflection point instream flow method (WETP) is not based on flow-induced changes in fish habitat. The method considers potential effects of reduced flow on fish energetics. This method recommends a single flow that maintains wetted perimeter in riffles areas. Because riffles are important to aquatic invertebrate populations, the primary food for many stream fishes, it is assumed that maintaining wetted perimeter will minimize flow-induced reductions in food availability to fish (Leathe and Nelson 1986; Nelson 1989). Also, since physical conditions in riffles are more severely affected by discharge reductions than other stream areas, the method further assumes that flows maintaining riffle wetted perimeter will provide adequate habitat for fish in other stream habitats.

Artificial stream channels have been used to assess the relative roles of food availability and habitat features on stream salmonids, with overhead and instream cover as the habitat features of interest. Wilzbach (1985) varied food availability and cover to cutthroat trout (*O. clarki*) for 7 d in artificial stream channels and found more trout remained in channels receiving high rations, and that ration level influenced cover use. In contrast, Mesick (1988) found that cover was the primary factor determining residency of brown trout (*Salmo trutta*) and Apache trout (*O. apache*) in artificial stream channels. Unfed, adult trout remained in channels when cover was present. While the different conclusions of these studies may be related to species specific responses, the studies illustrate the importance of potential interactions of habitat and food.

Because water depth is a feature of salmonid habitat strongly dependent on stream discharge, I evaluated the relative roles of food availability and two incremental reductions in water depth on short-term residency of juvenile cutthroat trout in artificial stream channels. Two experiments were conducted using two sizes of trout. The null hypotheses tested were that ration level and depth reduction would have no effect on the number of trout remaining in channels.

Methods

The study was conducted in two indoor stream channels at the Bozeman Fish Technology Center, U.S. Fish and Wildlife Service, Bozeman, Montana. Channels were rectangular (outer dimensions: 6.50 m long, 2.00 m wide, 0.41 m deep) with outer walls and floor constructed of coated plywood (opaque black). Glass inner walls formed a central observation area (Figure 41). A single channel consisted of two long arms 0.60 m wide connected by two short arms at the ends; channels were 1.2 m above the floor.

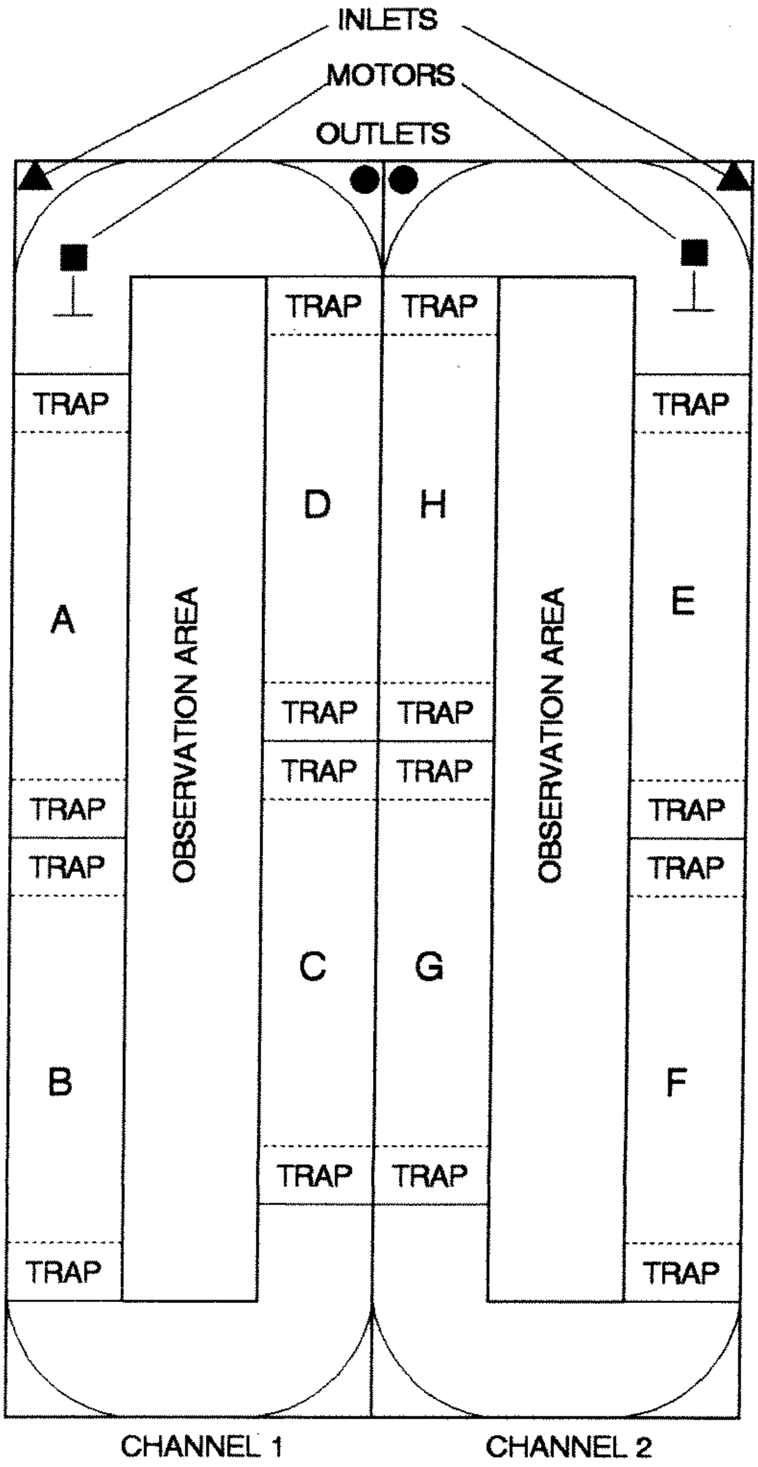

Figure 41.-Overview of experimental channels showing locations of individual chambers (A-H), fish traps, electric motors, water inlets, and water outlets.

Channels received water from warm and cold springs (mixed to 8-10 C, 10-12 L/min) and water depth was controlled by a standpipe placed in outlet drains. An electric outboard motor continuously circulated water in each channel (Figure 41). Channels were exposed to three light levels. The highest light intensity was supplied by five pairs of fluorescent lamps (40 W/lamp) located 1.1 m above each long arm of the channels. Translucent plastic sheets suspended below the lamps diffused light so that mean light intensity was 7.9-10.8 $\mu E/s/m^2$ at the water surface in the long arms of the channels. Incandescent flood lamps (120 W), one located 1 m above each short arm of a channel, produced intermediate light intensities (0.12-0.28 $\mu E/s/m^2$). The lowest light level (0.06-0.09 $\mu E/s/m^2$) was produced by strings of miniature white lights attached to the undersides of the translucent plastic sheets below the fluorescent lamps. All light sources were controlled by timers. Channels were illuminated at the highest light intensity for 12 h (0800 to 2000) each day. Gradual increases in light intensity in the mornings were achieved by setting the miniature lights to turn on at 0730. These were followed by the flood lights at 0745 which were turned off after the fluorescent lights came on at 800. This sequence was reversed at 2000.

Four experimental chambers were formed by equally partitioning the long arms of each channel with 1.5 mm mesh plastic screens. Each chamber was 2.35 m long (designated A-H; Figure 41) with fish traps (V-shaped, 6 mm nylon mesh) at both ends. The floor of each channel was covered with 2-3 cm diameter gravel forming a regular series of shallow-deep-shallow areas (Figure 42). Two solid blocks (5.7 cm

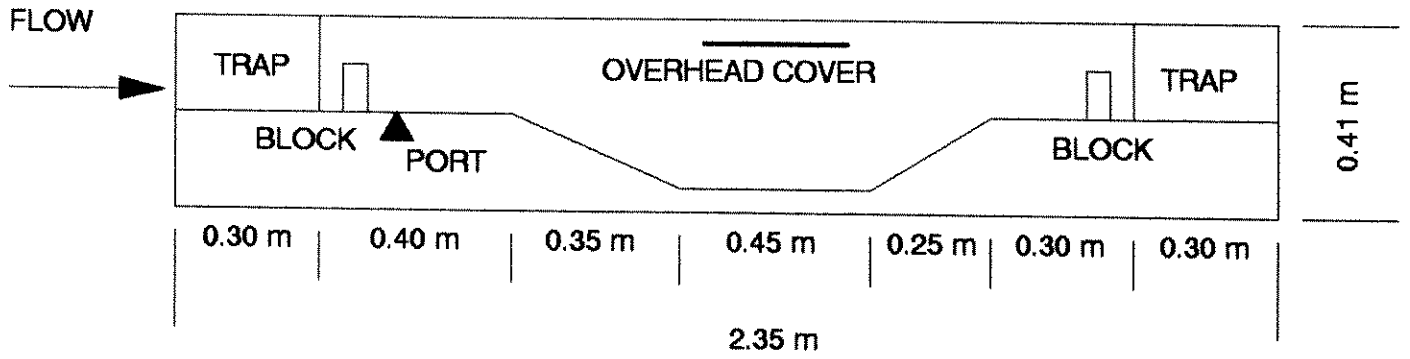

Figure 42.-Individual chamber showing direction of water flow, dimensions and locations of fish traps, overhead cover, blocks, and food delivery port.

wide, 9.2 cm high, and 19.9 cm long) were placed with the longest side perpendicular to water flow and the narrow side against the outer wall in the two shallow areas in each chamber. Overhead cover was provided by a styrofoam square (900 cm^2) placed against the inner wall at the midpoint of the deep area in each chamber. The squares, held in place with a 41 cm wooden rod extending from the gravel floor, floated on the water surface.

Water depths tested were 18.0 cm, 9.0 cm, and 4.5 cm in shallow areas of each experimental chamber. Corresponding water volumes were 0.26 m^3, 0.16 m^3, and 0.11 m^3 while surface area (1.05 m^2) was not affected. Water volumes were reduced 37% and 55%. When changing standpipes, water depth stabilized in about 30 min.

Water depth and velocity (0.6 depth) were measured in each chamber at the three water levels with an electronic current meter and a section of a top-setting rod. Measurements were taken at five equally spaced locations across the width of each chamber every 10 cm along the shallow and deep areas. Water velocity ranged from 0.03 to 0.11 cm/s and was similar in all chambers. Mean water velocity for a chamber was 0.06 to 0.07 cm/s and differed by $<$ 1 cm/s at the three water depths tested.

Tops of all chambers were covered with clear plastic sheets and a 1.5 mm mesh plastic screen was placed over each trap to prevent fish from leaping out. Each chamber was surrounded by black plastic curtains; black cloth curtains with viewing slits covered the inner glass walls of the channels.

Food was supplied to each chamber through a single plastic tube, perforated with six 5-mm holes, buried below the gravel in the upstream shallow area. Tubes extended the width of the channels and were attached to 3-L containers located above the channels. Frozen brine shrimp (Murex Aqua Foods Inc.) were placed in the containers with water. As shrimp thawed, they were maintained in suspension by an air stone and pump and gravity fed into the chambers.

Experiment 1 was conducted from April to June 1990 and used small Yellowstone cutthroat trout (*O. c. bouvieri*; 51-75 mm total length). Fish were cultured from eggs and sperm of wild fish (3 females and 4 males) collected in Brackett Creek, Gallatin County, Montana, on 26 June 1989.

Approximately 450 trout were available for the experiment in April 1990. Fourteen days before beginning tests, fish were offered thawed brine shrimp in addition to pelleted food. Seven days later, trout were moved from a hatchery trough into a 420 L holding tank located under the experimental channels. The tank received water from the channels (3 L/min) and fish were exposed to the experimental light regime. Trout were fed 2% of total fish biomass of frozen brine shrimp (dry weight) per day, half in the morning and evening.

An individual test consisted of selecting two ration levels (0, 1%, or 2% of initial fish biomass) of which one was assigned to each chamber. Identical ordering of ration levels for chambers was used in each channel and unfed chambers were always located in front of a fed chamber. One channel received water depth reductions while the other channel served as a control. Three tests were conducted so that every combination of ration and water depth was repeated four times.

Ten to 15 trout were netted from the holding tank and anesthetized with tricane methanesulfonate. Total length (mm) and weight (0.1 g) were recorded. Trout were introduced into a chamber after fish had recovered from anesthesia. This process was repeated by adding groups of trout to randomly selected chambers until 35 individuals had been introduced into each chamber. During a 5 d acclimation period, traps were closed. Throughout the tests, food was supplied at 0900 and 1800 daily. Traps were opened on the evening of day 5 and were inspected daily after the morning feeding. Date, trout total length, weight, and direction of movement were recorded for trapped individuals. Emigrants were moved to the holding tank. Water depth was reduced in one channel on the evenings of days 10 and 15. Trout that had emigrated during these days prior to water depth reduction in the evening were removed from traps in all chambers. On the morning of day 20, the test was concluded and all trout were removed from the chambers, counted, and lengths and weights recorded. Channels were then drained, cleaned, and filled with water and trout were introduced for the next test.

Because of limited number of trout, test fish were reused in the second and third tests. To minimize potential effects, only trout emigrating during the first 10 days were used in subsequent tests. Thus, reused trout had at least a 10 d period before being used in later tests.

Experiment 2 was conducted from March to June 1991 using larger trout (122-159 mm total length). Two hundred cutthroat trout were obtained from the Montana Department of Fish, Wildlife, and Parks hatchery in Big Timber, Montana. Tests were similar to experiment 1 except that 10 trout were introduced into each chamber and ration levels were 1%, 2%, and 4% of initial fish biomass of frozen brine shrimp (dry weight). Also, the amount of overhead cover was increased to 2800 cm^2 and the acclimation period was 9 d.

The number of trout remaining in each chamber at the end of the tests were ranked. An extension of the Kruskal-Wallis test for two-factor designs (Zar 1984) was used to test for the effects of ration and water depth reduction. A nonparametric analog of the Newman-Keuls multiple range test was used to compare differences in ration (Zar 1984). A significance level of 0.05 was used in all tests.

Results

Because three tests were required to replicate each combination of water depth and ration level four times in both experiments, 20-24 d separated day 1 of tests. Trout used in the experiments grew in length and weight between tests (Table 16). Trout significantly differed in length and weight ($P<0.001$, Kruskal-Wallis tests) among the three tests. Maximum differences in the means for length and weight were 10 mm and 1.0 g, respectively, in experiment 1, and 16.3 mm and 8.7 g in experiment 2 (Table 16).

Volitional residency of small trout was significantly influenced by ration level ($P<0.001$, Kruskal-Wallis test) but not by water depth

Table 16.-Summary of ration levels, water depth reductions, and mean (SE) trout length and weight for experiment 1 with small (51-75 mm) and experiment 2 with large (122-159 mm) cutthroat trout conducted in two artificial stream channels at Bozeman Fish Technology Center.

Test	Ration levels	Water depth		Mean fish	
		channel 1	channel 2	length (mm)	weight (g)
			Experiment 1		
1	0, 2%	reduced	constant	59.5(0.2)	1.8(0.1)
2	1%, 2%	constant	reduced	63.9(0.3)	2.3(0.1)
3	0, 1%	reduced	constant	69.5(0.3)	2.8(0.1)
			Experiment 2		
1	1%, 2%	reduced	constant	130.8(0.5)	19.1(0.3)
2	2%, 4%	constant	reduced	137.0(0.7)	22.6(0.4)
3	1%, 4%	reduced	constant	147.1(0.9)	27.8(0.6)

reductions (P=0.769, Kruskal-Wallis test; Figure 43). There was no interaction effect between the factors (P=0.976, Kruskal-Wallis test). Without regard to water depth, mean number of trout remaining in chambers was 0.4 for 0 ration, 3.5 for 1% ration, and 14.8 for 2% ration. Although there was considerable variation, rank of number of trout associated with each ration level at the end of tests significantly different among all levels (P<0.05, nonparametric Newman-Keuls test). While the number of trout remaining in each chamber ranged from 0 to 1 and 0 to 9 for 0 and 1% rations, respectively, 10 or more trout typically remained in chambers receiving 2% rations (in one instance only one remained; Figure 43).

Excluding this chamber yielded a mean of 19.3 trout (range 15-25) remaining at the end of the 2% ration tests.

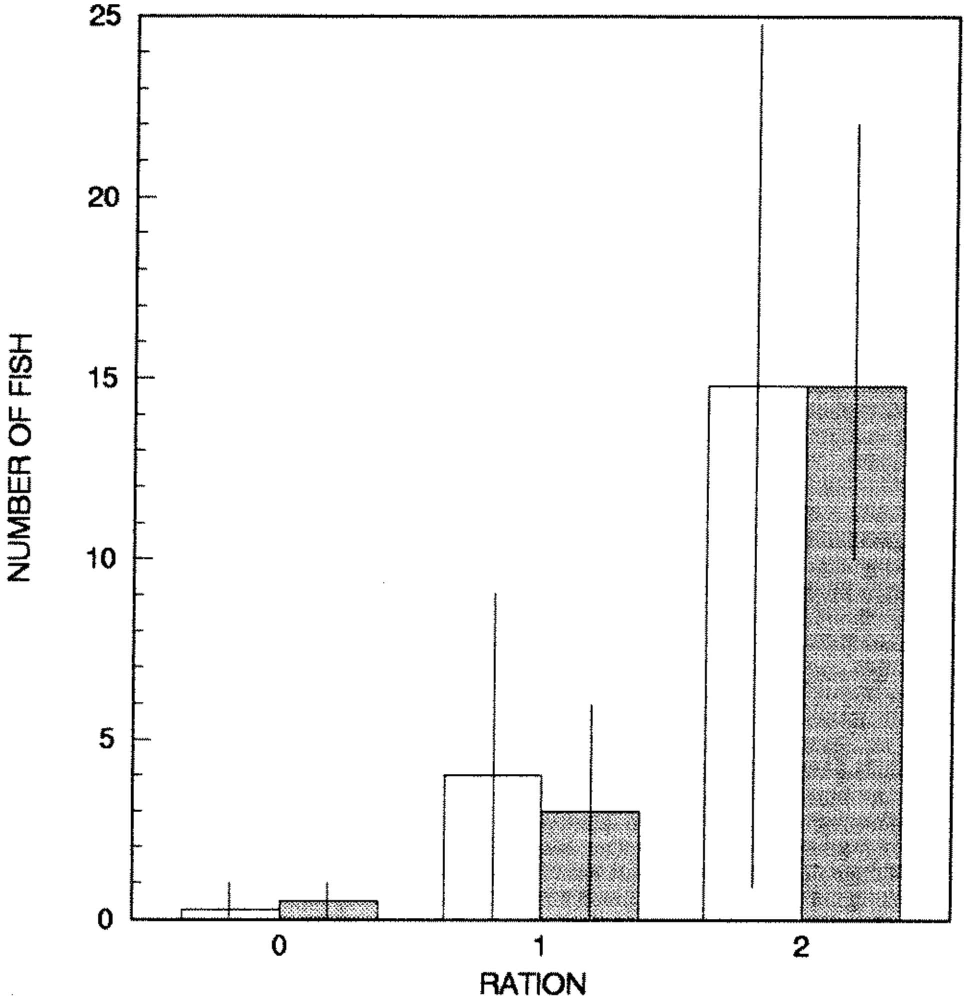

Figure 43.-Mean number of small cutthroat trout (51-75 mm, experiment 1) remaining in chambers at end of tests by ration (0, 1%, and 2% initial trout biomass) for constant (open bars) and reduced (shaded bars) water depth channels. Vertical bars are ranges, N=4 chambers.

Mean number of trout remaining in a chamber on each test day was similar for each ration level between channels with reduced and constant water depths (Figure 44). A substantial proportion of trout emigrated from chambers in the 5 d that traps were open but before

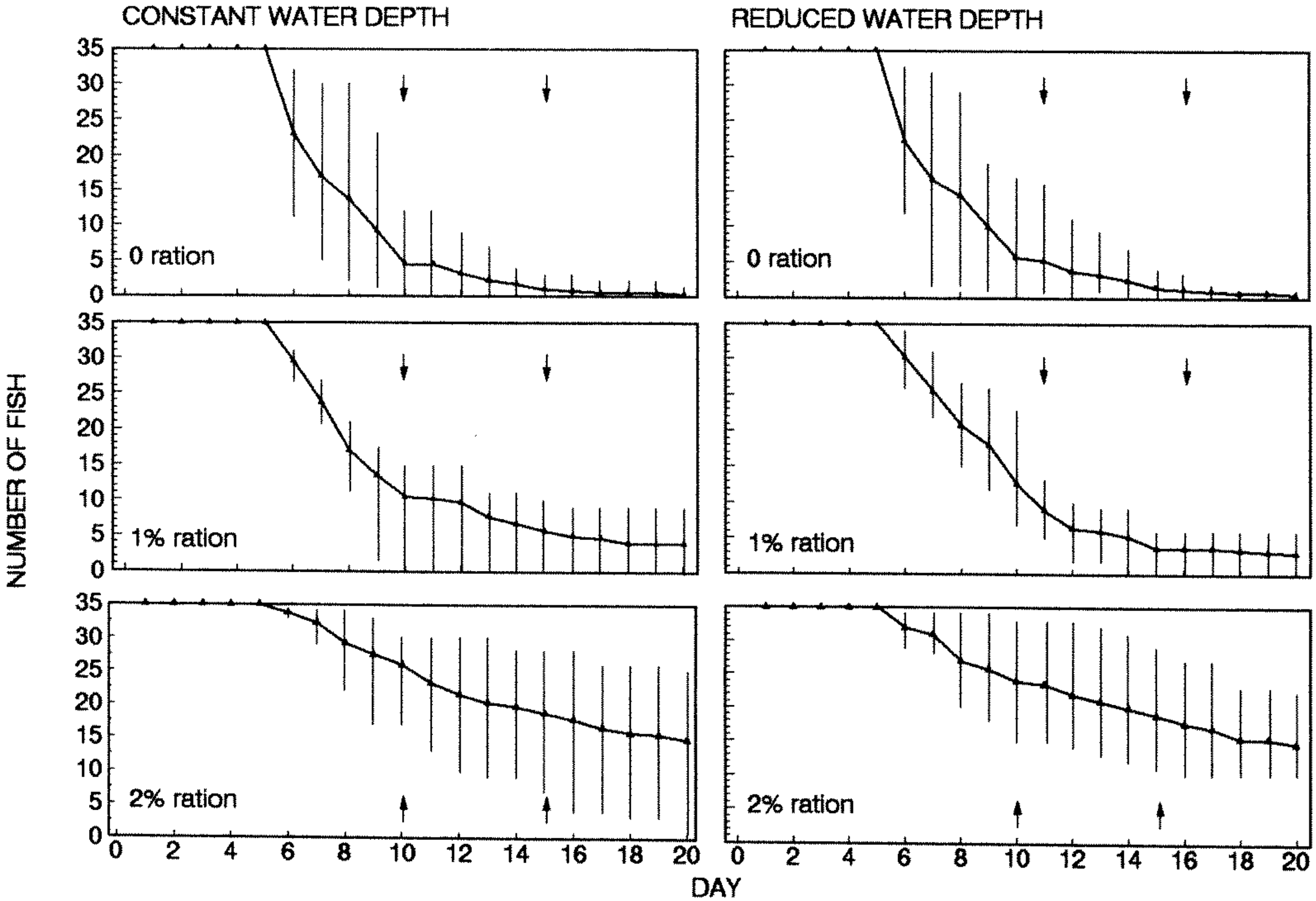

Figure 44.-Mean number of small cutthroat trout (51-75 mm, experiment 1) in chambers per day by ration (0, 1%, and 2% initial trout biomass) and water depth (constant and reduced). Water depths were reduced on the evenings of days 10 and 15 (arrows). Vertical bars are ranges, N=4.

water level was reduced. The percentage of trout that emigrated on day 1 ranged from 6% to 69% for unfed trout, 3% to 26% for 1% rations, and from 3% to 17% for 2% rations. Before the first water depth reduction, all trout had emigrated from some chambers receiving 0 and 1% rations. Although daily number of trout in a chamber greatly varied for ration levels, emigration was lowest for trout that received 2% ration and highest for unfed trout.

Most trout emigrated in an upstream direction, but more of the unfed trout moved downstream than did the trout that were on 1% or 2% rations (Figure 45). More than 50% of emigrating trout from unfed chambers entered downstream traps in over half of the chambers, over 50% of trout on 1% and 2% rations entered upstream traps of most chambers. Trout emigrated exclusively upstream from some fed chambers.

Size of fed trout increased during the tests. Mean length and weight increased for emigrants and residents compared to initial mean length and weight.

For analysis of trout length and weight at the end of tests, only chambers with more than one trout remaining were considered. Also, lengths and weights from trout in test 1 were not considered because of mechanical problems with an outboard motor at the start of the test. Four days lapsed between the time trout were introduced into the chambers and the start of the 5 d acclimation period. Fish were allowed to remain in the channels but received 2% rations during this time.

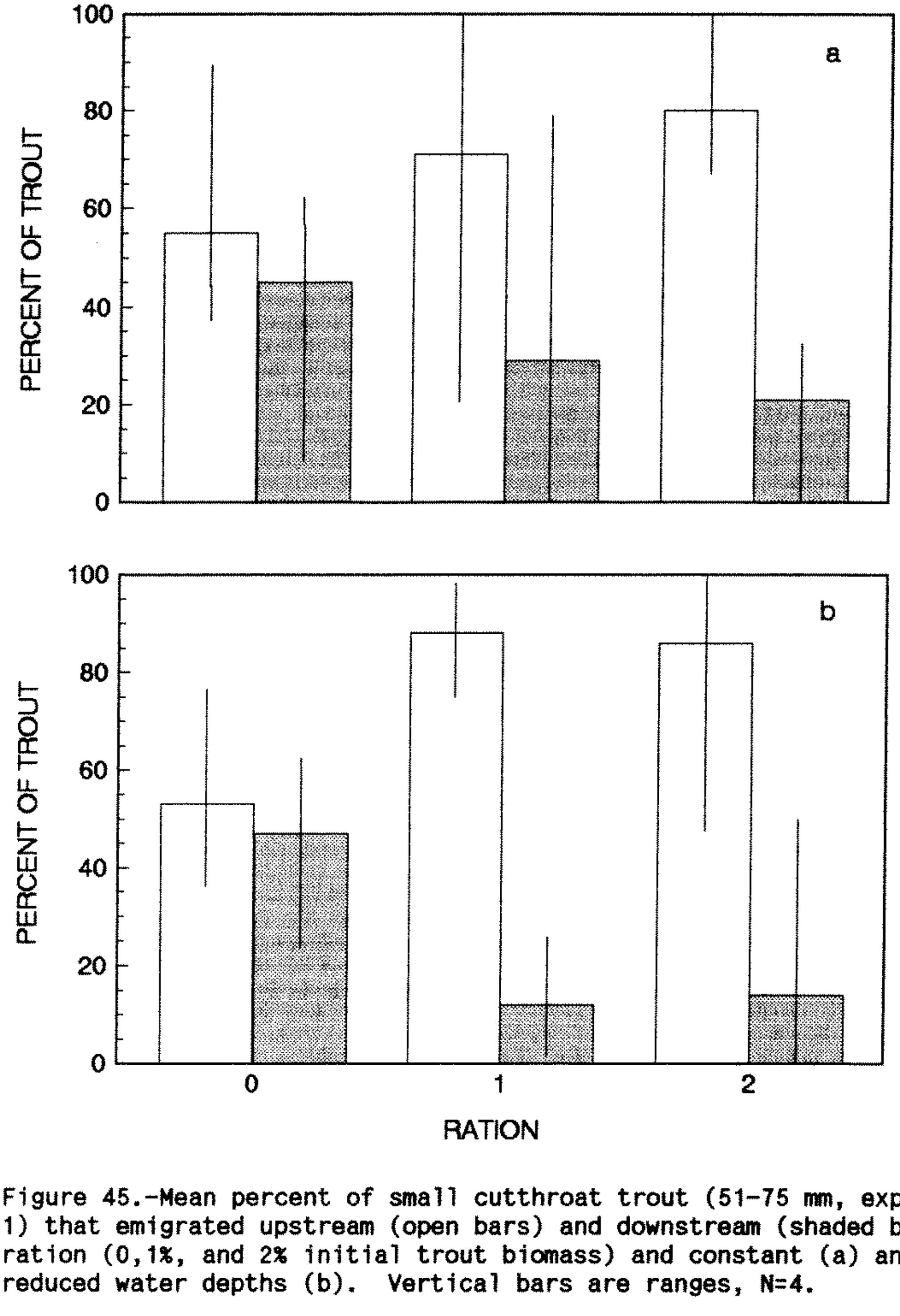

Figure 45.-Mean percent of small cutthroat trout (51-75 mm, experiment 1) that emigrated upstream (open bars) and downstream (shaded bars) by ration (0,1%, and 2% initial trout biomass) and constant (a) and reduced water depths (b). Vertical bars are ranges, N=4.

Percent change in mean length and weight of emigrant and resident trout during the tests was similar for trout exposed to constant and reduced water depth tests (Table 17). Mean percent change in both length and weight was negative for unfed emigrant trout and only one trout remained in three chambers at the end of tests. Trout that emigrated in the 1% ration tests increased in length and weight by 2.6% and 6.5%, respectively, compared to 4.0% and 21.0% increase in the 2% ration tests (Table 17). Percent change in length and weight of trout remaining in chambers was 6.3% and 34.4%, respectively, for 1% ration tests and 9.0% and 40.1% for the 2% ration tests.

For larger trout in experiment 2, food availability and water depth reductions did not affect volitional residency of trout. Virtually all trout emigrated from experimental chambers by the end of the tests. A single trout remained in five chambers that received various rations, and two trout remained in a chamber that received 1% ration at the end of the tests. Although the number of trout in a chamber per day varied, higher rations slightly decreased emigration rate (Figure 46). Mean percentage of trout that emigrated on the first day after traps were opened was 13%, 10%, and 5% for 1%, 2%, and 4% rations, respectively. By day 5 (depth unchanged), mean percentage of trout that had emigrated was 76%, 66%, and 55% for 1%, 2%, and 4% rations, respectively. Overall, trout emigrated in an upstream direction (Figure 47); trout receiving 1% ration in constant water depth showed this more than trout in other treatments.

Table 17.-Mean (SE) percent change in mean cutthroat trout length and weight from start of tests for trout recovered in traps (emigrants) and at the end of tests (residents) by ration and water depth for experiment 1. Only chambers with > 1 trout at end of tests 2 and 3 were used. N=number of chambers.

	Ration level					
Measure	0	N	1%	N	2%	N
			Constant water depth			
Length emigrants (mm)	-0.5(0.10)	2	1.1(3.48)	4	4.3(0.13)	2
Weight emigrants (g)	-4.8(0.83)	2	5.6(0.96)	4	19.6(0.28)	2
Length residents (mm)	-	-	6.3(1.20)	2	8.7 -	1
Weight residents (g)	-	-	37.8(9.93)	2	41.0 -	1
			Reduced water depth			
Length emigrants (mm)	-0.7(0.24)	2	4.0(2.00)	4	3.8(3.94)	2
Weight emigrants (g)	-5.3(0.71)	2	7.5(1.02)	4	22.3(2.03)	2
Length residents (mm)	-	-	6.3(1.22)	3	9.2(0.59)	2
Weight residents (g)	-	-	32.1(7.29)	3	39.6(6.38)	2
			Constant and reduced water depth combined			
Length emigrants (mm)	-0.6(0.13)	4	2.6(1.09)	8	4.0(1.62)	4
Weight emigrants (g)	-5.1(0.47)	4	6.5(0.75)	8	21.0(2.41)	4
Length residents (mm)	-	-	6.3(0.77)	5	9.0(0.39)	3
Weight residents (g)	-		34.4(5.16)	5	40.1(3.71)	3

Percent change in initial length and weight for trout that emigrated varied directly with ration level (Table 18). Mean length for trout that received 1% ration slightly increased but trout exhibited loss of weight. Trout that received 2% and 4% rations

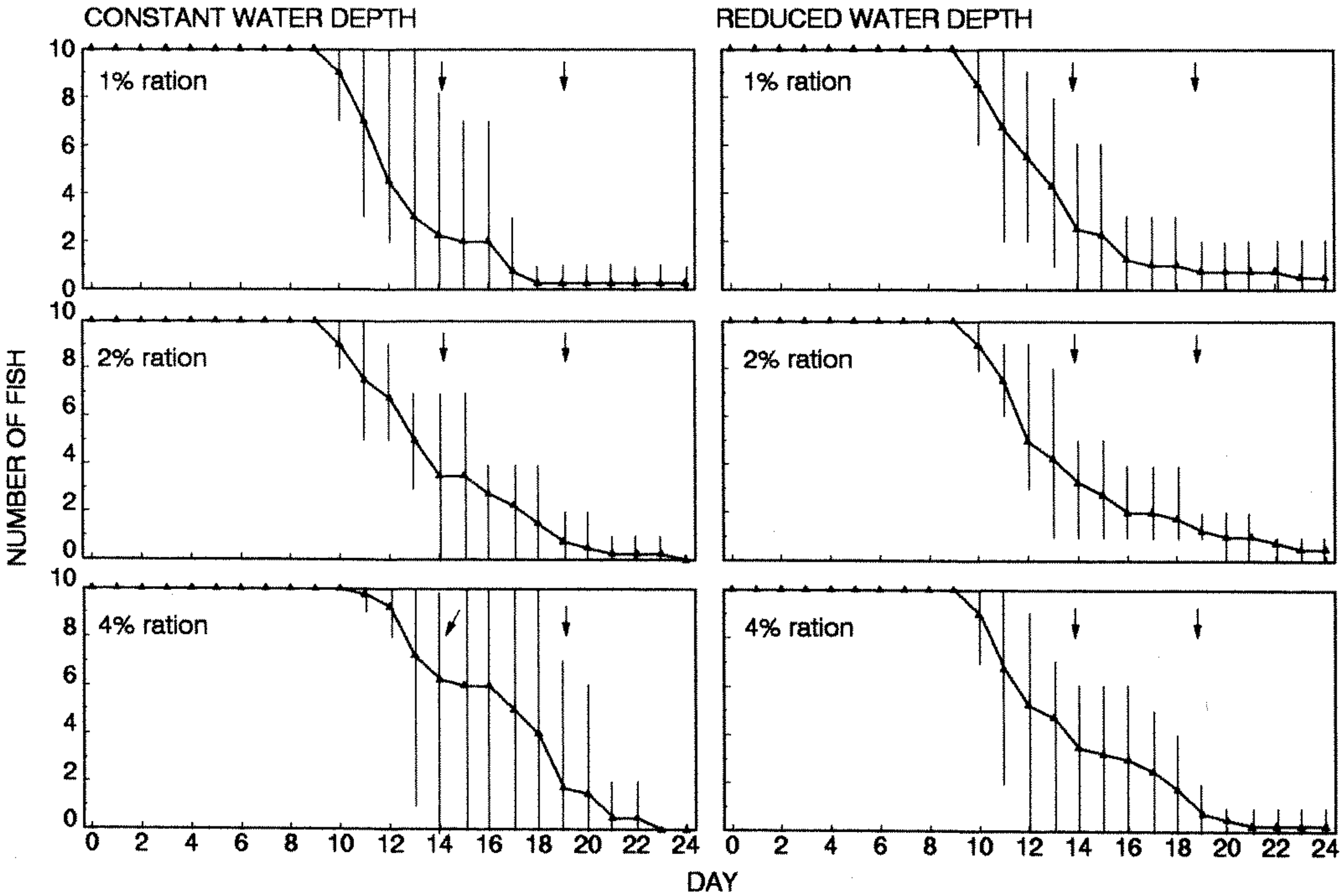

Figure 46.-Mean number of large cutthroat trout (122-159 mm, experiment 2) in chambers per day by ration (1%, 2%, and 4% initial trout biomass) and water depth (constant and reduced). Water depths were reduced on the evenings of days 14 and 19 (arrows). Vertical bars are ranges, N=4.

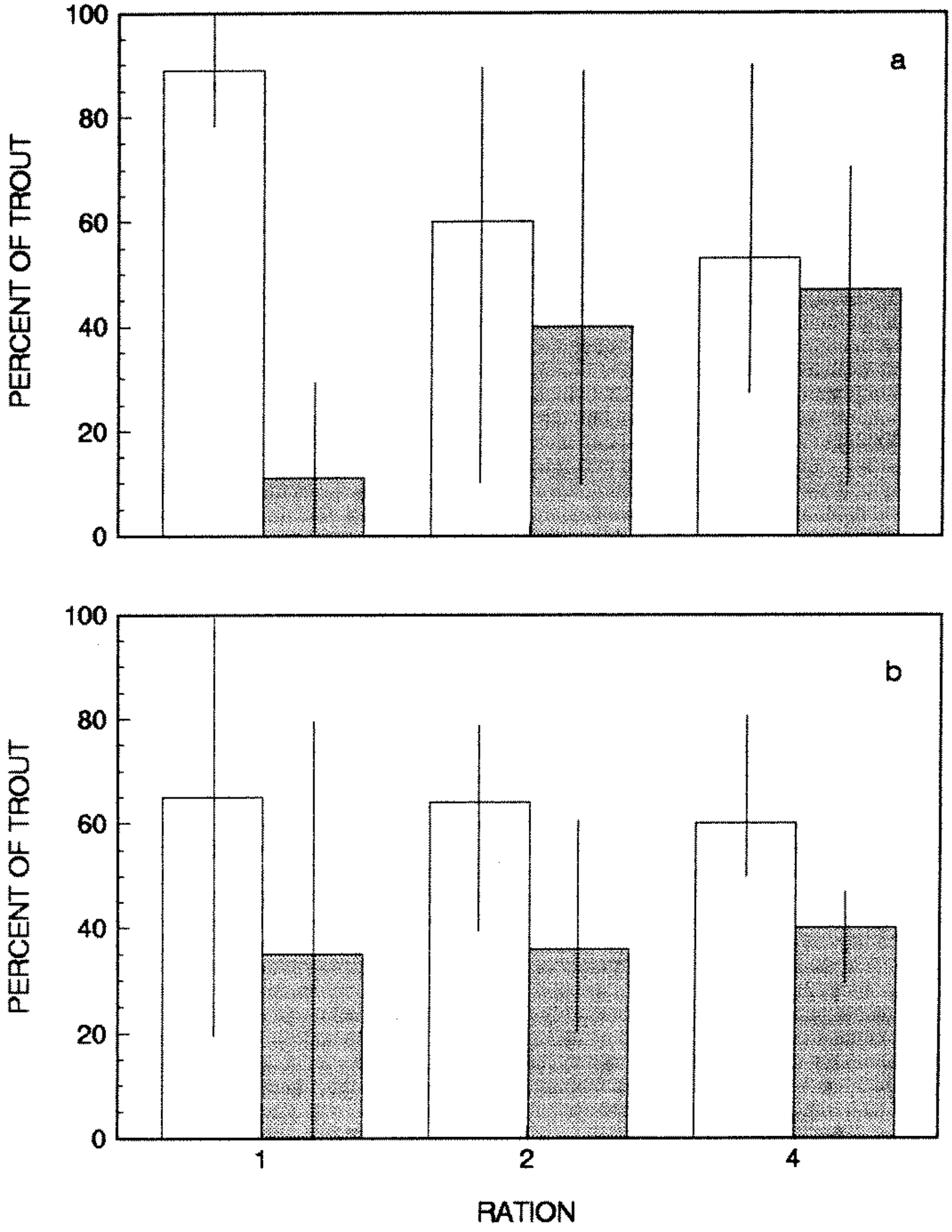

Figure 47.-Mean percent of large cutthroat trout (122-159 mm, experiment 2) that emigrated upstream (open bars) and downstream (shaded bars) by ration (1%, 2%, and 4% initial trout biomass) and constant (a) and reduced water depths (b). Vertical bars are ranges, N=4.

increased in both length and weight. Percent increase in weight was about three times greater for trout that received 4% ration than for trout given 2% rations.

Table 18.-Mean (SE) percent change in mean cutthroat trout length and weight from start of tests for trout recovered in traps by ration and water depth for experiment 2. N=number of chambers.

Measure	Ration level					
	1%	N	2%	N	4%	N
			Constant water depth			
Length (mm)	0.8(0.3)	4	2.9(0.3)	4	5.4(0.8)	4
Weight (g)	-0.7(0.9)	4	8.5(1.7)	4	16.5(6.1)	4
			Reduced water depth			
Length (mm)	1.0(0.3)	4	2.2(0.7)	4	3.4(1.0)	4
Weight (g)	-0.4(1.4)	4	5.0(2.7)	4	15.1(2.2)	4
			Constant and reduced water depth combined			
Length (mm)	0.9(0.2)	8	2.6(0.4)	8	4.4(0.4)	8
Weight (g)	-0.5(0.8)	8	6.8(1.6)	8	15.8(3.0)	8

Discussion

Food availability influenced short-term, volitional residency of small (51-75 mm) cutthroat trout in artificial stream channels. Studies with rainbow trout (Slaney and Northcote 1974), cutthroat trout (Wilzbach 1985), and Atlantic salmon, *S. solar*, (Symons 1971) showed that fish adjusted densities relative to food availability through emigration from experimental stream channels. In my study, the mean number of small trout remaining in experimental chambers varied directly with food availability.

As food availability increased, the range of the number of resident trout increased as did the variation in emigration rate during the tests. Two factors that may have affected this were the relatively high density of trout introduced into experimental chambers and the reuse of some trout in tests. In addressing these problems, Mesick (1988) found that reusing individual fish had no effect on subsequent behavior if fish were held in darkened holding tanks for at least 6 h. He also reported that high stocking densities produced high numbers of residents and increased variability of tests lasting 6 d. At least a 10 d period intervened between reusing trout in my study, and tests were over twice as long as Mesick's (1988) preliminary tests. I assumed these time intervals minimized potential problems associated with reusing trout and with trout density. Even with high variability in my results, trends in the number of resident trout existed.

Changes in mean length and weight of both emigrants and resident trout varied directly with food availability. Konopacky (1984) found a direct relationship between fish density, growth, and production of chinook salmon (*O. tshawytscha*) fry and four levels of food availability in artificial stream channels. While virtually all unfed trout in my study lost weight and emigrated, trout on 1% and 2% rations (both emigrants and residents) increased in length and weight with higher rations resulting in greater gain.

Larger cutthroat trout failed to consistently establish residency in experimental chambers even when lower numbers were introduced and the amount of overhead cover and length of the acclimation period were increased. Mesick (1988) found differential responses in residency for fed and starved Apache and brown trout relative to fish size. Small Apache trout (7.0-8.9 cm standard length) were more likely to emigrate from channels when starved than larger trout, whereas all sizes of brown trout were unaffected by feeding regime. Because most large (122-159 mm total length) cutthroat trout emigrated in my study, presumably the chambers did not afford adequate habitat for short-term residency. Wilzbach (1985) observed that cutthroat trout (10-15 cm) densities varied with food availability. While the size range of trout used was similar to that in my experiment 2, her channels were considerably larger. Even though trout did not remain in chambers, changes in mean length and weight varied directly with food availability.

Although water depth has been identified as an important component of salmonid habitat (Chapman and Bjornn 1969; Stewart 1970), providing space and cover, I found no effect of two incremental reductions in water depth on the number of resident cutthroat trout in experimental chambers. Easterbrooks (1981) observed that wild rainbow and cutthroat trout emigrated from experimental channels at a constant rate relative to depth reductions ranging from 25% to 85%. Also, rainbow trout and cutthroat trout of hatchery origin differed by increasing emigration rate at depth reductions below 50%. In my study, water depth reductions may not have been large enough to influence trout residency. Although volume of experimental chambers was reduced 55% from the highest to lowest water levels, water depth decreased 75% in shallow areas but only 13% in the deep areas. Also, large trout were of hatchery origin and small trout had been reared under hatchery conditions which may have influenced behavior.

Trout emigration was rapid with most trout emigrating within the first few days of tests. Bjornn (1971) and Konopacky (1984) reported similar results. In my study, most trout had left chambers before water depth was reduced, suggesting that trout were responding primarily to differences in food availability since habitat was similar among chambers.

I was unable to discern any behavioral differences between trout exposed to constant and reduced water depth. Changes in water velocity were minimal with reductions in water depth. Small trout frequently changed positions and I was unable to associate individual trout with specific locations in the chambers. In general, trout congregated in the deep and upstream shallow areas of a chamber. Fed trout became conditioned to the location of the food delivery port, and during feeding sessions, most trout moved to the food port and became aggressive. Unfed trout cruised about the chambers showing little association with any particular area. Large trout were found under the overhead cover in the deep area of the chambers but moved to the upstream shallow area during feeding sessions.

Food availability was more important than limited reductions in water depth in determining residency of small cutthroat trout in artificial stream channels. Higher food availability increased residency and growth of small cutthroat trout and lowered trout emigration rates while no effects were observed for reductions in water depth. In a natural stream, supplemental feeding had similar effects on juvenile coho salmon, *O. kisutch*, (Mason 1976) during summer months. Reductions in stream flow that do not influence food availability and maintain stream depths of 4.5 to 20 cm would probably have minimal effects on cutthroat trout fry, but such stream conditions can be expected to severely limit the number of larger trout.

Summary

Tests were conducted in artificial stream channels to determine the relative influence of ration and water depth reductions on short term residency (< 20 d) of two size classes of cutthroat trout. Trout were exposed to three ration levels and water depth was incrementally reduced during tests resulting in a 55% reduction in habitat volume. Number of small trout (51-75 mm TL) remaining in channels at the end of tests varied directly with ration level, whereas water depth reductions had no effect on trout residency. Changes in mean weight of small trout that remained in channels also varied directly with ration. Larger trout (122-159 mm TL) did not establish residency, regardless of ration level, suggesting that habitat was inadequate in artificial stream channels. The relative influence of food abundance and habitat on cutthroat trout residency may be dependent on trout size.

GENERAL SUMMARY, CONCLUSIONS AND MANAGEMENT IMPLICATIONS

General Summary

Montana Department of Fish, Wildlife and Parks applies the wetted perimeter inflection point instream flow method in recommending stream flow reservations to protect aquatic resources. Major considerations in selecting this approach were a method that: 1) used on-site field data, 2) produced a single flow recommendation to simplify compliancy by water users, 3) was cost-effective when applied in a state-wide water reservation program, and 4) maintained aquatic resources at existing levels. Nelson (1980) applied several instream flow methods to four southwestern Montana rivers and evaluated minimum flow recommendations relative to those derived from long-term trout population and stream flow records. He found stream flows corresponding to wetted perimeter inflection points for riffles concurred with those from flow and trout population records. He concluded that a wetted perimeter method, using several riffle transects and calibrated at three stream flows, provided an adequate and cost-effective means to derive minimum instream flow recommendations fulfilling objectives of the Montana Department of Fish, Wildlife and Parks.

The wetted perimeter method produces a composite wetted perimeter-discharge curve for stream riffles. Flow recommendations are made relative to inflection point(s) on the curve to minimize losses in riffle wetted perimeter. Biological assumptions linking discharge-wetted perimeter dynamics to behavior of stream biota are: 1) abundance of aquatic invertebrates is proportional to wetted riffle area, 2) wetted perimeter can be used as an index of riffle area, 3) reductions in discharge below the wetted perimeter inflection point reduces invertebrate abundance, resulting in potential food limitation for fish (i.e. fish abundance and growth are reduced to levels lower than would be realized without reductions in stream discharge). Flow recommendations are proposed to maintain existing aquatic resources.

The goal of my study was to evaluate biological assumptions of the wetted perimeter instream flow method. Specific objectives were to: determine if aquatic macroinvertebrate abundance declines in response to decreases in stream discharge and riffle wetted perimeter, discern the effects of increased food availability on cutthroat trout density and growth rate, and evaluate the relative importance of food availability and habitat influencing trout residency.

Stream discharge directly affects invertebrate abundance in riffles by controlling amount of wetted area present at various flows and by determining hydraulic characteristics of water flow. Riffle wetted area establishes amount of potential invertebrate habitat available, whereas hydraulic characteristics determine water velocity and depth, and influences invertebrate distribution through effects on substrate composition, retention of detritus, and water temperature.

In comparing invertebrate abundance between reference riffles exposed to the natural flow regime and dewatered, test riffles, total benthic invertebrate densities were largely unaffected by water diversion. Although benthic densities varied considerably among samples, densities were not significantly different between the reference and test riffles on four sample dates in Bozeman Creek, despite differences of 20% to 47% and 6% to 29% for stream discharge and wetted perimeter, respectively. I found no differences between riffles in densities of the dominant taxa. However, density estimates were made for riffle areas that remained submersed, so that absolute invertebrate abundance, per riffle length, differed according to riffle area, which is proportional to riffle wetted perimeter. Discharge was below the wetted perimeter inflection at the test riffle on the final sample date when the lowest stream flow was measured.

Body length of total invertebrates and *Baetis* spp. was significantly smaller at the test than the reference riffle when discharge was below the wetted perimeter inflection point in Bozeman Creek. This resulted in significant reductions for biomass and caloric density at the test riffle. Size differences between riffles were unlikely due to phenological events since the riffles were relatively close, water temperatures were identical between riffles, and measures of community overlap were relatively high on all sample dates. Water velocities were almost twice as great on the reference than the test riffle on most sample dates. I speculate that differences in water velocities between the riffles were either below tolerance ranges for late instar individuals at the dewatered riffle, or that conditions favored early instars at the dewatered riffle, resulting in the size and biomass differences for invertebrates between sites.

At Big Creek, where successive water diversion structures allowed me to establish two test riffles, total benthic density was significantly lower at a dewatered riffle on the first sample date when discharge was 27% and 38% lower at the dewatered than at the reference riffles. Densities were similar among riffles after discharge was reduced by 88% and 95% at the two dewatered riffles on the second sample date. Channel profiles varied considerably between riffles so that wetted perimeter at the reference riffle was substantially greater than at the test riffles, and therefore, absolute invertebrate abundance. Even though only two calibration flows for the wetted perimeter instream flow method were used on Big Creek, severe water diversion caused discharge to fall below the wetted perimeter inflection points at the dewatered riffles on the second sample date. I observed no differences in body length and biomass for total benthic taxa among riffles, even with substantial differences in hydraulic conditions in the riffles. Presumably, time between sample dates and dewatering may have been insufficient for invertebrates to respond to new conditions.

In both Bozeman Creek and Big Creek, reductions in stream discharge between test and reference riffles elicited overall increases in invertebrate drift density. Declines in stream discharge were not great enough to override nocturnal drift patterns for invertebrates since the greatest differences between riffles typically occurred at nights whereas drift was generally similar at noon sample periods. However, invertebrate drift rate was reduced at dewatered riffles since drift rate is a function of both drift density and stream discharge. Drift density at dewatered riffles may have greatly exceeded that of reference riffles, but with reductions in stream discharge, numeric drift rate at dewatered riffles ranged from 6% greater to 94% less than numeric drift rate at reference riffles.

At Bozeman Creek, smaller body length of drifting and benthic invertebrates effectively reduced invertebrate biomass and caloric value at the dewatered riffle. Smaller body length and reductions in drift rates resulted in 15% to 71% lower caloric drift rates at the dewatered riffle. Although differences in body length of drifting invertebrates at Big Creek were not as great as in Bozeman Creek, caloric drift rates were 85% to 94% lower at the two dewatered riffles than the reference riffle on the second sample date. In both streams, drift rate was more closely related to stream discharge than to riffle wetted perimeter and mean water velocity.

To address assumptions of the wetted perimeter instream flow method concerning food limitation in fish populations, field tests using cutthroat trout (≥ 90 mm TL) in stream enclosures, open to emigration, were conducted during two late summer field seasons. Tests were designed to investigate effects of supplemental feeding of brine shrimp and krill on trout density and growth. I observed no consistent trends in supplemental feeding and trout density. Additionally, density of trout at the end of tests was not significantly associated with habitat features of the enclosures (e.g. surface area, mean water depth and velocity, and amount of cover).

Ending cutthroat trout numbers, biomass, and numeric density in all enclosures generally exceeded pretest conditions, suggesting that characteristics of the unaltered trout populations were influenced by factors operating at times other than my study period. Also, the natural trout community of Brackett Creek included individuals smaller (≤ 90 mm) than I used in my tests.

Growth of cutthroat trout in experimental enclosures was greater than in control enclosures. While some trout in each enclosure either lost weight or did not grow, the number of trout that increased in weight was significantly greater in experimental enclosures. Trout that had emigrated from enclosures typically lost weight and no consistent trend in length of trout that emigrated or remained in enclosures was observed. Virtually all trout increased in total length between the beginning of the tests and when they were collected in traps or recovered at the end of the tests. This suggests that resources were used for structural tissues at the expense of body weight in cases where trout lost weight.

The general increase in total length of cutthroat trout elicited either a significant reduction or no change in trout condition factors during the tests. Slopes of initial and final length and weight regressions were significantly greater for trout in experimental enclosures in 1990 but not in 1989. This corresponds to significantly greater specific growth rates of trout in experimental enclosures compared to controls in 1990; growth rates were similar among all experimental enclosures and in one control enclosure in 1989. For experimental enclosures, mean growth rates were higher in 1990 than in 1989 when ambient drift rates were lower in the later year.

Analysis of stomach contents indicated that trout in experimental enclosures readily fed on supplemental brine shrimp and krill. Trout in all enclosures generally selected dipterans in greater proportion to their abundance in the final drift samples while most other food categories were present in lower proportions than their availability. Fish selected food items that were larger than mean size collected in the drift. Relative food consumption rates of trout were generally similar between control and experimental enclosures, but stomach contents from trout in experimental enclosures often had greater caloric value.

Trout in experimental enclosures attained a greater percentage of their potential maximum growth rates (EGC), predicted by bioenergetic equations, than trout in control enclosures. Bioenergetic equations were used to predict maximum, maintenance, and observed food consumption rates and compared to invertebrate drift rates to evaluate potential food limitation. Drift in all enclosures was more than adequate to achieve predicted maintenance and observed food consumption rates in both years, but was sometimes inadequate for maximum consumption rates in control enclosures in 1990. Drift rates were generally higher for most enclosures in 1989 than 1990, when trout growth rates were lower in the former year. This suggests that actual food availability to trout is modified by other factors and that measures of food abundance (i.e. invertebrate drift rate) may overestimate food availability. Also, potential benthic feeding by trout was not considered in my tests.

Cutthroat trout residency in artificial stream channels was found to be influenced more by ration than reductions in water depth, and this relationship varied with size of trout used in tests. Number and weight of small trout (51-75 mm TL) remaining in channels at the end of 20-d tests varied directly with ration level, but a 55% decrease in habitat volume had no effect. Larger trout (122-159 mm TL) did not establish residency during tests regardless of ration level, suggesting that habitat was inadequate in artificial stream channels.

To relate flow induced changes in potential fish-food abundance (Bozeman Creek study) to feeding by cutthroat trout (Brackett Creek study), I assumed that the differences in mean daily caloric drift rate between the test and reference riffles at Bozeman Creek were proportional to stream discharge at each riffle. I then scaled mean daily drift rates for each enclosure at Brackett Creek by the percent difference in drift on the four sample dates for each discharge difference at Bozeman Creek. I calculated foraging efficiencies for 0, 20, 28, 32, and 47% reductions in discharge on every invertebrate sample date at Brackett Creek (Appendix G). Although food was adequate for all trout to potentially achieve maximum consumption rates in all experimental enclosures (foraging efficiency < 1), this was not the case in control enclosures except for a few instances in 1989. Predicted reductions in drift abundance, however, would limit trout consumption rates in several instances in 1990. The greatest reductions in food abundance would occur if discharge was reduced 47%, which corresponded to a 70% reduction in caloric drift rate.

This argument implies the unlikely situation where trout would detect and feed on all prey drifting into enclosures. The limited growth of trout in 1989 tests compared to 1990, when ambient drift rates were higher in 1989, suggests that this situation would not exist. Reductions in discharge that reduce invertebrate drift rate can be expected to reduce actual food availability to trout.

Conclusions

Biological assumptions of the wetted perimeter instream flow method were generally supported by the findings of this study. Differences in abundance of invertebrates were observed between artificially dewatered riffles and riffles exposed to the natural flow regime. Additionally, differences in food abundance were shown to affect growth rates of cutthroat trout in field enclosures, as well as density of small trout in artificial stream channels.

Although benthic invertebrate densities were generally similar between test and reference riffles in both streams studied, absolute invertebrate abundance varied because of differences in riffle area as indicated by riffle wetted perimeter. Given similar benthic densities in riffles of equal length, the absolute number of invertebrates inhabiting each riffle would be proportional to some measure of riffle width, e.g. riffle wetted perimeter. Thus, the greatest rate of invertebrate habitat loss, relative to stream discharge, would occur when discharge falls below the wetted perimeter-discharge inflection point. For potential food value of benthic invertebrates, reductions in stream discharge presumably created hydraulic conditions favoring smaller taxa or instars which severely reduced benthic biomass and caloric value.

Reductions in stream discharge elicited an increase in invertebrate drift density, but drift rate was reduced. Drift rate is an function of drift density, discharge, and riffle area. Relative changes in drift rate were associated more closely with discharge than with riffle wetted perimeter. Reductions in drift rate were accompanied by decreased invertebrate size which severely reduced drift biomass and caloric value.

Evidence for food limitation in cutthroat trout was shown. Supplemental feeding increased food abundance for trout (≥ 90 mm TL) in experimental enclosures in field tests. While supplemental feeding produced higher growth rates of trout in experimental enclosures compared to unfed control enclosures, no effects on trout density were observed. Comparing predicted food consumption rates to drift rate, a measure of food abundance, indicated that food was more than adequate for trout to attain higher growth rates than observed. This demonstrated discrepancies between food abundance and food availability for trout.

Density of small trout varied directly with ration in artificial stream channels while reductions in water depth had no effect on trout residency. Larger trout did not establish residency in stream channels, suggesting that adequate habitat was not afforded by the channels and that habitat characteristics may exert a greater influence on density of large cutthroat trout than short-term food abundance.

Management Implications

While this study supports the validity of some biological assumptions made by the wetted perimeter instream flow method, namely that invertebrate abundance and biomass declines with reduced stream flow and fish may become food limited, it should be emphasized that these assumptions address trends. That is, the assumptions relate to overall changes in the behavior of stream communities subjected to reductions in discharge (e.g. invertebrate abundance is higher at greater flows, hence potential fish-food is more abundant), and not to strict quantitative changes in invertebrate and fish populations.

Because the wetted perimeter method addresses relative changes, the need for additional information concerning fish population structure is essential when recommending minimum flows for streams possessing a highly valued fishery or a threatened or endangered species. For example, drift rates may possibly decline to the point that fish growth is inhibited at discharges above the wetted perimeter-discharge inflection point. Setting conservative minimum flows substantially above an inflection point may be prudent in instances where the fishery resources have high value. Other criteria should be considered in recommending a minimum flow other than that corresponding to the wetted perimeter-discharge inflection point.

Results of this study may be applicable only to conditions present during my test periods. For example, cutthroat trout density did not vary with habitat in Brackett Creek tests. This suggests that the enclosed pools afforded adequate habitat. However, fish habitat requirements may vary seasonally. Impacts of chronically low flows relative to the wetted perimeter-inflection point should be considered in view of habitat requirements of fish in other seasons such as winter if flow recommendations are desired for instances where water diversions are of a prolonged nature.

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LITERATURE CITED

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APPENDICES

APPENDIX A

INVERTEBRATES - BOZEMAN CREEK AND BIG CREEK

Table 19.-List of taxa collected in drift and benthic samples in Bozeman Creek, July-September 1989.

Group/order	Family	Taxa
Oligochaeta		
Turbellaria		
Nematomorpha		
Acarina		
Terrestrials		
Ephemeroptera	Baetidae	unidentified nymphs
		Acentrella turbida McDunnough
		Baetis spp.
		Cloeon sp.
	Siphlonuridae	*Ameletus* sp.
	Leptophlebiidae	*Paraleptophlebia* sp.
	Heptageniidae	unidentified nymphs
		Cingymula spp.
		Epeorus spp.
		Rhithrogena spp.
	Ephemerellidae	unidentified nymphs
		Caudatella sp.
		C. hystrix (Traver)
		Drunella spp.
		D. doddsi (Needham)
		D. grandis (McDunnough)
		Ephemerella spp.
		Serratella tibialis (McDunnough)
Plecoptera	Peltoperlidae	*Yoraperla brevis* (Banks)
	Nemouridae	unidentified nymphs
		Zapada spp.
		Amphinemura banksi Baumann and Gaufin
	Leuctridae	unidentified nymphs
	Perlidae	unidentified nymphs
		Hesperoperla pacifica (Banks)
		Doroneuria theodora (Needham and Classen)
	Chloroperlidae	unidentified nymphs
	Perlodidae	unidentified nymphs
		Isoperla sp.
		Megarcys sp.
		Kogotus sp.
Hemiptera	Corixidae	unidentified adults
Trichoptera		unidentified larvae

Table 19.-Continued.....

Group/order	Family	Taxa
	Brachycentridae	*Brachycentrus* spp.
		Micrasema bactro Ross
	Hydropsychidae	unidentified larvae
		Arctopsyche grandis (Banks)
	Glossosomatidae	*Glossosoma* sp.
	Lepidostomatidae	*Lepidostoma* sp.
	Limnephilidae	*Apatania* spp.
		Onocosmoecus unicolor (Banks)
	Philopotamidae	*Dolophilodes* sp.
	Rhyacophilaidae	*Rhyacophila* spp.
	Uenoidae	*Neothrema alicia* Dodds and Hisaw
		Oligophlebodes sp.
		Neophylax sp.
Coleoptera	Amphizoidae	*Amphizoa* sp. adult
	Gyrinidae	*Gyrinus* sp. adult
	Haliplidae	*Haliplus* sp. adult
	Dytiscidae	unidentified larvae
		Oreodytes spp. adult
		Agabus spp. adult
		Dytiscus sp. adult
	Hydrophilidae	unidentified larvae
	Elmidae	unidentified larvae
		Narpus concolor (LeConte) adult
		Cleptelmis ornata (Schaeffer) adult
		Optioservus sp. adult
		Zaitzevia sp. adult
		Heterlimnius corpulentus (LeConte) adult
Diptera		unidentified pupae
	Tipulidae	unidentified larvae
	Deuterophlebiidae	*Deuterphlebia nielsoni* Kennedy
	Dixidae	*Dixa* sp.
	Simuliidae	*Simulium* spp.
	Ceratopogonidae	unidentified larvae
	Chironomidae	unidentified larvae
	Psychodidae	*Pericoma* sp.
	Anthericidae	*Antherix pachypus* Bigot
	Psycomyidae	unidentified larvae

Table 20.-Mean percentage of each taxon in the benthos for numeric density (D) and dry biomass (B) for the test and reference riffles on four sample dates in Bozeman Creek, July-September 1989.

	19 July				4 August				31 August				17 September			
	Test		Reference		Test		Reference		Test		Reference		Test		Reference	
Taxa	D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B
								Ephemeroptera								
Acentrella turbida	2.7	0.6	6.3	1.1	0.1	<0.1	0.4	0.1	-	-	<0.1	<0.1	-	-	-	-
Baetis spp.	14.3	4.6	11.2	3.5	18.9	4.2	28.4	5.5	12.2	8.4	15.8	5.2	4.7	3.9	7.8	5.7
Ameletus sp.	-	-	<0.1	0.2	0.7	0.8	0.1	<0.1	0.3	0.9	<0.1	<0.1	0.2	1.1	-	-
Paraleptophlebia sp.	-	-	<0.1	<0.1	0.3	0.1	<0.1	<0.1	0.7	0.4	0.4	<0.1	0.1	<0.1	0.1	0.1
Heptageniidae	2.1	<0.1	2.7	<0.1	1.8	<0.1	1.1	<0.1	6.0	0.1	4.4	<0.1	6.4	0.1	3.9	<0.1
Cingymula spp.	4.5	4.5	6.4	5.9	1.9	2.3	2.3	1.4	3.1	2.1	2.4	1.1	3.8	1.5	5.5	1.3
Epeorus spp.	2.3	0.8	1.5	0.8	0.1	<0.1	2.3	1.2	0.1	0.2	1.3	0.6	-	-	0.5	0.8
Rhithrogenia spp.	-	-	0.1	<0.1	0.4	0.1	2.0	0.6	2.6	2.0	5.0	2.3	2.3	3.0	5.8	3.1
Ephemerellidae	0.7	<0.1	0.4	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Ephemerella spp.	1.4	<0.1	2.2	<0.1	0.5	<0.1	1.9	<0.1	0.8	<0.1	0.7	<0.1	2.4	<0.1	1.3	<0.1
Drunella spp.	0.5	0.9	0.7	1.7	1.8	1.9	3.1	0.7	3.9	1.0	2.8	0.6	2.5	1.1	3.9	3.4
D. doddsi	0.1	1.4	0.4	4.7	-	-	-	-	-	-	1.5	0.1	-	-	0.4	0.1
D. grandis	0.1	3.0	-	-	0.1	0.9	-	-	-	-	-	-	-	-	-	-
Serratella tibialis	4.5	2.3	5.9	5.4	4.8	8.2	2.4	3.5	1.6	2.7	0.8	0.8	0.6	1.2	2.8	1.5
Total	33.2	18.1	37.8	23.3	31.4	18.5	44.0	13.0	31.3	17.8	35.1	10.7	23.0	11.9	32.0	16.0
								Plecoptera								
Yoraperla brevis	0.1	<0.1	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Nemouridae	0.7	<0.1	3.7	<0.1	2.2	<0.1	1.3	<0.1	1.3	0.1	1.4	<0.1	1.4	<0.1	2.3	<0.1
Zapada spp.	1.1	0.2	1.8	0.5	2.3	0.4	1.9	0.2	3.1	0.8	2.6	0.4	2.0	0.4	8.0	1.1
Amphinemura banksi	0.1	<0.1	0.2	<0.1	0.3	0.1	0.1	<0.1	0.2	<0.1	0.1	<0.1	<0.1	<0.1	0.1	<0.1
Leuctridae	0.4	0.5	0.1	<0.1	0.4	0.3	0.5	0.6	0.4	0.1	0.4	0.3	0.6	0.1	0.7	0.7

Table 20.-Continued.....

Taxa	19 July				4 August				31 August				17 September			
	Test		Reference		Test		Reference		Test		Reference		Test		Reference	
	D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B
Perlidae	0.6	0.3	0.6	0.4	2.1	0.7	1.1	0.4	1.5	0.4	0.5	0.1	1.3	0.9	1.3	0.9
Hesperperla pacifica	-	-	-	-	0.1	2.1	-	-	-	-	-	-	-	-	<0.1	3.1
Doroneuria theodora	0.9	4.0	1.0	16.9	0.3	3.2	0.6	8.2	0.5	11.7	0.7	22.1	0.4	5.9	0.5	6.8
Chloroperlidae	3.0	2.7	6.6	8.2	5.5	4.9	2.9	2.0	2.3	2.7	3.9	2.2	2.6	3.9	2.6	2.5
Perlodidae	5.2	0.2	3.6	0.4	7.9	2.8	2.4	0.8	3.6	1.0	3.1	0.6	1.7	0.8	3.0	1.1
Megarcys sp.	-	-	-	-	-	-	-	-	-	-	0.1	0.3	-	-	-	-
Kogotus sp.	0.4	3.4	0.5	3.5	0.1	0.4	-	-	0.1	0.2	0.2	0.3	<0.1	0.5	0.2	1.1
Total	12.5	11.3	18.1	29.9	21.2	14.9	10.8	12.2	13.0	16.9	13.0	26.3	10.0	12.5	18.7	17.3
	Hemiptera															
Corixidae	0.1	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Trichoptera															
Unidentified	3.4	<0.1	1.3	<0.1	6.9	<0.1	1.8	<0.1	8.9	<0.1	8.3	<0.1	21.5	0.1	2.3	<0.1
Brachycentrus spp.	0.7	0.5	0.4	0.3	0.3	0.1	0.2	0.2	0.4	0.5	0.2	0.2	0.4	0.9	0.6	0.7
Micrasema bactro	0.6	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1	0.1	<0.1	1.3	<0.1	0.1	<0.1	0.1	<0.1
Arctopsyche grandis	0.2	2.1	0.2	1.3	1.0	1.2	0.4	2.6	4.2	4.0	4.5	4.6	5.1	6.4	4.1	12.6
Glossosoma sp.	-	-	-	-	0.1	0.1	-	-	0.2	0.1	0.4	0.4	<0.1	0.1	0.7	0.8
Apatania spp.	-	-	-	-	0.1	<0.1	-	-	-	-	<0.1	<0.1	-	-	0.1	<0.1
Dolophilodes sp.	0.7	0.3	0.9	0.3	0.2	0.4	0.4	1.0	0.1	0.3	0.2	0.3	<0.1	<0.1	0.6	1.2
Rhyacophila spp.	2.4	6.4	2.5	9.4	3.9	1.8	3.6	3.7	3.7	3.8	2.2	2.7	3.2	7.1	1.7	3.4
Neothremma sp.	0.2	<0.1	0.5	0.1	-	-	-	-	0.1	<0.1	<0.1	<0.1	-	-	-	-
Oligophlebodes sp.	-	-	-	-	-	-	-	-	-	-	<0.1	<0.1	0.1	0.1	-	-
Neophylax sp.	0.1	0.1	-	-	-	-	-	-	0.1	<0.1	-	-	-	-	-	-

Table 20.-Continued.....

	19 July				4 August				31 August				17 September			
	Test		Reference		Test		Reference		Test		Reference		Test		Reference	
Taxa	D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B
Pupae	1.0	1.7	0.2	0.8	0.4	1.7	0.7	2.7	0.1	0.3	0.1	0.4	-	-	0.1	0.3
Total	0.093	0.111	0.060	0.122	0.130	0.053	0.071	0.102	0.179	0.090	0.172	0.086	0.304	0.147	0.103	0.190
Coleoptera																
Oreodytes spp.	-	-	-	-	0.1	0.1	-	-	-	-	-	-	-	-	-	-
Elmidae larvae	28.4	51.1	19.9	28.9	17.5	54.1	16.9	58.0	20.0	47.2	17.3	42.4	20.0	55.7	16.7	40.9
Cleptelmis ornata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<0.1	0.1
Optioservus sp.	-	-	0.2	0.7	0.2	0.5	0.1	0.3	0.1	0.6	0.2	0.6	<0.1	0.2	0.2	0.5
Zaitzevia sp.	-	-	-		-	-	-	-	-	-	-	-	-	-	0.1	0.3
Heterlimnius corpulentus	0.1	0.3	0.1	0.5	0.5	1.7	0.8	2.4	0.7	3.0	0.7	1.8	0.2	1.1	0.7	2.3
Total	28.5	51.4	20.2	30.1	18.3	56.4	17.8	60.2	20.8	50.8	18.2	44.8	20.2	57.0	17.7	44.1
Diptera																
Tipulidae	0.4	2.0	0.4	0.4	0.1	0.8	<0.1	0.6	0.1	0.1	0.1	6.8	0.1	0.1	0.1	<0.1
Deuterphlebia spp.	-	-	-	-	-	-	<0.1	<0.1	-	-	-	-	-	-	<0.1	<0.1
Simulium spp.	0.7	0.4	0.7	0.1	0.4	<0.1	2.9	<0.1	<0.1	<0.1	2.3	0.4	<0.1	<0.1	1.3	0.8
Pericoma spp.	-	-	2.7	<0.1	1.0	<0.1	1.1	<0.1	5.8	0.1	2.7	<0.1	7.9	0.2	9.6	0.3
Chironomidae	14.1	4.8	12.2	3.6	13.5	2.8	15.4	2.4	9.7	3.7	10.7	2.1	6.4	1.3	8.8	1.7
Psycomyidae	-	-	<0.1	<0.1	-	-	-	-	0.1	1.4	-	-	-	-	<0.1	0.4
Antherix pachypus	<0.1	0.3	<0.1	0.3	0.1	0.7	0.1	0.3	<0.1	<0.1	<0.1	0.1	0.1	1.9	0.1	0.1
Ceratopogonidae	0.1	0.1	0.1	<0.1	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.1	0.2	0.5	0.1	0.2

Table 20.-Continued.....

Taxa	19 July				4 August				31 August				17 September			
	Test		Reference		Test		Reference		Test		Reference		Test		Reference	
	D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B
Pupae	1.4	<0.1	1.5	<0.1	1.4	0.1	0.7	0.2	0.9	<0.1	0.7	<0.1	1.4	<0.1	1.4	0.1
Total	16.8	7.6	17.6	4.4	16.6	4.5	20.3	3.7	16.7	5.5	16.6	9.5	16.1	4.0	21.4	3.6

Table 21.-Mean percentage of each taxon in the drift for mean daily numeric drift density (DD) and dry biomass (DB) for the test and reference riffles on four sample dates in Bozeman Creek, July-September 1989.

Taxa	18-19 July				2-3 August				28-29 August				14-15 September			
	Test		Reference		Test		Reference		Test		Reference		Test		Reference	
	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB
									Ephemeroptera							
Acentrella turbida	9.8	3.5	10.9	3.0	3.0	2.1	2.6	1.0	0.4	1.4	0.2	<0.1	0.1	<0.1	-	-
Baetis spp.	38.9	46.0	40.3	44.9	57.2	42.21	57.8	28.8	73.0	62.5	66.5	53.6	52.3	59.3	61.3	47.2
Cloeon sp.	0.3	0.3	0.2	<0.1	1.3	1.4	5.6	4.7	0.1	0.2	0.1	0.2	0.2	0.7	-	-
Ameletus sp.	0.6	0.7	0.3	0.2	0.4	1.9	0.4	0.6	-	-	0.1	0.1	-	-	0.3	0.8
Paraleptophlebia sp.	0.2	0.1	<0.1	<0.1	0.2	0.1	0.2	0.1	0.2	0.3	0.1	0.1	-	-	<0.1	<0.1
Heptageniidae	1.0	<0.1	0.6	<0.1	0.5	<0.1	0.4	<0.1	0.1	<0.1	1.2	<0.1	1.2	<0.1	0.8	<0.1
Cingymula spp.	1.9	1.6	1.3	1.3	0.2	0.6	0.6	0.7	0.5	<0.1	0.2	0.3	1.8	0.5	0.7	0.1
Epeorus spp.	4.0	3.6	5.8	5.1	2.7	2.0	4.1	3.1	0.9	0.9	0.9	0.8	1.1	0.7	1.3	1.5
Rhithrogenia spp.	-	-	-	-	0.6	0.4	0.1	<0.1	0.5	0.3	0.4	0.3	0.8	1.2	0.6	0.2
Drunella spp.	0.2	0.5	0.3	1.3	<0.1	0.3	0.1	1.2	0.1	<0.1	0.2	0.1	-	-	0.4	0.2
D. doddsi	-	-	<0.1	0.2	-	-	-	-	-	-	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Serratella tibialis	2.9	1.2	4.0	2.8	1.2	1.6	2.5	2.6	1.0	0.7	1.8	1.6	0.3	0.2	1.1	1.2
Caudatella sp.	-	-	-	-	-	-	0.1	0.1	-	-	0.1	<0.1	0.1	0.1	-	-
C. hystrix	-	-	-	-	-	-	-	-	-	-	<0.1	<0.1	0.2	<0.1	-	-
Total	59.8	57.5	63.7	58.8	67.3	52.5	74.5	42.9	73.8	65.3	71.8	57.1	58.2	62.7	66.5	51.2
									Plecoptera							
Nemouridae	0.3	<.0.	0.1	<0.1	0.4	0.1	0.1	<0.1	1.6	<0.1	1.2	<0.1	0.5	<0.1	1.0	<0.1
Zapada spp.	1.4	0.2	2.2	0.4	1.3	0.5	1.1	0.3	2.1	0.3	4.2	1.2	3.6	0.9	8.3	1.7
Amphinemura banksi	0.6	0.2	0.4	0.1	0.5	0.1	0.4	0.2	-	-	0.5	0.4	-	-	0.5	0.3
Perlidae	-	-	<0.1	<0.1	-	-	-	-	0.1	<0.1	0.2	0.1	0.4	0.1	-	-
Hesperperla pacifica	<0.1	0.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 21.-Continued.....

Taxa	18-19 July				2-3 August				28-29 August				14-15 September			
	Test		Reference		Test		Reference		Test		Reference		Test		Reference	
	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB
Doroneuria theodora	-	-	-	-	-	-	<0.1	4.9	-	-	-	-	-	-	0.2	0.9
Chloroperlidae	1.1	3.4	1.4	4.8	0.4	1.3	0.6	0.7	0.2	0.2	0.9	1.0	0.5	0.2	1.8	1.7
Perlodidae	0.5	0.2	0.5	0.1	0.9	0.1	0.5	0.2	2.1	0.9	1.1	0.6	1.2	0.3	1.0	0.6
Isoperla sp.	-	-	-	-	-	-	<0.1	0.3	0.1	<0.1	-	-	-	-	-	-
Kogotus sp.	-	-	0.1	1.1	-	-	0.1	3.2	-	-	-	-	-	-	-	-
Total	3.9	4.8	4.7	6.5	3.5	2.0	2.8	9.8	6.2	1.4	8.1	3.3	6.2	1.5	12.8	5.2
Hemiptera																
Corixidae	0.1	0.1	-	-	-	-	<0.1	0.1	0.1	0.2	-	-	-	-	0.2	0.5
Trichoptera																
Unidentified	0.3	<0.1	0.2	<0.1	0.5	<0.1	<0.1	<0.1	4.2	<0.1	-	-	7.3	<0.1	-	-
Brachycentridae	0.4	<0.1	0.3	<0.1	0.7	<0.1	0.3	<0.1	1.1	<0.1	1.8	<0.1	3.0	<0.1	0.4	<0.1
Brachycentrus spp.	0.2	0.2	0.1	0.1	0.1	0.1	0.2	<0.1	-	-	0.2	0.5	-	-	0.3	0.2
Micrasema bactro	0.2	<0.1	0.1	<0.1	-	-	0.3	<0.1	0.1	<0.1	0.3	<0.1	0.4	0.1	-	-
Hydropsychidae	-	-	-	-	-	-	<0.1	<0.1	-	-	<0.1	<0.1	-	-	<0.1	<0.1
Arctopsyche grandis	-	-	-	-	<0.1	<0.1	<0.1	0.8	0.9	0.7	0.2	0.1	1.4	1.9	0.2	0.1
Glossosoma sp.	-	-	-	-	-	-	0.1	<0.1	-	-	-	-	-	-	-	-
Lepidostoma spp.	-	-	-	-	-	-	-	-	-	-	0.1	<0.1	-	-	-	-
Apatania spp.	0.1	<0.1	<0.1	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Onocosmoecus unicolor	-	-	<0.1	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Dolophilodes sp.	0.3	0.1	0.7	0.2	0.6	0.7	0.5	0.7	0.2	0.4	0.2	0.3	0.1	0.1	0.2	0.2
Rhyacophila spp.	0.7	3.1	0.4	0.3	0.2	0.8	0.2	0.7	0.1	<0.1	0.3	0.2	1.1	0.1	0.5	0.8
Oligophlebodes sp.	-	-	-	-	-	-	-	-	-	-	<0.1	<0.1	-	-	-	-
Neophylax sp.	-	-	-	-	-	-	-	-	-	-	0.1	<0.1	-	-	-	-

Table 21.-Continued.....

Taxa	18-19 July				2-3 August				28-29 August				14-15 September			
	Test		Reference		Test		Reference		Test		Reference		Test		Reference	
	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB
Pupae	0.4	0.9	0.1	0.7	-	-	-	-	-	-	0.3	1.6	0.1	0.4	0.3	1.0
Total	2.6	4.3	1.9	1.5	2.1	1.6	1.6	2.2	6.6	1.1	3.5	2.7	13.4	2.6	1.9	2.3
Coleoptera																
Amphizoa sp.	-	-	<0.1	1.2	-	-	-	-	-	-	-	-	-	-	0.2	13.7
Gyrinus sp.	-	-	-	-	-	-	<0.1	0.5	-	-	-	-	-	-	-	-
Haliplus sp.	-	-	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	0.1	0.4
Dytiscidae	-	-	<0.1	<0.1	0.3	<0.1	-	-	0.2	<0.1	-	-	-	-	-	-
Oreodytes spp.	0.2	0.7	0.2	0.6	0.2	0.1	0.1	0.3	0.3	0.3	-	-	-	-	0.5	3.5
Agabus spp.	<0.1	0.2	<0.1	0.2	-	-	-	-	-	-	-	-	0.1	1.2	-	-
Dytiscus spp.	<0.1	0.3	0.3	0.2	-	-	-	-	0.1	3.1	-	-	-	-	-	-
Hydrophilidae	0.4	0.8	<0.1	<0.1	0.1	<0.1	<0.1	<0.1	0.1	0.2	-	-	-	-	-	-
Elmidae larvae	2.0	9.4	1.2	7.0	0.5	4.6	1.8	15.1	1.6	17.2	2.3	19.4	1.5	6.2	3.3	13.3
Narpus concolor	0.7	9.4	0.7	7.4	0.6	14.4	0.5	8.7	-	-	-	-	-	-	-	-
Cleptelmis ornata	<0.1	0.2	-	-	0.4	2.3	<0.1	0.2	0.1	0.6	0.1	0.4	0.2	1.0	0.2	0.3
Optioservus sp.	0.3	1.0	0.3	0.9	1.5	8.3	0.8	3.8	0.2	1.2	0.4	1.6	0.2	0.8	-	-
Zaitzevia sp.	0.2	0.7	0.2	0.7	<0.1	0.2	0.1	0.4	-	-	0.1	0.5	-	-	-	-
Heterlimnius corpulentus	0.9	6.0	1.5	9.0	0.9	9.4	1.3	12.4	0.5	5.6	1.4	11.8	1.9	13.1	1.7	7.5
Total	4.7	28.7	4.3	27.7	4.5	39.3	4.6	41.4	3.1	29.2	4.3	33.7	3.9	22.3	6.0	38.7
Diptera																
Tipulidae	-	-	-	-	-	-	<0.1	0.5	-	-	-	-	0.5	7.0	-	-
Deuterphlebia sp.	-	-	<0.1	<0.1	-	-	<0.1	<0.1	-	-	-	-	-	-	-	-
Dixa sp.	-	-	-	-	-	-	-	-	-	-	0.1	0.1	0.1	0.2	<0.1	0.1

Table 21.-Continued.....

Taxa	18-19 July				2-3 August				28-29 August				14-15 September			
	Test		Reference		Test		Reference		Test		Reference		Test		Reference	
	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB
Simulium sp.	18.2	3.2	16.4	4.0	13.1	3.2	8.0	2.1	4.0	1.7	3.0	0.9	5.2	2.7	2.0	0.7
Pericoma sp.	-	-	<0.1	<0.1	-	-	-	-	0.2	0.1	-	-	0.7	<0.1	0.2	<0.1
Chironomidae	8.5	1.2	5.3	1.3	5.1	1.0	6.1	0.9	1.7	0.7	3.5	1.4	2.6	0.3	2.0	0.6
Psycomyidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1	<0.1
Pupae	2.3	0.2	3.1	0.2	4.4	0.4	1.8	0.1	1.6	0.2	5.7	0.6	9.0	0.7	8.5	0.7
Total	29.0	4.6	25.2	5.5	22.6	4.6	15.9	3.6	7.5	2.7	12.3	3.0	18.1	10.9	12.8	2.1

Table 22.-Mean number of individuals (rounded to nearest integer) collected by paired driftnets at the test (T) and reference (R) riffles for total taxa, *Baetis* spp., *Zapada* spp., and Chironomidae for each time period (TP; N-noon, S-sunset, M-midnight, R-sunrise) on four sample dates and results of G-tests (P-values) for taxa counts weighted equally between riffles (E), and proportional to stream discharge (Q)^{b}, wetted perimeter (WP)^{c}, and mean water velocity (VEL)^{d} in Bozeman Creek, July-September 1989.

Date	TP	Total taxa						*Baetis* spp.						*Zapada* spp.						Chironomidae					
		T	R	E	Q	WP	VEL	T	R	E	Q	WP	VEL	T	R	E	Q	WP	VEL	T	R	E	Q	WP	VEL
18- 19/7	N	146	137	0.593	0.022	0.315	0.051	29	44	0.079	0.383	0.129	0.297	0	0	--^{a}	--^{a}	--^{a}	--^{a}	26	12	0.022	0.004	0.014	0.105
	S	902	1163	<0.001	0.306	<0.001	0.053	487	572	0.009	0.438	0.089	0.903	12	21	0.118	0.329	0.160	0.276	16	19	0.611	0.914	0.734	0.992
	M	368	285	0.001	<0.001	<0.001	<0.001	156	103	0.001	<0.001	0.002	<0.001	15	12	0.566	0.263	0.474	0.315	15	17	0.726	0.815	0.846	0.904
	R	207	79	<0.001	<0.001	<0.001	<0.001	111	29	<0.001	<0.001	<0.001	<0.001	3	2	--^{a}	--^{a}	--^{a}	--^{a}	9	8	0.500	0.331	0.453	0.362
2- 3/8	N	81	101	0.138	0.461	0.434	0.915	22	47	0.002	0.091	0.009	0.028	0	0	--^{a}	--^{a}	--^{a}	--^{a}	11	14	0.552	0.826	0.736	0.929
	S	695	794	0.010	<0.001	0.576	0.169	509	516	0.827	<0.001	0.148	0.002	2	7	--^{a}	--^{a}	--^{a}	--^{a}	8	9	0.686	0.418	0.605	0.522
	M	444	398	0.113	<0.001	0.002	<0.001	259	241	0.421	<0.001	0.049	<0.001	12	8	0.252	0.078	0.183	0.129	13	16	0.580	0.744	0.783	0.992
	R	184	138	0.010	<0.001	<0.001	<0.001	103	68	0.007	<0.001	0.049	<0.001	0	0	--^{a}	--^{a}	--^{a}	--^{a}	14	23	0.140	0.626	0.244	0.388
28- 29/8	N	94	93	0.942	0.003	0.222	0.127	32	47	0.092	0.870	0.345	0.453	2	3	--^{a}	--^{a}	--^{a}	--^{a}	0	0	--^{a}	--^{a}	--^{a}	--^{a}
	S	453	275	<0.001	<0.001	<0.001	<0.001	389	208	<0.001	<0.001	0.049	<0.001	6	9	0.849	0.584	0.759	0.828	4	4	--^{a}	--^{a}	--^{a}	--^{a}
	M	189	130	<0.001	<0.001	<0.001	<0.001	138	87	<0.001	<0.001	0.049	<0.001	6	9	0.849	0.584	0.759	0.828	2	5	--^{a}	--^{a}	--^{a}	--^{a}
	R	379	95	<0.001	<0.001	<0.001	<0.001	291	63	<0.001	<0.001	0.049	<0.001	9	2	--^{a}	--^{a}	--^{a}	--^{a}	16	7	0.047	0.004	0.019	0.014

Table 22.-Continued.....

Date	TP	Total taxa						*Baetis* spp.						*Zapada* spp.						Chironomidae					
		T	R	E	Q	WP	VEL	T	R	E	Q	WP	VEL	T	R	E	Q	WP	VEL	T	R	E	Q	WP	VEL
14- 15/9	N	62	55	0.518	<0.001	0.013	0.023	12	31	0.003	0.394	0.064	0.049	3	1	--[a]	--[a]	--[a]	--[a]	1	2	--[a]	--[a]	--[a]	--[a]
	S	210	254	0.041	<0.001	0.111	0.705	146	159	0.457	<0.001	0.027	0.059	7	21	0.007	0.307	0.069	0.056	7	3	0.172	--[a]	--[a]	--[a]
	M	163	184	0.260	<0.001	0.044	0.093	98	116	0.219	<0.001	0.216	0.332	8	19	0.033	0.631	0.202	0.172	3	4	--[a]	--[a]	--[a]	--[a]
	R	78	61	0.150	<0.001	<0.001	0.001	55	39	0.099	<0.001	0.001	0.002	4	5	--[a]	--[a]	--[a]	--[a]	3	1	--[a]	--[a]	--[a]	--[a]

[a] Inadequate sample size for tests.

[b] Proportion of stream discharge at the test and reference riffles on four sample dates were: 0.45 and 0.55, 0.42 and 0.58, 0.40 and 0.60, 0.34 and 0.66.

[c] Proportion of wetted perimeter at the test and reference riffles on four sample dates were: 0.49 and 0.51, 0.47 and 0.53, 0.46 and 0.54, 0.42 and 0.58.

[d] Proportion of mean water velocity at the test and reference riffles on four sample dates were: 0.46 and 0.54, 0.45 and 0.55, 0.45 and 0.55, 0.42 and 0.58.

Table 23.-Mean daily number of individuals (no./100 m^3; rounded to nearest integer) collected by paired driftnets at the test (T) and reference (R) riffles for total taxa, *Baetis* spp., *Zapada* spp., and Chironomidae on four sample dates and results of G-tests (P-values) for taxa counts weighted equally between riffles (E), and proportional to stream discharge (Q)^b, wetted perimeter (WP)^c, and mean water velocity (VEL)^d in Bozeman Creek, July-September 1989.

Date	Total taxa						*Baetis* spp.						*Zapada* spp.						Chironomidae					
	T	R	E	Q	WP	VEL	T	R	E	Q	WP	VEL	T	R	E	Q	WP	VEL	T	R	E	Q	WP	VEL
18-19/7	469	450	0.539	<0.001	0.140	0.002	183	181	0.917	0.036	0.523	0.087	7	10	0.517	0.767	0.515	0.705	40	23	0.032	0.003	0.018	0.005
2-3/8	573	609	0.295	<0.001	0.459	0.014	325	352	0.300	0.001	0.752	0.105	8	7	0.799	0.377	0.651	0.520	30	38	0.333	0.700	0.589	0.897
28 29/8	431	267	<0.001	<0.001	<0.001	<0.001	313	177	<0.001	<0.001	<0.001	<0.001	9	11	0.659	0.628	0.944	0.980	8	10	0.642	0.680	0.909	0.982
14-15/9	142	146	0.814	<0.001	0.009	0.020	74	89	0.240	0.003	0.328	0.456	5	12	0.089	0.690	0.305	0.272	4	3	--[a]	--[a]	--[a]	--[a]

[a] Inadequate sample size for tests.

[b] Proportion of stream discharge at the test and reference riffles on four sample dates were: 0.45 and 0.55, 0.42 and 0.58, 0.40 and 0.60, 0.34 and 0.66.

[c] Proportion of wetted perimeter at the test and reference riffles on four sample dates were: 0.49 and 0.51, 0.47 and 0.53, 0.46 and 0.54, 0.42 and 0.58.

[d] Proportion of mean water velocity at the test and reference riffles on four sample dates were: 0.46 and 0.54, 0.45 and 0.55, 0.45 and 0.55, 0.42 and 0.58.

Table 24.-List of taxa collected in drift and benthic samples in Big Creek, July-August 1990.

Group/order	Family	Taxa
Oligochaeta		
Turbellaria		
Nematomorpha		
Acarina		
Terrestrials		
Ephemeroptera	Baetidae	unidentified nymphs
		Acentrella turbida McDunnough
		Baetis spp.
		Cloeon sp.
	Siphlonuridae	*Ameletus* sp.
	Leptophlebiidae	*Paraleptophlebia* sp.
	Heptageniidae	unidentified nymphs
		Cingymula spp.
		Epeorus spp.
		Rhithrogena spp.
	Ephemerellidae	unidentified nymphs
		Drunella spp.
		D. doddsi (Needham)
		D. grandis (McDunnough)
		Serratella tibialis (McDunnough)
Plecoptera	Nemouridae	unidentified nymphs
		Zapada spp.
		Amphinemura banksi Baumann and Gaufin
	Leuctridae	unidentified nymphs
	Perlidae	unidentified nymphs
		Hesperoperla pacifica (Banks)
		Doroneuria theodora (Needham and Classen)
	Chloroperlidae	unidentified nymphs
	Perlodidae	unidentified nymphs
		Megarcys sp.
		Kogotus sp.
Hemiptera	Corixidae	unidentified adults
Trichoptera		unidentified larvae
	Brachycentridae	*Amiocentrus aspilus* Ross
		Brachycentrus spp.
		Micrasema bactro Ross
	Hydropsychidae	*Arctopsyche grandis* (Banks)
	Lepidostomatidae	*Lepidostoma* sp.
	Limnephilidae	*Apatania* spp.

Table 24.-Continued.....

Group/order	Family	Taxa
		Dicosmoecus spp.
	Philopotamidae	*Dolophilodes* sp.
	Rhyacophilaidae	*Rhyacophila* spp.
	Uenoidae	*Neophylax*
Coleoptera	Haliplidae	*Haliplus* sp.
	Dytiscidae	unidentified larvae and adults
		Oreodytes spp.
	Hydrophilidae	unidentified larvae
	Elmidae	unidentified larvae
		Narpus concolor (LeConte) adult
		Cleptelmis ornata (Schaeffer) adult
		Optioservus sp. adult
		Zaitzevia sp. adult
		Heterlimnius corpulentus (LeConte) adult
Diptera		unidentified pupae
	Tipulidae	unidentified larvae
	Deuterophlebiidae	*Deuterphlebia nielsoni* Kennedy
	Dixidae	*Dixa* sp.
	Simuliidae	*Simulium* spp.
	Ceratopogonidae	unidentified larvae
	Chironomidae	unidentified larvae
	Anthericidae	*Antherix pachypus* Bigot

Table 25.-Mean percentage of each taxon in the benthos for numeric density (D) and dry biomass (B) for the downstream, middle, and upstream riffles on two sample dates in Big Creek, July-August 1990.

Taxa	Downstream				Middle				Upstream			
	18 July		1 August		18 July		1 August		18 July		1 August	
	D	B	D	B	D	B	D	B	D	B	D	B
Ephemeroptera												
Acentrella turbida	3.3	0.1	0.2	<0.1	6.8	0.4	0.3	<0.1	7.7	0.4	3.2	0.3
Baetis spp.	19.9	10.5	25.6	11.6	16.1	12.5	20.3	9.2	14.5	9.0	22.1	7.4
Cloeon sp.	2.0	0.7	-	-	1.1	0.6	-	-	2.0	0.7	0.3	0.1
Ameletus sp.	0.1	0.2	6.0	6.4	0.3	1.8	7.8	10.4	-	-	-	-
Paraleptophlebia sp.	-	-	-	-	-	-	-	-	0.1	<0.1	-	-
Heptageniidae	1.3	<0.1	0.3	<0.1	1.0	<0.1	1.1	<0.1	1.0	<0.1	0.8	<0.1
Cingymula spp.	5.4	3.6	7.2	8.3	4.7	3.7	9.2	11.6	8.8	4.9	6.6	5.6
Epeorus spp.	1.9	1.1	2.3	0.3	1.0	0.3	0.6	<0.1	1.8	0.6	5.3	0.7
Rhithrogenia spp.	1.2	2.7	0.4	0.4	0.5	2.0	0.1	<0.1	0.8	1.4	-	-
Ephemerellidae	0.5	<0.1	0.5	<0.1	0.6	<0.	1.3	<0.1	0.5	<0.1	1.1	<0.1
Drunella	4.3	9.0	2.5	13.6	3.0	8.3	1.8	8.4	1.4	2.8	2.9	8.7
D. doddsi	0.5	7.2	-	-	0.4	8.1	-	-	0.9	11.5	0.2	1.8
D. grandis	0.4	3.7	0.1	1.0	-	-	-	-	-	-	0.1	0.4
Serratella tibialis	12.9	4.3	13.1	14.5	7.8	3.6	9.4	11.0	9.7	4.3	14.0	10.9
Total	54.1	43.1	58.2	56.1	43.3	41.3	51.9	50.6	49.2	35.6	56.6	35.9
Plecoptera												
Nemouridae	0.4	<0.1	0.7	<0.1	0.3	<0.1	0.5	<0.1	0.6	<0.1	0.8	<0.1
Zapada spp.	0.3	<0.1	0.8	0.2	0.6	0.1	0.2	<0.1	1.8	0.1	0.3	<0.1
Amphinemura banksi	1.1	<0.1	2.5	0.1	1.5	<0.1	1.0	0.1	1.9	0.1	1.3	<0.1
Leuctridae	-	-	-	-	0.2	0.3	1.0	1.0	-	-	0.2	0.1
Perlidae	-	-	0.5	<0.1	0.2	<0.1	-	-	0.1	<0.1	0.1	<0.1
Hesperperla pacifica	0.4	0.4	-	-	-	-	-	-	-	-	-	-

Table 25.-Continued.....

Taxa	Downstream				Middle				Upstream			
	18 July		1 August		18 July		1 August		18 July		1 August	
	D	B	D	B	D	B	D	B	D	B	D	B
Doroneuria theodora	0.3	22.5	1.8	13.3	0.9	6.4	0.9	3.6	1.8	33.8	1.8	44.3
Chloroperlidae	2.8	2.1	4.9	9.6	5.3	6.5	10.2	15.5	4.6	5.3	4.9	3.7
Perlodidae	0.8	<0.1	1.6	<0.1	1.2	<0.1	2.2	0.2	1.4	1.0	1.4	<0.1
Megarcys sp.	-	-	-	-	-	-	-	-	-	-	0.1	<0.1
Kogotus sp.	1.7	5.0	0.2	1.6	1.3	0.3	0.4	1.5	0.7	2.0	0.2	0.5
Total	7.8	33.0	13.0	24.8	11.0	16.5	16.4	21.9	12.9	42.3	11.1	48.6
					Hemiptera							
Corixidae	-	-	0.1	0.6	-	-	-	-	-	-	-	-
					Trichoptera							
Unidentified	1.3	<0.1	1.4	<0.1	0.8	<0.1	1.2	<0.1	1.7	<0.1	2.3	0.3
Brachycentrus spp.	-	-	0.1	<0.1	0.1	<0.1	0.1	0.1	-	-	0.2	0.1
Micrasema bactro	-	-	0.1	<0.1	-	-	-	-	-	-	0.1	<0.1
Arctopsyche grandis	-	-	-	-	0.1	0.8	-	-	-	-	-	-
Lepidostoma spp.	-	-	-	-	0.1	<0.	-	-	0.1	0.1	-	-
Apatania spp.	0.1	<0.1	-	-	-	-	-	-	-	-	-	-
Dolophilodes sp.	0.9	0.1	-	-	2.3	0.6	0.1	<0.1	0.8	0.1	3.8	1.6
Rhyacophila spp.	2.4	9.6	0.5	0.5	2.0	3.3	0.8	1.2	1.5	4.4	3.2	4.0
Neophylax sp.	-	-	-	-	0.3	0.1	0.1	0.1	-	-	0.1	<0.1
Pupae	1.1	3.8	-	-	1.6	9.7	0.1	0.1	0.1	<0.1	0.2	0.1
Total	5.8	13.5	2.1	0.5	7.3	14.5	2.4	1.5	4.2	4.6	9.0	6.1

Table 25.-Continued....

Taxa	Downstream				Middle				Upstream			
	18 July		1 August		18 July		1 August		18 July		1 August	
	D	B	D	B	D	B	D	B	D	B	D	B
					Coleoptera							
Elmidae larvae	4.0	3.0	3.6	5.9	14.1	15.9	14.6	15.1	8.0	9.4	6.2	4.0
Narpus concolor	-	-	-	-	-	-	0.1	1.0	-	-	0.1	0.5
Cleptelmis ornata	-	-	-	-	-	-	-	-	-	-	0.1	0.1
Optioservus sp.	1.1	2.0	0.8	1.9	1.3	3.4	2.6	6.1	0.9	2.0	1.3	2.1
Zaitzevia sp.	-	-	-	-	-	-	-	-	-	-	0.1	0.1
Heterlimnius corpulentus	0.1	0.2	0.8	1.9	0.4	0.9	0.5	1.1	0.1	0.1	0.2	0.4
Total	5.2	5.2	4.9	9.0	15.8	20.2	17.8	23.3	9.0	11.5	8.0	7.2
					Diptera							
Tipulidae	0.7	0.3	0.3	0.1	0.6	0.5	0.2	1.0	0.3	1.2	0.2	0.4
Deuterphlebia spp.	0.1	<0.1	-	-	0.9	<0.1	-	-	0.7	<0.1	1.2	<0.1
Simulium spp.	0.4	<0.1	1.4	0.7	0.1	<0.1	0.1	0.1	0.1	<0.1	0.1	<0.1
Chironomidae	21.3	3.9	17.6	6.1	19.2	6.4	7.7	0.9	19.6	3.6	11.3	1.4
Antherix pachypus	-	-	0.4	1.8	-	-	-	-	0.1	0.5	-	-
Ceratopogonidae	-	-	-	-	-	-	0.1	<0.1	-	-	-	-
Pupae	4.8	0.6	2.2	0.4	2.2	0.4	3.7	0.7	4.0	0.8	1.8	0.2
Total	27.3	4.8	21.9	9.1	23.0	7.3	11.8	2.7	24.8	6.1	14.6	2.0

Table 26.-Mean percentage of each taxon in the drift for mean daily numeric drift density (DD) and dry biomass (DB) for the downstream, middle, and upstream riffles on two sample dates in Big Creek, July 1990.

Taxa	Downstream				Middle				Upstream			
	16-17 July		30-31 July		16-17 July		30-31 July		16-17 July		30-31 July	
	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB
					Ephemeroptera							
Acentrella turbida	4.9	1.1	0.025	0.5	4.3	0.8	4.4	1.1	4.9	1.3	6.5	1.4
Baetis spp.	66.1	74.0	55.7	47.2	55.5	63.6	67.3	60.4	53.1	44.4	71.9	74.9
Cloeon sp.	0.1	0.1	0.1	0.1	0.4	0.4	-	-	0.2	0.3	0.5	0.2
Ameletus sp.	0.2	0.5	0.1	1.0	0.3	0.6	0.1	<0.1	0.6	1.5	0.2	0.3
Paraleptophlebia sp.	-	-	-	-	-	-	-	-	<0.1	<0.1	-	-
Heptageniidae	0.1	<0.1	1.1	<0.1	0.2	<0.1	1.0	<0.1	0.3	<0.1	0.6	<0.1
Cingymula spp.	0.3	0.2	0.4	0.3	0.4	0.3	0.2	0.1	1.0	1.0	0.9	1.6
Epeorus spp.	2.3	3.7	6.5	8.5	5.9	7.5	5.4	12.6	4.1	15.8	1.7	1.3
Rhithrogenia spp.	0.1	0.5	0.1	<0.1	0.2	1.3	<0.1	<0.1	0.3	2.3	-	-
Ephemerellidae	0.2	<0.1	0.8	<0.1	0.3	<0.1	0.5	<0.1	0.1	<0.1	0.1	<0.1
Drunella spp.	0.6	1.7	0.6	3.0	0.4	1.6	0.3	0.6	0.9	3.1	0.2	0.8
D. doddsi	<0.1	0.4	-	-	<0.1	1.2	<0.1	<0.1	<0.1	1.8	0.2	2.2
D. grandis	<0.1	0.4	-	-	<0.1	0.3	-	-	-	-	-	-
Serratella tibialis	1.6	0.7	11.1	15.6	2.7	1.6	5.6	6.4	3.7	1.1	1.4	1.5
Total	76.5	83.3	79.0	76.2	70.1	79.2	84.8	81.2	69.2	72.6	84.2	84.2
					Plecoptera							
Nemouridae	<0.1	<0.1	0.6	<0.1	<0.1	<0.1	0.7	<0.1	0.1	<0.1	0.1	<0.1
Zapada spp.	0.4	<0.1	0.7	0.1	0.7	0.1	0.5	0.1	0.8	0.1	0.4	<0.1
Amphinemura banksi	0.3	<0.1	2.4	0.3	0.2	<0.1	2.3	0.2	0.2	<0.1	1.3	0.2
Perlidae	-	-	-	-	-	-	0.1	<0.1	-	-	0.1	0.1
Doroneuria theodora	-	-	-	-	0.1	0.1	-	-	-	-	0.1	0.1
Chloroperlidae	0.7	2.5	0.1	0.5	1.1	3.4	0.3	1.1	1.2	2.3	0.9	1.9

Table 26.-Continued.....

Taxa	Downstream 16-17 July DD	 DB	 30-31 July DD	 DB	Middle 16-17 July DD	 DB	 30-31 July DD	 DB	Upstream 16-17 July DD	 DB	 30-31 July DD	 DB
Perlodidae	<0.1	<0.1	0.2	<0.1	0.2	0.2	0.3	<0.1	0.2	0.1	0.1	0.1
Megarcys sp.	-	-	-	-	<0.1	<0.1	-	-	-	-	-	-
Kogotus sp.	<0.1	0.4	0.1	0.6	-	-	<0.1	0.3	<0.1	0.4	0.1	1.0
Total	1.4	2.9	4.1	1.5	2.3	3.8	4.2	1.7	2.5	2.9	3.1	3.5
						Hemiptera						
Corixidae	<0.1	0.2	-	-	<0.1	0.2	-	-	<0.1	0.4	<0.1	0.2
						Trichoptera						
Unidentified	0.5	<0.1	2.8	<0.1	1.0	<0.1	1.3	<0.1	0.2	<0.1	0.3	<0.1
Brachycentrus spp.	<0.1	<0.1	0.5	0.5	0.1	0.1	0.5	0.6	0.1	<0.1	-	-
Ameniocentus sp.	0.1	0.1	-	-	-	-	-	-	-	-	-	-
Micrasema bactro	<0.1	<0.1	0.1	<0.1	-	-	<0.1	<0.1	-	-	-	-
Arctopsyche grandis	-	-	<0.1	<0.1	-	-	0.1	5.0	-	-	-	-
Lepidostoma spp.	0.1	0.2	-	-	<0.1	<0.1	-	-	-	-	-	-
Dolophilodes sp.	0.3	<0.1	3.9	2.9	0.4	0.1	2.0	1.4	0.7	0.1	0.8	0.5
Rhyacophila spp.	0.6	1.4	0.6	0.7	0.5	0.6	0.4	0.8	0.7	0.9	0.6	1.4
Discomeous sp.	<0.1	<0.1	-	-	-	-	-	-	<0.1	0.1	-	-
Pupae	0.1	0.2	-	-	0.1	0.2	<0.1	<0.1	0.1	0.3	<0.1	0.2
Total	1.7	1.9	7.9	4.1	2.1	1.0	4.3	7.8	1.8	1.4	1.7	2.1
						Coleoptera						
Haliplus sp.	<0.1	0.2	-	-	-	-	-	-	<0.1	0.1	-	-
Dytiscidae	-	-	0.4	0.9	0.3	0.3	<0.1	0.4	<0.1	<0.1	0.1	0.1

Table 26.-Continued.....

Taxa	Downstream				Middle				Upstream			
	16-17 July		30-31 July		16-17 July		30-31 July		16-17 July		30-31 July	
	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB	DD	DB
Oreodytes spp.	<0.1	0.1	-	-	<0.1	0.1	<0.1	0.1	<0.1	0.6	<0.1	0.5
Hydrophilidae	-	-	0.1	1.7	-	-	-	-	<0.1	0.4	0.1	0.4
Elmidae larvae	0.2	1.2	0.4	0.9	0.3	1.4	0.3	0.2	0.1	0.6	0.3	1.5
Narpus concolor	<0.1	0.7	0.1	1.4	0.1	1.5	<0.1	0.5	<0.1	0.5	0.2	3.4
Cleptelmis ornata	<0.1	<0.1	0.1	0.3	-	-	-	-	-	-	-	-
Optioservus sp.	0.6	2.4	3.1	11.0	0.6	2.2	1.0	4.4	1.6	7.9	0.3	0.9
Zaitzevia sp.	<0.1	0.1	<0.1	0.1	0.1	0.3	0.2	0.7	<0.1	1.4	-	-
Heterlimnius corpulentus	0.2	0.7	0.7	2.3	0.2	0.9	0.5	2.2	0.4	1.7	0.2	0.8
Total	1.0	5.4	4.5	17.7	1.6	6.6	2.0	8.5	2.1	13.2	1.2	7.6
Diptera												
Tipulidae	<0.1	<0.1	-	-	<0.1	0.4	<0.1	<0.1	<0.1	0.8	<0.1	<0.1
Deuterphlebia sp.	3.3	0.4	0.6	<0.1	3.2	0.3	1.0	0.1	1.4	0.2	2.1	0.1
Dixa sp.	-	-	-	-	-	-	-	-	-	-	<0.1	<0.1
Simulium spp.	1.1	0.4	1.3	0.2	1.4	0.3	1.1	0.1	1.7	0.5	1.3	0.3
Chironomidae	11.1	5.2	1.7	0.3	15.0	8.0	1.5	0.4	14.7	7.4	4.4	1.9
Antherix pachypus	-	-	-	-	-	-	-	-	<0.1	<0.1	-	-
Pupae	3.7	0.1	0.9	<0.1	4.2	0.1	1.1	<0.1	6.2	0.3	1.7	0.1
Total	19.2	6.1	4.5	0.5	23.8	9.1	4.7	0.6	24.0	9.2	9.5	2.4

Table 27.-Mean number of individuals (rounded to nearest integer) collected by paired dirftnets at the downstream (D), middle (M), and upstream (U) riffles for total taxa for each time period (TP; N-noon, S-sunset, M-midnight, R-sunrise) on two sample dates and results of G-test (P-values) for taxa counts weighted equally among riffles (E), and proportional to stream discharge (Q)[a], wetted perimeter (WP)[b], and mean water velocity (VEL)[c] in Big Creek, July 1990.

Date	TP	L	M	H	E	Q	WP	VEL
16-17/7	N	69	88	100	0.042	0.442	<0.001	0.261
	S	1462	1400	878	<0.001	<0.001	<0.001	<0.001
	M	434	446	373	0.007	<0.001	<0.001	<0.001
	R	327	296	193	<0.001	<0.001	<0.001	<0.001
30-31/7	N	183	169	145	0.064	<0.001	<0.001	<0.001
	S	598	1413	796	<0.001	<0.001	<0.001	<0.001
	M	946	905	324	<0.001	<0.001	<0.001	<0.001
	R	210	242	436	<0.001	<0.001	<0.001	0.034

[a] Proportion of stream discharge at the downstream, middle, and upstream riffles on two sample dates were: 0.26, 0.31, 0.43; and 0.05, 0.11, 0.84.

[b] Proportion of wetted perimeter at the downstream, middle, and upstream rifles on two sample dates were: 0.22, 0.26, 0.52; and 0.16, 0.24, 0.60.

[c] Proportion of water velocity at the downstream, middle, and upstream riffles two sample dates were: 0.31, 0.30, 0.39; and 0.25, 0.24, 0.52.

Table 28.-Mean daily number of individuals (no./100 m^3; rounded to nearest integer) collected by paired driftnets at the downstream (D), middle (M), and upstream (U) riffles for total taxa on two sample dates and results of G-tests (P-values) for taxa counts weighted equally among riffles (E, and proportional to stream discharge (Q)[a], wetted perimeter (WP)[b], and mean water velocity (VEL)[c] in Big Creek, July 1990.

Date	L	M	H	E	Q	WP	VEL
16-17/7	977	990	758	<0.001	<0.001	<0.001	<0.001
30-31/7	1895	2715	1669	<0.001	<0.001	<0.001	<0.001

[a] Proportion of stream discharge at the downstream, middle, and upstream riffles on two sample dates were: 0.26, 0.31, 0.43; and 0.05, 0.11, 0.84.

[b] Proportion of wetted perimeter at the downstream, middle, and upstream rifles on two sample dates were: 0.22, 0.26, 0.52; and 0.16, 0.24, 0.60.

[c] Proportion of water velocity at the downstream, middle, and upstream riffles two sample dates were: 0.31, 0.30, 0.39; and 0.25, 0.24, 0.52.

APPENDIX B

BIOENERGETIC EQUATIONS AND MODELS

Table 29.-Description of bioenergetic equations and models used in the study.

Elliott (1975a, b, c, d; 1976a, b, c) developed bioenergetic equations for brown trout from laboratory tests investigating the influence of water temperature, ration, and fish weight on the energy budget of immature trout. Trout had been reared under hatchery conditions and ranged in size from 5 to 300 g. Water temperature varied from 3.8 to either 19.5, 20.4, or 21.7 C. Energy required for gonadal development was not addressed by the equations.

To conceptualize the various metabolic pathways of ingested materials, Elliott used the general energy budget:

$$C=F+U+B+R$$

where C is energy consumed, F is energy lost as feces, U is energy lost as excretory products, B is change in energy content of the trout, and R is energy required for respiration. All components were directly measured in tests except R, which was calculated by balancing the energy budget after other components had been estimated. In all tests, a continuous flow of water was supplied to tanks containing experimental trout so that fish were exercised. Therefore, the component R included all possible respiratory losses, e.g. standard metabolism, activity, and energy needed in acquisition and processing of food.

Several inflection points were noted for the relationships among components of the energy budget and water temperature. Elliott developed separate multiple regression equations predicting the various components, in energetic terms (cal./d) of the energy budget corresponding to areas between inflection points. The equations used trout weight and water temperature as independent variables and different regression coefficients for specific temperature ranges.

Both food consumption and respiration were estimated with the equation:

$$C \text{ and } R = a_i W^{b_{1i}} e^{b_{2i}T}$$

where W is trout live weight, T is water temperature, e is the base of the natural logarithm, and a_i, b_{1i}, and b_{2i} are constants appropriate for temperature range *i*. Two levels of C and R may be calculated from the equation; maximum level, the amount of energy consumed and respired by a fish feeding to satiation (temperature range tested: 3.8 to 21.7 C) and maintenance level, the amount of energy consumed and respired that produces no change in the energy content of the trout (temperature range tested: 3.8 to 19.5 C).

Elliott calculated the amount of energy lost as feces and excretory products, as proportions of consumption, P_F and P_U, respectively. He found that these proportions were unaffected by trout weight, but varied with water temperature and consumption rate (C) relative to maximum consumption rate, C/C_{max}. Both P_F and P_U were estimated by the equation:

$$P_F \text{ and } P_U = aT^{b_1} W^{b_2(C/C_{max})}$$

where a, b_1, and b_2 are constants applicable for temperatures between 3.8 to 20.4 C. To relate changes in energy content of a trout to biomass, Elliott performed proximate analysis on experimental fish and developed a regression equation using fish weight and condition factor as independent variables to predict energy content per gram of trout tissue (EG). This relationship was described by the equation:

$$EG = ae^{b_1K}W^{b_2}$$

where EG is energy content of trout tissue (cal./g), K is the Fulton condition factor of the trout, and a, b_1, and b_2 are constants. Also, Elliott (1975c) derived a multiple regress equation that directly predicts maximum weight gain for a brown trout over a time interval. The equation is:

$$W_t=(b_1(a+b_2T)t+W_o^{b_1})^{(1/b_1)}$$

where W_t is trout weight (g) at end of the time interval, W_o is fish weight (g) at the start of the time interval, T is water temperature, t is time (d), and a, b_1, and b_2 are temperature specific constants for the ranges 3.8 to 12.8 C and 13.6 to 19.5 C.

Preall and Ringler (1989) translated Elliott's equations for C_{max}, R_{max}, P_F, P_U, and EG into a simulation model (TROUT). By reworking the basic energy budget, they estimated maximum change in energy content of a fish as:

$$B_{max} = C_{max}(1-P_F-P_U)-R_{max}.$$

By converting B_{max} to a weight increment (B_{max}/EG), Preall and Ringler (1989) were able to estimate maximum growth rate of a fish given water temperature, fish weight and condition factor. They developed a second model (EQMAX) that directly predicted maximum weight gain

(Elliott 1975c) given water temperature, fish weight, and time interval. Changes in energy density of fish tissue were not considered in this model. Both models were tested and EQMAX produced estimates closer to experimental results (Elliott 1975c) than did TROUT, but Preall and Ringler (1989) concluded that TROUT may be a better model in instances where large changes in condition factors of trout occur. Both models were used to estimate maximum growth rates and ecological growth coefficient (EGC, the percent of maximum growth actually attained) for brown trout in three streams with differing temperature regimes and trout populations.

I converted Elliott's bioenergetic equations into a simulation model (BIOE1). The basic organization of the model was similar to that employed by Preall and Ringler (1989) and Preall (1985) for their TROUT model. I selected this approach since trout in Brackett Creek exhibited substantial changes in condition factors. This model differed from Preall and Ringler's in that trout growth was incremented daily as opposed to weekly and C_{main} was also calculated. Data requirements were the number of days for the time interval of interest, mean daily water temperatures, and trout lengths and weights at the start and end of the time interval. The model calculates the ecological growth coefficient used by Preall and Ringler (1989) as well as C_{max} and C_{main} for each trout while it was in an enclosure and the model sums these variables for the test period per trout and daily totals for all trout in an enclosure.

A second model (BIOE2) used EGC and daily energy increment for each fish calculated by BIOE1 to estimate consumption rates that would produce observed trout growth for the time interval. This was estimated daily as the difference between C_{max} and C_{main} weighted by EGC and added to C_{main} for trout that grew. C_{main} was used for trout that did not grow while C_{main} was scaled proportional to specific growth rates for trout that lost weight during the study.

Figure 48.-FORTRAN source code for bioenergetics model BIOE1.

```
      PROGRAM BIOE1
C.....PROGRAM TO USE ELLIOTT'S (1975A,B,C,D; 1976A,B,C) BIOENERGETIC
C.....EQUATIONS IN A SIMULATION MODEL TO CALCULATE MAXIMUM AND
C.....MAINTENANCE CONSUMPTION RATE, METABOLISM, PROPORTION OF
C.....CONSUMPTION LOST AS WASTE, AND MAXIMUM GROWTH IN CALORIES.
C.....THE PROGRAM CONVERTS MAXIMUM GROWTH INCREMENT TO WEIGHT (G)
C.....USING FISH CONDITION FACTOR.  OBSERVED AND MAXIMUM SPECIFIC
C.....GROWTH RATES ARE CALCULATED AND THEIR RATIO*100 (EGC).
C.....MAINTENANCE CALCULATIONS ASSUME THAT FISH DO NOT CHANGE
C.....IN LENGTH OR WEIGHT DURING SIMULATIONS.  DATA INPUT IS A
C.....FILE WITH NUMBER OF DAYS FOR SIMULATIONS AND MEAN DAILY WATER
C.....TEMPERATURE AND A FILE OF FISH LENGTHS AND WEIGHTS (INITIAL AND
C.....FINAL) AND THE FIRST AND LAST DAY THAT FISH WERE IN THE TEST.
C.....3 OUTPUT FILES CONSIST OF 1) DAILY VALUES PER FISH (UNIT 3)
C.....2) DAILY TOTALS FOR ALL FISH IN ENCLOSURES (UNIT 4), AND
C.....3) TOTAL PER FISH FOR THE DURATION OF THE TEST (UNIT 5).
C.........................SCL...5/28/92..........rev.12/9/92.
C
      CHARACTER TAG*4
      INTEGER DIN,DOUT,DTOT,SECTION
      REAL LI,LF,LINC,LII
      DIMENSION T(100),CX(100),CN(100),RX(100),RN(100)
C
         WRITE(*,*)' TEMPERATURE SOURCE FILE'
         OPEN(1,FILE='  ')
         WRITE(*,*)' FISH DATA FILE'
         OPEN(2,FILE='  ')
         WRITE(*,*)' FILE FOR DAILY GROWTH RESULTS PER FISH'
         OPEN(3,FILE='  ')
         WRITE(*,*)' FILE FOR DAILY TOTALS OF ALL FISH'
         OPEN(4,FILE='  ')
         WRITE(*,*)' FILE FOR TOTAL PER FISH'
         OPEN(5,FILE='  ')
C
C.....READ FILE WITH TEST LENGTH IN DAYS (NODAY) AND MEAN DAILY
C.....WATER TEMPERATURE INTO ARRAY T(J). TEMPERATURES OUTSIDE RANGE
C.....USED BY ELLIOTT ARE SET TO CLOSEST EXTREME (3.8 AND 21.7).
            READ(1,10)NODAY
 10         FORMAT(1X,I2)
               DO 30,J=1,NODAY
                  READ(1,20)TEMP
 20               FORMAT(1X,F5.1)
                    IF (TEMP.LT.3.8) THEN
                        TEMP=3.8
                     ELSEIF (TEMP.GT.21.7) THEN
                        TEMP=21.7
                    ENDIF
                    T(J)=TEMP
```

```
                  N=0
 30          CONTINUE
C
C.....ZERO VARIABLES FOR TRACKING TOTAL MAX.CONSUMPTION (CMXT)
C.....AND METABOLISM (RMXT),MAIN.CONSUMPTION (CMNT) AND METABOLISM
C.....(RMNT) FOR INDIVIDUAL FISH OVER TEST
C
 35          CONTINUE
                CMXT=0
                CMNT=0
                RMXT=0
                RMNT=0
C
C.....READ FILE OF FISH DATA--SECTION=ENCLOSURE,TAG=FISH TAG CODE,
C.....LI AND WI=INITIAL FISH LENGTH AND WEIGHT,LF AND WF=LENGTH AND
C.....WEIGHT AT END OF TEST OR WHEN FISH ENTERED TRAP,DIN=DAY FISH
C.....WAS RELEASED INTO ENCLOSURE,DOUT=DAY FISH WAS COLLECTED.
C
            READ(2,40,END=300)SECTION,TAG,LI,WI,LF,WF,DIN,DOUT
 40         FORMAT(1X,I2,1X,A4,1X,4(F5.1,1X)2(I4,1X))
C.....CALCULATE CONDITION FACTORS(CFI,CFF),TOTAL DAYS FISH WAS IN
C.....TEST(DTOT),AND DAILY INCREMENTS FOR L,W,CF
C
             CFI=(WI/(LI**3))*100000
             CFF=(WF/(LF**3))*100000
             DTOT=DOUT-DIN
             DIN=DIN+1
             LINC=(LF-LI)/DTOT
             WINC=(WF-WI)/DTOT
             CFINC=(CFF-CFI)/DTOT
C
C.....INITIALIZE CONDITION FACTORS AND WEIGHTS FOR MAXIMUM
C.....(*MX),MAINTENANCE(*MN),OBSERVED(*O) VALUES
C
             CFMX=CFI
             WMX=WI
             WMN=WI
             WO=WI
             CFO=CFI
             LII=LI
C
C.....DO LOOP CALLS SUBROUTINES MAX AND MN OF ELLIOTT'S
C.....BIOENERGETIC EQUATIONS TO CALCULATE MAXIMUM
C.....AND MAINTENANCE CONSUMPTION, METABOLISM, PROPORTIONS LOST AS
C.....FECES AND EXCRETION, CALORIC INCREMENT, AND WEIGHT INCREMENT
C.....USING CONDITION FACTORS.  ITERATES FOR DTOT.
C
          DO 50,J=DIN,DOUT
             TEMP=T(J)
             CALL MAX(TEMP,WMX,CMX,RMX,PMX,EMX,CFMX,GMX,CC)
             CALL MN(TEMP,WMN,CMN,RMN,CMX,PMN)
C
```

```
C.....INCREMENT AND WRITE DAILY RESULTS PER FISH TO UNIT 3
C
               WO=WO+WINC
               LII=LII+LINC
               WMX=WMX+GMX
               CFMX=(WMX/(LII**3))*100000
               CFO=CFO+CFINC
         WRITE(3,45)J,SECTION,TAG,CMX,CMN,RMX,RMN,PMX,PMN,WMX,
     &WMN,WO,CFMX,CFI,CFO,CC
  45     FORMAT(1X,I2,1X,I2,1X,A4,1X,4(F8.2,1X),2(F5.3,1X),
     &3(F7.3,1X),3(F5.3,1X),F10.3)
C
C.....TALLY FOR TOTALS PER FISH
C
                   CMXT=CMXT+CMX
                   CMNT=CMNT+CMN
                   RMXT=RMXT+RMX
                   RMNT=RMNT+RMN
C
C.....TALLY FOR DAILY TOTAL FOR ALL FISH
C
                   CX(J)=CX(J)+CMX
                   CN(J)=CN(J)+CMN
                   RX(J)=RX(J)+RMX
                   RN(J)=RN(J)+RMN
  50        CONTINUE
C
C.....CALCULATES MAXIMUM SPECIFIC GROWTH RATE(SGRM), OBSERVED
C.....SPECIFIC GROWTH RATE(SGRO), AND RATIO (EGC)
          N=N+1
        SGRM=((LOG(WMX)-LOG(WI))/DTOT)*100
        SGRO=((LOG(WF)-LOG(WI))/DTOT)*100
        EGC=(SGRO/SGRM)*100
C
C.....WRITE TOTALS PER FISH TO UNIT 5
C
        WRITE(*,60)N,DTOT,TAG,SGRM,SGRO,EGC,CMXT,CMNT,RMXT,RMNT,
     &WMX,WI,WF,LI,LF,CFMX,CFI,CFO
        WRITE(5,60)N,DTOT,TAG,SGRM,SGRO,EGC,CMXT,CMNT,RMXT,RMNT,
     &WMX,WI,WF,LI,LF,CFMX,CFI,CFO
  60    FORMAT(1X,I2,1X,I3,1X,A4,1X,3(F6.3),1X,4(F12.2,1X),5(F7.3,1X),
     &3(F6.3,1X))
         GOTO 35
 300    CONTINUE
C
C.....DO LOOP TO WRITE DAILY FISH TOTALS TO UNIT 4
C
          DO 320 J=1,100
            WRITE(4,310)J,CX(J),CN(J),RX(J),RN(J)
 310        FORMAT(1X,I3,1X,4(F12.2,1X))
 320       CONTINUE
```

```
        ENDFILE(5)
        ENDFILE(4)
        ENDFILE(3)
        CLOSE(1)
        CLOSE(2)
        CLOSE(3)
        CLOSE(4)
        CLOSE(5)
        STOP
        END

      SUBROUTINE MAX(TP,WX,CX,RX,PX,EX,CFX,GX,DCX)
C.....SUBROUTINE MAX READS TEMPERATURE,FISH WEIGHT,AND CONDITION
C.....FACTOR AND CALCULATES MAXIMUM DAILY CONSUMPTION,METABOLISM,
C.....PROPORTION OF CONSUMPTION LOST AS WASTE,CALORIC INCREMENT,
C.....AND WEIGHT INCREMENT ACCORDING TO TEMPERATURE RANGE.
C.....WASTE LOSS EQUATIONS RANGE=3.8-20.4, TEMPERATURES BEYOND
C.....RANGES ARE CONVERTED TO NEAREST EXTREME.
C
        IF(TP.LT.6.6) THEN
           CX=(2.902*WX**0.762*EXP(0.418*TP))
         ELSEIF((TP.GE.6.6).AND.(TP.LT.13.3)) THEN
           CX=(15.018*WX**0.759*EXP(0.171*TP))
         ELSEIF((TP.GE.13.3).AND.(TP.LT.17.8)) THEN
           CX=(26.433*WX**0.767*EXP(0.126*TP))
         ELSEIF(TP.GE.17.8) THEN
          CX=(3.241E7*WX**0.753*EXP(-0.662*TP))
         ENDIF
C
          IF(TP.LT.17.8) THEN
           RX=(3.890*WX**0.770*EXP(0.204*TP))
          ELSEIF((TP.GE.17.8).AND.(TP.LT.19.5)) THEN
           RX=(2.215E7*WX**0.757*EXP(-0.663*TP))
          ELSE
           RX=(28.833*WX**0.756*EXP(0.0325*TP))
          ENDIF
C
         IF (TP.LE.20.4) THEN
            T=TP
          ELSE
            T=20.4
         ENDIF
           PFX=(0.212*T**(-0.222)*EXP(0.631))
           PUX=(0.0259*T**(0.580)*EXP(-0.299))
           PX=1-PFX-PUX
C
           DCX=CX*PX-RX
           EX=751.9*EXP(0.332*CFX)*WX**0.072
           GX=DCX/EX
         END
```

```
      SUBROUTINE MN(TP1,WX1,CX1,RX1,CXX1,PX1)
C.....SUBROUTINE MAIN READS TEMPERATURE AND FISH WEIGHT
C.....AND CALCULATES MAINTENANCE DAILY CONSUMPTION,METABOLISM,
C.....AND PROPORTION OF CONSUMPTION LOST AS WASTE ACCORDING TO
C.....TEMPERATURE RANGES.  C AND R RANGE=3.8-19.5 AND WASTE
C.....LOSS RANGE=3.8-20.4, TEMPERATURES BEYOND RANGES ARE
C.....CONVERTED TO NEAREST EXTREME. NO CHANGE IN FISH LENGTH
C.....AND WEIGHT ARE ASSUMED FOR MAINTENANCE ESTIMATES.
C
        IF(TP1.LT.6.6) THEN
           CX1=(6.169*WX1**0.716*EXP(0.224*TP1))
         ELSEIF((TP1.GE.6.6).AND.(TP1.LE.19.5)) THEN
           CX1=(12.031*WX1**0.737*EXP(0.105*TP1))
         ELSE
           CX1=(12.031*WX1**0.737*EXP(0.105*19.5))
        ENDIF
C
          IF(TP1.LT.7.1) THEN
           RX1=(3.802*WX1**0.723*EXP(0.245*TP1))
          ELSEIF((TP1.GE.7.1).AND.(TP1.LE.19.5)) THEN
           RX1=(11.866*WX1**0.721*EXP(0.0915*TP1))
          ELSE
           RX1=(11.866*WX1**0.721*EXP(0.0915*19.5))
          ENDIF
C
          IF (TP1.LE.20.4) THEN
            T=TP1
          ELSE
            T=20.4
         ENDIF
           PFX1=0.212*T**(-0.222)*EXP(0.631*(CX1/CXX1))
           PUX1=0.0259*T**(0.580)*EXP(-0.299*(CX1/CXX1))
           PX1=1-PFX1-PUX1
         END
```

Figure 49.-FORTRAN source code for bioenergetics model BIOE2.

```
      PROGRAM BIOE2
C.....PROGRAM TO READ MAX. AND MAIN. CONSUMPTION RATES AND OBSERVED
C.....SPECIFIC GROWTH RATES AND EGC FROM BIOE1 TO CALCULATE
CONSUMPTION
C.....RATES PRODUCING OBSERVED GROWTH RATES..SCL.5/29/92.rev.12/9/92
      CHARACTER TAG*4,TAG1*4
      DIMENSION C(100)
      WRITE(*,*)' FILE OF EGC'
      OPEN(1,FILE='  ')
      WRITE(*,*)' DAILY GROWTH RESULTS PER FISH'
      OPEN(2,FILE='  ')
      WRITE(*,*)' FILE FOR TOTAL ESTIMATED CONSUMPTION RATES'
      OPEN(3,FILE='  ')
C
  10  CONTINUE
C.....READ FILE WITH OBSERVED SPECIFIC GROWTH RATES AND EGC
        READ(1,20,END=100)TAG,SGRO,EGC
  20    FORMAT(1X,A4,1X,2(F6.3))
  25  CONTINUE
C.....READ FILE WITH DAILY MAX. AND MAIN. CONSUMPTION RATES
         READ(2,30,END=100)J,TAG1,CMX,CMN
  30     FORMAT(1X,I2,1X,A4,1X,2(F8.2,1X))
C
C.....SCALE DAILY CONSUMPTION RATES BY EGC OR GROWTH RATES BASED
C.....ON POSITIVE, NEGATIVE, OR NO FISH GROWTH AND TALLY TOTALS IN
C.....ARRAY C(I) BY DAY (I)
       IF((TAG.EQ.TAG1).AND.(SGRO.GT.0.0)) THEN
           I=J
           CON=(EGC*(CMX-CMN))+CMN
           C(I)=C(I)+CON
           GOTO 25
        ELSEIF((TAG.EQ.TAG1).AND.(SGRO.EQ.0.0)) THEN
           I=J
           CON=CMN
           C(I)=C(I)+CON
           GOTO 25
         ELSEIF((TAG.EQ.TAG1).AND.(SGRO.LT.0.0)) THEN
           I=J
           CON=(1+(SGRO*0.01))*CMN
           C(I)=C(I)+CON
           GOTO 25
        ELSE
C.....READ FILE 2 FOR NEXT TROUT
          ENDIF
          BACKSPACE(2)
          GOTO 10
 100    CONTINUE
C.....WRITE TOTAL DAILY CONSUMPTION RATES TO FILE 3
```

```
          DO 120,I=1,100
            WRITE(*,115)I,C(I)
            WRITE(3,115)I,C(I)
115         FORMAT(1X,I4,1X,F15.2)
120       CONTINUE
      ENDFILE(3)
      CLOSE(1)
      CLOSE(2)
      CLOSE(3)
      STOP
      END
```

APPENDIX C

INVERTEBRATES - BRACKETT CREEK

Table 30.-List of taxa collected in drift samples from Brackett Creek, July-September 1989 and 1990.

Group/order	Family	Taxa
Oligochaeta		
Turbellaria		
Nematomorpha		
Acarina		
Terrestrials		
Ephemeroptera	Baetidae	unidentified nymphs
		Acentrella turbida McDunnough
		Baetis spp.
		Cloeon sp.
	Siphlonuridae	*Ameletus* sp.
	Leptophlebiidae	*Paraleptophlebia* sp.
	Heptageniidae	unidentified nymphs
		Cingymula spp.
		Epeorus spp.
	Ephemerellidae	*Caudatella* sp.
		Drunella spp.
		D. doddsi (Needham)
		Ephemerella spp.
		Serratella tibialis (McDunnough)
Plecoptera		unidentified nymphs
	Nemouridae	unidentified nymphs
		Zapada spp.
		Amphinemura banksi Baumann and Gaufin
	Leuctridae	unidentified nymphs
	Perlidae	unidentified nymphs
		Doroneuria theodora (Needham and Classen)
	Chloroperlidae	unidentified nymphs
	Perlodidae	unidentified nymphs
		Kogotus sp.
Hemiptera	Corixidae	unidentified nymphs
	Gerridae	unidentified adults
Trichoptera		unidentified larvae and pupae
	Brachycentridae	*Brachycentrus* spp.
		Micrasema bactro Ross
	Hydropsychidae	unidentified larvae
		Hydropsyche sp.
		Arctopsyche grandis (Banks)
	Glossosomatidae	*Glossosoma* sp.
	Limnephilidae	*Apatania* spp.

Table 30.-Continued.....

Group/order	Family	Taxa
		Onocosmoecus unicolor (Banks)
		Dicosmoecus sp.
		Cryptochia furcata Denning
	Rhyacophilaidae	*Rhyacophila* spp.
	Uenoidae	*Oligophlebodes* sp.
		Neophylax sp.
Coleoptera	Amphizoidae	*Amphizoa* sp. adult
	Gyrinidae	*Gyrinus* sp. adult
	Haliplidae	*Haliplus* sp. adult
	Dytiscidae	unidentified larvae
		Oreodytes spp. adult
		Agabus spp. adult
		Hydroporus sp. adult
	Hydrophilidae	unidentified larvae
	Elmidae	unidentified larvae
		Narpus concolor (LeConte) adult
		Cleptelmis ornata (Schaeffer) adult
		Optioservus sp. adult
		Zaitzevia sp. adult
		Heterlimnius corpulentus (LeConte) adult
Diptera		unidentified pupae
	Tipulidae	unidentified larvae
	Dixidae	*Dixa* sp.
		Meringodixa sp.
	Simuliidae	*Simulium* spp.
	Chironomidae	unidentified larvae
	Psychodidae	*Pericoma* sp.
	Anthericidae	*Antherix pachypus* Bigot
	Stratiomyidae	unidentified larvae

Table 31.-Mean percentage of each drift category (aquatic insect orders, terrestrials, Acarina, and worms (Oligochaeta, Turbellaria, and Nematomorpha)) for total daily drift by mean numeric drift density (DD) and drift biomass (DB) for all enclosures with and without brine shrimp and krill on each sample date in Brackett Creek, 1989. N=5 enclosures.

	16-17 August		5-6 September		21-22 September	
Category	DD	DB	DD	DB	DD	DB
Without brine shrimp and krill						
Ephemeroptera	33.2	16.2	16.9	5.1	10.2	2.3
Plecoptera	1.9	0.5	3.8	0.9	1.7	0.3
Hemiptera	0.1	0.1	0.1	0.6	0.2	0.7
Trichoptera	0.8	0.7	0.4	0.5	0.1	0.5
Coleoptera	1.9	6.9	1.1	2.9	0.7	2.0
Diptera	13.1	5.0	19.8	2.6	18.4	1.3
Acarina	10.9	0.5	10.4	0.4	3.4	0.2
Worm	0.2	<0.1	0.2	<0.1	0.1	<0.1
Terrestrial	37.8	70.1	47.4	87.1	65.0	92.8
With brine shrimp and krill						
Ephemeroptera	13.7	4.6	5.0	1.3	4.2	0.8
Plecoptera	0.8	0.1	1.1	0.2	0.7	0.1
Hemiptera	<0.1	<0.1	<0.1	0.2	0.1	0.3
Trichoptera	0.3	0.2	0.1	0.1	0.1	0.2
Coleoptera	0.8	2.0	0.3	0.8	0.3	0.7
Diptera	5.4	1.4	5.8	0.7	7.5	0.5
Acarina	4.5	0.1	3.1	0.1	1.4	0.1
Worm	0.1	<0.1	0.1	<0.1	<0.1	<0.1
Terrestrial	15.6	19.8	14.0	22.7	26.5	34.1
Brine shrimp	57.2	50.6	68.7	55.2	57.6	44.7
Krill	1.6	21.1	1.9	21.7	1.6	18.6

Table 32.-Mean percentage of each drift category (aquatic insect orders, terrestrials, Acarina, and worms (Oligochaeta, Turbellaria, and Nematomorpha)) for total daily drift by mean numeric drift density (DD) and drift biomass (DB) for all enclosures with and without brine shrimp and krill on each sample date in Brackett Creek, 1990. N=6 enclosures.

Category	24-25 July		9-10 August		21-22 August		12-13 September	
	DD	DB	DD	DB	DD	DB	DD	DB
				Without brine shrimp and krill				
Ephemeroptera	50.3	41.0	42.4	49.7	57.7	25.7	35.2	15.9
Plecoptera	1.9	2.2	2.0	4.4	8.3	1.0	0.8	1.9
Trichoptera	1.3	1.4	0.7	1.1	3.6	0.9	1.4	1.0
Coleoptera	1.5	4.5	2.4	2.2	7.4	16.5	10.2	11.8
Diptera	8.0	8.6	7.2	5.7	2.1	1.5	1.7	2.0
Acarina	19.5	7.7	19.8	13.2	0.7	0.4	1.5	1.5
Worm	0.3	0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Terrestrial	17.4	34.7	25.4	23.8	20.2	54.0	49.1	66.0
				With brine shrimp and krill				
Ephemeroptera	14.8	14.8	12.9	14.0	7.3	4.8	3.8	1.5
Plecoptera	0.6	0.8	0.6	1.2	1.1	0.2	0.1	0.2
Trichoptera	0.4	0.5	0.2	0.3	0.5	0.2	0.1	0.1
Coleoptera	0.4	1.6	0.7	0.6	0.9	3.1	1.1	1.1
Diptera	2.4	3.1	2.2	1.6	0.3	0.3	0.2	0.2
Acarina	5.7	2.8	6.0	3.7	0.1	0.1	0.2	0.1
Worm	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Terrestrial	5.1	12.5	7.7	6.7	2.6	10.2	5.2	6.2
Brine shrimp	67.9	61.5	67.1	69.0	54.4	50.6	55.7	56.5
Krill	2.6	2.4	2.6	2.7	32.9	30.6	33.7	34.2

APPENDIX D

INVERTEBRATES - INDIVIDUAL ENCLOSURES

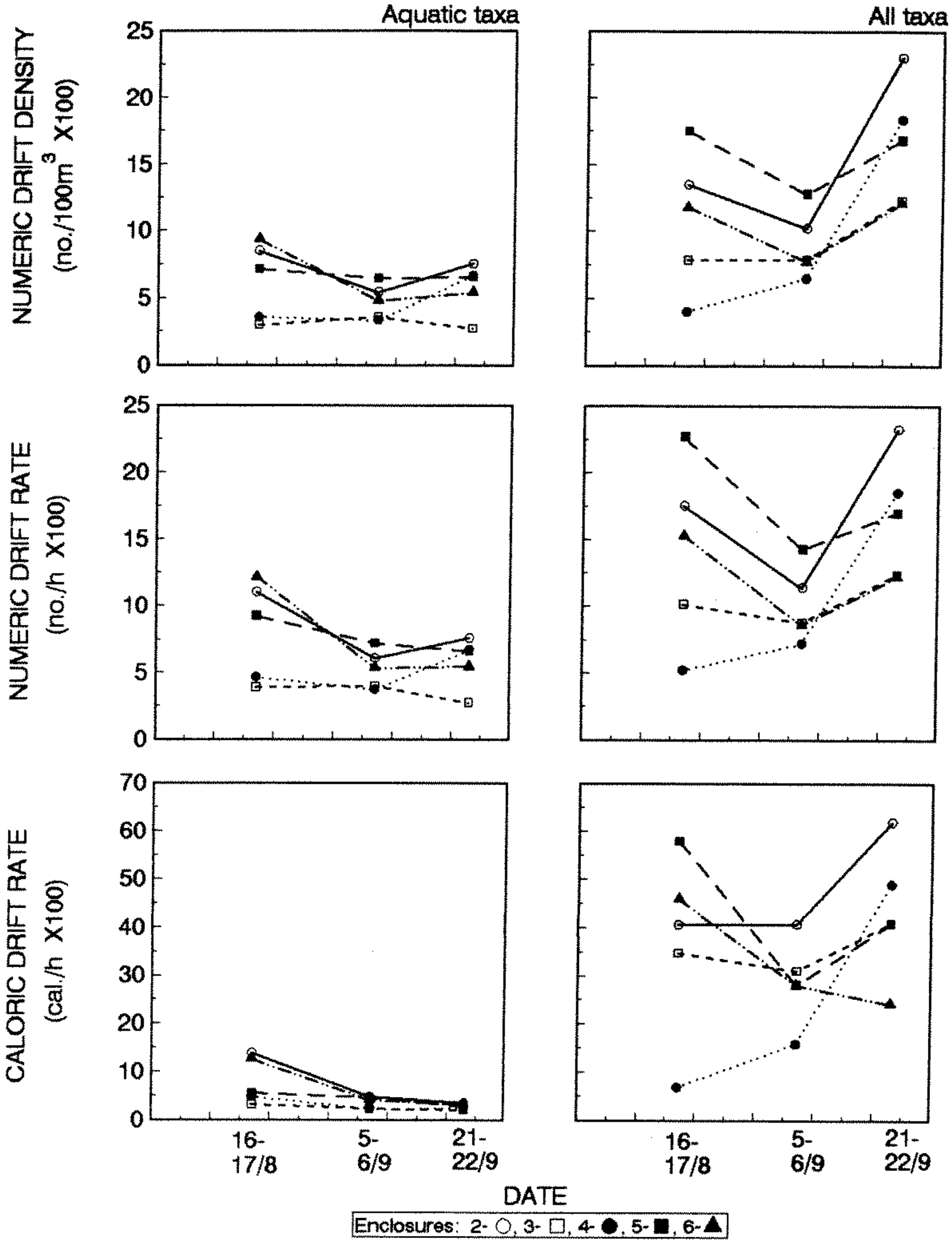

Figure 50.-Mean daily drift density, numeric drift rate, and caloric drift rate of aquatic and all taxa for each enclosure on three sample dates in Brackett Creek, 1989.

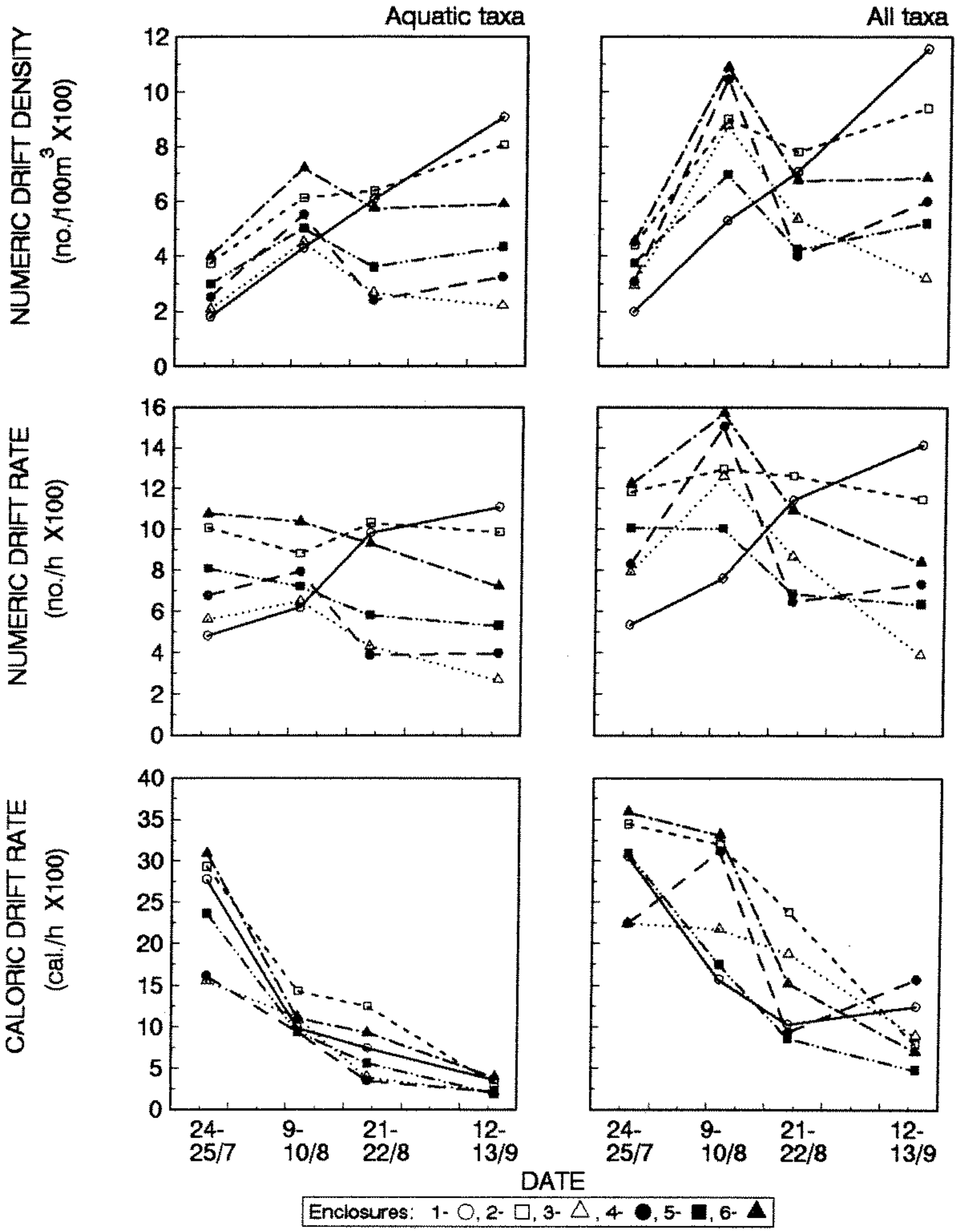

Figure 51.-Mean daily drift density, numeric drift rate, and caloric drift rate of aquatic and all taxa for each enclosure on three sample dates in Brackett Creek, 1990.

APPENDIX E

LENGTH FREQUENCY DISTRIBUTIONS OF CUTTHROAT TROUT

Table 33.-Length frequency distribution for cutthroat trout introduced into each enclosure at the start of tests and recovered at the end of tests in Brackett Creek 1989.

Length (mm)	Enclosure									
	Start of tests					End of tests				
	2	3	4	5	6	2	3	4	5	6
90-99	4	2	4	4	3	1				
100-109	4	5	6	4	5	1	2	3		1
110-119	2	7	7	6	6	4	2	4	2	2
120-129	11	6	7	5	6	2	2	3	1	3
130-139	6	6	4	5	7	4	3	4	2	1
140-149	2	2	3		1	3	4		1	2
150-159	3	3	1	1				2	1	
160-169		1	1	2	3	1	1	2	1	
170-179	1	1	1		1		1			
180-189	1			2			1			1
190-199									2	
200-209	1		1							
210-219		1			1	1	1	1		
220-229	1	1								
Total	36	35	35	29	33	16	18	19	10	10

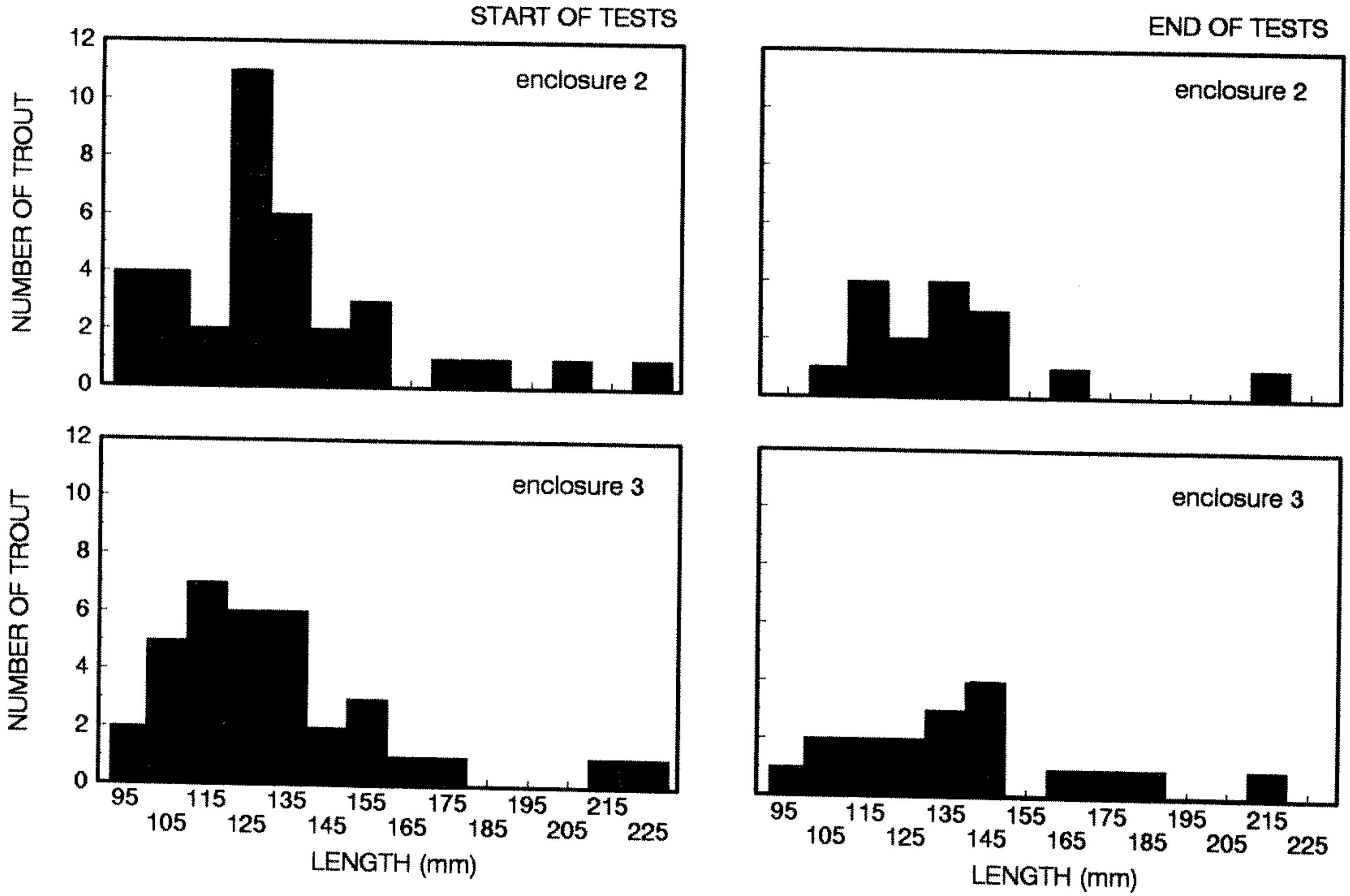

Figure 52.-Length frequency distribution for cutthroat trout introduced into each enclosure at the start of tests and recovered at the end of tests in Brackett Creek 1989.

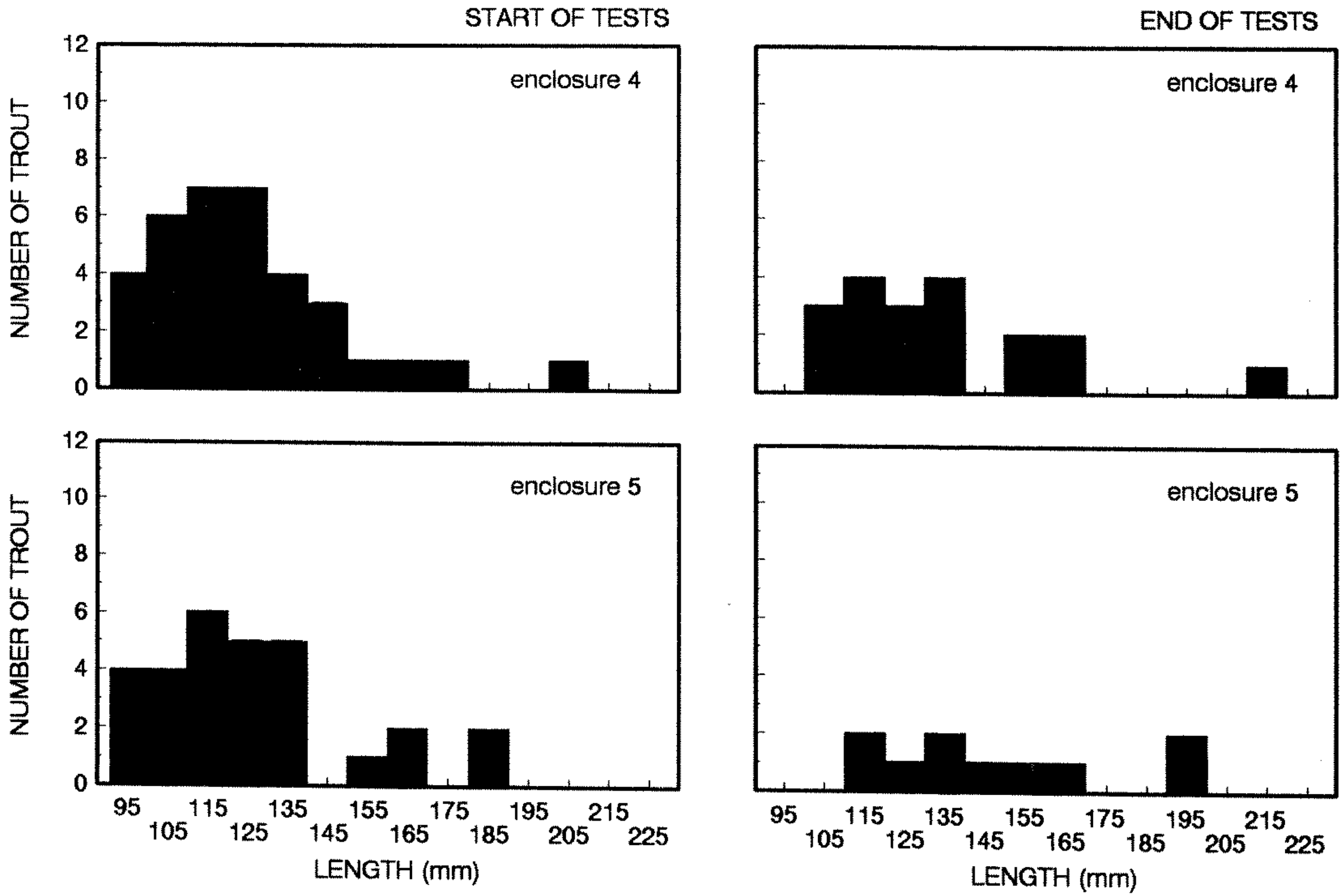

Figure 52.-Continued.....

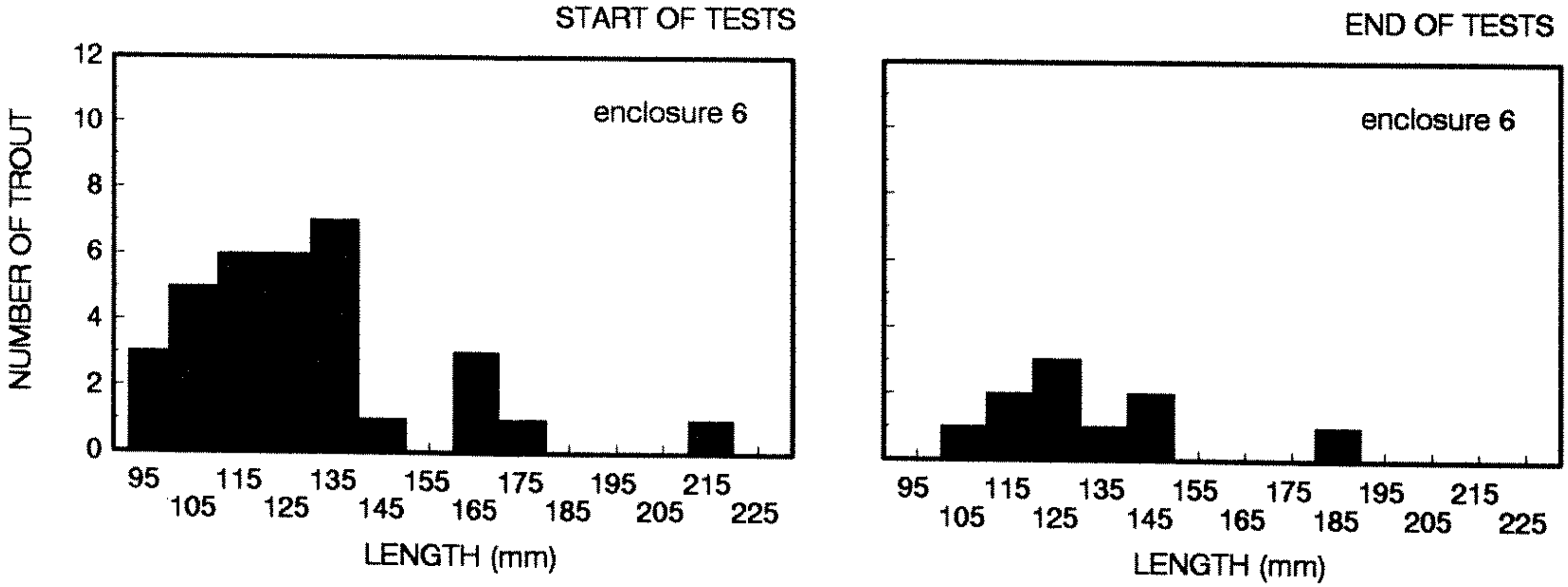

Figure 52.-Continued.....

Table 34.-Length frequency distribution for cutthroat trout introduced into each enclosure at the start of tests and recovered at the end of tests in Brackett Creek 1990.

	Enclosure											
	Start of tests						End of tests					
Length (mm)	1	2	3	4	5	6	1	2	3	4	5	6
90-99	3	4	4	3	6	4						
100-109	9	10	7	7	7	8			1		2	2
110-119	8	7	10	6	9	8	4		5	1	5	5
120-129	5	5	5	3	5	7	8	6	6		4	4
130-139	3	2	2	1	1	2	2	3	3	1	3	7
140-149	3	4	2	4	3	2	4	1	1		2	1
150-159	3	3	3	2	2	4	4		4			1
160-169	2	2	3	3	3	2	1	2	2	1	3	2
170-179	2	2	2	2	2	1	1	2	2		2	1
180-189	2	1	1	1	1	1	1	2			1	
190-199	1	2	2	1	1	1	1					
200-209				1		1	1		1	2		
210-219		2		1		2		1	2	2	2	1
220-229	3	1	2					1		1		1
230-239								1				1
240-249				1					1	1		
250-259										1		
260-269												
270-279	1											
Total	45	45	43	36	40	43	27	19	28	10	24	26

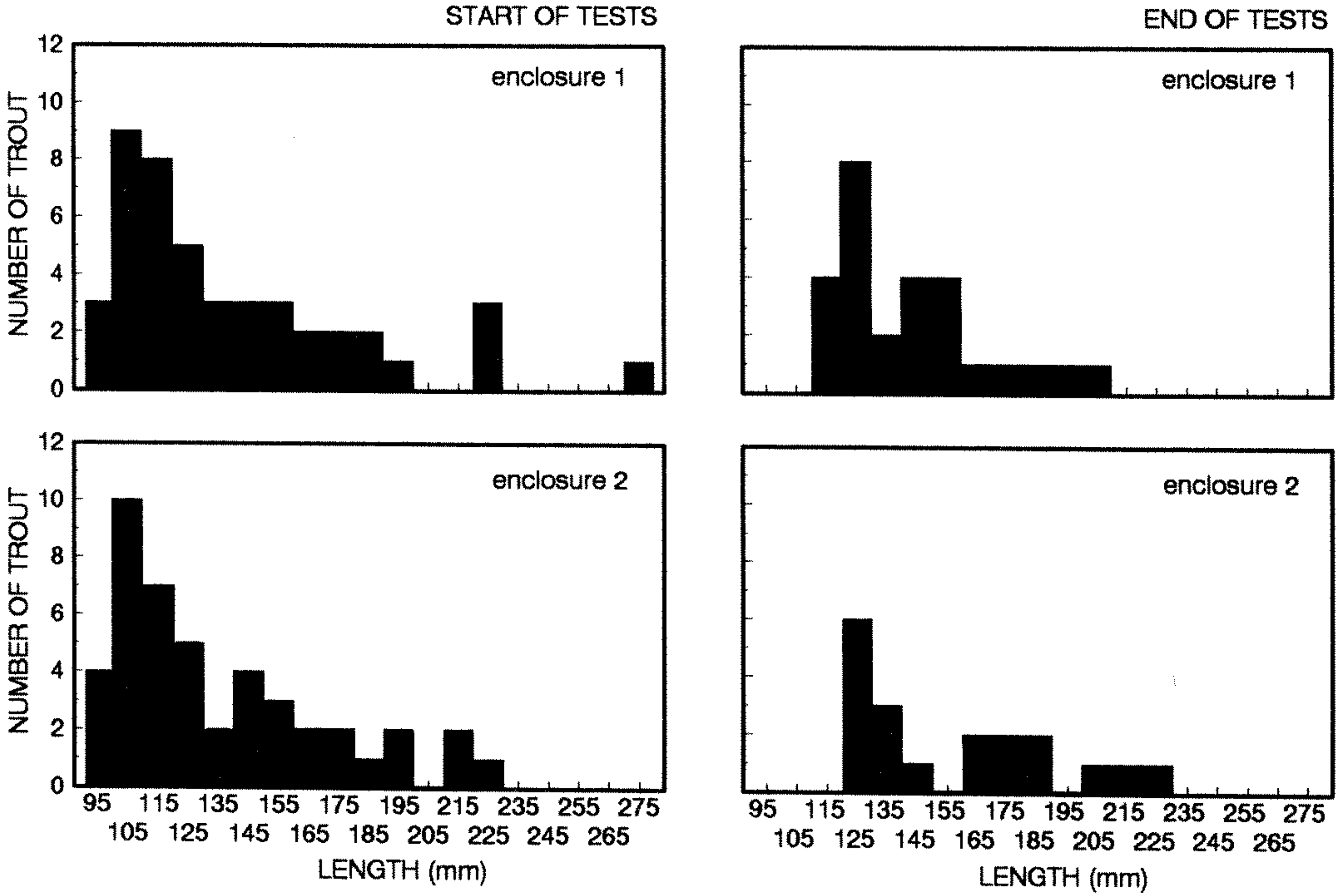

Figure 53.-Length frequency distribution for cutthroat trout introduced into each enclosure at the start of tests and recovered at the end of tests in Brackett Creek 1990.

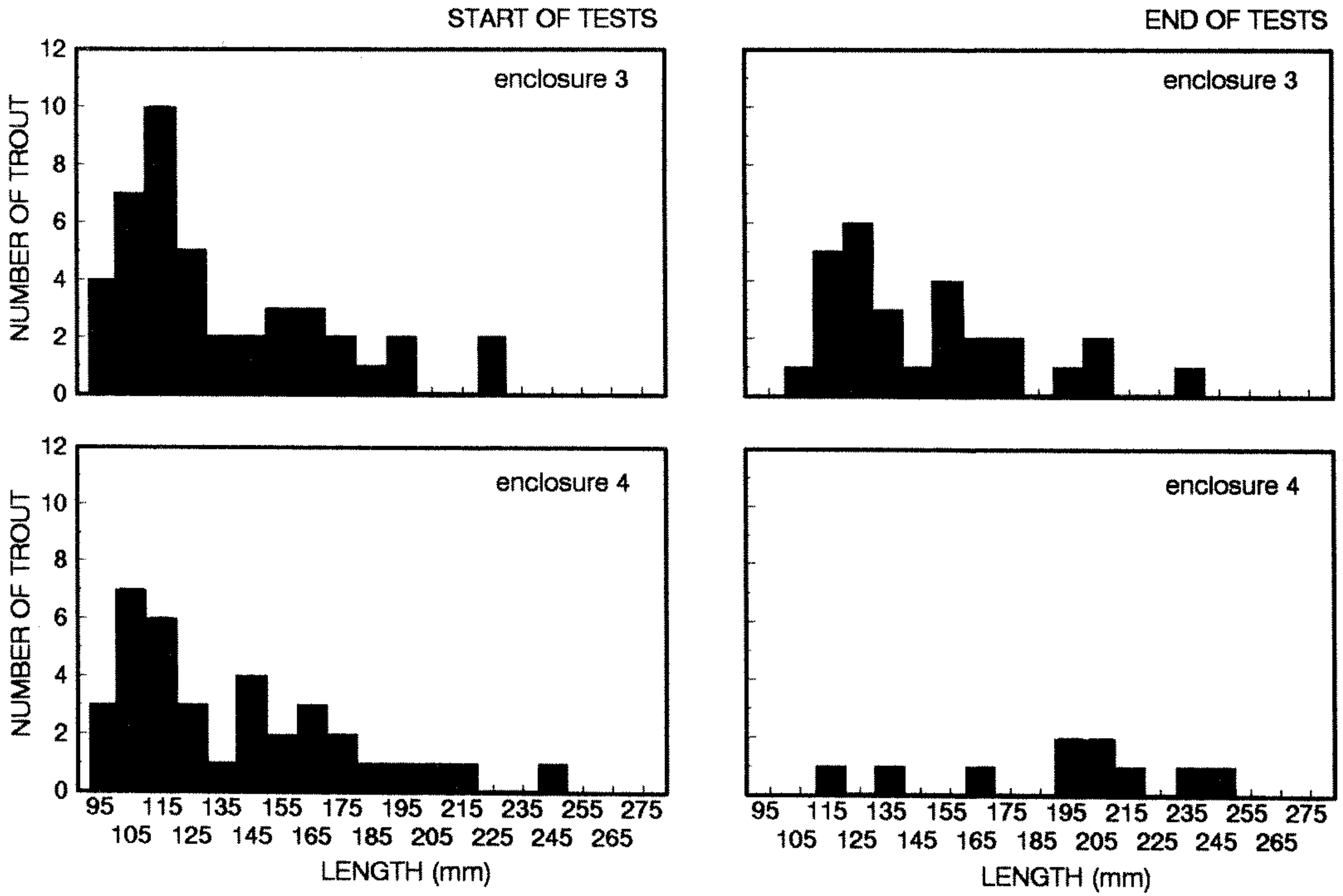

Figure 53.-Continued.....

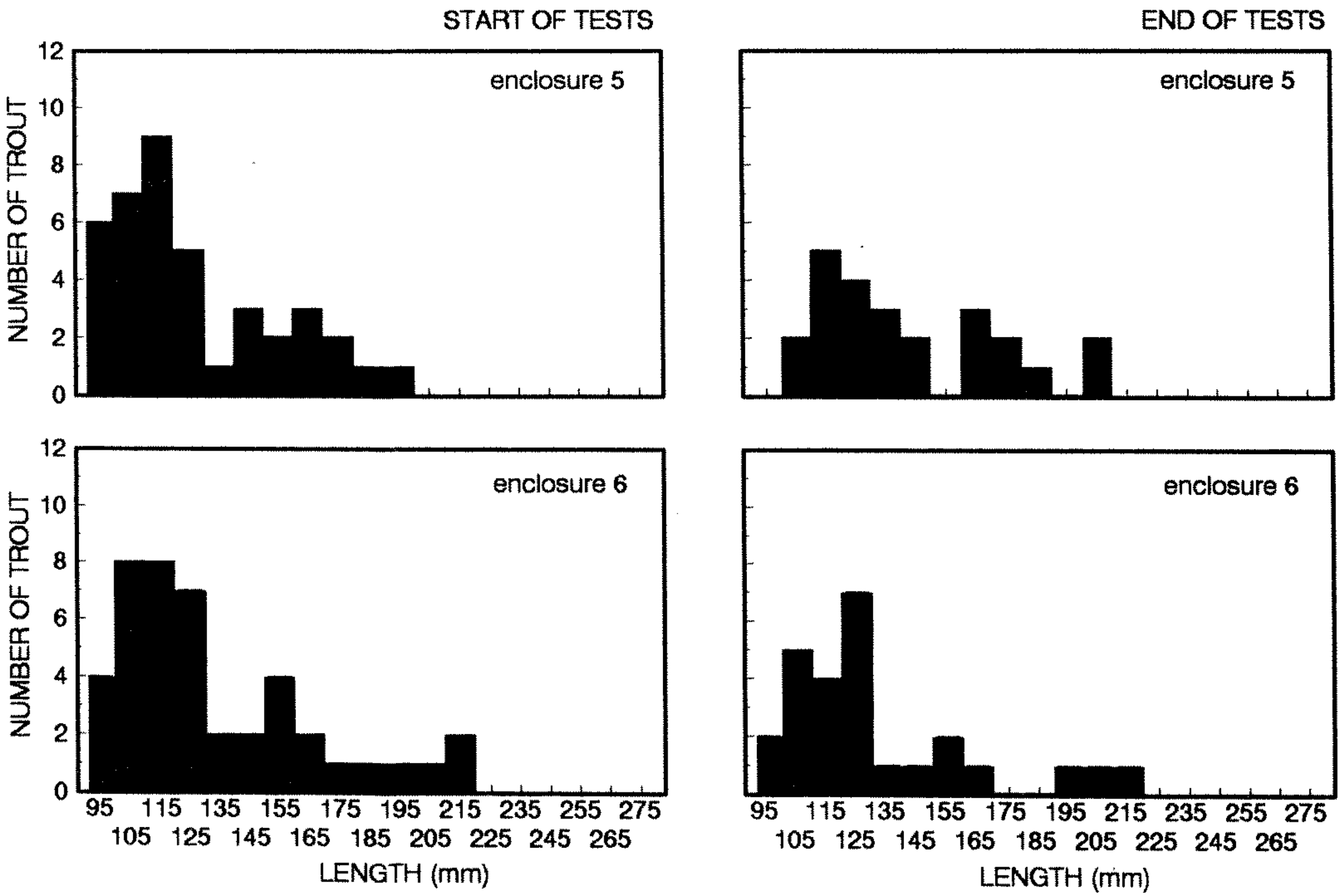

Figure 53.-Continued.....

APPENDIX F

SPEARMAN RANK CORRELATIONS

Table 35.-Spearman rank correlation coefficients (P in parentheses) between characteristics of cutthroat trout in enclosures and physical habitat for Brackett Creek, 1989 and 1990. N=5 enclosures in 1989, N=6 enclosures in 1990.

Habitat variable rate	Fish number	Density (no./m^2)	Biomass (g)	Standing crop (g/m^2)	Specific growth
			1989		
Area (m^2)	0.205 (0.682)	-0.500 (0.317)	0.100 (0.842)	-0.300 (0.549)	-0.600 (0.230)
Mean depth (m)	0.460 (0.358)	-0.211 (0.673)	0.369 (0.461)	0.000 (1.000)	-0.791 (0.114)
Maximum depth(m)	0.205 (0.682)	-0.300 (0.548)	0.300 (0.548)	0.100 (0.842)	-0.800 (0.110)
Mean velocity (m/s)	0.718 (0.151)	0.800 (0.110)	0.800 (0.110)	0.900 (0.072)	-0.700 (0.162)
Overhead cover (m^2)	0.205 (0.682)	0.300 (0.549)	0.300 (0.549)	0.400 (0.424)	0.300 (0.549)
Percent cover	0.051 (0.918)	0.400 (0.424)	0.100 (0.842)	0.300 (0.549)	0.600 (0.230)
Volume (m^3)	0.205 (0.682)	-0.500 (0.317)	0.100 (0.842)	-0.300 (0.549)	-0.600 (0.230)
Mean drift rate (cal/d)	-0.667 (0.182)	-0.100 (0.842)	-0.600 (0.230)	-0.300 (0.549)	0.900 (0.072)
Specific growth rate	-0.667 (0.182)	-0.200 (0.689)	-0.700 (0.162)	-0.500 (0.317)	-- --

Table 35.-Continued.......

Habitat variable rate	Fish number	Density (no./m^2)	Biomass (g)	Standing crop (g/m^2)	Specific growth
1990					
Area (m^2)	0.143 (0.749)	-0.314 (0.482)	-0.429 (0.338)	-0.943 (0.035)	-0.464 (0.300)
Mean depth (m)	0.371 (0.406)	0.257 (0.565)	-0.257 (0.565)	-0.371 (0.406)	-0.754 (0.092)
Maximum depth(m)	0.232 (0.604)	0.406 (0.364)	-0.029 (0.948)	-0.116 (0.795)	-0.544 (0.224)
Mean velocity (m/s)	-0.736 (0.100)	-0.500 (0.263)	0.000 (1.000)	0.206 (0.645)	0.806 (0.072)
Overhead cover (m^2)	-0.657 (0.142)	-0.429 (0.338)	0.086 (0.848)	-0.371 (0.406)	0.203 (0.650)
Percent cover	-0.600 (0.180)	-0.143 (0.749)	-0.086 (0.848)	-0.086 (0.848)	0.290 (0.517)
Volume (m^3)	0.429 (0.238)	0.200 (0.655)	-0.143 (0.749)	-0.543 (0.225)	-0.753 (0.092)
Mean drift rate (cal/d)	-0.543 (0.225)	-0.200 (0.655)	0.429 (0.338)	0.200 (0.655)	0.725 (0.105)
Specific growth rate	-0.348 (0.437)	0.058 (0.897)	0.029 (0.949)	0.200 (0.655)	-- --

APPENDIX G

FORAGING EFFICIENCIES

Table 36.-Foraging efficiency (food consumption rate (cal./d)/mean daily drift rate per enclosure (cal./d)) for predicted maximum (C_{max}) and maintenance (C_{main}) rations and estimates for observed consumption rate (C_{obs}) for all cutthroat trout in an enclosure (E) on invertebrate sample dates in Brackett Creek, 1989. Foraging efficiencies were calculated using actual caloric drift rates from Brackett Creek and at drift reductions corresponding to discharge differences at Bozeman Creek (QD).

		16-17 August			5-6 September			21-22 September		
E	QD	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}
2	0	0.46	0.14	0.16	0.21	0.07	0.09	0.07	0.03	0.03
	-20	0.56	0.17	0.20	0.27	0.09	0.10	0.09	0.04	0.04
	-28	0.83	0.25	0.29	0.39	0.13	0.15	0.13	0.05	0.06
	-32	0.54	0.16	0.19	0.26	0.09	0.10	0.09	0.03	0.04
	-47	1.56	0.47	0.54	0.74	0.25	0.29	0.25	0.10	0.11
3	0	0.51	0.16	0.17	0.28	0.10	0.11	0.15	0.06	0.07
	-20	0.62	0.19	0.21	0.34	0.12	0.13	0.18	0.07	0.08
	-28	0.92	0.28	0.31	0.51	0.17	0.19	0.27	0.11	0.12
	-32	0.60	0.18	0.20	0.33	0.11	0.13	0.18	0.07	0.08
	-47	1.73	0.53	0.58	0.95	0.33	0.36	0.51	0.21	0.22
4	0	0.21	0.06	0.08	0.10	0.03	0.04	0.05	0.02	0.02
	-20	0.26	0.08	0.10	0.12	0.04	0.05	0.06	0.02	0.03
	-28	0.39	0.11	0.15	0.18	0.06	0.08	0.08	0.03	0.04
	-32	0.25	0.08	0.10	0.11	0.04	0.05	0.05	0.02	0.03
	-47	0.71	0.22	0.28	0.33	0.11	0.15	0.15	0.06	0.08
5	0	0.13	0.04	0.06	0.08	0.03	0.04	0.03	0.01	0.02
	-20	0.15	0.05	0.07	0.09	0.03	0.05	0.04	0.02	0.02
	-28	0.23	0.07	0.11	0.14	0.05	0.07	0.05	0.02	0.03
	-32	0.15	0.05	0.07	0.09	0.03	0.05	0.04	0.01	0.02
	-47	0.43	0.13	0.20	0.25	0.09	0.13	0.10	0.04	0.06
6	0	0.12	0.04	0.05	0.04	0.01	0.02	0.03	0.01	0.02
	-20	0.15	0.05	0.06	0.05	0.02	0.03	0.04	0.01	0.02
	-28	0.22	0.07	0.09	0.07	0.02	0.04	0.05	0.02	0.03
	-32	0.14	0.04	0.06	0.05	0.02	0.03	0.04	0.01	0.02
	-47	0.41	0.12	0.16	0.14	0.05	0.07	0.10	0.04	0.06

Table 37-Foraging efficiency (food consumption rate (cal./d)/mean daily drift rate per enclosure (cal./d)) for predicted maximum (C_{max}) and maintenance (C_{main}) rations and estimates for observed consumption rate (C_{obs}) for all cutthroat trout in an enclosure (E) on invertebrate sample dates in Brackett Creek, 1990. Foraging efficiencies were calculated using actual caloric drift rates from Brackett Creek and at drift reductions corresponding to discharge differences at Bozeman Creek (QD).

		24-25 July			8-9 August			21-22 August			12-13 September		
E	QD	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}
1	0	0.600	0.24	0.28	1.72	0.53	0.67	1.33	0.42	0.55	1.03	0.31	0.42
	-20	0.73	0.29	0.33	2.09	0.64	0.81	1.62	0.51	0.67	1.25	0.38	0.51
	-28	1.08	0.42	0.49	3.09	0.95	1.20	2.40	0.75	0.99	1.84	0.56	0.75
	-32	0.71	0.28	0.32	2.03	0.62	0.79	1.57	0.49	0.65	1.21	0.36	0.49
	-47	2.03	0.80	0.93	5.83	1.80	2.26	4.52	1.42	1.86	3.48	1.05	1.41
2	0	0.43	0.17	0.19	0.66	0.20	0.25	0.59	0.19	0.24	1.48	0.46	0.61
	-20	0.53	0.21	0.24	0.80	0.25	0.30	0.71	0.23	0.29	1.80	0.56	0.74
	-28	0.78	0.31	0.35	1.18	0.36	0.45	1.05	0.34	0.43	2.67	0.83	1.10
	-32	0.51	0.20	0.23	0.77	0.24	0.29	0.69	0.22	0.28	1.75	0.55	0.72
	-47	1.47	0.58	0.66	2.22	0.69	0.85	1.98	0.64	0.81	5.03	1.57	2.07
3	0	0.65	0.26	0.27	0.93	0.29	0.32	0.87	0.28	0.31	1.68	0.52	0.58
	-20	0.79	0.31	0.33	1.13	0.35	0.39	1.06	0.34	0.38	2.04	0.63	0.71
	-28	1.17	0.46	0.49	1.67	0.51	0.58	1.57	0.50	0.56	3.02	0.93	1.05
	-32	0.77	0.30	0.32	1.10	0.34	0.38	1.03	0.33	0.37	1.98	0.61	0.69
	-47	2.20	0.87	0.93	3.15	0.97	1.10	2.96	0.95	1.06	5.70	1.76	1.97
4	0	0.16	0.06	0.11	0.20	0.06	0.14	0.15	0.05	0.12	0.13	0.04	0.10
	-20	0.19	0.07	0.13	0.25	0.08	0.17	0.18	0.06	0.14	0.15	0.05	0.12
	-28	0.28	0.11	0.19	0.37	0.11	0.25	0.26	0.09	0.21	0.23	0.07	0.18
	-32	0.18	0.07	0.12	0.24	0.07	0.16	0.17	0.07	0.14	0.15	0.05	0.12
	-47	0.53	0.21	0.35	0.69	0.21	0.47	0.50	0.16	0.40	0.43	0.13	0.34

Table 37.-Continued.....

		24-25 July			8-9 August			21-22 August			12-13 September		
E	QD	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}	C_{max}	C_{main}	C_{obs}
5	0	0.11	0.04	0.08	0.21	0.06	0.14	0.16	0.05	0.12	0.16	0.05	0.12
	-20	0.13	0.05	0.09	0.25	0.08	0.17	0.19	0.06	0.14	0.20	0.06	0.14
	-28	0.20	0.08	0.14	0.37	0.11	0.25	0.29	0.08	0.21	0.29	0.09	0.21
	-32	0.13	0.05	0.09	0.24	0.07	0.17	0.19	0.06	0.14	0.19	0.06	0.14
	-47	0.37	0.15	0.26	0.70	0.21	0.48	0.54	0.17	0.39	0.54	0.16	0.39
6	0	0.13	0.05	0.10	0.18	0.06	0.15	0.15	0.05	0.12	0.16	0.05	0.12
	-20	0.16	0.06	0.12	0.22	0.07	0.18	0.18	0.06	0.14	0.20	0.06	0.15
	-28	0.23	0.09	0.18	0.33	0.10	0.27	0.27	0.08	0.21	0.29	0.09	0.22
	-32	0.15	0.06	0.12	0.22	0.07	0.18	0.18	0.06	0.14	0.19	0.06	0.15
	-47	0.44	0.17	0.34	0.62	0.19	0.51	0.51	0.16	0.39	0.54	0.16	0.42