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

by Samuel Clark Lohr

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

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

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

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

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

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

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

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Montana State University
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APPROVAL

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Samuel Clark Lohr

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

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STATEMENT OF PERMISSION TO USE

VITA

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

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ABSTRACT

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

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GENERAL INTRODUCTION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

INVERTEBRATE ABUNDANCE AND REDUCTIONS IN STREAM DISCHARGE

Introduction

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

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

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

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

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

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

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

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

Methods

Study Sites

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

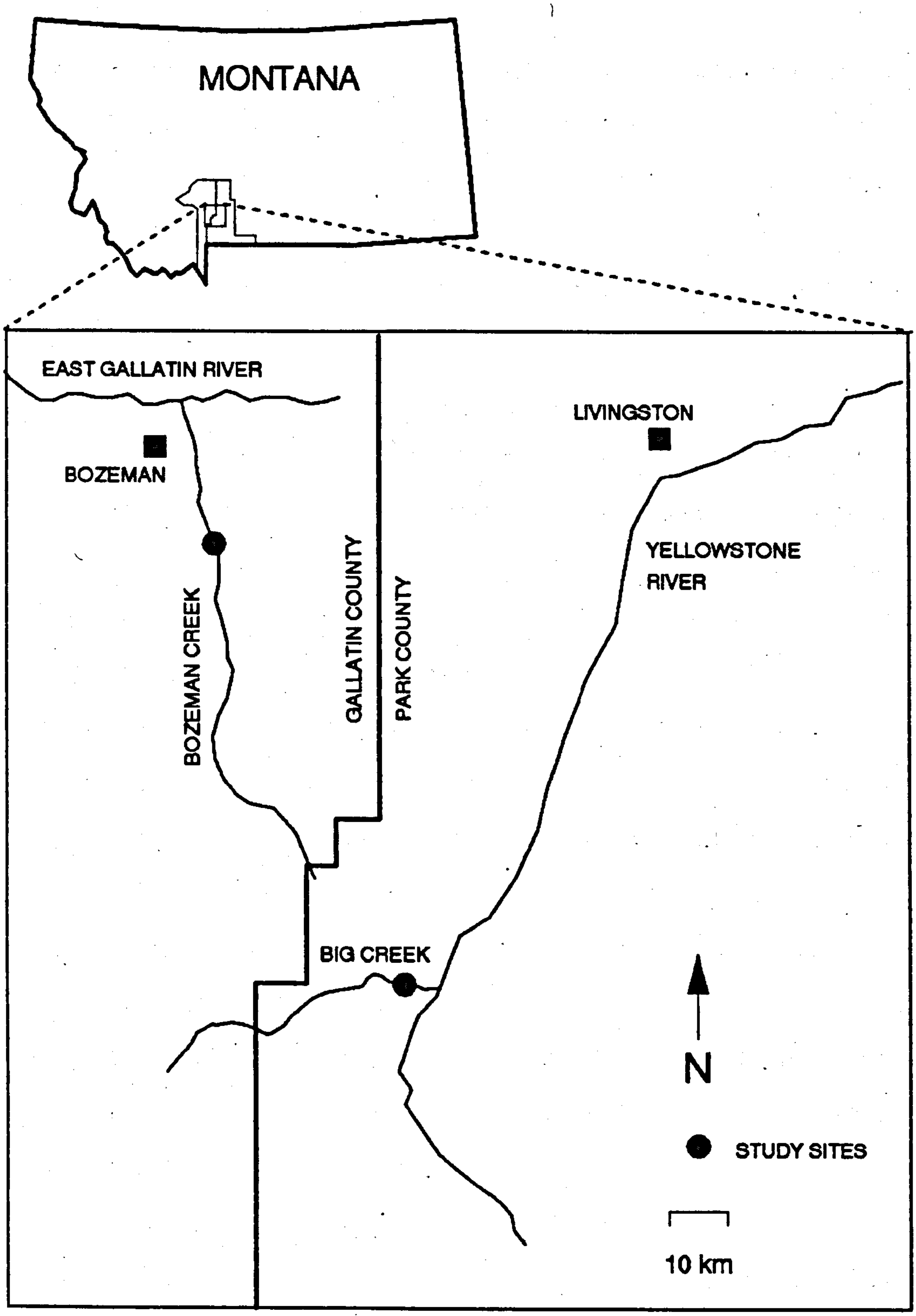

Figure 1.-Location of study sites in Bozeman Creek and Big Creek.

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

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

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

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

Drift Collections

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

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

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

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

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

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

Benthic Collections

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

Data Analyses

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

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

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

Results

Bozeman Creek

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

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

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

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

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

Table 1.-Continued.....

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

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

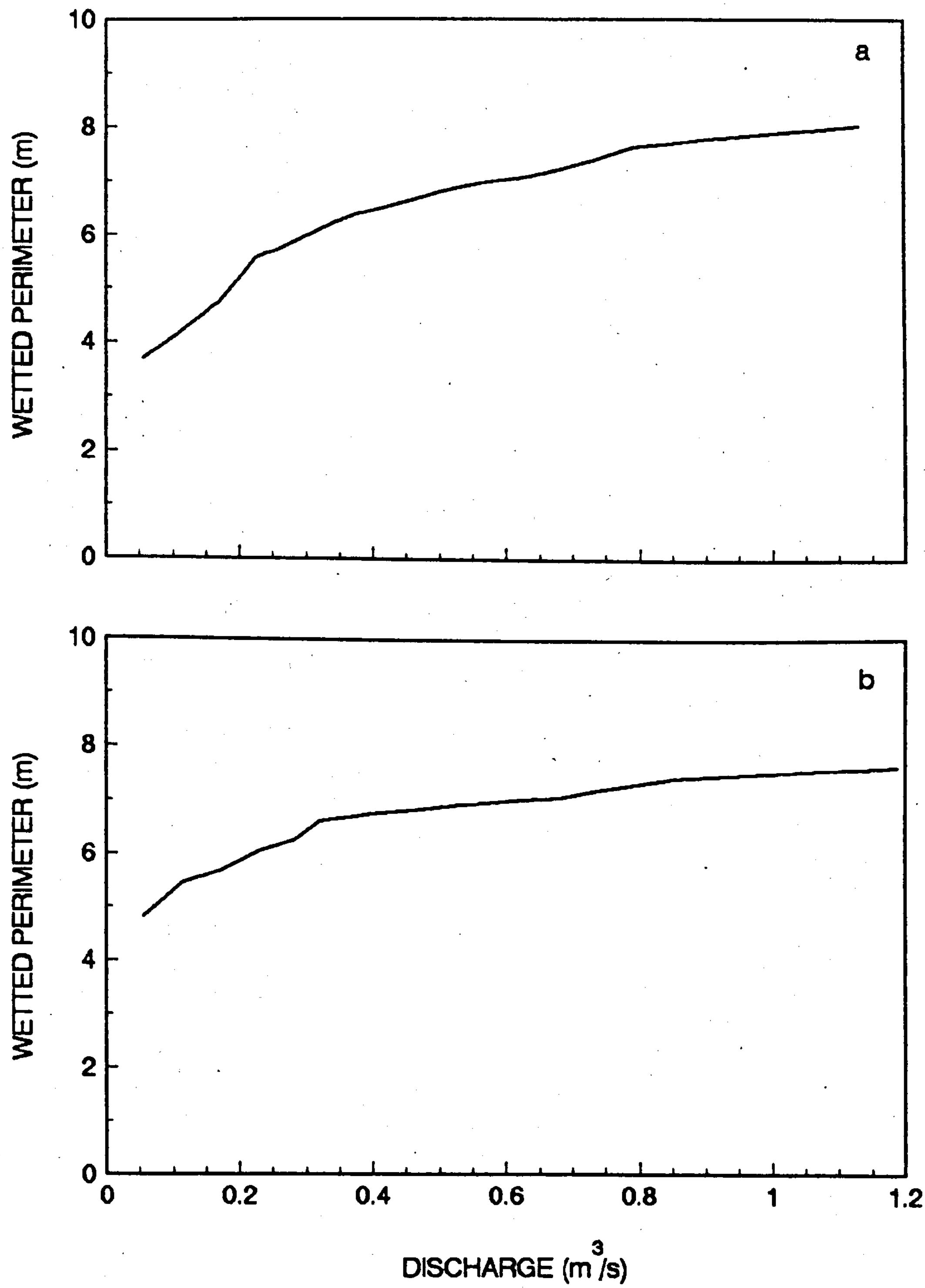

Figure 2.-Mean wetted perimeter-discharge relationships for the test (a) and reference (b) riffles in Bozeman Creek, July-September 1989.

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

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

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

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

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

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

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

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