INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313/761-4700 800/521-0600

EVALUATION OF THE IMPACTS OF A SIMULATED IRRIGATION WITHDRAWAL ON THE HABITAT AND POPULATIONS OF BROOK TROUT AND BENTHIC MACROINVERTEBRATES IN HUNT CREEK, MICHIGAN

By

Edward Allen Baker

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Fisheries and Wildlife

1995

ABSTRACT

EVALUATION OF THE IMPACTS OF A SIMULATED IRRIGATION WITHDRAWAL ON THE HABITAT AND POPULATIONS OF BROOK TROUT AND BENTHIC MACROINVERTEBRATES IN HUNT CREEK, MICHIGAN USING PHABSIM

By

Edward Allen Baker

The state of Michigan has many valued stream fishery resources. However, the integrity of the stream resources of the state are threatened by the increased use of water for the irrigation of lawns, golf courses, and agricultural crops. I diverted approximately 50% of the summer streamflow from a treatment section of Hunt Creek, Michigan to simulate an irrigation withdrawal. I evaluated the Physical Habitat Simulation System (PHABSIM) to determine its effectiveness in modeling the impacts of the withdrawal on the brook trout *Salvelinus fontinalis* and benthic macroinvertebrate habitat in Hunt Creek. I used diurnal habitat suitability criteria (HSC) for brook trout to model the withdrawal impacts on diurnal brook trout habitat. I also developed alternative HSC for brook trout from nocturnal habitat use data and from bioenergetic models of foraging microhabitats. I used these HSC to model the impacts of the withdrawal on the brook trout habitat in Hunt Creek and compared the predictions of the PHABSIM model to brook trout population data. I also modeled benthic macroinvertebrate habitat from habitat use data collected in Hunt Creek and compared the habitat modeling output with population density data to determine if the predictions of the PHABSIM model matched observed population responses to the withdrawal. The PHABSIM model indicated that the withdrawal did not reduce the amount or quality of brook trout or benthic macroinvertebrate habitat in the treatment section of Hunt Creek. Population abundance data for brook trout and benthic macroinvertebrates also indicated that the withdrawal had no impact on the numbers of either group in the treatment section. The PHABSIM model did indicate that a withdrawal of greater than 50% would result in reductions in benthic macroinvertebrate habitat but brook trout habitat would not be reduced until discharge was reduced approximately 80%. These results suggest the PHABSIM modeling system may be effective in predicting impacts of altered streamflows on the stream resources of Michigan. However, I recommend continued study in Hunt Creek to validate the effectiveness of the PHABSIM model.

For my wife. Her understanding, patience, and hard work made this possible.

ACKNOWLEDGEMENTS

I thank my guidance committee members: Dr. Gary Mittelbach, Dr. Rich Merritt, and Dr. Scott Winterstein. I especially thank my advisor, Dr. Tom Coon, for his guidance, support and friendship.

I also am grateful to the personnel of the Michigan Department of Natural Resources' Hunt Creek Fisheries Research Station: Gaylord Alexander, Andy Nuhfer, Jack Rodgers, Tom Adams, and Tim Smigelski. Their cooperation during this study was invaluable. Many undergraduate and graduate students also helped with various aspects of the field and laboratory work for this study. I thank all of them but especially K. Meyer, D. Simpkins, and J. Anicka.

Financial support for this study came from the Michigan Department of Natural Resources, the Michigan State University Agricultural Experimental Station, the Michigan Polar-Equator Club, the West Michigan Chapter of Trout Unlimited, and the Kalamazoo Valley Chapter of Trout Unlimited.

Finally, I thank my friends and especially my family for their endless support and encouragement.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The state of Michigan has abundant water resources that provide a myriad of recreational opportunities for the state's residents and many non-residents. The stream resources of Michigan are particularly valuable and are widely recognized as some of the finest in North America. However, the streams of the state and the Midwest are threatened by the increasing use of water for out-of-stream uses including irrigation of agricultural crops, golf courses and lawns. The use of water for seasonal irrigation has the potential to adversely impact streams if water is removed directly from a stream or is removed from an aquifer that supplies water to a stream.

The need to protect streams from excessive water withdrawals was first recognized in the western United States in the 1970's. This recognition resulted in the formulation of several standard setting methods which provide recommended flows in streams that are designed to protect instream resources (fisheries, recreational uses, wildlife) from excessive degradation resulting from withdrawals. The most common of these methods is the Instream Flow Incremental Methodology (IFIM). The IFIM was designed to provide an estimate of the impacts of water withdrawals from streams on instream fish, wildlife, or recreational habitat. The habitat modeling component of IFIM is the PHysical HABitat SIMulation system (PHABSIM). PHABSIM is widely used in the western

United States to evaluate the impacts of altered streamflows but has not been widely applied in the midwest.

The objectives of this research were to: develop alternative habitat suitability criteria for brook trout that could be used in a PHABSIM analysis of stream habitat; evaluate the impacts of a simulated irrigation withdrawal on aspects of the ecology of the brook trout and benthic macroinvertebrate populations in Hunt Creek; to evaluate the impacts of the simulated withdrawal on the brook trout and benthic macroinvertebrate habitat using PHABSIM; and to compare the changes in brook trout and benthic macroinvertebrate abundance predicted by PHABSIM with observed changes.

CHAPTER 1

DEVELOPMENT AND EVALUATION OF ALTERNATIVE HABITAT SUITABILITY CRITERIA FOR BROOK TROUT *SALVELINUS FONTINALIS*

ABSTRACT

I developed diurnal habitat suitability criteria from net bioenergetic benefit models (bioenergetic-HSC) for drift feeding brook trout in Hunt Creek, MI and compared these to criteria developed from frequency-of-use data (use-HSC). I also constructed nocturnal use-HSC from frequency-of-use data collected in Hunt Creek. Bioenergetic-HSC were more restrictive in predictions of optimal velocity: a single velocity was optimal and depended on fish size, as opposed to a range of optimal velocities predicted from frequency-of-use data. The optimal velocities predicted for yearling and older fish from bioenergetic-HSC (range 33-46 $cm \cdot s^{-1}$) were greater than the highest optimal velocity (27 $cm \cdot s^{-1}$) predicted by use-HSC. Optimal velocities for young of the year fish predicted from bioenergetic-HSC (23 and 28 $cm \cdot s^{-1}$ for 5 and 7.5 cm fish respectively) were within the range of optimal velocities (6-30 $cm \cdot s^{-1}$) predicted from use-HSC. The predicted range of usable velocities was narrower for bioenergetic-HSC than for use-HSC, regardless of fish size. Use-HSC suitability scores for an independent set of habitat use observations in Hunt Creek were significantly higher than bioenergetic-HSC for young of the year fish but not for yearling and older fish. This may indicate that use-HSC are too general and do not represent the actual suitability of foraging microhabitats in Hunt Creek. Young of the year and yearling and older brook trout selected microhabitats with lower mean column velocities and shallower depths at night than when

foraging in daytime. Also, yearling and older brook trout used microhabitats with higher mean column velocities and greater depths than young of the year fish during diurnal and nocturnal periods.

Introduction

The construction and use of habitat suitability criteria (HSC) is an important step in the evaluation of stream fish habitat, particularly in conjunction with the use of the Physical Habitat Simulation System (PHABSIM). The HSC used in stream habitat modeling are quantitative models that represent the suitability of particular habitat parameters for stream fish. The value of HSC ranges between zero for an unusable habitat state to on for an optimal habitat state (Bovee 1986; Thomas and Bovee 1993). The four habitat parameters typically used in a PHABSIM evaluation of stream habitat are water depth, water velocity, substrate and instream cover (Milhous et al. 1989). Previous stream habitat evaluations have been based on HSC for the species and life stage of interest and constructed by use of one of three methods as suggested by Bovee (1986): 1)the construction of HSC from expert opinion, 2)collection of frequency-of-use data in the stream under investigation and subsequent conversion of frequency-of-use data to HSC by one of several methods and 3)frequency-of-use data corrected to reflect habitat availability in the stream of interest so that HSC reflect the preference of the species for specific microhabitat attributes. The HSC generated from these three methods are termed Category I, II and III models respectively (Bovee 1986). Category II criteria are the most widely used in investigations of stream habitat.

Classifying the suitability of microhabitats based on frequency-of-use data alone may not be accurate. It is possible for less frequently selected microhabitats to be more suitable than those most frequently selected if competition for microhabitats is intense in a particular stream. For example, a stream reach with N microhabitat units that are truly optimal and 2N microhabitat units that are half as suitable as the optimal microhabitats would have enough usable habitat units for 3N fish. If the stream supports 3N fish the microhabitats that are less than optimal would be used most frequently and would therefore be classified as optimal based on frequency-of-use data. Also, in this simple case, if the HSC were corrected for habitat availability the optimal and suboptimal habitats would be equally suitable.

Several factors influence habitat use by drift feeding salmonids in streams including energetic gains (Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993), predation risk, and cover availability (McNicol et al. 1985; Grant and Noakes 1987; Huntingford et al. 1988), all of which may evoke territorial behavior (Grant and Noakes 1988; Hughes and Dill 1990; Hill and Grossman 1993). Previous studies on stream fish have stressed the importance of energetic gains associated with drift feeding and have demonstrated that drift feeding fish select microhabitats that optimize energetic gains during foraging (Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993). Juvenile coho salmon *Onchorhyncus kisutch* form dominance hierarchies and experience growth rate constraints inversely related to position in the dominance hierarchy and related to microhabitat selected (Nielsen 1992). Optimal foraging theory (Schoener 1971) also predicts that, among other factors, position choice for a drift feeding fish should be influenced by energetic costs and benefits associated with the microhabitat, and that drift feeding fish should select microhabitats that maximize the net energetic gains during foraging. This suggests the suitability of a microhabitat location for a drift feeding stream fish should be related to the energetic costs and benefits associated with the location.

Bioenergetic costs and benefits associated with microhabitats for drift feeding stream fishes may be a more appropriate measure of the suitability of microhabitats than data on frequency of habitat use. Further, if HSC derived from bioenergetic models more accurately represent the actual suitability of microhabitats, they may provide more accurate predictions of the impacts of altered stream flows on drift feeding stream fishes. The use of bioenergetic modeling for microhabitat suitability could also be used in individual based models to predict growth rates of fish in particular microhabitats and to evaluate the spatial array of microhabitats in a stream (Rose and Cowan 1993; Brandt and Kirsch 1993; Goyke and Brandt 1993).

The objectives of this work were to develop HSC derived from bioenergetic cost and benefit models for foraging brook trout *Salvelinus fontinalis* (bioenergetic-HSC in remainder of text) and to compare these to HSC based on frequency-of-use data (use-HSC in remainder of text). I describe a method for developing bioenergetic-HSC based on water velocity and depth and then test these against use-HSC on an independent data set from Hunt Creek. The hypothesis was that bioenergetic-HSC suitability scores calculated from an independent data set of depth and velocity use data would be lower than suitability scores calculated from use-HSC.

This hypothesis was based on three assumptions. The first assumption was that the brook trout population in Hunt Creek was at or near carrying capacity and competition for foraging microhabitats was intense. Evidence from Hunt Creek supports this assumption because Hunt

Creek is closed to fishing, and there are few piscivorous predators in the research area of Hunt Creek. In addition, an artificial increase of the sand bed load in Hunt Creek reduced benthic invertebrate abundance and brook trout abundance, presumably by reducing the habitat available to both and food availability for trout (Alexander and Hansen 1986).

The second assumption is that the brook trout in Hunt Creek select foraging microhabitats based on the net energetic gain available. The third assumption follows the second: substrate and cover in the immediate vicinity of a foraging fish's position do not influence the net energetic gain available from a microhabitat.

I suggest that the output of a PHABSIM analysis using bioenergetic-HSC may be more biologically meaningful in terms of expected changes in fish population parameters (i.e. predictions of growth rate) when changes in stream flow are modeled. Use of bioenergetically derived HSC may also lead to a better relationship between the output of a PHABSIM analysis (WUA) and fish population parameters in a hydraulically altered stream if they more accurately reflect the suitability of microhabitats than HSC constructed from frequency-of-use data. Also, because the criteria are based on bioenergetics instead of habitat use and availability the bioenergetic-HSC may be easier to transfer to other streams (Thomas and Bovee 1993) with possible adjustments for food availability in the target stream.

Methods

Study Area

This study was conducted at the Michigan Department of Natural Resources' (MDNR) Hunt Creek Fisheries Research Station in northern Oscoda and southern Montmorency counties of Michigan's lower peninsula.

Hunt Creek is a third order stream which drains glacial sands and gravels deposited during the last glaciation of the region, approximately 10,000 years ago (Dorr and Eschman 1970). Hunt Creek and surrounding watersheds have extremely stable discharge and temperature regimes and are some of the most productive trout streams in Michigan (G. Alexander, personal communication). Hunt Creek was chosen as the study stream for this research because the brook trout population in Hunt Creek is self sustaining and has been monitored by the MDNR since 1949: a continuous record of population density estimates exists from spring and fall mark-recapture electrofishing. In addition, the entire Hunt Creek research area has been closed to fishing since 1966. Therefore, any response of the brook trout population to experimental treatment should be attributable to an increase in the natural mortality rate, emigration rate, or some other factor related to the treatment.

The portion of Hunt Creek that flows through the research area is divided into four sections: three nontreatment sections (sections A, C and Z) and a treatment section (section B; Figure 1). Hunt Creek is a second order stream upstream of the confluence with Fuller Creek and is a third order stream through the remainder of the study area. Section C, the source of the independent data set of habitat use observations, is immediately upstream of the treatment section B. Distribution of mean velocities in section C are not significantly different from section B (Mann-Whitney U, $p=0.36$) but depths are significantly shallower in section C (Mann-Whitney U, $p<0.001$).

The brook trout population in Hunt Creek is composed primarily of small fish; approximately 96% of the fish in section B are less than 17.7 cm total length (Alexander and Hansen 1986). The only common fish species in Hunt Creek are brook trout, mottled sculpin *Cottus bairdi* and

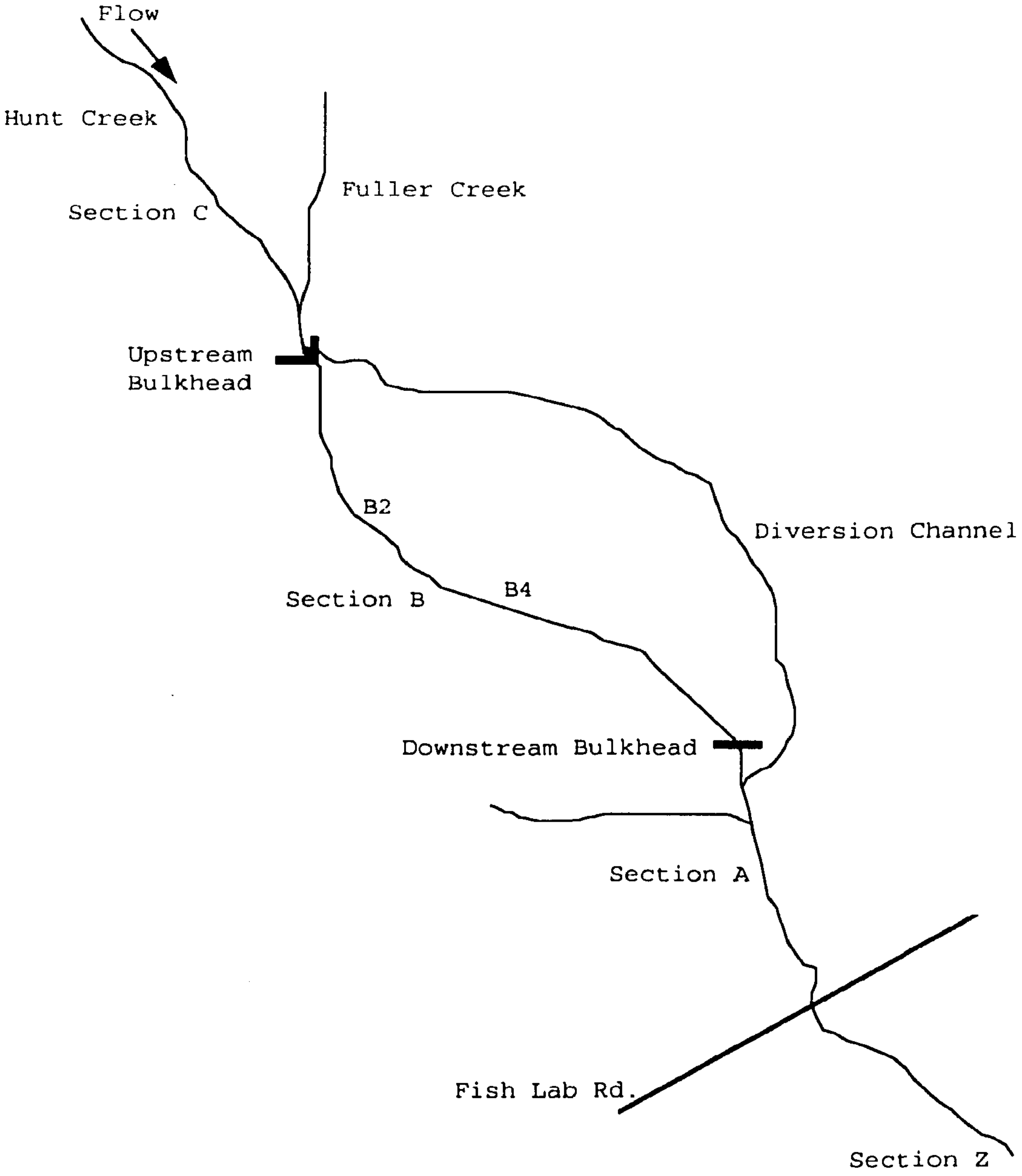

Figure 1. Map of Hunt Creek study area. The upstream bulkhead is the boundary between sections C and B, the downstream bulkhead is the boundary between sections B and A, and Fish Lab Rd. is the boundary between sections A and Z.

slimy sculpin *Cottus cognatus* (Alexander and Hansen 1986). In 1989-90 the MDNR excavated a diversion channel around the treatment section and installed bulkheads at the upstream and downstream ends of the treatment section (Figure 1, referred to as the upstream and downstream bulkheads respectively in remainder of text). The bulkheads allowed us to control the flow of water through the treatment section of Hunt Creek. The MDNR also installed inclined screen traps on the bulkheads to monitor downstream fish movement into and out of the treatment section. The traps were operated during each summer of the treatment. In addition, to provide a baseline estimate of fish movement in Hunt Creek, the traps on the downstream bulkhead were monitored during the summer of 1990 before the experiment was initiated. The traps only caught fish moving downstream, and prevented upstream fish movement.

Bioenergetic-HSC Construction

I followed the methods described by Hill and Grossman (1993) to model the bioenergetic costs and benefits associated with specific microhabitats based on water velocity and depth. The net energetic benefit (E_X) of a microhabitat is a function of the water velocity and depth. Water velocity is expected to affect the costs and benefits of the microhabitat and the fish's foraging area, and depth is expected to affect the foraging area of the fish. E_X is equal to the difference between the benefits gained by holding the position (B_X) and the costs of maintaining the position (C_X):

$$E_X = B_X - C_X. \qquad (1)$$

I derived seven net benefit models for brook trout between 5 and 20 cm total length at increments of 2.5 cm. Data necessary for estimating model parameters came from a variety of sources given in the description that follows.

I based estimates of microhabitat benefit on invertebrate drift density data collected in Hunt Creek during 1993 and 1994. I collected invertebrate drift on a fixed transect in Hunt Creek during summer, 1993 from dawn to dusk. I sampled the invertebrate drift for 20 minutes every four hours at three locations across the transect approximately every 30 days. Preceding each sample I measured depth to the nearest cm and measured mean column velocity to the nearest $cm \cdot s^{-1}$ at each net location with either a Marsh-McBirney electronic current meter or a pygmy-Gurley mechanical current meter. I compared velocity measurements between the two meters in Hunt Creek on several occasions by measuring velocity at specific points in the stream with both meters. I found no consistent differences in measurements of velocity between the two meters and velocity measurements were always in close agreement. I sampled invertebrate drift with a rectangular drift net (64 µm mesh, 15.5 x 75 cm and 80 cm deep). I also collected invertebrate drift samples at locations where brook trout were observed feeding in 1993 and 1994. The duration of drift sampling was 10 minutes at fish locations as opposed to 20 minutes for the fixed locations.

I separated the invertebrates from the rest of the material collected in the nets by floating the samples in a saturated sugar solution (Anderson 1959). I then preserved invertebrates in 95% ethyl alcohol until they were identified and measured in the lab.

I identified aquatic organisms in the drift to family by use of the keys in Merritt and Cummins (1984) and identified the terrestrial invertebrates to order (Barnes 1987). I measured invertebrate lengths to the nearest 0.1 mm using an ocular micrometer. I only included invertebrates ≥ 2 mm total length in the calculation of benefit because this appears to be the smallest size prey item taken by other drift feeding salmonids (Bisson 1978; Tippets and Moyle 1978). I converted invertebrate lengths to weights with length-weight equations given in Rogers et al. (1977) and Smock (1980) and converted weights to caloric values according to Cummins and Wuycheck (1971).

I converted calories per sample to calories per hour and, because the drift net sampled the entire water column, corrected the sample caloric values to a standard depth of 25 cm (constant sampled area of 387.5 cm^2). I made this correction by dividing 387.5 cm^2 by the area sampled by the drift net and multiplied this by the calories per hour for each sample. I related calories per hour to mean column velocity by use of linear regression in which the regression was forced through the origin. This yielded estimates of caloric benefit of microhabitats based on current velocity for a constant sampled area of 387.5 cm^2.

Because fish size and water velocity are important in determining the foraging success of a fish (Hughes and Dill 1990; Hill and Grossman 1993), I adjusted the caloric benefit of a microhabitat by the maximum capture distance (MCD) as defined in Hughes and Dill (1990). Maximum Capture Distance (cm) is a function of fish size, water velocity, and the size of the invertebrate prey:

$$MCD = \sqrt{RD^2 - (V * RD / VMAX)^2} \qquad (2)$$

where:

$$RD = 12 * PL(1 - e^{(-0.2 * FL)}) \qquad (3)$$

$$VMAX = 17 * FL^{0.58} \qquad (4).$$

RD is the fish's reaction distance (cm), PL is prey length (mm), FL is the fish's fork length (cm, Hughes and Dill 1990), VMAX is the fish's maximum sustainable swimming speed ($cm \cdot s^{-1}$, Jones et al. 1974) and V is the microhabitat's mean column velocity ($cm \cdot s^{-1}$) (Figure 2).

I estimated PL as a function of mean column velocity from the invertebrate drift data collected in Hunt Creek by use of linear regression. I derived the regression equation by calculating the mean invertebrate length for each drift sample and regressing these mean invertebrate lengths against mean column velocity for the drift samples.

I used the MCD to estimate the fish's foraging area (FA, cm^2) as a semicircle, perpendicular to the current (Hughes and Dill 1990), with radius equal to the MCD:

$$FA=0.5(\Pi MCD^2) \qquad (5).$$

I used a semicircle because over 95% of the fish observed foraging in Hunt Creek were maintaining positions just above the substrate and therefore could only feed on drift in an area defined as a semicircle above the fish with radius equal to the MCD.

I adjusted the estimated caloric benefit of a microhabitat to reflect the fish's FA as determined by the MCD. I made this adjustment by multiplying the benefit of the microhabitat (determined by the mean column velocity) by the quotient FA/387.5 cm^2 (standardized area for the drift samples). Therefore, if the fish's foraging area was greater than the 387.5 cm^2 the benefit estimate of the microhabitat was increased accordingly. The MCD increases with increasing velocity from 0 $cm \cdot s^{-1}$ to a maximum, the value of which depends on fish size, and then decreases to zero, again dependent on fish size (Hughes and Dill 1990).

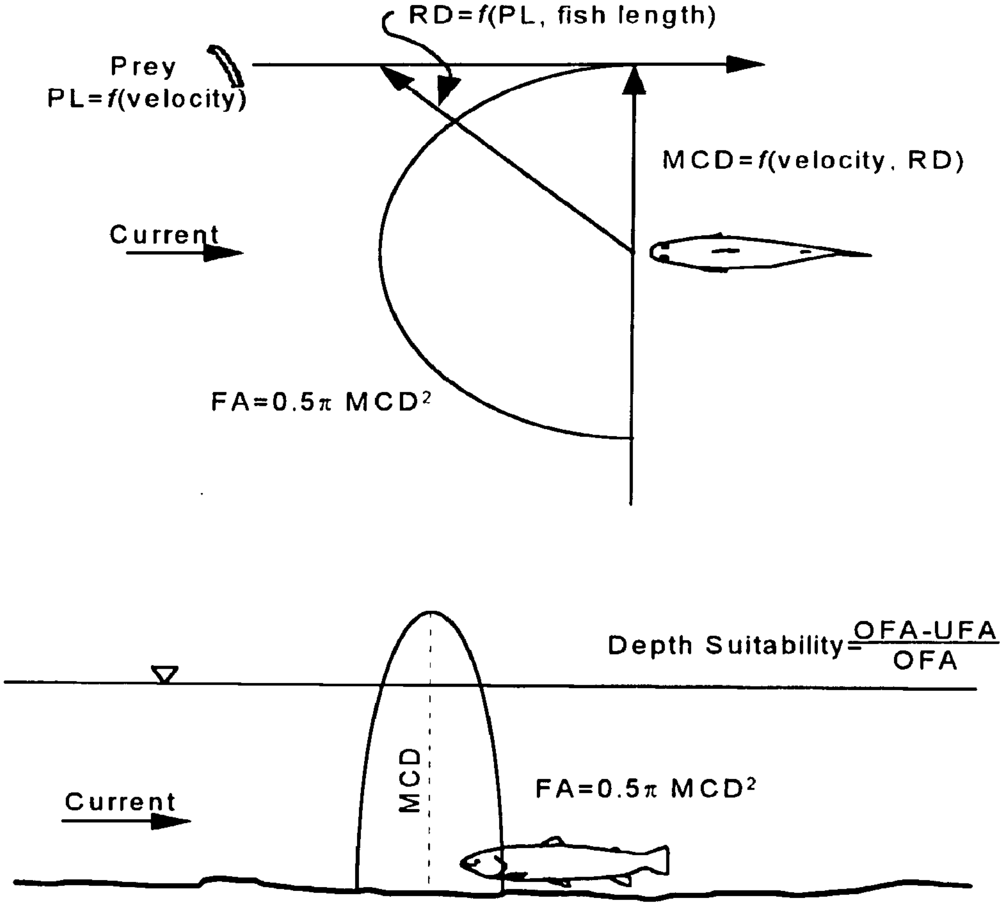

Figure 2. Parameters used in estimating bioenergetic benefits of brook trout foraging microhabitats (adapted from Hughes and Dill 1990). The foraging area (FA) is a two dimensional semi-circular plane perpendicular to the direction of the current with radius equal to the maximum capture distance (MCD). RD, PL, OFA, and UFA are defined in the text.

I did not include the benthic prey available to the fish because data indicated that brook trout in Hunt Creek foraged on the benthos only rarely. Behavioral observations collected in section B of Hunt Creek demonstrated that only 10% of the feeding attempts were directed at the substrate and none of the fish observed fed exclusively on benthos (E. A. Baker unpublished data). This is similar to results in McNicol et al. (1985), which showed that young of year brook trout in a small stream in Manitoba, Canada directed only 3% of their foraging effort toward the benthos.

I developed regression equations to estimate the cost of maintaining position at a microhabitat location (C_x, cost of swimming) from data in Beamish (1980, Table 1). Because I only modeled summer microhabitats I used the equations derived for brook trout swimming at 15° C. This temperature is similar to the average daily maximum temperature in Hunt Creek. In the summers of 1993-94, average daily maximum temperature for the period June 1 to August 31 was 15.1 and 15.8 respectively. The equations presented by Beamish (1980) related swimming cost to current velocity and weight for brook trout at velocities of 25, 30, 35, 40 and 45 $cm \cdot s^{-1}$. I determined size specific (i.e. 5, 7.5, 10 cm etc.) swimming cost estimates at each of these five velocities for brook trout and calculated the linear regression of swimming cost versus current velocity for fish of a specific size (Table 1). I derived weight estimates for the brook trout in Hunt Creek from length-weight data collected in the spring and fall, 1993 and 1994 in Hunt Creek. I estimated swimming cost in mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$ at velocities from 0 to 100 $cm \cdot s^{-1}$ from the equations in Table 1 and converted these cost estimates to $calories \cdot hr^{-1}$ by use of the energetic equivalents given in Elliot and Davison (1975). I used a nonlinear regression

Table 1. Parameters for the linear regression equation Log (C)=I+S*FV, where C=the cost of swimming (mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$) for brook trout developed from data in Beamish (1980). I=y-intercept, S=regression slope and FV=focal velocity ($cm \cdot s^{-1}$). Fish weights were estimated from length-weight regressions developed from data collected in Hunt Creek.

Length (cm)	**Weight (g)**	**I**	**S**	**r^2**	**p**
5	1.0	2.605	0.020	0.49	0.19
7.5	3.6	2.366	0.019	0.57	0.14
10	8.8	2.196	0.019	0.64	0.10
12.5	17.4	2.064	0.019	0.70	0.08
15	30.5	1.956	0.019	0.75	0.06
17.5	48.9	1.865	0.018	0.79	0.05
20	73.8	1.786	0.018	0.82	0.04

equation to predict focal point velocity as a function of mean column velocity developed from data collected in Hunt Creek, and used the estimates of focal point velocity to calculate C_x for specific microhabitats by use of the equations in Table 1.

I modeled the net benefits of microhabitats with equation 1. I constructed the bioenergetic-HSC from the 7 net benefit curves by standardizing each of the curves as outlined in Bovee (1986).

Because the suitability of a particular microhabitat location chosen by a drift feeding brook trout is dependent on the fish's foraging area, I developed bioenergetic-HSC for depth which were dependent on MCD and therefore, dependent on velocity. The suitability of the depth at a microhabitat is defined as follows:

$$\text{if depth} \geq \text{MCD, } HSC_d=1.0 \qquad (6)$$

$$\text{if depth} < \text{MCD, } HSC_d=\frac{OFA-UFA}{OFA}, \qquad (7)$$

where HSC_d=depth suitability, OFA=foraging area available at optimal depth (depth≥MCD), and UFA=unavailable foraging area at depth<MCD. This assumes that depth is not limiting if it is greater than the MCD. Because the MCD is dependent on the current velocity it is possible for the suitability of a particular depth to vary as velocity changes. Depth is defined as unsuitable when it is less than or equal to the maximum body depth for brook trout (22.3% of total length, estimated from data in Balon 1980).

Use-HSC Construction

I collected diurnal and nocturnal brook trout habitat use data during May through August, 1991-93 in Hunt Creek by instream observation with mask and snorkel. I randomly selected a 50 m reach for sampling and moved from the downstream end through the entire reach to the upstream end. No 50 m reach was sampled twice during the diurnal or nocturnal period in any year unless all reaches had been sampled previously. For each undisturbed fish observed, I estimated fish size to the nearest 1.25 cm (0.5 in), classified substrate and cover at the fish's location according to the codes in Table 2, measured depth to the nearest cm, and measured mean and focal point velocity to the nearest $cm \cdot s^{-1}$. I also noted the fish's activity as either actively foraging or resting. A fish was considered resting if it was immobile and on the substrate, and actively foraging if it was above the substrate and swimming to maintain a position in the stream. I only included data collected from actively foraging fish for constructing diurnal use-HSC and only included data from fish that were resting for constructing nocturnal use-HSC. Because Hunt Creek is a narrow stream in the study section I was able to observe the entire stream width and thus sampled all available habitats for habitat use data.

I constructed depth and mean column velocity use-HSC for the diurnal and nocturnal periods for young of the year (<8.9 cm) and yearling and older ($\geq$8.9 cm) brook trout based on habitat use in Hunt Creek using the nonparametric tolerance limits method (Bovee 1986). Use-HSC were constructed using the formula:

$$NSI=2(1-P), \qquad (8)$$

where NSI is the normalized suitability index and P is the central proportion of the data distribution under the curve (Bovee 1986). I constructed use-HSC for depth and mean column velocity by this approach

Table 2. Codes used to classify substrate and cover use and availability in Hunt Creek.

Cover Code	**Cover Description**
1	No cover
2	Velocity shelter protruding out of substrate but not providing visual isolation
3	Combination cover providing both visual isolation and velocity shelter
Substrate Code*	**Substrate Description**
1	Fines composed of sand and silt
2	Sand
3.X	Small gravel, Diameter < 0.6 cm
4.X	Medium gravel, diameter $\geq$ 0.6 cm and less than 2.5 cm
5.X	Large gravel, diameter > 2.5 cm

*Substrate classifications for gravels included an estimate of the embeddedness of the gravel, X=1,2,3, and 4 where 1=up to 25%, 2=26-50%, 3=51-75%, and 4=76-100% embedded. For example, a substrate classification of 4.2 denotes medium gravel embedded between 26-50%.

and defined P as the 50, 75, 90, and 95% portions of the distribution according to Somerville (1958) and a confidence level of 95%.

I compared microhabitat suitability values from the diurnal use- and bioenergetic-HSC models for independent observations of microhabitat use by brook trout in section C of Hunt Creek. I collected the habitat use data in section C of Hunt Creek during summer, 1991-92 with the same methods employed in section B and calculated microhabitat suitability scores by multiplying depth and velocity suitability values, as in a PHABSIM analysis (Milhous et al. 1989). I tested the null hypothesis that median suitability scores for these observations would be equal with these two methods with the Wilcoxon sign rank test for paired samples (Zar 1984).

Results

Bioenergetic-HSC

I collected invertebrate drift samples over a range of mean column velocities from 2 to 82 $cm \cdot s^{-1}$. Invertebrate drift availability (corrected to a depth of 25 cm, $calories \cdot hr^{-1}$) ranged from 2.1 to 1428.2. The regression of $calories \cdot hr^{-1}$ on mean column velocity was significant ($F=41.6$, $df=1,148$, $p<0.001$; Figure 3). However, because I forced the regression through the origin I was unable to calculate a meaningful coefficient of determination. These results are similar to those of Hill and Grossman (1993) who also found a linear relationship between energetic content of the drift and velocity. Aquatic invertebrates captured in the drift samples represented 28 families. However, chironomid larvae and pupae represented 52.6% of the invertebrates captured in the drift.

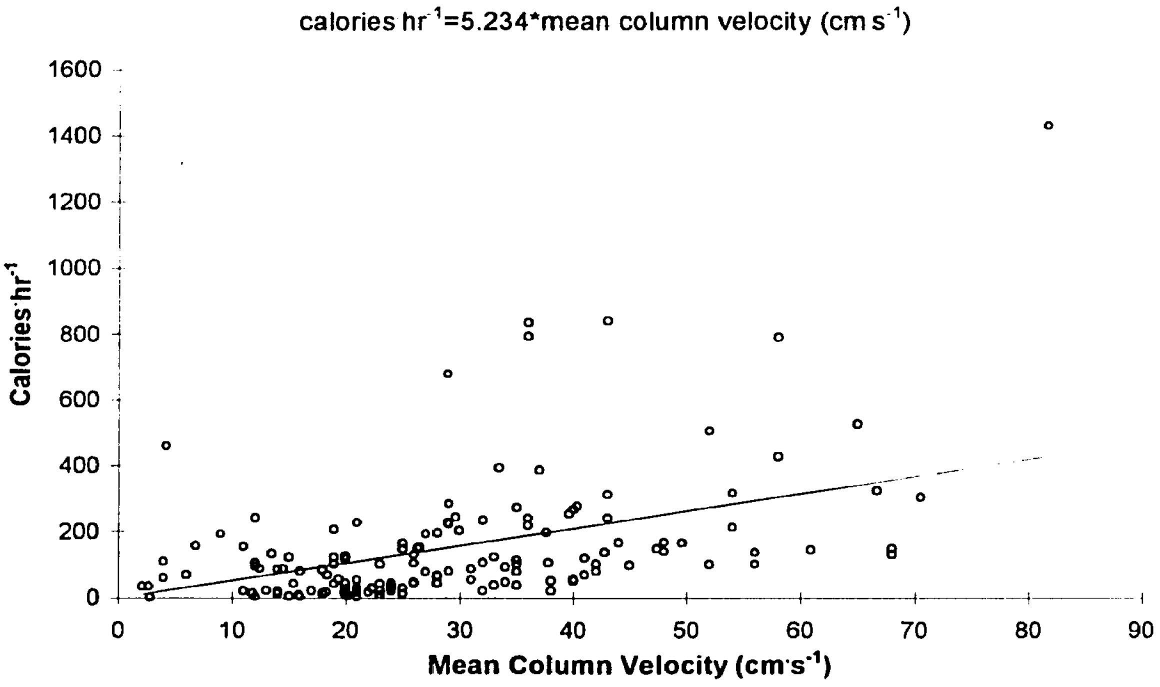

Figure 3. Invertebrate drift availability (calories·hr^{-1}) in relation to mean column velocity (cm·s^{-1}) from drift samples collected in Hunt Creek at locations where brook trout were observed feeding in section B and on the fixed transect in section B.

The relationship between mean invertebrate length (mm) and mean velocity was linear and positive over the range of velocities sampled (Figure 4; F=26.4, df=1,144, $p<0.01$, $r^2=0.16$). I used this regression equation to predict prey length (PL) in the calculation of fish reactive distance (RD). Based on the prey length and fish length the RD increased linearly with water velocity (Figure 5). The ratio of RD to fish length was greatest for the smallest fish, RD for a 5 cm fish at a velocity of 0 $cm \cdot s^{-1}$ was 20.6 cm, 4.1 times the fish length. In contrast, RD for a 20 cm fish at a velocity of 0 $cm \cdot s^{-1}$ was only 1.6 times the fish length or 31.9 cm.

MCD was equal to RD at 0 $cm \cdot s^{-1}$, increased slightly for fish of all sizes with increasing velocity to a maximum, and then decreased at higher velocities to zero (Figure 6). Maximum values of MCD occurred at velocities between 5 $cm \cdot s^{-1}$ for 5 cm fish and 25 $cm \cdot s^{-1}$ for 20 cm fish.

In the model, benefit of a microhabitat location was related to caloric value of the drift via a regression forced through the origin. Thus, the model predicted B_x of all foraging microhabitats at 0 $cm \cdot s^{-1}$ to be zero for fish of all sizes. B_x of foraging microhabitats increased with increasing velocity and reached maxima at mean column velocities between 23 and 48 $cm \cdot s^{-1}$, depending on fish size (Figure 7). Small fish had a narrower range of mean column velocities that provided a net caloric benefit than larger fish, and optimal velocities increased as fish size increased. The maximum velocity with benefit greater than zero for a fish of any particular size was equal to the maximum velocity at which the fish's MCD was greater than zero (Figure 6).

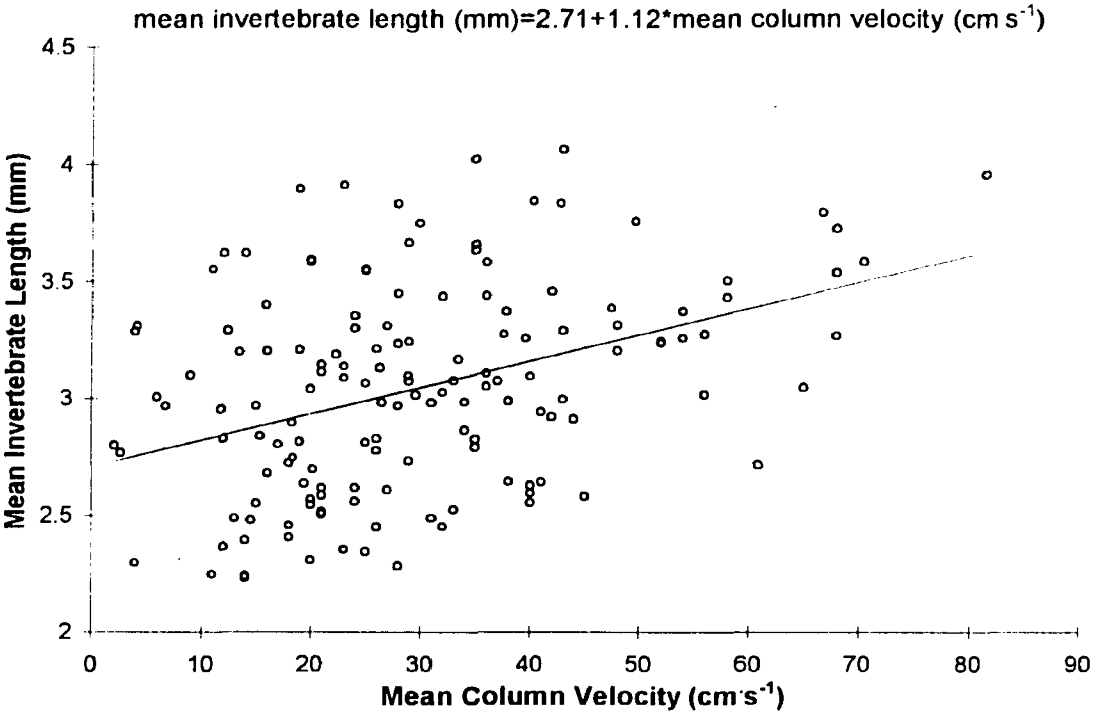

Figure 4. Mean invertebrate length (mm) in relation to mean column velocity (cm·s^{-1}) for drift samples collected in Hunt Creek at locations where brook trout were observed feeding in section B and on the fixed transect in section B.

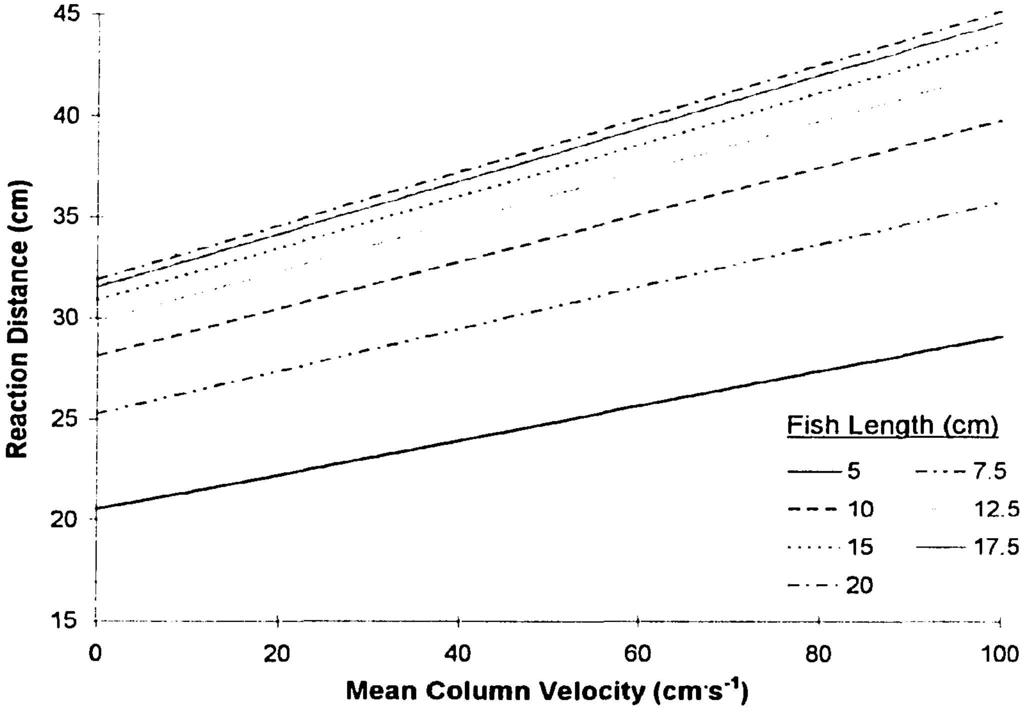

Figure 5. Reaction distance (RD) in relation to current velocity ($cm \cdot s^{-1}$) for foraging brook trout in Hunt Creek.

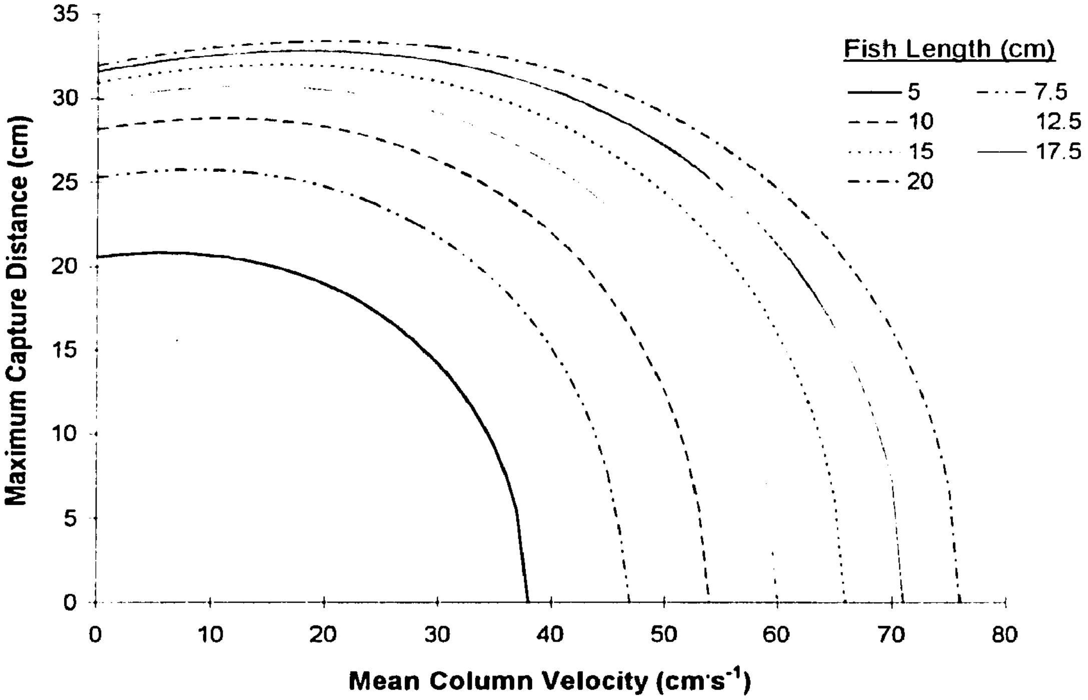

Figure 6. Maximum capture distance (MCD) in relation to current velocity (cm·s^{-1}) for foraging brook trout in Hunt Creek.

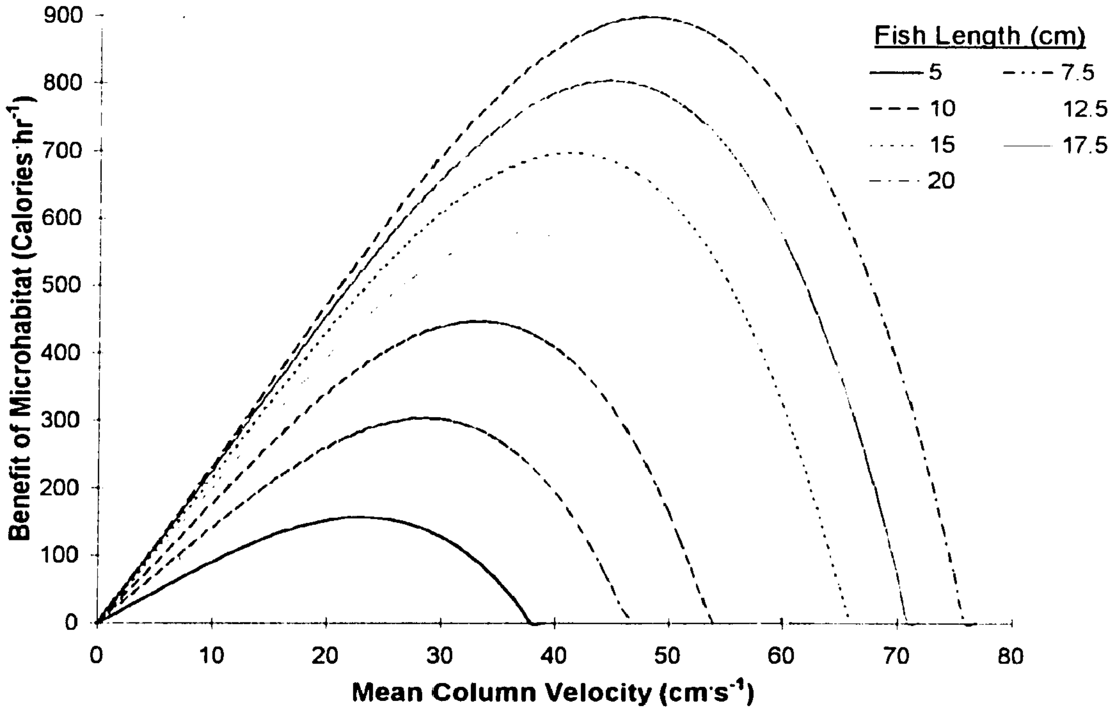

Figure 7. Microhabitat benefit estimates based on length (cm) of brook trout and current velocity (cm·s^{-1}) for foraging microhabitats in Hunt Creek. Benefit estimates are based on a microhabitat depth greater than or equal to the fish's MCD.

A nonlinear regression equation related focal point velocity (FPV, $cm \cdot s^{-1}$) to mean column velocity (MCV, $cm \cdot s^{-1}$), based on 287 observations of foraging brook trout:

$$FPV=2.973*MCV^{0.5},\ r^{2}=0.782. \qquad (9)$$

I used this equation to predict swimming cost for foraging microhabitats from the mean column velocity and used the swimming cost estimate in the calculation of the net benefit curves.

Brook trout swimming cost estimates for velocities from 0 to 100 $cm \cdot s^{-1}$ demonstrated that the cost of swimming was small for fish of all sizes at slow velocities (Figure 8). The cost of swimming increased as velocity increased and exceeded the benefits gained at a velocity of 40 $cm \cdot s^{-1}$ for 5 cm fish and at 71 $cm \cdot s^{-1}$ for a 20 cm fish. The cost of swimming was greater than zero at zero velocity, because the equations in Beamish (1980) included the standard metabolic rate.

The net benefit estimates for foraging brook trout (Figure 9) demonstrated that the cost of swimming exceeded the benefit of a microhabitat at low, as well as high, mean column velocities for fish of all sizes. The influence of fish size on the net benefit curves was dramatic: the minimum velocity at which a 5 cm fish received a net benefit was slightly higher than 0 $cm \cdot s^{-1}$, but the largest fish (20 cm) required a microhabitat with a mean column velocity of at least 6 $cm \cdot s^{-1}$ to receive a net benefit. These curves indicated that as brook trout grew they required microhabitats with greater velocities to maximize their energetic gains during foraging. Net energetic gains were greatest for the largest fish: a 20 cm fish foraging in an optimal microhabitat could potentially receive a benefit of approximately 650 $calories \cdot hr^{-1}$, but a 5 cm fish foraging at an optimal location could

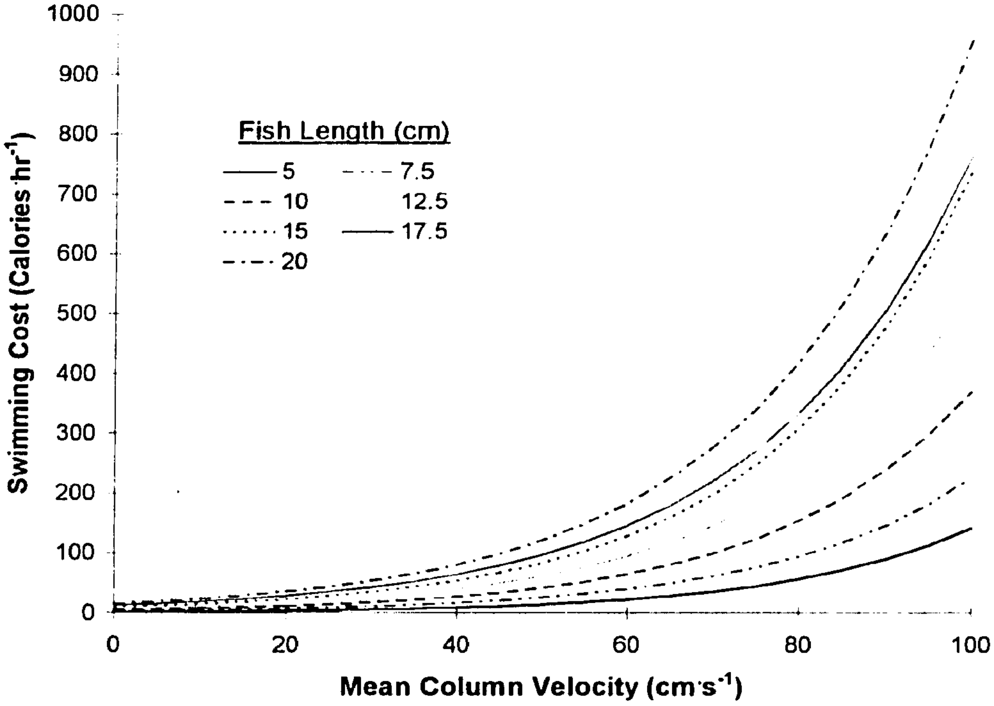

Figure 8. Brook trout length specific swimming cost estimates (calories·hr^{-1}) in relation to current velocity (cm·s^{-1}) based on equations given in Beamish (1980).

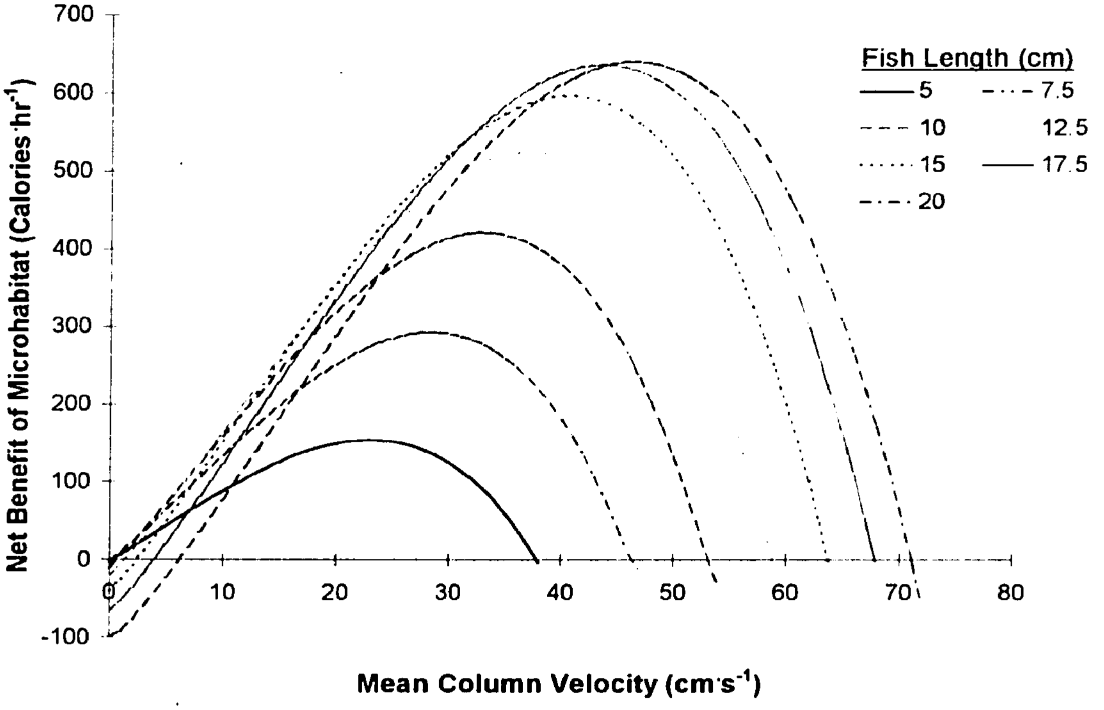

Figure 9. Length specific net caloric benefit (calories·hr^{-1}) estimates for brook trout foraging microhabitats in Hunt Creek in relation to current velocity (cm·s^{-1}).

receive a maximum benefit of 150 calories$\cdot$hr^{-1} (Figure 9). The maximum velocity which could provide a net benefit also varied with fish size and increased with increasing fish size. The maximum suitable velocity (net benefit>0) for a 20 cm fish was approximately 71 cm$\cdot$s^{-1} while the maximum suitable velocity for a 5 cm fish was only 38 cm$\cdot$s^{-1}.

The bioenergetic-HSC for velocity generated from the net benefit curves (Figure 10) again demonstrated the importance of fish size and mean column velocity on habitat suitability. As brook trout size increased the mean column velocity that was most suitable (suitability=1.0) for foraging increased as well. The most suitable microhabitat for 5 cm brook trout was at a velocity of 25 cm$\cdot$s^{-1} and the most suitable microhabitat location for a 20 cm brook trout was at a velocity of 46 cm$\cdot$s^{-1}. The bioenergetic-HSC for velocity assumed the depth at the microhabitat location was at least equal to the MCD for the fish.

The bioenergetic-HSC for depth (Figure 11) at a particular microhabitat location in a stream depended on current velocity for a fish of a particular size. As velocity increased from 0 cm$\cdot$s^{-1} the suitability of a specific depth increased to a maximum until the depth equaled the MCD. Also, the suitability of depth at a particular velocity was dependent on fish size. For example, the suitability at a depth of 20 cm and a velocity of 10 cm$\cdot$s^{-1} was 0.94 for a 5 cm fish, but it was only 0.86 for a 15 cm fish. The dependence of depth suitability on the current velocity is contrary to the current method of calculating habitat area in a PHABSIM analysis in which the habitat parameters are considered to be independent in their influence on fish habitat selection.

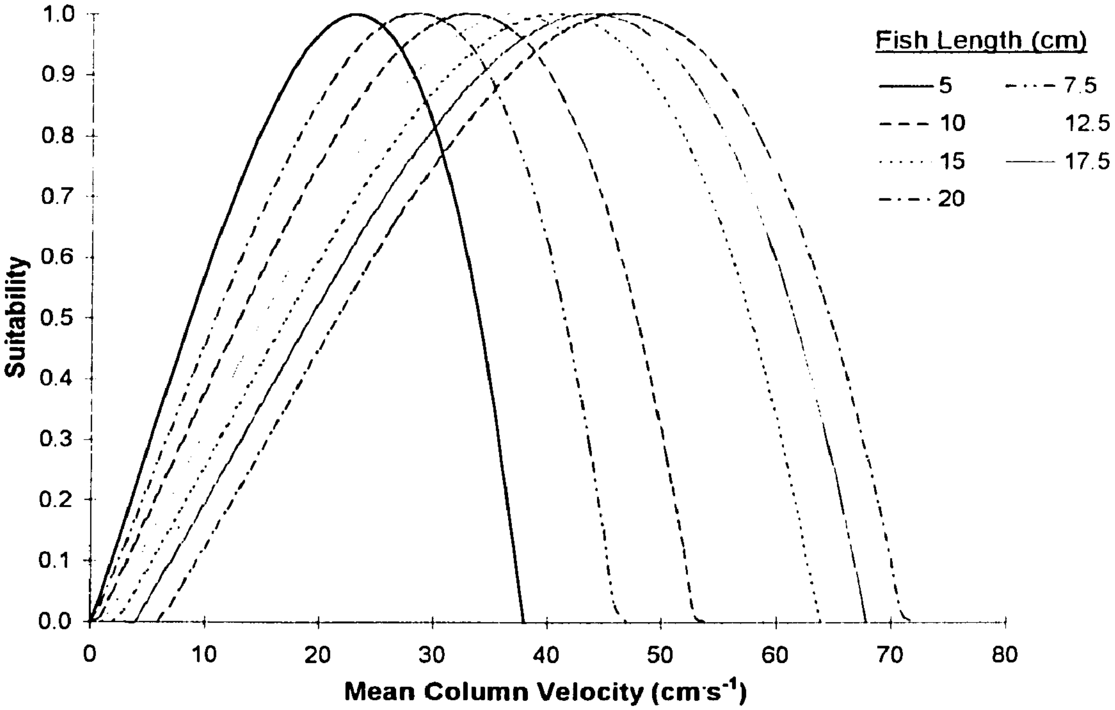

Figure 10. Brook trout length specific bioenergetically derived velocity habitat suitability criteria for foraging microhabitats in Hunt Creek.

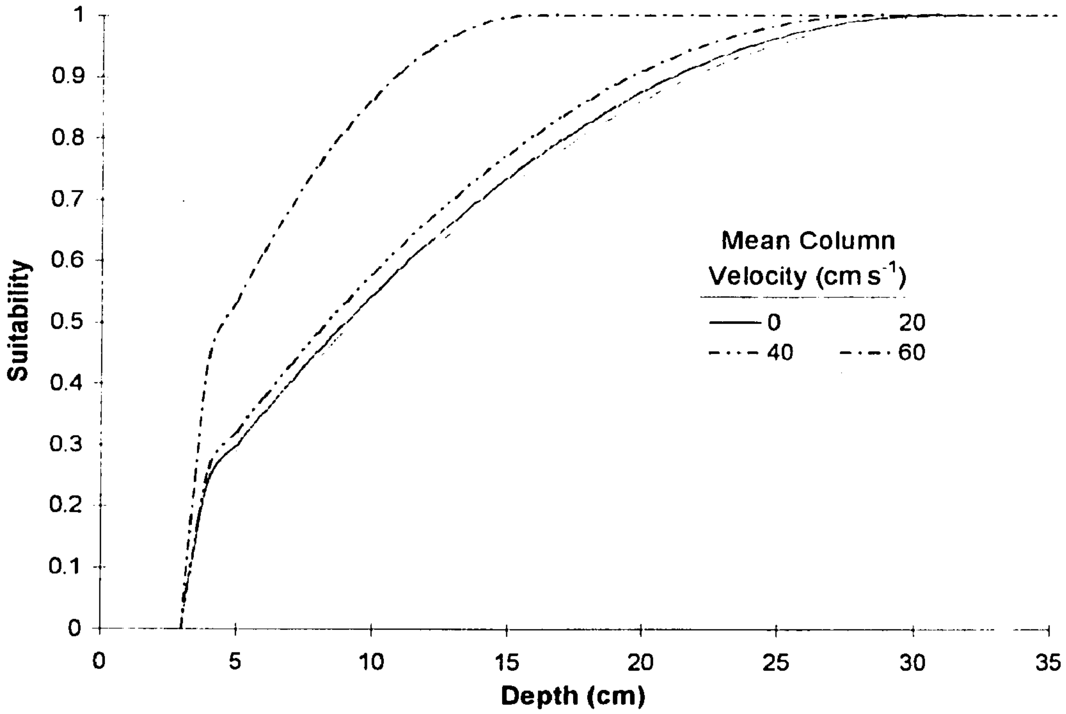

Figure 11. Sample depth suitability criteria for 15 cm brook trout in relation to current velocity in Hunt Creek.

Use-HSC

I constructed diurnal use-HSC for mean column velocity and depth from observations of 149 young of the year and 138 yearling and older foraging brook trout in section B of Hunt Creek (Figures 12 and 13). The optimal velocities (suitability=1.0) predicted for young of the year brook trout in Hunt Creek were from 6 to 30 $cm \cdot s^{-1}$, almost identical to the optimal range for yearling and older brook trout (6 to 27 $cm \cdot s^{-1}$). The range of usable velocities (suitability>0.0) predicted from use-HSC for young of the year fish was from 0 to 66 $cm \cdot s^{-1}$ (Figure 13). A velocity of 0 $cm \cdot s^{-1}$ had a predicted suitability value of 0.5 for yearling and older fish and the maximum usable velocity predicted for yearling and older fish was 98 $cm \cdot s^{-1}$.

The range of optimal depths based on diurnal use-HSC was narrower ans shallower for young of the year fish (15-34 cm) than for yearling and older fish (27-55 cm; Figure 13). Usable depths for young of the year fish more closely overlapped the range of useable depths for yearling and older fish (3-67 cm and 12-85 cm, respectively). The minimum depths used by both young of the year and yearling and older fish were close to the minimum suitable depths predicted using the maximum body depth from Balon (1980), although no young of the year or yearling and older fish were observed in water equal to the minimum depth predicted from the body depth. It should be noted however, that it was very difficult for the snorkeler to see in water less than about 8 cm deep.

I constructed nocturnal use-HSC from observations of 31 young of the year and 62 yearling and older brook trout in sections C and B combined. The optimal velocity range was 5-23 $cm \cdot s^{-1}$ for young of the

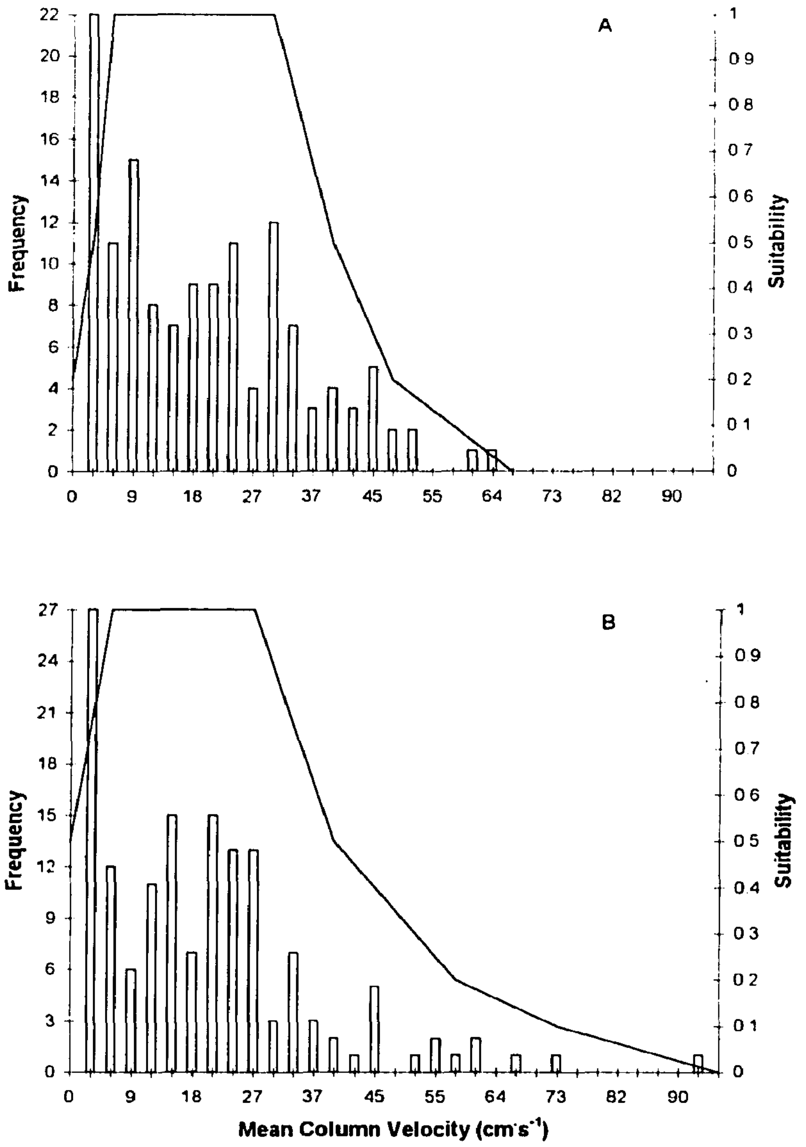

Figure 12. Mean column velocity (cm·s^{-1}) frequency-of-use data and use-HSC for foraging young of the year (A) and yearling and older (B) brook trout in Hunt Creek. Histogram represents use data and line represents suitability.

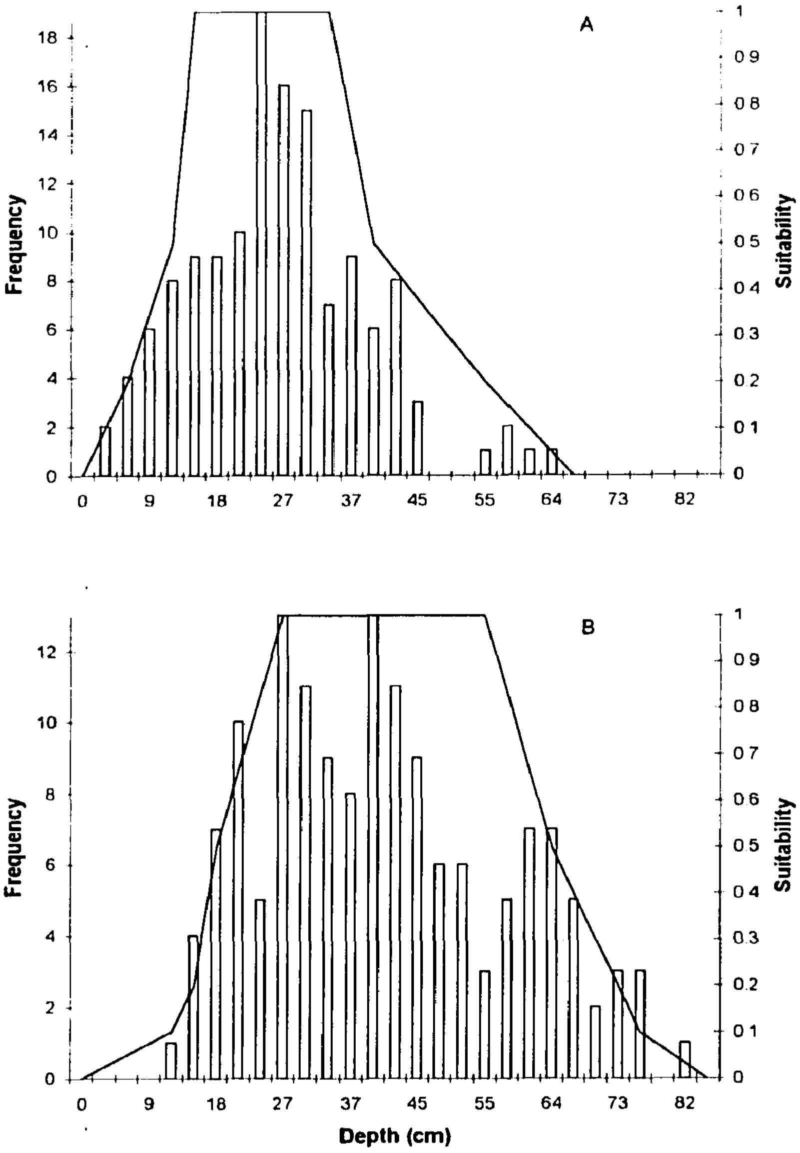

Figure 13. Depth (cm) frequency-of-use data and use-HSC for foraging young of the year (A) and yearling and older (B) brook trout in Hunt Creek. Histogram represents use data and line represents suitability.

year brook trout, and was 4-22 $cm^{\cdot}s^{-1}$ for yearling and older brook trout (Figure 14). The range of usable velocities was narrower for young of the year fish (0-39 $cm^{\cdot}s^{-1}$) than for yearling and older fish (0-54 $cm^{\cdot}s^{-1}$). The range of optimal depths was from 12 to 29 cm for young of the year and was from 20 to 46 cm for yearling and older brook trout (Figure 15). Usable depths were from 2 to 75 cm for young of the year and were from 6 to 72 cm for yearling and older fish.

Brook trout use of depth and mean column velocity micro-habitat attributes differed between young of the year and yearling and older fish (MANOVA, F=31.6, df=2,375, p<0.001). Depth and velocity use also differed significantly between the nocturnal and diurnal period (MANOVA, F=6.9, df=2,375, p=0.001), but the interaction between life stage and period was not a significant source of variation in the model (MANOVA, F=0.11, df=2,375, p=0.90). Young of the year fish occupied microhabitats that were shallower and had slower mean column velocity than those occupied by yearling and older fish during both nocturnal and diurnal periods. Also, both young of the year and yearling and older fish moved to microhabitat locations that had lower mean column velocity during the nocturnal period but depth use was not different between periods within life stage.

Comparison of Diurnal Foraging HSC

The optimal velocities predicted from the bioenergetic models were in general greater and narrower than those predicted from frequency-of-use data (Figures 16 and 17). The optimal velocities predicted for 5 and 7.5 cm fish (equivalent to young of the year size range) from bioenergetic-HSC were within the optimal velocity range predicted from use-HSC. However, the optimal velocities predicted from bioenergetic-

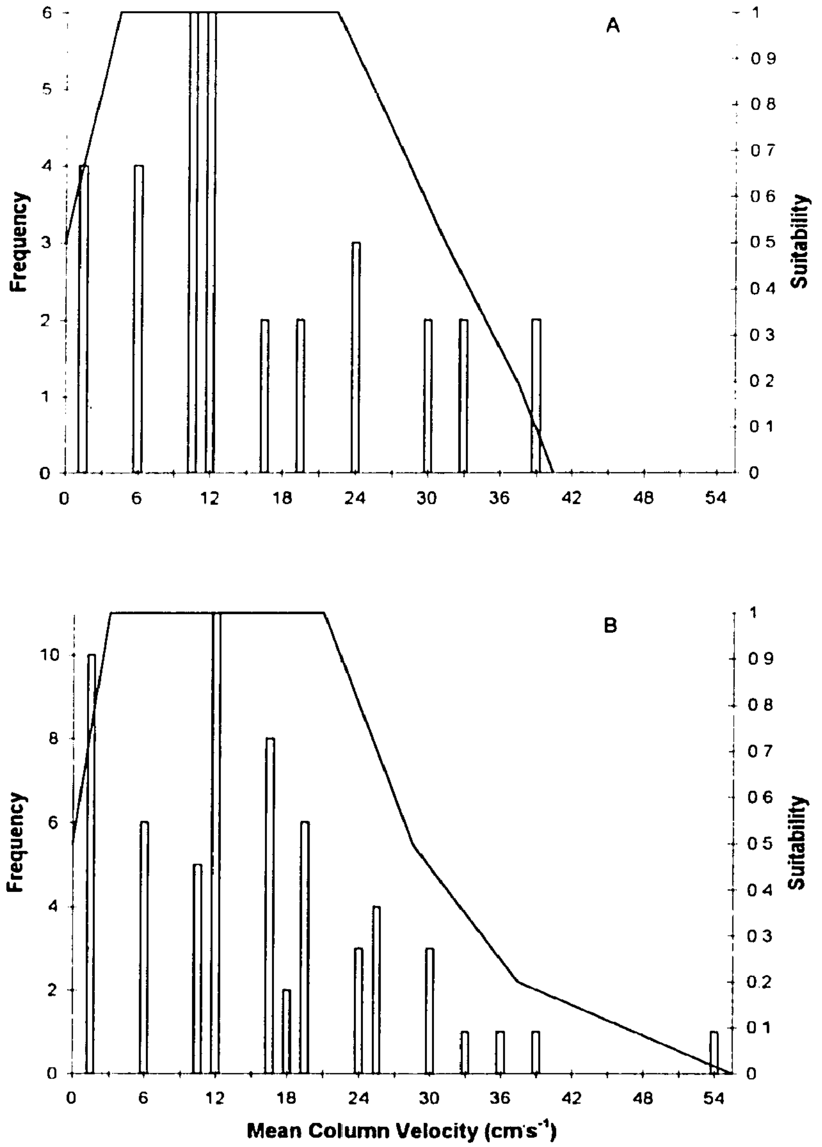

Figure 14. Mean column velocity (cm·s^{-1}) frequency-of-use data and use-HSC for resting young of the year (A) and yearling and older (B) brook trout in Hunt Creek. Histogram represents use data and line represents suitability.

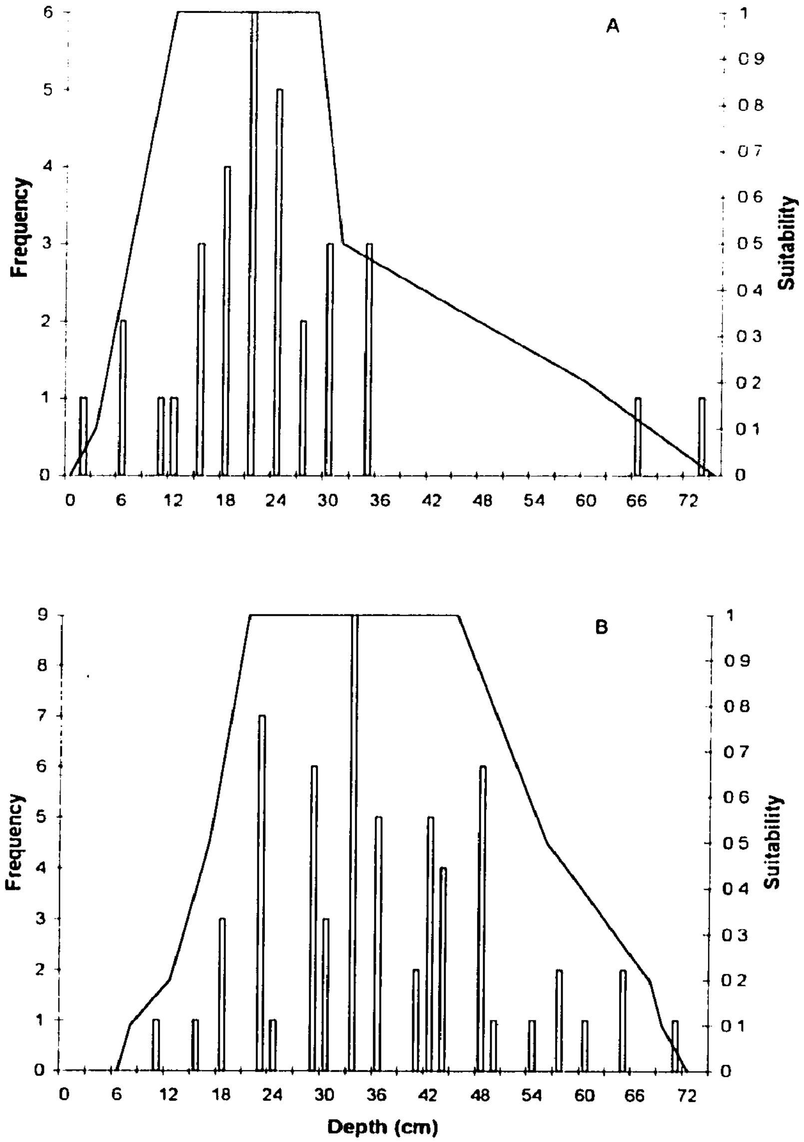

Figure 15. Depth (cm) frequency-of-use data and use-HSC for resting young of the year (A) and yearling and older (B) brook trout in Hunt Creek. Histogram represents use data and line represents suitability.

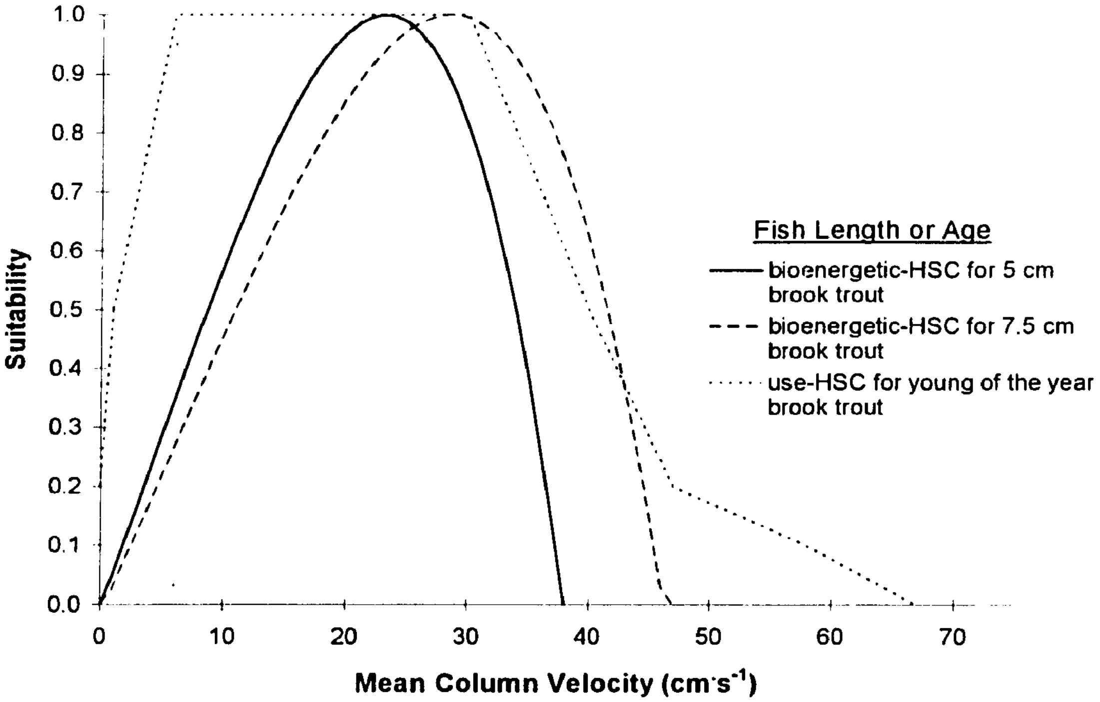

Figure 16. Mean column velocity use-HSC and bioenergetic-HSC for foraging young of the year brook trout in Hunt Creek.

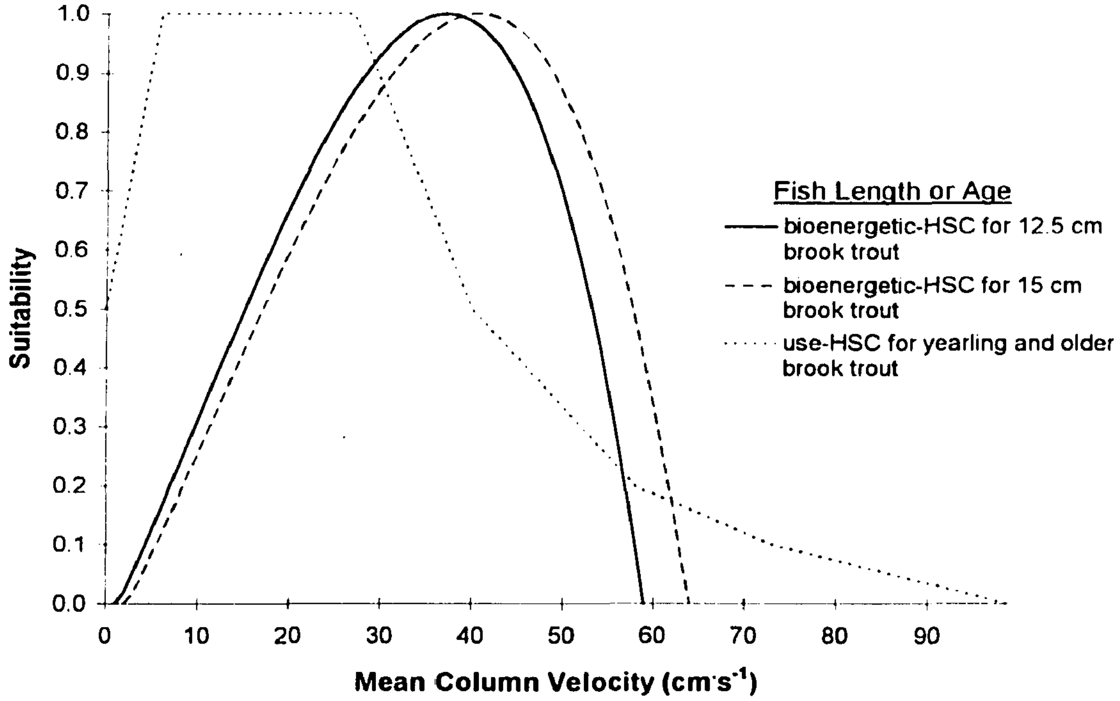

Figure 17. Mean column velocity use-HSC and bioenergetic-HSC for foraging yearling and older brook trout in Hunt Creek.

HSC for fish 10 cm and larger (yearling and older) were all greater than the optimal velocities predicted from use-HSC. Comparisons of the depth suitability values are difficult because the suitability of depth depends on velocity for bioenergetic-HSC.

I tested the null hypothesis of no difference in suitability scores between the two methods for 146 habitat use observations collected in section C of Hunt Creek that were independent of the data used to construct the HSC models. The null hypothesis that microhabitat suitability scores calculated from both models were equal was rejected for young of the year fish (Wilcoxon signed rank test, Z=5.167, p=0.<001) but not for yearling and older fish (Z=1.087, p=0.277). The suitability scores for young of the year fish were significantly higher based on the use-HSC model (median=0.875) than for the bioenergetic-HSC model (median=0.498) in section C. This is in spite of the fact that velocity availability distributions were similar between sections C and B (see description of study area). Also, habitat use distributions were similar for young of the year fish between sections C and B (n=136 in section B, n=141 in section C, Mann-Whitney U=8562.5, p=0.124, df=1).

Discussion

The bioenergetic-HSC differed from the use-HSC in several ways. Bioeneretic-HSC predicted narrower renges of optimal and usable mean column velocity for both young of the year and yearling and older foraging brook trout. From the bioenergetic-HSC, a single velocity provided a maximum energetic gain and thus, was optimally suitable for foraging brook trout. In contrast, the use-HSC predicted a range of optimal velocities.

The predicted use suitability scores at 0 $cm \cdot s^{-1}$ seem unrealistic based on the energy maximization principle for drift feeding stream fishes (Smith and Li 1983; Fausch 1984; Godin and Rangely 1989; Hill and Grossman 1993). This is because drift feeding fish depend on the current for food delivery, and the benefit of the drift is positively related to the current velocity (Hill and Grossman 1993). Therefore, a drift feeding fish occupying a foraging microhabitat with zero velocity should not receive a benefit from foraging, and the suitability of those microhabitat locations should be comparatively low.

The fact that foraging brook trout in Hunt Creek occupied microhabitats that were less than optimal based on bioenergetic-HSC may be an indication that optimal foraging sites are limited. This would result in competition for foraging stations forcing some fish to occupy suboptimal sites. Others have noted that a linear dominance hierarchy exists in foraging salmonids and that the dominant fish select microhabitats that provide the greatest benefit in foraging (Fausch 1984; Hughes 1992; Nielsen 1992). Brook trout competition for optimal foraging sites in Hunt Creek could also explain the differences in predicted optimal velocities from the two sets of HSC. One alternative explanation is that net energy gain from foraging is not what determines brook trout foraging habitat use in Hunt Creek. Other alternatives are that the measuring instrument is not accurate at low velocity or the fish were feeding on non-drift food items. Alexander and Gowing (1976) determined that oligochaetes were an important component of the diet of two and three year old brook trout in Hunt Creek. Although I did find oligochaetes in the drift samples I collected, they were a very minor component of the drift.

The bioenergetic-HSC predicted a narrower range of velocities that provide usable foraging habitat for brook trout in comparison to the range predicted by use-HSC. One potential explanation for this difference is that foraging brook trout in Hunt Creek may have selected foraging stations that were shielded from the current but were adjacent to a region of high velocity where foraging occurs. This behavior has been well documented for other foraging salmonids (Everest and Chapman 1972; Fausch and White 1981) and was also documented in observations in Hunt Creek. However, most of the foraging brook trout in Hunt Creek maintained foraging stations just above the substrate and pursued food items that were in the overlying water column. Fewer than 1% of the foraging brook trout I observed in Hunt Creek were holding position in calm water and feeding in faster adjacent water.

Another difference between bioenergetic-HSC and use-HSC was that optimal velocity was different for brook trout of different lengths. Use-HSC predicted an optimal velocity range for yearling and older foraging brook trout that was nearly identical to the range of predicted optimal velocities for young of the year brook trout. In contrast, optimal velocities predicted from bioenergetic-HSC increased with increasing fish size and the optimal predicted velocities for yearling and older fish from bioenergetic-HSC were greater than those predicted from use-HSC. Again, this could be explained through competition for the most suitable microhabitats. Competition for foraging microhabitats in Hunt Creek could force subordinate fish to choose microhabitats with mean column velocities that are either greater or less than optimal velocity. The results of that choice should also provide the subordinate fish with the maximum energetic gain available. The use-HSC suggest that brook trout select microhabitats with a velocity that is less than the optimal velocity (predicted by bioenergetic-HSC) in greater proportion than they select microhabitats with a velocity greater than optimal. The net benefit curves also suggest that microhabitats with a velocity less than optimal are more suitable than those with higher than optimal velocity (Figure 10). For example, a 5 cm brook trout faced with the choice of occupying a microhabitat with a velocity 15% lower than optimal or 15% higher than optimal velocity should select the microhabitat with the lower velocity because it provides a greater net benefit. The observation that optimal predicted velocity from bioenergetic-HSC increased with fish size suggests that, in the absence of competition, the mean column velocity at a foraging station selected by a drift feeding brook trout should be correlated with the length of the fish.

Differences in the depth HSC between the methods are difficult to assess because the suitability of a particular depth based on fish foraging area is dependent on velocity. Use-HSC for depth agreed reasonably well with bioenergetic-HSC in the predictions of minimum suitable depth although bioenergetic-HSC predicted suitable depths that were slightly lower than those predicted from use-HSC.

The fact that bioenergetic-HSC yielded lower suitability scores than use-HSC for young of the year brook trout observational data collected in section C but not for yearling and older observational data could also be explained by competition between young of the year fish. If competition between young of the year fish was intense in section C it could result in density dependent mortality or emigration of young of the year fish. This could reduce the density of the remaining fish to a level low enough that competition between yearling and older fish for foraging microhabitats is not as intense and therefore, a higher proportion of the yearling and older fish can use foraging microhabitats that have a relatively higher suitability. It also could mean that there is a greater availability of foraging microhabitats with high suitability values for yearling and older fish than for young of the year fish.

The tendency for both young of the year and yearling and older fish to select microhabitats with lower mean column velocities during the nocturnal period than during the diurnal period is further evidence that the fish selected microhabitats that maximized energetic benefit. Although there was no energetic gain during the nocturnal period because the fish were not foraging, the fish minimized energetic expenditure during the resting period. By minimizing energy expenditure for swimming, the fish maximized the amount of energy gained during active foraging that was available for growth of soma and reproductive organs.

The differences between bioenergetic-HSC and use-HSC have important implications for stream habitat analysis using the PHABSIM modeling system. A PHABSIM analysis of summer foraging habitat in Hunt Creek, (Chapter 2) documented differences in both the shape and magnitude of the weighted usable area (WUA, the measure of habitat area and quality calculated in a PHABSIM analysis) curves that were calculated from bioenergetic-HSC versus use-HSC. WUA values at a particular discharge were generally lower when bioenergetic-HSC were used in the calculations. In addition, the PHABSIM model predicted a reduction in discharge of 98% in section B of Hunt Creek would reduce WUA 37-70% based on use-HSC and 75-99% based on bioenergetic-HSC.

I did not include cover and substrate components in the bioenergetic-HSC model. However, observational data collected in Hunt Creek demonstrated that brook trout seek out velocity shelters and combination cover types (those that provide both velocity shelter and visual isolation). I speculate that this results from the fish's desire to evade predators and to increase the net benefit of microhabitats by reducing the cost of swimming. Therefore, the relationship between focal point velocity and mean column velocity does reflect the use of cover as it affects the fish's focal point velocity choice. In addition, I propose that substrate composition in the immediate vicinity of the fish is of minor importance when the fish is selecting a feeding station to maximize its energetic gain during foraging. It is more likely that substrate composition upstream of the fish is more important because it influences upstream invertebrate abundance and drift composition (Minshall 1984). Furthermore, the substrate in Hunt Creek is composed almost entirely of small and medium gravels.

The tradeoffs between potential energetic gain and predation risk have been implicated as an important factor in fish habitat choice decisions (Mittelbach 1984; Gilliam and Fraser 1987; Huntingford et al. 1988). However, it does not appear that predator avoidance influenced position choice decisions for foraging brook trout in Hunt Creek. Piscivorous fish are only rarely present in the study sections of Hunt Creek (E. A. Baker, personal observation). A variety of avian, mammalian, and reptilian predators of trout (Alexander 1979) are present in the study area but I only rarely observed great blue herons *Ardea herodias* and belted kingfishers *Megaceryle alcyon* and never observed any mammalian or reptilian predators.

The bioenergetic-HSC presented here were developed from modeling principles that have already been shown to accurately reflect the position choice preferences of drift feeding stream fishes under field and laboratory conditions (Hughes and Dill 1990; Hill and Grossman 1993). Therefore, HSC constructed by this methodology may offer an improvement to those based on frequency-of-use data, and may accurately represent the suitability of foraging microhabitats in Hunt Creek.

However, further research is needed to validate the mechanistic basis for construction and use of bioenergetically-derived HSC and to improve the predictive capacity of bioenergetic-HSC. For example, the estimates of RD presented here were based on data collected from Arctic grayling *Thymallus arcticus* feeding on zooplankton in a laboratory under controlled conditions (Schmidt and O'Brien 1982). Research is needed regarding the relationship between prey size, actual RD, water velocity, and light intensity that would provide a more accurate prediction of foraging area as a function of current velocity and light intensity. Further, quantitative measures of swimming speed for brook trout intercepting drift would also improve the estimates of MCD. It is possible that foraging brook trout may travel at burst swimming speeds during foraging attempts. If this were the case, it would be necessary to increase the foraging area estimates used in the calculation of net benefits of a microhabitat and to adjust the depth suitability estimates based on MCD. If foraging brook trout were found to swim at burst speeds during foraging this would result in even higher estimates of optimal velocities. The importance of cover and substrate composition for drift feeding fish as they affect predator avoidance and swimming cost also needs to be addressed.

Literature Cited

Alexander, G. R. 1979. Predators of fish in coldwater streams. Pages 153-170 *in* H. Clepper, editor. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D. C.

Alexander, G. R., and H. Gowing. 1976. Relationships between diet and growth in rainbow trout (*Salmo gairdneri*), brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*). Michigan Department of Natural Resources Fisheries Research Report No. 1841, Ann Arbor, MI.

Alexander, G. R. and E. A. Hansen. 1986. Sand bed load in a brook trout stream. North American Journal of Fisheries Management 6:9-23.

Anderson, R. O. 1959. A modified flotation technique for sorting bottom fauna samples. Limnology and Oceanography. 4:223-225.

Balon, E. K. 1980. Early ontogeny of the brook charr, *Salvelinus* (*Baione*) *fontinalis*. Pages 631-666 *in* E. K. Balon, editor. Charrs, salmonid fishes of the genus *Salvelinus*. Dr. W. Junk, The Hague, Netherlands.

Barnes, R. D. 1987. Invertebrate Zoology, Fifth Edition. Saunders College Publishing, Philadelphia, PA.

Beamish, F. W. H. 1980. Swimming performance and oxygen consumption of the charrs. Pages 739-748 *in* E. K. Balon, editor. Charrs, salmonid fishes of the genus *Salvelinus*. Dr. W. Junk, The Hague, Netherlands.

Bisson, P. A. 1978. Diel food selection by two sizes of rainbow trout (*Salmo gairdneri*) in an experimental stream. Journal of the Fisheries Research Board of Canada 35:971-975.

Bovee, K. D. 1986. Development and evaluation of habitat suitability criteria for use in the Instream Flow Incremental Methodology. Instream Flow Information Paper 21. U.S. Fish and Wildlife Service Biological Report 86(7). 235 pp.

Brandt, S. B., and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. Transactions of the American Fisheries Society 122:845-869.

Cummins, K. W. and J. C. Wuychek. 1971. Caloric equivalents for investigations in ecological energetics. Internationale Vereinigung fur theoretishe und angewandte Limnologie, Verhandlungen 18:1-58.

Dorr, J. A., and D. F. Eschman. 1970. Geology of Michigan. University of Michigan Press, Ann Arbor. 476 pages.

Elliott, J. M. and W. Davison. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia (Berlin) 19:195-201.

Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29:91-100.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441-451.

Fausch, K. D. and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220-1227.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856-1862.

Godin, J. J.-G. and R. W. Rangeley. 1989. Living in the fast lane:effects of cost of locomotion on foraging behaviour on Atlantic salmon. Animal Behaviour 37:943-954.

Goyke, A. P., and S. B. Brandt. 1993. Spatial models of salmonine growth rates in Lake Ontario. Transactions of the American Fisheries Society 122:870-833.

Grant, J. W. A., and D. L. G. Noakes. 1987. Escape behaviour and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 44:1390-1396.

Grant, J. W. A. and D. L. G. Noakes. 1988. Aggressiveness and foraging mode of young-of-the-year brook charr, *Salvelinus fontinalis* (Pisces, Salmonidae). Behavioral Ecology and Sociobiology 22:435-445.

Hill, J. and G. D. Grossman. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology 74(3):685-698.

Hughes, N. F. 1992. Ranking of feeding positions by drift-feeding Arctic grayling (Thymallus arcticus) in dominance hierarchies. Canadian Journal of Fisheries and Aquatic Sciences 49:1994-1998.

Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: models and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:2039-2048.

Huntingford, F. A., N. B. Metcalfe, and J. E. Thorpe. 1988. Choice of feeding station in Atlantic salmon, *Salmo salar*, parr: effects of predation risk, season and life history strategy. Journal of Fish Biology 33:917-924

Jones, D. R., J. W. Kiceniuk, and O. S. Bamford. 1974. Evaluation of the swimming performance of several fish species from the Mackenzie River. Journal of the Fisheries Research Board of Canada 31:1641-1647.

McNicol, R. E., E. Scherer, and E. J. Murkin. 1985. Quantitative field investigations of feeding and territorial behaviour of young-of-the-year brook charr, *Salvelinus fontinalis.* Environmental Biology of Fishes 12(3):219-229.

Merritt, R. W. and K. W. Cummins, editors. 1984. An Introduction to the Aquatic Insects of North America 2nd Edition. Kendall/Hunt Publishing Company of America. Dubuque, Iowa.

Milhous, R. T., M. A. Updike, and D. M. Schneider. 1989. Physical Habitat Simulation System Reference Manual-Version II. Instream Flow Information Paper No. 26. U.S. Fish and Wildlife Service Report 89(16).

Minshall, G. W. 1984. Aquatic insect-substratum relationships. Pages 358-400 *in* Resh, V. H., and D. M. Rosenberg, editors, The Ecology of Aquatic Insects. Praeger Publishers, New York, NY.

Mittelbach, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65:499-513.

Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121:617-634.

Rogers, L. E., R. L. Buschbom, and C. R. Watson. 1977. Length-weight relationships of shrubsteppe invertebrates. Annals of the Entomological Society of America 70:51-53.

Rose, K. A., and J. H. Cowan, Jr. 1993. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and baseline simulations. Transactions of the American Fisheries Society 122:415-438.

Schmidt, D., and W. J. O'Brien. 1982. Planktivorous feeding ecology of Arctic grayling (*Thymallus arcticus*). Canadian Journal of Fisheries and Aquatic Science 39:475-482.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369-404.

Smith, J. J. and H. W. Li. 1983. Energetic factors influencing foraging of juvenile steelhead trout, *Salmo gairdneri*. Pages 173-180 *in* Noakes, D. L. G., D. G. Lindquist, G. S. Helfman, and J. A. Ward, eds. Predators and Prey in Fishes. Dr. W. Junk Publishers, The Hague, Netherlands.

Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10:375-383.

Somerville, P. N. 1958. Tables for obtaining non-parametric tolerance limits. Annals of Mathematics and Statistics 29:599-601.

Thomas, J. A., and K. D. Bovee. 1993. Application and testing of a procedure to evaluate transferability of habitat suitability criteria. Regulated Rivers: Research and Management 8:285-294.

Tippets, W. E. and P. B. Moyle. 1978. Epibenthic feeding by rainbow trout (Salmo gairdneri) in the McCloud River, California. Journal of Animal Ecology 47:549-559.

Zar, J. H. 1984. Biostatistical Analysis, 2nd Edition. Prentice-Hall, Inc. Englewood Cliffs, New Jersey. 718 pp.

CHAPTER 2

COMPARISON OF PREDICTED HABITAT CHANGE AND BROOK TROUT POPULATION RESPONSE TO A SIMULATED IRRIGATION WITHDRAWAL IN HUNT CREEK, MICHIGAN

ABSTRACT

I used three types of habitat suitability criteria (nocturnal, diurnal frequency-of-use, and diurnal bioenergetically based) to evaluate the impacts of a seasonal 50% withdrawal on brook trout habitat in Hunt Creek, MI by use of the Physical Habitat Simulation System (PHABSIM). Young of the year diurnal Weighted Usable Area (WUA) increased 16-31%, regardless of HSC used. Yearling and older diurnal WUA calculated from frequency-of-use HSC decreased 1.5-1.9%. Yearling and older WUA calculated from bioenergetically based HSC increased for fish ≤ 15 cm and decreased for fish >15 cm. Nocturnal WUA increased 18-29% for young of the year fish and 9-15% for yearling and older fish. Biannual brook trout density estimates in treatment and control sections of Hunt Creek were very similar for ten years preceding the withdrawal and during the withdrawal period and not significantly different after the treatment. The PHABSIM model predicted a summer withdrawal equal to 88% of baseflow would produce a statistically detectable reduction in brook trout density and that yearling and older brook trout habitat would be reduced more than young of the year habitat at that level of flow reduction.

Introduction

Changes in stream flow regime can influence the ecology of stream fishes in a variety of ways (Orth 1987). Stream flows are important in determining reproductive success (Starrett 1951), fish community structure and habitat use (Bain et al. 1988), and habitat availability (Kraft 1972). In midwestern trout streams the input of groundwater is recognized as an important abiotic factor influencing trout populations. For example, Latta (1965) found a significant positive relationship between young of the year brook trout *Salvelinus fontinalis* density and groundwater levels during a nine year study on the Pigeon River, Michigan. Similarly, White et al. (1976) determined that trout streams in Michigan and Wisconsin that had the most stable flow regime also had the greatest trout abundance and standing crop. Clearly, protecting flows in midwestern trout streams is important for the maintenance of healthy trout populations.

The Physical Habitat Simulation System (PHABSIM) is the computer based habitat modeling component of the Instream Flow Incremental Methodology (IFIM) that predicts stream habitat quality and quantity as a function of discharge (Milhous et al. 1989). PHABSIM was developed in the western U.S. with the purpose of evaluating the impacts of changes in streamflow on stream habitat. The PHABSIM system is widely used in the western U.S. to evaluate the impacts of water development projects on stream resources and is a legal requirement in the state of California (Reiser et al. 1989). However, the PHABSIM system has only recently been applied to streams in the midwestern U.S. where the geology, hydrology, and composition of the fauna are distinctly different from western streams (Gowan 1984; Bovee et al. 1994).

The PHABSIM system works on the premise that water depth, water velocity, substrate, and cover are the four microhabitat parameters that determine a fish's use of habitat. Data input into PHABSIM are in the form of habitat suitability criteria (HSC) and habitat availability data for these four parameters for the species and life history stage of interest and the stream under investigation (Figure 18; Milhous et al. 1989). The output of a PHABSIM analysis is a measure of habitat, Weighted Usable Area (WUA). WUA is a measure of the amount of habitat in a stream that is suitable for the target species and life stage and is calculated for a range of simulated discharges in the stream of interest. The resulting WUA versus discharge relation is used to evaluate proposed changes in the flow regime in a stream and to predict the impacts of altered flows on the fish population(s) in the stream. An assumption of the PHABSIM system is that WUA is linearly and positively related to fish standing crop (Bovee 1978; Orth and Maughan 1982; Mathur et al. 1985). Orth and Maughan (1982) and Milhous et al. (1989) reviewed the computational procedures of the PHABSIM modeling procedure and the assumptions associated with a PHABSIM analysis.

The PHABSIM system has been criticized for several reasons including the technical simplicity of the habitat calculations and the complexity and expense of its application. More importantly, it has been critized for the assumption that WUA is positively related to fish abundance (Mathur et al. 1985; Morhardt 1986; Scott and Shirvell 1987; Morhardt and Mesick 1988; Reiser et al. 1989; Armour and Taylor 1991). Numerous studies have attempted to document a relationship between WUA and fish population parameters with limited success (for example: Orth and Maughan 1982; Gowan 1984; Shirvell and Morantz 1983; Conder and

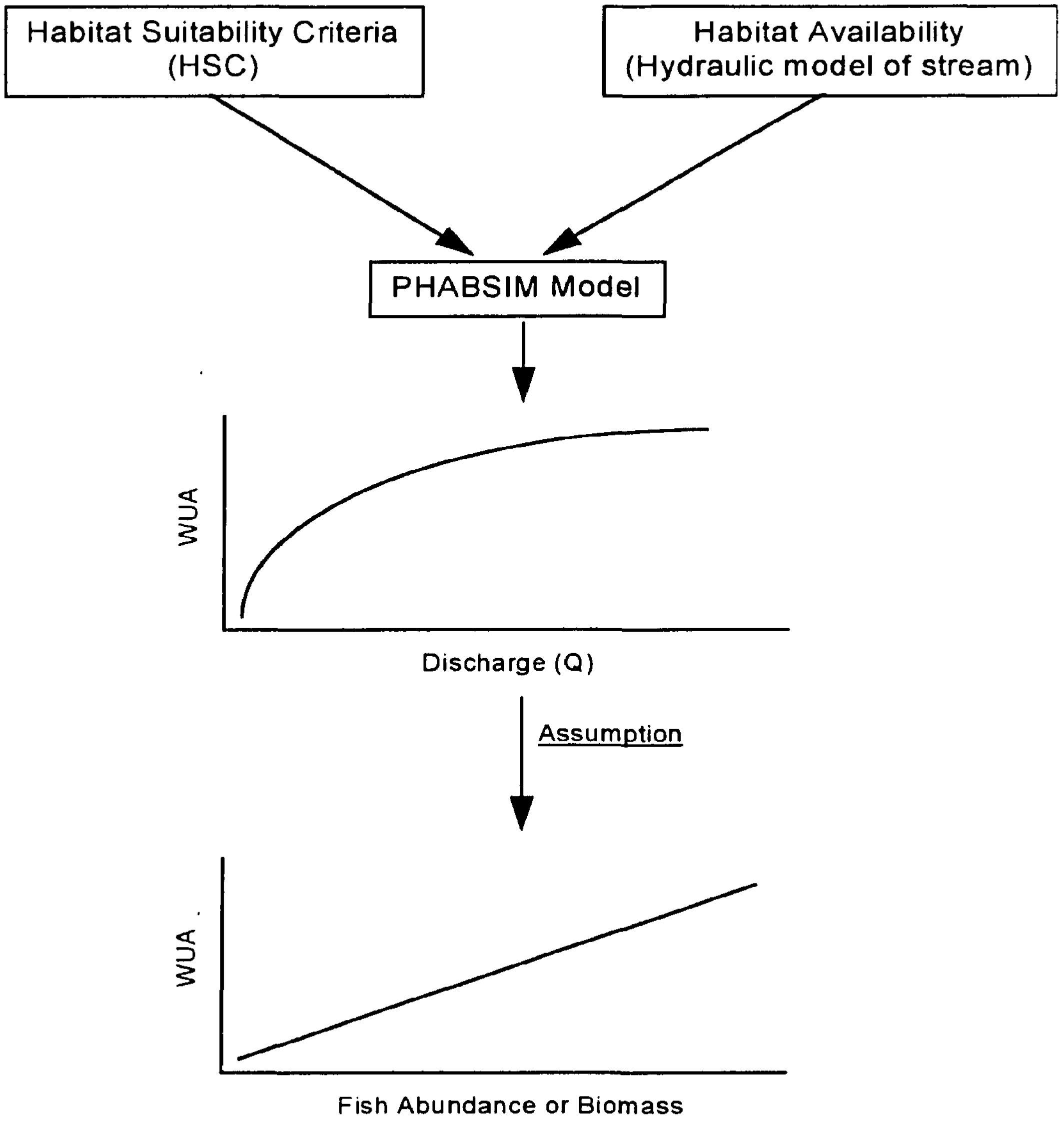

Figure 18. Logical sequence of the PHABSIM model process. Data are entered in the form of habitat suitability criteria and hydraulic status of the stream. The model predicts weighted usable area over a range of discharges. Weighted usable area is assumed to be linearly related to fish abundance or biomass.

Annear 1987; Scott and Shirvell 1987). However, none of these studies used experimental manipulation of streamflow to measure the response of the fish population in a control site or a pretreatment period. The objectives of this study were to: 1) evaluate the impacts of a simulated irrigation withdrawal on the brook trout *Salvelinus fontinalis* population in Hunt Creek; 2) evaluate the PHABSIM system in Hunt Creek by comparing the output of the PHABSIM analysis to the observed response of the brook trout population; 3) evaluate nocturnal resting HSC and bioenergetically derived HSC for foraging microhabitats (bioenergetic-HSC, Chapter 1) to determine if these alter the PHABSIM predictions.

Methods

Beginning on June 1 or 2 and continuing through August 31, 1991-94 I diverted approximately 50% of the summer stream flow around the treatment section of Hunt Creek to simulate the effects of a seasonal water withdrawal for irrigation. During the withdrawal period I monitored the traps on the bulkheads at the upstream and downstream ends of the treatment section (Figure 1, Chapter 1) to determine if the trout moved in response to the dewatering. I did not operate traps during the period of full flow (September 1-May 31) and, brook trout were free to move into and out of the treatment section. In addition to the 50% reduction of summer flow, I reduced flow to 25% of summer baseflow (0.11 $m^3 \cdot s^{-1}$) during a three day period in August, 1993 to collect hydraulic data needed to calibrate the hydraulic modeling component of PHABSIM.

I modeled diurnal and nocturnal habitat of young of the year ($\leq$8.9 cm total length) and yearling and older (>8.9 cm total length) brook trout habitat based on several different sets of habitat suitability criteria (use-HSC, Chapter 1). I used two sets of habitat suitability criteria developed from frequency-of-use data collected in sections B and C of Hunt Creek in 1991-93 over the range of flows from baseflow (0.46 $m^3 \cdot s^{-1}$) to 25% of baseflow (0.11 $m^3 \cdot s^{-1}$). One set was based on observations of habitat use in diurnal conditions (diurnal use-HSC) and the other set was based on observations of habitat use in nocturnal conditions (nocturnal use-HSC). I also modeled diurnal foraging habitat from habitat suitability criteria based on bioenergetic cost and benefit models (bioenergetic-HSC) from data collected in 1993-94 in section B (Chapter 1). Bioenergetic-HSC were size-specific for brook trout and were constructed for fish at 5 cm intervals between 5 and 20 cm total length.

I used a representative reach approach for modeling the habitat in section B of Hunt Creek with PHABSIM. To select representative reaches I first measured and marked section B into approximately 50 m contiguous reaches, omitting the small area of impounded water at the downstream end of the section as well as the short reach of disturbed habitat immediately downstream of the diversion bulkhead (Figure 1, Chapter 1). Two of the 50 m reaches in section B were randomly selected to model by use of PHABSIM (reaches B2 and B4 in Figure 1, Chapter 1). I established transect locations in each of the reaches, and used changes in meso habitat (riffle, run, pool) within the reach to guide transect placement. Substrate and cover along each transect were classified by use of the same codes used for the brook trout habitat use observations (Table 2, Chapter 1). The dominant cover type was recorded for each PHABSIM cell. I collected flow data in the two reaches in section B at three discharges; 0.46, 0.23, and 0.11 $m^3 \cdot s^{-1}$: depths were measured to the nearest cm with a wading rod and velocities to the nearest $cm \cdot s^{-1}$

with either a mechanical Pygmy-Gurley or an electronic March-McBirney current meter. I compared velocity measurements obtained from both meters at the same location in Hunt Creek on several occasions and could not detect any differences between the meters. I calibrated the PHABSIM model and simulated habitat over a range of flows from summer baseflow to 0.01 $m^3 \cdot s^{-1}$ (2% of baseflow) for the reaches in sections B.

Brook trout population abundance data were collected in cooperation with Michigan DNR staff in all four sections of Hunt Creek by conducting mark-recapture electrofishing in April and September of each year of the study and following the same protocol that has been followed for nearly five decades in Hunt Creek (Alexander and Hansen 1986). The entire length of Hunt Creek was sampled from the downstream end of section Z to the upstream end of section C (approximately 6.5 km of stream). Recapture sampling efforts always followed marking within 72 hours. All fish were measured to the nearest 0.25 cm and a subsample of 10 fish per 2.5 cm length interval from each section were weighed to the nearest 0.1 g in spring and fall, 1993 and 1994. I used Bailey's modification (Bailey 1951) of the Petersen method to estimate brook trout population density for 2.5 cm length intervals and used the equations in Ricker (1975) to estimate 95% confidence limits.

I measured brook trout lengths and weights during electrofishing sampling and developed length-weight regressions for each section and season. I tested the length-weight regressions developed from each section, season and year with ANCOVA and determined there were no significant differences between the regressions ($F=0.97$ $df=5,2723$, $p=0.43$). Therefore, the length-weight data were pooled and the regression was recalculated and used to predict brook trout weights for use in biomass calculations. I multiplied the number of fish in each 2.5 cm length interval by the weight of a fish at the midpoint of the interval, obtained from the length-weight regression, and then summed biomass over all length intervals.

I formulated hypotheses concerning the impact of the withdrawal on the brook trout population numbers and total standing crop in section B (treatment section) based on the predicted relationship between WUA and discharge for section B and the assumed positive linear relationship between WUA and fish population standing stock and population density. I tested these hypotheses by use of BACI statistics (Stewart-Oaten et al. 1986, 1992). For the analysis I calculated spring and fall mean population density estimates for sections A and Z combined (control section) and determined differences between these estimates and the density estimates for section B for the ten year period preceding the treatment and the four years of treatment. I repeated the analysis for the total biomass data for the same period. I used the Student's t-test to compare pretreatment period mean difference with the treatment period mean difference.

I did not include the upstream nontreatment section C in the statistical analysis because the brook trout population in section C was influenced by environmental factors that did not impact the population in sections A, B, and Z.

Results

Summer baseflow in section C at the confluence with Fuller Creek (Figure 1, Chapter 1) was approximately 0.23 $m^3 \cdot s^{-1}$. Fuller Creek delivered an additional 0.23 $m^3 \cdot s^{-1}$ to produce a summer baseflow of 0.46 $m^3 \cdot s^{-1}$ through the treatment section (B). A small tributary enters Hunt

Creek just downstream of the treatment section and delivers approximately 0.11 m^3/s, increasing discharge in Hunt Creek to approximately 0.57 m^3/s. Hunt Creek continues to gain flow as it flows downstream and out of the research area.

Characteristics of Study Reaches

Reaches B2 and B4 were 47.1 and 55.2 m long respectively. I established 19 transects and measured habitat availability at 385 locations (cells) in reach B2. I established 21 transects and measured habitat availability at 530 locations (cells) in reach B4. Mean distance between transects was 2.5 m in reach B2 and 2.6 m in reach B4, and the maximum distance between any two transects was 6.6 m in reach B2 and 5.2 m in reach B4.

Several important differences existed between the two reaches used in habitat modeling, and these affected the output of the PHABSIM analysis. First, the mean water surface slope at baseflow (0.46 $m^3 \cdot s^{-1}$) in reach B2 (4.2 $m \cdot km^{-1}$) was nearly twice the slope (2.2 $m \cdot km^{-1}$) in reach B4. As a result, the mean water velocities were greater in reach B2: at baseflow the mean of all mean column velocity measurements was 34 $cm \cdot s^{-1}$ in reach B2 and 28 $cm \cdot s^{-1}$ in reach B4. Differences in velocity distributions between modeled reaches were significant (Mann-Whitney U test, $p=0.002$). A second difference between the modeled reaches was that the mean channel width in reach B2 (4.15 m) was less than in B4 (5.00 m).

The substrate and cover composition in the two modeled reaches was similar. In both reaches the substrate was composed primarily of gravels less than 2.5 cm diameter. Sand and silt were also common in both reaches. Substrate composition in the reaches differed significantly (X^2=64.1, df=9, p<0.001), primarily due to the presence of more cells in reach B2 with large gravel than in B4 and a greater number of cells in reach B4 with the substrate embedded more than 25%.

The majority of the cells (>93%) in both reaches had instream cover present, either in the form of a velocity shelter or a combination cover type. Availability of cover composition did not differ between the reaches (X^2=1.13, df=2, p<0.01).

Habitat Suitability Criteria

The HSC developed from frequency-of-use data and from bioenergetic models are fully presented in Chapter 1 and are only summarized here (Table 3). The diurnal use-HSC represent the suitability of foraging microhabitats for brook trout in Hunt Creek because only data from actively foraging fish were used (87% of all diurnal observations) in the construction of diurnal use-HSC. In contrast, nocturnal use-HSC were based on observations of inactive fish (93% of all nocturnal observations) and represented the suitability of resting microhabitats (Table 3). All of the inactive brook trout observed at night were in direct contact with the substrate, and some were burrowed into vegetation (primarily watercress, *Nasturtium officinale*) or wedged between sticks.

PHABSIM Model Results

The relation between surface area and discharge for the two modeled reaches in section B indicated that a 50% reduction in summer stream flow in the treatment section resulted in a very minor loss of stream surface area (Figure 19). In reach B2, total surface area was reduced from 206 to 195 $m^2 \cdot 100\ m^{-1}$, a reduction of 5.6%. In reach B4, total surface area decreased 292 to 275 $m^2 \cdot 100\ m^{-1}$, a reduction of 5.7%.

Table 3. Optimal and suitable habitat suitability criteria values for diurnal and nocturnal periods. Data for all HSC are from Chapter 1. Bioenergetic-HSC were size specific and are presented here only for 7.5 and 15 cm fish (sizes equivalent to young of the year and yearling and older fish respectively).

		Depth (cm)	**Mean Column Velocity ($cm \cdot s^{-1}$)**	**Substrate**	**Cover**
Diurnal Use-HSC					
young of the year	Optimal Range	15-34	6-30	1-5.4	3
	Suitable Range	3-67	0-66	1-5.4	2 & 3
yearling and older	Optimal Range	27-55	6-27	1-5.4	3
	Suitable Range	12-85	0-98	1-5.4	2 & 3
Diurnal Bioenergetic-HSC					
7.5 cm	Optimal Value	Varies	28	1-5.4	3
	Suitable Range	>1.7	1-46	1-5.4	2 & 3
15 cm	Optimal Value	Varies	41	1-5.4	3
	Suitable Range	>3.3	3-63	1-5.4	2 & 3
Nocturnal Use-HSC					
young of the year	Optimal Range	12-29	5-23	1-5.4	3
	Suitable Range	1-73	0-39	1-5.4	2 & 3
yearling and older	Optimal Range	20-46	4-22	1-5.4	3
	Suitable Range	7-73	0-52	1-5.4	2 & 3

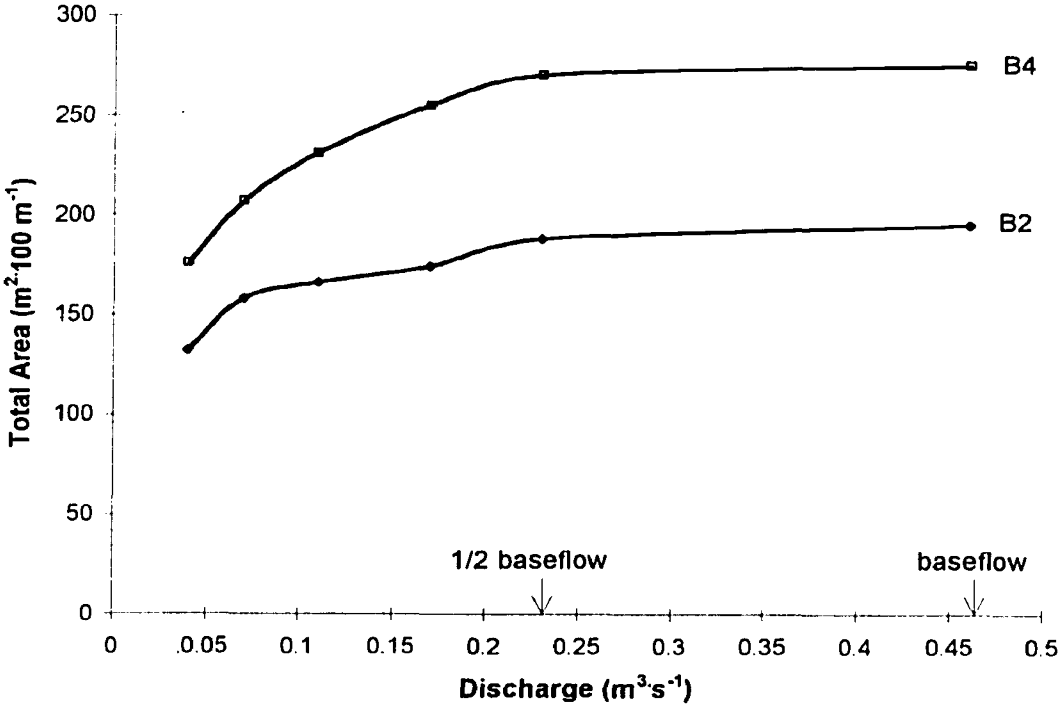

Figure 19. Total area ($m^2 \cdot 100\ m^{-1}$) in relation to discharge ($m^3 \cdot s^{-1}$) for reaches B2 (solid diamonds) and B4 (open squares) in Hunt Creek.

Model results also predicted that reducing flow in section B by 98% to a discharge of 0.01 $m^3 \cdot s^{-1}$ would decrease total surface area to 132 $m^2 \cdot 100\ m^{-1}$ in reach B2 (35.9% loss) and 176 $m^2 \cdot 100\ m^{-1}$ in reach B4 (39.7% loss). The difference in the total surface area estimates between the two modeled reaches is due to the greater width and lower slope in reach B4.

The 50% reduction of summer stream flow actually resulted in an increase in WUA for young of the year fish based on diurnal use-HSC in reaches B2 and B4 (Figures 20 and 21). Suitable habitat area increased 27% in reach B2 and 16% in reach B4 with a 50% reduction of summer flow. The maximum WUA value over the range of discharges modeled occurred at a discharge of 0.17 $m^3 \cdot s^{-1}$ (37% of baseflow) in both modeled reaches. In reach B2 maximum WUA was 160 $m^2 \cdot 100\ m^{-1}$ and in reach B4 it was 217 $m^2 \cdot 100\ m^{-1}$. The PHABSIM model also predicted that if discharge in section B of Hunt Creek was reduced to 0.01 $m^3 \cdot s^{-1}$ young of the year WUA would only be reduced to 76 $m^2 \cdot 100\ m^{-1}$ in reach B2 and 82 $m^2 \cdot 100\ m^{-1}$ in reach B4. This represents a reduction in young of the year WUA of 37% and 56% in reaches B2 and B4 respectively, with a 98% reduction of summer baseflow.

In contrast to the young of the year WUA estimates, yearling and older diurnal WUA in the two modeled reaches was slightly reduced with a 50% reduction in baseflow (Figures 20 and 21). The yearling and older diurnal WUA in reach B2 decreased from 134 to 132 $m^2 \cdot 100\ m^{-1}$, a loss of 1.5% of suitable habitat area. Yearling and older WUA in reach B4 decreased from 162 to 159 $m^2 \cdot 100\ m^{-1}$, a reduction of 1.9%. The model also predicted that a 98% reduction in summer stream flow would reduce yearling and older WUA by 65% in reach B2 and 70% in B4.

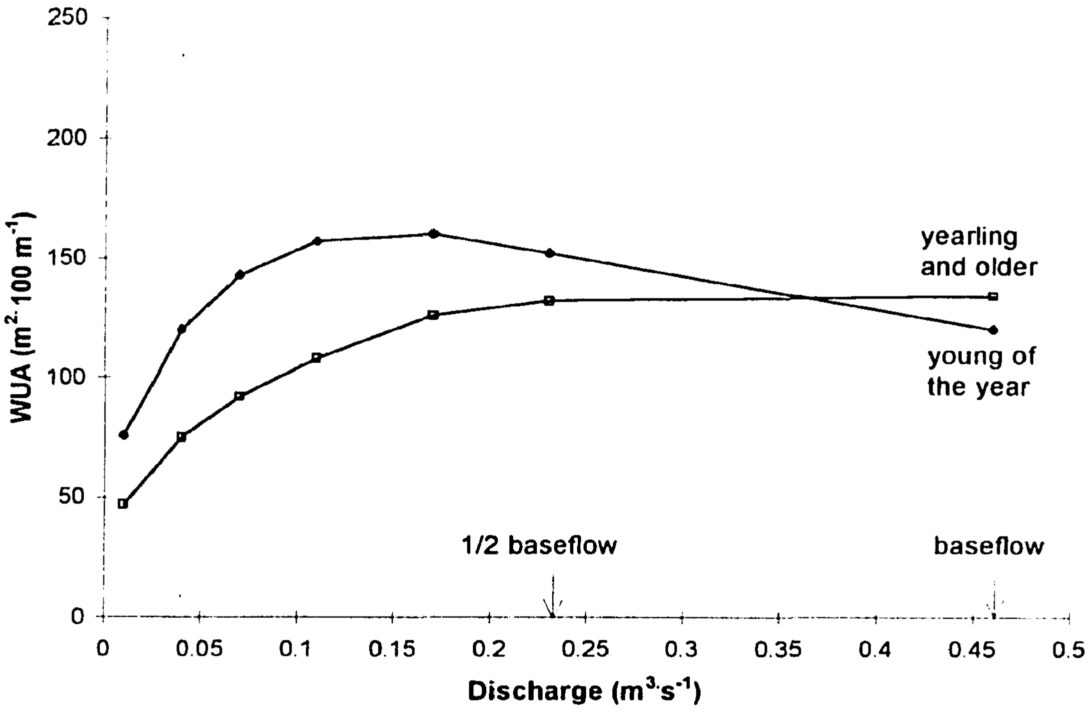

Figure 20. Diurnal WUA ($m^2 \cdot 100\ m^{-1}$) estimates derived from diurnal use-HSC as a function of discharge ($m^3 \cdot s^{-1}$) for young of the year (solid diamonds) and yearling and older brook trout (open squares) in reach B2 of Hunt Creek.

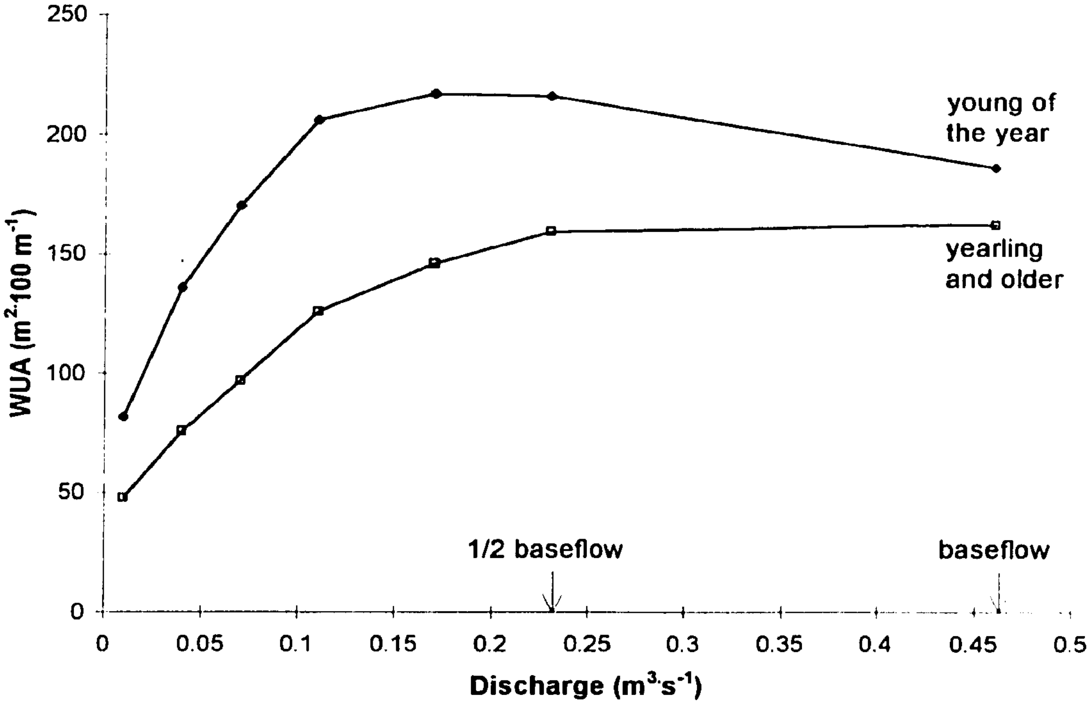

Figure 21. Diurnal WUA ($m^2 \cdot 100\ m^{-1}$ of stream) estimates derived from diurnal use-HSC as a function of discharge ($m^3 \cdot s^{-1}$) for young of the year (solid diamonds) and yearling and older brook trout (open squares) in reach B4 of Hunt Creek.

Diurnal WUA estimates based on bioenergetic-HSC for brook trout 5 and 7.5 cm total length (length range equivalent to young of the year fish) also increased with the 50% reduction in summer stream flow (Figures 22 and 23). In reach B2 WUA estimates increased approximately 24% and 21% for 5 and 7.5 cm fish, respectively. The magnitude of the increase was slightly lower than the 27% increase in WUA predicted for young of the year fish from the diurnal use-HSC. In reach B4, WUA increased approximately 31% and 17% for 5 and 7.5 cm fish, respectively. This increase in WUA estimates was slightly higher than the 16% increase WUA for young of the year fish in reach B4 from diurnal use-HSC.

The maximum WUA estimates for 5 and 7.5 cm fish in reach B2 occurred at Q=0.11 $m^3 \cdot s^{-1}$ and Q=0.17 $m^3 \cdot s^{-1}$ respectively. This is similar to the predicted discharge of 0.17 $m^3 \cdot s^{-1}$ that yielded maximum WUA for all young of the year fish from the diurnal use-HSC. The maximum WUA values for 5 and 7.5 cm fish in reach B4 occurred at Q=0.17 $m^3 \cdot s^{-1}$ and Q=0.23 $m^3 \cdot s^{-1}$ respectively. This is also similar to the results for reach B4 from the diurnal use-HSC which indicated maximum WUA occurred at Q=0.17 $m^3 \cdot s^{-1}$ for all young of the year fish. Finally, the model predicted a 98% reduction in flow (Q=0.01 $m^3 \cdot s^{-1}$) would reduce WUA in reach B2 for 5 and 7.5 cm fish approximately 75% and 86%, respectively and 82% and 91%, respectively in reach B4. The magnitude of the WUA reduction based on the bioenergetic-HSC is nearly twice that predicted on the basis of diurnal use-HSC.

For yearling and older brook trout, the PHABSIM model predicted WUA would increase with the 50% reduction in flow for fish 10 cm to 15 cm total length in reach B2, but would decrease for larger fish in B2 and all fish 10 cm or larger in B4. WUA increased 16% for 10 cm fish,

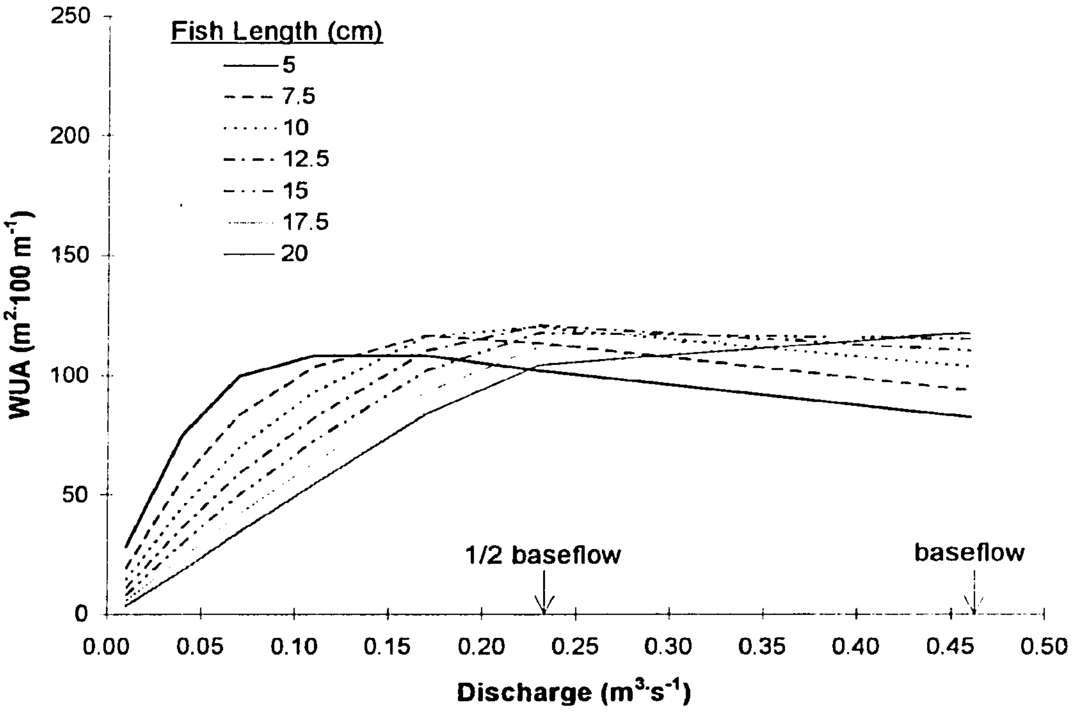

Figure 22. Diurnal WUA ($m^2 \cdot 100\ m^{-1}$ of stream) estimates derived from bioenergetic-HSC as a function of discharge ($m^3 \cdot s^{-1}$) for brook trout in reach B2 of Hunt Creek.

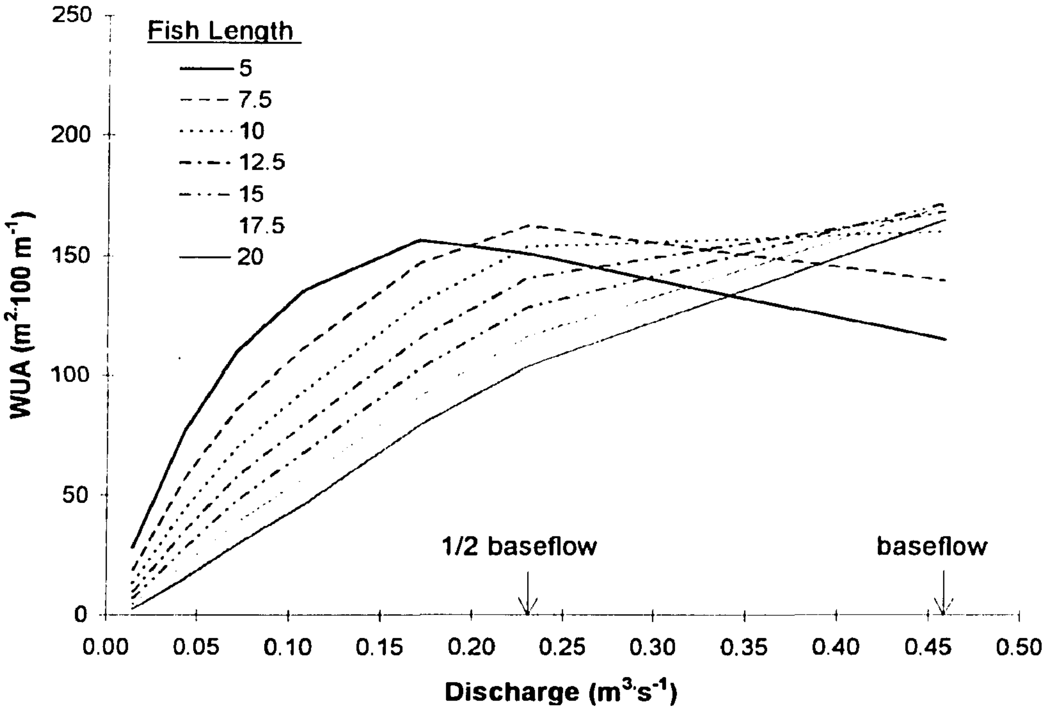

Figure 23. Diurnal WUA ($m^2 \cdot 100\ m^{-1}$ of stream) estimates derived from bioenergetic-HSC as a function of discharge ($m^3 \cdot s^{-1}$) for brook trout in reach B4 of Hunt Creek.

10% for 12.5 cm fish and 2% for 15 cm fish (Figure 22). In reach B2, WUA decreased 5% and 11% for 17.5 and 20 cm fish, respectively. The reduction in WUA for fish in reach B4 was greater than in reach B2 (Figure 23), and ranged from 4% to 37% for fish 10 cm to 20 cm, respectively. Reductions in WUA were greatest for the largest fish in both reaches (Figures 22 and 23). The model predicted that WUA for fish between 10 and 20 cm total length would be reduced between 75% and 98% in reach B2 and from 82% to 99% in reach B4 if summer stream flow was reduced 98% to 0.01 $m^3 \cdot s^{-1}$.

The PHABSIM model results for nocturnal habitat were similar to the results from diurnal use-HSC. Nocturnal WUA increased with the 50% reduction in stream flow for both young of the year and yearling and older brook trout in section B (Figure 24). WUA for young of the year fish increased 18% in reach B2 and 29% in reach B4. At 98% reduction in flow, the model predicted greater WUA than at baseflow in reach B2 and a 16% reduction in reach B4.

The 50% reduction in flow increased nocturnal WUA for yearling and older brook trout 9% in reach B2 and 15% in reach B4. In contrast to the results for young of the year nocturnal habitat, the model predicted that a 98% reduction in flow would result in substantial reductions (42% and 56% in B2 and B4, respectively) in yearling and older nocturnal WUA.

PHABSIM Predictions

The analysis of the PHABSIM model output yielded two different sets of hypotheses concerning the impact of the 50% flow reduction on the brook trout population. The first hypothesis is that standing stock and density would not change in rsponse to the withdrawal for young of the year or yearling and older brook trout. This conclusion stems from

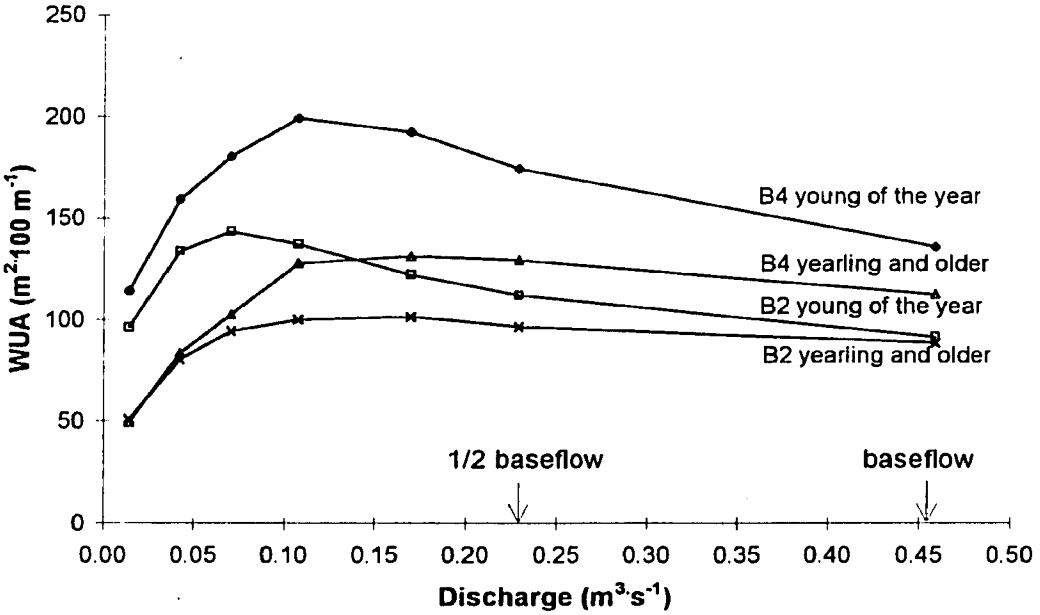

Figure 24. Nocturnal WUA ($m^2 \cdot 100\ m^{-1}$) as a function of discharge ($m^3 \cdot s^{-1}$) estimates for young of the year and yearling and older brook trout in reaches B2 and B4 of Hunt Creek.

the model predictions based on use-HSC that diurnal and nocturnal WUA increased substantially in both modeled reaches for young of the year fish, diurnal WUA decreased only slightly for yearling and older fish and nocturnal WUA increased for yearling and older fish when summer flow was reduced 50% (Figures 20, 21, and 24). The second hypothesis is based on the PHABSIM predictions generated with the bioenergetic-HSC. The WUA data from reaches B2 and B4 predict no change in standing stock or density of young of the year fish in section B2 (Figures 22 and 23). However, the WUA data predicted that density or standing stock of yearling and older fish in section B would be reduced, particularly for fish 20 cm or larger. The expected reduction in density was as much as 16-37%, depending on fish size (Figure 23). The expected reduction in brook trout abundance was based on an assumed one to one relationship between WUA and fish standing stock (Bovee 1978).

The summer withdrawal had no effect on brook trout density or biomass. The pretreatment period mean difference in density between the control and treatment sections was not significantly different from the treatment period mean difference for young of the year (Figure 25, Student's t=0.43, p=0.65, df=12) or yearling and older fish (Figure 26, Student's t=1.21, p=0.28, df=12). The pretreatment period mean difference in total standing crop was also not significantly different from the treatment period mean difference (Student's t, p=0.97, df=12).

I tested the predictions of the PHABSIM model generated from the bioenergetic-HSC using BACI statistics. I calculated the densities of brook trout in the control and treatment sections of Hunt Creek for 2.5 cm length intervals from 5 to 20 cm (e.g. 5-7.49 cm) and then tested for impacts on each of these length classes of fish. I found a significant

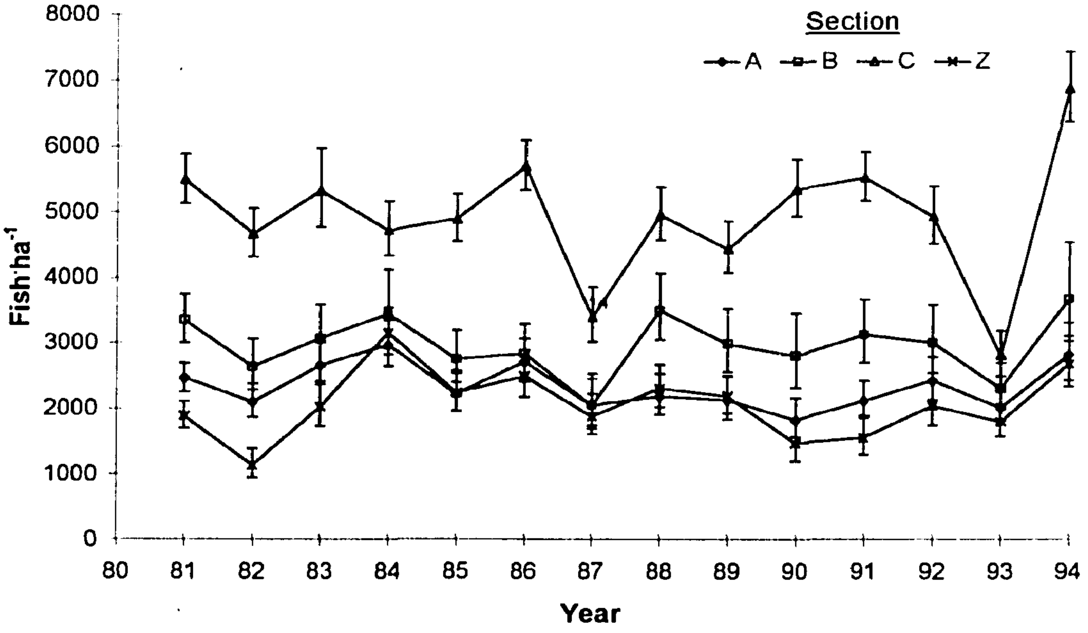

Figure 25. Fall young of the year brook trout population density (fish·ha^{-1}) estimates for sections A, B, C, and Z of Hunt Creek for 1981-1994. The withdrawal period was from 1991-94. Error bars represent 95% confidence limits of the mean.

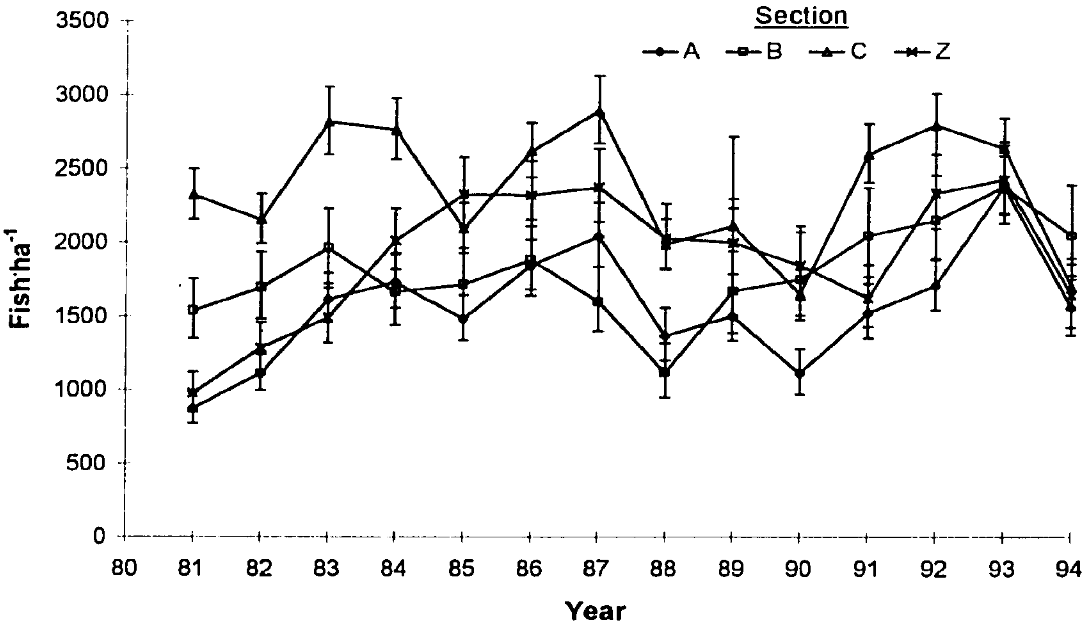

Figure 26. Fall yearling and older brook trout population density (fish·ha^{-1}) estimates for sections A, B, C, and Z of Hunt Creek for 1981-1994. The withdrawal period was from 1991-94. Error bars represent 95% confidence limits of the mean.

difference between the pretreatment and treatment period differences in densities only for the fish in the 10-12.5 cm length interval (Figure 27, Student's t=4.01, p=0.002, df=12). However, the change in this size group was opposite the predicted change: from 1981-1988, density of 10-12.5 cm brook trout decreased, and from 1989-1993 it increased (Figure 27). For all other length groups of fish there was no measurable impact from the withdrawal (p values between 0.09 and 0.78).

Because I was interested in the magnitude of the change in fish density that would be needed to detect a difference I calculated the minimum detectable difference and statistical power (Zar 1984) for the BACI analysis. A minimum difference of approximately 823.1 and 842.3 $\text{fish}\cdot\text{ha}^{-1}$ would be necessary between the pretreatment and treatment mean differences to conclude that there was an impact on young of the year and yearling and older fish, respectively. Also, power estimates for the BACI analysis were all less than 0.20, indicating that if there was an impact of the experimental treatment, the chances of detecting it were 20% or less at $\alpha=0.05$.

I also used the minimum detectable difference estimates to predict the reduction in discharge necessary to produce a measurable impact on the fish population. For this calculation I subtracted the minimum detectable difference estimate from the mean density of fish in the control section (sections A and Z combined) over the pretreatment period to estimate the mean density of fish in the treatment section that would produce a statistically detectable result. I then calculated the proportional change in density that this represents, relative to the pretreatment density and multiplied the WUA at base flow by this proportion to determine the change in WUA needed to obtain a detectable

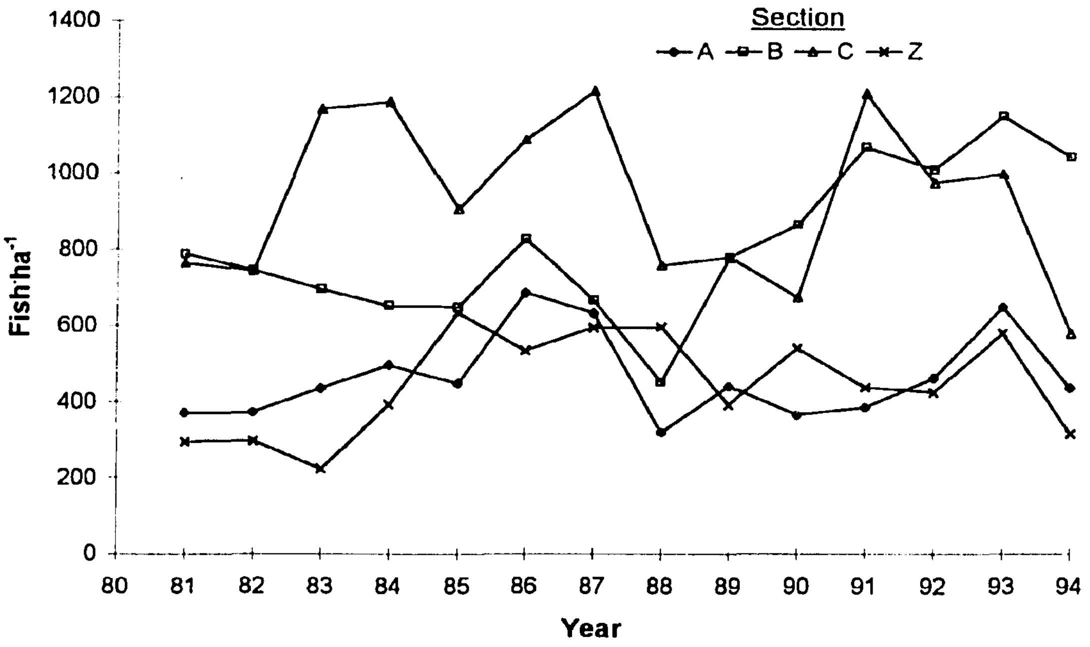

Figure 27. Fall brook trout population density (fish·ha^{-1}) estimates for fish 10-12.5 cm total length in sections A, B, C, and Z of Hunt Creek for 1981-1994. The withdrawal period was from 1991-94.

change in density. From this, I estimated the discharge reduction that would produce this reduced WUA.

The reduction in WUA that would be needed to produce a statistically detectable impact on both young of the year and yearling and older brook trout densities in section B was approximately 50% of the WUA available at baseflow (Table 4). The discharge values that would produce a statistically detectable result differed depending on the type of HSC used to calculate WUA. The WUA curves calculated from diurnal use-HSC indicated that flow would need to be reduced to 0.02 $m^3 \cdot s^{-1}$ (reach B2) and 0.01 $m^3 \cdot s^{-1}$ (reach B2) to reduce young of the year densities 50% and to 0.03 $m^3 \cdot s^{-1}$ (reach B2) and 0.05 $m^3 \cdot s^{-1}$ (reach B4) to reduce yearling and older densities 50% (Table 4). This represents a reduction in flow of at least 88% to reduce fish densities a detectable amount. The discharge needed to produce a measurable impact on fish densities based on the WUA curves calculated from bioenergetic-HSC was between 0.02 and 0.06 $m^3 \cdot s^{-1}$ for fish equal to young of the year size and between 0.05 and 0.16 $m^3 \cdot s^{-1}$ for fish equal to yearling and older size (Table 4). Because the nocturnal WUA estimates at a 98% reduction in flow were only slightly lower than those at baseflow, it was impossible to evaluate a discharge which would produce a measurable decrease in population standing crop from nocturnal WUA.

Fish Movement

Brook trout moved downstream and out of the treatment section throughout summer, 1990, a pretreatment year (Table 5). Fish movement was relatively steady throughout the summer because the number of brook trout caught on any date never exceeded four. Trap data for the treatment period (1991-94) were inconsistent between years and even

Table 4. Estimated discharges (Q, $m^3 s^{-1}$) for reaches B2 and B4 and corresponding WUA (m^2 100 m^{-1}) estimates that would produce a statistically detectable reduction in brook trout density or biomass in section B.

		Use-HSC		Bioenergetic-HSC	
		Q	WUA	Q	WUA
Reach	**Fish Size**	**($m^3 s^{-1}$)**	**(m^2 100 m^{-1})**	**($m^3 s^{-1}$)**	**(m^2 100 m^{-1})**
B2	young of the year	<0.01	76		
	5 cm			0.02	43
	7.5 cm			0.04	56
	yearling and older	0.03	66		
	10 cm			0.05	53
	12.5 cm			0.07	58
	15 cm			0.08	55
	17.5 cm			0.10	68
	20 cm			0.12	59
B4	young of the year	0.02	100		
	5 cm			0.03	60
	7.5 cm			0.06	76
	yearling and older	0.05	83		
	10 cm			0.09	81
	12.5 cm			0.12	82
	15 cm			0.14	85
	17.5 cm			0.16	85
	20 cm			0.18	83

Table 5. Size and number of brook trout caught in inclined screen traps during the treatment period (1991-94) and for the summer prior to withdrawal from traps at the upstream and downstream bulkheads.

	Upstream Bulkhead		Downstream Bulkhead	
Year	**mean length (cm)**	**n**	**mean length (cm)**	**n**
1990	not recorded		10.9	69
1991	10.2	39	10.3	43
1992	11.3	30	9.0	53
1993	12.6	199	12.6	132
1994	8.5	183	8.3	50

between the upstream and downstream traps. However, brook trout in section B did not respond to the withdrawal consistently by moving downstream (Table 5). The rate of fish movement into section B was similar to the rate of movement out of the section in 1991-93, and movement into section B exceeded the rate of movement out in 1994 by a factor of four. However, the number of trout that moved into and out of the treatment section during any one summer was small in comparison to the total number of trout in the treatment section (mean=1269 fish in fall, 1991-94). The mean length of fish captured in traps was also similar among years and between the upstream and downstream traps.

Discussion

The brook trout population in Hunt Creek was not affected by the 50% reduction in summer stream flow and the habitat analysis predicted no effects. Hunt Creek is a groundwater fed stream with stable discharge and high quality physical and biotic habitat under summer baseflow conditions. Given the high quality of the habitat under summer baseflow conditions it is not surprising that habitat was not severely impacted by a 50% reduction in baseflow. The results of the PHABSIM modeling support this conclusion because the diurnal WUA estimates for young of the year fish were substantially higher at reduced flow and WUA was only slightly reduced for yearling and older fish. These results were similar whether use-HSC or bioenergetic-HSC were used to estimate WUA. Furthermore, nocturnal WUA increased for young of the year and yearling and older fish as a result of the reduced flow.

Because the PHABSIM model only varied the depths and velocities with changes in discharge, these two parameters determined the shape of the WUA-discharge relation. Therefore, the increased WUA estimates at half of the mean summer stream flow were due to either more locations with improved depth suitability, improved velocity suitability, or both. The change in the velocity availability was likely the primary cause of the increased WUA estimates. This conclusion is based on the observation that the optimal mean column velocities from the use-HSC were less than the mean of the mean column velocity measurements at summer baseflow in section B of Hunt Creek for young of the year and yearling and older fish. Therefore, as discharge decreased, locations with greater than optimal mean column velocity at summer baseflow became more suitable because mean column velocity decreased as discharge decreased. It is also likely that depth suitability in parts of the modeled reaches decreased as discharge decreased.

The results from this study are very similar to those from a study by Kraft (1972), who evaluated the impact of a seasonal withdrawal on the brook trout habitat and population in a Montana stream. He dewatered a section of stream by up to 90% during the summer months and monitored brook trout population density. Brook trout moved from shallow runs to pools as flow was reduced but the number of trout did not change significantly (Kraft 1972). Brook trout did move out of the dewatered section of the Montana stream, but not until the reduction in flow was equal to 90% of mean flow. Also, when fish moved out of the test section it was in an upstream direction (Kraft 1972). Clothier (1954) reported similar upstream movement of brook trout, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss* during extreme irrigation withdrawals in the Gallatin River, Montana. Upstream movement was not possible for the brook trout in the treatment section of Hunt Creek, and downstream movement from the treatment section generally matched movement rates from the upstream control section. The large number of brook trout caught in the traps in 1993 may have been a result of the unusually wet summer. Several heavy rains fell during the summer and each was followed by large numbers of fish caught in the traps. For example, during the three day period of 7 to 9 June, 82 fish were captured in the traps at the upstream and downstream bulkheads (41 fish at each bulkhead). These three days corresponded to a period of heavy rainfall which ultimately caused the failure of a beaver dam just upstream of section C.

Although physical habitat is important in determining fish abundance and distribution in a variety of habitats, other biotic and abiotic factors can influence fish abundance and distribution in streams (Latta 1965; Chapman 1966; Sheldon 1968; Gorman and Karr 1978; Finger 1982; Bowlby and Roff 1986). Other factors which could change under reduced flow conditions are predation risk, disease transmission rates, water temperature, competitive interactions, and food availability (Orth 1987). The magnitude of the changes in any of these parameters is almost certainly dependent on the magnitude of the reduction in flow.

It does not appear that risk of predation was increased by the reduction in summer stream flow in Hunt Creek because fish density in the treatment section did not decrease. Also, although I did not measure disease occurrence during this study, I did not notice any obvious differences in the occurrence of diseased fish between sections during the spring and fall electrofishing sampling. Water temperature also did not appear to increase in the treatment section of Hunt Creek due to the reduced flow. Temperature recorders installed at the upstream and downstream ends of the treatment section recorded mean daily maximum temperatures for June 1-August 31 in 1993 that were 0.3° C higher at the downstream end of section B and in 1994 were 0.4° C lower at the downstream end (Michigan DNR unpublished data). These differences could be due to differences in calibration of the recording devices or may be real differences. In either case, there is no evidence for an increase in temperature as a result of the reduced flow. Finally, brook trout food was not reduced as a result of the reduced flow because neither benthic invertebrate density or habitat were impacted by the reduction in flow (Chapter 3).

Factors other than mean summer stream flow may serve to determine the density of the brook trout population in Hunt Creek. A large reduction in fall young of the year brook trout density in the upstream section C of Hunt Creek in 1993 was not evident in the other sections of Hunt Creek (Figure 25). This reduction in fall young of the year density of brook trout may have been due to the intense rain which caused the failure of a beaver dam just upstream of section C in June, 1993. I was unable to measure stream gage or discharge during the spate, however, the flow was over bank full in section C. This occurred during the first week of June when the young of the year brook trout were approximately 2-3 cm total length. This flood event may have caused high mortality or emigration of young of the year fish in section C, but not in section B, because half of the flood flow was diverted through the diversion channel. This high mortality or emigration of young of the year in 1993 also apparently caused the reduction in yearling and older density in fall 1994 (Figure 26).

The alternate HSC showed that an investigator's *a priori* choice of HSC used in modeling habitat can affect the output of a PHABSIM analysis. However, the question still remains as to which type(s) of HSC provide the best prediction of the impacts of a change in flow regime in a PHABSIM analysis. The magnitude of the withdrawal in this study was insufficient to produce an impact on the brook trout. However, the fact that the shape and magnitude of the WUA-discharge curves differ indicate that the analysis based on bioenergetic-HSC may provide a different prediction of impacts. The magnitude of the decrease in diurnal WUA predicted at a reduced flow equal to 2% of baseflow was only 37-70% when diurnal use-HSC were used in the calculation of WUA but was 75-91% when bioenergetic-HSC were used to calculate WUA. It is more likely that a 98% reduction in discharge would reduce the suitable drift foraging habitat area approximately the same amount. Therefore, the bioenergetic-HSC may be more accurate predictors of the changes in foraging microhabitat availability in Hunt Creek than diurnal use-HSC.

The differences in the magnitude of WUA between the two methods is likely a result of the more conservative estimates of optimal velocities based on bioenergetic modeling and the interdependence of the suitability of depth to velocity. However, the magnitude of WUA is less important than the shape of a WUA-discharge curve in attempting to assess the impacts of a proposed withdrawal on the fish population in a stream (Bovee 1978). In that respect, both types of HSC were accurate predictors of the lack of impact from the reduction of summer stream flow in Hunt Creek. However, this is not an adequate test of the PHABSIM modeling procedure. Rather, WUA curves developed from this study could be used to establish a withdrawal level expected to produce an impact on the brook trout population in Hunt Creek and the study continued for four more years. Only then can the predictions of the PHABSIM model be tested sufficiently.

It is important to stress that the results of this study are unique to Hunt Creek and are not necessarily applicable to other streams in Michigan or the Midwest. The fact that the 50% reduction in summer streamflow did not reduce fish densities in Hunt Creek is probably because Hunt Creek is a very stable stream with high quality brook trout habitat under baseflow conditions. If Hunt Creek was a marginal trout stream the 50% reduction in summer baseflow may have resulted in a reduction in WUA and fish densities. For example, in an evaluation of impacts of irrigation withdrawals on the brown trout population in a marginal trout stream in southern Michigan, the PHABSIM model indicated that a 50% reduction of summer baseflow would reduce brown trout WUA approximately 40% (estimated from figures in Gowan 1984). It is also likely that a 50% reduction of summer stream flow in Hunt Creek would have an adverse impact on the trout in Hunt Creek if the population in Hunt Creek was brown trout or rainbow trout instead on brook trout. I modeled the habitat in section B of Hunt Creek with HSC for brown trout (Gowan 1984; Raleigh et al. 1986) and rainbow trout (Raleigh et al. 1984). The WUA-discharge curves indicated that if brown trout was the only salmonid present in Hunt Creek, a 50% reduction in summer flow would reduce adult habitat approximately 8% and would reduce juvenile habitat 12-16%. If rainbow trout were the only salmonid species in Hunt Creek, juvenile habitat would be increased approximately 4% and adult habitat would be reduced 14-23% with a 50% reduction in summer flow (Appendix A).

Although this study could not evaluate the effectiveness of the bioenergetic-HSC relative to the use-HSC used to calculate WUA estimates for foraging microhabitats, bioenergetic-HSC offer several potential advantages. First, bioenergetic-HSC could be used to construct a spatial model of foraging habitats in the stream of interest, which could be used to predict the locations of suitable foraging microhabitats. This information in conjunction with territory size predictions (Grant and Kramer 1990) could be used to predict the actual number of fish in a reach of stream and how that number may change with reduced streamflow. Also, the use of bioenergetic-HSC with a spatial model of stream habitat could also be used to predict fish growth rates (Nielsen 1992) as well as to predict expected changes in growth rates in relation to changes in flow. Information on the expected changes in abundance and growth rates of stream fish in relation to flow could therefore be used to predict changes in biomass as well.

Literature Cited

Alexander, G. R. and E. A. Hansen. 1986. Sand bed load in a brook trout stream. North American Journal of Fisheries Management 6:9-23.

Armour, C. L. and J. G. Taylor. 1991. Evaluation of the Instream Flow Incremental Methodology by U.S. Fish and Wildlife Service field users. Fisheries 16(5):36-43.

Bailey, N. J. J. 1951. On estimating the size of mobile populations from recapture data. Biometrika 38:293-306.

Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Streamflow regulation and fish community structure. Ecology 69(2):382-392.

Bovee, K. D. 1978. The incremental method of assessing habitat potential for coolwater species, with management implications. Transactions of the American Fisheries Society Special Publication 11:340-346.

Bovee, K. D., T. J. Newcomb, and T. G. Coon. 1994. Relations between habitat variability and population dynamics of bass in the Huron River, Michigan. National Biological Survey Biological Report 1994(21). 63 pp.

Bowlby, J. N., and J. C. Roff. 1986. Trout biomass and habitat relationships in southern Ontario streams. Transactions of the American Fisheries Society 115(4):503-514.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. The American Naturalist 100(913):345-357.

Clothier, W. D. 1954. Effect of water reductions on fish movement in irrigation diversions. Journal of Wildlife Management 18:150-160.

Conder, A. L. and T. C. Annear. 1987. Test of weighted usable area estimates derived from a PHABSIM model for instream flow studies on trout streams. North American Journal of Fisheries Management 7:339-350.

Finger, T. R. 1982. Fish community relations in a small central New York stream. Journal of Freshwater Ecology 1(4):343-352.

Gorman, O. T., and J. R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59(3):507-515.

Gowan, C. 1984. The impacts of irrigation water withdrawals on brown trout (*Salmo trutta*) and two species of benthic macroinvertebrates in a typical southern Michigan stream. M. S. thesis, Michigan State University, East Lansing. 127 pp.

Grant, J. W. A., and D. L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Science 47:1724-1737.

Kraft, M. E. 1972. Effects of controlled flow reduction on a trout stream. Journal of the Fisheries Research Board of Canada 29:14055-1411.

Latta, W. C. 1965. Relationship of young-of-the-year trout to mature trout and groundwater. Transactions of the American Fisheries Society 94:32-39.

Mathur, D., W. H. Bason, E. J. Purdy, Jr., and C. A. Silver. 1985. A Critique of the Instream Flow Incremental Methodology. Canadian Journal of Fisheries and Aquatic Science 42:825-831.

Milhous, R. T., M. A. Updike, and D. M. Schneider. 1989. Physical Habitat Simulation System Reference Manual-Version II. Instream Flow Information Paper No. 26. U.S. Fish and Wildlife Service Report 89(16).

Morhardt, J. E. 1986. Instream flow methodologies. Research Project 2194-2. Prepared for the Electric Power Research Institute by EA Engineering, Science and Technology, Inc., Lafayette, CA.

Morhardt, J. E. and C. F. Mesick. 1988. Behavioral carrying capacity as a possible short term response variable. Hydro Review 7(2):32-40.

Nielsen, J. L. 1992. Microhabitat specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121:617-634.

Orth, D. J. 1987. Ecological considerations in the development and application of instream flow-habitat models. Regulated Rivers: Research and Management 1:171-181.

Orth, D. J., and O. E. Maughan. 1982. Evaluation of the Incremental Methodology for recommending instream flows for fishes. Transactions of the American Fisheries Society 111:413-445.

Raleigh, R. F., T. Hickman, R. C. Solomon, and P. C. Nelson. 1984. Habitat suitability information: rainbow trout. U.S. Fish and Wildlife Service FWS/OBS-82/10.60. 64 pp.

Raleigh, R. F., L. D. Zuckerman, and P. C. Nelson. 1986. Habitat suitability index models and instream flow suitability curves: brown trout, revised. U.S. Fish and Wildlife Service Biological Report 82(10.124).

Reiser, D. W., T. A. Wesche, and C. Estes. 1989. Status of Instream Flow legislation and practices in North America. Fisheries 14(2):22-29.

Ricker, W. E. 1975. Computation and Interpretation of Biological Statistics of Fish populations. Bulletin of the Fisheries Research Board of Canada 191. 382 pp.

Scott, D. and C. S. Shirvell. 1987. A critique of the instream flow incremental methodology and observations on flow determination in New Zealand. Pages 27-43 *in* J. F. Craig and J. R. Kemper, eds. Regulated Streams Advances in Ecology. Plenum Press, NY.

Sheldon, A. L. 1968. Species diversity and longitudinal succession in stream fishes. Ecology 49(2):193-198.

Shirvell, C., and D. Morantz. 1983. Assessment of the instream flow incremental methodology for Atlantic salmon in Nova Scotia. Transactions of the Canadian Electrical Association, Engineering and Operating Division 22:83-H-108.

Starrett, W. C. 1951. Some factors affecting the abundance of minnows in the Des Moines River, Iowa. Ecology 32:13-27.

Stewart-Oaten, A., W. W. Parker, and K. R. Parker. 1986. Environmental impact assessment: "pseudoreplication" in time? Ecology 67:929-940.

Stewart-Oaten, A., J. R. Bence, and C. W. Osenberg. 1992. Assessing effects of unreplicated perturbations: no simple solutions. Ecology 73:1396-1404.

White, R. J., E. A. Hansen, and G. R. Alexander. 1976. Relationship of trout abundance to stream flow in midwestern streams. Pages 597-615 *in* Osborn, J. F., and C. H. Allman, editors, Instream Flow Needs, Volume 2. American Fisheries Society, Bethesda, MD.

Zar, J. H. 1984. Biostatistical Analysis, 2nd Edition. Prentice-Hall, Inc. Englewood Cliffs, New Jersey. 718 pp.

CHAPTER 3

COMPARISON OF PREDICTED HABITAT CHANGE AND BENTHIC MACROINVERTEBRATE RESPONSE TO A SIMULATED IRRIGATION WITHDRAWAL IN HUNT CREEK, MICHIGAN

ABSTRACT

I diverted approximately 50% of the summer flow from a 0.7 km section of Hunt Creek from June 1-August 31, 1992-94, simulated the impacts of the withdrawal on the benthic macroinvertebrate habitat in the treatment section by use of the Physical Habitat Simulation System (PHABSIM), and compared the changes in habitat with observed densities of benthic macroinvertebrates in the treated section of Hunt Creek. The withdrawal of 50% did not decrease the benthic macroinvertebrate habitat of most of the taxa examined, but did reduce habitat of riffle dwelling taxa (e.g. Heptageniidae) by up to 38%. The total density of benthic macroinvertebrates in the treatment section of Hunt Creek did not change as a result of the reduced flow in relation to the total density of benthic macroinvertebrates in a control section. However, the densities of Heptageniidae in a riffle sampled in 1994 did decrease in relation to a control riffle ($p=0.05$), indicating that reduced flow may have resulted in a reduction of Heptageniidae density.

Introduction

The Physical Habitat Simulation System (PHABSIM) is the computer based habitat modeling component of the Instream Flow Incremental Methodology (IFIM) developed by the U.S. Fish and Wildlife Service that models stream physical habitat as a function of discharge (Milhous et al. 1989). PHABSIM is widely used to evaluate the impact of altered flow regimes on stream fish habitat (Reiser et al. 1989) with the assumption that stream physical habitat is directly related to stream fish population abundance or biomass (Bovee 1978; Orth and Maughan 1982; Mathur et al. 1985). The PHABSIM is widely used in the western United States for fish habitat evaluations (Reiser et al. 1989), but has not been as widely used for modeling stream benthic macroinvertebrate habitat. Also, the PHABSIM system has not been widely applied in the midwestern United States where the geology, hydrology, and faunal composition are different from western streams.

In addition to evaluating the effects of reduced streamflows on fish populations, it is necessary to determine impacts on the benthic macroinvertebrates because the benthic macroinvertebrates are the primary source of food for fishes, particularly game species such as the trouts and charrs (Elliott 1973; Alexander and Gowing 1976; Allan 1981; Bechara, Morceau and Planas 1992; Nielsen 1992). In many trout streams the density of benthic macroinvertebrates and the occurrence of macroinvertebrates in the drift may limit the growth rate of individual fish or may limit the population size (Chapman 1966). Orth (1987) also argued for consideration of ecological factors other than space occupied by fish alone when evaluating the impacts of altered streamflows, yet most PHABSIM analyses of altered streamflows are centered on the changes in game fish habitat. I am only aware of one published study which applied the PHABSIM system to benthic macroinvertebrates. Bovee (1985) studied the impacts of a peaking hydropower operation on the benthic macroinvertebrate habitat in a Colorado stream, but no comparison was made between the output of the PHABSIM modeling and observed benthic macroinvertebrate abundance. Gowan (1984) also modeled the habitat of two genera of macroinvertebrates in a marginal trout stream in Michigan and determined that withdrawals for irrigation reduced habitat by up to 11%, but that fish habitat losses were more severe. However, he did not compare PHABSIM model output with observed benthic macroinvertebrate densities.

Several studies have documented benthic macroinvertebrate habitat use patterns and have published habitat suitability criteria (HSC) which could be used in a PHABSIM analysis (Gore and Judy 1981; Orth and Maughan 1983; Gore 1989). However, the availability of these data have not led to an increase in the use of benthic macroinvertebrates in predicting impacts of flow regulation in streams.

Very little is known about the relationships between natural streamflow patterns and benthic macroinvertebrate communities and abundance. Ward (1976) reviewed the impacts of regulated streamflows on the benthos below large dams and noted that streamflow regulation can result in changes in community composition and enhancement or reduction of standing crop, depending on flow regime. Others (Minshall and Winger 1968; Corrarino and Brusven 1983; Poff and Ward 1991) have documented the impacts of altered streamflows on invertebrate drift, noting that altered streamflows can result in increased drift rates. Current velocity (Rabeni and Minshall 1977; Orth and Maughan 1983; Degani et al. 1993), depth (Degani et al. 1993) and substrate composition (Minshall 1984) are important factors influencing the distribution and abundance of benthic macroinvertebrates. Of these three factors, depth and velocity will change as streamflow is altered. Also, substrates may become embedded with fines if velocity is sufficiently reduced. Therefore, altered streamflows can be expected to have an influence on benthic macroinvertebrate communities.

Here I present the results of a PHABSIM analysis of benthic macroinvertebrate habitat in a Michigan stream during a simulated irrigation withdrawal. The objectives were to determine the impacts of a simulated irrigation withdrawal on the benthic macroinvertebrates in Hunt Creek, and to evaluate the PHABSIM model as a quantitative predictor of the changes in the benthic macroinvertebrate assemblage resulting from the altered streamflow.

Methods

I examined macroinvertebrate habitat and populations in two sections of Hunt Creek: one nontreatment section (section C) and a treatment section (section B; Figure 1, Chapter 1). Prior to sampling macroinvertebrates and macroinvertebrate habitat I measured and marked sections B and C (Figure 1, Chapter 1) into approximately 50 m contiguous reaches, and omitted the small area of impounded water at the downstream end of sections B and C and the disturbed habitat at the upstream end of section B immediately below the bulkhead. I was left with four 50 m reaches in section C and seven reaches in section B.

I sampled benthic macroinvertebrates from randomly selected locations in sections B and C during May-September, 1992 and April-

September, 1993 to construct habitat suitability criteria (HSC). I moved upstream through the sections and collected 20 samples each month in each section from randomly selected locations. I sampled macroinvertebrates using a modified Hess sampler or a petite Ponar grab in water that was either too deep or too shallow to sample with the Hess sampler. The net on the Hess sampler was constructed of 500 µm mesh and the area sampled by the Hess sampler was 0.023 m^2. The Ponar grab sampled 0.026 m^2. I preserved benthic samples in the field in 95% ethyl alcohol. At each sample location, I also measured depth to the nearest cm, water velocity to the nearest $cm \cdot s^{-1}$, and visually estimated dominant substrate composition using the codes in Table 2, Chapter 1. I measured water velocity with either a mechanical pygmy Gurley or an electronic Marsh-McBirney current meter. There was no difference in measurements between the meters (Chapter 2).

I separated macroinvertebrates from inorganic material in the samples by floating the sample contents in a saturated sugar solution (Anderson 1959). I also thoroughly sorted a second time through 20 samples from a variety of habitats (depositional, erosional) after they were sorted once to evaluate the effectiveness of the initial sorting.

I identified macroinvertebrates to family using the keys in Merritt and Cummins (1984) and Pennak (1989). I counted the number of organisms by family in the samples and converted these to density estimates by dividing by the sampled area.

I constructed HSC from the combined data collected in 1992-93 in section B using the nonparametric tolerance limits method (Bovee 1986). HSC were constructed from habitat use data by use of the formula:

$$NSI=2(1-P), \qquad (10)$$

where NSI is the normalized suitability index and P is the central proportion of the data frequency distribution (Bovee 1986). I constructed the HSC for depth and mean column velocity with this approach by defining P as the central 50, 75, 90, and 95% portions of the distribution by use of the nonparametric tolerance limits table found in Somerville (1958) and a confidence level of 95%. I constructed the HSC for substrate by normalizing the frequency-of-use data for each of the substrate categories. I normalized the substrate data by dividing the frequency-of-use data in each category by the frequency for the most commonly used substrate (Bovee 1986). I combined the substrate data by largest particle size and ignored the percent embeddeded classification because sample sizes were small for some of the substrate categories. Because I was concerned about statistical independence of the observations, I did not weight the value of the habitat measured at a sample location by the number of organisms in the sample. This resulted in HSC constructed from presence-absence data only. I also did not correct the HSC based on habitat availability because I randomly selected sample sites and therefore sampled all habitat types in approximate proportion to their availability.

I used the same reaches in section B to model macroinvertebrate habitat that were used to model brook trout habitat (Figure 1, Chapter 1). I simulated benthic macroinvertebrate habitat for selected families over a range of flows from baseflow to 2% of baseflow for the reaches in section B. I selected families based on their frequency of occurrence in the 1992-93 samples and based on habitat use characteristics. I modeled habitat for macroinvertebrate families that occurred in 20-80% of the samples in 1992-93 and selected additional families to provide data for habitat types that were not sufficiently represented in the initial selection procedure.

Because early results of the PHABSIM modeling indicated that riffle dwelling macroinvertebrates (e.g. Hydropsychidae) were more likely to be impacted by the reduction in flow than macroinvertebrates found more commonly in pool or depositional habitats, I altered the macroinvertebrate sampling design during the final year of the study. Prior to the withdrawal period in 1994 I selected two riffles, one in section C and one in section B, that had similar microhabitat characteristics under baseflow conditions. The riffle selected in section B was approximately 25 m upstream of the upper end of modeled reach B2. The depths, mean column velocities, and substrate characteristics of the selected riffle were very similar to those found in the riffle habitats in reach B2. I measured the width and length of each of the selected riffles and established a two dimensional grid of cells using permanent markers in the stream bank. The cells were approximately the same size as the area sampled by the Hess sampler. I then collected benthic samples in seven randomly selected cells in each riffle at three week intervals from May 12-August 23. I used the same sampling protocol as for the 1992-93 samples.

I formulated hypotheses concerning the impacts of the reduced streamflow on the density of benthic macroinvertebrate families in section B of Hunt Creek in 1992 and 1993 based on the relation between WUA and discharge curves and the assumption that WUA is positively and linearly related to macroinvertebrate abundance (Bovee 1978; Orth and Maughan 1982; Mathur et al. 1985). I used profile analysis (Morrison 1990) to compare the total benthic macroinvertebrate density trends between sections B and C during the summer for the 1992 data and used Before After Control Impact (BACI) analysis (Stewart-Oaten et al. 1986, 1992) to evaluate the predictions of the PHABSIM model for the 1993 data. For the BACI analysis of the 1993 and 1994 macroinvertebrate data, I determined the mean pretreatment difference between sections B and C from the benthic samples collected prior to 1 June and compared that mean difference to the mean difference between the sections from the samples collected after 1 June. Because the riffle sampled in 1994 in section B was close to reach B2 and was similar to the riffles in reach B2, I evaluated the relation between WUA and discharge for riffle transects in reach B2 to formulate hypotheses concerning the impacts of the withdrawal on the macroinvertebrate assemblage in the sampled riffle. I evaluated hypotheses of withdrawal impacts on the total macroinvertebrate density and on the densities of the most abundant families in 1994 by use of BACI statistics by again comparing the pretreatment mean difference to the treatment mean difference.

I also evaluated the impacts of reduced flow on the macroinvertebrate drift density in Hunt Creek. I collected macroinvertebrate drift data across a fixed transect in the treatment and the control sections of Hunt Creek. I sampled the drift by use of rectangular drift nets with a mouth opening 75 cm x 15.5 cm and 80 cm deep. Drift nets were constructed from 64 μm mesh nylon netting. Three nets were set across the transect which bisected a riffle, and the nets sampled the entire water column. I sampled the invertebrate drift for 20 minutes at four-hour intervals over 24 hours approximately every four weeks during summer, 1993 in section C and sampled the drift in section B on approximately the same dates but for up to 48 hours, depending on the withdrawal schedule. I measured depth and velocity at each net location immediately prior to sampling and used these data to estimate the volume sampled in the 20 minute period. I sorted the drift samples in a saturated sugar solution immediately after collection and preserved macroinvertebrates in 95% ethyl alcohol as they were retrieved from the samples. I thoroughly sorted through 15 samples a second time to determine the effectiveness of the procedure. I calculated total number of invertebrates in the drift per m^3 for each sample and determined the mean number of invertebrates per m^3 for each sample date and time. I used BACI analysis to evaluate the impacts of the withdrawal on the macroinvertebrate drift densities by comparing pretreatment mean difference in drift density between section B and C for the 24 hour period prior to the withdrawal on June 2 with the treatment period mean differences for the remaining sample dates.

Results

Benthic Macroinvertebrate Assemblage

I collected 199 benthic samples in 1992 and 237 benthic samples during 1993. I sorted 26 benthic samples a second time after sugar floating and determined I was retrieving 88% (range 69-100%) of the macroinvertebrates from the samples with the sugar floating procedure. Because I retrieved nearly all invertebrates from the samples I did not adjust the sample data by the efficiency of the initial sorting procedure. The benthic samples contained macroinvertebrates from 45 families representing 13 orders (Table 6). I collected 83 benthic samples in 1994, 42 from the riffle in section B and 41 from the riffle in section C. The 1994 samples contained macroinvertebrates from 29 families representing 11 orders (Table 6). Oligochaetes, baetids,

Table 6. Benthic macroinvertebrate taxa collected and percent frequency of occurrence in benthic samples in sections B and C of Hunt Creek, 1992-94. Taxa selected for habitat modeling are in bold face type.

Class	Order	Family	% Occurrence in 1992-93 (n=436)	% Occurrence in 1994 (n=83)
Insecta	Ephemeroptera	**Baetidae**	72.5	97.6
		Ephemerellidae	37.6	53.0
		Ephemeridae	5.1	
		Heptageniidae	38.8	83.1
		Leptophlebiidae	1.6	2.4
		Tricorythidae	0.2	
	Trichoptera	**Hydropsychidae**	31.9	47.0
		Glossosomatidae	67.7	90.4
		Limnephilidae	23.6	33.7
		Rhyacophilidae	36.2	53.0
		Philopotamidae	12.6	20.5
		Brachycentridae	15.8	14.5
		Lepidostomatidae	3.2	
		Hydroptilidae	1.6	4.8
		Psychomyiidae	0.2	
	Plecoptera	**Perlodidae**	23.2	32.5
		Nemouridae	30.3	69.9
		Taenyopterygidae	0.2	
		Leuctridae	6.0	26.5
		Perlidae	0.2	
	Odonata	Cordulegasteridae	9.2	1.2
		Gomphidae	1.4	
		Aeshnidae	0.2	
		Calopterygidae	0.7	

Table 6 (cont'd)

	Coleoptera	Elmidae larvae	81.9	98.8
		Elmidae adults	33.5	84.3
		Dytiscidae (larvae)	0.2	
	Diptera	Chironomidae	90.6	86.7
		Tipulidae	16.3	3.6
		Simuliidae	34.9	51.8
		Empididae	50.7	68.7
		Ceratopogonidae	25.0	6.0
		Tabanidae	9.2	2.4
		Athericidae	3.7	10.8
		Ptychopteridae	0.7	
		Muscidae	0.2	1.2
		Dixidae	0.9	
		Stratomyiidae	0.2	
	Megaloptera	Corydalidae	7.1	10.8
		Sialidae	1.8	
	Lepidoptera	Pyralidae	0.2	
Arachnida	Acari	Hydracarina	1.4	15.7
Bivalvia	Pelecypoda	Sphaeriidae	0.9	
Malacostraca	Amphipoda	Gammaridae	91.7	97.6
	Isopoda	Asselidae	6.7	14.5
Oligochaeta	Undetermined	Undetermined	100.0	100.0
Hirudinea	Undetermined	Undetermined		1.2

gammarids, elmid larvae and chironomids were the most frequently occurring taxa in 1992-93, when samples were collected at random locations throughout sections B and C. Oligochaetes were the most frequently collected taxa in the 1994 samples in sections B and C. Other frequently occurring taxa in 1994 were baetids, heptageniids, glossosomatids, chironomids, elmid larvae, and gammarids (Table 6).

I selected 13 families of macroinvertebrates for habitat modeling using PHABSIM (Table 6). In addition to the families selected based on frequency of occurrence, I selected the Tipulidae (present in 16.3% of the 1992-93 samples) to provide an additional taxon that occurs primarily in pool or depositional habitats. I also excluded the Limnephilidae because the genera of limnephilids found in Hunt Creek included both scrapers (*Goera* sp.) and shredders-herbivores (*Limnephilus* sp.) which occupy different habitats (Merritt and Cummins 1984). The majority of the taxa selected were found primarily in riffles (Table 6) and the remaining taxa were habitat generalists found primarily in runs and depositional habitats but also in riffles.

Habitat suitability criteria (HSC) for depth were very similar for all the taxa irrespective of the habitat type selected most frequently (Table 7). The narrowest optimal (suitability=1.0) depth range was from 16-31 cm for the Hydropsychidae and the widest optimal depth range was from 13-33 cm for the Ceratopogonidae. The range of usable (0.0<suitability<1.0) depths was also very similar between taxa and was also similar to the range of depths sampled in 1992-93. The minimum usable depth was 2 cm (Ceratopogonidae) and the maximum usable depth was 61 cm (6 taxa, Table 7). The depth HSC did not differ between taxa that primarily occupied riffles in comparison to taxa that primarily occupied

Table 7. Mean column velocity ($cm \cdot s^{-1}$) and depth (cm) habitat suitability ranges for the 13 families of benthic macroinvertebrates selected for habitat modeling in Hunt Creek. Column headings (1, 0.5, 0.2, 0.1, and usable) are suitability values.

			Mean Velocity ($cm \cdot s^{-1}$)		
Taxa	**1**	**0.5**	**0.2**	**0.1**	**Usable**
Baetidae	21-56	9-64	0-73	0-78	0-80
Ephemerellidae	21-55	12-63	1-70	0-74	0-79
Heptageniidae	42-65	27-73	6-78	4-79	0-80
Hydropsychidae	34-61	23-69	15-77	7-78	4-79
Glossosomatidae	30-58	16-65	10-74	2-79	0-80
Rhyacophilidae	34-63	27-70	12-78	0-79	0-80
Perlodidae	32-63	22-73	15-79	4-80	3-81
Nemouridae	27-58	10-66	2-73	0-79	0-80
Elmidae Adult	34-60	27-70	15-78	11-79	0-80
Tipulidae	24-58	5-64	0-69	0-70	0-71
Simuliidae	28-59	21-73	14-78	14-79	4-80
Empididae	27-57	14-65	8-77	0-79	0-81
Ceratopogonidae	4-43	0-54	0-73	0-77	0-78
			Depth (cm)		
Baetidae	17-36	12-46	8-58	5-61	4-63
Ephemerellidae	17-37	11-47	5-58	4-58	2-63
Heptageniidae	20-38	13-49	11-58	6-61	4-63
Hydropsychidae	16-31	11-42	6-49	4-55	4-58
Glossosomatidae	17-37	12-47	6-55	4-61	4-63

Table 7 (cont'd)

Rhyacophilidae	17-36	13-44	11-50	7-56	6-61
Perlodidae	13-38	7-43	5-47	4-61	3-62
Nemouridae	13-31	8-40	5-47	4-58	3-59
Elmidae Adult	17-37	13-46	7-58	5-61	3-64
Tipulidae	15-35	11-43	9-49	6-56	5-57
Simuliidae	13-30	11-46	6-58	4-58	3-59
Empididae	16-37	12-48	8-56	4-61	2-64
Ceratopogonidae	13-33	10-48	3-52	2-56	1-57

pool or depositional habitats (Figure 28). For example, the optimal depth range for Hydropsychidae (riffles) was from 16-31 cm and was from 15-35 cm for Tipulidae and 13-33 cm for Ceratopogonidae, both found primarily in depositional areas (Table 7).

Although there was considerable overlap in usable mean column velocities between the taxa, mean column velocity HSC were less similar between taxa than depth HSC and were better indicators of the habitat types selected by the taxa (Table 7). For example, the optimal velocity range for Hydropsychidae was 34-61 $cm \cdot s^{-1}$ and 24-58 $cm \cdot s^{-1}$ for Tipulidae (Figure 29). Usable velocity ranges also overlapped considerably for the taxa selected for habitat modeling. The maximum usable velocity was between 71-81 $cm \cdot s^{-1}$. The minimum usable velocity was 0 $cm \cdot s^{-1}$ for most taxa but was as high as 4 $cm \cdot s^{-1}$ for the Simuliidae and the Hydropsychidae, both filter feeding taxa (Merritt and Cummins 1984).

Substrate HSC also reflected the habitat selectivity of the taxa (Table 8, Figure 30). The optimal substrate size (medium gravel) was the same for all the taxa selected for modeling. However, this undoubtedly reflects the fact that medium gravel was the most frequently sampled substrate during 1992-93. Large gravel was the most suitable substrate after medium gravel for all taxa except Ceratopogonidae (Table 8). Sand and silt in combination and sand alone were the second most suitable substrates for the ceratopogonids.

PHABSIM Model Results

The 50% reduction in summer stream flow in the treatment section resulted in a very minor loss of stream surface area in both modeled reaches (Figure 19, Chapter 2). In reach B2 total surface area decreased from 206 to 195 $m^2 \cdot 100\ m^{-1}$, a reduction of only 5.6%. In

Table 8. Substrate suitability values for the 13 families of benthic macroinvertebrates selected for habitat modeling in section B of Hunt Creek. Percent embeddedness of the substrate was not included in the substrate suitability calculations.

	Substrate Code				
Taxa	**1 (sand and silt)**	**2 (sand)**	**3 (small gravel)**	**4 (medium gravel)**	**5 (large gravel)**
Baetidae	0.13	0.13	0.17	1	0.70
Ephemerellidae	0.11	0.11	0.2	1	0.65
Heptageniidae	0.02	0	0.02	1	0.83
Hydropsychidae	0	0.11	0.11	1	0.80
Glossosomatidae	0	0.04	0.13	1	0.55
Rhyacophilidae	0.02	0.08	0.06	1	0.67
Perlodidae	0	0.04	0.04	1	0.88
Nemouridae	0.08	0.24	0.20	1	0.76
Elmidae Adult	0	0	0.07	1	0.65
Tipulidae	0.23	0.14	0.09	1	0.82
Simuliidae	0.04	0.12	0.27	1	0.96
Empididae	0.08	0.12	0.17	1	0.61
Ceratopogonidae	0.69	0.41	0.14	1	0.38

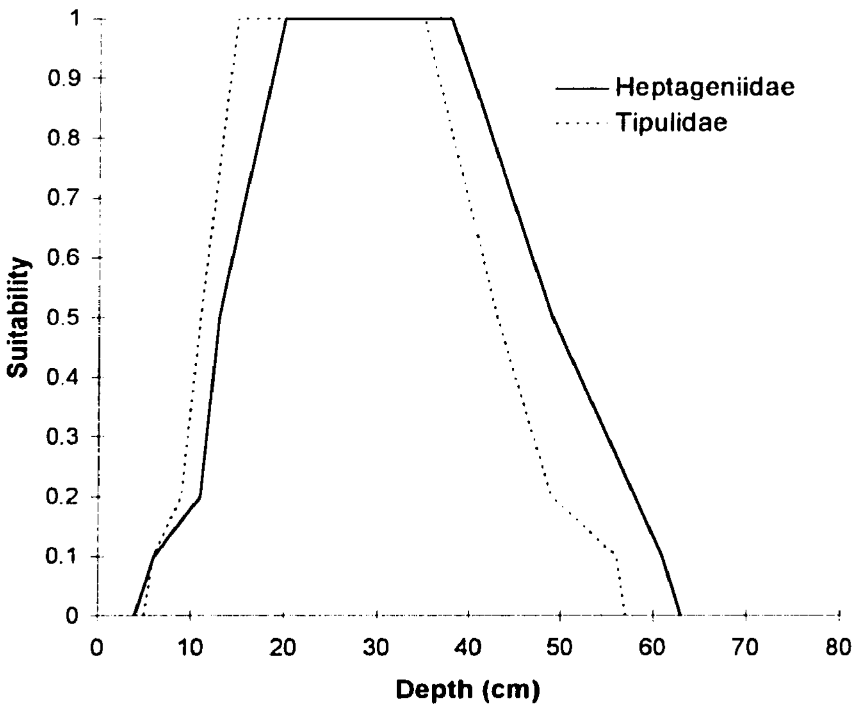

Figure 28. Depth habitat suitability criteria for Heptageniidae and Tipulidae calculated from habitat use data collected in section B of Hunt Creek, summer 1992-93.

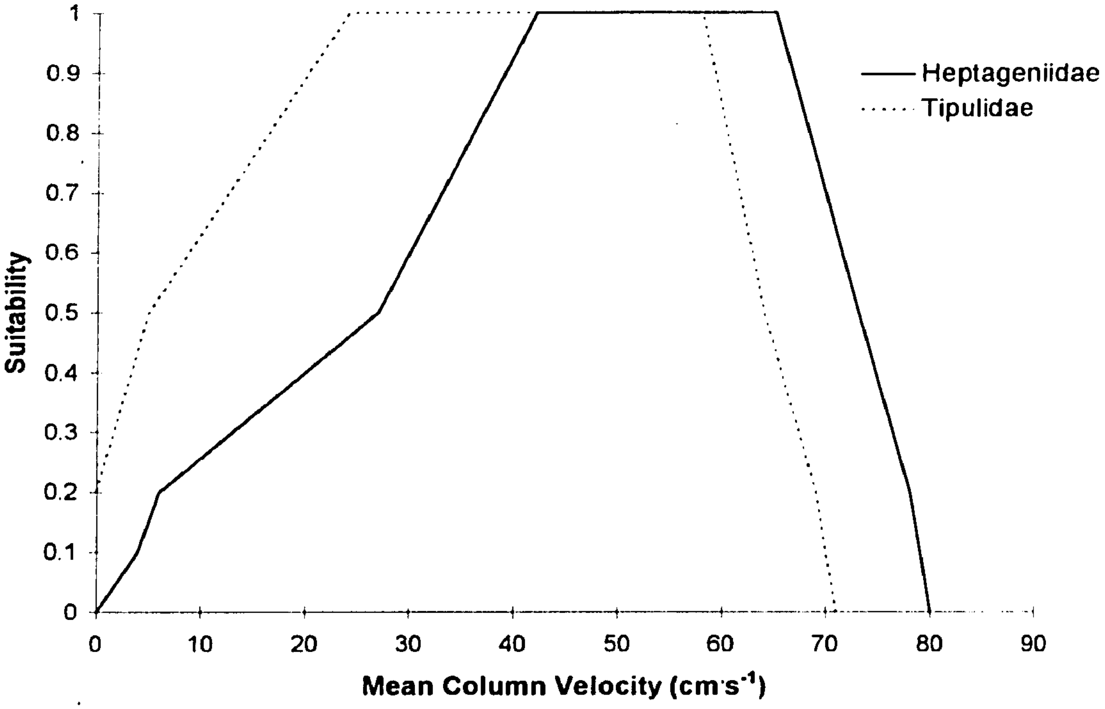

Figure 29. Mean column velocity habitat suitability criteria for Heptageniidae and Tipulidae calculated from habitat use data collected in section B of Hunt Creek, summer, 1992-93.

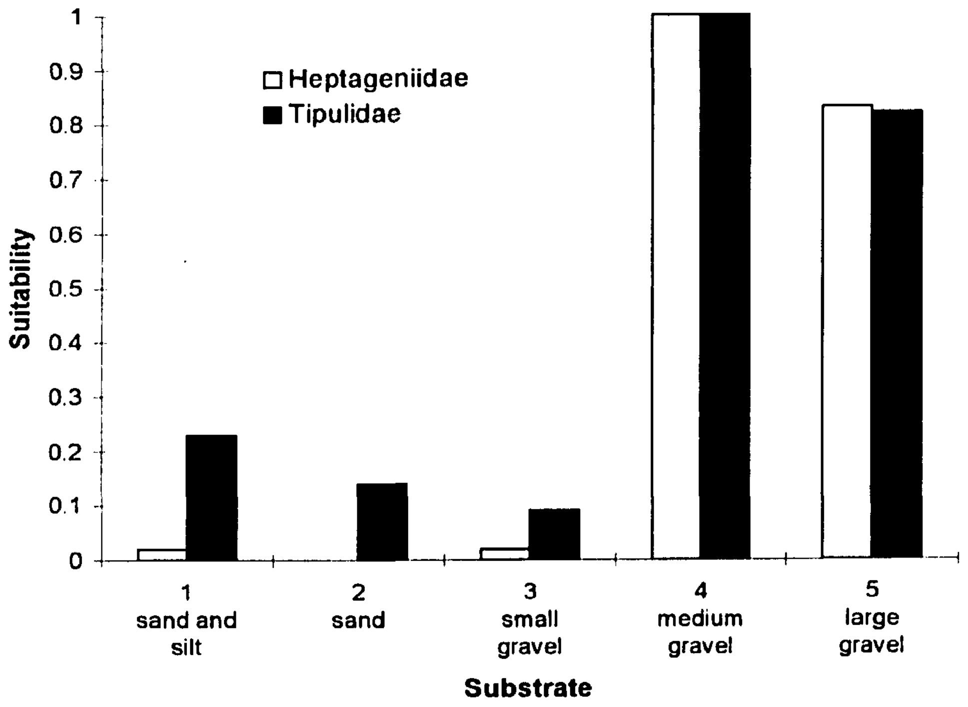

Figure 30. Substrate suitability criteria for Heptageniidae and Tipulidae calculated from habitat use data collected in section B of Hunt Creek, summer, 1992-93.

reach B4, total surface area decreased from 292 to 275 $m^2 \cdot 100\ m^{-1}$, a reduction of only 5.7%. Model results indicated that reducing flow in section B to a discharge of 0.01 $m^3 \cdot s^{-1}$ would reduce total surface area to 132 $m^2 \cdot 100\ m^{-1}$ in reach B2 (35.9% loss in surface area) and 176 $m^2 \cdot 100\ m^{-1}$ in reach B4 (39.7% loss of surface area). This result suggests that considerable pool habitat would remain in section B if discharge was reduced to 0.01 $m^3 \cdot s^{-1}$. The difference in the total surface area estimates between the two modeled reaches is due to differences in channel width.

The reduction of summer stream flow by 50% increased WUA for all but three of the taxa in reach B2 (Heptageniidae, Rhyacophilidae, and Elmidae adults, Table 9). The increases in WUA ranged from 1% to 22% (Perlodidae and Tipulidae, respectively). In general, the taxa that were most commonly found in pool and depositional habitats had the largest increases in WUA. The Heptageniidae, Rhyacophilidae, and Elmidae adults all had reduced WUA as a result of the 50% reduction in summer stream flow, although the losses were minor (4-15%). In contrast, WUA decreased in reach B4 for all taxa except Ceratopogonidae when summer stream flow was reduced 50%. The WUA estimate at 50% reduced flow for ceratopogonids remained virtually unchanged (from 279.8 $m^2 \cdot 100\ m^{-1}$ to 280.3 $m^2 \cdot 100\ m^{-1}$) (Table 9). For the remaining taxa, WUA decreased between 9% and 38% (Nemouridae and Heptageniidae, respectively). The WUA estimates for taxa most commonly found in pool and depositional habitats decreased less than for riffle dwelling taxa (e.g. Figure 31).

Reducing flow to less than 50% of baseflow during the summer months would result in reduced WUA for all taxa modeled (Table 9).

Table 9. Weighted Usable Area (WUA, $m^2 \cdot 100\ m^{-1}$) in relation to discharge for the 13 benthic macroinvertebrate families selected for habitat modeling in section B of Hunt Creek.

	Discharge ($m^3 \cdot s^{-1}$)						
Reach B2	**0.01**	**0.04**	**0.07**	**0.11**	**0.17**	**0.23**	**0.46**
Baetidae	24.8	60.0	91.3	123.1	160.7	180.5	160.0
Ephemerellidae	26.2	64.5	96.9	127.8	162.8	180.6	155.8
Heptageniidae	6.7	20.8	35.9	59.1	99.2	130.7	153.4
Hydropsychidae	5.2	24.7	50.6	85.7	130.9	155.1	147.8
Glossosomatidae	11.0	37.4	66.2	97.8	138.1	161.2	148.0
Rhyacophilidae	7.4	17.8	33.7	62.3	109.1	140.0	146.5
Perlodidae	9.1	36.2	68.6	104.8	145.3	166.6	165.4
Nemouridae	29.8	77.0	115.1	148.4	180.2	193.1	164.7
Elmidae Adult	3.4	16.6	35.5	65.0	111.0	141.3	147.3
Tipulidae	30.8	66.0	99.7	135.8	173.8	192.2	157.4
Simuliidae	4.7	29.6	65.7	108.7	153.0	175.8	169.2
Empididae	13.9	42.1	72.8	107.4	148.7	171.0	156.6
Ceratopogonidae	88.1	132.8	163.1	188.9	212.2	217.3	180.3
Reach B4							
Baetidae	28.5	67.5	108.1	156.7	197.2	216.7	249.4
Ephemerellidae	30.6	67.9	108.2	157.5	201.1	219.8	247.0
Heptageniidae	6.5	22.4	40.5	63.8	99.5	131.9	212.8
Hydropsychidae	3.9	21.5	43.9	75.5	131.6	166.6	225.7
Glossosomatidae	11.8	36.4	66.9	108.8	162.1	190.8	234.1
Rhyacophilidae	8.4	19.4	35.7	62.0	108.8	142.6	220.3
Perlodidae	8.5	34.2	58.8	91.1	153.9	189.2	242.3

Table 9 (cont'd)

Nemouridae	34.5	86.0	125.2	163.7	208.6	230.0	252.2
Elmidae Adult	3.2	14.6	30.6	57.1	109.9	145.3	220.2
Tipulidae	33.0	80.2	123.6	166.1	201.3	220.8	254.1
Simuliidae	3.2	23.5	54.3	93.8	156.6	194.6	241.7
Empididae	15.0	42.8	79.1	125.3	174.7	202.3	244.4
Ceratopogonidae	109.1	171.8	217.1	249.0	265.6	280.3	279.8

Also, the model predicted that reducing flow to 2% of baseflow (0.01 $m^3 \cdot s^{-1}$) would reduce WUA between 51-96% in reach B2 (Ceratopogonidae larvae and Elmidae adults respectively) and 61-99% in reach B4 Ceratopogonidae and Simuliidae larvae/Elmidae adults respectively).

Based on the WUA curves for reaches B2 and B4 I hypothesized that the 50% reduction in flow should not have resulted in a decrease in total benthic macroinvertebrate density in section B in 1992 or 1993. The profile analysis of the 1992 density data support this hypothesis because the test indicated the trends in total macroinvertebrate densities (Table 10, Figure 32) were not different between the sections ($F=0.30$, $df=4,194$, $p<0.001$). Similarly, the results of the BACI analysis of the 1993 data (Table 10, Figure 33) support the conclusion that the withdrawal did not reduce total macroinvertebrate density in section B (Student's t test, $p=0.84$).

The relation between WUA and discharge for the riffle transects in reach B2 were virtually unchanged by excluding the run and pool habitats, although the magnitude of the WUA estimates at any one discharge did decrease. Therefore, I hypothesized that the 50% reduction in summer stream flow would have no impact on the abundance of any of the benthic macroinvertebrate taxa in the sampled riffle in section B during summer, 1994. I tested these hypotheses on the taxa for which I modeled habitat and also on the Gammaridae, Chironomidae, and Elmidae larvae. The 50% reduction in summer stream flow did not impact the abundance of the families tested nor did it impact the total macroinvertebrate abundance estimates in section B (Table 11). Total macroinvertebrate density in section B did not decline as a result of the withdrawal and the trend in total density through the summer closely

Table 10. Benthic macroinvertebrate density estimates (number$\cdot$m^{-2}, standard error estimates in parentheses) from random sample locations in sections B and C for 1992-93.

Family	**Year**	**Section**	**April**	**May**	**June**	**July**	**August**	**September**
Baetidae	**1992**	B		75(21)	110(30)	273(87)	321(106)	18(6)
		C		136(41)	641(106)	427(85)	318(112)	185(68)
Ephemerellidae		B		138(38)	112(27)	104(24)	9(6)	2(2)
		C		91(37)	40(17)	47(13)	5(3)	11(5)
Heptageniidae		B		236(56)	11(8)	4(3)	9(4)	90(24)
		C		460(109)	65(23)	14(8)	20(20)	91(37)
Hydropsychidae		B		61(33)	24(11)	258(93)	446(222)	256(145)
		C		11(5)	9(5)	12(7)	241(106)	510(307)
Glossosomatidae		B		1042(253)	661(190)	927(334)	410(141)	845(156)
		C		173(57)	234(63)	366(140)	310(90)	1108(265)
Rhyacophilidae		B		37(12)	2(2)	27(9)	111(35)	198(55)
		C		33(10)	31(21)	23(10)	31(14)	107(30)
Perlodidae		B		4(3)	11(5)	18(12)	38(14)	62(18)

Table 10 (cont'd).

		C		5(3)	29(10)	42(15)	36(15)	111(28)
Nemouridae		B		44(23)	78(59)	62(30)	13(7)	0(0)
		C		20(8)	698(317)	206(104)	20(9)	2(2)
Elmidae adults		B		94(41)	35(12)	36(20)	58(20)	76(29)
		C		0(0)	0(0)	0(0)	0(0)	0(0)
Tipulidae		B		18(6)	13(6)	11(4)	36(10)	13(5)
		C		7(5)	2(2)	14(7)	2(2)	13(6)
Simuliidae		B		13(7)	13(8)	322(202)	125(58)	4(3)
		C		57(29)	546(298)	330(157)	138(106)	120(82)
Empididae		B		24(8)	52(18)	79(21)	20(9)	22(7)
		C		2(2)	80(25)	66(24)	38(10)	18(8)
Ceratopogonidae		B		20(14)	26(10)	37(14)	49(16)	44(11)
		C		13(9)	22(10)	19(9)	29(17)	29(16)
Total		B		4031(647)	5569(771)	8301(1256)	6109(940)	4148(470)
		C		2309(315)	6078(1050)	8865(1195)	6451(1001)	5443(963)
Baetidae	**1993**	B	277(58)	114(25)	110(29)	244(33)	392(71)	130(26)
		C	251(82)	78(19)	180(72)	592(125)	435(117)	300(70)

Table 10 (cont'd).

Ephemerellidae	B	317(81)	168(38)	191(39)	175(36)	21(12)	13(9)
	C	49(16)	26(13)	26(15)	0(0)	2(2)	0(0)
Heptageniidae	B	239(134)	275(93)	38(18)	7(5)	12(8)	141(51)
	C	378(93)	321(86)	236(81)	81(28)	40(18)	18(9)
Hydropsychidae	B	146(81)	61(26)	38(18)	404(120)	442(202)	280(168)
	C	45(24)	5(3)	0(0)	14(8)	25(16)	58(24)
Glossosomatidae	B	306(72)	248(71)	249(75)	245(79)	222(56)	630(182)
	C	448(159)	109(36)	28(13)	236(77)	305(102)	117(48)
Rhyacophilidae	B	131(38)	11(6)	9(7)	20(10)	59(18)	150(32)
	C	36(12)	12(7)	21(9)	14(7)	29(12)	36(13)
Perlodidae	B	11(6)	5(3)	5(5)	7(4)	7(4)	49(16)
	C	7(4)	2(2)	5(5)	2(2)	11(4)	16(8)
Nemouridae	B	70(40)	90(39)	40(23)	54(25)	5(5)	0(0)
	C	61(26)	31(14)	99(57)	36(13)	16(5)	2(2)
Elmidae adults	B	33(9)	90(27)	74(25)	52(24)	116(39)	146(42)
	C	40(20)	59(21)	45(19)	31(12)	29(9)	119(54)
Tipulidae	B	18(7)	14(7)	7(4)	9(5)	7(5)	0(0)

Table 10 (cont'd).

	C	11(7)	0(0)	2(2)	5(3)	25(22)	0(0)
Simuliidae	B	16(10)	491(427)	5(3)	168(60)	113(52)	11(4)
	C	20(11)	83(47)	5(3)	139(58)	94(39)	38(12)
Empididae	B	47(11)	105(30)	186(55)	197(57)	90(30)	61(21)
	C	85(22)	59(21)	66(29)	96(29)	88(33)	108(29)
Ceratopogonidae	B	45(29)	38(18)	29(11)	49(23)	38(13)	52(20)
	C	2(2)	52(50)	2(2)	5(3)	9(9)	7(5)
Total	B	6236(1043)	4509(655)	5308(713)	9053(1131)	6312(751)	4480(727)
	C	4241(783)	2403(346)	2984(737)	4036(690)	4646(751)	4030(918)

Table 11. Benthic macroinvertebrate density estimates (number·m^{-2}, standard error estimates in parentheses) from one riffle each in sections B and C, 1994.

		Date					
Taxa	**Section**	**May 12**	**June 1**	**June 20**	**July 12**	**August 3**	**August 23**
Baetidae	B	448(83)	91(33)	149(42)	1143(218)	2331(576)	1052(210)
	C	759(142)	442(92)	545(74)	992(187)	2182(389)	935(215)
Ephemerellidae	B	643(55)	350(78)	253(33)	117(41)	39(21)	19(14)
	C	58(16)	26(13)	13(8)	0(0)	13(13)	0(0)
Heptageniidae	B	1149(136)	851(106)	273(49)	110(31)	39(15)	26(13)
	C	649(106)	539(83)	487(62)	326(84)	130(30)	19(13)
Hydropsychidae	B	195(55)	84(50)	208(67)	32(13)	636(148)	740(180)
	C	6(6)	6(6)	0(0)	0(0)	13(13)	26(13)
Glossosomatidae	B	1818(483)	1117(269)	1442(263)	234(73)	312(38)	130(47)
	C	571(141)	253(31)	221(53)	76(22)	65(17)	84(40)
Rhyacophilidae	B	52(25)	13(8)	52(38)	13(13)	136(37)	52(15)
	C	39(15)	39(6)	52(15)	38(18)	19(9)	19(9)

Table 11 (cont'd).

Perlodidae	B	6(6)	0(0)	26(9)	0(0)	97(48)	39(12)
	C	6(6)	6(6)	19(9)	23(16)	45(24)	6(6)
Nemouridae	B	162(47)	104(32)	435(90)	45(24)	97(44)	26(13)
	C	117(61)	162(78)	539(166)	159(66)	104(45)	19(14)
Elmidae adults	B	377(80)	214(56)	273(44)	149(52)	299(62)	390(66)
	C	78(32)	162(65)	182(65)	106(46)	84(27)	84(51)
Tipulidae	B	0(0)	0(0)	0(0)	0(0)	19(14)	6(6)
	C	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Simuliidae	B	52(27)	32(22)	6(6)	104(38)	156(119)	32(26)
	C	468(250)	156(80)	26(26)	60(19)	149(72)	65(40)
Empididae	B	136(49)	130(55)	208(70)	117(28)	65(34)	13(8)
	C	149(43)	136(43)	227(95)	98(36)	97(34)	32(19)
Ceratopogonidae	B	13(13)	0(0)	6(6)	0(0)	13(8)	6(6)
	C	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Total	B	7188(485)	4188(713)	6195(892)	6948(727)	7591(1031)	5409(726)
	C	4844(441)	2981(366)	4500(805)	3614(524)	6325(805)	4149(1262)

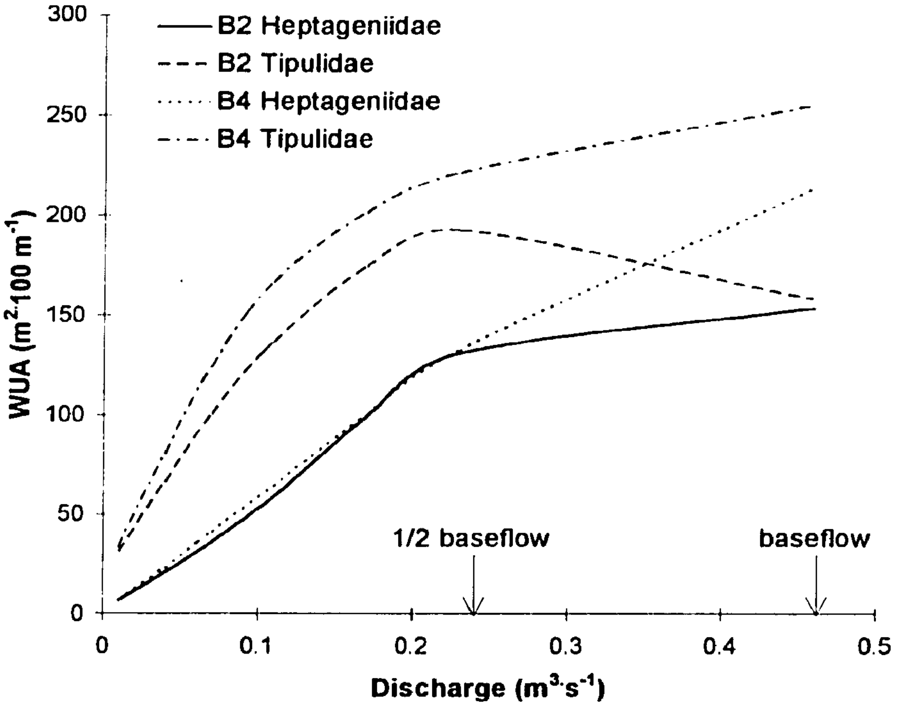

Figure 31. Weighted usable area ($m^2 \cdot 100\ m^{-1}$) at discharge ($m^3 \cdot s^{-1}$) for Heptageniidae and Tipulidae in section B of Hunt Creek.

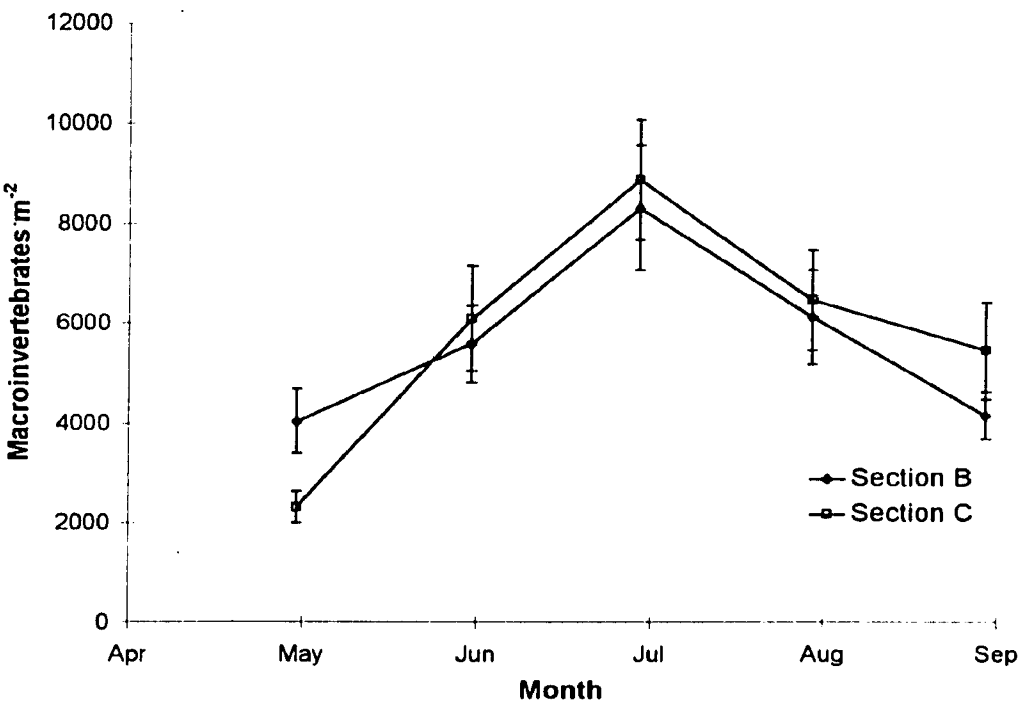

Figure 32. Total macroinvertebrate density (number·m^{-2}, with standard error bars) in sections B and C of Hunt Creek, summer, 1992.

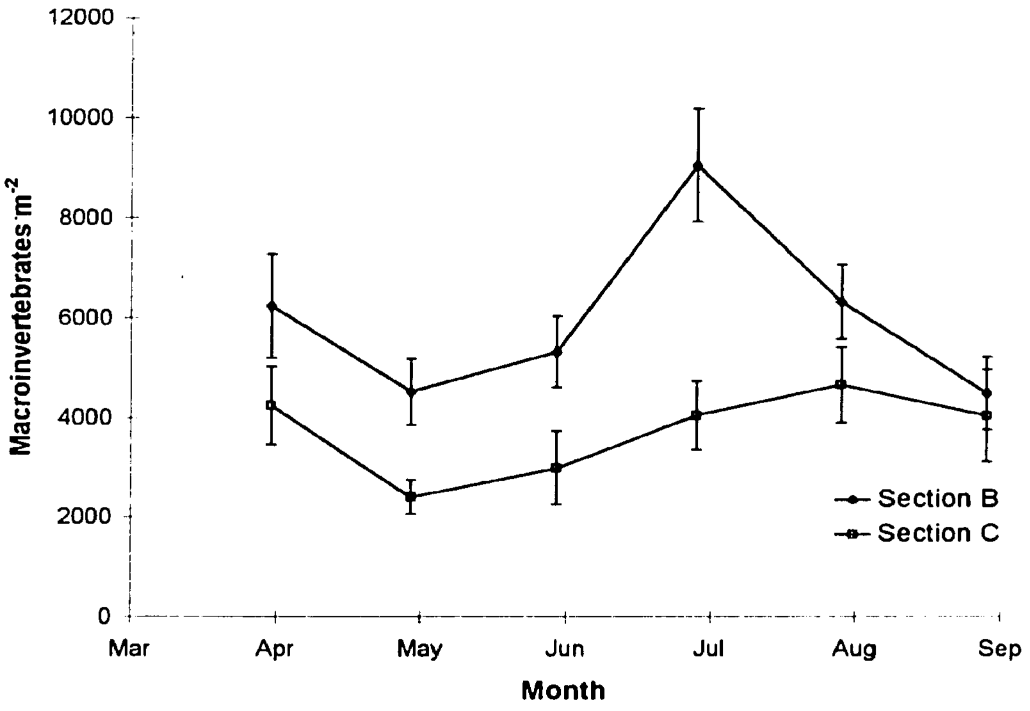

Figure 33. Total macroinvertebrate density (number·m^{-2} with standard error bars) in sections B and C of Hunt Creek, summer, 1993.

matched the trend in section C (Table 11). The only instance in which the trends in total macroinvertebrate numbers departed was between the samples collected on July 12 when the total numbers in section C declined slightly from the previous sample whereas the total number in section B on July 12 increased over the previous sample period (Figure 34).

The only taxa-specific BACI test that produced a significant result was for the Heptageniidae (Table 12). However, it is not clear whether the difference between pretreatment and treatment mean differences was due to the reduced flow because the densities of Heptageniidae in both sections B and C were declining prior to the withdrawal period and continued to decline through the summer. However, the rate of decline in Heptageniidae density was faster in section B before the withdrawal was initiated and continued at a faster rate through most of the summer, although the densities of Heptageniidae in sections B and C were virtually identical at the time the final sample was collected (Table 11). This difference in rates of decline between the sections resulted in the sign and magnitude of the treatment mean difference changing after the withdrawal was initiated. I also was unable to detect a mean differences for the three most abundant taxa (Gammaridae, Chironomidae, and Elmidae larvae, Table 12).

Invertebrate Drift

Invertebrate drift density (individuals$\cdot m^{-3}$) was elevated in section B immediately following the initiation of each water withdrawal event (June 2 and August 22) but returned to prewithdrawal levels within 24 hours (Figures 35-37). The elevated drift densities on June 2 were

Table 12. Mean difference between pretreatment and treatment period benthic macroinvertebrate density estimates between sections B and C and BACI analysis resullts for 1994 data (df=4 for all tests).

Taxa	**Pretreatment Mean Difference (# m^{-2})**	**Treatment Mean Difference (# m^{-2})**	**t statistic**	**p value**
Baetidae	-331.0	5.3	-2.5	0.09
Ephemerellidae	454.5	100.5	2.5	0.19
Heptageniidae	406.0	-128.5	4.9	0.05
Hydropsychidae	133.5	394.3	-1.5	0.21
Glossosomatidae	1055.5	418.0	1.9	0.13
Rhyacophilidae	-6.5	31.3	-1.0	0.36
Perlodidae	-3.0	17.3	-1.2	0.30
Nemouridae	-6.5	-54.5	0.8	0.52
Elmidae adult	175.5	163.8	0.1	0.94
Elmidae larvae	571.5	1198.8	-2.7	0.06
Simuliidae	-270.0	-0.5	-1.8	0.31
Empididae	-9.5	-12.8	0.3	0.79
Ceratopogonidae	6.5	6.3	0.04	0.98
Chironomidae	-90.9	29.5	-0.7	0.51
Gammeridae	-419.0	-736.7	0.5	0.63
Total Density	1775.5	1888.8	-0.15	0.89

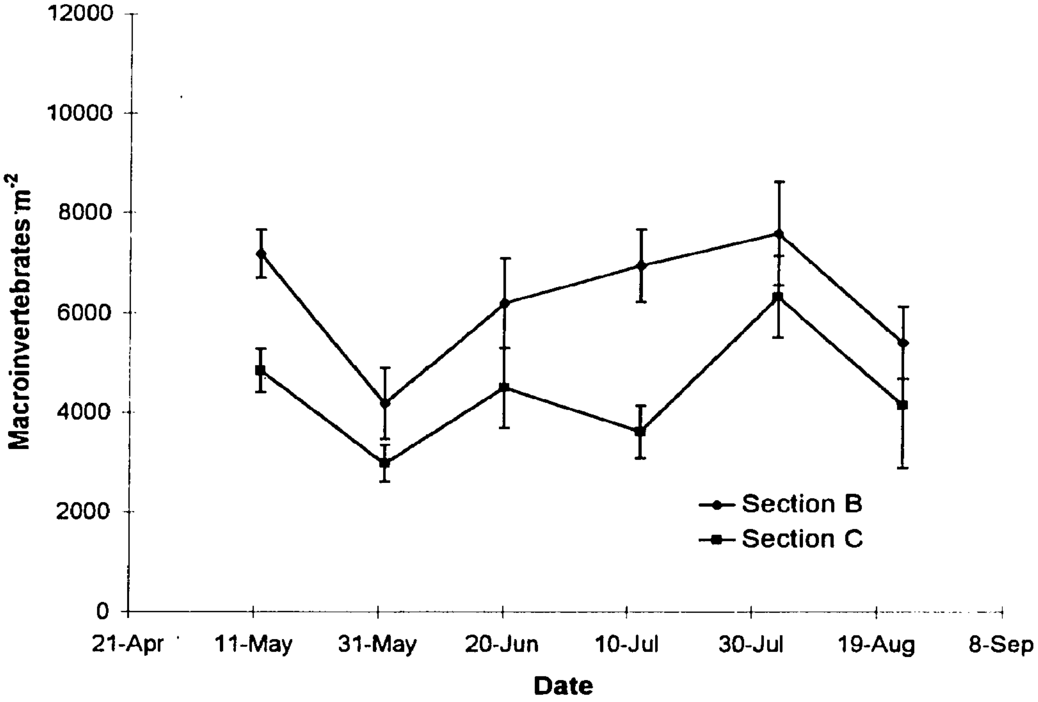

Figure 34. Total macroinvertebrate density (number·m^{-2}, with standard error bars) in sampled riffles in sections B and C of Hunt Creek, summer, 1994. June 1 samples were collected immediately prior to the start of the withdrawal period.

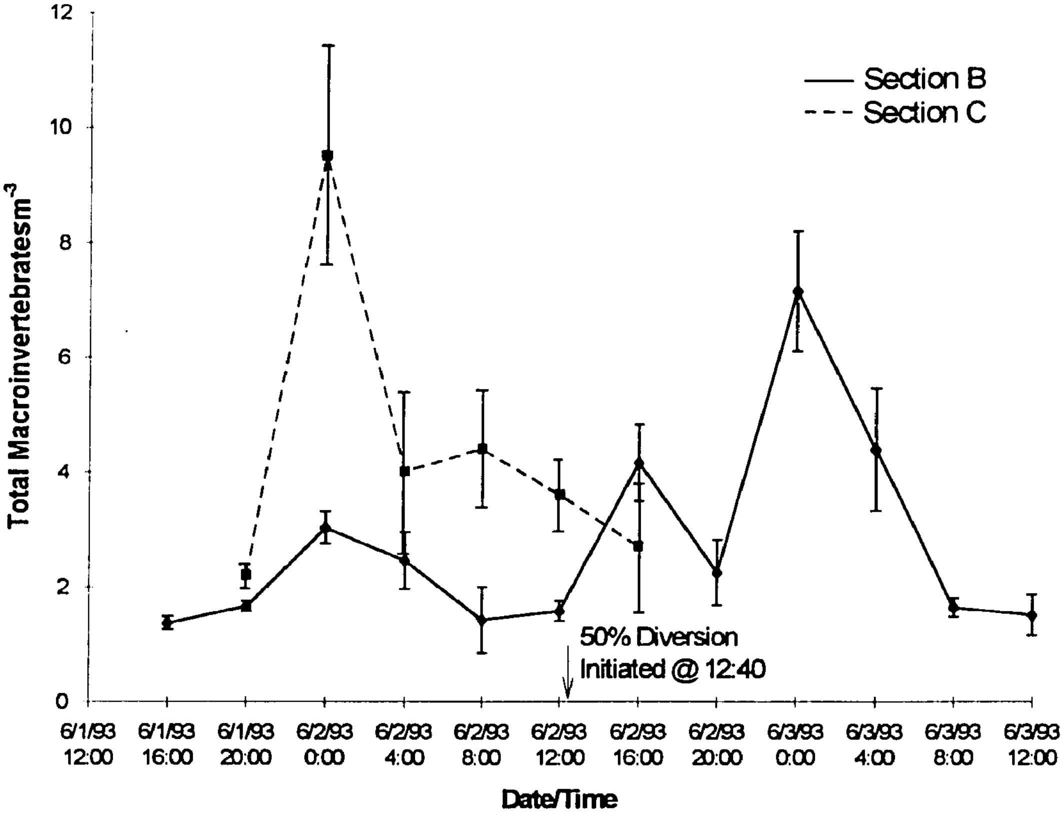

Figure 35. Macroinvertebrate drift density (number$\cdot$m^{-3}, with standard error bars) in section B immediately before and after the initiation of the withdrawal period in 1993 and in section C. Withdrawal period began at approximately 12:40 on June 2, after the 12:00 sampling was completed. Section C drift samples were collected on June 6 and 7.

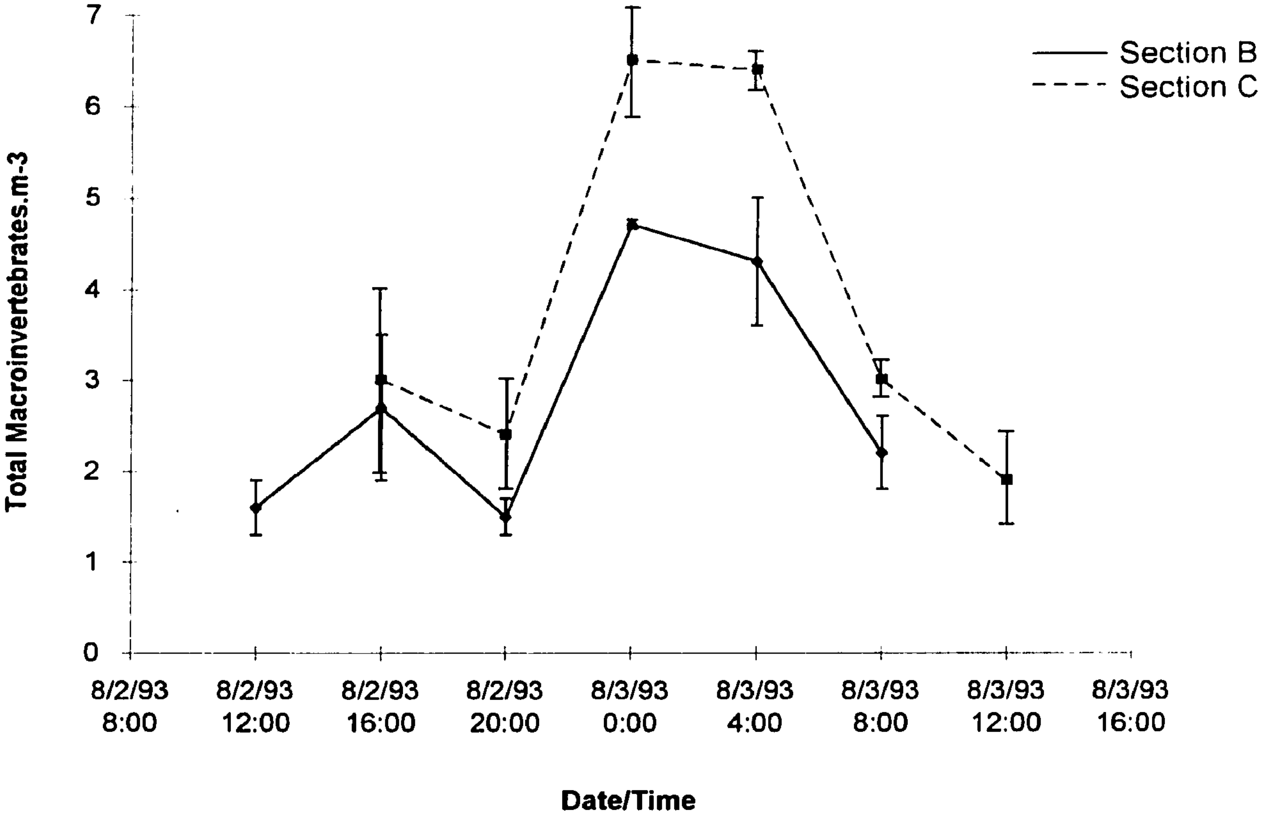

Figure 36. Macroinvertebrate drift density (number·m^{-3}, with standard error bars) in section B on August 1-3, 1993. Section B samples were collected on August 1 and 2 and section C samples were collected on August 2-3.

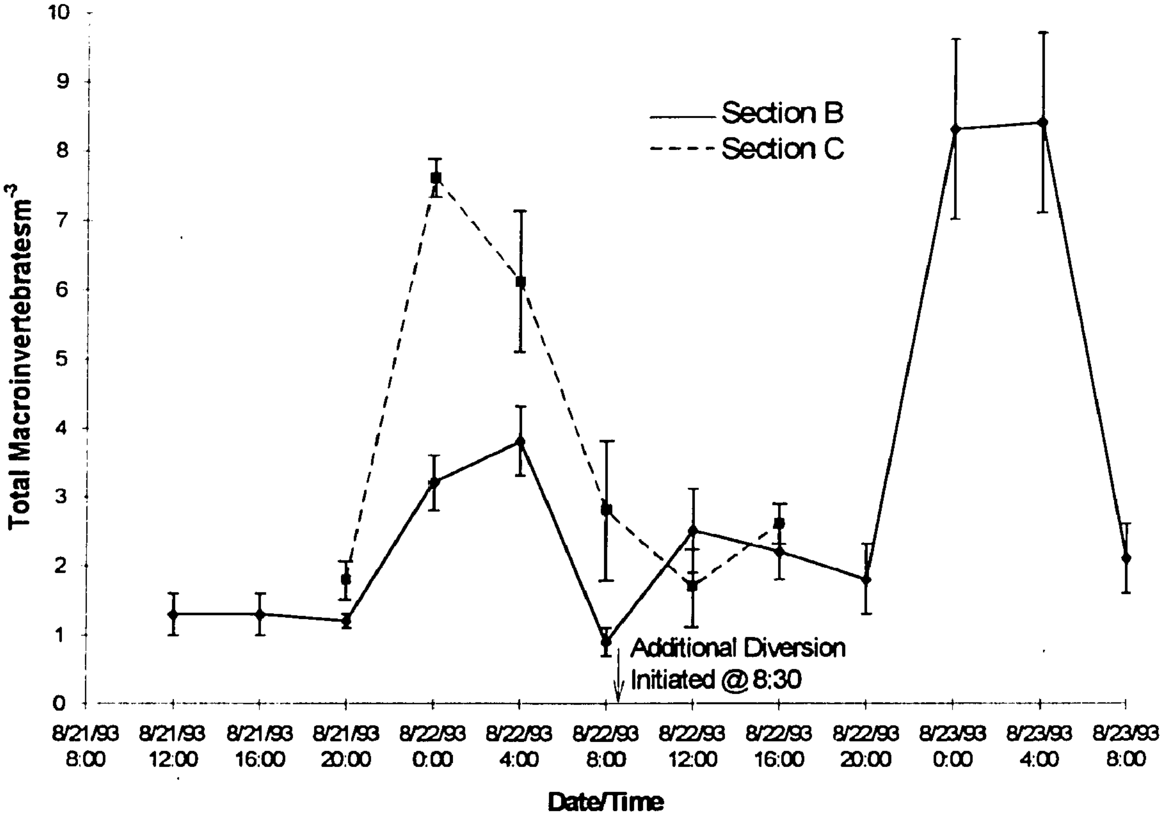

Figure 37. Macroinvertebrate drift density (number$\cdot$m^{-3}, with standard error bars) in section B immediately before and after the initiation of the additional withdrawal period in August, 1993. Withdrawal period began at approximately 8:30 on August 22. Section C samples were collected on August 25 and 26.

not significantly different from pretreatment levels (t=-1.39, df=10, p=0.19) but the elevated densities on August 22 were significantly different (t=-2.98, df=10, p=0.02). Also, total drift densities were similar between sections B and C during the July and early August sampling.

Discussion

Total benthic macroinvertebrate density in Hunt Creek did not decline as a result of the 50% reduction in summer stream flow in the treatment section. Further, there is no evidence for an impact on any of the individual families examined except, perhaps, the Heptageniidae (Table 11). The significance of the test result for Heptageniidae density may be due to chance alone because I did not adjust p values for multiple comparisons as suggested by Smith et al. (1993). The families I selected for habitat modeling and the additional three families selected for BACI analysis represented 93% of the benthic macroinvertebrate fauna in Hunt Creek. It is unlikely that any of the remaining taxa were impacted by the reduced flow. This result is consistent with the observation that the withdrawal reduced the total surface area of the stream less than 6%. I recognize that I probably did not adequately sample the first and second instars of many of the taxa because of the mesh size used on the Hess sampler. However, it is unlikely that sampling the early instars would have influenced the results of the study because the model predictions matched the observed trends in density of the macroinvertebrates.

The PHABSIM model indicated that reducing stream flow more than 50% would reduce WUA in both reaches for all taxa and that WUA losses would be substantial. A PHABSIM analysis of brook trout habitat in section B of Hunt Creek during the same period indicated that brook trout WUA would not be substantially reduced by reducing the streamflow until the discharge was equal to approximately 20% of baseflow, or to 0.09 $m^3 \cdot s^{-1}$ (Chapter 2). These results indicated that brook trout food resources may be impacted by a lesser reduction in flow, one that would not be sufficient to reduce brook trout foraging or resting habitat. The benthic macroinvertebrates in Hunt Creek comprise over 85% of the diet of the brook trout, both by volume and caloric value (Alexander and Gowing 1976). A flow reduction in Hunt Creek greater than 50% could adversely affect the brook trout population even if other measures of brook trout habitat did not decline.

There were no obvious differences in the relation between WUA and discharge among the various taxa. The relation between WUA and discharge for taxa that were most common in riffle habitats (e.g. Heptageniidae and Hydropsychidae) had a similar shape when compared to the relations for taxa that were more common in depositional or pool habitats (e.g. Tipulidae and Empididae) (Figure 32). The only clear difference in the relation between WUA and discharge was between reaches B2 and B4. In general, the WUA relations for reach B4 indicated a reduction in WUA for benthic macroinvertebrates in Hunt Creek when summer stream flow was reduced 50%, although the reductions were minor. In contrast, WUA curves from reach B2 indicated a modest increase in WUA when summer stream flow was reduced 50%. The differences in the WUA curves between reaches B2 and B4 are undoubtedly due to the differences in velocity and depth between the two reaches.

The similarity between the HSC and the WUA-discharge relations for the taxa modeled is probably due to the methods used to construct the HSC. I did not weight the value of the habitat parameters for the individual samples because the habitat parameters measured and modeled with PHABSIM (depth and mean column velocity) may not be the most important parameters influencing the abundance of macroinvertebrates at the sample location. For example, Peckarsky (1984) noted that predation can be an important factor influencing the distribution and abundance of both predator and prey species of macroinvertebrates in localized areas. Further, it is unlikely that mean column velocity and depth are as important as the shear stress and thickness of the boundary layer in determining the abundance of macroinvertebrate taxa at specific locations in a stream (Osborne et al. 1985). The substrate composition at a location is undoubtedly important in determining the abundance of specific taxa of macroinvertebrates at locations in a stream (Minshall 1984). However, the PHABSIM system assumes substrate composition is constant and therefore, is not as important in determining the shape of WUA-discharge relation as depth and mean column velocity.

I did not conduct the PHABSIM analysis on the habitat of the macroinvertebrate families that occurred in less than 20% of the samples because these families represented less than 7% of the benthic organisms encountered during sampling and habitat suitability criteria constructed for extremely small sample sizes are generally not representative of the actual habitat suitability requirements of the taxa (Bovee 1986). If a habitat analysis for the infrequently occurring taxa was necessary it would require altering the sampling protocol to more adequately sample those taxa. In addition, I did not analyze the habitat for the most frequently encountered taxa (found in more than 80% of the samples) because nearly all microhabitats sampled were suitable for those taxa. As a result, the HSC for those taxa would have been too broad to be useful as a predictor or the change in habitat for those taxa and the WUA-discharge relation would have looked similar to the Total Area-discharge relation (Figure 19, Chapter 2).

In addition to macroinvertebrate habitat, invertebrate drift can be affected by changes in discharge (Anderson and Lehmkuhl 1968; Minshall and Winger 1968; Hooper and Ottey 1988; Poff and Ward 1991). Poff and Ward (1991) demonstrated that drift increased for most taxa during simultaneous experimental streamflow reductions and elevations. I documented an increase in invertebrate drift densities (number$\cdot$m^{-3}) in the 24 hour period immediately following flow reduction but drift densities returned to prewithdrawal levels quickly, indicating the response of the invertebrates in section B to the reduced discharge was a short term, catastrophic drift response (Waters 1972). The only aspect of the total macroinvertebrate drift that might have been altered by the reduction of flow was the rate of downstream movement of the invertebrates due to the reduced velocity in the treatment section. This reduced rate of downstream movement may alter macroinvertebrate colonization dynamics in dewatered streams, even if other measures of habitat quality and quantity are not reduced by reduced flows.

Although I was not able to document a short term response to the reduced flow in Hunt Creek, it is possible that reduced flows could have a long term impact, particularly if stream edge habitats important for oviposition are subjected to drying over successive years. If stream edge habitats were dewatered it could lead to reduced reproductive success for taxa that use overhanging vegetation and stream edge substrates for egg laying. This in turn could lead to reduced production of macroinvertebrates in the stream.

The results presented here also point out that habitat components normally not considered in a PHABSIM analysis may be important in determining the response of fish to reduced flows. Orth (1987) argued for including broader ecological analyses in impact assessment, yet most of the PHABSIM studies conducted since 1987 have focused on fish microhabitat alone (Conder and Annear 1987; Scott and Shirvell 1987; Bovee et al. 1994). In this study I found that brook trout food-producing habitat may be decreased by a reduction in flow that would not produce a reduction in brook trout WUA (Chapter 2). For example, the PHABSIM model indicated benthic macroinvertebrate WUA in section B would be reduced approximately 52% and 66% in reaches B2 and B4, respectively if summer flow was reduced 85% but brook trout WUA would only be reduced 10%.

Finally, I want to stress that the results presented here are unique to Hunt Creek and should not be applied to streams throughout Michigan or the midwest. It is likely that a withdrawal of 50% of summer baseflow would have a greater impact on both fish and benthic macroinvertebrate habitat in marginal trout streams or streams that do not have high quality habitat under summer baseflow conditions. For example, a withdrawal of 50% of summer baseflow in Fish Creek, a marginal brown trout stream in Ingham County, Michigan would result in a 30% reduction of WUA for Hydropsyche spp. and a 25% reduction of WUA for Ephemerella spp. (esimated from figures in Gowan 1984). Clearly, the potential impacts of proposed water withdrawals from streams must be evaluated stream by stream.

Literature Cited

Alexander, G. R. and H. Gowing. 1976. Relationships between diet and growth in rainbow trout (*Salmo gairdneri*), brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*). Michigan Department of Natural Resources Fisheries Research Report No. 1841.

Alexander, G. R. and E. A. Hansen. 1986. Sand bed load in a brook trout stream. North American Journal of Fisheries Management 6:9-23.

Allan, J. D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 38:184-192.

Anderson, N. H., and D. M. Lehmkuhl. 1968. Catastrophic drift of insects in a woodland stream. Ecology 49:198-206.

Anderson, R. O. 1959. A modified flotation technique for sorting bottom fauna samples. Limnology and Oceanography 4:223-225.

Bechara, J. S., G. Moreau, and D. Planas. 1992. Top-down effects of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. Canadian Journal of Fisheries and Aquatic Sciences 49:2093-2103.

Bovee, K. D. 1978. The incremental method of assessing habitat potential for coolwater species, with management implications. Transactions of the American Fisheries Society Special Publication 11:340-346.

Bovee, K. D. 1985. Evaluation of the effects of hydropeaking on aquatic macroinvertebtrates using PHABSIM. Pages 236-241 *in* Proceedings of the Symposium of Small Hydropower and Fisheries. Olson, F. W., R. G. White, and R. H. Hamre editors. American Fisheries Society, Bethesda, MD.

Bovee, K. D. 1986 Development and evaluation of habitat suitability criteria for use in the Instream Flow Incremental Methodology.

Instream Flow Information Paper 21. U.S. Fish and Wildlife Service Biological Report 86(7). 235 pp.

Bovee, K. D., T. J. Newcomb, and T. G. Coon. 1994. Relations between habitat variability and population dynamics of bass in the Huron River, Michigan. National Biological Survey Biological Report 1994(21). 63 pp.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. The American Naturalist 100(913):345-357.

Conder, A. L. and T. C. Annear. 1987. Test of weighted usable area estimates derived from a PHABSIM model for instream flow studies on trout streams. North American Journal of Fisheries Management 7:339-350.

Corrarino, C. A., and M. A. Brusven. 1983. The effects of reduced stream discharge on insect drift and stranding of near shore insects. Freshwater Invertebrate Biology 2:88-98.

Degani, G., G. N. Herbst, R. Ortal, H. J. Bromley, D. Levanon, Y. Netzer, N. Harari, and H. Glazman. 1993. Relationship between current velocity, depth and the invertebrate community in a stable river system. Hydrobiologia 263:163-172.

Elliott, J. M. 1973. The food of brown and rainbow trout (*Salmo trutta and S. gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. Oecologia 12:329-347.

Gore, J. A. and R. D. Judy, Jr. 1981. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. Canadian Journal of Fisheries and Aquatic Sciences 38:1363-1370.

Gore, J. A. 1989. Models for predicting benthic macroinvertebrate habitat suitability under regulated flows. Pages 253-265 *in* Gore, J. A. and G. E. Petts, editors. Alternatives in regulated river management. CRC Press, Boca Raton, FL.

Gowan, C. 1984. The impacts of irrigation water withdrawals on brown trout (*Salmo trutta*) and two species of benthic macroinvertebrates in a typical southern Michigan stream. M. S. thesis, Michigan State University, East Lansing. 127 pp.

Hooper, F. F., and D. R. Ottey. 1988. Responses of macroinvertebrates of two headwater streams to discharge fluctations. Verh. Int. Ver. Limnol. 23:1159-1166.

Mathur, D., W. H. Bason, E. J. Purdy, Jr., and C. A. Silver. 1985. A Critique of the Instream Flow Incremental Methodology. Canadian Journal of Fisheries and Aquatic Science 42:825-831.

Merritt, R. W., and K. W. Cummins. 1984. An introduction to the aquatic insects of North America, second edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Milhous, R. T., M. A. Updike, and D. M. Schneider. 1989. Physical Habitat Simulation System Reference Manual-Version II. Instream Flow Information Paper No. 26. U.S. Fish and Wildlife Service Report 89(16).

Minshall, G. W. 1984. Aquatic insect-substratum relationships. Pages 358-400 *in* Resh, V. H. and D. M. Rosenberg, editors. The Ecology of Aquatic Insects. Praeger Publishers, New York.

Minshall, G. W., and F. V. Winger. 1968. The effect of reduction in stream flow on invertebrate drift. Ecology 49:580-582.

Morrison, D. F. 1990. Multivariate Statistical Methods, third edition. McGraw-Hill Publishing Company, New York.

Nielsen, J. L. 1992. Microhabitat specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121:617-634.

Orth, D. J., and O. E. Maughan. 1982. Evaluation of the Incremental Methodology for recommending instream flows for fishes. Transactions of the American Fisheries Society 111:413-445.

Orth, D. J. and O. E. Maughan. 1983. Microhabitat preferences of benthic fauna in a woodland stream. Hydrobiologia 106:157-168.

Osborne, L. L., Herricks, E. E., and Alavian, V. Characterizationof benthic microhabitat: an experimental system for aquatic insects. Hydrobiologia, 123:153-160.

Peckarsky, B. L. 1984. Predator-prey interactions among aquatic insects. Pages 196-254 *in* Resh, V. H. and D. M. Rosenberg, editors. The Ecology of Aquatic Insects. Praeger Publishers, New York.

Pennak, R. W. 1989. Freshwater inbertebrates of the United States Protozoa to Mollusca, third edition. John Wiley and Sons, Inc. New York.

Poff, N. L., and J. V. Ward. 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. Canadian Journal of Fisheries and Aquatic Sciences 48:1926-1936.

Rabeni, C. F., and G. W. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. Oikos 29:33-43.

Reiser, D. W., T. A. Wesche, and C. Estes. 1989. Status of Instream Flow legislation and practices in North America. Fisheries 14(2):22-29.

Scott, D. and C. S. Shirvell. 1987. A critique of the instream flow incremental methodology and observations on flow determination in New Zealand. Pages 27-43 *in* J. F. Craig and J. R. Kemper, eds. Regulated Streams Advances in Ecology. Plenum Press, NY.

Smith, E. P., D. R. Orvos, and J. Cairns, Jr. 1993. Impact assessment using the before-after-control-impact (BACI) model: concerns and comments. Canadian Journal of Fisheries and Aquatic Sciences 50:627-637.

Somerville, P. N. 1958. Tables for obtaining non-parametric tolerance limits. The Annals of Mathematical Statistics 29:599-601.

Stewart-Oaten, A., J. R. Bence, and C. W. Osenberg. 1992. Assessing effects of unreplicated perturbations: no simple solutions. Ecology 73:1396-1404.

Stewart-Oaten, A., W. W. Parker, and K. R. Parker. 1986. Environmental impact assessment: pseudoreplication in time? Ecology 67:929-940.

Ward, J. V. 1976. Effects of flow patterns below large dams on stream benthos: a review. Pages 235-253 *in* J. F. Osborn and G. H. Allman, editors, Instream Flow Needs, Solutions to Technical, Legal, and Social Problems Caused by Increasing Competition for Limited Stream Flow. Symposium and Speciality Conference, Boise, ID, May, 1976. American Fisheries Society, Bethesda, MD.

Waters, T. F. 1972. The drift of stream insects. Annual Review of Entomology 17:253-272.

SUMMARY

The results presented here clearly illustrate that a 50% reduction of summer baseflow in Hunt Creek did not reduce the population density of brook trout or the benthic macroinvertebrate assemblage. The results also indicate that the PHABSIM modeling system may be appropriate for use in Michigan streams for predicting the impacts of altered stream flows on stream fish populations because the predictions of the model matched the observed trends in fish abundance. The model indicated that the withdrawal of 50% did not reduce the foraging, resting, or food producing habitat available for brook trout. However, it is not certain that the PHABSIM procedure is an accurate predictor of the changes in a fish population that result from altered flows, because the flow reduction applied to Hunt Creek was not large enough to produce an effect. A much more rigorous test of the model would be to reduce the flow in Hunt Creek to a level that would be expected to produce a reduction of brook trout standing crop or abundance and compare population response to the predicted effect size.

These results should not be interpreted to mean that all streams in Michigan or the Midwest could withstand a 50% reduction in summer flow with no adverse impact to the fish or other biota. The response of the biota in a particular stream to a flow reduction depends to a large extent on local watershed attributes, the resident species assemblage, and stream characteristics such as channel shape and water source. Therefore, the results presented here are unique to Hunt Creek. Future water withdrawals from streams in Michigan need to be evaluated on a case by case basis.

The alternative HSC presented here also offer a potential improvement over existing HSC developed from frequency-of-use data. However, the model developed here could be improved by developing all model paramaters based on performance of brook trout (e.g. maximum capture distance) and by verifying that bioenergetic criteria accurately describe the habitat selection tendencies of foraging brook trout.

Appendix A

Appendix A

Brown trout and rainbow trout WUA ($m^2 \cdot 100\ m^{-1}$) in relation to discharge ($m^3 \cdot s^{-1}$) in reaches B2 and B4, Hunt Creek.

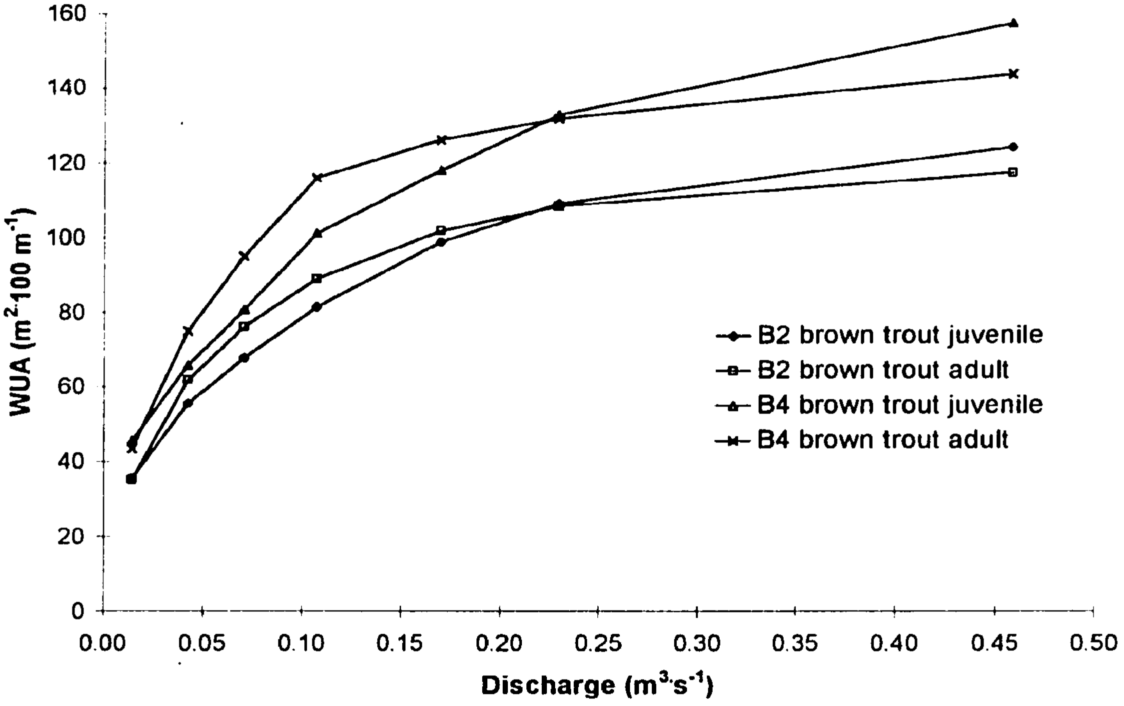

Figure 38. Juvenile and adult brown trout WUA in relation to discharge in reaches B2 and B4, Hunt Creek derived from HSC data presented in Raleigh et al. (1986; see Literature Cited fo Chapter 2).

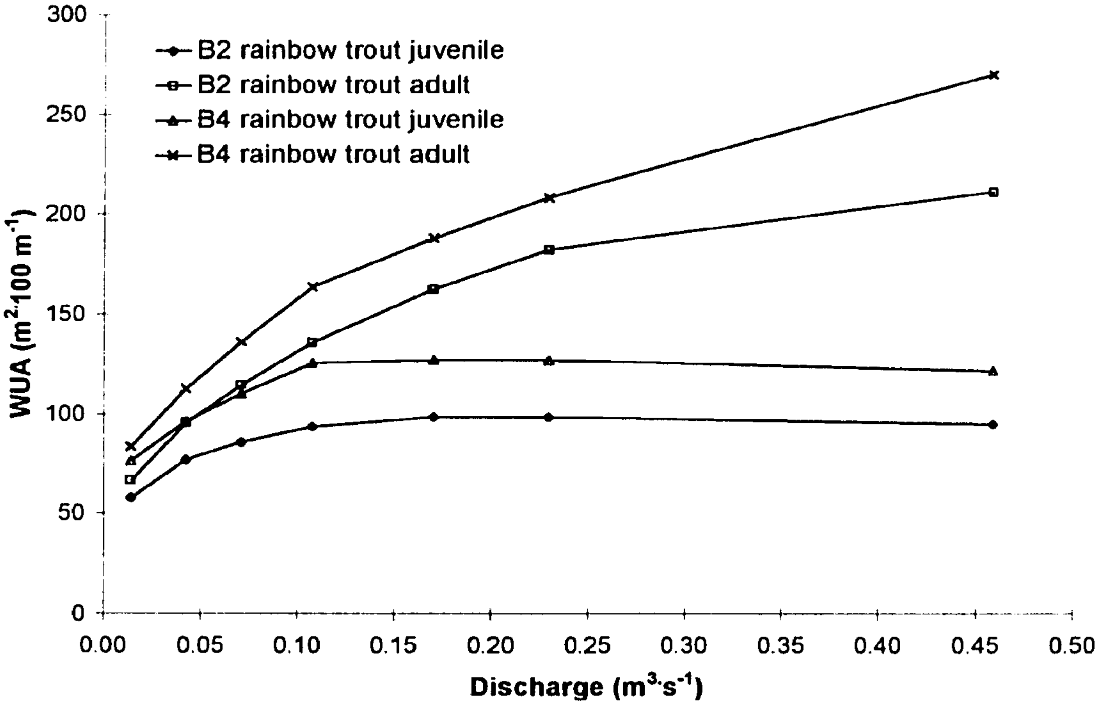

Figure 39. Juvenile and adult rainbow trout WUA in relation to discharge in reaches B2 and B4, Hunt Creek derived from HSC data presented in Raleigh et al. (1984; see Literature Cited for Chapter 2).