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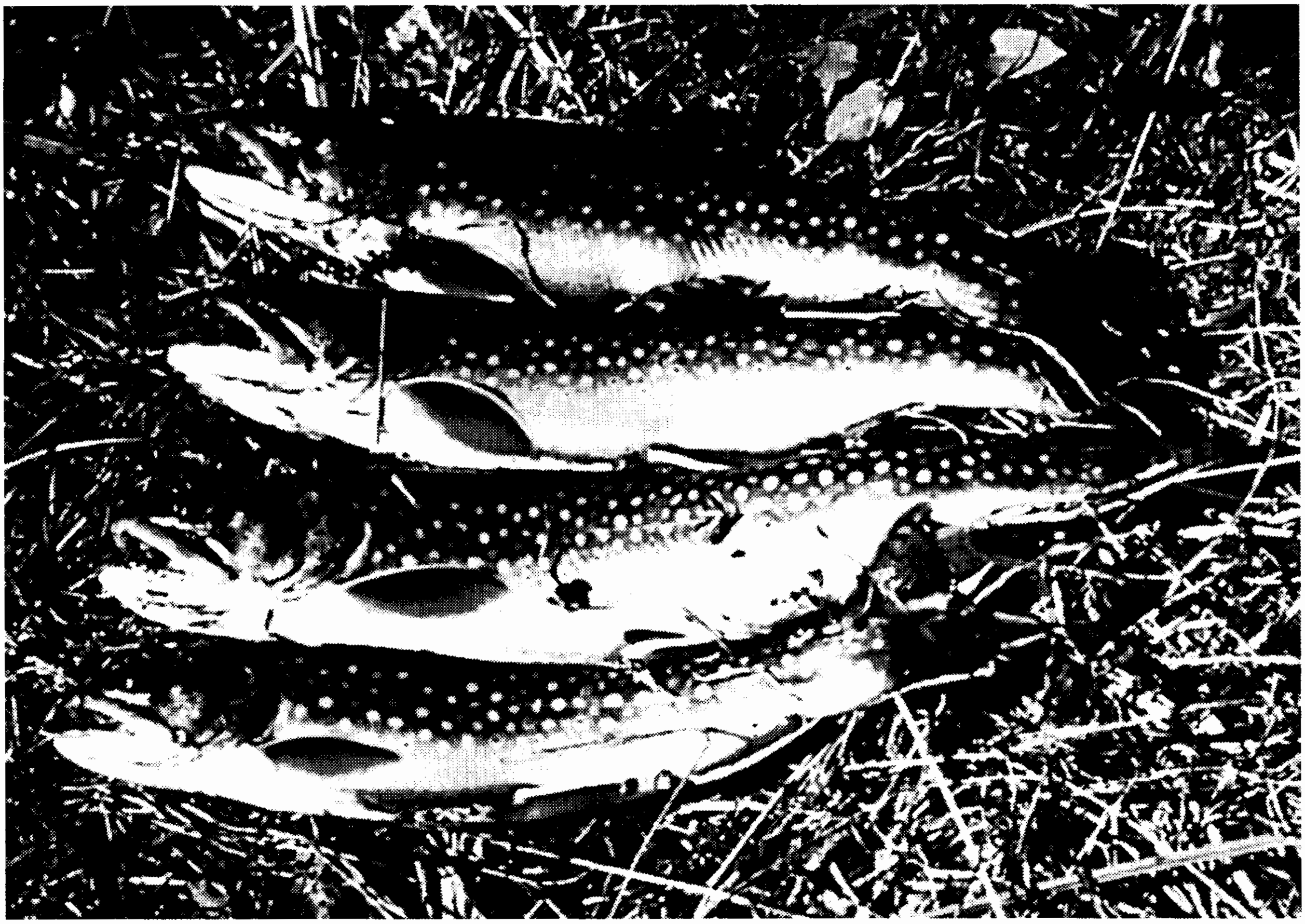

STATE OF MICHIGAN
DEPARTMENT OF NATURAL RESOURCES

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

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

## ABSTRACT

We used bioenergetic modeling to derive diurnal foraging habitat suitability criteria (bioenergetic-HSC) for mean column velocity and depth for brook trout *Salvelinus fontinalis*. We compared these to diurnal foraging habitat suitability criteria (HSC) derived from frequency-of-use data (use-HSC) for brook trout in Hunt Creek, MI. We also constructed nocturnal use-HSC from frequency-of-use data collected in Hunt Creek. Bioenergetic benefits were estimated by use of an empirical invertebrate drift density x current velocity model that adjusted fish foraging area as a function of fish size, depth, and current velocity. Metabolic costs were modeled from published swimming energetics equations for brook trout. Size-specific net benefit curves were constructed for the range of observed current velocities and bioenergetic-HSC were constructed by standardizing these curves. We constructed use-HSC from Hunt Creek frequency-of-use data using nonparametric tolerance limits. 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. Also, the optimal velocities predicted for yearling and older fish from bioenergetic-HSC were greater than the highest optimal velocity predicted by use-HSC. Young of the year optimal velocities predicted from bioenergetic-HSC were within the range of optimal velocities predicted from use-HSC but were at the upper end of the range. Also, the predicted range of usable velocities was narrower for bioenergetic-HSC than for use-HSC. Nocturnal use-HSC indicated young of the year and yearling and older brook trout selected microhabitats with lower mean column velocities at night. Yearling and older brook trout used microhabitats with higher mean column velocities and greater depths than young of the year fish during both the diurnal and nocturnal periods. Bioenergetic-HSC provided a more conservative assessment of microhabitat suitability for drift feeding brook trout. A comparison of bioenergetic and use-HSC suitability scores for an independent data set of habitat use observations in Hunt Creek indicated that use-HSC predicted suitability values greater than bioenergetic-HSC. We suggest this is because use-HSC are too general and do not represent the actual suitability of foraging microhabitats in Hunt Creek.

## 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). HSC are quantitative models which represent the suitability of particular habitat parameters for stream fish. Habitat suitability ranges between zero and one, with zero meaning the habitat parameter is unsuitable and a value of one indicating the habitat is optimally suitable (Thomas and Bovee 1993, Bovee 1986). The four habitat parameters typically used in a PHABSIM evaluation of stream habitat are water depth, water velocity, substrate and cover (Milhous et al. 1989). Previous stream habitat evaluations have been based on HSC for the species and life stage of interest constructed using 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 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 result in territoriality (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). A recent study on juvenile coho salmon *Onchorhyncus kisutch* has demonstrated the formation of dominance hierarchies and that growth rate was directly related to position in the dominance hierarchy and also to the 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 objective of this work was 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). We 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 two assumptions. The first assumption was the brook trout population in Hunt Creek was at or near carrying capacity and as a result 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 (occasionally a few large brown trout are collected during fall electrofishing, but these fish are removed). 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 by reducing food availability (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.

We 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.

We stress that this is the first step in this approach to HSC construction. We recognize that it may be more instructive and accurate to include substrate and cover components in the suitability model. However, we did not evaluate or include substrate and cover in model construction.

## 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 (Gaylord Alexander, personal communication). Hunt Creek was chosen as the study stream for this research because the brook trout population in Hunt Creek is naturally reproducing, has been monitored by the MDNR since 1949 and a continuos 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.

The portion of Hunt Creek that flows through the research area is divided into two sections (sections B and C; 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.

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 slimy sculpin *Cottus cognatus* (Alexander and Hansen 1986).

### Bioenergetic-HSC Construction

We 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. Using this approach, 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 microhabitat position ($C_x$):

$$E_x = B_x - C_x. \qquad (1)$$

We derived net benefit models for brook trout between 5 and 20 cm total length at increments of 2.5 cm. We thus constructed 7 net benefit models. Data necessary for estimating model parameters came from a variety of sources including published literature and are given in the description that follows.

We based estimates of microhabitat benefit on invertebrate drift data collected in section B of Hunt Creek during 1993 and 1994. We collected invertebrate drift on a fixed transect in Hunt Creek during summer, 1993 from dawn to dusk. We sampled the invertebrate drift for

20 minutes every four hours at three locations across the transect approximately every 30 days. Preceding each sample we 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. We 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. We found no consistent differences in measurements of velocity between the two meters and velocity measurements were always in close agreement. We sampled invertebrate drift using a 64 mm mesh rectangular drift net with a mouth opening 15.5 cm by 75 cm. We also collected invertebrate drift samples at locations where brook trout were observed feeding in section B during 1993 and 1994. We used the same methods for sampling drift at fish locations except the duration of drift sampling was 10 minutes as opposed to 20 minutes for the fixed location samples.

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

We identified aquatic organisms in the drift to family using the keys in Merritt and Cummins (1984) and identified the terrestrial invertebrates to order. We measured invertebrate lengths to the nearest 0.1 mm using an ocular micrometer. We only included invertebrates $\geq 2$ 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). We converted invertebrate lengths to weights using length-weight equations given in Rogers et al.

(1977) and Smock (1980) and converted weights to caloric values using data in Cummins and Wuycheck (1971).

We 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 constant depth of 25 cm (constant sampled area of 387.5 $cm^2$). We made this correction by dividing 387.5 $cm^2$ by the area sampled by the drift net. We multiplied the calories per hour for each sample by the sample correction factor to determine calories per hour for the constant area. We related calories per hour to mean column velocity with a linear regression equation, forcing the regression through the origin, to obtain estimates of caloric benefit of microhabitats based on current velocity for a constant sampled area of 387.5 $cm^2$.

Because the size of the fish and water velocity are important in determining the foraging success of a fish (Hughes and Dill 1990, Hill and Grossman 1993), we adjusted the caloric benefit of a microhabitat by the maximum capture distance (MCD) as defined in Hughes and Dill (1990). Using the approach of Hughes and Dill (1990) MCD (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). We estimated PL as a function of mean column velocity from the invertebrate drift data collected in Hunt Creek by use of linear regression. We 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. We 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:

$$FA=0.5(\boldsymbol{P}MCD^2) \qquad (5).$$

We 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. We adjusted the estimated caloric benefit of a microhabitat to reflect the fish's FA as determined by the MCD. We 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 value depending on fish size and then decreases to zero, again dependent on fish size (Hughes and Dill 1990). We 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 no 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 efforts toward the benthos.

We 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 we were only modeling summer microhabitats we used the equations derived for brook trout swimming at $15^\circ$ 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 $cm \cdot s^{-1}$. We 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 specific size fish (Table 1). We derived weight estimates for the brook trout in Hunt Creek from length-weight data collected in the spring and fall of 1993 and 1994 in Hunt Creek. We 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 $calories \cdot hr^{-1}$ using the energetic equivalents given in Elliot and Davison (1975). We used a nonlinear regression equation describing 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.

We modeled the net benefits of microhabitats using equation 1. We 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 we developed bioenergetic-HSC for depth which were dependent on MCD and therefore, dependent on velocity. Using this approach, the suitability of the depth at a microhabitat is a function of the MCD: if the depth is equal to or greater than the MCD then it is optimally suitable. We based this on the simplifying assumption that depth was not limiting if it was greater than the MCD. For depths less than the fish's MCD we calculated the suitability of the depth by determining the fraction of the area available for foraging in relation to the optimal foraging area as determined by the MCD:

$$\text{Depth Suitability} = \frac{\mathrm{OFA} - \mathrm{UFA}}{\mathrm{OFA}} \qquad (6)$$

where OFA is the foraging area available at an optimal depth ($\text{depth} \geq \text{MCD}$) and UFA is the unavailable foraging area when depth is less 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. We considered depth as unsuitable when it was 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

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

We 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). We constructed diurnal use-HSC from data collected in section B, but because of small sample sizes combined data from sections B and C for constructing nocturnal use-HSC. Use-HSC were constructed using the formula:

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

where NSI is the normalized suitability index and P is the central proportion of the data distribution under the curve (Bovee 1986). We constructed the use-HSC for depth and mean column velocity using this approach by defining P as the 50, 75, 90, and 95% portions of the distribution using the nonparametric tolerance limits table found in Somerville (1958) and a confidence level of 95%.

We graphically compared the diurnal use and bioenergetic-HSC to evaluate differences. We also compared microhabitat suitability values from the two diurnal HSC models calculated from independent observations of microhabitat use by brook trout in section C of Hunt Creek. We collected the diurnal habitat use data in section C of Hunt Creek during the summers of 1991-92 using the same methods employed in section B. We made the comparison between the two models by calculating suitability values for observational data collected in section C of Hunt Creek using both HSC models and evaluated the hypothesis that suitability scores would be equal between the two methods. We tested the null hypothesis with the Wilcoxon sign rank test for paired samples (Zar 1984). We calculated microhabitat suitability scores by multiplying depth and velocity suitability values, as in a PHABSIM analysis (Milhous et al. 1989).

## Results

### Bioenergetic-HSC

We collected invertebrate drift samples over a range of mean column velocities from 2 to 82 $cm \cdot s^{-1}$. Total $calories \cdot hr^{-1}$, corrected to a depth of 25 cm, ranged from 2.1 to 1428.2. The regression of $calories \cdot hr^{-1}$ versus mean column velocity was significant (F=41.6, df=1,148, p<0.001; Figure 3). However, because we forced the regression through the origin we were 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.

The relationship between mean invertebrate length (mm) and mean velocity was linear and positive over the range of velocities sampled (Figure 4). This regression was also significant ($F=26.4$, $df=1,144$, $p<0.01$, $r^2=0.16$). We used the regression equation describing the relationship between velocity and mean invertebrate length 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 RD as a proportion of 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 before reaching a maximum and then decreased to zero (Figure 6). Maximum values of MCD occurred at velocities between 5 and 25 $cm \cdot s^{-1}$ depending on fish size.

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

We developed two nonlinear regression equations relating focal point velocity (FPV, $cm \cdot s^{-1}$) to mean column velocity (MCV, $cm \cdot s^{-1}$) from 287 observations of foraging brook trout. The equations were:

$$FPV = MCV^{0.819}, \; r^2 = 0.789 \quad \text{and} \qquad (3)$$

$$FPV = 2.973 * MCV^{0.5}, \; r^2 = 0.782. \qquad (4)$$

We predicted swimming cost from both equations in the calculation of the net benefit curves and found little difference in the results. Therefore, the results presented here were all calculated using equation (4) because we believe it more accurately reflects the selection of microhabitats with the smallest swimming cost in relation to benefit at higher velocities.

Brook trout swimming cost curves 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 is greater than zero at zero velocity, because the equations in Beamish (1980) included the standard metabolic rate.

The net benefit curves 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 is dramatic: the minimum velocity at which a 5 cm fish received a net benefit is slightly higher than 0 $cm \cdot s^{-1}$, but the largest fish (20 cm) must occupy a microhabitat with a mean column velocity of at least 6 $cm \cdot s^{-1}$ to receive a net benefit. These curves indicate that as brook trout increase in length they must seek out 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 receive a maximum benefit of only approximately 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 approximately 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 assume the depth at the microhabitat location is at least equal to the MCD for the fish.

The bioenergetic-HSC for depth (Figure 11) demonstrated that the suitability of the depth at a particular microhabitat location in a stream is dependent on 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 while it was only 0.86 for a 15 cm fish. The dependence of the suitability of the depth on the 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.

## Use-HSC

We 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 was 98 $cm \cdot s^{-1}$.

Diurnal use-HSC for depth also indicated a range of optimal depths for both young of the year and yearling and older fish (Figure 13). The range of optimal depths for young of the year fish was from 15 to 34 cm and usable depths were from 3 to 67 cm. The optimal depth range for yearling and older fish was from 27 to 55 cm while the range of usable depths was from 12 to 85 cm. 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. Yearling and older brook trout used a wider range of depths than young of the year and tended to be found in deeper water.

We 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 for young of the year brook trout was from 5 to 23 $cm \cdot s^{-1}$ and was from 4 to 22 $cm \cdot s^{-1}$ for yearling and older brook trout (Figure 14). The range of usable velocities was from 0 to 39 $cm \cdot s^{-1}$ for young of the year and was from 0 to 54 $cm \cdot s^{-1}$ for yearling and older fish. 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 depth and mean column velocity habitat use 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 lifestage 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 lifestage.

### 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-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.

We 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 was not rejected 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 (mean=0.691) than for the bioenergetic-HSC model (mean=0.497) in section C but not for yearling and older fish. 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 and were more restrictive in predictions of optimal as well as usable mean column velocity ranges for both young of the year and yearling and older foraging brook trout. An important distinction between the two sets of HSC is that bioenergetic-HSC curves indicated that there was a single velocity that 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 of 0.2 and 0.5 for young of the year and yearling and older fish respectively at a velocity equal to zero 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). 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, and competition for foraging stations forces some fish to occupy suboptimal sites or net energy gain from foraging is not what determines brook trout foraging habitat use in Hunt Creek. In addition, the fact that foraging fish were observed in microhabitats with a mean column velocity of zero may be the result of insufficient sensitivity of the measuring instrument 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 we did find oligochaetes in the drift samples we collected, they were a very minor component of the drift. It may also result from fish occupying habitats with a focal point velocity greater than zero but a mean column velocity of zero. 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.

A second difference between the HSC was that 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 we observed in

Hunt Creek were found holding position in calm water and feeding in faster adjacent water.

Another difference between bioenergetic-HSC and use-HSC was in the prediction of optimal velocity 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 abscence 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 were minimizing energetic expenditure during the resting period. By minimizing energy expenditure for swimming the fish were maximizing the amount of energy gained during foraging 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, (Baker and Coon 1995) 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 indicated that a reduction in discharge of 98% in section B of Hunt Creek would reduce WUA 37-70% based on use-HSC, but bioenergetic-HSC predicted a WUA 75-99% reduction in WUA.

We did not include cover and substrate components in bioenergetic-HSC modeling directly. 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). We 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 fishes focal point velocity choice. In addition, we 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 almost entirely composed 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), but have no abundance data on avian or mammalian predators. A variety of avian, mammalian, and reptilian predators of trout (Alexander 1979) are present in the study area but we only rarely observed great blue herons *Ardea herodias* and belted kingfishers *Megaceryle alcyon* and never observed any mammalian 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 using the methodology presented here may offer an improvement to those based on frequency-of-use data alone and bioenergetic-HSC may be a more accurate representation of the suitability of foraging microhabitats in Hunt Creek.

However, we suggest that further research should be completed to validate the mechanistic basis for construction and use of bioenergetically-derived HSC as well as 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). We suggest research into 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 as well as 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. Although we did not quantify swimming speed during foraging attempts, observational data collected in Hunt Creek indicate that foraging brook trout do not swim at burst speed when foraging. We also suggest research into the importance of cover and substrate composition to drift feeding fish as they affect predator avoidance and swimming cost.

Previous research on stream-dwelling salmonids as well as other stream-dwelling drift feeders has demonstrated that drift-feeding fishes in streams select microhabitats that maximize the energetic gains in foraging (Fausch 1984, Smith and Li 1983, Hughes and Dill 1990, Hill and Grossman 1993). We recommend this principal should be applied to the construction and use of bioenergetic-HSC for drift-feeding stream fish because bioenergetic-HSC should better represent the suitability of foraging microhabitats. As we hypothesized in the Introduction, HSC based on frequency-of-use data alone may not represent the suitability of microhabitats, particularly for territorial, drift-feeding fishes.

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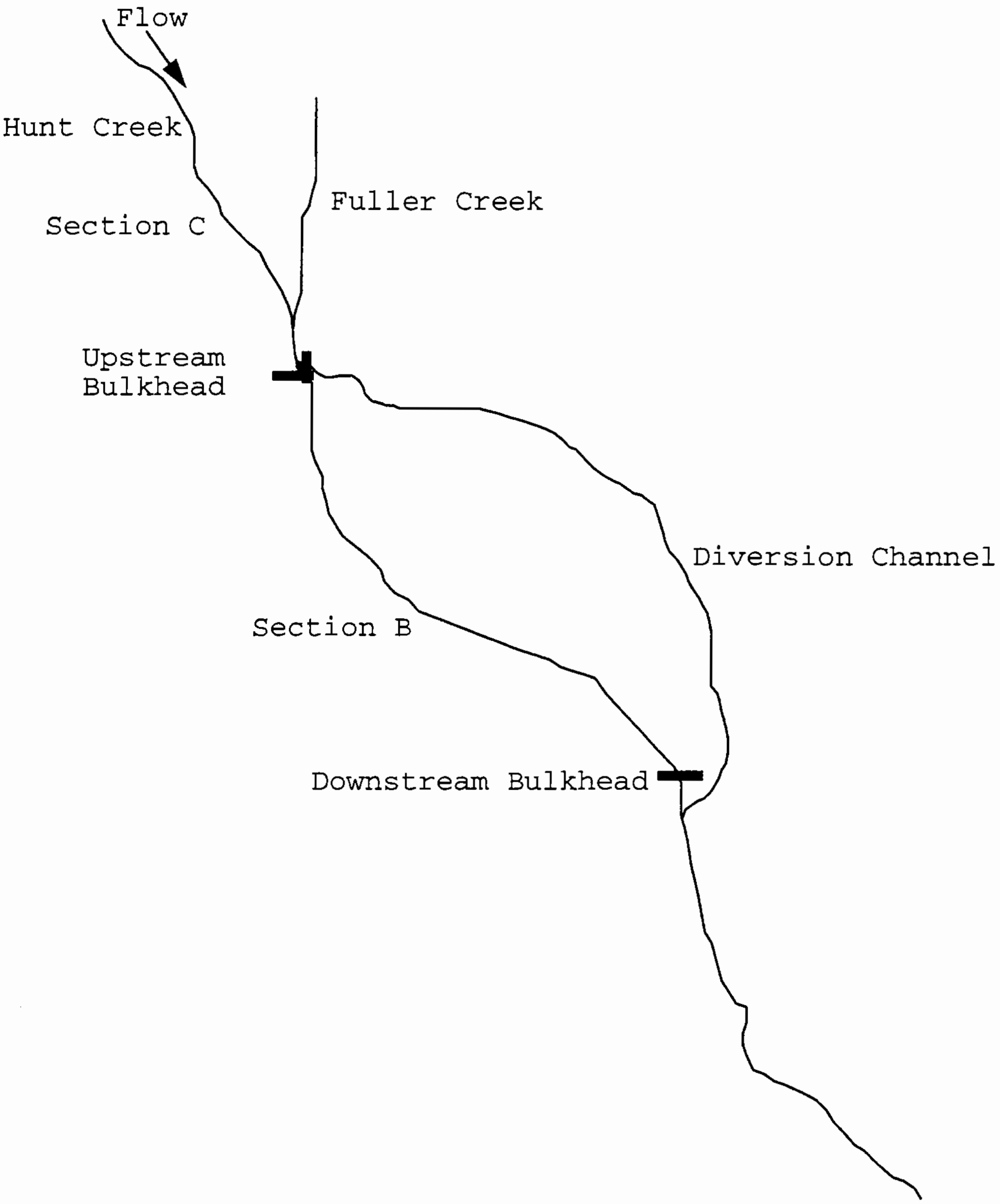

Figure 1. Map of Hunt Creek study area. The upstream bulkhead is the boundary between sections C and B, the downstream bulkhead is the downstream boundary of section B.

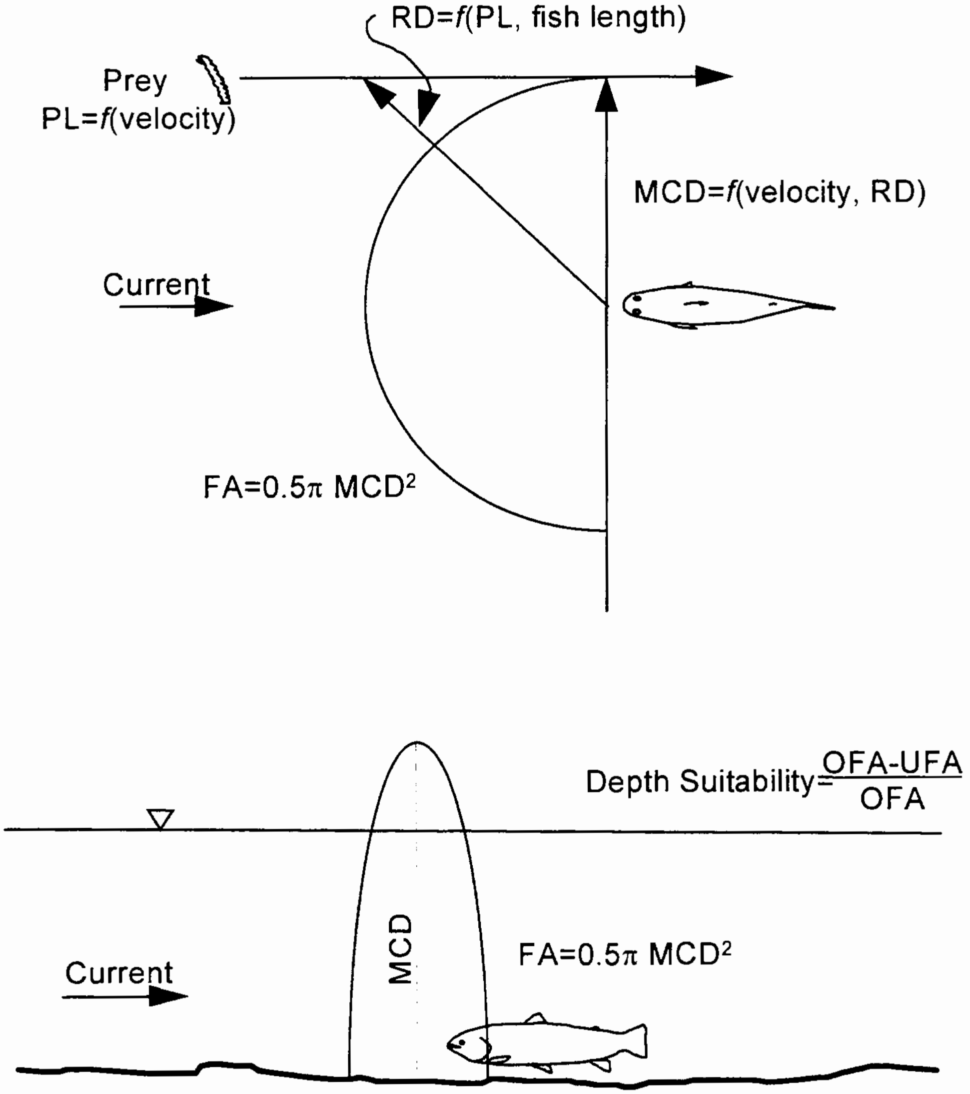

Figure 2. Parameters used in estimating bioenergetic benefits of brook trout foraging microhabitats (adapted from Hughes and Dill 1990). The foraging area (FA) is a two dimensional semi-circular plane perpendicular to the direction of the current with radius equal to the maximum capture distance (MCD).

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

| Length (cm) | Weight (g) | I (Intercept) | S (Slope) | $r^2$ | 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 |

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 ≥ 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%.

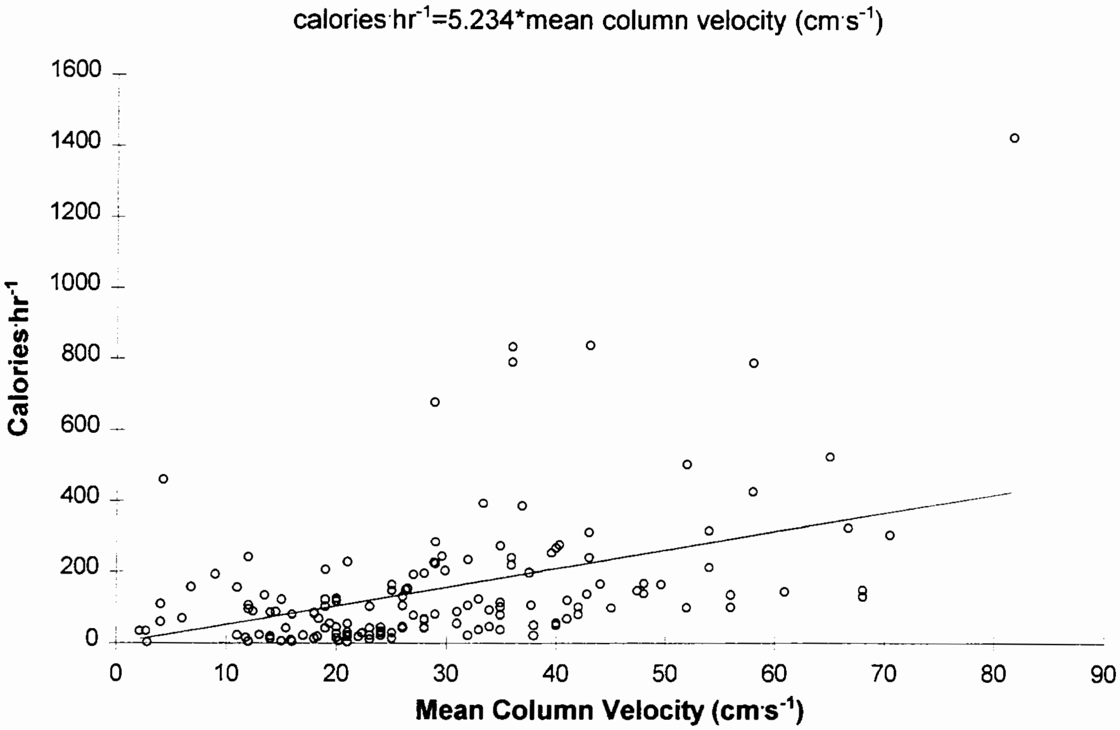

Figure 3. Calories·hr$^{-1}$ in relation to mean column velocity (cm·s$^{-1}$) from drift samples collected in Hunt Creek at locations where brook trout were observed feeding in section B and on the fixed transect in section B.

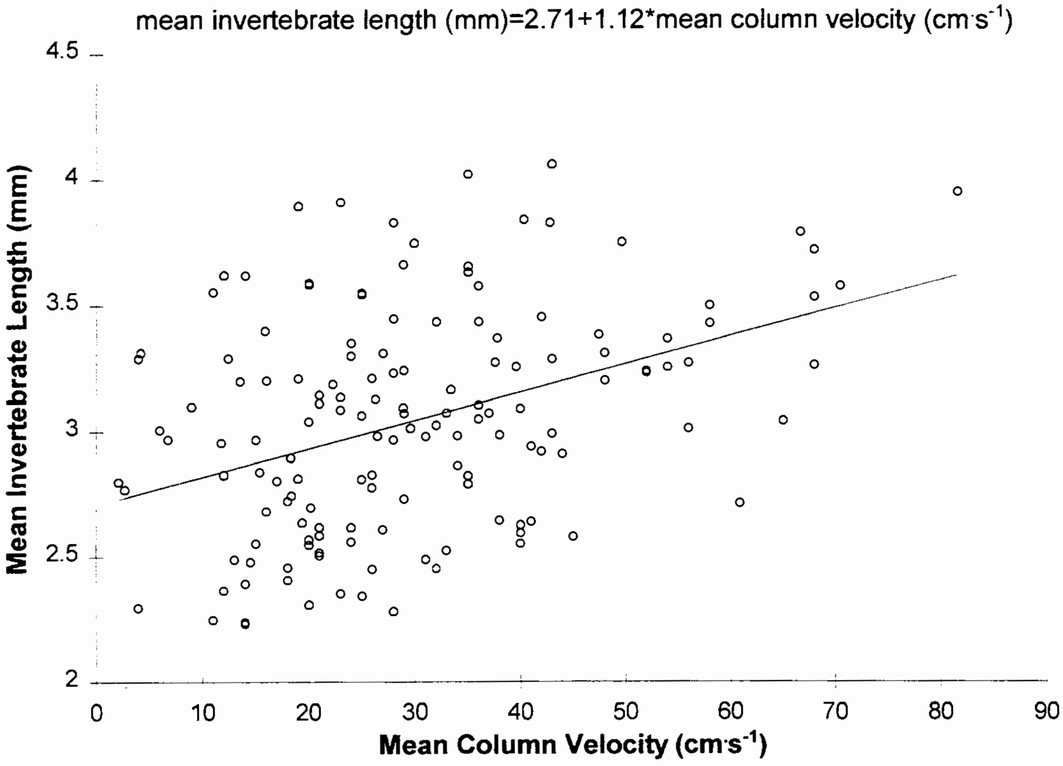

Figure 4. Mean invertebrate length (mm) in relation to mean column velocity ($cm \cdot s^{-1}$) for drift samples collected in Hunt Creek at locations where brook trout were observed feeding in section B and on the fixed transect in section B.

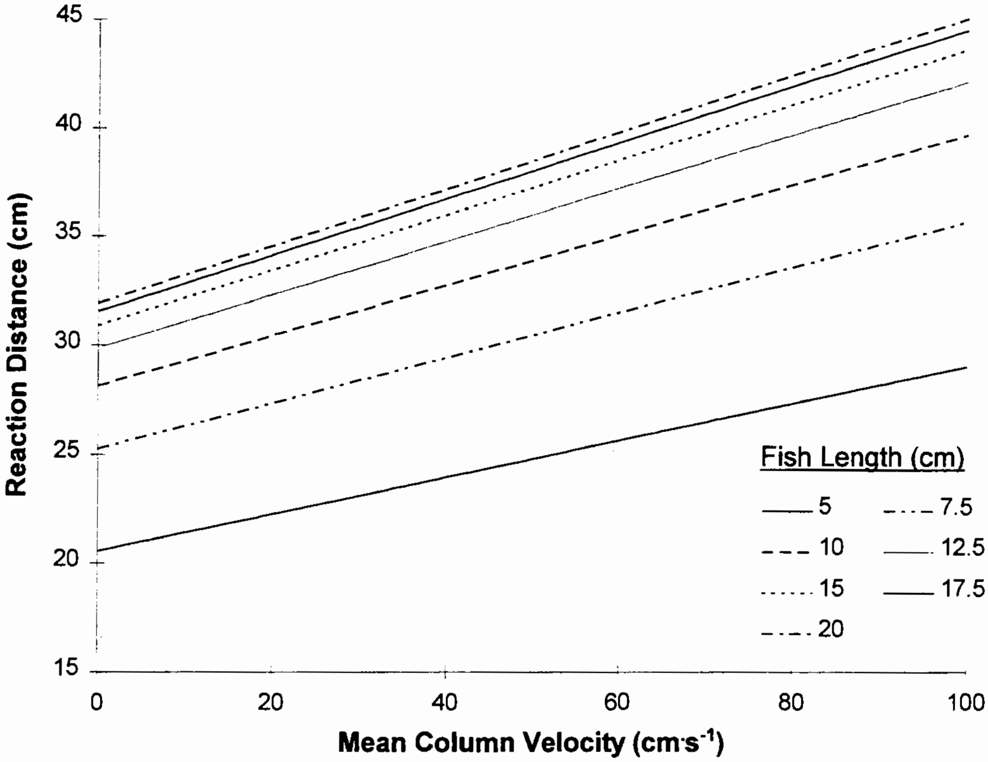

Figure 5. Reaction distance (RD) as a function of current velocity (cm·s$^{-1}$) for foraging brook trout in Hunt Creek.

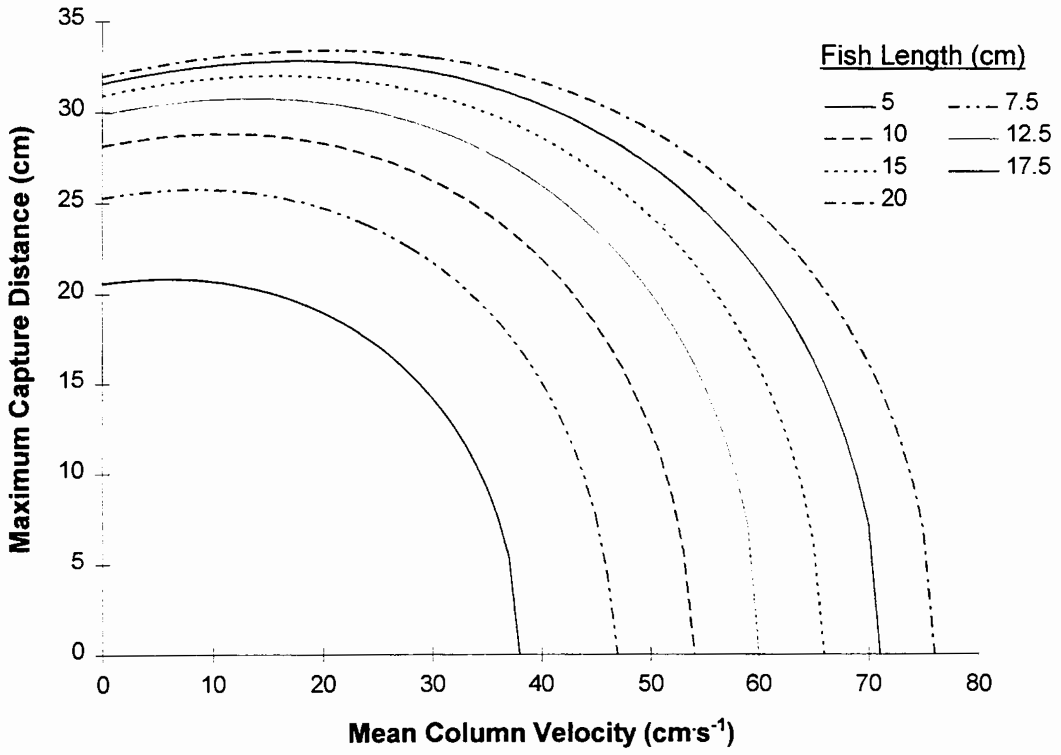

Figure 6. Maximum capture distance (MCD) as a function of current velocity (cm·s$^{-1}$) for foraging brook trout in Hunt Creek.

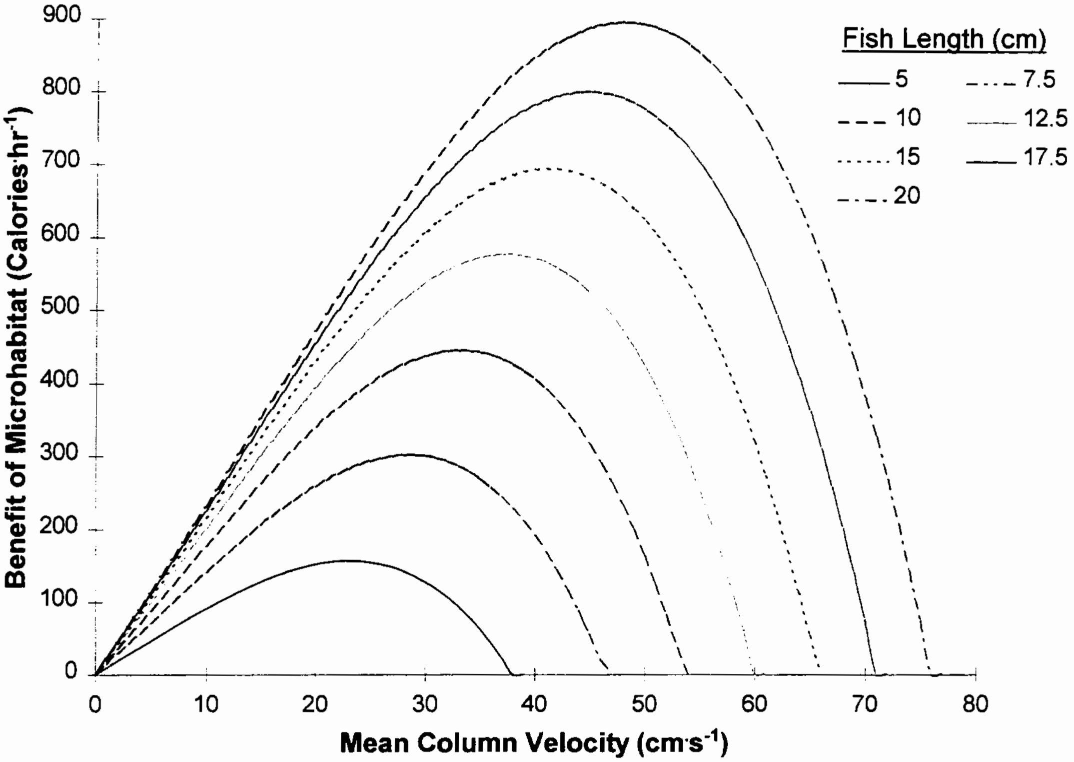

Figure 7. Benefit estimates based on length (cm) of brook trout and current velocity (cm·s$^{-1}$) for foraging microhabitats in Hunt Creek. Benefit estimates are based on a microhabitat depth greater than or equal to the fish's MCD.

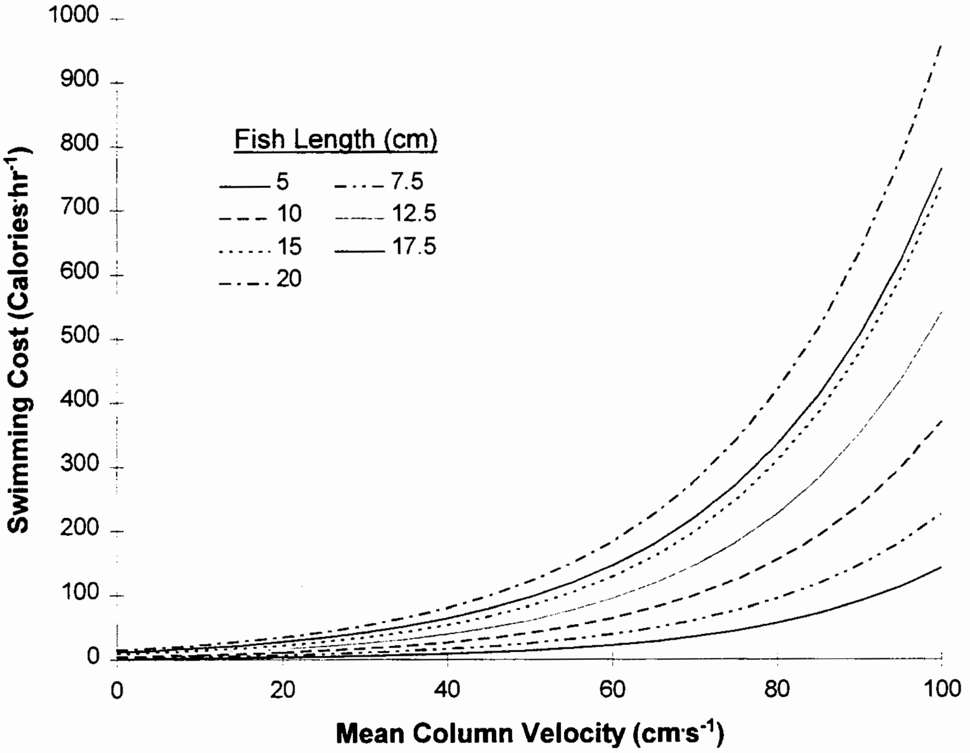

Figure 8. Brook trout length specific swimming cost estimates (calories·hr$^{-1}$) versus current velocity (cm·s$^{-1}$) based on equations given in Beamish (1980).

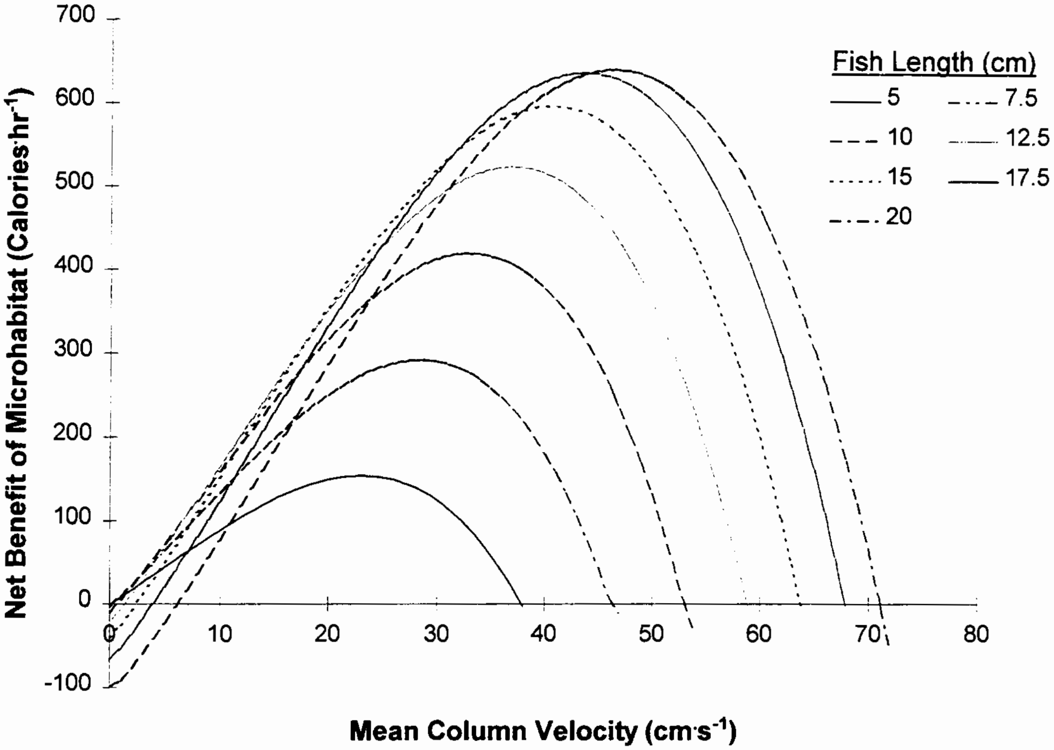

Figure 9. Length specific net caloric benefit (calories·hr$^{-1}$) curves for brook trout foraging microhabitats in Hunt Creek as a function of current velocity (cm·s$^{-1}$).

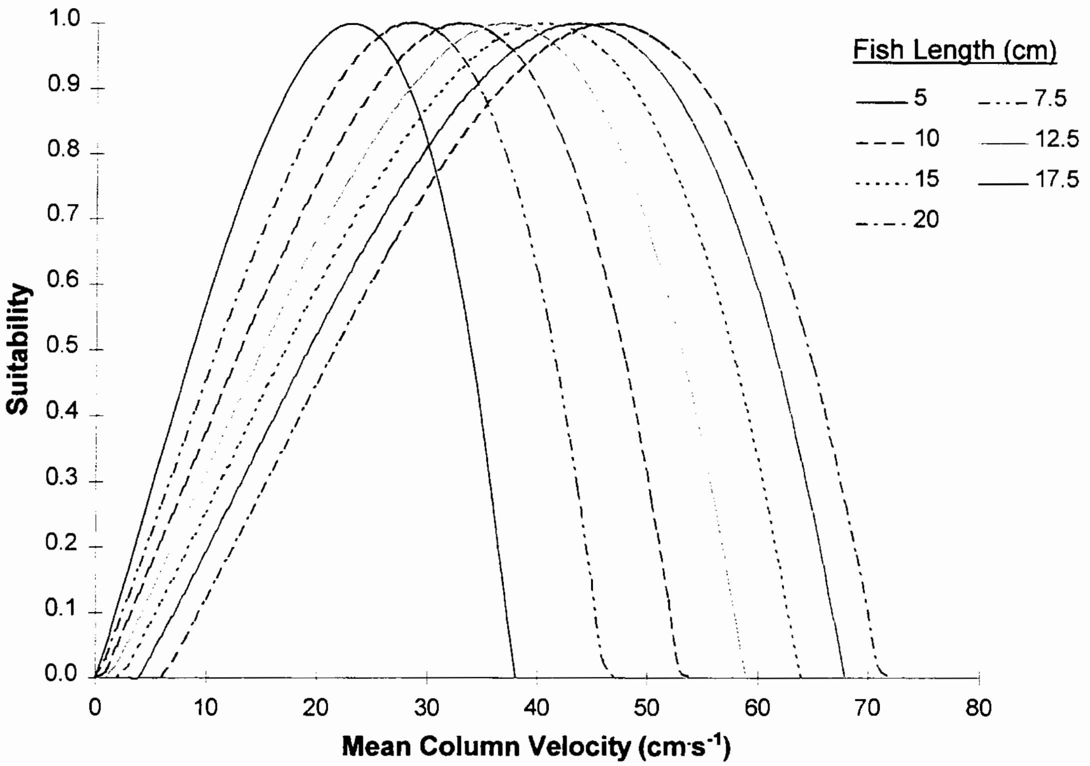

Figure 10. Brook trout length specific bioenergetically derived velocity habitat suitability criteria for foraging microhabitats in Hunt Creek.

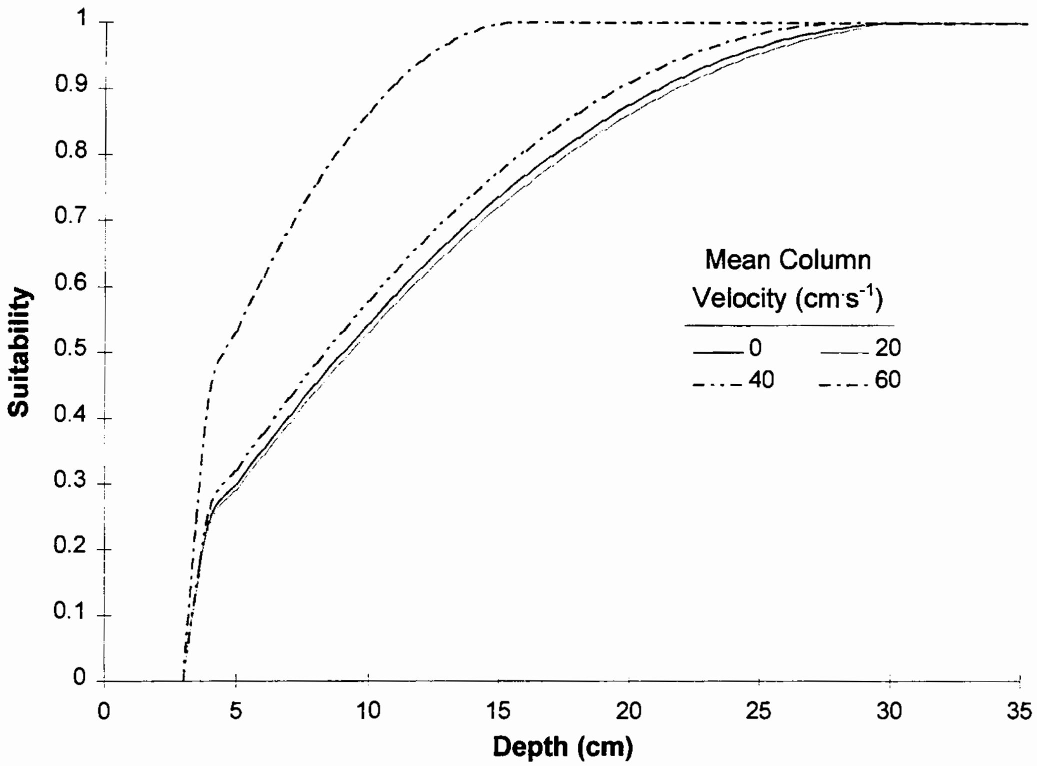

Figure 11. Example depth suitability curves for 15 cm brook trout in relation to current velocity in Hunt Creek.

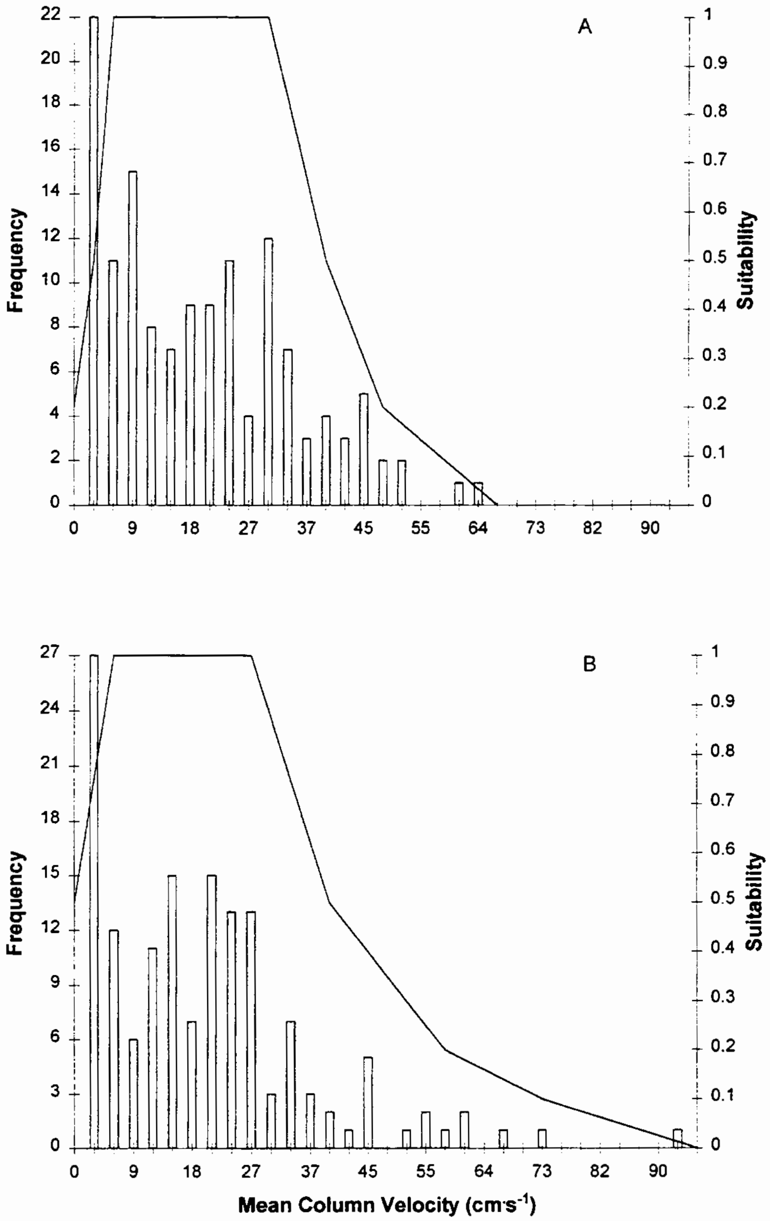

Figure 12. Mean column velocity (cm·s$^{-1}$) frequency-of-use data and use-HSC for foraging young of the year (A) and yearling and older (B) brook trout in Hunt Creek. Histogram represents use data and line represents suitability.

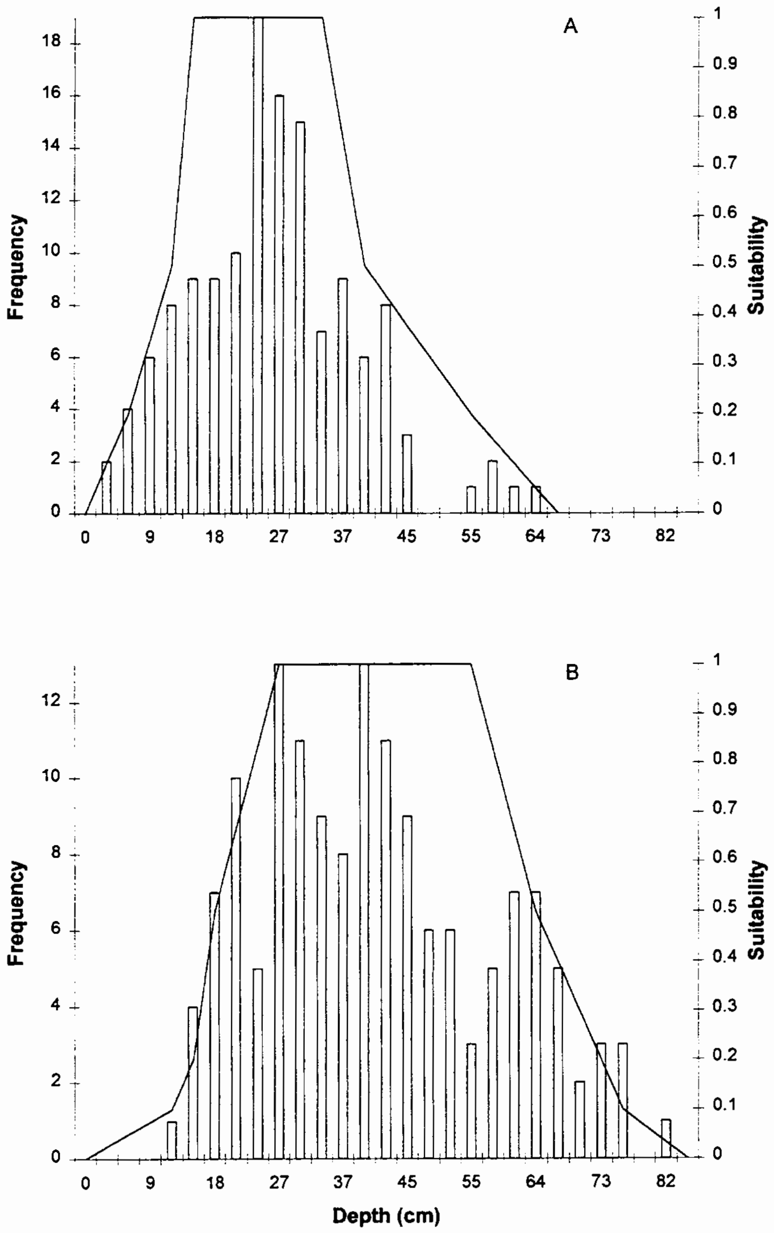

Figure 13. Depth (cm) frequency-of-use data and use-HSC for foraging young of the year (A) and yearling and older (B) brook trout in Hunt Creek. Histogram represents use data and line represents suitability.

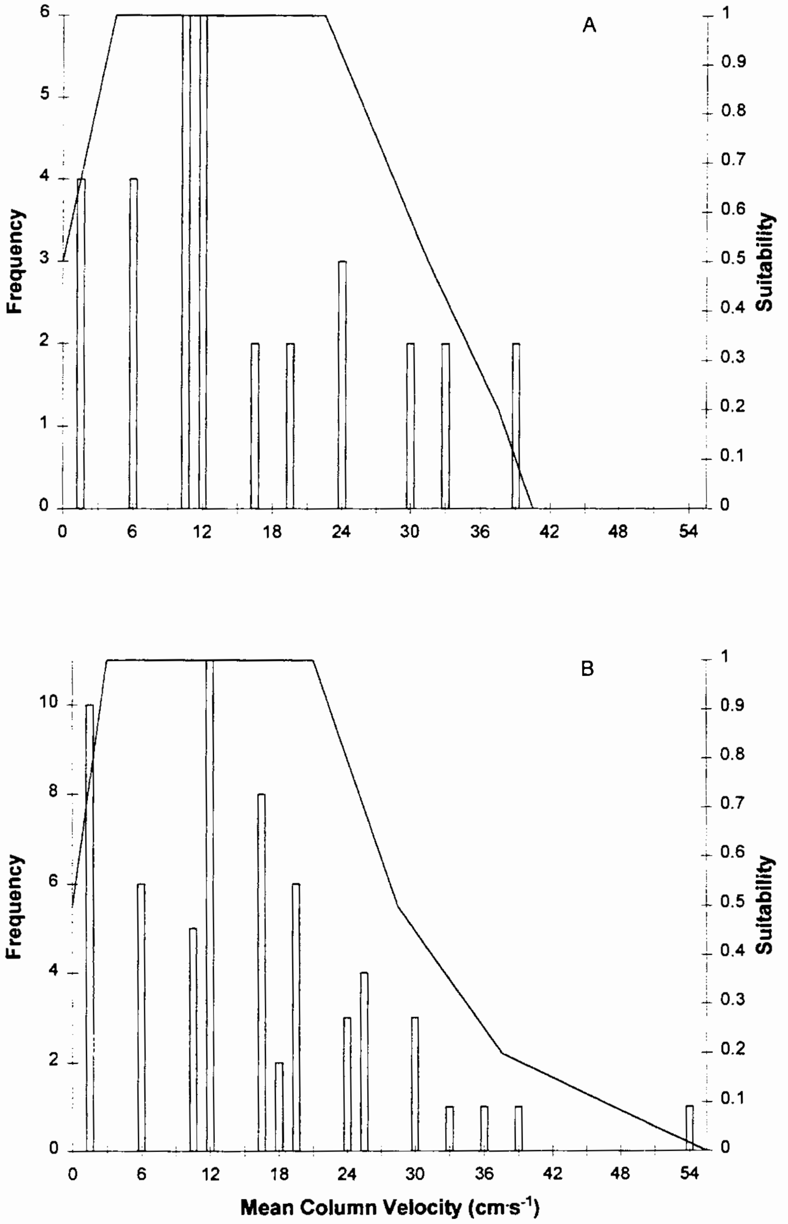

Figure 14. Mean column velocity ($cm \cdot s^{-1}$) frequency-of-use data and use-HSC for resting young of the year (A) and yearling and older (B) brook trout in Hunt Creek. Histogram represents use data and line represents suitability.

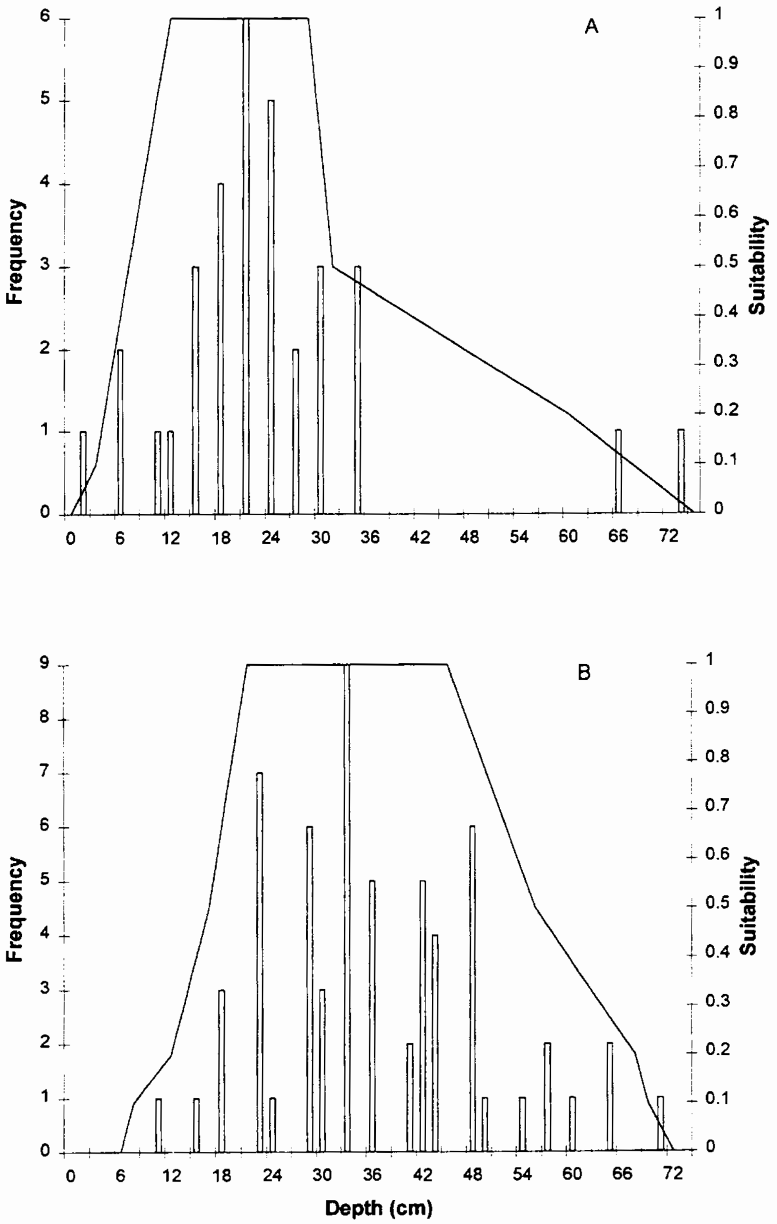

Figure 15. Depth (cm) frequency-of-use data and use-HSC for resting young of the year (A) and yearling and older (B) brook trout in Hunt Creek. Histogram represents use data and line represents suitability.

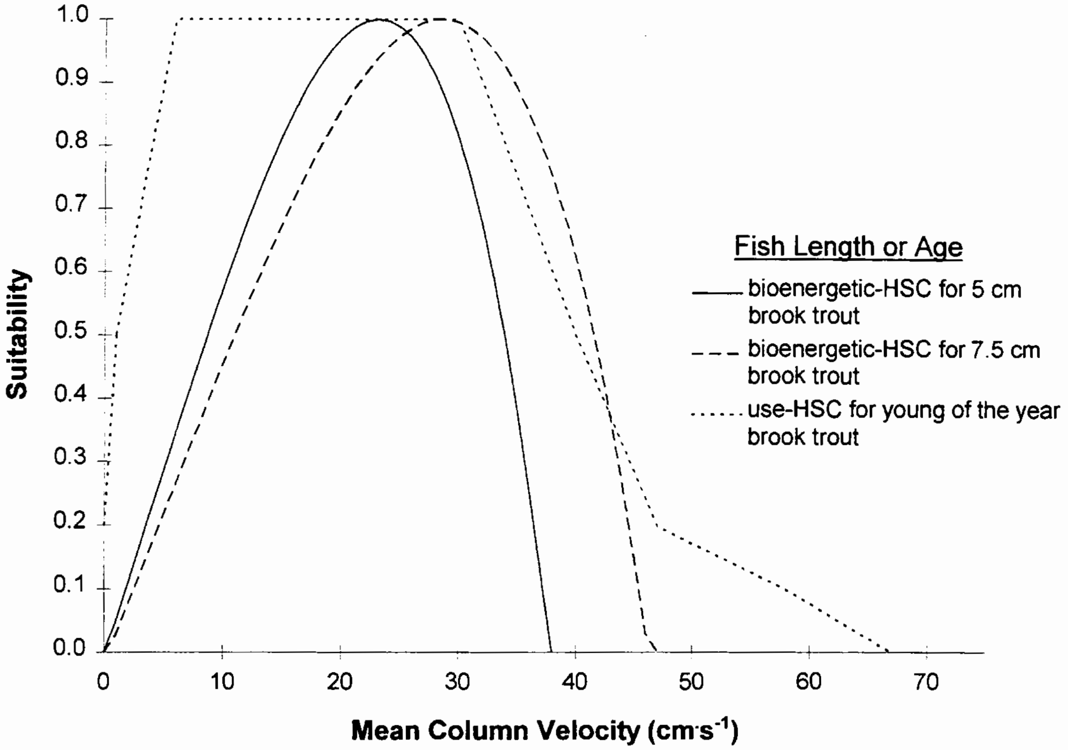

Figure 16. Graphical comparison of mean column velocity use-HSC and bioenergetic-HSC for foraging young of the year brook trout in Hunt Creek.

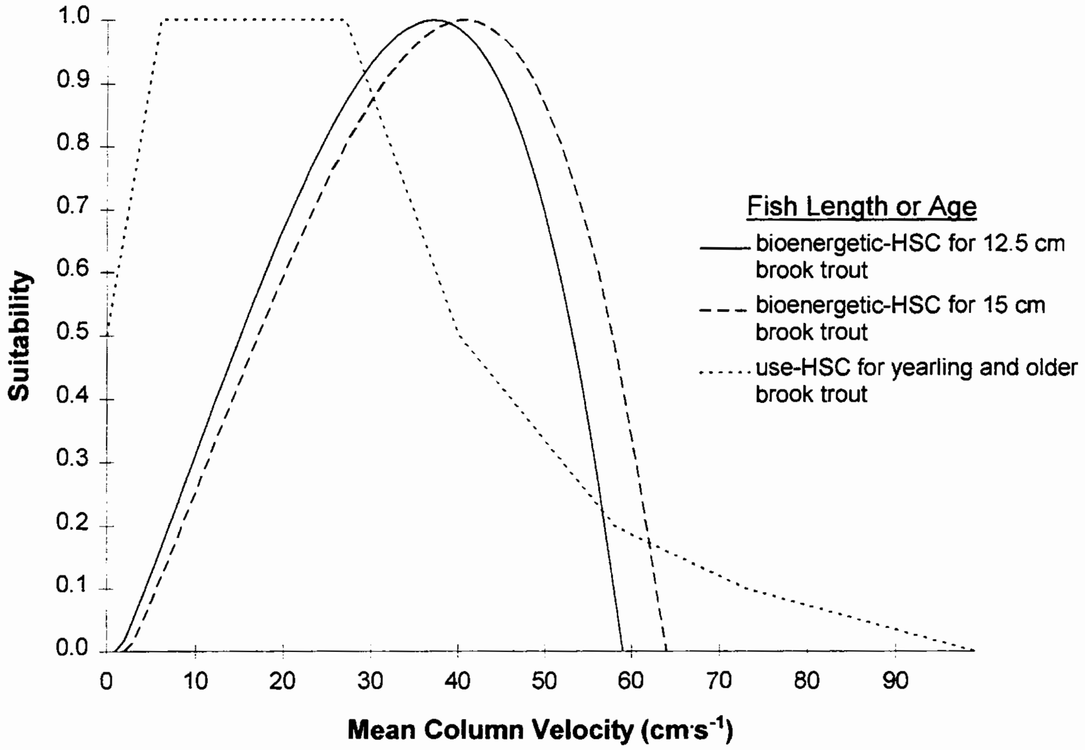

Figure 17. Graphical comparison of mean column velocity use-HSC and bioenergetic-HSC for foraging yearling and older brook trout in Hunt Creek.