

Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles

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Abstract: To assess freshwater habitat requirements of juvenile anadromous cutthroat trout, *Oncorhynchus clarki*, we measured habitat preference and growth rates of young-of-the-year (YOY) and 1- to 2-year-old fish confined to either pools or riffles in Hudson Creek, British Columbia, during 1999. YOY preferred pools to riffles in habitat-preference experiments, despite normally occurring at lower densities in pools. YOY grew in both pools and riffles when experimentally confined to either habitat, but growth rates were higher in pools. Larger juvenile cutthroat trout, on average, grew in pools, but consistently lost weight in riffles, indicating that pools are a habitat preference for YOY but a requirement for larger fish. A bioenergetic cost-benefit analysis (based on swimming costs and energy intake from invertebrate drift) indicates that energetics alone are sufficient to account for avoidance of riffles by larger cutthroat trout, without having to invoke greater predation risk in shallow habitats. Energetics modeling demonstrates that the smaller size and energetic needs of YOY allow exploitation of habitats (e.g., pocket pools in riffles) that are unavailable to larger fish.

Résumé : Dans le but de déterminer les exigences d'habitat des jeunes Truites fardées anadromes, nous avons mesuré la préférence d'habitat et les taux de croissance chez des jeunes de l'année (yoy) et des poissons de 1-2 ans, confinés dans des profonds ou dans des rapides de Hudson Creek en Colombie-Britannique, Canada, en 1999. Les jeunes Truites fardées de l'année préfèrent les profonds aux rapides dans des épreuves de choix d'habitat, bien qu'elles soient normalement moins nombreuses dans les profonds; ces truites croissent dans les deux habitats lorsqu'on les confine expérimentalement dans l'un ou l'autre milieu, mais les taux de croissance sont supérieurs dans les profonds. En moyenne, les truites plus grandes croissent dans les profonds, mais elles subissent systématiquement une perte de masse dans les rapides, ce qui indique que les profonds sont un habitat préféré pour les jeunes de l'année, mais un habitat essentiel pour les truites plus grandes. Une analyse bioénergétique de coûts/bénéfices (basée sur les coûts de la nage et les apports d'énergie tirés de la dérive des invertébrés) montre que les considérations énergétiques seules suffisent à expliquer pourquoi les truites plus grandes évitent les rapides, sans qu'il soit nécessaire d'invoquer le risque accru de prédation dans les habitats peu profonds. La modélisation des relations énergétiques démontre que la taille et les besoins énergétiques réduits des truites de l'année leur permettent d'exploiter des habitats (e.g. les petites fosses dans les zones de rapides) qui ne sont pas disponibles aux poissons plus grands.

[Traduit par la Rédaction]

Introduction

Defining habitat requirements of fish is a necessary first step towards identifying and protecting critical habitat features. Habitat "requirements" is a commonly used but poorly defined expression; by habitat requirements, we refer to features of the environment that are necessary for the growth and persistence of individuals and populations. The habitat requirements of mobile life stages of fish are typically inferred from field surveys documenting the selection of dif-

ferent habitats (e.g., Moyle and Baltz 1985), in which selection is measured in terms of differential use or occupancy of particular habitats. However, it has been demonstrated that habitat use in the wild may not necessarily reflect habitat preference in the absence of biotic interactions, particularly for juvenile fish, which may be forced into suboptimal habitats by competition or predation (Werner and Hall 1988; Harvey 1991). This may lead to erroneous conclusions with respect to habitat preference (Mathur et al. 1985), including, for instance, the construction of biased habitat suitability curves for use in instream flow type methodologies. It is also implicitly assumed that habitat selection (differential habitat use in the wild) or preference (habitat selection in controlled choice experiments) accurately reflects the true benefits of using different habitats, but this assumption is rarely validated by measuring the fitness consequences (e.g., growth or survival) of using different habitat types (but see Lonzarich and Quinn (1995) for a good example of the survival consequences of differential habitat use).

Juvenile cutthroat trout (*Oncorhynchus clarki*) rear in very small streams that are vulnerable to habitat degradation from

Received May 26, 2000. Accepted January 21, 2001.
Published on the NRC Research Press Web site on March 7, 2001.
J15788

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forestry and urbanization (Reeves et al. 1997), but their freshwater habitat requirements are poorly understood (Hall et al. 1997). Young-of-the-year (YOY) fish are most abundant in shallow riffle and glide habitat (Glova 1984), whereas larger parr are most abundant in deeper pool habitat (Rosenfeld et al. 2000). To determine whether habitat selection accurately reflects habitat preference, we performed habitat choice experiments with YOY in a natural stream. We then assessed the requirement for different habitats at summer low flow by measuring the growth rates of YOY (40–60 mm) and larger (120–160 mm) juvenile cutthroat trout confined to replicate pool and riffle habitats.

Preferential use of deeper pool habitat by fish is usually attributed to greater vulnerability to avian or terrestrial predators (Power 1984; Lonzarich and Quinn 1995). However, the costs and benefits of using shallow fast habitat versus deep slow habitat will also differ for drift-feeding fish, regardless of predation. Hughes and Dill (1990) developed a model for predicting microhabitat choice by drift-foraging Arctic grayling (*Thymallus arcticus*), based on the costs of swimming and the energy content of drifting invertebrate prey. We measured invertebrate drift rates in pools and riffles and used their model to estimate the energetic costs and benefits of exploiting pool versus riffle habitats for juvenile cutthroat trout. We then evaluated whether allometric differences in net energy gain were sufficient to account for observed differences in growth rates and habitat use by YOY and older fish, irrespective of predation risk.

Materials and methods

Experiments were performed in Husdon Creek, a small coastal British Columbia stream with an average bankfull width of 3.5 m and a summer base flow of approximately 30 L·s⁻¹. Husdon Creek was chosen because it typifies the small-stream habitat in which juvenile anadromous coastal cutthroat trout are most abundant (Rosenfeld et al. 2000). The Husdon Creek basin is primarily second-growth forest, with a drainage area of 3.4 km². The fish community consists of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout in three age-classes (YOY, 1+, and 2+ fish). Cutthroat trout and coho salmon densities are relatively high, averaging 0.92 and 0.2 fish/m², respectively, during summer base flow (J. Rosenfeld, unpublished data). The reach of stream used for experiments had approximately 75% canopy cover, a 1% gradient, substrate dominated by gravel and sand, and abundant large woody debris (LWD; 0.37 pieces of LWD/linear m) in a forced pool–riffle channel.

Enclosures were created by fencing off individual channel units, using 6.5 mm wire mesh supported by steel re-enforcing rod (the terms enclosure, channel unit, pool, or riffle are used interchangeably to refer to experimental units throughout the text). Fences were installed across the head and bottom of each pool or riffle, with the bottom skirt stapled to a wood two-by-four (1.625 × 3.625 in. (1 in. = 25.4 mm)) buried under the substrate. Substrate and cover within each channel unit were left intact. The 6.5-mm mesh was permeable to most invertebrates in the stream, with the exception of the largest instars of the stonefly *Pteronarcys* sp. Eight pools and seven riffles were isolated over a 400-m reach of stream, with five channel units as isolated enclosures and the remaining channel units in four separate groups of two to four adjacent channel units (adjacent channel units shared a common fence, with one channel unit upstream of the other). Channel units were selected on the basis of their obvious classification as pools or riffles (see Table 1 for differences in depth and velocity between habitats) and the additional criterion that fences could be installed without major habitat disturbance (e.g., removal of LWD). Channel units that met

these criteria were scattered throughout the reach, and were similar in depth and surface area to pools and riffles surveyed over a 600-m length of stream that included the study reach. Although all enclosures had sufficient instream cover (cutbank, boulder, small or large woody debris) to provide refuge from terrestrial predation, cover in riffles was usually not associated with optimal foraging locations where fish could observe drifting invertebrates. To test whether cover affected the growth of large fish in riffles and pools, a 45 cm wide strip of 3-mm plastic screening attached to a wooden frame was placed across the stream 5–10 cm above the water surface in three riffles and three pools.

Because of the limited number of enclosures, growth rate experiments with YOY and older trout were run sequentially. All 15 enclosures were used to measure growth rates of larger juvenile cutthroat trout from 28 June to 3 August 1999, and eight enclosures were used to measure growth rates of YOY from 5 to 31 August 1999. The growth of larger fish was measured first because YOY were too small to be retained by the 6.5-mm mesh until the beginning of August. Stream temperature was similar in July and August, averaging 11.4 and 12.4°C, respectively. Fewer replicates were used for YOY growth because YOY were stocked at a higher density than larger trout and were therefore less subject to loss of replication through individual fish mortality (most enclosures were stocked with three to six YOY vs. a single larger trout).

Fish were removed from enclosures prior to stocking using minnow traps and multiple-pass electrofishing. Large fish stocked in enclosures were captured with minnow traps from the reach in which the experiments were performed. Large fish were stocked at a relatively low density (0.17 fish/m²), to ensure that density-dependent effects did not confound habitat effects, and fish were stocked at equivalent densities in pools and riffles. Fewer large fish were stocked in pools than were captured in pools; however, large fish were not captured in riffles. Most enclosures had a relatively small surface area and were stocked with a single fish, but three of the larger pools received two fish and the largest pool received three fish. All fish were uniquely marked subcutaneously with visible implant elastomer (Northwest Marine Technology, Shaw Island, Wash.) to permit measurement of individual growth rates. Following marking, fish were held overnight to clear stomach contents, weighed to the nearest 0.01 g, measured to the nearest millimetre, and stocked in enclosures. Fish were collected 36 days later using minnow traps and electroshocking, and were again weighed and measured after being held overnight to clear gut contents.

Because many YOY were small enough to pass through a 6.5-mm mesh, a 3-mm mesh was placed over the original fencing. YOY were collected by electrofishing, because of low capture rates in minnow traps. YOY were individually marked, held overnight, weighed, measured, and released into four pools and four riffles (from 5 to 6 August) at the relatively low density of 0.5 fish/m² to prevent density-dependent effects. After 27 days, fish were recovered from enclosures by electrofishing, and were again weighed and measured after being held overnight. Screens were cleaned daily or as necessary throughout the experiments to maintain natural flow in enclosures.

Habitat preference of YOY

To assess the habitat preference of YOY, the center transverse fence separating adjacent pool and riffle channel units was removed to create three replicate pool–riffle sequences. The transverse wire-mesh fence separating each pool and riffle was replaced with a fine-mesh stop net buried beneath the substrate surface. We stocked individually marked fish at roughly equal densities (0.55 ± 0.13 fish/m² (mean ± SD)) in both pools and riffles on 8 August, leaving fish free to move between habitats within each replicate pool–riffle sequence. Fewer fish were stocked in riffles than in pools because riffles had smaller surface areas. Pools and riffles were isolated 1 week later when concealed observers on the stream

Table 1. Physical characteristics of the pools and riffles used for growth experiments performed in Husdon Creek, B.C., in 1999.

Habitat	<i>n</i>	Area (m ²)	Mean depth (cm)	Maximum depth (cm)	Mean velocity (cm·s ⁻¹)
Pool	8	14.4 (8.0–22)	21.6 (16.7–25.4)	45.4 (37–51)	6.6(3.9–8.9)
Riffle	7	7.4 (5.3–9.1)	6.2 (5.0–7.7)	14.1 (12–18)	21.0 (15.6–24.5)

Note: Values are mean, with range given in parentheses.

bank quickly lifted buried stop nets by pulling on ropes attached to net ends. Fish were then recovered from separate pool and riffle habitats by multiple-pass electroshocking.

To examine the potential effect of predation by larger trout on YOY distribution, stop nets were buried again, and fish were returned to the channel unit from which they had been collected in each pool–riffle sequence. Large cutthroat trout (124–173 mm) were then stocked in pools at twice the density used in the growth-rate experiment. After 1 week, stop nets were again raised and fish were collected as in the first habitat preference experiment.

Measurement of foraging windows

Observations were made on cutthroat trout focal depths and velocities to estimate the size of foraging windows available to fish in pools and riffles; a foraging window is defined as the cross-sectional area of a stream surrounding a fish's focal point where it is capable of intersecting drift (Hughes and Dill 1990). A single focal point location of a drift-feeding fish was recorded in each enclosure for both small and large fish separately during the growth rate experiments (*n* = 8 pools and 6 riffles for large fish; *n* = 4 pools and 4 riffles for small fish). Observations were made from behind a portable blind or from higher up the stream bank using binoculars. When fish were using cover and could not be directly observed, focal location was estimated from trajectories of fish striking at twigs thrown onto the water upstream of the focal point. Only one large fish was observed holding in a riffle enclosure during the experiment. The most probable focal-point location of fish in the remaining riffles was estimated on the basis of close proximity to cover, relatively low current velocity, and least obstructed view upstream. The focal point of a single YOY was directly observed in each pool (*n* = 4) and riffle (*n* = 4) enclosure used for the YOY growth rate experiments. In all cases, fish were estimated to be holding at 60% of total water depth.

The general method of Hughes and Dill (1990) was used to estimate the size of the window of drift available to a fish upstream of its focal point. Stream depth and velocity were measured at 10-cm intervals along a transect through the focal point perpendicular to the current, and along a second transect 30 cm upstream of the focal point. These data were then used to estimate the volume of water and the total energy content of invertebrates drifting past a fish holding at the focal point (see below).

Measurement of invertebrate drift

Invertebrate drift was measured following the removal of larger fish at the end of the first set of growth experiments. A 250 µm mesh drift net (19 cm square mouth) was placed at the observed or most probable focal point of large fish in each pool (*n* = 8) or riffle (*n* = 7) enclosure. Drift nets were left for a minimum of 6 h between 10:00 and 18:00, with sets staggered over a period of 5 days because only four drift nets were available. Maximum depth and velocity at the center of the mouth of each net were measured at the beginning and end of each set. Velocities declined by an average of 2 cm·s⁻¹ over the course of each set. Contents of drift nets were preserved in 5% formalin, and invertebrates were later sorted from detritus with a binocular microscope at 25× magnification and transferred to 80% isopropyl alcohol. Invertebrates were identified to genus using Merritt and Cummins (1984), with the exception of chironomids, which were identified to subfamily. Invertebrate length

was measured to the nearest 0.05 mm, using a digitizing system and a binocular microscope equipped with a drawing tube (Roff and Hopcroft 1986).

Data analysis

Growth rate

Relative daily growth rate of individual cutthroat trout was calculated as final weight less initial weight divided by duration of the experiment and initial body weight. When multiple fish were present in an enclosure, growth rate was estimated as the average for all fish in that enclosure. Size (YOY vs. larger trout), habitat (pool vs. riffle), and cover (screen addition vs. no screen addition) effects on growth were analyzed as a three-way analysis of variance (ANOVA, *n* = 23), following log (*x* + 0.008) transformation to normalize data and remove correlation of variance with the mean. Effects on growth were re-analyzed as a two-way ANOVA, because one of the factors (screen addition) was not significant. The constant *a* in the log (*x* + *a*) transformation was selected on the basis of the criterion of maximizing the normality of regression residuals (Berry 1987), which was assessed using the Shapiro–Wilk statistic (SAS Institute Inc. 1989) and a frequency histogram of residuals. The assumption of homogeneity of variance in ANOVA was evaluated by testing for a significant correlation between the absolute value of residuals and predicted values. All analyses met assumptions of normality and homogeneity of variance at *p* = 0.05. Data analyses were performed using PC SAS (SAS Institute Inc. 1989).

To better describe the effect of habitat on cutthroat trout over a broad range of fish sizes (rather than as two size-classes), the relative growth rate for all individual fish (*n* = 45) was regressed against initial fork length. Although individual fish from the same enclosure are not independent and cannot be treated as separate observations without inflating probability values (cf. pseudo-replication), trout are territorial and growth rates of individual fish were somewhat independent insofar as they experienced different microenvironments within each enclosure. Relative growth rates were log (*x* + 0.007) transformed, to normalize variance and remove correlation of residuals with the mean. The log–log relationship of growth rate on fork length was back-transformed to its arithmetic power function to facilitate interpretation. To adjust for the inherent bias in back-transformation of logged relationships, a correction factor (CF) for scaling back-transformed logged values to arithmetic means was calculated as $CF = e^{(MSE/2) \times 2.303}$ (where MSE is mean square error) (Baskerville 1971; Sprugel 1983).

YOY habitat choice

Change in distribution between pools and riffles during habitat preference experiments (based on single trials with three replicates) was expressed as the change in initial and final densities in riffles (initial riffle density less final riffle density for each pool–riffle sequence, evaluated as a paired *t* test, *n* = 3) and as differences in final YOY densities between pool and riffle habitats (evaluated as a simple *t* test comparing final pool and riffle densities, *n* = 3).

Drift rate

Invertebrate biomass was estimated using published length–weight relationships (Meyer 1989; Sample et al. 1993; Benke et al. 1999). Drift concentrations, as biomass per metre cubed, were cal-

culated by dividing the biomass of invertebrates collected during each drift set by the volume of water filtered by the drift net. Drift concentrations in pool and riffle habitats were then calculated as the mean for all drift sets in pools ($n = 8$) or riffles ($n = 7$). Separate drift concentrations were calculated for three size-classes of invertebrate (<2.5, 2.5–5.0, and >5.0 mm), as described by Hughes and Dill (1990), since reactive distance of drift-foraging fish depends on prey size. Differences in drift concentration between pool and riffle habitats were tested using a t test for each size-class. Drift concentrations in pools and riffles were combined to calculate an average concentration per size-class when there was no significant difference between habitats.

Estimation of energetic costs and benefits

Velocity and depth data collected along transects at fish focal points were used to estimate discharge (water volume per unit time crossing the lower transect) through adjacent 10 cm wide columns of water on either side of the focal point. Maximum lateral capture distances for the three size-classes of drifting prey were then used to estimate the volume of flow available to a fish striking prey from the focal point, as described in Hughes and Dill (1990). Three size-classes of prey were used because maximum capture distance (and therefore the volume of water scanned by a drift-foraging fish) depends on prey length (visibility). A more detailed description of the method for calculating the size of a drift-foraging window is presented in Hughes and Dill (1990).

Volume of water flowing through each 10 cm wide section of transect was calculated by multiplying cross-sectional area (CA) of the section by velocity (V). Total volume of water flowing through the drift window was then calculated by summing the discharge in each 10-cm section of transect within the reactive distance for each size-class of prey. Total energy content in the drift was calculated by multiplying total water volume and drift concentration (CONC) for each size-class of invertebrate. Invertebrate biomass was converted to energy content using a factor of 5200 Cal (= 21 790 J)·g⁻¹ dry weight (Cummins and Wuycheck 1971). Energy gain was then calculated as 60% of energy intake, to adjust for energy loss due to specific dynamic action (15%), excretion (15%), and egestion (10%) (Hewett and Johnson 1992; Tucker and Rasmussen 1999):

$$(1) \quad \text{energy gain} = \sum_{i=1}^3 \sum_{j=-n}^n C_{aij} \cdot V_j \cdot \text{CONC} \cdot 21\,790 \text{ J} \cdot \text{g}^{-1} \cdot 0.6 \cdot 3600 \cdot 10^{-6}$$

where $i = 1, 2, 3$ represents each of the three size-classes of prey, $j = -n, \dots, +n$ represents the number of sections to the left and right of the focal point, and 3600 and 10^{-6} are the respective factors to convert centimetres and seconds (the units of area and velocity, respectively) to metres and hours (see Hughes and Dill 1990).

Swimming costs (including basal metabolism) were calculated as a function of fish weight and focal velocity (V) using eq. 2 (Hughes and Dill 1990; adjusted to 10°C), assuming an average fish length and weight of 5.0 cm and 1.4 g, respectively, for YOY and 13.7 cm and 24.7 g, respectively, for larger juvenile trout:

$$(2) \quad \text{swimming cost} = 10 \cdot (C + M \cdot V) \cdot 19 \cdot \text{weight} / 1000$$

where C and M are dimensionless scalars ($C = 2.07 - 0.37 \cdot \log(\text{length})$ and $M = 0.041 - 0.0196 \cdot \log(\text{length})$) (Hughes and Dill 1990).

Net energy gain was calculated as energy gain less swimming cost for each observed holding position for YOY and larger trout in pools and riffles. Relative energy gain was expressed as the ratio of net energy gain to swimming cost (energy gain divided by metabolic costs) to produce an index of growth potential for fish of different sizes. Relative energy gain was considered preferable to simple energy intake as an index of fish growth potential because it scales energy intake to metabolic costs. Relative energy gain (net

energy intake/energy expenditure) was chosen over “efficiency” (gross energy intake/energy expenditure) because relative energy gain, like growth rate, can be negative; efficiency, on the other hand, can never be negative and is therefore a poor surrogate of growth potential for fish of different sizes.

Projections from energy modeling could not be normalized with data transformation, and habitat and size effects on energy gain, swimming cost, net energy gain, and relative energy gain were analyzed using a Wilcoxon rank sum (Mann–Whitney U) test evaluated with the Cochran–Mantel–Haenszel statistic (SAS Institute Inc. 1989), which is approximately χ^2 distributed. The ability of large fish to exploit riffle habitat was further evaluated by calculating net energy gain for large fish hypothetically foraging at observed focal points of small fish in riffle enclosures ($n = 4$).

Results

Growth rate

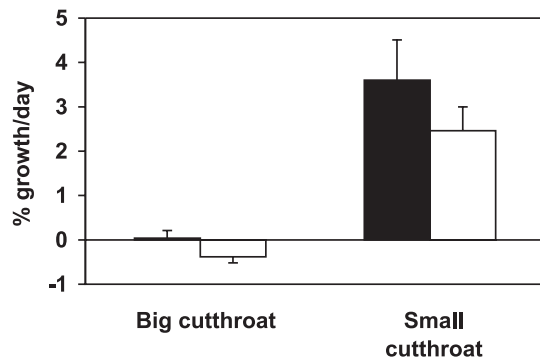
All large cutthroat trout were recovered from enclosures with no mortality over the course of the experiment; 33–100% of YOY were recovered from each enclosure (average of 67% in riffles and 82% in pools). These values probably overestimate mortality for YOY, since all stunned or killed YOY may not have been recovered in the complex natural stream habitat of enclosures despite multiple-pass electro-fishing.

There was no significant effect of the addition of cover (screen) on growth rate of large cutthroat trout ($F_{1,12} = 1.2$, $p = 0.30$). There was a significant size ($F_{1,20} = 238.5$, $p < 0.0001$) and habitat ($F_{1,20} = 24.4$, $p < 0.0001$) effect on average relative growth rate within enclosures (Fig. 1). Growth rates of YOY were positive in both pool and riffle habitat, although growth was lower in riffles. In contrast, the growth rate of larger cutthroat trout was positive in pools but negative in riffles. Growth rates of individual fish showed a typical allometric decline in relative growth rate with increasing size (Fig. 2), with growth consistently higher in pools than in riffles across the entire range of fish length ($F_{1,44} = 42.6$, $P < 0.0001$). Relative growth rate was best described by back-transforming the log–log relationship ($\log(\text{growth} + 0.007) = 1.44 - 1.82(\log \text{length}) + (0 \text{ for riffle}, 0.29 \text{ for pool})$, $R^2 = 0.92$) to the corresponding power function: percent growth = $((27.5 \cdot \text{length}^{-1.82} \cdot (1.94 \text{ for pool habitat}, 1 \text{ for riffle habitat})) - 0.007) \cdot 1.02 \cdot 100$, where 1.02 is the correction factor for back-transformation and growth is in percent body weight per day.

YOY habitat choice

YOY demonstrated a clear preference for pool habitat. In the absence of predation risk or competition, there was a net movement out of riffles into pools (Table 2). The change in density in riffles was $-0.42 \pm 0.07 \text{ fish/m}^2$ (paired t test, $t_2 = -10.8$, $p = 0.009$), with the final density in pools ($0.63 \pm 0.09 \text{ fish/m}^2$) roughly three times that in riffles ($0.23 \pm 0.13 \text{ fish/m}^2$) ($t_2 = 4.47$, $p = 0.01$ for a significant difference in final density between pools and riffles). When larger cutthroat trout were introduced to pools in the second habitat-choice experiment, there was no significant effect on YOY distribution ($t_2 = 1.13$, $p = 0.32$ for a difference in final density between habitats). However, there was a net movement of fish into riffle habitat in the pool–riffle sequence with the least instream pool cover (Table 2), suggesting that the effect of

Fig. 1. Average growth rate (% body weight/day) of small and large juvenile cutthroat trout in pools (filled bars) and riffles (open bars).



predation on habitat choice is dependent on the availability of instream cover. When the buried stop net was raised in this sequence, one of the larger trout was observed trying to swim back into the pool from the riffle and regurgitated a marked YOY when recovered, demonstrating that predation risk for YOY was substantial.

Drift rates

Drift concentrations were significantly higher in riffles than in pools for the smallest size-class of drifting invertebrate ($t_{13} = 2.31$, $p = 0.038$), but were not significantly different between pools and riffles for the large and medium size-classes (Table 3).

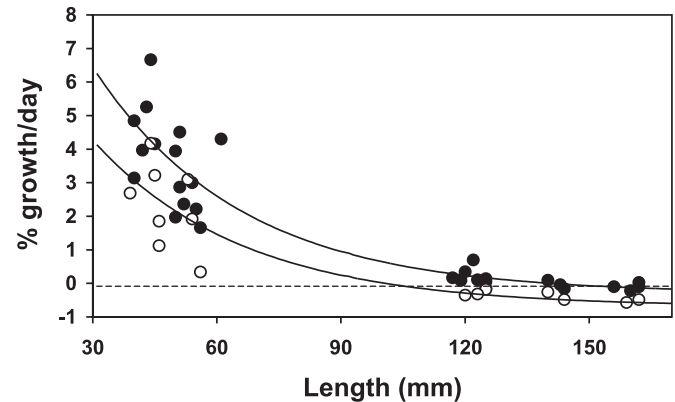
Energy costs and benefits

Observed focal velocities of YOY in pools and riffles were similar to those of larger juvenile cutthroat trout in pools, but estimated focal velocities for larger fish in riffles were higher and more variable (Table 4). Energy intake was significantly greater for large fish than for YOY (Fig. 3a) χ^2 ($= 5.10$, $p = 0.024$), and non-significantly higher in pools than in riffles χ^2 ($= 2.72$, $p = 0.10$). Swimming costs were significantly higher in riffles χ^2 ($= 4.09$, $p = 0.043$), although this was most pronounced for large fish (Fig. 3b). Net energy gain was higher in pools than in riffles χ^2 ($= 11.68$, $p = 0.001$) and positive for YOY in both habitats (Fig. 3c). Net energy gain was negative for larger trout in riffles ($-71.0 \pm 76.1 \text{ J}\cdot\text{h}^{-1}$ (mean \pm SD)) but positive in pools. Energy gain relative to metabolic costs was significantly higher in YOY than in larger trout χ^2 ($= 13.8$, $p = 0.001$; Fig. 3d) and showed a pattern very similar to that of observed relative growth rates. Projected net energy intake for a large fish at the observed focal positions occupied by small fish in riffles was negative for three of four observations.

Discussion

Habitat-choice experiments with YOY cutthroat trout clearly indicate that habitat selection in the wild does not accurately reflect preference in the absence of predation and competition. YOY preferred deep pool habitat, despite occurring at highest densities in shallow habitats in field surveys (Glova 1984; Rosenfeld et al. 2000). However, preference for pool habitat does appear to accurately reflect the

Fig. 2. Growth rates (% body weight/day) of individual juvenile cutthroat trout in pool (filled circles) and riffle (open circles) habitats as a function of body length. The cluster of points to the left are young-of-the-year trout; the cluster to the right are larger juvenile trout. The upper line represents growth rate in riffles; the lower line represents growth rate in pools.



fitness consequences of habitat choice, since YOY growth rates were higher in pools than in riffles. Low densities of larger cutthroat trout in shallow habitats in the wild (Fausch and Northcote 1992; Rosenfeld et al. 2000) is also consistent with observed negative growth rates of larger cutthroat trout in riffles, and confirms that habitat selection by larger juveniles also reflects the fitness consequences of habitat use.

Differential growth rates of YOY and larger cutthroat trout in pools and riffles indicate different habitat requirements at summer low flow. Pools are a preferred habitat for YOY, but not a requirement, since they are capable of growth in riffles. In contrast, pools are a habitat requirement for larger juvenile cutthroat trout, which could not maintain a positive energy balance in riffles. Negative growth in riffles supports the paradigm that riparian management practices leading to a loss of pool habitat (e.g., through decreased LWD inputs; Murphy and Koski 1989) causes a decline in suitable rearing habitat for older fish. This emphasizes the importance of pools at a population level, since the freshwater rearing phase of anadromous cutthroat trout in small gravel-cobble streams is probably limited by the number of 1- to 2-year-old smolts rather than by YOY abundance (Fausch and Northcote 1992).

Although fish predation has been widely demonstrated to influence habitat use by juvenile fish (Gilliam and Fraser 1987; Werner and Hall 1988), the effect of introducing large cutthroat trout to pools in the habitat-preference experiment was ambiguous. While there was no effect of large trout on YOY density in the two pools with abundant cover, there was net movement out of pool habitat in the third pool with the least cover; although this observation is clearly in need of further replication, it suggests that predator effects on habitat choice are cover dependent. An alternative mechanism to cannibalism for displacement of YOY into riffles is competition from larger juvenile coho salmon that hatch earlier in the spring and also prefer pools (Glova 1986; Nickleson et al. 1992), particularly at high coho salmon densities or when instream cover is abundant. This is both a management and a conservation issue, since stocking juvenile coho salmon on top of native cutthroat trout stocks is common in coastal streams.

Table 2. Number of young-of-the-year cutthroat trout at the start and end of habitat-choice experiments in the absence and presence of larger predatory trout for three replicate pool–riffle sequences.

	Initial no.		Final no.		Change in no. in riffle	Instream cover (m ²)
	Pool	Riffle	Pool	Riffle		
No large fish	7	4	10	1	-3	2.5
	7	4	9	2	-2	2.7
	5	4	8	1	-2	0.8
Large fish added	10	1	10	1	0	2.5
	9	2	8	1	-1	2.7
	8	1	5	4	+3	0.8

Table 3. Densities (mg·m⁻³ ± SD) of drifting invertebrates in three size-classes in pool (*n* = 8) and riffle (*n* = 7) habitats, or both habitats combined (*n* = 15).

	Size-class		
	<2.5 mm	2.5–5.0 mm	>5.0 mm
Pool	0.180±0.008	0.011±0.013	0.028±0.075
Riffle	0.281±0.009	0.021±0.010	0.023±0.038
<i>P</i>	0.038*	0.14	0.89
Both habitats	0.023±0.010	0.016±0.012	0.026±0.058

Note: *P* represents the probability of a significant difference between pool and riffle drift density for a given size-class; *, significant at *P* < 0.05.

Table 4. Velocities and total water depth at focal points of juvenile cutthroat trout in pools and riffles.

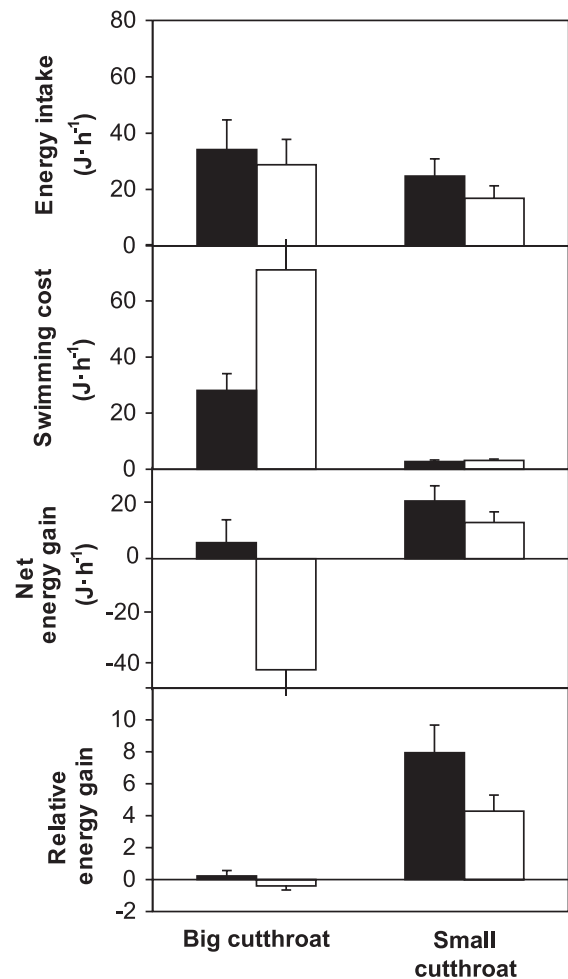
	Large fish		Young of the year	
	Pool	Riffle	Pool	Riffle
Total depth (cm)	17.2±4.4	6.3±1.7	16.5±3.8	6.0±1.3
Velocity (cm·s ⁻¹)	6.4±4.9	20.7±18.9	7.0±2.7	9.3±2.4

Note: Values are mean ± SD.

The net outcome of coho salmon – cutthroat trout interactions is potentially complex (Polis et al. 1989) because coho salmon juveniles are both a competitor with YOY cutthroat trout and a prey item for older fish, but stocking coho salmon appears to contribute to long-term declines of cutthroat trout in coastal streams (Johnson et al. 1999).

Net energy intake from the bioenergetics model generated results consistent with the observed pattern of fish growth in pool and riffle habitats. Large fish were projected to lose weight in riffles, whereas small fish were projected to grow in both pools and riffles, with energy intake relative to metabolic costs 15–30 times higher for YOY. Although energetic models for drift-feeding fish have been used primarily to predict microhabitat choice rather than growth rate (Hughes and Dill 1990; Hughes 1992; Hill and Grossman 1993), the concordance of modeled and observed growth indicates their utility for predicting growth rates of drift-feeding salmonids (see also Hayes et al. 2000). Because the drift-feeding model of Hughes and Dill (1990) takes into account depth and velocity and is inherently three-dimensional, it also offers an alternative to modeling habitat capacity based on two-dimensional area-based measures of territory size (e.g., Grant et al. 1998). Two-dimensional territory-size models have proven useful for retrospectively explaining when density-

Fig. 3. Projected energy intake, swimming cost, net energy gain, and relative energy gain for small and large cutthroat trout in pool (filled bars) and riffle (open bars) habitats based on bioenergetic modeling.



dependent effects occur in streams, but implicitly assume that territory size is independent of habitat quality (e.g., pool vs. riffle habitat). Grant and Kramer (1990) found that predictions associated with a two-dimensional territory-size model do not apply well in deeper pool habitats, suggesting that estimates of territory size and habitat capacity that take volume and quality of habitat into account are likely to be more biologically realistic.

Focal velocities of large fish in pools were partly based on strike trajectories rather than direct observation. This approximation of focal velocities is unlikely to have caused a serious bias in energetics calculations because of the relatively low variation in velocity and swimming costs within a pool, which would also have a minimal influence on the size of the foraging window. Because only one large fish was observed foraging in a riffle, focal velocities for estimating energetics in riffles were largely assumed using criteria of low velocity and proximity to cover. This was essentially a conservative assumption, since occupation of higher focal velocities would greatly increase swimming costs without appreciably increasing the size of the foraging window, leading to an even greater negative energy balance for larger trout in riffles. By selecting low-velocity focal points from the entire distribution of points in a riffle, we tested the extreme of the focal-point distribution most likely to give a positive energy gain for large fish in a riffle. Even at low focal velocities, the energetics model projected that fish would lose less energy by refuging than by foraging in most riffles, which is consistent with an absence of visibly foraging fish. In two of the riffles, the model predicted less energy loss by foraging than by refuging, which is consistent with the observation of a foraging fish (which lost weight) in one of these riffles.

Bioenergetic models used to estimate swimming cost are usually based on respiration rates of fish confined to swim tubes, in which flow is laminar and constant (Boisclair and Tang 1993), and may underestimate actual swimming costs of drift-feeding fish in turbulent flow (Daniel Boisclair, Université de Montréal, Department of Biological Sciences, Montreal, QC H3C 3J7, Canada, personal communication). Drift-feeding fish typically hold at a low-velocity focal point and strike at prey within a reactive radius that may carry them into higher-velocity locations. Fish striking from a focal point are likely to expend more energy leaving and returning to their focal point than predicted from a simple model based on holding at a single point in laminar flow. Despite the simplifying assumptions of present swimming-cost models, they appear to capture the average changes in swimming cost with current velocity and fish size, since the swimming-cost equation from Hughes and Dill (1990) (eq. 2 in Materials and methods) generates net energy gains consistent with the observed growth rates of cutthroat trout.

Selection of deeper pool habitat by larger fish is usually attributed to use of pools as refuges from avian or terrestrial predators (Power 1984; Lonzarich and Quinn 1995). Modeling net energy gain indicates that energetics alone is sufficient to account for the absence of larger juvenile cutthroat trout in shallow riffle habitats. We observed no mortality of larger juvenile cutthroat trout in either pools or riffles over the 30-day growth experiment, indicating little effect of terrestrial predators even in shallow habitats. In contrast, Lonzarich and Quinn (1995) showed that predation, most likely by herons, resulted in up to 50% mortality of larger juvenile steelhead trout in shallow pool habitat in small artificial channels adjacent to a larger stream in Washington. Lower mortality rates in Husdon Creek may reflect a lower abundance of avian predators in small forested streams, in contrast with higher densities of wading or diving birds in estuaries or riparian corridors adjacent to larger

streams and rivers. Differences in mortality rates highlight the spatially variable nature of predation risk from terrestrial predators in small streams (e.g., Heggenes and Borgstrom 1988), which will influence survival and habitat selection to unknown degrees.

The habitat-specific growth model indicates that juvenile cutthroat trout need to shift from riffles to pools at a size of approximately 90 mm to maintain a net energy balance at summer base flow. This is analogous to the ontogenetic habitat shift of juvenile bluegill sunfish from the littoral zone of lakes to the more resource-rich but predator-abundant pelagic zone (Werner and Hall 1988). Werner and Hall (1988) attributed this size-dependent habitat shift to a trade-off between lower resource acquisition in the littoral zone versus greater predation risk from gape-limited predators in the pelagic zone. However, while the presence of YOY cutthroat trout in riffles represents a probable trade-off between lower resource acquisition in riffles versus greater predation risk in pools (or interspecific competition from coho salmon), the shift of larger cutthroat trout out of riffle habitat appears to be driven by a ceiling on maximum energy intake imposed by the habitat structure of shallow riffles rather than a trade-off between predation risk and resource acquisition.

Despite higher overall growth rates of cutthroat trout in pool enclosures, the largest trout marginally lost weight even in pools. By removing forage fish (YOY cutthroat trout and coho salmon) from enclosures prior to stocking, we forced larger cutthroat trout to feed exclusively on invertebrates. Larger juvenile cutthroat trout appear to be energy-limited by a diet of invertebrate drift even in pools, indicating the requirement for an ontogenetic dietary shift to facultative piscivory to maintain positive growth as they become larger. Despite a shift to piscivory, maximum energy gain in small-stream habitat probably remains limited by pool size and prey encounter rate, selecting for the final ontogenetic habitat shift of migration to the ocean where habitat structure no longer limits energy intake.

Holling (1992) hypothesized that habitat structure constrains resource acquisition so that discrete body-size ranges are optimal for exploiting resources at different spatial scales. The ability of smaller fish to exploit habitats that are energetically unsuitable to larger fish is consistent with this hypothesis, which may apply to many stream salmonids and some lentic species as well. YOY cutthroat trout effectively function to transfer energy up the food chain from unsuitable habitats to larger predatory trout in streams, although YOY also compete for drifting invertebrates to an unknown degree. Lower absolute energy requirements of smaller fish may also be a major adaptive force selecting for differences in maximum body size between species and provides a plausible explanation for the general decrease in average body size of fish along an upstream gradient (Hughes and Reynolds 1994). Although smaller fish have a greater metabolic requirement per unit biomass, they have lower absolute energy requirements, permitting persistence in habitats with insufficient energy to meet the demands of larger fish (e.g., small streams or shallow habitats in rivers).

Understanding the mechanisms underlying growth in different habitats is a useful first step towards defining both habitat requirements and adaptive constraints on habitat use. Human land use practices frequently alter the complex habi-

tat structure that characterizes stream channels, thereby affecting the survival of both individuals and populations (Reeves et al. 1997). Logistic constraints often prevent the large-scale habitat perturbation experiments that are ideal for documenting the population-level effects of habitat change in streams (e.g., Hartman and Scrivener 1990). This study demonstrates an alternative way to infer population-level consequences of habitat change, by measuring the fitness consequences of using suboptimal habitats (e.g., riffles) that may become more abundant following disturbance.

Acknowledgements

We thank Mark D'Andrade and Carmen T. Kat for able assistance in the field; Grant McBain for facilitating permitting of instream work; Ernest Keeley, Eric Parkinson, and Marc Porter for providing helpful advice and logistic support; and Nick Hughes and Tom Quinn for providing useful comments on an early draft of the manuscript. This project was funded through Forest Renewal British Columbia.

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