

# Temporal and spatial variation in the energy intake of a brook trout (*Salvelinus fontinalis*) population in an Appalachian watershed

Ryan M. Utz and Kyle J. Hartman

**Abstract:** Stream-dwelling salmonids in eastern North America are often restricted to headwater watersheds, where productivity is low and thus feeding conditions are poor. We sought to quantify how energy intake varies with spatial and temporal variation by monitoring feeding rates in multiple sites over the course of two years. Daily rations were calculated for 939 fish by examining stomach contents. Maintenance rations were compared with daily rations using a bioenergetics model. Consumption peaked in spring, dropped substantially in summer, and remained low until the following spring. A minority of fish fed at very high levels during all seasons, elevating the mean consumption of the population. Fish occupying large sites with low trout densities consistently consumed more energy than fish in smaller streams with high trout densities. A direct relationship between trout density and mean consumption was observed during summer, when feeding conditions were poorest. Our findings suggest that within a headwater watershed, larger reaches of streams where fewer trout are found act as important feeding areas and thus may be important habitat for brook trout (*Salvelinus fontinalis*).

**Résumé :** Les salmonidés des cours d'eau dans l'est de l'Amérique du nord sont souvent confinés aux bassins versants d'amont où la productivité est faible et conséquemment les conditions alimentaires médiocres. Nous avons cherché à mesurer les variations spatiales et temporelles de l'ingestion d'énergie en suivant les taux d'alimentation à plusieurs sites durant deux années. L'analyse des contenus stomacaux de 939 poissons a permis de calculer les rations journalières. Un modèle bioénergétique a comparé les rations journalières aux rations de maintien. La consommation atteint un maximum au printemps, diminue considérablement en été et reste faible jusqu'au printemps suivant. Un minorité de poissons se nourrit à un taux élevé en toutes saisons, ce qui augmente la consommation moyenne de la population. Les poissons habitant de grands sites à faibles densités d'ombles consomment toujours plus d'énergie que les poissons dans les petits cours d'eau à forte densité d'ombles. On observe une relation directe entre la densité des ombles et la consommation moyenne en été, quand les conditions d'alimentation sont les moins bonnes. Nos observations indiquent que, dans un bassin versant d'amont, les grandes sections habitées par un nombre réduit d'ombles sont des lieux importants d'alimentation et peuvent donc être un habitat vital pour l'omble de fontaine (*Salvelinus fontinalis*).

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## Introduction

Brook trout (*Salvelinus fontinalis*) populations have declined in size and range as the result of a host of historic and persistent anthropogenic impacts, including uncontrolled logging, acidic precipitation, mine runoff, overfishing, and introduced species (Larson and Moore 1985; Marschall and Crowder 1996; Wigington et al. 1996). A number of institutions consider the restoration of brook trout a management goal because of its potential value as a recreational fishery. Recent work has highlighted the importance of small streams with high alkalinity and low levels of fine sediment in maintaining brook trout reproduction and populations (Petty et al. 2005; Hartman and Hakala 2006). However, be-

cause of the low productivity of the watersheds that brook trout often occupy in Appalachia and elsewhere, factors other than reproductive success may be important in sustaining and expanding existing populations.

Throughout eastern North America, brook trout are often restricted to headwater watersheds that are naturally infertile. As a result, trout in these watersheds may be subjected to prolonged periods of poor feeding conditions (Cada et al. 1987; Ensign et al. 1990; Forrester et al. 1994), and food abundance may affect trout production (Clarke and Scruton 1999). Such episodes of reduced feeding usually occur during summer when aquatic insect activity is relatively low, although other seasons may present poor foraging opportunities (Sweka and Hartman 2001). Although poor feeding has

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not been shown to reduce populations under normal conditions, severe summer drought may cause environmental conditions to deteriorate (Hakala and Hartman 2004) along with decreasing foraging rates, potentially resulting in mortality.

A growing body of evidence suggests that lotic salmonids operate under density-dependent processes, which has implications for feeding success. Fish density has been shown to affect growth (Vøllestad et al. 2002; Imre et al. 2004; Lobón-Cerviá 2005) in that fish occupying reaches of streams with less fish per unit area experienced significantly higher growth rates in both natural and simulated settings. The territorial nature of salmonids likely drives this relationship. Density has been found to be positively correlated with emigration and mortality as a result of competitive interactions (Nakano 1995; Imre et al. 2004). Multiple studies have concluded that brook trout may be highly mobile (Gowan and Fausch 1996; Petty et al. 2005). The ability to move coupled with the poor nature of high-density locations suggests that movement into low-density areas should be beneficial. Large adult brook trout have been shown to prefer larger reaches of streams where fish density is typically low (Petty et al. 2005). However, observational data pertaining to energy intake at the watershed scale for stream salmonids remain sparse in the literature.

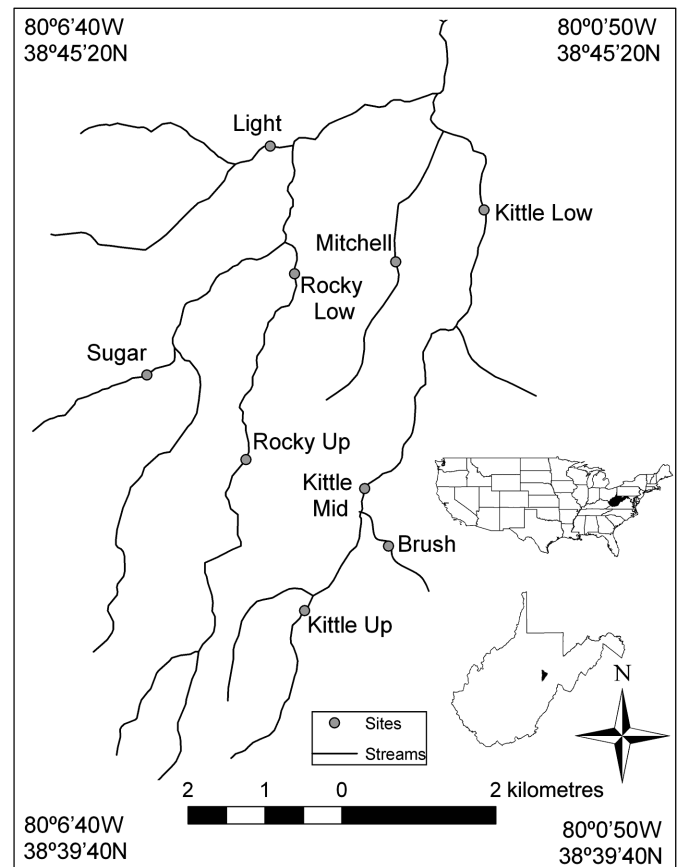
The concept that feeding intensity may be related to spatial variables has been established for salmonids with the general conclusion that larger bodies of water offer greater feeding potential (Keeley and Grant 2001). However, the extent to which this relationship exists within small watersheds remains to be described with detail. The relationship between density, watershed position, and feeding intensity may be of particular importance in eastern brook trout streams where food resources are often sparse. An understanding of temporal change in feeding intensity at the watershed scale may provide insight into how brook trout use different reaches of habitat to acquire energy. The recent development of a bioenergetics model for brook trout (Hartman and Sweka 2001) facilitates the calculations of a number of feeding variables, including daily ration and maintenance ration. In the current study, we sought to explain how consumption changes temporally and spatially by monitoring the energetic intake of a brook trout population throughout a headwater watershed over the course of two years.

## Materials and methods

### Study area

This study was conducted within the Middle Fork watershed, a north-flowing tributary of the Tygart River in the central Appalachian Mountains of Randolph County, West Virginia (Fig. 1). Most land cover within the watershed is that of secondary-growth hardwood deciduous forest. All sites in the study are located in the southernmost part of the watershed and are of low order and high gradient. We chose nine 200 m sites encompassing a range of stream sizes (Table 1). All sites met the following criteria: each contained brook trout, consistently held age-0 brook trout (indicating water quality was sufficient for spawning), and was devoid of fish barriers between other sites. Temperature regimens in these reaches are suitable for trout as temperatures rarely exceeded 20 °C through the duration of the study, determined

**Fig. 1.** The upper Middle Fork watershed and all sites described for this study.



by analysis of temperature logger data conducted for the current and previous studies. The West Virginia Division of Natural Resources (WVDNR) and the West Virginia Department of Environmental Protection have actively added limestone sand to riparian areas of streams within the watershed to remediate the effects of acid precipitation and acid mine drainage in the Middle Fork since the 1990s (WVDNR 2001). This process is commonly used in the region and successfully increases pH, restores fish communities, and increases invertebrate abundance (Clayton et al. 1998), though invertebrate productivity and diversity may not reach pre-acidification levels following treatment (McClurg 2004). Some sites selected in this study were not actively treated with lime. However, each site without a limestone treatment retained the ability to support brook trout spawning and carry fish populations. To quantify water quality in each site, water samples were taken in February, May, July, and October 2004 and tested for pH and alkalinity in a laboratory at the WVDNR office in Elkins, West Virginia. The means of both measurements were calculated for each site based on the four seasonal measurements; this calculation provided an estimate of average water quality across seasons.

Fish diversity differed across sites but was typical of Appalachian headwater streams. The number of species encountered increased with stream size. In nearly all sites, fish fauna was dominated by brook trout and mottled sculpin (*Cottus bairdii*). Other fish sampled include blacknose dace

**Table 1.** Physical features and number of fish species encountered for each site in the Middle Fork River watershed.

Site name	Stream	Limed (Y/N)	Stream class	Basin area (km <sup>2</sup> )	Mean wetted width (m)	Mean bankful width (m)	Mean pH	Mean alkalinity (mg·L <sup>-1</sup> )	Observed fish species
Brush	Brush Run	N	Upstream	0.83	1.46	3.97	5.17	1.38	1
Kittle Low	Kittle Creek	Y	Downstream	15.38	4.77	9.36	6.27	6.30	8
Kittle Mid	Kittle Creek	Y	Midstream	5.26	2.44	5.89	6.30	5.33	4
Kittle Up	Kittle Creek	Y	Upstream	2.05	2.19	3.98	6.73	15.78	2
Light	Light Run	N	Midstream	5.24	3.13	7.07	6.04	3.60	4
Mitchell	Mitchell Lick Fork	Y	Upstream	1.78	2.08	5.02	6.25	6.25	1
Rocky Low	Rocky Run	Y	Downstream	9.94	4.36	7.98	5.51	2.08	7
Rocky Up	Rocky Run	Y	Midstream	6.44	3.76	9.14	5.42	1.68	1
Sugar	Sugar Drain	N	Upstream	1.64	2.42	5.36	6.47	8.05	2

**Note:** The column titled "Limed" refers to whether or not (yes (Y) or no (N)) an active limestone treatment site existed above the site reach. If the site was not limed, water quality in the study reach retained the ability to hold young-of-the-year brook trout (*Salvelinus fontinalis*).

(*Rhynchichthys obtusus*), longnose dace (*Rhynchichthys cataractae*), creek chub (*Semotilus atromaculatus*), white sucker (*Catostomus commersonii*), northern hog sucker (*Hypentelium nigricans*), and fantail darter (*Etheostoma flabellare*).

**Fish and stream size sampling**

Fish sampling occurred 11 times over the course of two years (Table 2). Sampling was conducted between 0800 and 1600, and the order of sites to sample was randomly chosen during each day. A three-pass depletion electrofishing procedure (Platts and Nelson 1988) was used to estimate fish populations within each 200 m section. Before sampling, block nets were placed at the upstream and downstream ends of each section to restrict fish movement into or out of sections during sampling. Sampling teams used an electrofishing unit (DC, 60 hz, 500–750 V; Smith-Root, Vancouver, Washington) and dip nets to capture fish. Temperatures needed for bioenergetics modeling were recorded during fish sampling using an electronic thermometer.

Following collection, fish were processed at a streamside station. All fish were immobilized with a solution of clove oil and 95% ethanol. Brook trout were weighed to the nearest 0.5 g, and total length was taken to the nearest millimetre. We chose a subset of 10 brook trout per site per month for stomach content removal. Only fish > 110 mm fork length (FL) were considered eligible for gut content removal because of gear restrictions; the gape of fish below this size was usually about the same size of the flushing tube diameter (7 mm). This size class generally represented age-1+ fish, which was apparent in length-frequency histograms (Utz 2005). An attempt was made to collect an equal range of fish sizes to analyze for gut contents at each site; aside from this, fish were chosen randomly. Stomach contents were removed by directing a constant flow of stream water into the foregut (Twomey and Giller 1990). Gut items were filtered through a 250 µm sieve and transferred to 95% ethanol, a process that has proven effective (Light et al. 1983; Sweka 2003). All fish other than trout were counted and weighed. Each fish was allowed to recover from the clove oil treatment and returned to the stream reach within 2 h. A sample of 10 trout, selected for gastric lavage, was randomly collected from sites, frozen, and kept for dry weight analysis during four select sampling periods. This resulted in a removal of 40 fish during the entire course of the study. Brook trout dry weights were needed to estimate fish energy density, a necessary component of bioenergetics modeling.

To determine if fish density was related to consumption at the watershed scale, select habitat variables were calculated at each site. Habitat measurements within each site were recorded during base flow on 17 August 2005. Variables were measured on each 200 m reach of stream. Habitat units within each site were classified as riffle or pool, and the length of each unit was measured. Within each habitat unit, the wetted width and bankful width were taken along a linear transect perpendicular to the stream. The number of transects measured within a habitat unit depended on the length of the unit, with measurements made approximately every 20 m in riffles and every 2 m in pools. Pools were more represented than riffles in mean width estimation because of the tendency for large adults to use this habitat; however, riffles and pools did not differ markedly in widths.

**Table 2.** Middle Fork River brook trout (*Salvelinus fontinalis*) sampling start and end dates and mean temperatures at all sites for each month.

Sampling period	Start date	End date	Mean temperature (°C)	Designated season
March 2004	13 March	20 March	5.3	Winter
May 2004	5 May	12 May	11.0	Spring
June 2004	13 June	16 June	15.9	Spring
July 2004	16 July	19 July	16.2	Summer–fall
August 2004	16 August	18 August	18.0	Summer–fall
September 2004	24 September	26 September	14.4	Summer–fall
December 2004	2 December	5 December	5.2	Winter
March 2005	12 March	18 March	2.6	Winter
May 2005	9 May	11 May	12.5	Spring
June 2005	9 June	11 June	15.4	Spring
July 2005	12 July	13 July	16.9	Summer–fall

The basin area (km<sup>2</sup>) of each site was determined using coordinates derived from a global positioning system at the midpoint of each site and calculated using geographic information systems (GIS).

### Laboratory procedures

All prey items were identified to family or the lowest taxonomic classification possible (Merritt and Cummins 1996; Borror et al. 1989) to quantify prey exploitation by frequency and energy. Extremely small (<0.5 mm) organisms or organisms partially destroyed beyond identification to family were classified to order. The lengths of prey items were measured (to estimate dry weight) via an ocular micrometer to the nearest 0.1 mm; when lengths were unavailable, head capsule widths were measured to the nearest 0.1 mm. Crayfish (*Cambarus bartoni*) carapace lengths were measured rather than head capsule width or body length. The dry mass of each organism was estimated using published length or head width to dry mass equations, with the exception of crayfish where a carapace to dry mass equation was used (Sample et al. 1993; Benke et al. 1999; Johnston and Cunjak 1999; Sabo et al. 2002). Vertebrate food items such as frogs, salamanders, and fish were dried at 60 °C for 48 h to calculate dry weight. Frozen brook trout were thawed, weighed to the nearest 0.1 g, and dried at 60 °C for 72 h to calculate percent dry weight used in energy density analysis.

### Estimates of consumption and daily ration

Estimates of consumption and maintenance ration were calculated to determine seasonal and spatial variation in energy intake. Comparing estimated consumption with maintenance ration determines if fish are obtaining enough energy to maintain body weight. Estimated maintenance rations (EMR, in joules per gram fish wet weight per day) were calculated based on a bioenergetics model for brook trout (Hartman and Sweka 2001) using fish weight, fish energy density, and observed water temperature (taken with an electronic thermometer streamside during sampling) as variables. Maintenance ration was determined by calculating the energy required to obtain zero weight growth over the course of a day. This calculation was conducted for each fish over 110 mm FL (i.e., the size range of fish targeted for diets). Brook trout energy densities were calculated from observed

mean energy density in collected fish using a Salmonidae dry weight – energy equation (Hartman and Brandt 1995) and were interpolated from energy densities taken before and after a given collection period. Mean fish energy density was assumed equal across sites during a given month. Consumption estimates were calculated based on a model proposed by Eggers (1977). Each prey item was converted to energy using published dry weight – energy equations based on taxonomy and life stage (Cummins and Wuycheck 1971), and the total energy in the gut was summarized for each fish.

The total energy intake was multiplied by the brook trout gastric evacuation rates (based on temperature; Sweka et al. 2004) and divided by fish weight to calculate an observed consumption value (J·g<sup>-1</sup> fish·h<sup>-1</sup>) as suggested by Eggers (1977). This estimate was multiplied by 24 to convert it to a daily ration. The mean daily consumption estimates in this study were based on stomach contents obtained during the daylight hours only. Though daily consumption typically requires estimates of feeding activity across a diel cycle (Bowen 1996), multiple studies of indigenous brook trout feeding trends revealed no significant diel pattern (Forrester et al. 1994; Sweka 2003; Mookerji et al. 2004). Further, the evacuation rate of brook trout has proven to be low relative to that of other salmonids (Sweka et al. 2004), meaning that food items remain in the gut long after they have been ingested. Thus the current study made the assumption that a measurement of diet during daylight hours provided sufficient data to calculate daily ration.

### Statistical procedures

We calculated population estimates in each site per month and all sites combined per month to determine population change, estimate fish density, and allow comparison of consumption and population variables. Population estimates were calculated for each stream using the depletion process of Zippin in the program CAPTURE (White et al. 1982). If fewer than 30 fish were captured, then the actual number of fish caught was substituted for an estimate (Riley and Fausch 1992). Fish density per site was calculated as the population estimate divided by the wetted area (m<sup>2</sup>) at base flow. Although densities were determined via monthly fish populations and one estimate of wetted area per site, we

assumed that wetted width estimates among sites would change proportionally to each other over time. This assumption was based on the close proximity of all sites, with a high likelihood that the watersheds are subject to identical climatic conditions. In addition to calculating fish populations and density, we calculated percent habitat saturation (PHS) as an estimate of fish abundance (Grant et al. 1998). We found this variable to be desirable because it incorporates fish size, fish density, and territorial requirements for individual fish, resulting in a single number that considers all variables potentially affecting density-dependent processes. PHS was calculated using the equations derived by Grant and Kramer (1990):

$$\text{PHS} = \sum DT \times 100$$

where  $D$  is the density (number·m<sup>-2</sup>) of fish and  $T$  is territory size (m<sup>2</sup>), which was calculated using the following equation derived for salmonids similar in size to those encountered in the current study:  $\log(\text{territory size}) = 2.61\log(\text{FL (cm)}) - 2.83$ . Because we recorded total length in the field, we first converted total length to FL using the equation  $\text{FL} = \text{total length}/1.0326$  (Carlander 1969).

For analysis of consumption by site, each site was placed into one of three classes (upstream, midstream, or downstream; see Table 1) based on similarities in basin area, trout density, wetted width, and other fish species present. Early analyses showed that each month could be classified into one of three broad seasons (winter, spring, and summer–fall; see Table 2) by means of similarities in temperature and consumption; each season was analyzed separately. Consumption estimates were first square root transformed to approximate normality. Because differences existed in fish size and temperature (at time of sampling) among sites, we tested for the effects of these variables on consumption first (as continuous variables) when testing for differences in consumption rates among sites. If fish size (i.e., weight) or temperature was found to be linearly related to consumption at the  $\alpha = 0.05$  level, the variable was retained. Differences in square root transformed consumption estimates across stream classes within each season were tested using analysis of covariance (ANCOVA) if weight or temperature was significant (analysis of variance, ANOVA, if neither weight nor temperature entered the model) and Duncan's repeated-measures test post hoc. Interaction effects were included if weight or temperature entered into the model. For all ANCOVA and ANOVA models, the type III sum of squares was analyzed. If site class did influence consumption, potential relationships between PHS and mean consumption estimates were explored. Nonlinear relationships were considered to test for best fit during these analyses by plotting both original and log-transformed variables. All statistical and analytical procedures were completed using PROC GLM and PROC REG in SAS<sup>®</sup> 9.1 (SAS Institute Inc. 2003).

## Results

### Consumption and seasonal change

A total of 939 brook trout was sampled for stomach contents throughout the course of the study, yielding mean estimates of consumption on monthly and seasonal intervals.

Brook trout consumption varied significantly throughout the year (Fig. 2). Middle Fork brook trout appeared to exceed metabolic demands only during select seasons. Mean consumption during all spring months was significantly higher than maintenance ration. Only marginal differences were observed between consumption and maintenance ration during the summer or fall. Maintenance ration estimates were higher than mean observed consumptions for both March samples. Despite low consumption estimates during certain months, the number of fish encountered with no food items retrieved was small, with a high of 10 fish in August 2004 and between 0 and 4 fish during all other months. Fish with empty stomach were included in all analyses.

Although comparisons between consumption and maintenance rations suggest that fish were meeting metabolic demands, this mean was elevated by a minority of fish feeding exceptionally well. The distribution of consumption values during each season was skewed to the right, where a minority of individuals consumed a disproportionately large amount of energy relative to the mode (Fig. 3).

### Consumption and watershed position

Throughout the year, brook trout density was significantly correlated with watershed position. Trout density was negatively correlated with basin area at the log–log scale ( $F = 51.14$ ,  $n = 26$ ,  $p < 0.0001$ ; Fig. 4).

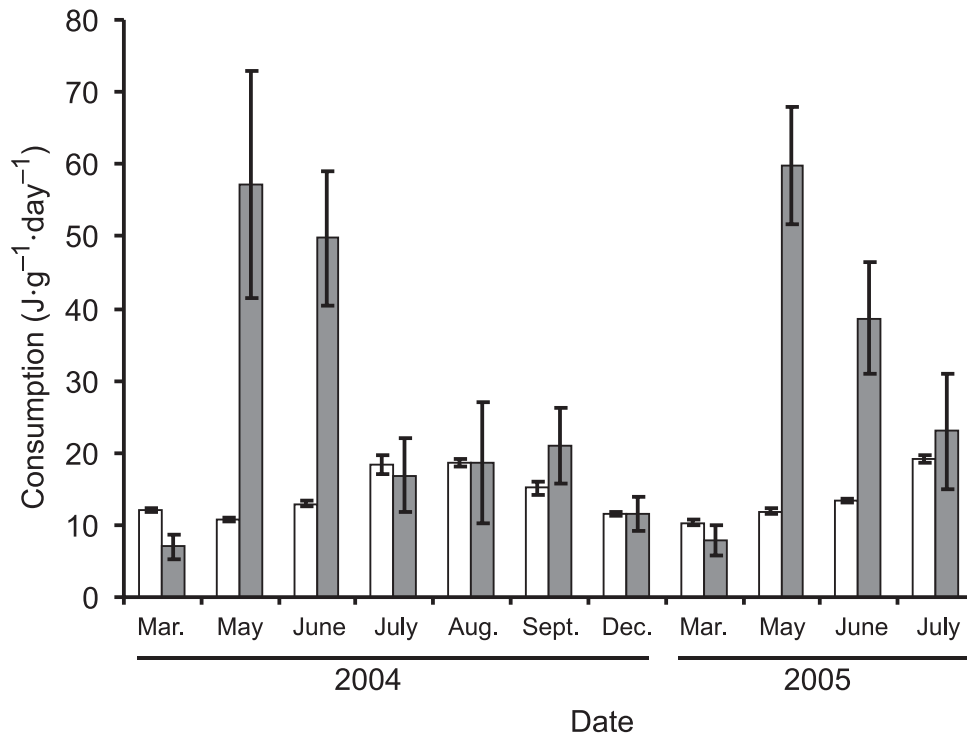
The location of fish collection seemed to affect feeding conditions. During each of the three seasons, significant differences in consumption were apparent among positions in the watershed, despite differences in fish size or temperature among site classifications (Table 3). Fish size alone was never significantly related to consumption; however, temperature was retained in the model during spring and winter. The interaction of watershed location and temperature, rather than temperature alone, was significantly related to consumption during spring once the full model was explored. In winter, temperature, rather than an interaction effect, was significantly related to consumption estimates. During summer, only watershed location significantly explained variation in consumption estimates. With the exception of winter, site location explained the majority of variation in consumption estimates among sites. Fish in upstream locations consumed significantly less energy than fish occupying downstream and midstream reaches during spring and summer (Table 4). The trend shifted in winter, with upstream consumption significantly greater than mid-order reaches, but not downstream reaches.

Each season was tested separately for an effect of trout PHS on mean consumption. No relationship was found between the two variables during spring or winter (Fig. 5). However, during the summer–fall season, a significant negative nonlinear relationship existed between mean consumption and PHS ( $F = 20.41$ ,  $n = 9$ ,  $p = 0.0027$ ).

## Discussion

The relationship detected between watershed position and energy intake highlights the importance of watershed position in successful feeding. With the exception of winter, fish occupying upstream sites fed at significantly lower rates than fish at other sites. During winter, however, temperatures

**Fig. 2.** Mean ( $\pm 95\%$  confidence intervals) monthly estimated maintenance ration (open bars) and observed consumption values (shaded bars) across all sites.



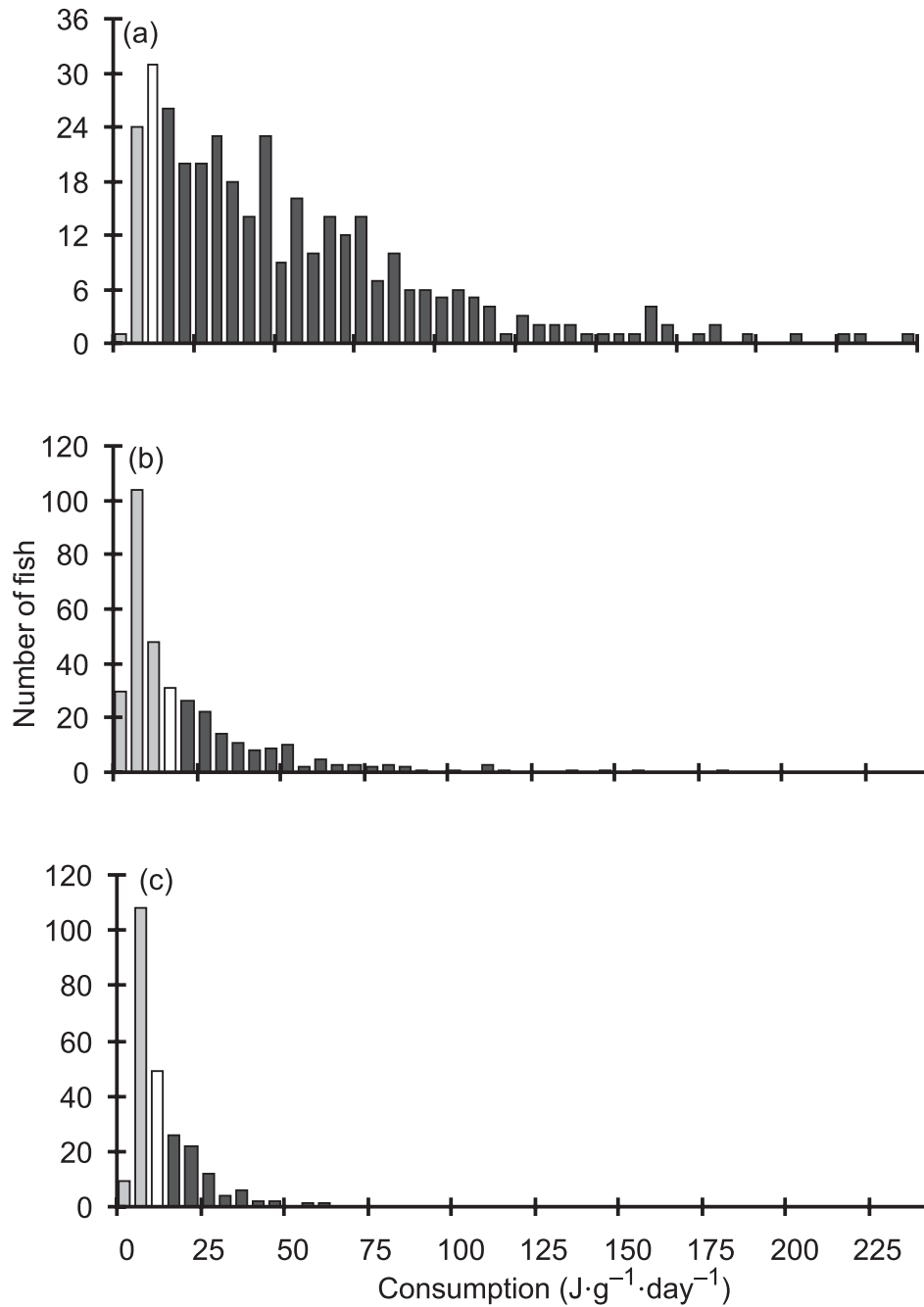
were low and metabolic costs were correspondingly low. Therefore, poor feeding conditions existed in upstream sites during the most critical seasons regarding temperature (spring through fall). An absence of a relationship between PHS and mean consumption during the spring could have been attributed to the abundant food resources available during that season, as territory size may shrink during periods of abundant food resources (Grant et al. 1998). During the summer–fall, however, a direct relationship was detected between PHS and consumption. Therefore, during the season of greatest metabolic costs and lowest food resources (Cada et al. 1987; Ensign et al. 1990; Utz 2005), fish density was particularly important in determining mean energy intake. These findings imply that density-dependent processes or differences in food abundance by site regulate feeding in Appalachian brook trout during certain times of the year.

A number of studies have recently confirmed density-dependent growth in lotic salmonids (Jenkins et al. 1999; Imre et al. 2004; Lobón-Cerviá 2005), a concept that is consistent with findings in the current study. Unfortunately, sufficient data to compare growth rates in our study were not available because of the likelihood that multiple shocking events would have affected growth (Dwyer and White 1995, 1997; Hughes 1998) and the low number of trout encountered in the downstream reaches disallowed sufficient estimates of mean growth. Our findings concur with those examining density-dependent growth, as higher rates of energy intake likely correspond to increased growth rates. Higher values of trout density imply that fish spend more time defending territories and less time foraging, resulting in decreased energy acquisition and (or) increased allocation of

energy towards territory defense rather than growth (Elliot 1994; Nakano 1995; Steingrímsson and Grant 1999). Although density-dependent processes have been shown to appear at PHS values of  $\geq 27\%$  (Grant and Kramer 1990), we observed a relationship between mean consumption and PHS at values  $< 27\%$ . If density-dependent processes were occurring at relatively low densities in the Middle Fork watershed, this could have occurred because of lower food resources compared with those in Grant and Kramer (1990).

Alternatively, food abundance may have increased with stream size. Food resource abundance for salmonids typically increases with habitat volume (Keeley and Grant 2001), though few have examined this idea at the scale of a headwater watershed. No measures of food abundance were collected for this study. An attempt at calculating food abundance would be difficult at the large spatial and temporal scales, as well as the ability to quantify both aquatic and terrestrial food abundance. Further, brook trout tend to select for certain items in the drift and also feed on nondrifting prey (Sweka and Hartman 2001). Salmonids in watersheds similar to the Middle Fork have been found to derive most of their energy from terrestrial invertebrates (Forrester et al. 1994; Nakano et al. 1999; Hilderbrand and Kershner 2004b), as was the case in our study (Utz 2005). Riparian forest cover and composition in each of the sites were identical; therefore terrestrial insect biomass was likely similar among sites. The finding that temperature was occasionally significantly related to mean consumption among locations was not surprising; temperature is a primary component of the bioenergetics model for brook trout. However, differences in temperature on a larger temporal scale do not likely affect

**Fig. 3.** Distributions of daily ration estimates by season for (a) spring, (b) summer and fall, and (c) winter. Bars are in increments of five. Solid bars represent estimates above mean maintenance ration for the corresponding season, shaded bars represent estimates below mean maintenance ration, and open bars represent the number of fish either slightly above or slightly below mean maintenance ration.



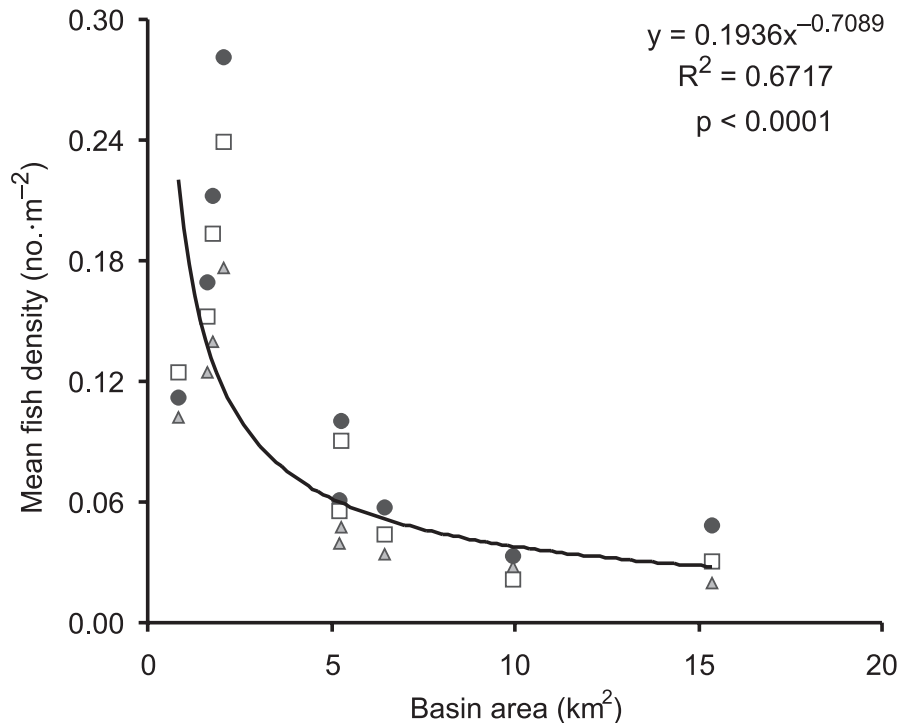
consumption rates at the same scale. Long-term temperature profiles among sites were nearly identical over the course of the study (Utz 2005).

A potential mechanism explaining greater consumption downstream is that of increased piscivory, as fish typically provide more energy than invertebrates (Jonsson et al. 1999; Neveu 1999; Keeley and Grant 2001). Piscivory was rarely encountered in the Middle Fork watershed ( $n = 19$  out of 939 observed fish), though the highest rate was observed at the largest site (Kittle Creek-Low,  $n = 11$ ). Regardless of

whether the trends observed in the Middle Fork were driven by trout density or food abundance, feeding conditions improved with increasing stream size.

The notion that stream-dwelling salmonids, including brook trout in eastern North America (Rodriguez 2002; Logan 2003; Petty et al. 2005), are highly mobile (Gowan et al. 1994; Gowan and Fausch 1996, 2002), as well as the propensity for large adults to seek large reaches of streams, suggests that a proportion of the population may move to seek food resources. Few studies have shown this to be the case

**Fig. 4.** Fish densities as a function of basin area across all seasons: solid diamonds, summer estimates; shaded triangles, winter estimates; and open squares, spring estimates.



**Table 3.** Model parameters of the analysis of variance (ANOVA) or analysis of covariance (ANCOVA) models run on square root transformed mean consumption by watershed location (i.e., downstream, midstream, upstream) for each season.

Effect	df	F value	p
<b>Spring</b>			
Overall model	4	8.68	<0.0001
Watershed location	2	10.37	<0.0001
Temperature	1	3.28	0.0709
Site type × temperature	2	8.44	0.0003
<b>Summer–fall</b>			
Watershed location	2	13.57	<0.0001
<b>Winter</b>			
Overall model	4	6.93	<0.0001
Watershed location	2	3.32	0.0380
Temperature	1	6.40	0.0121
Site type × temperature	2	2.69	0.0699

within a headwater watershed. The trends documented in the current study together with the distributional patterns observed in the Shaver's Fork watershed (Petty et al. 2005) suggest that although spawning areas are essential for brook trout abundance, larger reaches of streams with lower trout densities are important in providing improved feeding and growth conditions. However, these concepts must be considered with caution, as other factors may contribute to the tendency for individual fish to move.

Salmonids in lotic environments that undergo movement invoke an energetic cost and other potential risks. As a result, some studies (Naslund et al. 1993; Gowan and Fausch

**Table 4.** Post-hoc analysis of the analysis of variance (ANOVA) or analysis of covariance (ANCOVA) models on mean consumption by watershed location for each season.

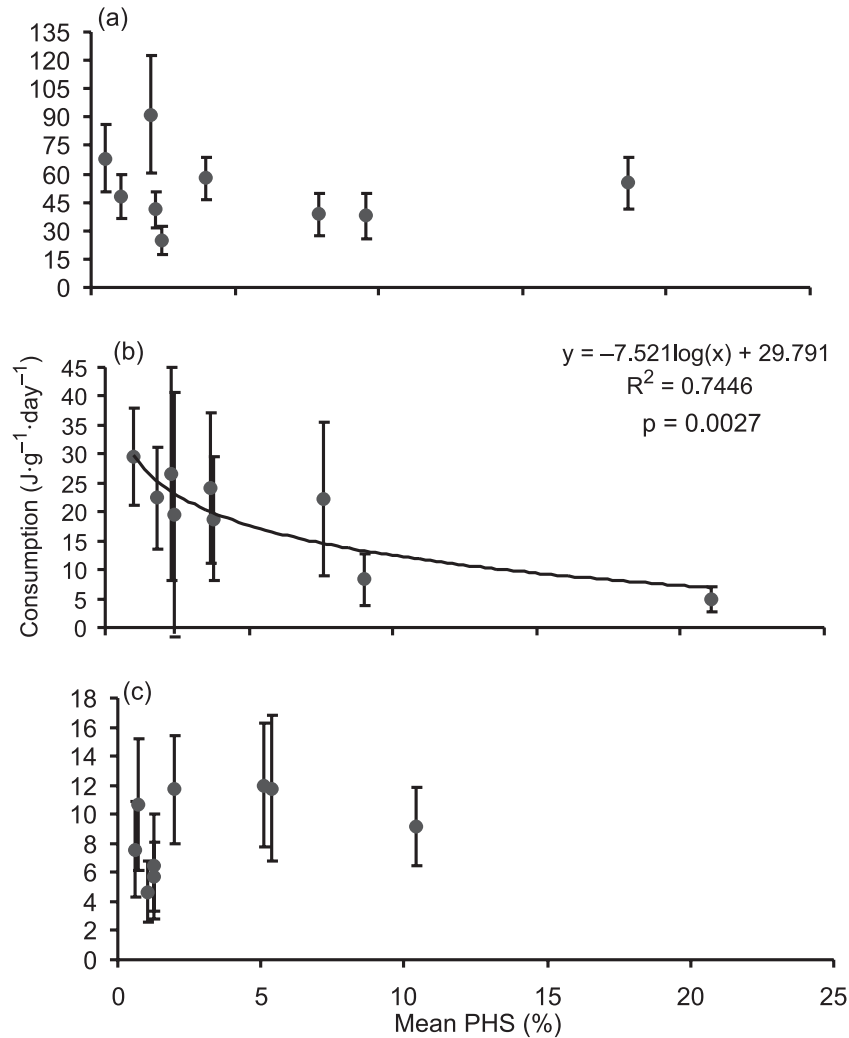
Stream classification	Mean consumption (J·g <sup>-1</sup> ·day <sup>-1</sup> )	Standard error
<b>Spring</b>		
Downstream	58.03a	5.47
Midstream	62.95a	6.01
Upstream	39.42b	3.01
<b>Summer–fall</b>		
Downstream	24.88a	2.60
Midstream	25.74a	3.50
Upstream	13.13b	2.43
<b>Winter</b>		
Downstream	8.89a	1.38
Midstream	5.61b	0.79
Upstream	11.12a	1.03

**Note:** Means with different letters within a season are significantly different (following a square root transformation) at the  $\alpha = 0.05$  level using Duncan's repeated-measures test.

1996) suggested that mobile trout were in poorer condition than resident trout. However, movement from areas as a result of poor feeding conditions does occur (Wilzbach 1985; Nakano 1995), and in some cases, mobile trout have been shown to be in better condition than the population average (Hilderbrand and Kershner 2004a). In addition to the energetic costs of movement, an individual choosing to move downstream may risk higher rates of predation in the form of angling.



**Fig. 5.** Mean consumption as a function of percent habitat saturation (PHS) by site for (a) spring, (b) summer and fall, and (c) winter. Vertical bars represent 95% confidence intervals. Lines were fitted when the relationship between variables was significant at the  $\alpha = 0.05$  level.



Trends in these data differ somewhat from those of other studies that have observed mean daily ration significantly below maintenance levels during the summer; a lack of such a finding in our study may be attributed to a minority of fish feeding at very high levels when resources were low. Mean estimated daily ration fell below maintenance ration only during winter months. Limitations in summer food intake have previously been inferred or observed in Appalachian salmonids. Cada et al. (1987), Ensign et al. (1990), and Thorne (2004) observed a substantial drop in the number of items and (or) mean stomach content weight found in brook trout stomachs from spring to summer in populations of Appalachian salmonids. Ensign et al. (1990) found that the drop in brook trout consumption was calculated below maintenance ration. Such low food intake was similar to summer rates of the current study, yet our fish consistently attained maintenance ration on average. One potential explanation may be our sampling of a large number of fish per season, which captured the data of a minority of fish that fed exceptionally well.

Environmental conditions for brook trout may be highly variable between years because of drought and flooding

(Carline and McCullough 2003; Hakala and Hartman 2004). The summers in the current study were not particularly severe, and it is likely that consumption values during drought years would drop below those observed in this study. Of particular importance is the finding in this study that a minority of fish feeding on large or abundant organisms during the summer elevated the mean consumption estimate of the fish population. Therefore, chance encounters with large prey items may be critical in maintaining brook trout through stressful periods.

Though this study examined the feeding dynamics of brook trout within a single watershed in central Appalachia, the findings of this study are likely applicable to populations of brook trout elsewhere and stream-dwelling salmonids in general. Brook trout populations are often confined to similar-sized, unproductive watersheds throughout their range, including the upper midwestern United States (Zorn et al. 2002), eastern Canada (Clarke and Scruton 1999), and the southern Appalachians, where brook trout populations are critically threatened (Habera and Moore 2005). Further, food resources may limit brook trout production in such watersheds outside of Appalachia (Clarke and Scruton 1999).

Trout populations other than brook trout may be isolated into headwater watersheds by anthropogenic impacts, such as cutthroat trout in western North America (Hilderbrand 2003). If density dependence plays a role in trout feeding capacity as suggested here, applying our results to other trout species may allow insight into the restoration and maintenance of threatened populations.

The intense regimen of electrofishing (monthly in some periods) may have had an effect on individual fish, as growth and short-term behavior are usually affected by the process (Dwyer and White 1995, 1997; Hughes 1998). However, electrofishing effects at the population level have not been observed (Kocovsky et al. 1997). Variables critical to the current study, such as movement or feeding behavior, were not affected by electrofishing when examined in other salmonids (Twomey and Giller 1990; Dunham et al. 2002). An inability of gastric lavage to remove all contents in the gut is another potential source of error. However, previous examinations of gear efficiency for the gear used in this study showed that little to no contents remain after a thorough lavage (Sweka 2003). Further, the items that potentially remain in the gut despite lavage are likely smaller organisms (as larger organisms can be detected outside of the fish) that would not dramatically affect consumption estimates.

Movement downstream by Middle Fork brook trout from areas of high population density to areas of low population density appears to increase foraging success. In systems where food may be potentially limiting, as in the Middle Fork and elsewhere in the brook trout range, migration to downstream reaches may be particularly important. Future management decisions concerning the rehabilitation of brook trout populations will need to consider the spatial heterogeneity of habitats within a watershed. Although small, alkaline streams are crucial for spawning, larger-order reaches of streams provide significantly better feeding conditions than the smaller streams where rearing occurs. Barriers and risks associated with movement into these larger stream reaches, such as acid mine drainage and high angling mortality, may prevent brook trout from exploiting more productive areas in a watershed.

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