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**Effects of Drifting Prey Abundance on Food Consumption and Growth
of Brook Trout in Shenandoah National Park.**

by

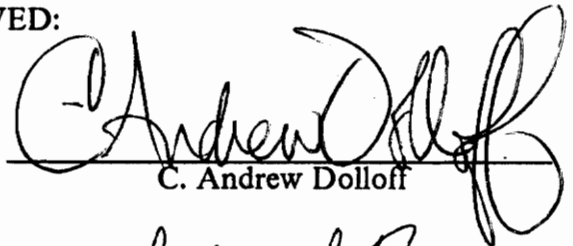
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APPROVED:



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(ABSTRACT)

The relation between prey density and brook trout *Salvelinus fontinalis* food consumption has not been quantified in natural streams. This relation may be most critical in the summer when southern Appalachian trout have demonstrated poor growth. It is not known whether the poor growth is due to the low food densities or to excess temperatures and increased metabolic costs. Purposes of this study were to quantify the relation between prey density and food consumption in brook trout, identify how diel feeding and prey size selectivity by brook trout affect the relation, and to determine if slow growth in the summer was caused by low daily rations or other factors. Daily consumption was estimated in May, July and September of 1989, for four streams in Shenandoah National Park. Sampling was performed at 6-hour intervals over 24 hours. Adult and yearling trout did not consume more food at one specific time throughout the summer, but juvenile trout (< 100 mm) fed significantly less at night in both July and September. All sizes of fish selected for prey longer than 4mm. The best predictor of daily ration (corrected for temperature) over the summer was the number of prey longer than 4mm/m³. Models parameterized to quantify the relation between prey density and food consumption showed that adult trout were significantly more likely to have a higher daily ration per gram body weight (temperature and size corrected) than yearling trout at low (< 1.0 prey longer than 4mm/m³) prey densities. Daily ration of juvenile trout

was independent of prey abundance. The prey density-consumption relation was more consistent within streams than among streams, which suggests that habitat or population characteristics may influence the prey density-consumption relation. Trout had the most energy available for growth in July followed by May and then September. Daily ration was most dependent on temperature in May and on prey density in July and September. Juvenile trout did not decrease daily ration as much from July to September as did yearling and adult trout. All sizes of trout met maintenance costs in both early and late summer, yet yearling and adult trout did not grow in late summer although stream temperature was optimum for growth. Growth was negatively correlated with daily ration in the late summer, suggesting that activity costs may be more important in determining growth in late summer than prey densities. Activity costs varied substantially among streams. The effect of food consumption and habitat on activity costs needs to be defined to improve understanding of the determinants of growth in stream environments.

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INTRODUCTION

The distribution of brook trout *Salvelinus fontinalis* in the southeastern U.S. has been drastically reduced in the past century because of changes in land use and the introduction of exotic salmonids. Currently, this range is stable in some areas while it is still declining substantially in others (Seehorn 1978). Bivens et al. (1985) found that brook trout habitat declined by 50 to 70% in Tennessee from 1978 to 1984 and hypothesized that the species may become extinct in the state in thirty to fifty years if the habitat continues to decline at the same rate.

While brook trout habitat and populations are declining, the demand for brook trout angling is increasing (Flebbe et al. 1988). Flather and Hoekstra (1989) projected that coldwater fishing on Forest Service land in the southeast would increase almost 200% by 2040. Brook trout also appeal to environmentalists because they are the only native salmonid in the southeastern U.S. and are indicators of a pristine environment. Government agencies, recognizing the increasing importance of brook trout, have increased their efforts to protect and improve these fisheries. At Great Smoky Mountain National

Park, managers are trying to re-establish native brook trout in parts of their historical range (Moore 1979, Moore et al. 1983).

Logging practices, fires, overharvesting, and the introduction of exotic salmonids were critical factors affecting brook trout in the early 1900s. More recent and perhaps of greater concern are chronic regional problems such as climate warming, acid rain, and gypsy moth defoliation. These chronic problems may affect the temperature regime or the timing and abundance of invertebrates in the stream. This study was undertaken to develop a better understanding of how variations in temperature and prey abundance affect brook trout consumption and growth.

Effects of temperature and prey abundance on trout feeding have been described in laboratory systems, but there is a need to identify if the same effects hold in natural environments. Previous studies of salmonids in controlled environments measured the influence of temperature (Baldwin 1956, Elliott 1975a, 1975b) on consumption. Laboratory studies have also described the effect of prey density on food consumption in trout (Ringler and Brodowski 1983, Ware 1972). Ringler and Brodowski (1983) found that the type-2 predator response of Holling (1959) described the relation between trout consumption and increasing levels of prey. As prey densities increased, consumption also increased but eventually reached a plateau, where increases in prey densities did not increase consumption. In laboratory studies, trout were often in artificial environments, the temperature was constant, the fish were starved before the experiment, only one type of prey was offered, and consumption was measured for only a short time. Consequently, the laboratory relation between daily consumption and prey density may not hold in a natural stream with fluctuating temperatures, a diverse prey resource, a more complex habitat and a social dominance hierarchy. Some field studies have suggested

that fish consume more or have more food in their stomachs at sites with higher prey densities (Allan 1981, Cada et al. 1987). However, none have tried to quantify the relation between daily ration (i.e. food eaten over a 24 hour period) and prey densities in natural streams.

Prey characteristics that directly influence consumption need to be taken into account when trying to predict the prey density-consumption relation. Trout in streams have been shown to consistently select for larger prey. Noakes and Grant (1986) stated that practically all studies that examined food size-selection by salmonids have found positive selection for large prey.

Behavioral characteristics of the trout populations may also affect food consumption. Ney (1990) identified distributional availability, the presence of prey and predator at the same location at the same time, as one condition of prey being available. Salmonids may exhibit feeding periodicity (Johnson and Johnson 1981), therefore, high prey densities when trout are not feeding will have little affect on consumption. Larger trout also feed differently from younger fish both for morphological (Wankowski 1979) and behavioral reasons (Bachman 1984); the relation between prey density and consumption may differ among fish sizes.

Measuring the energy budget, energy consumed versus energy spent, will indicate if the trout are able to meet their energy costs and grow. In general, brook trout in the southeast Appalachians have poor growth during the summer compared with the rest of the year (Neves and Pardue 1983, Lucchetti 1983). However, this poor growth is not consistent among size classes of fish; juvenile trout grow more during the summer than larger trout (Lucchetti 1983, Ensign et al. in press). It is not known whether the poor growth is due to high temperatures (which increase metabolic costs), low food densities,

or increased costs due to activity or gonadal development. Estimating the energy allocated to different energetic fates may be useful in determining the factors limiting growth and when growth should be limited.

How prey abundance and temperature affect trout consumption and eventually growth is a complex set of relations. I approached the problem in four steps. (1) Determined when brook trout feed and what size of prey they select because these factors could affect the prey abundance-food consumption relation. I determined when brook trout were eating by estimating feeding periodicity in May, July, and September of 1989 for four streams in Shenandoah National Park, Virginia. I measured prey sizes in the drift and in trout stomachs in one of the streams in May, July and September to estimate prey size selection. (2) Quantified the relation between prey abundance and trout consumption. I measured prey densities and daily rations throughout 24 hrs in the four streams on the three months. Information on prey density and daily ration were used to fit a model that predicts how prey density affects trout consumption. (3) Described the energy budget (energetic fate of food eaten) to find whether fish are meeting minimum energetic costs. The consumption measured at the streams was allocated to different energetic fates using parameter values from previously published studies on salmonids. (4) Compared excess energy after meeting minimum costs with growth of trout. Excess energy after meeting minimum cost was estimated in early and late summer and compared with trout growth. Specific objectives and hypothesis were:

1. To identify characteristics of trout feeding behavior that may affect the prey density-consumption relation. I hypothesized that size selectivity and rigid feeding periodicity by trout might affect the relation between prey density and food consumption.

2. To quantify the effects of prey density on daily ration of brook trout independent of temperature and fish size. I hypothesized that daily ration corrected for temperature and fish size would increase asymptotically with increasing prey density.
3. To compare energy consumed with minimum energetic costs. I hypothesized the difference between consumed energy and costs would be highest in May when trout are growing and low in July and September when they are not.
4. To compare observed growth with excess energy, energy after meeting minimum energetic costs, over the summer for different sizes of brook trout. I hypothesized that trout that obtained the most energy after meeting fixed metabolic costs would have the highest growth.

METHODS.

Study Areas

Four study streams were selected in Shenandoah National Park located in northern Virginia in the Blue Ridge Mountains. Steep ridges and peaks rise 1000 to 3000 feet in the Park, causing the streams to be short and steep (Lennon 1961). I chose sites in different areas of the park to ensure wider variations in prey densities (Figure 1). I expected that topographic and geographic differences would cause changes in vegetation and consequently prey densities. Streams and their dominant geological formations are Piney River (Catoctin, Pedlar), White Oak Canyon Creek (Catoctin), Little Hawksbill Creek (Pedlar) and Madison Run (Hampton, Weverton, and Catoctin; Dise 1984). Streams were selected to have a wide range in alkalinity, (range 138 to 225 micromoles/liter; Dise 1984) because alkalinity has been found to be correlated with invertebrate production (Krueger and Waters 1983). Table 1 presents selected water quality parameters (Dise 1984), latitude and longitude, elevation and mean slope for the four streams. All the streams were first order except Madison Run, which was second

order. Creek chubs *Semotilus atromaculatus* and blacknose dace *Rhinichthys atratulus* were present in Madison Run; nonsalmonid biomass was not measured but I would estimate it made up 20% of total fish biomass. The other three study streams only had brook trout.

Gypsy moth *Lymantria dispar* defoliation has had a large impact in the Park especially in the northern end. In summer of 1989, White Oak Canyon was heavily infested by gypsy moths and Piney River was moderately infested. Little Hawksbill was lightly infested and Madison Run was free of gypsy moths.

Field Measurements and Laboratory Analysis

Sampling schedule

The four streams were sampled once every two months over a 24 hour period. Dates sampled ranged from May 8 to 16, July 8 to 20 and September 2 to 12, 1989. Piney River was sampled first in May, followed by White Oak Canyon, Madison, and Little Hawksbill. In July and September, the streams were sampled in the same order except White Oak Canyon was sampled before Piney River. Samples were started at the same location each month, but the length of stream sampled varied by month and stream. I sampled the site until I captured the number of fish required. Size of sites sampled ranged from little over 200 meters for Little Hawksbill Creek to over a km for Madison Run.

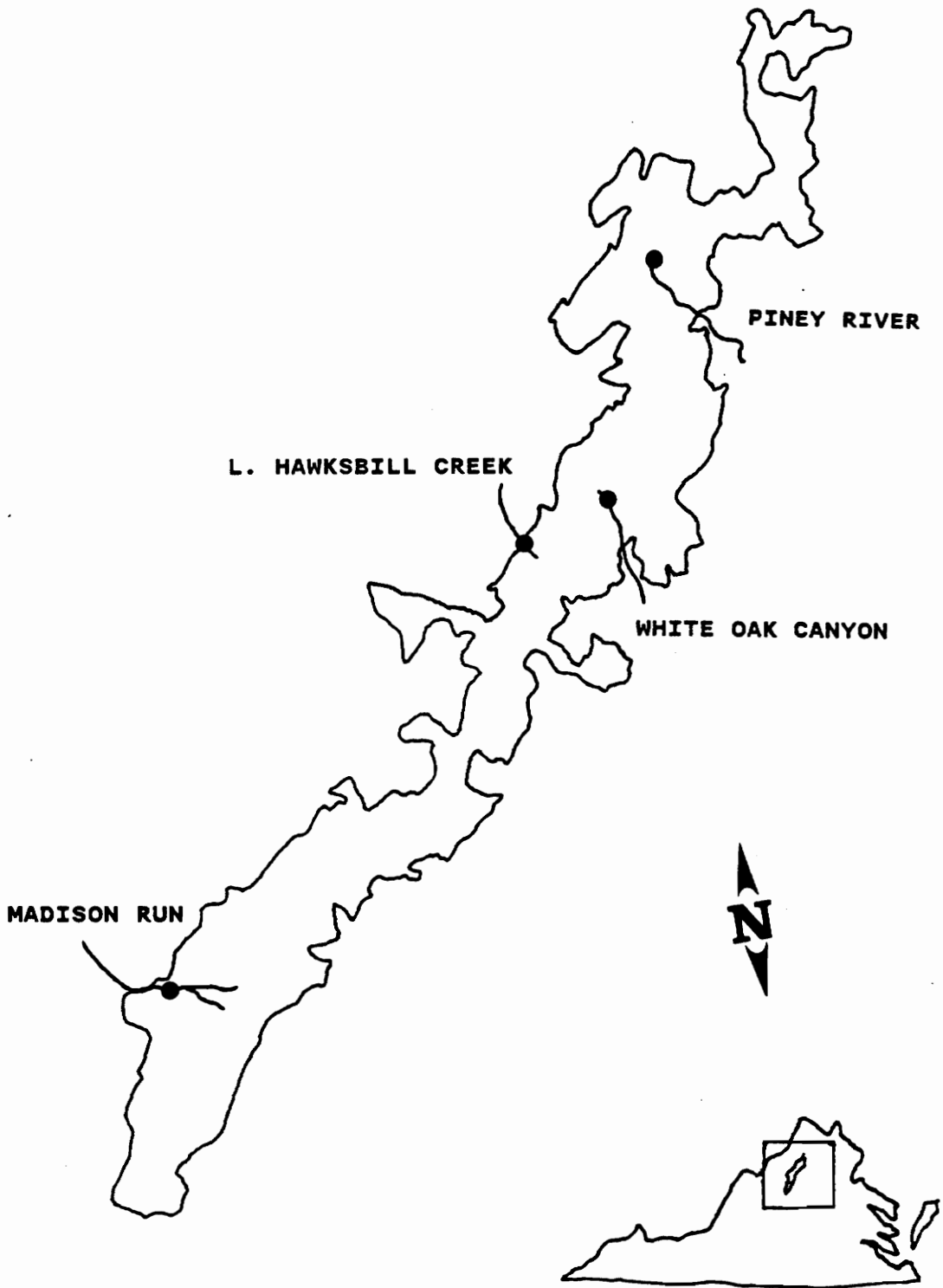


Figure 1. Location of the study streams in Shenandoah National Park.

Table 1. Selected physical characteristics of study streams in Shenandoah National Park measured from U.S. geological survey maps, and summary of water quality data from Dise (1984).

	Piney	White Oak	Madison	Hawksbill
Location ^a				
Latitude	38°44'15"	38°33'52"	38°15'20"	38°32'59"
Longitude	78°17'24"	78°21'53"	78°45'57"	78°26'06"
Mean slope (%) ^b	8.4	15.1	1.6	9.8
Elevation (ft) ^c	2160	2570	1460	1640
Location of sites ^d				
Latitude	38°41'46"	38°32'23"	38°15'05"	38°33'23"
Longitude	78°15'30"	78°20'53"	78°44'50"	78°25'55"
Water quality (micromoles/liter)				
conductivity ^e	36	30	31	28
pH ^f	7.2	7.0	6.3	6.8
Ca	130	99	51	93
Mg	123	91	90	53
Na	92	50	59	81
K	6	3	28	5
Alk	225	187	144	138
SO ₄	63	57	72	78
Cl	27	27	24	24
Si	262	151	145	207
NO ₃	4	5	2	14
NH ₄	< 1	< 1	< 1	< 1

^aLocation is the downstream end of the trout study sites.

^bMean slope measured for the length of stream shocked.

^cElevation for downstream end of trout study sites.

^dAll water quality data taken August 18-21, 1981. Water quality sites were approximately 3 miles down stream from trout site at Piney River, two miles downstream from trout site at White Oak Canyon, and at the same location of trout site for Madison Run and Little Hawksbill Creek (Dise 1984).

^eMeasured in micromhos/cm².

^fpH units

Habitat measurements and analysis

Finding differences in habitat among the four streams was not a major objective of this study; however, food consumption in trout can be dependent on habitat (Ware 1972) and light intensity (Wilzbach et al. 1986). Therefore, I measured some habitat variables that might be useful in explaining variations in the prey abundance-consumption relation. All habitat measurements were taken over a 100 meter section at the downstream end of the study site. Width, substrate, and light intensity were measured with cross sectional transects every 10 meters. Substrate was observed and classified (Wentworth 1922) as bedrock, boulder, rubble, gravel, or sand-silt every 0.5 meters on the transects and the percent of each substrate was calculated. Percent of light shaded was estimated by measuring light intensity in the stream and dividing by maximum light intensity in an unshaded area. Light intensity in the stream was measured in Einsteins at the center of each transect with a photometer once between 1000 and 1400 hours. Proportion of pools was estimated by measuring the the areas of the pools in the 100 meter sections and dividing by the total area. I also counted the number of pools in 100 meters of stream length. Temperature was measured continuously with a Ryan J thermograph over four months in each stream. Water discharge was estimated by measuring cross sectional areas and water velocities (at 0.6 x total depth) with a pygmy-current meter at at least six sites (length among sites ranged from 10 to 50 cm depending on the width of the stream) across a single transect.

Fish sampling

Trout were captured with a backpack electroshocker (Coffelt Model BP-1C) set to output 100 volts DC. Physiological relations may be determined more by size than age (McCormick and Naiman 1984), therefore, captured trout were separated into three size categories on the basis of gaps in the length frequencies for each stream (Table 15). These size classes closely corresponded to juvenile, yearling, and adult fish; and differed slightly among streams. Throughout this thesis I will also refer to these classes as 0, 1, and 2+, respectively. Gaps in the length frequencies sometimes changed between periods, when that happened, I changed the size limit of the size class accordingly.

Fish used to estimate daily ration were captured at four 6-hr intervals beginning at either 0900 or 1500 hrs. At each interval, I shocked the stream until I got the number of trout required for each size class: ten juveniles, ten yearlings and five adults. I did not sample the same numbers of trout in May as in July and September. When sampling in May, I did not distinguish between 1 or 2+ size class and I captured ten or more fish per sampling interval that were a combination of 1 and 2+ fish. Few age 0 fish were captured in May and they were excluded from analysis. Time spent sampling fish ranged from 15 to 60 minutes (median = 25 minutes). The crew always shocked upstream and started each sample at a previously unshocked pool to prevent resampling fish.

After capture, fish were anesthetized with MS-222 (tricane methane sulfonate), and their lengths and weights were measured. Stomach contents were flushed into a plastic bag using a stomach lavage technique (Light et al. 1983) and preserved with formalin. In the few cases where the trout died, I weighed the contents remaining after flushing. The median percent flushed for 0-size fish was 100 % (n= 16); with more than 90% of the

stomach contents flushed for 14 of 16 stomachs. The median percent flushed for 1 and 2+ size fish was 99% (n=13); with more than 90% of the stomach contents flushed for 8 of 13 stomachs.

Fish density was not a major focus of this study, however fish density could affect the amount of food per fish and perhaps energetic costs (Li and Brocksen 1977). Fish density was estimated at 100-meter sections at each stream using the two-catch removal method (Seber and LeCren 1967). I waited at least one hour after the first pass before starting the second pass. The number of fish in each size class was estimated separately and their average weight was used to calculate biomass.

Laboratory analysis of stomach contents

I determined the dry weight of all the stomachs sampled. In the laboratory, the stomach contents of each fish were separated by dissecting microscope into six prey categories: terrestrial origin, terrestrial life stages of aquatic invertebrates, aquatic invertebrates, crayfish, vertebrates (including fish and salamanders), and unidentified prey. All inorganic material was removed. Prey were dried separately by category at 60 C for at least 48 hours and weighed with a Mettler balance to the nearest 0.1 mg.

I measured individual prey sizes eaten, in one randomly selected stream to study prey size selection by brook trout. Prey sizes in the stomachs were measured for the May, July and September samples of White Oak Canyon. All whole prey items were classified (aquatic, terrestrial, or terrestrial from aquatic origins), counted, and measured (total length minus appendages) with an ocular micrometer.

Prey sampling and analysis

Prey abundance was measured to provide indices for predicting food consumption by trout. Drifting prey was measured for one hour immediately before fish capture. Drift nets were 45 cm wide by 30 cm high and had a mesh size of 0.5 mm; the nets were held upright in the stream by two metal stakes. Two nets were set for each sampling interval in May, and one net was set for each interval in July and September because of lower flows. The nets were set in riffles with the top above the water surface to sample drifting terrestrial insects. Water velocity through the drift net was measured with a pygmy current meter to estimate the volume (m³) of water strained. Percent of total stream discharge sampled ranged from 6 to 89% with a median of 23%. Drift net samples were preserved in 5% formalin.

Drift samples were sorted in the laboratory and prey greater than 1.5 mm long were removed. This size was found to be the smallest size eaten by trout in May. In July and September, 98% of the prey eaten by trout were longer than 1.5 mm. Samples collected after May were dyed with eosin Y to speed the sorting process. Larger July samples were subsampled. I sorted and removed prey longer than 1 cm from the entire sample, the remaining sample was placed in a splitter that separated the sample into eight equal subsamples. At least three of the eight subsamples were sorted because an initial sample showed that three subsamples explained an acceptable level of variation. The initial sample had 142 organisms; three subsamples generated a 90 percent confidence interval of 112 to 172 organisms. Prey were counted and separated in the same prey categories as the stomach contents and dried at 60 C for at least 48 hours.

Trout may be selecting larger prey than in the drift, so I measured size of the prey in the drift to adjust prey indices to more accurately reflect available prey. The total length of prey, minus appendages, was measured with an ocular micrometer in all drift samples before drying. In samples with numerous prey, I measured lengths of 100 prey selected randomly. After sorting, prey and water were poured into a petri dish that had grid markings at 1 cm intervals; I measured all prey that touched the lines.

Data Analysis

Diel feeding

Diel feeding is the measure of when fish are eating during the day; it was estimated for brook trout in this study because it could affect the prey abundance-consumption relation. All stomach contents were converted to relative weight by dividing the stomach contents (mg dry wt) by the live body weight (g wet wt) of the fish. Relative weights of stomach contents were averaged for each time of day and trout size class. Times sampled were morning (0300-0900), midday (0900-1500), evening (1500-2100), and night (2100-0300). I used the Elliott and Persson (1978) model to estimate consumption per 6-hr interval because it is the most appropriate for estimating temporal consumption patterns (Boisclair and Leggett 1988).

$$C_t = \frac{(S_t - S_0 e^{-R6})R6}{1 - e^{-R6}} \quad [1]$$

Where C_i is the consumption per six hours ($\text{mg dry wt} \cdot \text{g}^{-1}$), S_i is the stomach contents at the end of the 6 hours ($\text{mg dry wt} \cdot \text{g}^{-1}$), S_o is the stomach contents at the beginning of the 6 hours ($\text{mg dry wt} \cdot \text{g}^{-1}$), and R is the evacuation rate (hr^{-1}). The evacuation rate was estimated from Elliott's (1972) work on brown trout.

$$R = 0.053e^{0.112T} \quad [2]$$

Where R is the proportion of food evacuated per hour and T is the water temperature (C). This evacuation rate is applicable to temperatures of 3.8 to 19.1 C and for *Gammarus*, *Baetis*, chironomids, and oligochaetes (Elliott 1972). Elliott (1972) found evacuation rates were consistent among meal size and fish size. Evacuation rates can change by food type; the use of this equation assumes that the prey have similar evacuation rates or trout do not change the type of prey eaten by time of day. Evacuation rates may be consistent among salmonid species; Cunjak et al. (1987) quoted studies that found salmonid species had similar physiological rates. Elliott (1972) is considered to have made the most reliable estimate of the evacuation rate and it has been used in studies on other salmonids (Cunjak and Power 1987, Cunjak et al. 1987, Amundsen and Klemetsen 1988, and Ensign et al. in press). The proportion of diel feeding during each interval was estimated by dividing the C_i of each 6-hr interval by the total food consumed in the four intervals. A Kruskal-Wallis one-way layout was used to test if fish fed significantly more at certain intervals throughout the summer. The number of replicates for the layout were twelve for yearlings and adults (four streams x three months), and eight for juveniles (four streams by two months).

Prey size selectivity

Prey size selectivity was estimated by comparing the size of prey selected by trout with the size of prey in the drift. Size selectivity was estimated because it could affect the prey abundance-consumption relation. I estimated size selectivity for trout in White Oak Canyon in May, July and September. The length frequencies of prey in the stomachs were pooled into the three size classes to determine prey selectivity. I used a Mann-Whitney U test ($P < 0.05$) to determine which size classes of fish selected for larger prey than in the drift.

I used Ivlev's (1961) selectivity index to describe sizes of prey selected by trout. The prey in the stomach and drift were separated into categories with a lower category of 1.5-2mm, five or six intermediate categories with increments of 1mm, and an upper category of prey longer than 8mm for May, and 7mm for July and September. Lower thresholds for the upper category were chosen so that trout had consumed at least five prey in the size category. Size selectivity by brook trout was calculated by Ivlev's (1961) formula:

$$E_i = \frac{r_i - p_i}{r_i + p_i} \quad [3]$$

Where E_i is the electivity for each size class of prey (i) and ranges from -1 to 1; higher numbers represent positive selection and negative numbers represent negative selection. The parameter r_i is the proportion of prey in the ration in the i size category and p_i is the proportion of prey in the drift in the i size category.

Prey abundance

Sixteen different indices were estimated to find the best predictor of consumption. I estimated four measures of prey abundance in the drift: total weight (including crayfish and salamanders) (mg), total weight of small invertebrates (excluding salamanders and crayfish) (mg), number of prey drifting (no), and number of prey longer than 4mm (no). Total weight of small invertebrates was used as a measure because crayfish and salamanders accounted for a large portion of the total weight when present, yet were rare in the drift. Capture of larger drift items may have been incidental. I used 4mm as a threshold because the size selection results indicated that brook trout positively selected for prey longer than 4mm. These measures were averaged for the entire day to get daily measures of prey availability. Because there were four streams sampled on three occasions there were twelve separate estimates of the four prey measures. Sixteen indices were calculated from these four abundance measures: drift density (prey measures \cdot m³), drift rate (prey measures \cdot hr⁻¹), drift density per fish (prey measures \cdot hr⁻¹ \cdot gm wet wt⁻¹ \cdot m²), and drift rate per fish (prey measures \cdot hr⁻¹ \cdot gm wet wt⁻¹ \cdot m²). Drift density (prey measures \cdot m³) may be good estimates if fish are feeding on drift at similar velocities among streams. However, other indices may better reflect the prey available to individual trout. Alternatives include estimates of prey passing a cross-section of stream per unit time (drift rate) and estimates of prey per fish. I calculated drift rates (prey measures \cdot hr⁻¹) by multiplying the four prey measures by stream discharge to get the amount of prey passing through a cross-section of the stream in an hour. I estimated prey per fish indices by dividing the four drift density indices and the four drift rate indices by fish biomass. For juveniles I used juvenile biomass and for yearlings and adults I used the sum of yearling and adult biomass in the denominator of the indices.

Daily consumption

Daily consumption was calculated by the Eggers method (1977). I used the Eggers method in all calculations instead of the Elliott and Persson's method (equation 1) because it is more robust to variation in the sampling interval (Boisclair and Leggett 1988). Elliott and Persson recommended 3 hrs per interval and I used 6 hrs because of logistic constraints. The formula for Eggers method (1977) is:

$$C = \bar{S} \cdot 24 \text{ hours} \cdot R \quad [4]$$

Where C equals the daily ration (mg dry wt • g wet wt⁻¹ • day⁻¹), \bar{S} is the average stomach content over the day (mg dry wt • g wet wt⁻¹) and R is the evacuation rate (% digested • hrs⁻¹) at a specific temperature (equation 2). Daily ration was converted to percent dry weight/trout dry weight for comparison with other studies, otherwise I kept the units in mg dry wt • g wet wt⁻¹ • day⁻¹. I assumed that trout body composition was 75% water when converting daily ration to dry weight/ trout dry weight.

The amount of food eaten is directly dependent on temperature and fish size (Elliott 1975b, Hewett and Johnson 1987). Therefore, consumption needs to be adjusted so that changes in food consumption are a reflection in changes of prey abundance and not changes in temperature or fish size. A measure of adjusted consumption is P-value, the proportion of maximum consumption (given trout size and temperature) consumed (Hewett and Johnson 1987). The parameter P-value is estimated by dividing daily ration (C) by the maximum potential consumption (C_{\max}) where C_{\max} is a function of fish size and temperature. Estimates of maximum consumption (C_{\max}) were adapted from

Elliott's (1975b, 1976) relation for brown trout maximum consumption using temperature data for brook trout; the adapted formula is:

$$C_{\max} = 56.104W^{-0.233}r_c \quad [5]$$

Where C_{\max} is maximum consumption (mg dry wt \cdot g⁻¹ \cdot day⁻¹), W is wet weight (g), and r_c is the effect of temperature on consumption (ranging from 0 to 1). This formula adapts a formula from Elliott (1976) to predict the effect of trout size on consumption and uses studies on brook trout (Baldwin 1956, Coutant 1977) to predict the effect of temperature on maximum consumption. Elliott's (1976) formula predicted brown trout would consume the most food at 17.8 C. I used his formula at 17.8 C to estimate the amount of food consumed by brook trout at their temperature of maximum consumption (which is 16.0 C). I converted Elliott's equation from calories to mg by using the conversion 4.438 cal/ mg dry wt (Elliott 1976).

The effect of temperature on maximum consumption r_c was estimated from laboratory studies on brook trout (Figure 2). The temperature correction factor, r_c , was estimated by fitting Thornton-Lessem (1978) functions to the data in Baldwin (1956) and Coutant (1977). Hewett and Johnson (1987) presented three possible functions for describing the affect of temperature on consumption; they stated the Thornton-Lessem algorithm was the most appropriate for cold water fish. The Thornton-Lessem algorithm requires information at three temperatures: consumption at a relatively cold temperature, consumption at optimal temperature (where consumption is highest) and consumption at a relatively high temperature. Baldwin (1956) measured brook trout consumption at different temperatures and I used his data for the low and the high temperature in the algorithm. Baldwin (1956) measured the highest consumption at 13 C but the next highest

temperature tested was 17 C. It is probable maximum consumption lies between 13 and 17 C; growth studies have found optimal growth at 15.4 C (McCormick et al. 1972) and 16.0 C (Hokansen 1973, Dwyer et al. 1983). One estimate of optimal food consumption for fish is their preference temperature. Kitchell et al. (1977) used temperature preference data to estimate the temperature of highest consumption for perch *Perca flavescens*. I used a similar approach to find optimal temperature for brook trout in this study. Coutant (1977) listed studies that presented brook trout temperature preferences; the median of the temperature preferences for these studies was 16.0 C. Therefore, the parameters used in the algorithm were lower threshold = 3.5 C with P-value = 20% and upper threshold = 21 C with P-value = 13% (from Baldwin 1956) and optimum temperature = 16.0 C with P-value = 100% (from Coutant 1977). Figure 2 shows this algorithm with data from Baldwin (1956) and Coutant (1977).

Prey density versus consumption

Prey densities and consumption were entered in a model to quantify the prey abundance-consumption relation. Earlier, I identified sixteen prey indices that might predict consumption. To eliminate the worst predictors of consumption, I tested the correlation between the prey indices and corrected consumption (P-value) using Spearman's rank correlation. Only indices with significant correlations were entered in Ivlev's (1961) equation which relates prey density and consumption:

$$C = C_{\max}(1 - e^{-kp}) \quad [6]$$

where:

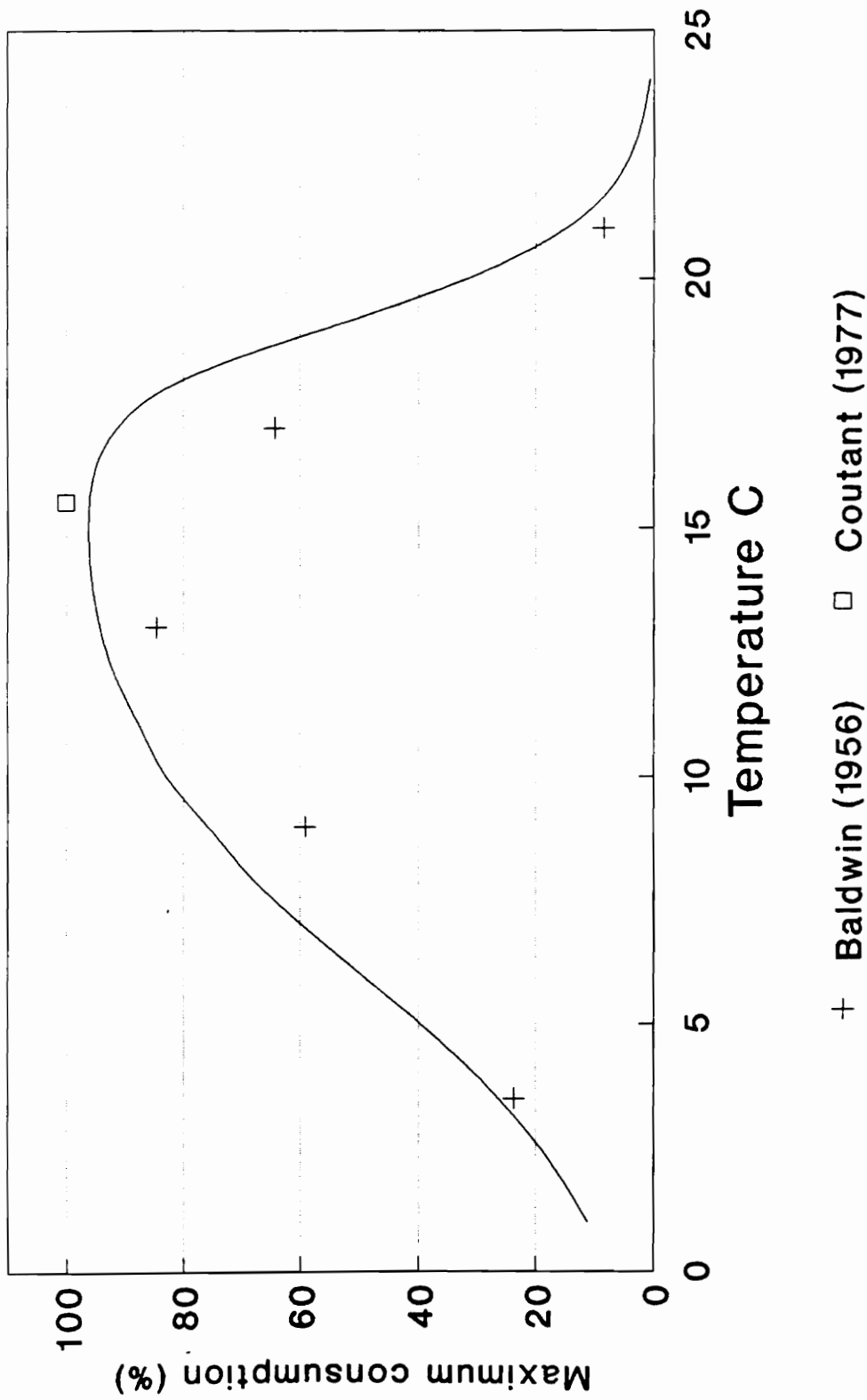


Figure 2. Brook trout feeding as a function of temperature as fitted by a Thornton-Lessem function. Daily rations from Baldwin (1956) was converted to the proportion of maximum consumption (P-value) by dividing by maximum consumption. Maximum consumption was estimated from maximum consumption for brown trout at the optimum temperature (Elliott 1976). Brook trout temperature preferences from Coutant (1977) was used to estimate the temperature at maximum consumption.

C = daily ration of fish (mg dry wt • g wet wt⁻¹ • day⁻¹)

C_{\max} = maximum potential consumption (mg dry wt • g wet wt⁻¹ • day⁻¹)

p = prey index

k = constant that represents the rate of increase in consumption with increasing prey

Because $P\text{-value} = C/C_{\max}$ the equation becomes

$$P\text{-value} = 1 - e^{-kp} \quad [7]$$

I used nonlinear regression (SAS procedure NLIN, SAS 1985) to estimate the constant k . When k is known, the above equation can be used to predict consumption when temperature and prey density are known.

Energy budget

I estimated energy budgets of trout on a daily scale to find if trout were meeting minimum energetic costs throughout the summer. Energy consumed is allocated to different fates (Webb 1978); the energy budget can be represented as:

$$G = C - F - U - R_{\text{sda}} - R_s - R_a \quad [8]$$

Where G is energy used for somatic and gonadal growth, C is energy consumed, F is energy egested, U is energy excreted, R_{sda} is energy used to digest food, R_s is energy used for basal respiration, and R_a is energy used for activity metabolism. In my calculations, all units are in joules/g wet weight. The energy allocated to activity is difficult to

measure accurately. Therefore, I combined the parameters G and R_a into E , the energy available to growth and activity. The new energy budget is:

$$E = C - F - U - R_{sda} - R_s \quad [9]$$

Consumed energy (C) in each size class was estimated by multiplying the daily ration (equation 4) of each prey category by caloric density (Cummins and Wuychek 1971). Prey in the unidentified category were assigned a caloric density intermediate between the terrestrial and aquatic categories. All caloric densities were converted to joules (4.190 joules/calorie).

Energy allocated to F , U and R_{sda} can be estimated as a function of consumption. Elliott (1976) reported that energy allocated to the sum of F and U was a direct proportion of food consumed and did not depend on temperature, meal size, or trout size. However, egested energy (F) and excreted energy (U) vary with different types of food. More energy is egested with foods high in carbohydrates than foods high in protein (Webb 1978). In this study, egestion (F) was estimated as $(C \times 0.267)$ and U was estimated as $(C \times 0.06)$ from (Elliott 1975). Elliott (1975) estimated F and U for brown trout feeding on invertebrates (*Gammarus*). Brook trout feed mostly on invertebrates, so I felt Elliott's estimate of F and U were probably accurate. Elliott's (1975) estimates of F and U were 2% higher than those derived for other carnivorous fish (Brett and Groves 1979). Respiration used for digestion is also a function of consumption. The parameter R_{sda} was estimated as $((C-F) \times 0.172)$ from Stewart et al. (1983). Stewart et al. (1983) measured the energy used by lake trout *Salvelinus namaycush* to digest fish. Foods with a higher protein content, such as fish, take more energy to digest, thus, this estimate of R_{sda} is probably an overestimate for brook trout. Brett and Groves (1979) found the

average R_{std} of carnivorous fish to be 14%. I felt it would be better to overestimate the energy used to digest food if I was unsure of the exact value because this would make the estimate of E more conservative. Energy available to trout after subtracting F , U , and R_{std} is net energy (Brett and Groves 1979) and is the energy remaining after meeting the cost of processing food. Estimates of net energy are equal to $(C \times 0.55)$ in this study. These formulas simplify equation (9) to:

$$E = (0.55C) - R_s \quad [10]$$

Basal metabolism R_s was estimated by taking data from Jobb (1955) for brook trout and using multiple regression to correlate respiration with temperature and fish size. Jobb (1955) measured basal metabolism for a wide range of brook trout sizes (5 to 1000g) and temperatures (5 to 20 C). I used the means of basal metabolism for groups of 5 to 10 trout (at specific weights and temperatures) as data points in the regression ($P < 0.0001$, $R^2 = 0.993$). The final equation was:

$$R_s = 18.532 W^{-0.1653} e^{0.0821T} \quad [11]$$

where R_s is basal metabolism ($j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$), W is fish size (g), and T is temperature in C (Figure 3).

I estimated energy budgets on a seasonal scale to find the relation between energy available for growth and activity (\bar{E}) averaged over two months and trout growth (\bar{G}). One of the hypotheses was that growth would increase with more energy available for growth and activity.

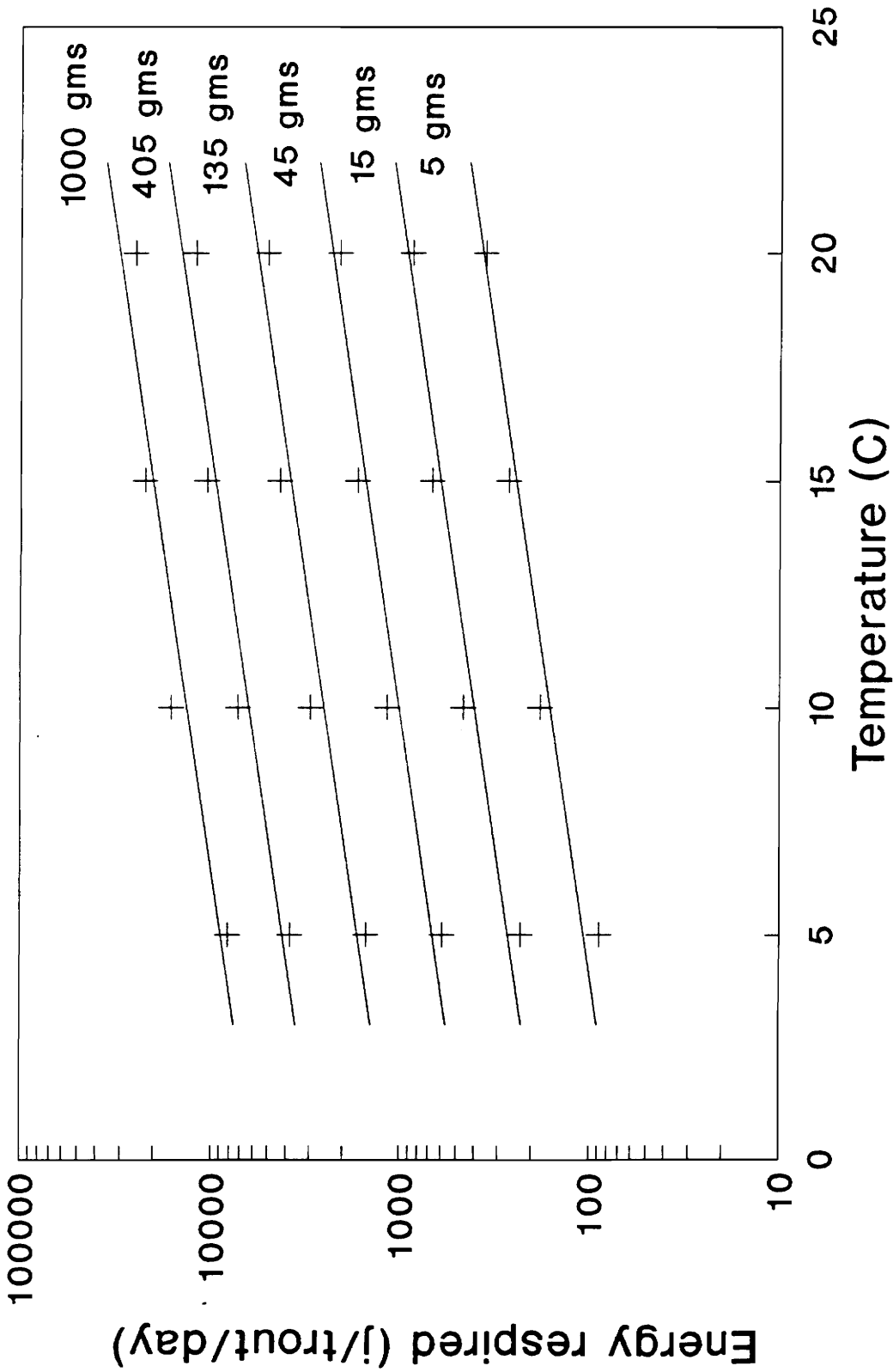


Figure 3. Standard metabolism ($j \cdot \text{trout}^{-1} \cdot \text{day}^{-1}$) of brook trout at different temperatures (C) and fish weights (g wet wt). Points are means of consumption measured by Jobb (1955), lines were found from multiple regression of temperature and weight, the formula is $18.532W^{0.8347}e^{T \cdot 0.0821}$

I estimated the energy available for growth and activity over the interval as:

$$\bar{E} = \frac{E_1 + E_2}{2} \quad [12]$$

Where \bar{E} is the mean energy available for growth and activity over the two month interval, E_1 is the energy available for growth and activity at the beginning of the interval (equation 10) and E_2 is the energy available for growth and activity at the end of the interval. All units are in $\text{j} \cdot \text{g wet wt}^{-1} \cdot \text{day}^{-1}$.

I estimated the energy available for growth over the two month intervals as:

$$\bar{G} = \left[\frac{(W_2 - W_1)}{\bar{W}} / t \right] D_c \quad [13]$$

Where \bar{G} is the mean energy allocated to growth during the interval ($\text{j} \cdot \text{g wet wt}^{-1} \cdot \text{day}^{-1}$), W_2 is the weight at the end of the interval (g wet wt), W_1 is the weight at the beginning of the interval (g wet wt), \bar{W} is the mean weight of the trout during the interval (g wet wt), D_c is the caloric density of the fish (I am assuming a constant derived from Elliott 1976; $6058 \text{ j} \cdot \text{g wet wt}^{-1}$), and t is the days in the interval. The caloric density of fish is not constant and could change by season. Unfortunately, I did not have information on changes in caloric densities. A trend of increasing caloric density would result in an underestimate of \bar{G} and decreasing caloric density would lead to overestimating \bar{G} .

Growth (\bar{G}) and energy available for growth and activity (\bar{E}) over two month intervals were compared graphically to examine possible relations. I expected to see a strong positive relation between excess energy after meeting excess costs (\bar{E}) and growth (\bar{G}).

Respiration allocated to activity (R_a) is difficult to measure on a daily scale but can be indirectly estimated over longer intervals. The formula is:

$$\bar{R}_a = \bar{E} - \bar{G} \quad [14]$$

Where \bar{R}_a is the mean activity cost ($j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$), \bar{G} is the mean energy used for growth ($j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$), \bar{E} is the mean energy remaining for activity and growth ($j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$). Estimates of activity costs \bar{R}_a may be suspect because biases in \bar{G} and \bar{E} are included in the estimate.

I estimated gross conversion efficiencies and growth rates for comparison with other studies. Gross conversion efficiency is the proportion of energy consumed that is converted to growth.

$$C_e = (\bar{G}/\bar{C}) \times 100 \quad [15]$$

Where C_e is the conversion efficiency (%), \bar{G} is the mean energy allocated to growth $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$, and \bar{C} is the mean daily ration $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$ over the two month interval. Mean daily ration is found by:

$$\bar{C} = \frac{C_1 + C_2}{2} \quad [16]$$

Where \bar{C} is the mean energy in the daily ration over the two month interval, C_1 is the energy in the daily ration at the beginning of the interval and C_2 is the energy in the daily ration at the end of the interval. All units are in $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$.

Instantaneous growth rates were calculated for each size class over two month intervals for comparison with other studies.

$$G = \frac{(\ln W_2 - \ln W_1) \times 100}{t} \quad [17]$$

Where G is the instantaneous growth rate ($\text{percent wet wt} \cdot \text{day}^{-1}$), W_2 is the mean weight of the size class at the end of the two months (g), W_1 is the mean weight at the beginning of the two months (g) and t is the days between sampling. The parameter G and \bar{G} are different, G refers to the growth rate and is the average growth rate in weight ($\text{percent wet wt} \cdot \text{day}^{-1}$). The parameter (\bar{G}) is the average energy allocated to growth on a daily basis ($j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$).

RESULTS

Study streams varied in habitat and trout population characteristics (Table 2 and Appendix I). Appendix I contains information on the populations of the stream in numbers/ha and kg/ha, the intervals used to place the fish in different size classes, and the mean length, weight, and condition of the size classes. Piney River had a substrate dominated by bedrock, boulder, and rubble; it had a moderate slope (8%) and had a fish density twice as large as the other streams. White Oak Canyon had a steep slope (15%) and the substrate was mostly bedrock; fish density was intermediate. Madison Run was a low elevation low slope (1%) stream with a substrate dominated by rubble and gravel and had the lowest population density (a quarter the density of Piney River). Little Hawksbill Creek had a low elevation, 8 % slope, the most habitat heterogeneity, and was the most heavily shaded. It had an intermediate density of fish, but most were juveniles. The size of the streams from largest to smallest by September discharge was White Oak, Madison, Little Hawksbill, and Piney (Table 2).

Temperature was near optimum for food consumption during the summer (according to Figure 2). The mean temperatures in May (Table 14) would allow the fish to consume

Table 2. Selected physical characteristics of study streams in Shenandoah National Park (Summer 1989).

	Piney	White Oak	Madison	Hawksbill
Substrate(%)				
bedrock	23	65	3	33
boulder	26	16	18	36
rubble	23	8	41	26
gravel	18	11	32	2
sand-silt	9	1	5	3
Percent pool				
May	24	35	37	73
July	35	39	25	21 ^a
Number of pools per 100m	12	12	8	23
Mean width (meters)				
May	5.34	6.60	7.66	4.10
July	2.7	4.59	4.14	-
Sept	2.68	4.34	4.78	2.65
Area for population estimate(m ²)				
May	374	660	766	410
July	235	459	415	241 ^b
Sept	257	434	454	241
Shading (percent of light obstructed)				
May	-	34	38	78
July	58	75	61	92
Sept	-	-	-	-
Light intensity (einsteins)				
May	10	110	117	2
July	51	1004	74	100
Sept	-	-	-	-
Discharge(m ³ × s ⁻¹)				
May	.4899 ^c	.4285	.2474	.1890
July	.0313	.0823	.0304 ^d	.2740 ^e
Sept	.0135	.0851	.0506 ^d	.0208
Temperature day of sampling(°C)				
May	9.0	7.5	11.0	9.2
July	18.0	17.0	17.2	16.0
Sept	15.7	15.0	16.3	16.2

^aPool percentage was measured in September because of high water levels in July.

^bArea was estimated using the average width from September because of a flood event before measuring width in July.

^cDischarge was taken at the end of the 24 hours after a flood event there were no discharge measurements before the rain

^dIn some locations the flow was subterranean.

^eDischarge was taken at the end of the 24 hours after a flood event the flow before the flood was .0232m³ × s⁻¹

80% of maximum. The mean temperature the rest of the summer would allow the fish to consume 90% of maximum. Madison Run was the warmest stream, followed by Piney River, Little Hawksbill and White Oak Canyon. Temperatures were relatively cool; the warmest temperature measured ranged from 16.7 C for White Oak to 19.4 C for Madison Run.

Diel feeding

Adult and yearling trout did not consistently consume more food at one time period throughout the summer ($P = 0.45$ and $P = 0.26$ respectively; Kruskal-Wallis from May to September). However, juvenile trout had significant diel differences in consumption ($P = 0.03$). Juveniles fed less at night than at other times throughout the summer. Juveniles ate significantly more ($P < 0.05$) during midday (0900-1500) and evening (1500-2100) than at night (2100-0300). Consumption in the early morning (0300-0900) was not significantly different ($P > 0.05$) from consumption at night. Table 20 contains information on the mean stomach contents by stream for each interval.

Only juvenile trout significantly consumed more food at certain times throughout the summer, yet there were times of the day when yearling and adult trout consumed more food (Table 3). These peaks in consumption differed among trout size and month. In May, all trout ate more during the day; yearling trout fed more in the evening (37% of daily total) and adult trout ate more at midday (45%). Conversely, in July, yearlings and adults had the highest consumption at night (43 and 44% respectively). Juveniles had the most consumption in the evenings, intermediate consumption during morning and midday but had the lowest consumption (14% of total) at night. In September, all the sizes of fish followed the same patterns as July; juveniles ate the most in the evening,

followed by midday, morning, and night. Yearlings and adults fed slightly more at night (29 and 35% of daily consumption respectively). Even though yearlings and adults consumed more at night in September, the increase in consumption was slight. The range between the lowest and the highest amount eaten per interval only differed by 8% for yearlings and 16% for adults.

Prey size selectivity

There were significant differences (Mann-Whitney U, $P < 0.05$) between prey sizes in the drift and in the stomachs for all sizes of brook trout in White Oak Canyon (Table 4). Fish were more likely to select larger prey as they got larger. Median sizes of prey eaten were significantly ($P < 0.05$) higher than the drift in 11 of 12 sample times for adults, 10 of 12 for yearlings and 4 of 8 for juveniles.

Figures 4 to 6 contain information on selectivity of brook trout for particular size classes of prey. Larger prey had higher electivity values than smaller prey. Brook trout in White Oak Canyon consistently selected for prey in the prey category 4 to 5 mm and larger; Figures 4 to 6 show the phenomena for the different seasons. There is some scatter in the figures at low size categories especially in May.

Prey abundance

Prey densities were highest in May for prey per unit time and highest in July for prey per cubic meter (Table 5). Streams had the highest drift rates (prey measures hr^{-1}) in May for all measures, followed by July and then September (Table 5). The mean weight of prey drifting per hour dropped from 1024 mg/hr in May to 554 mg/hr in July and 82

Table 3. Diel feeding (% of food consumed in day) of brook trout in the summer in four streams of Shenandoah National Park.

Trout size/ Stream	Morning 0300-0900	Midday 0900-1500	Evening 1500-2100	Night 2100-0300
MAY				
1+				
Piney ^a	58.8	40.0	-0.2	1.0
White Oak	30.0	9.0	42.2	18.8
Madison	8.3	23.2	28.7	39.9
Hawksbill	37.4	22.1	39.7	0.7
Average	25.2	18.1	36.9	19.8
2+				
Piney ^a	51.3	9.4	18.7	20.5
White Oak	22.3	49.8	27.9	0.0
Madison	37.8	41.4	10.4	10.4
Hawksbill	13.5	44.9	0.0	41.6
Average	24.5	45.4	12.8	17.3
JULY				
0+				
Piney	11.4	35.2	39.5	13.9
White Oak	31.0	24.1	37.4	7.5
Madison	28.9	28.4	21.5	21.2
Hawksbill ^b	14.5	40.4	32.2	12.9
Average	23.8	29.2	32.8	14.2
1+				
Piney	22.3	14.2	24.3	39.2
White Oak	22.4	28.5	12.1	36.9
Madison	15.7	24.1	8.8	51.5
Hawksbill ^b	20.5	21.4	23.5	34.5
Average	20.1	22.3	15.1	43.3
2+				
Piney	30.0	8.2	41.0	20.8
White Oak	29.1	23.4	13.1	34.4
Madison	18.4	4.6	7.0	70.0
Hawksbill ^b	34.6	18.7	29.0	17.6
average	25.8	12.1	20.4	41.7
SEPT				
0+				
Piney	20.7	23.3	44.8	11.3
White Oak	12.0	25.7	60.0	2.3
Madison	7.3	28.7	29.4	34.6
Hawksbill	32.0	40.3	11.3	16.4
Average	18.0	29.5	36.4	16.1
1+				
Piney	20.8	35.7	25.7	17.8
White Oak	22.4	14.7	39.1	23.8
Madison	37.7	12.1	6.0	44.2
Hawksbill	19.0	22.9	27.5	30.7
Average	25.0	21.4	24.5	29.1
2+				
Piney	6.0	58.7	13.6	21.7
White Oak	7.3	20.0	36.0	36.6
Madison	8.5	23.0	8.2	60.3
Hawksbill	53.9	0.0	24.0	22.1
Average	18.9	26.5	20.5	35.2

^aHeavy rains fell at 1500, this sample was not used to calculate the averages.

^bHeavy rains fell at 2100, this sample was not used to calculate the averages.

Table 4. Median sizes (mm) of prey in the drift and fish stomachs at different times of the day in White Oak Canyon, Shenandoah National Park. Mann-Whiney U tests were used to test whether sizes of prey in the drift were different from the stomachs. Number of prey measured are in parentheses.

Time	Drift	Juvenile	Yearling	Adult
MAY				
0200	5.0 (252)	-	5.6* (76)	5.3 (29) (NS)
0800	3.4 (40)	-	5.3*** (45)	6.1*** (52)
1400	4.0 (156)	-	4.4 (48) (NS)	5.6*** (130)
2000	3.6 (100)	-	5.0*** (106)	5.4*** (79)
JULY				
0200	3.7 (127)	2.85 (32) (NS)	5.5*** (126)	5.5*** (39)
0800	2.3 (141)	3.7*** (86)	3.8*** (144)	5.1*** (206)
1400	2.5 (129)	3.0* (186)	4.0*** (282)	5.2*** (136)
2000	3.0 (195)	3.5*** (122)	4.2*** (31)	5.8*** (36)
SEPT				
0200	3.2 (122)	2.6 (5) (NS)	3.6 (20) (NS)	7.2*** (20)
0800	2.6 (19)	3.6 (67) (NS)	4.0** (100)	4.2** (120)
1400	2.8 (33)	3.2 (163) (NS)	3.2 (157) (NS)	4.0*** (109)
2000	3.0 (209)	4.2*** (42)	4.5*** (58)	4.5*** (44)

*Significantly different from drift ($P < 0.05$).

**Significantly different from drift ($P < 0.01$).

***Significantly different from drift ($P < 0.001$).

(NS) non significant ($P > 0.05$).

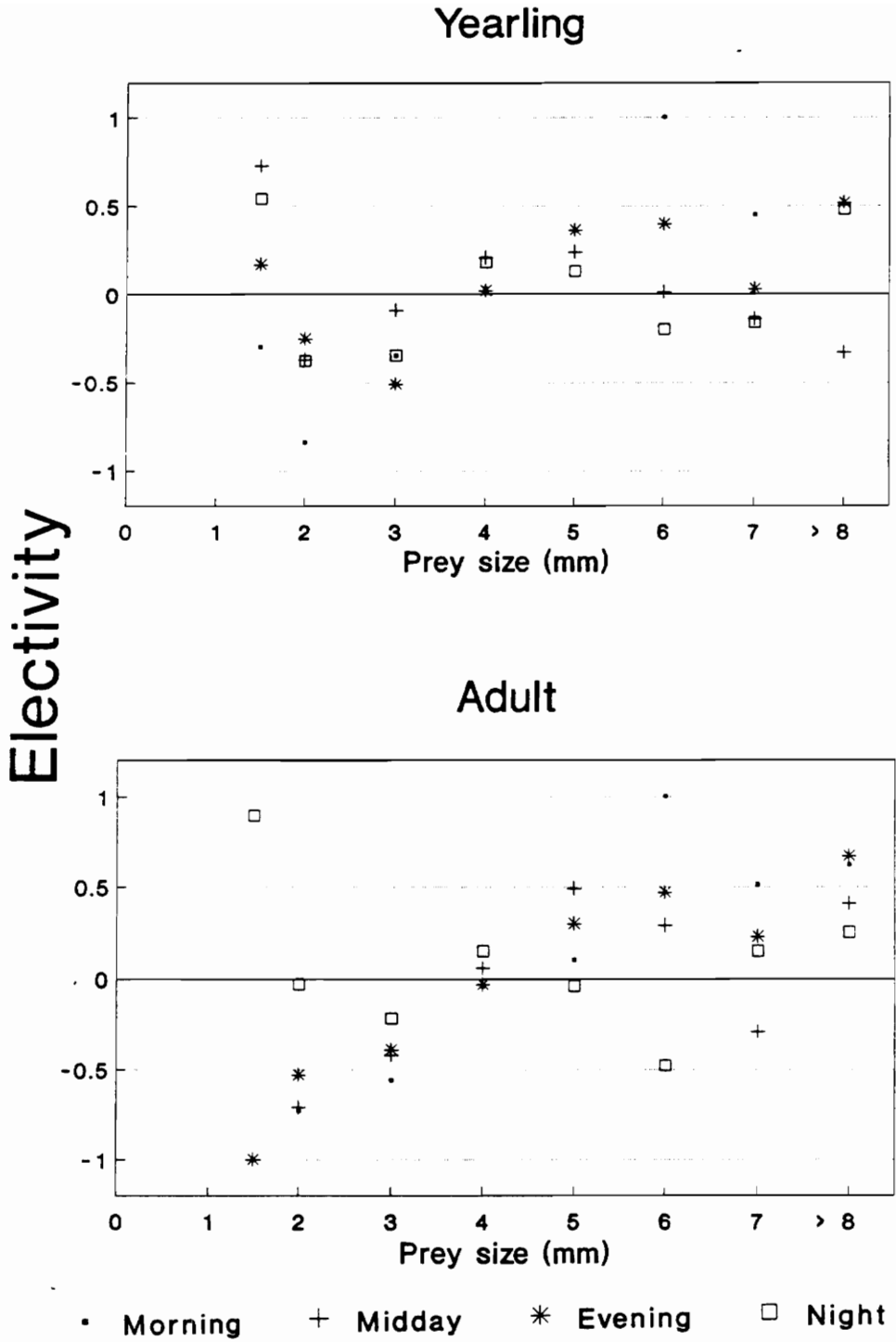


Figure 4. May selectivity (Ivlev 1961) for different sizes of prey at different times of the day for brook trout in White Oak Canyon of Shenandoah National Park.

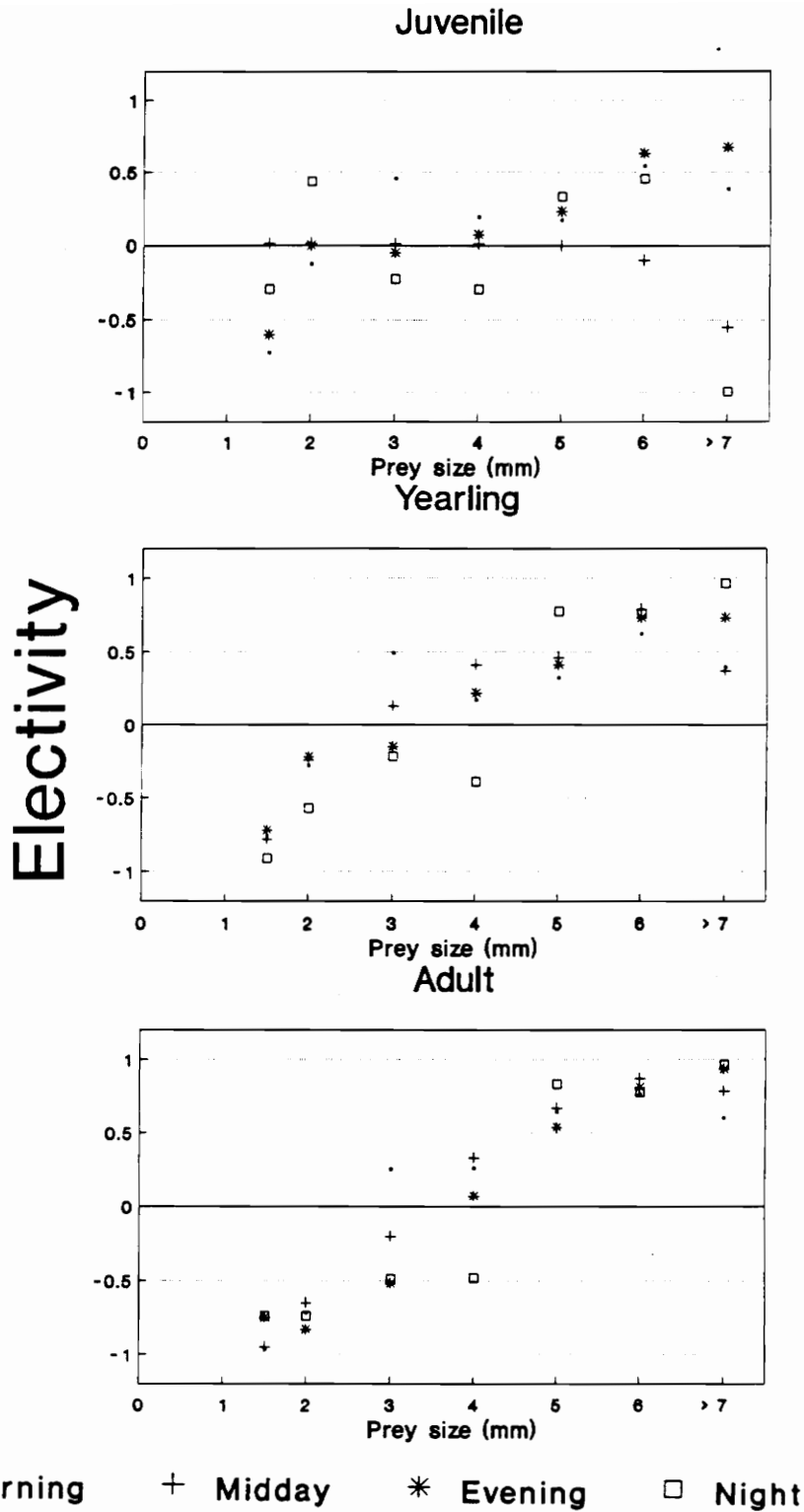


Figure 5. July selectivity (Ivlev 1961) for different sizes of prey at different times of the day for brook trout in White Oak Canyon of Shenandoah National Park.

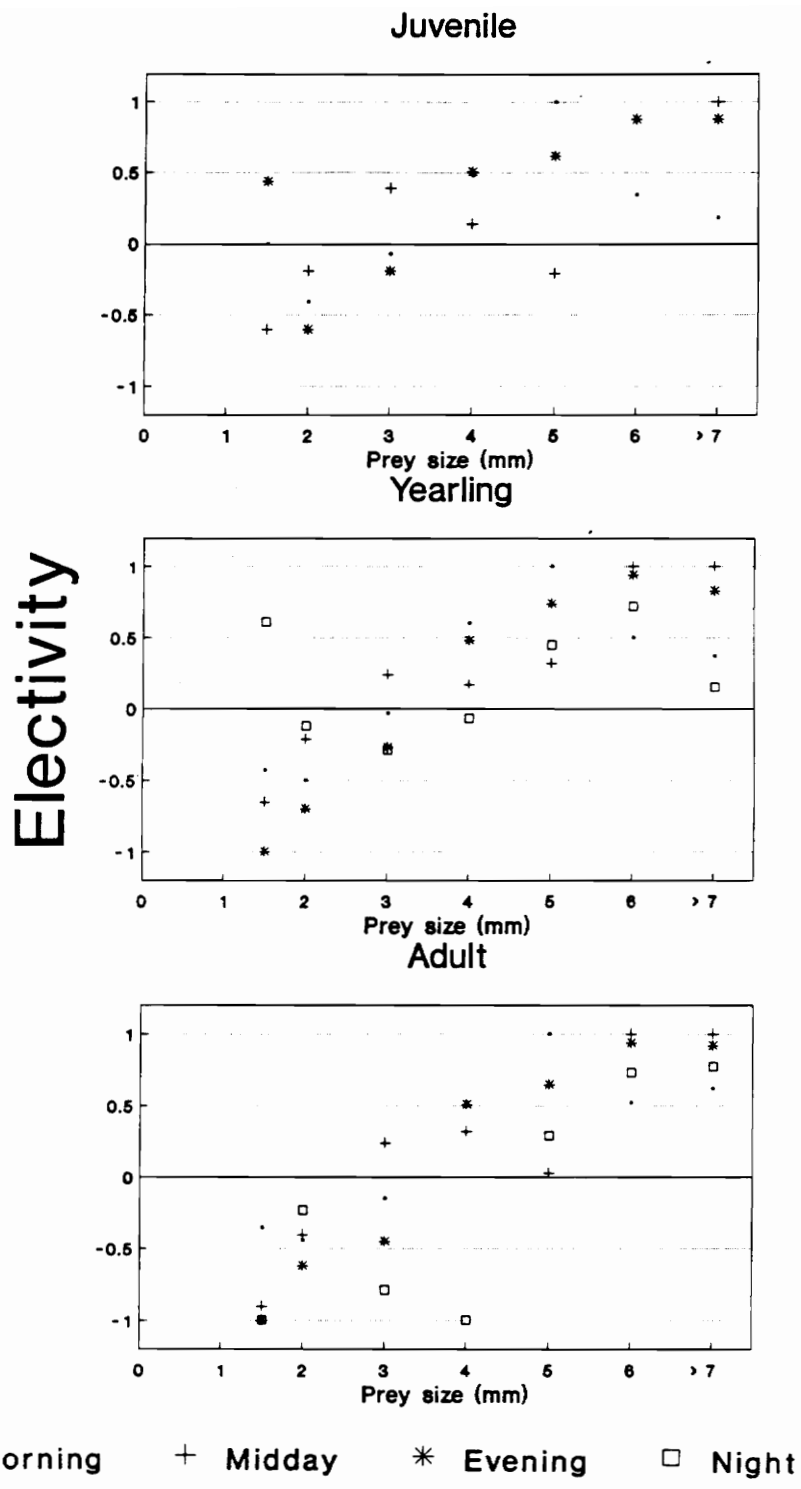


Figure 6. September selectivity (Ivlev 1961) for different sizes of prey at different times of the day for brook trout in White Oak Canyon of Shenandoah National Park.

mg/hr in September. May had high drift rates because the streams had higher discharges than the rest of the summer. Prey density indices (measures/m³) were highest in July followed by May and September; the only exception was mean number of prey (no/m³), which was 24 % higher in September than in May. Mean total weight (small invertebrates only) per m³ in July was twice as high as May and four times higher than September. The proportion of prey greater than 4 mm decreased over the summer, from 46% in May to 27% in July, and 17% in September. Prey densities were highest at 0200 hrs than the other times; prey densities were also high at 2000 hrs in September (Figure 7).

Variability in prey indices among streams were highest in July. Biomass of prey (mg/m³) in the stream ranged from 0.693 to 5.032 in July versus 0.266 to 1.019 in September and 0.870 to 1.162 in May. None of the streams had consistently higher or lower prey measures among months except White Oak Canyon; it had consistently higher drift rates than the other streams. The higher drift rates were partially due to White Oak having consistently higher water discharge.

Daily consumption

The average amount of food consumed by yearlings and adults as a percent of maximum was intermediate in May (29 to 47% respectively) was highest in July (50 to 76%) and fell to the lowest levels in September (27 to 30%; Table 6). Adults in July had the largest range in P-values among streams (15 to 109%) followed by September (13 to 61%) and May (36 to 55%). Yearlings also had the largest range (17 to 79%) in July, followed by May (15 to 45%) and September (16 to 39%). Juvenile trout had similar P-values in July (38%) and September (35%), with none of the P-values greater than 46%.

RESULTS

Table 5. Average prey densities over 24 hours at each site and date in Shenandoah National Park in summer of 1989. TOT is the total weight of prey (mg dry wt), SMA is the weight of prey excluding vertebrates and crayfish (mg dry wt), NTOT is the total number of prey, and LTOT is the total number of prey longer than 4mm.

	Drift Densities				Drift rates			
	TOT mg/m ³	SMA mg/m ³	NTOT no/m ³	LTOT no/m ³	TOT mg/hr	SMA mg/hr	NTOT no/hr	LTOT no/hr
	MAY							
Piney ^a	0.349	0.349	0.685	0.439	616	616	1209	774
White Oak	0.870	0.851	0.988	0.560	1342	1313	1524	864
Madison	1.054	0.925	1.642	0.784	939	823	1462	698
Hawksbill	1.162	1.007	1.610	0.621	791	685	1095	423
Average	1.029	0.928	1.413	0.655	1024	940	1360	662
	JULY							
Piney	0.837	0.707	2.660	0.862	94	80	300	97
White Oak	5.032	5.032	9.943	2.674	1492	1492	2948	792
Madison	0.693	0.290	1.596	0.249	76	32	174	27
Hawksbill ^b	1.562	1.485	4.302	0.870	892	848	2456	497
Average	2.187	2.010	4.733	1.262	554	535	1141	305
	SEPT							
Piney	1.019	0.429	2.010	0.154	50	21	98	7
White Oak	0.505	0.505	2.632	0.477	155	155	806	146
Madison	0.575	0.435	1.647	0.381	105	79	300	69
Hawksbill	0.266	0.232	0.708	0.159	20	17	53	12
Average	0.591	0.400	1.749	0.293	82	68	314	58

^aUsed water flow after the rain event to estimate prey indices/hr. This stream was not used in the average for May.
^bUsed mean of discharge before and after rain event to estimate prey indices/hr. This stream was not used in the average for July.

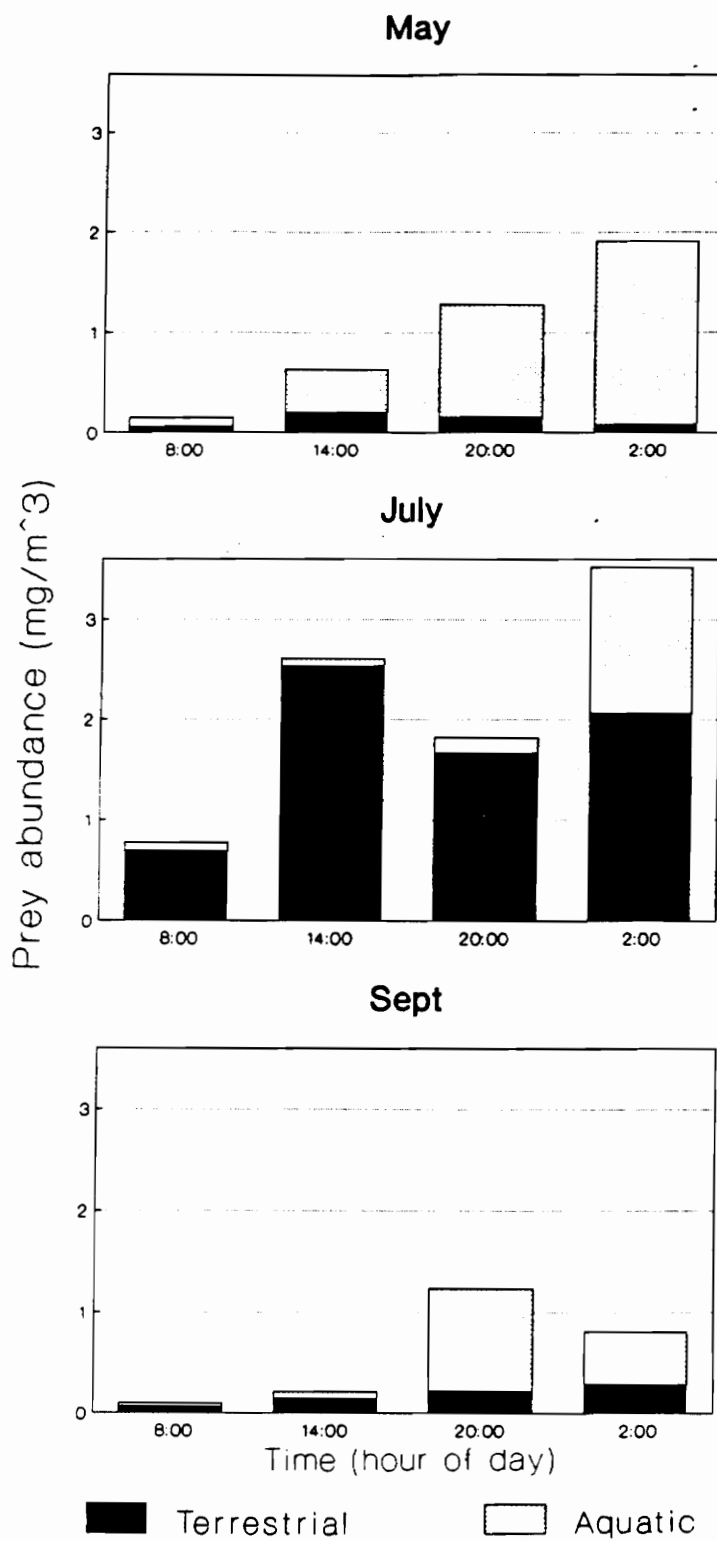


Figure 7. Mean prey abundance (mg/m^3) throughout the day in Shenandoah National Park. Prey abundance was estimated using drift nets set for one hour. The numbers on the x axis is the start of the sampling interval.

Adults had higher P-values than yearlings at all months but the difference was less in September. Juvenile trout had lower P-values than both yearlings and adults in July but higher P-values in September. Most streams did not have consistent pattern of consumption (e.g. fish in Madison fed well in May but poorly in July). Little Hawksbill was the only exception with higher P-values than the three other streams on 75% of the age x month combinations.

Stomach contents

All sizes of trout ate mostly aquatic invertebrates in May and terrestrial invertebrates in July and September (Figure 8). Table 22 presents the energetic contributions of the prey categories to the trout at different seasons.

Prey density versus consumption

Tables 7 and 8 present the results of the Spearman rank correlation of prey indices versus P-values. I excluded the Piney River May sample and the Little Hawksbill July sample because of flood events that may have caused atypical feeding behavior. Of the sixteen indices tested, only the number of prey greater than 4mm per m³ was significantly correlated with P-values. It was significant for yearlings and adults but not juveniles. Because juveniles did not feed at night, I correlated prey densities excluding night drift with P-values. The correlation increased on six of eight prey indices but none of the correlations were significant (Table 7). Prey indices adjusted for fish densities did not increase the strength of the correlations. In fact, when the prey indices were adjusted for the amount of prey available per gram of fish (Table 18) none of the correlations

RESULTS

Table 6. Daily ration in percent (g dry wt/g dry wt x 100) and P-value (the percent of maximum consumption) for different sizes of fish in the summer in Shenandoah National Park.

	Juvenile		Yearling		Adult	
	Ration (%)	P-value	Ration (%)	P-value	Ration (%)	P-value
	MAY					
Piney	-	-	2.20	24	2.40	35
White oak	-	-	1.22	15	2.88	48
Madison	-	-	4.34	45	3.65	50
Hawksbill	-	-	3.11	32	3.88	55
Average			2.72	29	3.20	47
	JULY					
Piney	5.66	39	4.82	52	5.47	79
White oak	7.49	44	5.71	53	8.48	109
Madison	3.22	22	1.72	17	1.14	15
Hawksbill	7.42	46	8.79	79	8.49	98
Average	5.96	38	5.26	50	5.80	75
	SEPT					
Piney	3.32	21	2.34	22	1.10	13
White oak	3.83	25	1.72	16	1.56	18
Madison	6.64	45	3.21	31	2.08	26
Hawksbill	7.04	46	4.38	39	5.31	61
Average	5.21	34	2.91	27	2.51	30

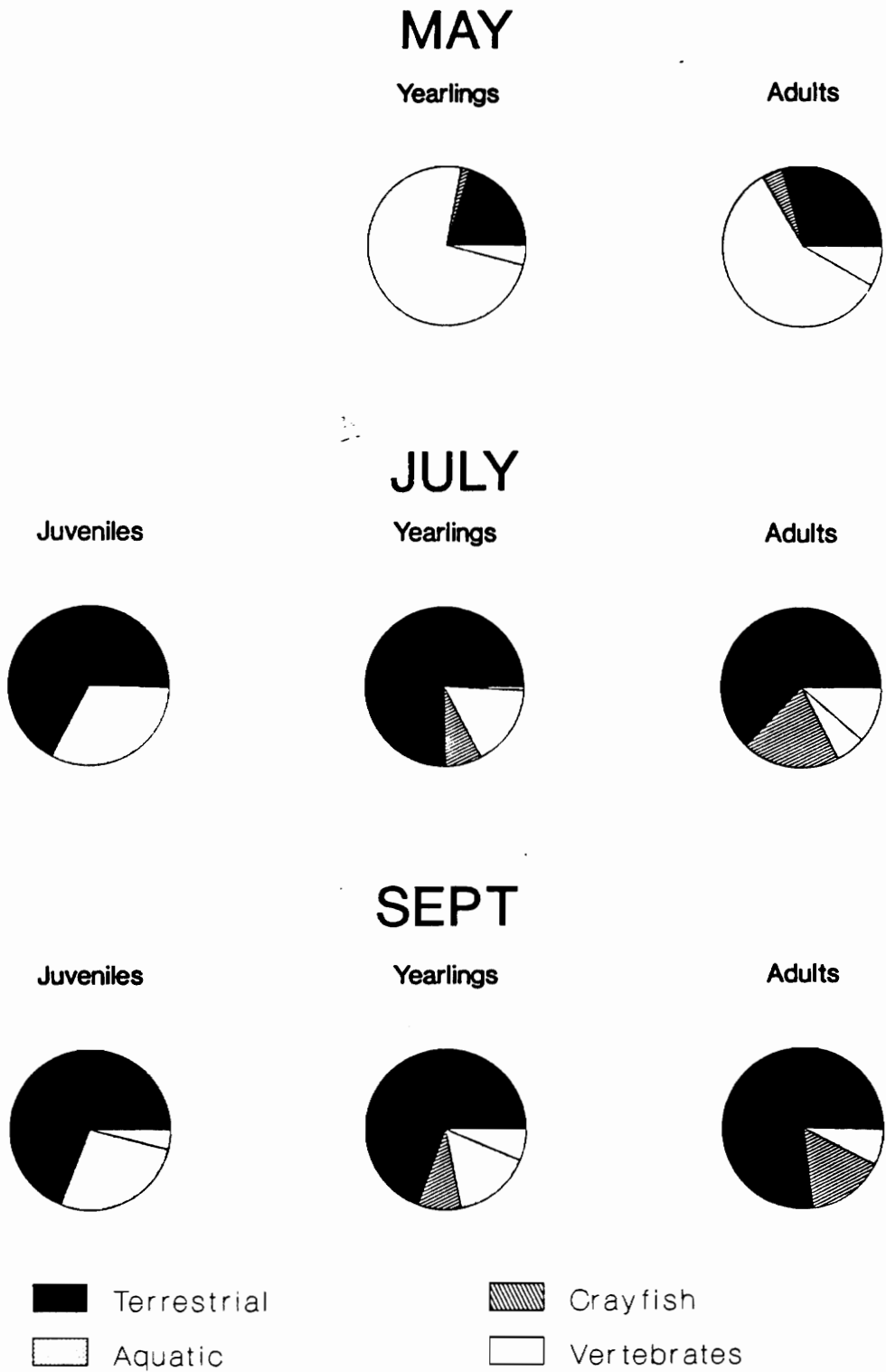


Figure 8. Mean food habits by weight (%) of brook trout by month for four streams in Shenandoah National Park.

were significant (Table 8). Fifty percent of the correlations between prey indices and consumption were weaker after adjustment for fish density.

Fit of the data on number of large prey (no/m³) and consumption with Ivlev's curve was good for yearlings and adults but not juveniles. Variance was high for estimates of k (constant that represents the increase in consumption with increases in prey abundance; Table 9). Variance for k was lowest for yearlings (SE = 0.13) followed by juveniles (SE = 0.23) and adults (SE = 0.25). The curve of food consumption rose more steeply for adults than yearlings (Figures 10 and 11). The parameter k was significantly larger for adults than yearlings (t-test, $P < 0.05$). The nonlinear regression estimated the parameter k to be 0.5259 for juveniles, 0.5773 for yearlings and 1.1596 for adults (Table 9).

Within streams, there was a more clear positive relation between prey abundance (no > 4mm/m³) and food consumption of trout. When prey density increased or decreased over the season, P-values increased or decreased accordingly. Of the 20 month x size combinations 19 had concordance between changes in prey density and changes in P-value (Figure 9). The only exception, juvenile trout in Piney River from July to September, had no difference in P-value when prey was reduced.

Energy budget

Estimated energy available for growth and activity (E) was generally positive throughout the summer (Table 10). Of the thirty-two possible stream x date x age combinations, only two were negative. Only adult trout in Madison Run in July and Piney River in September had energy deficits.

RESULTS

Table 7. Correlation (Spearman's Rank) between eight prey measures and daily consumption (P-value) for May, July and September. TOT is total weight of prey (dry wt), SMA is the weight of prey excluding vertebrates and crayfish, NTOT is the total number of prey, and LTOT is the number of prey longer than 4mm.

Age	N	Drift densities (per m ³)				Drift rates (per hour)			
		TOT mg/m ³	SMA mg/m ³	NTOT no/m ³	LTOT no/m ³	TOT mg/hr	SMA mg/hr	NTOT no/hr	LTOT no/hr
Drift measures over 24 hours									
0	7	-0.428	0.000	-0.214	0.250	0.071	0.000	0.000	0.214
1	10	0.394	0.381	0.418	0.575*	0.109	0.164	0.164	0.091
2	10	0.297	0.527	0.188	0.721*	0.358	0.418	0.418	0.442
Drift measures excluding night samples									
0	7	-0.179	0.143	-0.214	0.321	0.036	0.286	0.071	0.321

* statistically significant (P < 0.05)

RESULTS

Table 8. Correlation (Spearman's Rank) between eight prey measures (adjusted for density of fish) and daily consumption (P-value) for May, July and September. Prey indices were divided by biomass of yearlings and adults for correlations with yearling and adult consumption. For correlation with juvenile consumption prey indices were divided by juvenile biomass. TOT is total weight of prey (dry wt), SMA is the weight of prey excluding vertebrates and crayfish, NTOT is the total number of prey, and LTOT is the number of prey longer than 4mm.

Age N	Drift densities (per m ³ per trout biomass)				Drift rates (per hour per trout biomass)			
	TOT mg/m ³ /g ^a	SMA mg/m ³ /g	NTOT no/m ³ /g	LTOT no/m ³ /g	TOT mg/hr/g	SMA mg/hr/g	NTOT no/hr/g	LTOT no/hr/g
0 7	-0.179	0.107	-0.179	0.321	-0.054	0.286	0.286	0.321
1 10	0.176	0.224	0.151	0.333	0.079	0.079	0.164	0.321
2 10	0.236	0.370	0.115	0.491	0.248	0.367	0.272	0.527
Drift measures over 24 hours								
0 7	-0.036	0.286	-0.179	0.393	0.107	0.214	0.000	0.321
Drift measures excluding night samples								

^a statistically significant (P < 0.05)

^a mg/m³/g is actually mg dry wt • m⁻³ • g wet wt⁻¹ • m²,
 no/m³/g is no • m⁻³ • g wet wt⁻¹ • m²,
 mg/hr/g is mg dry wt • hr⁻¹ • g wet wt⁻¹ • m²,
 and no/hr/g is no • hr⁻¹ • g wet wt⁻¹ • m².

Table 9. Estimate of k (the constant that represents how fast consumption reaches maximum with increasing prey) for prey longer than 4mm.

Age	N	k	SE	95% CI
0	7	0.5259	0.2321	-0.0421 to 1.0939
1	10	0.5773	0.1318	0.2792 to 0.8755
2	10	1.1596*	0.2509	0.5921 to 1.7271

* Significantly ($P < 0.05$) larger than k for yearlings (t-test).

Juvenile

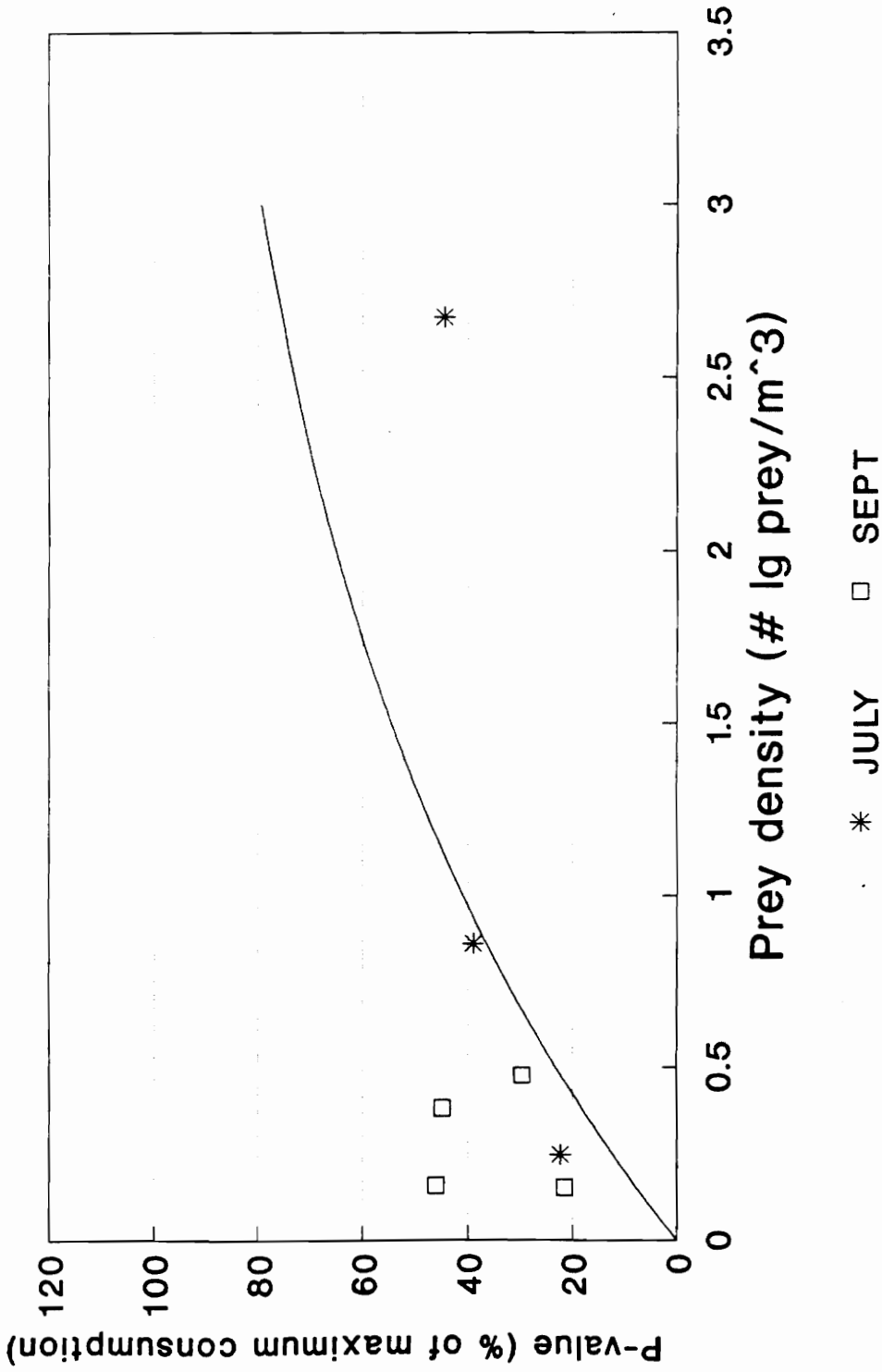


Figure 9. Consumption of prey (P-value) versus prey density (number of prey > 4mm / m³) for juvenile trout in four streams of Shenandoah National Park. Little Hawkbill Creek in July was excluded because of heavy rains.

Yearling

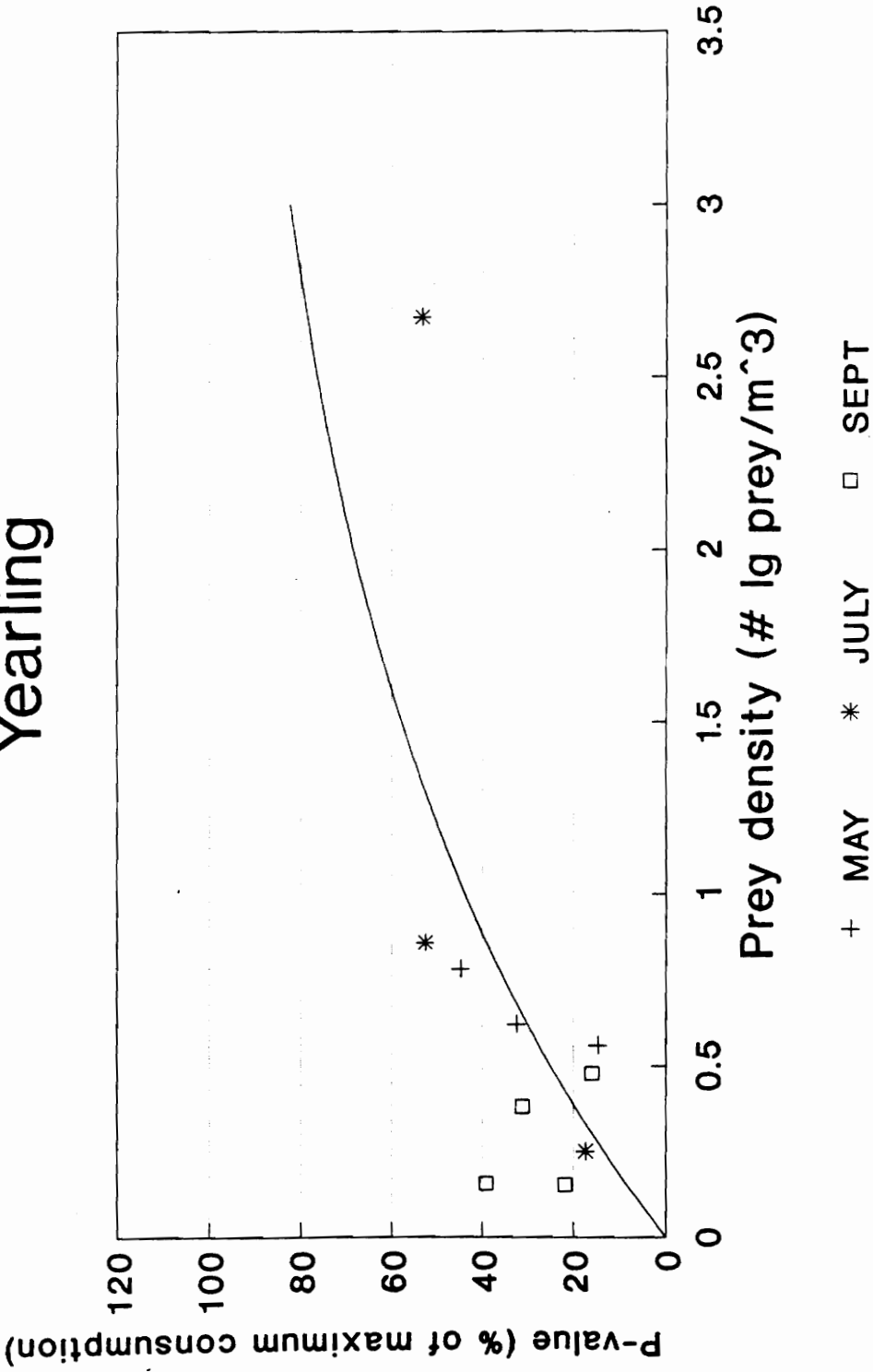


Figure 10. Consumption of prey (P-value) versus prey density (number of prey > 4mm / m³) for yearling trout in four streams of Shenandoah National Park.

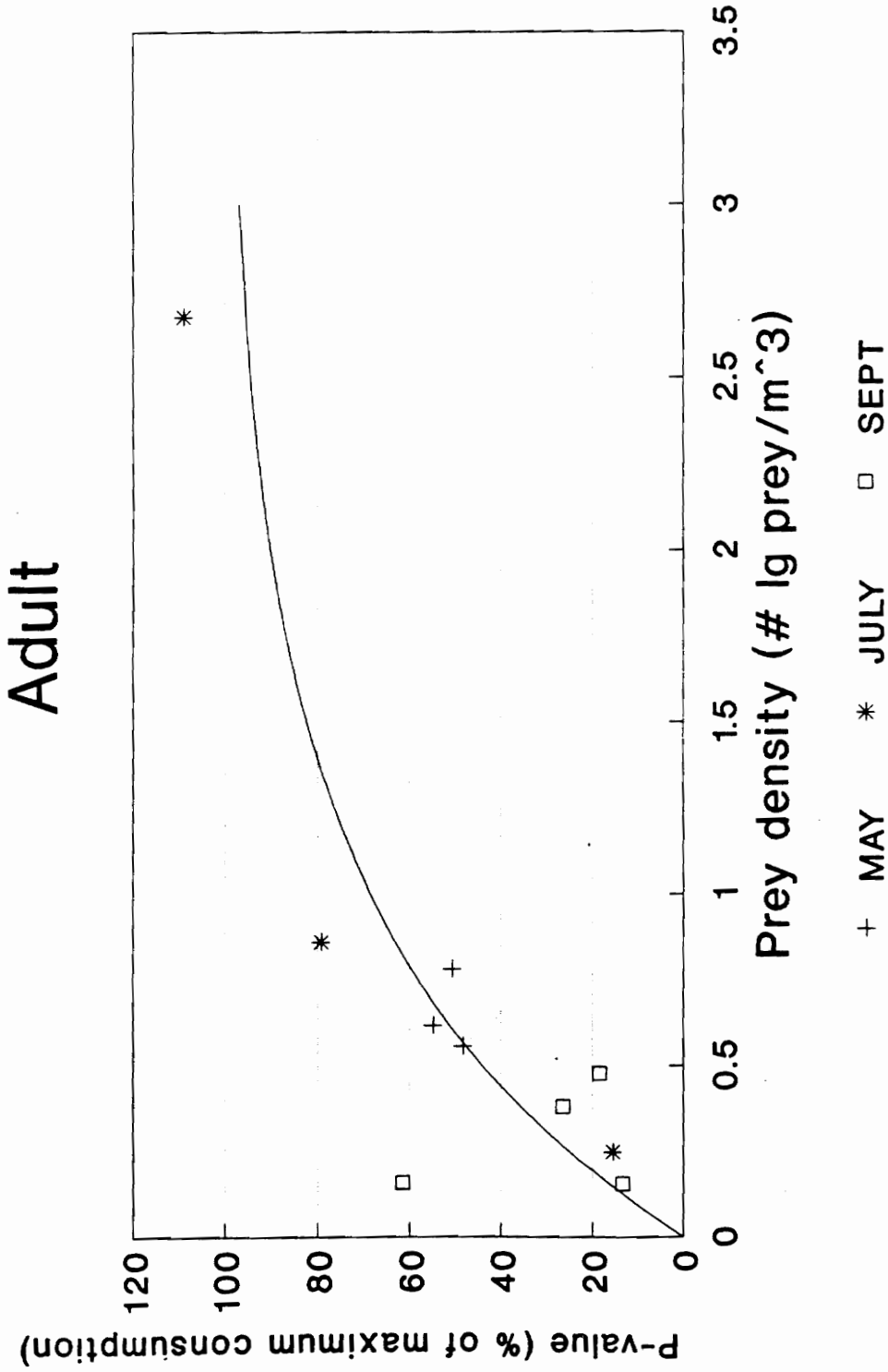


Figure 11. Consumption of prey (P-value) versus prey density (number of prey > 4mm / m³) for adult trout in four streams of Shenandoah National Park. Piney River in May and Little Hawksbill Creek in July were excluded because of heavy rains.

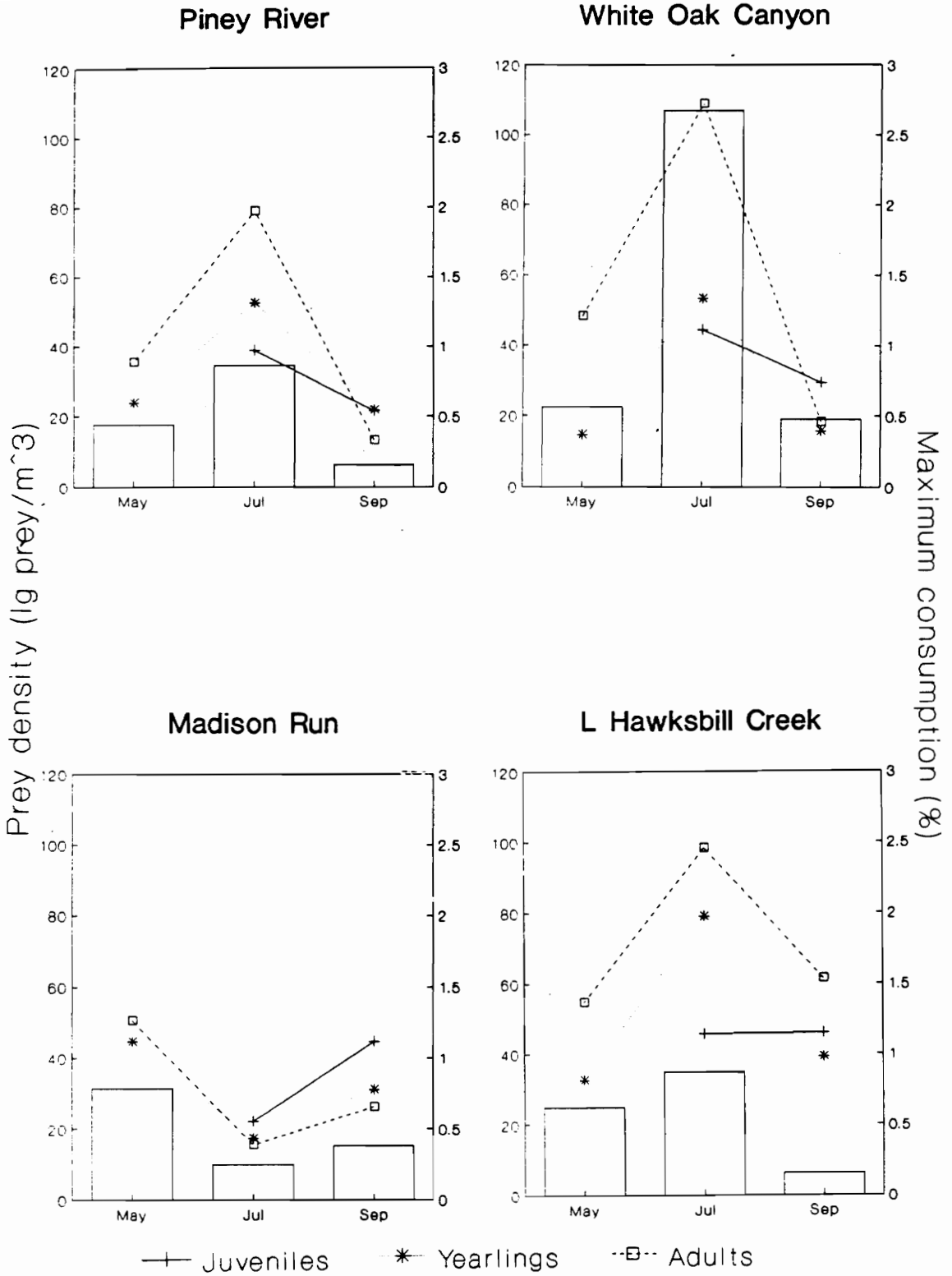


Figure 12. Consumption (P-value or percent of maximum consumption) versus prey density (prey > 4mm/m³) for streams in Shenandoah National Park over the summer. Consumption is represented by lines and prey abundance is represented by the bars.

Estimated energy available for growth and activity (E) for yearlings and adults was intermediate in May (65 and 96 $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$), high in July (113 and 134 $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$) and lowest in September (46 and 39 $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$) (Table 10, Figure 13). The variability in E was large among streams, especially in July. The variation in E was due to variation in consumption, not maintenance costs (Table 10). Unlike larger trout, juvenile trout had as much energy for growth and activity in September as July (115 in July and 107 in September $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$).

Adult trout had more energy available for growth and activity (E) than yearlings but allocated less energy to growth, especially in the late summer (Table 11). Energy used for adult and yearling growth was higher in early summer (31 and 11 $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$) than late summer (2 and 0 $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$). Juveniles allocated relatively more energy for growth (31 $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$) than both yearling and adult fish in the late summer.

Seasonally, activity costs increased from early summer to late summer for yearling trout, except for fish in Madison Run (Table 11). Activity costs for adult trout did not show any clear trend; activity costs in the late summer increased slightly for White Oak Canyon and Little Hawksbill and decreased slightly for Piney River and substantially for Madison Run.

Adults spent relatively more energy on activity than yearlings on seven of eight two month intervals. The difference was less pronounced in late summer than early summer. Juveniles in late summer had similar activity costs to yearlings and adults (within 10%).

Activity costs were variable among streams. All sizes of fish in Little Hawksbill spent from 30 to 100% more energy on activity costs in early and late summer than the aver-

Table 10. Consumed energy (C), net energy (energy left after meeting processing costs)(N), energy required for standard metabolism (R_s), and energy available for growth and activity (E). All units are ($J \cdot g^{-1} \cdot day^{-1}$)

Trout size/ Stream	Consumption	Net energy	Maintenance	Growth & Activity
MAY				
Yearling				
Piney	110.6	60.8	24.9	36.0
White Oak	62.0	34.1	23.1	11.0
Madison	323.1	177.7	27.6	150.1
Hawksbill	162.1	89.2	25.8	63.3
Average	164.5	90.4	25.3	65.1
Adult				
Piney	121.7	67.0	19.9	47.1
White Oak	144.4	79.4	18.3	61.1
Madison	345.8	190.2	21.9	168.3
Hawksbill	235.5	129.5	20.8	108.7
Average	211.9	116.5	20.3	96.3
JULY				
Juvenile				
Piney	303.0	166.6	67.3	99.4
White Oak	399.6	219.8	63.2	156.6
Madison	178.3	98.1	59.5	38.6
Hawksbill	400.1	220.1	56.0	164.1
Average	320.3	176.1	61.5	114.7
Yearling				
Piney	268.0	147.4	48.9	98.5
White Oak	331.4	182.3	46.2	136.1
Madison	84.9	46.7	45.3	1.4
Hawksbill	475.3	261.4	42.3	219.1
Average	289.9	159.5	45.7	113.8
Adult				
Piney	303.7	167.0	40.0	127.0
White Oak	431.1	237.1	37.5	199.8
Madison	55.0	30.3	35.8	-5.6
Hawksbill	456.6	251.1	35.6	215.5
Average	311.6	171.4	37.2	134.2
SEPT				
Juvenile				
Piney	183.0	100.7	55.1	45.6
White Oak	213.7	117.5	54.3	63.2
Madison	370.6	203.8	48.6	155.3
Hawksbill	391.5	215.3	52.7	162.6
Average	289.7	159.3	52.7	106.7
Yearling				
Piney	124.7	68.6	42.6	26.0
White Oak	90.4	49.7	42.9	6.9
Madison	177.6	97.7	37.5	60.1
Hawksbill	239.6	131.8	42.3	89.5
Average	158.1	86.9	41.3	45.6
Adult				
Piney	60.3	33.2	35.6	-2.4
White Oak	79.0	43.5	35.9	7.6
Madison	116.9	64.3	30.1	34.2
Hawksbill	277.9	152.9	35.2	117.7
Average	133.6	73.5	34.2	39.3

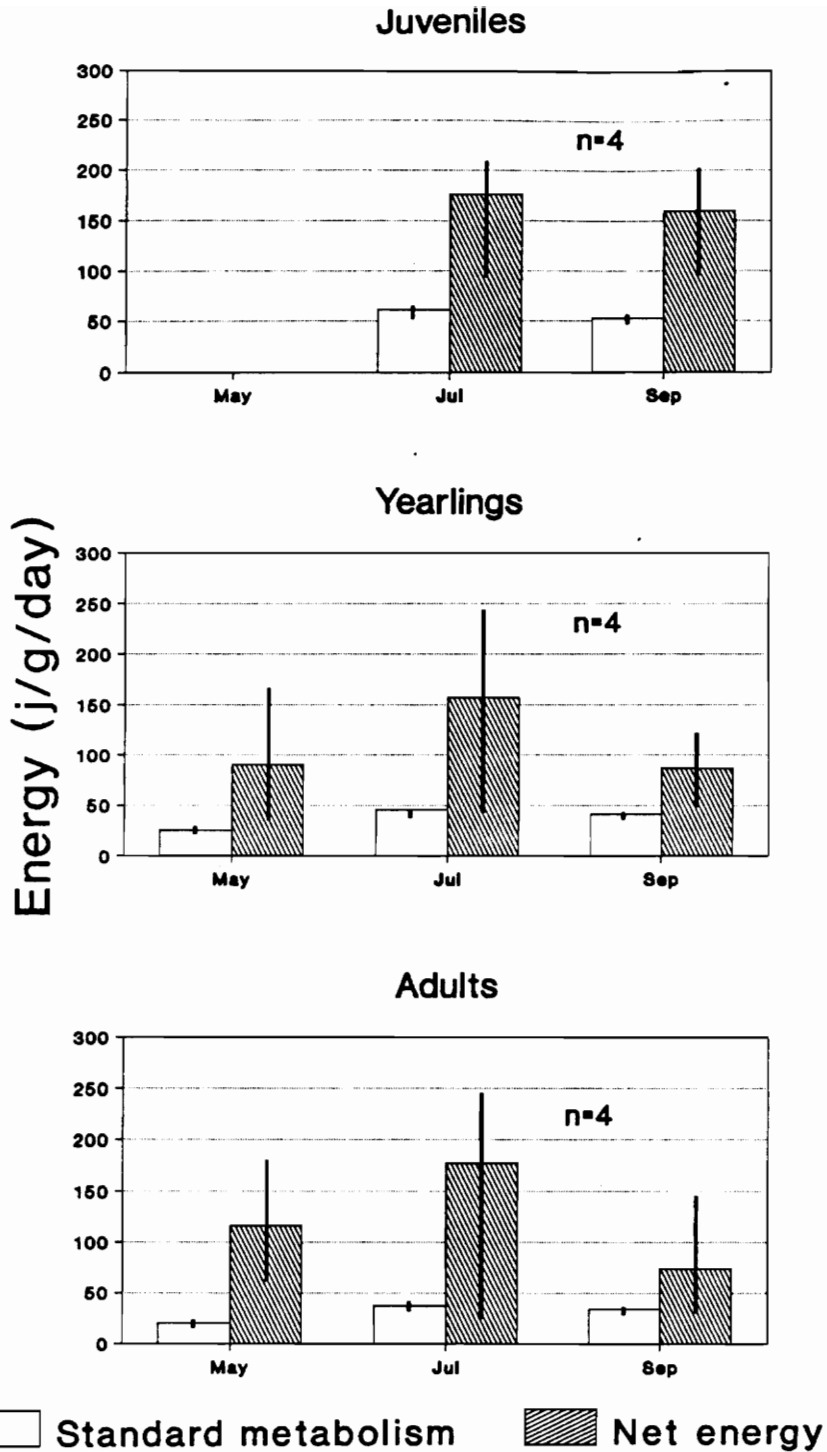


Figure 13. Net energy and maintenance energy ($\text{j} \cdot \text{g wet wt}^{-1} \cdot \text{day}^{-1}$) for different sizes of fish over the summer. Differences between the two energy estimates is the energy available for growth and activity. Vertical bars mark the range of the estimates among streams.

Table 11. Energy used for growth and activity in early and late summer. \bar{E} is the mean energy available for growth and activity (j/g wet wt/day), \bar{G} is the mean energy used for growth (j/g wet wt/day) and \bar{A} is the mean energy used for activity, (j/g wet wt/day) in early and late summer of 1989 in Shenandoah National Park. All units are in j • g wet wt⁻¹ • day⁻¹

	Growth & Activity (\bar{E})	Growth (\bar{G})	Activity (\bar{A})
MAY-JULY			
Yearling			
Piney ^a	67.3	34.4	32.8
White Oak	73.6	46.5	27.0
Madison	75.8	13.4	62.4
Hawksbill ^b	141.2	28.2	113.0
Average	89.4	30.6	58.8
Adult			
Piney ^a	87.0	12.8	74.2
White Oak	130.4	31.4	99.1
Madison	81.4	-5.7	87.0
Hawksbill ^b	162.1	7.6	154.5
Average	115.2	11.5	103.7
JULY-SEPTEMBER			
Juvenile			
Piney	72.5	33.0	39.5
White Oak	109.9	47.3	62.6
Madison	96.9	14.0	82.9
Hawksbill ^b	163.4	30.7	132.6
Average	110.7	31.3	79.4
Yearling			
Piney	62.3	1.0	61.3
White Oak	71.5	12.8	58.7
Madison	30.7	2.1	28.6
Hawksbill ^b	154.3	-8.6	162.9
Average	79.7	1.8	77.9
Adult			
Piney	62.3	0.5	61.8
White Oak	103.7	-4.5	108.2
Madison	14.3	11.0	3.3
Hawksbill ^b	166.6	-6.4	173.0
Average	86.7	0.2	86.6

^aHeavy rains fell in May and could have affected the \bar{E} estimate.

^bHeavy rains fell in July and could have affected the \bar{E} estimate.

age. Yearling and adult trout in Madison Run had low activity costs in late summer (37 and 4% of the average).

Growth versus excess energy

Energy available for growth and activity (E) did not correlate well with growth (Figures 14 and 15). In early summer, there were no clear relations in Figure 14. Adults may have showed an increase in growth with excess energy but yearlings did not. In late summer, adults and yearlings showed a negative relation between (E) and growth; the more excess energy the poorer the growth. Juveniles in late summer did not show any clear relation (Figure 15).

Growth of yearlings and adults was highest in early summer from May to July (0.52 and 0.20% per day) and lowest in late summer from July to September (0.04 and 0.00% per day; Table 12). Growth of juveniles was higher (0.59% per day) than larger fish in late summer.

Gross conversion efficiencies were generally higher for smaller fish in both early and late summer (Table 13). In early summer, conversion efficiency ranged from 7 to 24% for yearlings and -3 to 11% for adults. Efficiencies were lower in the late summer than the early summer for yearlings and adults. Juveniles had higher efficiencies (5 to 15%) than yearlings and adults in late summer.

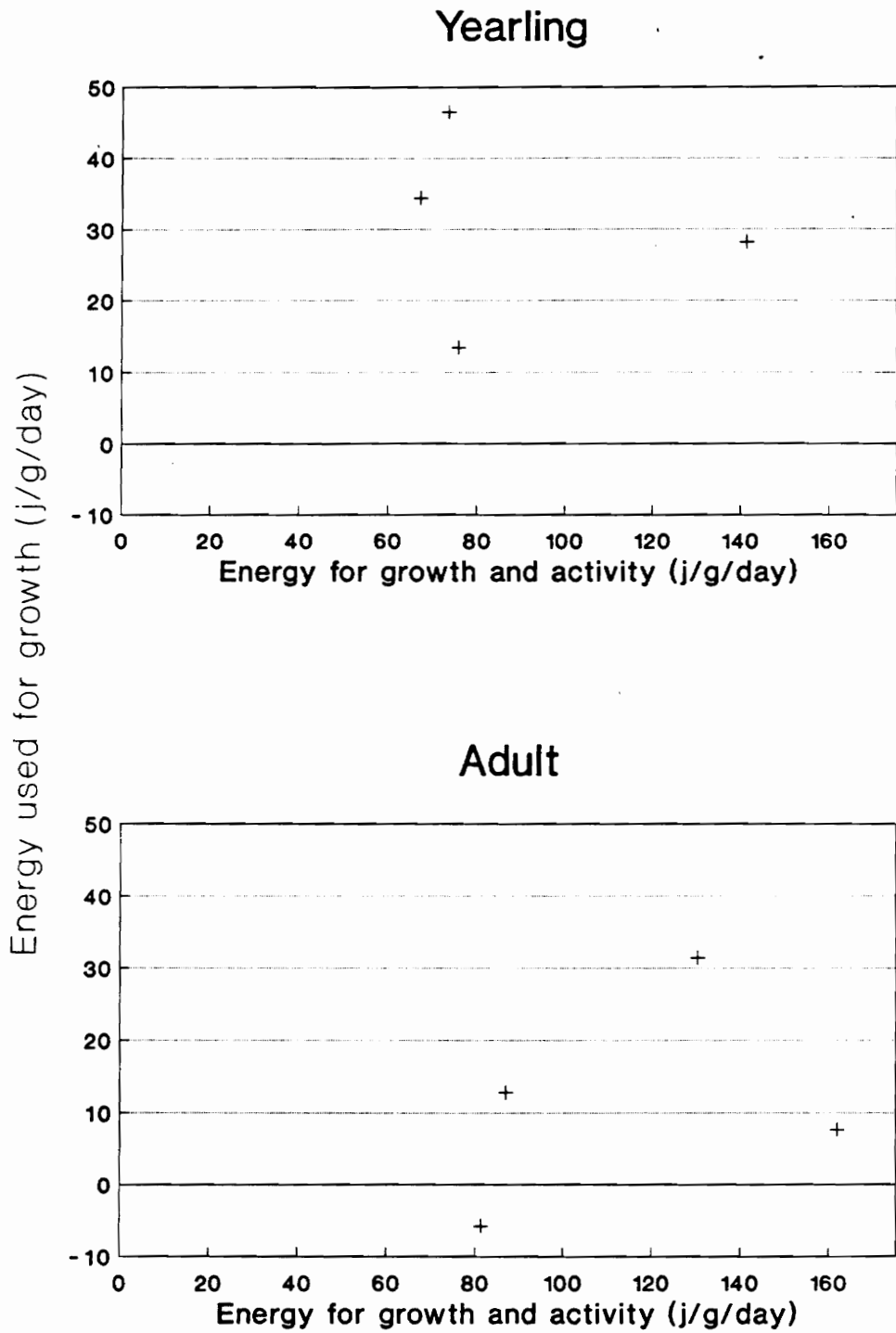


Figure 14. Energy available for growth (j/g/day) versus energy available for growth and activity (j/g/day) in early summer (May to July).

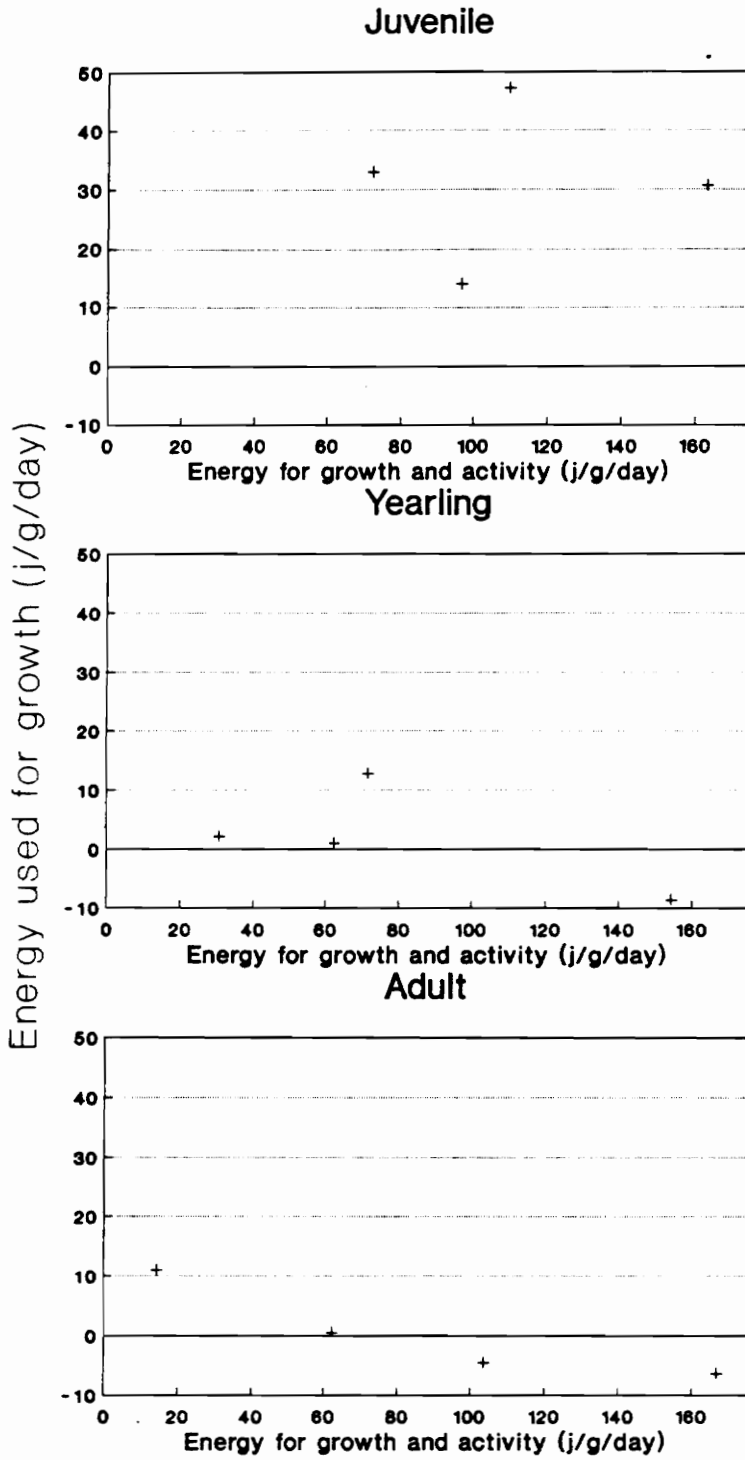


Figure 15. Energy available for growth (j/g/day) versus energy available for growth and activity (j/g/day) in late summer (July to September).

Table 12. Instantaneous daily growth rate (day^{-1}) and mean energy available for growth and activity (\bar{E}) ($\text{j} \cdot \text{g wet wt}^{-1} \cdot \text{day}^{-1}$) in early and late summer of 1989 in Shenandoah National Park. \bar{E} is estimated over two months.

Trout size/ Stream	Growth day^{-1}	(\bar{E}) $\text{j} \cdot \text{g wet wt}^{-1} \cdot \text{day}^{-1}$
MAY-JULY		
Yearling		
Piney ^a	0.5749	67
White Oak	0.8002	74
Madison	0.2212	76
Hawksbill ^b	0.4698	141
Average	0.5165	89
Adult		
Piney ^a	0.2119	87
White Oak	0.5404	130
Madison	-0.0936	81
Hawksbill ^b	0.1252	162
Average	0.1960	115
JULY-SEPTEMBER		
Juvenile		
Piney	0.5487	72
White Oak	0.7931	110
Madison	0.2320	97
Hawksbill ^b	0.5091	163
Average	0.5921	111
Yearling		
Piney	0.0161	62
White Oak	0.2676	71
Madison	0.0354	31
Hawksbill ^b	-0.1420	154
Average	0.0443	80
Adult		
Piney	0.0081	62
White Oak	-0.0818	104
Madison	0.1821	14
Hawksbill ^b	-0.106	167
Average	0.0024	87

^aHeavy rains fell in May and could have affected the estimates of \bar{E}

^bHeavy rains fell in July and could have affected the estimates of \bar{E}

Table 13. Gross conversion efficiencies (%) in early and late summer. \bar{C} is the mean energy consumed ($\text{j g}^{-1}\text{day}^{-1}$), \bar{G} is the mean energy used for growth ($\text{j g}^{-1}\text{day}^{-1}$) and C_e is the conversion efficiency (%), found by dividing energy used for growth ($\text{j g}^{-1}\text{day}^{-1}$) by energy consumed ($\text{j g}^{-1}\text{day}^{-1}$) X 100.

Trout size/ Stream	Consumption (\bar{C}) $\text{j g}^{-1}\text{day}^{-1}$	Growth (\bar{G}) $\text{j g}^{-1}\text{day}^{-1}$	Efficiency (C_e) %
MAY-JULY			
Yearling			
Piney ^a	189	34.4	18.2
White Oak	197	46.5	23.6
Madison	204	13.4	6.6
Hawksbill ^b	319	28.2	8.8
Average	227	30.6	13.5
Adult			
Piney ^a	212	12.8	6.0
White Oak	287	31.4	10.9
Madison	200	-5.7	-2.9
Hawksbill ^b	346	7.6	2.2
Average	262	11.5	4.4
JULY-SEPTEMBER			
Juvenile			
Piney	243	33.0	13.6
White Oak	307	47.3	15.4
Madison	274	14.0	5.1
Hawksbill ^b	396	30.7	7.8
Average	305	31.3	10.3
Yearling			
Piney	196	1.0	0.5
White Oak	211	12.8	6.1
Madison	131	2.1	1.6
Hawksbill ^b	357	-8.6	-2.4
Average	224	1.8	0.8
Adult			
Piney	182	0.5	0.3
White Oak	255	-4.5	-1.8
Madison	86	11.0	12.8
Hawksbill ^b	367	-6.4	-1.7
Average	223	0.2	0.1

^aHeavy rains fell in May and could have affected the \bar{C} estimate.

^bHeavy rains fell in July and could have affected the \bar{C} estimate.

DISCUSSION.

The goal of this study was to quantify the effect of prey density on consumption and growth of brook trout. First, I will examine how diel feeding and size selectivity affect the relation between prey density and consumption. Second, I will present the relation between consumption and prey density. Third, I will discuss whether trout were meeting energetic costs during the summer and whether growth is more dependent on the amount of food eaten or on other factors, i.e. activity costs.

Objective 1. Factors affecting the relation between prey abundance and consumption.

The hypothesis that diel feeding and prey size selectivity affect the prey abundance-consumption relation, was supported by the results of this study at least for some sizes

of fish. Trout of all sizes selected for prey longer than 4 mm and juvenile trout consumed less food at night.

Diel feeding

Diel feeding was estimated to find if the prey indices needed to be modified to account for rigid feeding periodicity. Adult and yearling trout did not have consistent peaks in consumption at specific times of the day throughout the summer; therefore, I did not modify the prey indices for different times of day. Juvenile brook trout consumed significantly less food at night than at other times. Exclusion of prey density at 0200 from the prey indices slightly improved predictability of consumption, although the indices were still not statistically significant.

Yearling and adult trout in July and September fed more at night (from 2100 to 0300 hrs) than any other time interval but it was not statistically significant. Although, there is no physiological reason trout could not feed at night (Tanaka 1970 as quoted from Elliott 1973), I did not find any other study that has found that brook trout feed more at night than during the day. Most studies have stated that brook trout have consumption peaks during the daylight hours (White 1967, Griffith 1974, Allan 1978a, Salli 1979, and Johnson and Johnson 1982). Further, Griffith (1974) reported that brook trout were not active from 2200 to 2400 hours in an Idaho stream. Twilight has been found to be a period of peak consumption for salmonids other than brook trout (Elliott 1970, Salli 1979). In this study, twilight consumption was probably not the cause of the high stomach contents at 0300; the streams in this study were dark by 2100 hours because of steep slopes adjacent to the stream. Further, the sun set an hour earlier in September than in July but the large fish still fed more at night. Moon phase probably

had little to do with the increase in night feeding in July and September compared to May. Most nights were overcast in July, yet yearling and adult trout still ate the most at night. Furthermore, Jenkins (1969) measured brown and rainbow trout feeding at different moon phases in an experimental stream; he concluded that moon phase did not cause a significant difference in food consumption. Salmonids other than brook trout, have been found to feed at night; Johnson and Johnson (1981) found that coho salmon *Oncorhynchus kisutch* fingerlings fed more at night. Elliott (1973) found that consumption by brown and rainbow trout peaked in the first two hours of darkness for a stream in France.

In this study, yearling and adult brook trout appeared to shift consumption peaks from daylight in May to nighttime in July and September. This shift could be attributed to higher risks to predators during the day, or to lower prey drift rates during the late summer. In late summer, water is typically lower and clearer than in May and fish may be more susceptible to predation by snakes and birds (Lennon 1961). Power (1984) found that catfish in Panama were more susceptible to predation during the daytime. Alternatively, trout may feed at night to take advantage of higher insect drift rates at night. In this study, prey abundance was higher at night; the 0300 to 0400 drift sample captured the most prey in May and July and the 0800 to 0900 drift sample captured the most prey in September (Figure 7). In May, prey was plentiful (Table 5) and temperatures were low enough that once fish were satiated they did not need to feed for 24 hours. Food density was lower in late summer; if the fish were hungry throughout the day they will feed at night when food densities are higher.

Juvenile brook trout consistently fed less at night, most likely because they inhabited riffles. The lack of night consumption by brook trout juveniles has been well docu-

mented (Salli 1979, Walsh et al. 1988). Juveniles may not feed at night because their feeding locations (focal points) are less beneficial at night in comparison with larger fish. Larger fish were almost always captured in pools in July and September while juveniles were mostly captured in riffles; a few were found at the lower edges of pools. Reactive distances to prey are lower at night (Cerri 1979), thus trout in faster water would have less time to respond to drifting prey at night. The decrease in response time may not be important when the prey is drifting slowly (pools) but may prevent the trout from capturing food when the prey is drifting quickly (riffles). Johnson and Johnson (1981) found that juvenile pool dwellers (coho salmon) fed most at night while riffle dwellers (steelhead trout, *Oncorhynchus mykiss*) fed most during the day. Cannibalism of smaller trout by larger trout could also be responsible for the lack of night consumption by juveniles. Smaller fish often do not feed at night because they do not see potential predators as soon as during daylight hours (Cerri 1983). Large brook trout feed more at night and may be cannibalizing juveniles; I flushed one juvenile from an adult brook trout in July. I think predation risk is less a factor in preventing night consumption in juveniles than consumption efficiency because adults and juveniles occupied different habitats and cannibalism was probably rare.

Prey size selectivity

Brook trout selected for large prey in the drift. Prey size has been found to be a major factor in prey selection because fish can see larger prey from a greater distance and therefore effectively scan more area (Dunbrack and Dill 1983, Grant and Noakes 1986). Grant and Noakes (1986) concluded that all studies which have examined size selection of salmonids have found positive selection for larger prey. Allan (1978b) observed that

trout selected smaller prey at night than during the day and hypothesized the tendency to select larger prey was reduced at night because of poor visibility.

Smaller trout did not select as strongly for large prey as did larger trout. Grant and Noakes (1986) observed that the preferred prey size of young-of-year brook trout increased over the summer as the fish grew. Elliott (1970) showed that larger brown trout selected for larger prey.

Brook trout at White Oak Canyon selected for prey larger than 4 mm. This threshold was generally consistent for season, size of fish, and time of day. Grant and Noakes (1986) also mention that juvenile brook trout begin to positively select prey at a threshold (0.6 mm width) that was consistent among the summer months. Bannon and Ringler (1986) measured size selectivity of brown trout in a New York stream and their figures indicate a threshold of 3 mm in length that was again consistent among seasons. Although Allan (1978b) and Sagar and Glova (1988) found that the mean of prey size selected by salmonids changed by time of day, I could not find evidence in their studies that the threshold changed.

Objective 2. Quantification of the prey density-consumption relation.

In this study, the relation between prey density and consumption was significant for yearlings and adult trout but not juveniles. Associations were generally weak among streams but not within streams suggesting stream habitat may have a disproportionate

effect on consumption. Other reasons for a weak correlation are: seasonal differences, benthic consumption at low drift densities, inappropriate measures of prey density, or biases in measuring consumption.

Prey density versus consumption

I was able to quantify the relation between prey abundance and consumption for yearling and adult trout but not juveniles. Consumption by juveniles did not correlate well with prey density, suggesting that juvenile consumption in these streams was independent of prey density. The correlation was poor because there was little variation in consumption, especially at the higher prey levels. More food available in a stream might not result in more food in stomachs on a population level, but higher survival of juvenile trout. Individual trout that are inefficient feeders and would die at low prey densities are more likely to survive at high prey densities. Thus, the estimate of mean daily ration for the population is not increased with increases in food because there is a higher proportion of inefficient feeders still surviving. Early life stages of salmonids in streams are often driven by density dependent factors (Gee et al. 1978, Elliott 1985).

Adult trout fed better at low prey densities than did yearlings. The parameter k (parameter that represents how quickly consumption reaches maximum with increasing prey abundance) was larger for adult trout than yearlings (Figures 10 and 11). The larger k for adults is important because adult trout will consume more than yearlings at all prey densities. It is not surprising that adult trout consume more energy than yearlings. Most of the yearlings and adults were in pools, where the larger fish probably had the most profitable focal points and monopolized food sources when feeding (Li and Brocksen 1977, Helfrich et al. 1982, Bachman 1984, Fausch 1984). Once prey levels be-

came high enough to satiate larger fish, then the yearlings would be able to increase consumption.

Changes in prey density would affect adult food consumption more at low prey densities and yearling food consumption at high prey densities because k is larger for adult trout. The relation between prey abundance and consumption is asymptotic (Figure 10 and 11). Thus, changes in prey abundance where the consumption is rising rapidly will have greater affect on the amount of food eaten than the same magnitude of change where the consumption response has already leveled off. If prey densities change at low levels (i.e. < 1.0 large prey/ m^3 ; Figure 10 and 11), adult consumption is going to be more affected than yearling consumption. Conversely, if prey densities are high (i.e. > 1.0 large prey/ m^3 ; Figure 10 and 11), changes in prey densities will affect yearling more than adult consumption.

The number of large prey (longer than 4mm) in the drift was the best predictor of trout consumption for yearlings and adults. Large prey may contribute more to consumption because: 1) fish have a larger reactive distance to larger prey; 2) fish are more likely to feed on larger prey when near satiation; and 3) larger prey weigh more and contribute more to daily ration. Fish see larger prey from further distances and will travel further to attack larger prey (Ware 1972, Dunbrack and Dill 1983). Encounter models have been built that predict what prey are eaten based on prey size and reactive distances (Newman 1987). Trout may be more likely to feed on larger prey when they are close to satiation. Ivlev (1961) observed that carp *Cyprinus carpio* became more selective as hunger decreased. Ringler (1979) did not find more selectivity with decreases in hunger for brown trout in a laboratory system but admitted the anomalous results may have been because of other effects (short consumption periods, and low differences in

electivity between prey types). The results from this study tend to support Ivlev's hypothesis because fish in White Oak Canyon were generally more size selective in July when the fish were closer to satiation (Table 4). Finally, large prey items are more likely to correlate with daily ration because the prey weigh more and contribute substantially to stomach content weights.

An asymptotic curve is better than a linear relation in describing the prey density-consumption relation because at high prey abundance fish become satiated and consumption reaches maximum. Holling's (1959) type-2 response has been found appropriate for both benthic (Ware 1972) and drift (Ringler and Brodowski 1983) feeding by salmonids. Cada et al. (1987) found a significant relation between prey density and weight of stomach contents for brown and rainbow trout using linear regression; however, they measured consumption at extremely low prey densities, so it is likely the regression only fit the rising portion of the type-2 curve. Fausch (1984) approximated a type-2 curve (using a Michaelis-Menton function) for specific growth (instead of consumption) and potential profit from a focal point (instead of prey density). He found the relation fit well for brook and brown trout but had the best fit for coho salmon.

Sources of variability in the prey density-consumption relation.

Correlations of prey density and consumption were generally weak (Table 7 and 8). A number of reasons could account for the poor correlation: 1) differences among months; 2) differences among streams, 3) facultative foraging strategy; 4) unsuitable measures of prey availability; 5) and possible biases in estimates of P-value.

Seasonal differences may have added variability in the prey density-consumption relation. Streams in May had higher water discharges (5-9 times summer discharge), and more large prey than in July and September. At high water levels, feeding may be less a function of prey availability than of the quantity or quality of available foraging sites. Focal points for feeding are characterized by low water velocity adjacent to faster water (Fausch 1984, Bachman 1984). Higher water discharges reduce the amount of pools and may reduce the number of focal points suited for feeding locations. If the number of sites is reduced, larger fish would continue to feed because they can withstand faster current velocities and can exclude subdominant fish from the remaining focal points. Seasonal differences may also affect the prey density-consumption correlation because fish may be less dependent on drifting prey at different seasons. Warren and Davis (1967) hypothesized that during warmer periods trout maximized energetic benefit/cost ratios by drift feeding. The notion that the energetic cost of swimming is offset by the increase in feeding was supported by the observation that steelhead fed in faster water velocities at higher temperatures (Smith and Li 1983).

Correlations of prey abundance and consumption were stronger within individual streams than over all the study streams, i.e. changes in P-values mirrored changes in prey density for all sizes of fish within streams (Figure 12). The consistent responses within streams suggest that effects of prey reduction can be predicted for individual streams but will not be the same for other streams. Therefore, it may be important to identify characteristics of the stream (such as habitat complexity, trout population density, and overhead cover) that may contribute to more effective consumption when attempting to predict changes in consumption with changes in prey density. A stream characteristic that seemed to increase consumption efficiency was habitat complexity. Trout in Little Hawksbill Creek consistently ate more than fish in other streams (Table 6), despite sim-

ilar prey densities (Table 5). One apparent difference between Little Hawksbill and the other study streams was that it had a more complex habitat, (because it had more pools per 100 meters and a higher proportion of boulders, Table 2). Habitat complexity could increase feeding efficiency by creating more velocity refuges for focal points and supporting more trout. The main focus of this study was not on habitat, and the number of pools per 100 meters may not be the best predictor of habitat complexity. Habitat complexity measurements that examined the number of optimal focal points (Bachman 1984, Fausch 1984) may be a better predictor of feeding efficiency.

Facultative foraging strategies may also have contributed to weak correlations between prey densities and consumption. Trout shifted feeding to benthic prey at lower drift densities. In this study, adult brook trout were more likely to feed on crayfish at low drift densities ($P < 0.05$, Spearman's Rank; Table 22). Yearlings also showed a negative correlation between drift density and the proportion of crayfish eaten, although it was nonsignificant ($0.10 < P < 0.20$).

The measure of prey may also have contributed to the variability in the prey abundance-consumption relation. Although drift nets are probably the single best measure of prey availability for drift feeding fish, setting the nets downstream from pools versus riffles may affect the number and distribution of prey captured. Prey items that drift through a pool are more likely to be cropped by trout than items drifting through a riffle. Trout could be depressing the apparent number of prey drifting by cropping prey before they enter the drift net. Wilzbach et al. (1986) found higher densities of drifting prey in pools after trout were removed. Some measure of benthic prey may be needed because of the likelihood of switching to benthic consumption at low drift densities.

Estimates of P-value could be biased and would affect the correlation of prey density and consumption. My purpose in calculating P-value from daily ration was to correct for differences in consumption caused by temperature and fish size. Two possible biases in daily ration and P-value could affect my interpretation of the prey density-consumption relation: P-values may be underestimated at low temperatures, and evacuation rates did not include corrections for different types of prey. The first bias would only affect the P-value estimate, the second would affect both P-value and daily ration.

The parameter (P-value) may be underestimated at low temperatures because of biases in the Thornton-Lessem curve (curve that estimates consumption at different temperatures). The study used to fit the curve (Baldwin 1956) presumably used trout from Ontario; it is possible that fish in the southern Appalachians do not feed as well at low temperatures. Bevelheimer et al. (1985) found regional differences in optimal temperature for consumption by northern pike *Esox lucius*; pike from lower latitudes had warmer temperature preferences. Ney (1990) warns that physiological parameters for fish may change by geographical region. These papers suggest care must be taken when using physiological relations from different species and perhaps different geographic regions. This bias would not affect daily ration but only the P-value estimate.

The evacuation rates were not corrected for different types of food. I used the evacuation rate for baetids, *Gammarus*, oligochaetes, and chironomidae to estimate daily ration for all months (Elliott 1972). Foods with higher fat contents have slower digestion rates, and their passage rate through the gut would be overestimated (Elliott 1972). I did not have evacuation rates on the most frequently eaten terrestrial invertebrates (Diptera, Lepidoptera, Coleoptera); therefore, I assumed terrestrial and aquatic invertebrates would have similar evacuation rates. To estimate the magnitude of possi-

ble biases, I compared the approach used by Cunjak and Power (1987); they used Elliott's (1972) slowest evacuation rate (on mealworms) to estimate evacuation of terrestrial invertebrates. Mealworms have a very high fat content relative to other prey and this approach would underestimate daily ration. Amundsen and Klemetsen (1988) assigned evacuation rates to food eaten by arctic charr; the evacuation rate for mealworms was only used for high protein food (fish and mollusks) because of mealworms' high fat content and low evacuation rates. Using the data on types of food in Table 22, daily ration and P-value would decrease by 14% in May and 41% in July and September. If terrestrial invertebrates have a slower evacuation rate, daily ration and P-value would be overestimated, especially in streams where fish feed mainly on terrestrial insects. P-values in July and September would be overestimated because more terrestrials insects are eaten in those months than May.

Possible biases in P-value would not change the major conclusions, i.e. juvenile consumption is independent of prey densities, adult trout have higher P-values than yearlings, and prey longer than 4 mm is the best predictor of trout consumption. However, the seasonality of consumption would be affected, i.e. consumption in July and September would be overestimated in comparison with May. Both possible biases of P-value (overestimating C_{max} at low temperatures and using inappropriate evacuation rates for terrestrial invertebrates) reduces the May P-values in comparison with July and September. Thus, most of the bias would affect the relation of May prey densities and consumption to the other months. Juveniles were not sampled in May and conclusions would remain unchanged. Adult trout would still have higher P-values than yearlings if both sizes of fish ate the same kinds of food within the month. Table 22 shows that yearlings and adults were generally within 10% of each other in each food category within a month. Prey greater than 4mm would still be the best predictor of trout con-

sumption. Large prey are more common in May, when P-values are underestimated; thus, if P-values in May were corrected for possible biases, the prey density-consumption correlations would be stronger. Other prey indices would also have stronger correlations with consumption, especially drift rates (hr^{-1}) because they were higher in May.

In future studies (especially for brown trout), there is a better method for calculating P-values. Measuring P-value as mean stomach contents divided by maximum mean stomach contents would eliminate the two biases mentioned for P-values (overestimating C_{max} at low temperatures and inappropriate evacuation rates). Elliott (1975a) determined maximum meal size at different temperatures and fish size for brown trout. Unfortunately, this function is probably inappropriate for brook trout because they are likely to eat larger meals than brown trout at lower temperatures (Allan 1981). I was unable to find information on brook trout maximum meal size in the literature.

Prey abundance

The range of prey densities during the summer was similar or higher than reported for other trout streams in the southern Appalachians. LaRoche (1979) looked at drifting prey densities in two Virginia streams and found ranges in number drifting to be almost exactly the same as this study. Prey abundance by weight in this study was ten times (Cada et al. 1987), four times (Lohr 1985), and equal to (Ensign 1988) prey densities found in the southern Appalachians during the summer. These comparisons suggest that streams in Shenandoah National Park generally have more food than other trout streams in the southern Appalachians. However, trout growth in Shenandoah National Park was similar to other streams in the southern Appalachians (Konopacky 1978).

Therefore, high prey abundance may not be correlated to better growth, but perhaps higher survival.

The streams in this study had large ranges in prey densities. This is fortunate because it makes the prey density-consumption relation more robust. July had the largest range in prey densities because of of gypsy moths. Gypsy moth infestation is spreading south into Shenandoah National Park. Gypsy moth abundance was highest in the center of the park at the crest of the invasion (White Oak Canyon) and moderate in the northern area of the park where the crest has already passed (Piney River). During moth breeding in July, larval and adult moths contributed substantially to the drift, at least in White Oak Canyon. Consequently, the July drift rate (mg/m^3) in White Oak Canyon was twice as high as other rates reported in southern Appalachian trout streams (LaRoche 1979, Lohr 1985, Cada et al. 1987, Ensign 1988). Yearling and adult trout consumed gypsy moth adults and larvae when available. The juvenile trout did not feed on adults and larvae (most likely because of their large size, larvae were approximately 30mm long and adults were approximately 15mm long).

Daily consumption

Estimates of daily ration suggests that the adult and yearling trout fed well in comparison to other studies. Daily ration of adult trout in Shenandoah National Park was five times higher in July and two and a half times higher in September than brook trout in the Smoky Mountains (Ensign, 1988). Admundsen and Klemetsen (1988) found that stunted arctic charr had daily rations of 0.4 to 1.1% (g wet wt/g wet wt) compared to this study's findings of 2.7 and 3.2% (g wet wt/g wet wt) at comparable temperatures (May).

Estimates of mean daily ration of yearlings and adult trout in this study was twice the estimates of Angradi and Griffith (1990) for rainbow trout in a large Idaho river.

Estimates of daily ration for juveniles, (5.9% in July and 5.2% in September) suggest that juveniles did not feed as well as in other studies. Godin (1981) and Sagar and Glova (1988) found juvenile salmonids in their studies had higher daily rations (8.3% and 6.6 to 13.1% respectively) than did the juveniles in this study. Walsh et al. (1988) found that juvenile brook trout in Quebec streams fed 25% more in July but 50% less in August than the juveniles in this study. Results of this study were similar to Ensign's (1988) estimate for juvenile daily ration (1.2 to 7.7%).

Objective 3. Consumed energy versus energetic costs.

The energy budget was estimated to examine whether trout were consuming enough energy to meet maintenance costs and what months during the summer were limiting growth. I hypothesized that the energy left after meeting minimum costs would be highest in May and low in July and September, because trout grow more in spring than summer (Whitworth and Strange 1983, Lucchetti 1983). Estimates of the energy budget did not support this hypothesis even though trout in the study stream had the growth rates expected; i.e. yearling and adult trout grew more from May to July than from July to September. Trout in May had high energy available for growth but trout in July had even more energy available for growth (Table 10).

The timing of growth over the summer was similar to the timing of growth for salmonids in other southern Appalachian streams (Whitworth and Strange 1983, Lucchetti 1983). Adult and yearling trout grew more in early summer and less in late summer. Generally, the fish in this study had lower growth rates than demonstrated in other Virginia streams in the early summer. Lucchetti (1983) estimated early summer growth in four Virginia streams that was 1.7 times higher for yearlings and 4.5 times higher for adults than this study. Late summer growth of yearlings and adults was similar between the two studies. Juvenile trout in this study grew well during the late summer in contrast with trout in Lucchetti's (1983) study. Cada et al. (1987) and Ensign et al. (in press) found that juvenile trout had higher growth rates in southern Appalachian streams than larger fish in the late summer.

Energy budget

Trout in July had more energy available for growth than trout in May and September, and ate substantially more than expected based on the original hypothesis of low food consumption in the summer. Although trout in July had the most energy for growth, the fish still had low growth rates from July to September. Either the July sample was not representative of the late summer interval or activity costs were higher in late summer than from May to July.

Estimates of energy available for growth and activity were greater in May and July than September, suggesting that food limitation was more likely in the late summer. Ensign et al. (in press) found that brook trout consumed the least energy in July, with more energy consumed in August and September. In this study, gypsy moths may have been responsible for the high amounts of energy consumed in July. The only stream without

gypsy moths, Madison Run, had trout that consumed the least energy in July. I did not measure the caloric contribution of gypsy moths. However, I estimated from stomach contents that gypsy moths contributed roughly 50% for White Oak Canyon and Piney River and 20% for Little Hawksbill of the stomach weights in July. If gypsy moths were subtracted from the total energy consumed in July, I believe the streams in September would still have less energy available for growth and activity than May or July.

Juveniles did not decrease food intake in September, unlike adult and yearling fish. Juvenile trout may be less susceptible to low prey densities than larger trout because of their habitat or behavior. Smaller trout spend more time feeding (Bachman 1984) and feed on smaller prey than larger trout (Wankowski 1979). Smaller prey are more prevalent than larger prey in late summer (Table 5), and smaller trout are more likely than larger trout to feed on small prey. Cada et al. (1987) and Ensign et al. (in press) have shown that juvenile trout eat more per body weight than larger trout in the summer when food may be more limiting.

The energy available for growth and activity was positive throughout the summer. This is in direct contrast to the findings of Ensign et al. (in press). They found none of the ages of brook trout in a Tennessee stream consumed enough energy to meet maintenance costs in the summer. This study found ranges in energy intake from 60 to 475 $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$; Ensign et al. (in press) found comparable ranges from 14 to 153 $j \cdot g \text{ wet wt}^{-1} \cdot \text{day}^{-1}$. This discrepancy may be due to year-to-year variation, variation among areas, or to differences in measurement. In this study, the summer was relatively wet and cool which kept the maintenance costs low. Gypsy moths and larvae contributed to the high consumption in this study and were not present in Tennessee. However, these moths contributed little to consumption in May and September and can not ex-

plain all the differences in consumption rates. Finally, Ensign et al. (in press) did not sample at night and may have underestimated consumption by older fish.

Consumed energy appears to be dependent on water temperature in May and prey densities later in the summer. In May, Madison Run was 2 C warmer and brook trout there consumed twice as much energy as brook trout in the other streams. White Oak Canyon had the coldest temperature, and fish there consumed the least energy, if the rain-impacted Piney River is excluded. Food abundance was less likely than temperature to explain the variation in consumption because prey densities were relatively equal among streams in May. Therefore, growth in spring may be more dependent on warm temperatures than food level. Elliott (1973) found that brown trout consumed more food and had more energy available for growth as temperatures got warmer in the spring. Energy available for growth in July and September was proportional to prey density. Trout consumed more energy in July when prey densities were high than September when prey densities were low. Madison Run was the only stream where both prey densities and consumed energy increased in September.

Objective 4. Growth versus excess energy.

I rejected the hypothesis that growth is associated with excess energy in the study streams, at least in the late summer. Trout populations that consumed the most energy in the late summer had the poorest growth. Therefore, activity costs may be more important in determining growth than food levels in these streams. In this section, I will

discuss the association between growth and energy available for growth, and possible reasons for large variations in activity costs.

Growth versus excess energy

Among streams, there was a poor correlation between growth and excess energy (energy available for growth and activity) in both early and late summer. In fact, in late summer there was a negative relation between excess energy and growth for yearling and adult fish, although it was not significant (Figure 15). These poor or negative correlations are probably due to differences in activity costs. Metcalfe (1986) reanalyzed data from Li and Brocksen (1977) and found a negative correlation between ration and growth for subdominant rainbow trout in crowded conditions. He attributed the poor growth (from increased consumption) to increased activity costs from using suboptimal focal points and from increasing the likelihood of being involved in agonistic encounters. He also quoted evidence from other studies to hypothesize that costs to subdominants would increase when food is restricted. Therefore, an energy-minimizing strategy would be more beneficial in late summer when prey abundance and water levels are low than an energy-maximizing strategy. In an energy-minimizing strategy, subdominant fish would not compete for focal points but would remain in stationary water and minimize energetic costs. In an energy-maximizing strategy, subdominant trout would try to maximize food intake. Maximizing food intake is likely to increase energetic costs because fish are competing for focal points and feeding in suboptimal locations.

The relation between food density and growth of trout is equivocal. Wilzbach et al. (1986) found a clear positive relation between the amount of prey drifting through a pool and growth rate when trout densities are the same. However, Cooper et al. (1962) con-

cluded that removal of fish did not increase the growth rates of larger trout and suggested that growth of larger salmonids in streams was not caused entirely by food limitation. The sampling scale could also help to explain the poor correlation in this study. Sampling once every two months may not be enough to determine excess energy. This is especially true when food abundance is changing rapidly, which may be the case in early summer. The method of estimating growth could also have affected the conclusions; if there was size dependent mortality, it would bias growth estimates. However, estimates of condition factors support the estimates of growth. If a fish loses weight (growth), the condition factor should also decrease. In late summer, changes in condition factors were generally in concordance with the estimates of growth (e.g. trout in Madison Run grew more than the trout in other streams and were the only trout that did not decrease in condition from July to September).

Activity Costs

Activity costs have a large effect on trout growth, as supported by the findings that trout ate plenty of food to meet metabolic costs but did not increase their mass. Presumed activity costs varied greatly among streams and sizes of fish and may be functions of: 1) fish size; 2) season; 3) stream characteristics; and 4) food consumption.

Estimates of gross conversion efficiency (Table 13) and estimates of activity costs (Table 11) suggest that adult trout had more activity costs than yearlings, especially in the early summer. Wurtsbaugh and Davis (1977) found that larger trout had better conversion efficiencies at the same ration (g/g of fish) because their energetic costs were less on a per weight basis. Adults in this study had daily rations as high or higher than yearlings (Table 6), yet their conversion rates were lower. Thus, the poorer conversion efficiencies

may be due to higher activity costs for adults than yearlings. The adults may have had higher energetic costs than yearlings if they fed at higher stream discharges and they were involved in more agonistic encounters. Stream discharges were high in the early summer. Because larger fish were feeding more than smaller trout in May (Table 6), they were exposed to higher water velocities than smaller fish. Larger trout are also involved in more agonistic encounters than smaller fish, and these encounters are more prevalent in the spring (Bachman 1984). The higher estimates of activity costs for adults than yearlings may have been caused by differences in caloric density. Adult trout may have been allocating more energy to gonads. Gonads could have a high energy content in comparison with weight and bias estimates of energy allocated to growth.

Activity costs generally increased for yearlings in late summer compared with early summer (Table 11). Activity costs could have increased because of warmer temperatures, consumption on terrestrials invertebrates, or consumption on smaller invertebrates. As water temperatures rise, fish feed in faster water velocities (Smith and Li 1983, Reeves et al. 1987) which could increase activity costs. Most of the food eaten in late summer was terrestrial, which requires more energy by the fish to capture. Surface strikes by brown trout took 40% longer to complete than a midwater foray and also took more tailbeats per second (Bachman 1984). The mean prey size was generally smaller in the summer (Table 3). If prey are smaller, fish would get less benefit from a foraging foray and grow more slowly (Wankowski and Thorpe 1979).

There were large variations in activity costs among streams. Some of these variations may be explained by differences in the physical characteristics in the streams. Streams that have larger pools with slower water should have less activity costs than streams with smaller pools. Gibson (1988) reported that trout in still water gave up drift feeding and

began schooling. Most of the adults and yearlings in Madison Run were captured in larger pools than the other streams; these fish spent less energy on activity than fish in the other streams (Table 11). Streams with more pools and more structure provide more focal points. Thus fish have more opportunities to find feeding locations where they can spend energy drift feeding. Little Hawksbill had the most fragmented habitat, and the fish in the stream consistently spent more energy on activity than fish in other streams. It is not known if schooling associated with larger pools reduces energetic costs in comparison with drift feeding. Actual observations of trout behavior in large versus small pools could answer the question. Energy costs in the two habitats could be estimated by counting tailbeats of individual trout.

Stream shading may also increase activity costs by decreasing light levels. Wilzbach et al. (1986) found that cutthroat trout *Oncorhynchus clarki* in forested sections of a stream had poorer feeding efficiencies than fish in a logged section. Thus, fish may have to spend more time and energy feeding when under low light conditions. Wilzbach et al. (1986) found that trout in forested sections of a stream had poorer growth than trout in open sections despite having more food in their stomachs at noon. They attributed the high midday stomach contents to trout in forested pools feeding only at the highest light levels. However, they did not examine feeding throughout the day. Alternatively, the poor growth may have been caused by greater activity costs in the shaded pools than the unshaded pools. Under low light levels, fish can not see as far and are scanning a smaller volume of water for prey. Thus, unless there were more prey at low light levels, a fish would increase benefits per cost by feeding at high light levels. Estimates of light intensities among streams and months was highly variable in this study (Table 2), so it is difficult to relate activity costs to shading. Trout consumption in southern Appalachians streams may be less influenced by shading than streams in Oregon.

Another reason fish in Little Hawksbill may have spent more energy on activity is that there is energy associated with capturing food. Trout in Little Hawksbill consumed more food than did trout in the other streams (Table 6). Boisclair and Leggett (1989) found that activity costs of perch *Perca flavescens* in the wild increased with higher food consumption. Activity costs associated with habitat complexity are linked with activity costs for feeding and hard to separate. More complex habitats allow trout to eat more so it is difficult to determine whether costs are associated with habitat or feeding.

I did not find a clear association between trout densities and activity costs. Densities for yearling and adult trout did not have a significant ($P > 0.1$) correlation with activity costs during the two months intervals (Spearman's Rank $R_s = 0.342$ for yearlings and -0.093 for adults, $n = 8$). Li and Brocksen (1977) found that activity costs of rainbow trout increased with crowding in an artificial environment; however, their fish were in the midst of stabilizing their social hierarchy. Density probably has an effect on activity costs, but it is probably inconsistent seasonally and among streams. If trout are in streams with low water discharge and few focal points, the trout may give up on drift feeding. Thus, no matter how many trout are in the stream it would not affect the average energy cost. Fish density may have had a relatively minor role in affecting activity costs in comparison with food consumption and habitat in the study streams over the summer.

Temperature conditions were optimal for growth in the late summer (Dwyer et al. 1983, Table 14) yet fish did not grow. Therefore, low food densities and the activity costs were limiting growth in late summer in Shenandoah National Park. Cada et al. (1987) and Ensign et al. (in press) concluded that trout populations in the southern Appalachians were food limited. Prey densities in Shenandoah National Park were substantially higher

than in the two previous studies, yet most of the fish did not grow in late summer. It may not only be the amount of food that is limiting growth but the type of food and the energy costs needed to obtain it. Hypothetically, fish should grow the best with larger prey, prey below the water surface, and prey that come in great enough abundance to minimize the time feeding. Stream characteristics are also important to growth by limiting energetic costs. Thus, if prey is scarce, caloric benefit per cost is increased in streams with slow water.

Management implications.

Results from this study could be useful in identifying habitat characteristics that could affect activity costs, in identifying possible short and long term effects of gypsy moth defoliation on brook trout, and in suggesting refinements in bioenergetic models for stream dwelling salmonids.

Studies are needed that examine the affect of habitat on trout activity costs. Activity costs were variable among streams, but I could not determine the exact cause of the variability. Two of the sources of variability in activity (habitat and prey characteristics) can be manipulated by managers. Further research could examine how changes in stream characteristics (increasing or decreasing pool size) or changes in prey characteristics (larger prey) affect activity costs, and more importantly, growth.

Results of this study suggest that gypsy moths had a possible positive impact on brook trout populations in the short term. Gypsy moth defoliation is one of the major con-

cerns in Shenandoah National Park and will be a growing concern throughout the southern Appalachians as the moths spread south. Gypsy moths contributed substantially to the drift in July, a month when Ensign (1988) had reported the lowest prey densities in a southern Appalachian stream. Yearling and adult trout ate gypsy moths and larvae in the streams where they were present. Of the four streams studied, White Oak Canyon had the greatest infestation of moths (personal observation) and had the highest growth rates compared to the three other study streams.

Longer term effects of gypsy moths on brook trout populations is not as clear. I have four concerns about the long term effects of gypsy moths. Does moth defoliation depress the number of terrestrials that enter the drift in late summer, will the contribution of moths to the trout diet be as great at warmer temperatures, does defoliation increase stream temperatures, and do moths depress allochthonous input to the system? The three streams that had gypsy moth infestation had late summer reductions in prey while the stream that was not infested (Madison Run) had an increase in prey from July to September (Figure 9). Therefore, moth defoliation may depress the number of terrestrial invertebrates in the late summer. This evidence is not strong because all the study streams were physically different from each other. Madison Run differed from the other streams in slope, substrate, and water temperature which also could have affected terrestrial invertebrates in the stream. Secondly, the summer of 1989 was relatively cool and wet compared to other summers, and the streams were all first or second order. Trout in warmer years or lower in the drainage would be exposed to warmer temperatures. If the temperatures get too high in July, due to decreased canopy shading, consumption will be depressed (Figure 2) and the fish will not be able to take full advantage of gypsy moths in the drift. This may be especially important if defoliation is going to increase stream temperatures. Finally, the moths may be reducing allochthonous mate-

rial input into the stream. The reduction in input would reduce the food of aquatic invertebrates (especially shredders). Aquatic invertebrates are important food sources for brook trout during cooler months (LaRoche 1979). Fortunately, Shenandoah National Park is currently monitoring invertebrates in the trout stream and should be able to observe any reductions in shredder invertebrates.

Bioenergetic models, such as Hewett and Johnson (1987), would have made two types of errors in predicting growth in the study streams. First, it would have made errors among streams, e.g. because trout in Little Hawksbill had the highest consumption among streams it would have predicted that the trout in the stream would have grown more than the trout in the other study streams. In fact, trout in Little Hawksbill had some of the lowest growth rates compared to the other study streams. Secondly, the model would have made errors in growth predictions among size classes. Adult trout ate more and had lower standard metabolic costs than yearling trout on a per gram basis. Hence, adult trout should have had better growth rates than the yearlings, but again this was not the case. Both of these types of errors could have been due to inaccurate measures of activity in the model.

Bioenergetic models need to be adjusted for activity costs before they can be of much use in predicting growth. Commonly, bioenergetic models estimate activity costs by assuming fish are swimming at a constant speed. This assumption implicitly assumes activity costs are constant among streams and trout size, if trout are assigned the same swimming speed. I can see two possible approaches to improve the estimate of activity costs: associate the activity costs with habitat characteristics or associate the activity costs with the amount of food consumed. The results suggested mean activity costs were higher for streams with more habitat complexity. The model could be improved by as-

signing higher activity costs to streams with more complex habitat. A simpler method to improve bioenergetic models would be to assign higher activity costs with more consumption. Kerr (1982) has developed an equation to predict activity costs as a function of consumption for pelagic feeders in marine systems. Kerr's equation may have some use in describing activity costs for brook trout, although the parameters may have to be changed. The adjustment (increased activity cost with feeding) would implicitly include the habitat complexity adjustment because the fish in more complex habitats would feed more (this study). More basic research is needed to examine whether activity costs are related more to habitat or feeding and to determine the effect of different seasons on activity costs.

CONCLUSIONS

1. Juvenile brook trout in streams of Shenandoah National Park consumed significantly less food at night than during the day in July and September. However, yearling and adult trout consumed the most food at night in July and September. In May, trout older than juveniles fed the most during the daylight. Thus, the times of peak consumption for yearling and adult trout were not consistent throughout the summer.
2. Trout of all sizes selected for prey longer than 4mm. Density of drifting prey larger than 4mm was also the best predictor of daily consumption by trout of all sizes.
3. Yearling and adult trout ate a higher proportion of maximum consumption in July and May than in September. Juvenile trout fed equally well in July and September.
4. Consumption appeared to be most dependent on temperature in May and prey density in July and September.

5. Consumption was positively correlated with prey density for yearling and adult brook trout. Juvenile consumption was independent of prey density. Changing the prey density at low abundance (< 1 prey larger than 4 mm/ m^3) influences adult consumption more than yearlings. Alternatively, changing prey densities at high abundance (> 1 prey larger than 4 mm/ m^3) changes yearling consumption more than adults.
6. The prey density-consumption relation was more consistent within streams than among streams. Stream characteristics such as habitat and trout population structure may be important in predicting consumption with changes in prey densities.
7. Brook trout in Little Hawksbill Creek ate consistently more than brook trout in the other streams despite low to medium prey densities. This anomaly suggests that fish may feed more efficiently in a more complex habitat.
8. Adult brook trout ate more than yearlings on a per gram basis, and also had a larger k (parameter that represents the increase in feeding with increases in prey). Social hierarchies may play a role in the prey density-consumption relation.
9. Energy available for growth and activity was positive throughout the summer, but yearling and adult fish grew only in early summer. Juveniles had more energy available for growth than yearlings and adults and were the only fish to grow in late summer.
10. Food limitation is more likely in September than in May or July. However, poor growth in the late summer may be due less to the amount of food than to charac-

teristics of the prey that increase activity costs (smaller size, surface drifting, and densities require continuous feeding to reach satiation).

11. Growth was not correlated with energy available for growth and activity (E) for adults in early summer. In late summer, there was a negative relation between growth (G) and energy available for growth and activity (E) for yearlings and adults. Therefore, trout that ate the most grew the least. An energy minimizing strategy may be more beneficial for subdominant trout growth in the late summer.
12. Activity costs presumably vary substantially among streams and may be linked to water discharge in early summer, light intensity, the size of pools, and the amount of food consumed. Bioenergetic models should have activity costs dependent on food consumption to make the model more accurate for brook trout streams.

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Appendix I

Selected information on habitat and brook trout populations in four streams of Shenandoah National Park.

Table 14. Temperatures (C) by different months in study streams of Shenandoah National Park. Parameters reported are monthly mean temperature, daily ranges within month, and number of days temperature was measured. Temperatures were measured continuously with Ryan J thermographs.

Month	Piney	White Oak	Madison	Hawksbill
MAY				
mean	10.4	10.2	11.7	11.2
range	7.5 - 13.2	7.3 - 13.0	9.1 - 14.2	10.0 - 12.7
n	22	20	24	15
JUNE				
mean	14.6	13.4	15.4	13.6
range	13.0 - 17.2	11.2 - 15.2	14.1 - 16.6	11.7 - 15.5
n	30	30	30	30
JULY				
mean	16.4	14.8	17.6	15.8
range	15.0 - 18.2	13.5 - 16.7	16.4 - 18.6	14.7 - 17.0
n	12	31	31	31
AUGUST				
mean	-	14.3	17.1	15.4
range	-	12.5 - 16.5	15.6 - 19.4	14.0 - 17.0
n	-	31	31	31
SEPTEMBER				
mean	-	15.0	16.3	15.0
range	-	15.0 - 15.0	15.9 - 17.1	14.2 - 15.7
n	-	2	7	10

Table 15. Trout lengths (mm) for each size class over the summer in streams of Shenandoah National Park. Lengths are reported in means, standard errors, and range. the number of fish measured is also reported.

Trout size/ Month	Piney	White Oak	Madison	Hawksbill
Age 0				
JULY				
mean	66	61	74	70
SE	0.747	1.154	0.919	0.682
range	49 - 84	46 - 83	55 - 94	55 - 88
n	107	49	84	100
SEPT				
mean	76	78	78	76
SE	0.797	1.174	0.736	0.740
range	58 - 97	62 - 98	59 - 99	59 - 94
n	112	51	130	112
Age 1				
MAY				
mean	114	100	125	109
SE	2.800	2.573	1.760	1.276
range	85 - 136	68 - 134	94 - 123	94 - 123
n	21	38	45	42
JULY				
mean	129	120	136	121
SE	1.423	1.548	1.441	1.354
range	90 - 152	87 - 150	107 - 160	100 - 142
n	87	92	84	66
SEPT				
mean	131	127	136	120
SE	1.401	1.177	1.480	1.337
range	103 - 154	105 - 154	106 - 157	101 - 144
n	71	101	75	65
Age 2+				
MAY				
mean	179	163	190	168
SE	4.879	5.101	7.953	3.421
range	143 - 235	137 - 205	150 - 252	145 - 208
n	23	18	16	20
JULY				
mean	184	177	191	170
SE	2.814	2.795	5.156	3.216
range	155 - 233	155 - 217	162 - 307	146 - 213
n	49	36	37	26
SEPT				
mean	187	175	193	171
SE	3.410	2.181	6.495	2.889
range	156 - 236	155 - 211	160 - 310	146 - 206
n	41	55	28	28

Table 16. Trout weights (g) for each size class over the summer in streams of Shenandoah National Park. Weights are reported in means, standard errors, and range. The number of fish measured is also reported.

Trout size/ Month	Piney	White Oak	Madison	Hawksbill
Age 0				
JULY				
mean	3.3	2.6	4.4	3.3
SE	0.109	0.160	0.160	0.099
range	0.9 - 6.1	1.0 - 5.7	1.9 - 8.9	1.1 - 6.2
n	107	49	84	100
SEPT				
mean	4.4	4.7	4.9	4.3
SE	0.144	0.231	0.146	0.119
range	1.7 - 9.4	2.0 - 10.0	2.1 - 10.0	2.3 - 8.1
n	112	51	130	112
Age 1				
MAY				
mean	15.	11.	21.	13.
SE	0.994	0.900	0.973	0.447
range	6.0 - 24.	2.4 - 28.	10. - 38.	8.5 - 19.
n	21	38	45	42
JULY				
mean	21.	18.	25.	18.
SE	0.735	0.760	0.814	0.576
range	8. - 40.	6.7 - 38.	11. - 41.	10. - 29.
n	87	92	84	66
SEPT				
mean	22.	21.	25.	17.
SE	0.777	0.641	0.846	0.587
range	9.4 - 36.	11. - 41.	13. - 40.	9.8 - 29.
n	71	101	75	65
Age 2+				
MAY				
mean	57.	44.	85.	49.
SE	4.591	4.539	11.604	3.925
range	26. - 111.	24. - 87.	33. - 180.	33. - 107.
n	23	18	16	20
JULY				
mean	65.	62.	80.	53.
SE	3.329	3.295	9.251	3.326
range	33. - 129.	37. - 116.	43. - 339.	31. - 100.
n	49	36	37	26
SEPT				
mean	65.	59.	85.	50.
SE	3.836	2.618	11.905	2.908
range	35. - 122.	32. - 108.	38. - 331.	29. - 92.
n	41	54	28	28

Table 17. Condition factors (K) for trout over the summer in streams of Shenandoah National Park. Condition factors are reported in means, standard errors, and range. The number of fish measured is also reported.

Trout size/ Month	Piney	White Oak	Madison	Hawksbill
Age 0				
JULY				
mean	1.13	1.08	1.04	0.93
SE	0.0178	0.0168	0.0162	0.0128
range	0.71 - 1.64	0.72 - 1.28	0.62 - 1.60	0.66 - 1.37
n	107	49	84	100
SEPT				
mean	0.96	0.95	0.99	0.98
SE	0.0071	0.0133	0.0096	0.0113
range	0.76 - 1.16	0.74 - 1.13	0.78 - 1.48	0.68 - 1.61
n	112	51	130	112
Age 1				
MAY				
mean	0.96	1.02	1.06	1.03
SE	0.0138	0.0155	0.0150	0.0110
range	0.87 - 1.10	0.74 - 1.17	0.91 - 1.38	0.93 - 1.21
n	21	38	45	42
JULY				
mean	0.97	1.01	0.95	0.99
SE	0.0080	0.0090	0.0066	0.0092
range	0.79 - 1.21	0.77 - 1.25	0.83 - 1.29	0.80 - 1.15
n	87	92	84	66
SEPT				
mean	0.94	0.99	0.95	0.93
SE	0.0088	0.0084	0.0096	0.0110
range	0.77 - 1.18	0.73 - 1.22	0.66 - 1.13	0.70 - 1.18
n	71	101	75	65
Age 2+				
MAY				
mean	0.94	0.96	1.14	1.01
SE	0.0121	0.0280	0.0282	0.0209
range	0.86 - 1.06	0.82 - 1.27	0.92 - 1.32	0.83 - 1.19
n	23	18	16	20
JULY				
mean	1.00	1.09	1.03	1.04
SE	0.0122	0.0136	0.0100	0.0164
range	0.81 - 1.25	0.85 - 1.25	0.92 - 1.17	0.90 - 1.26
n	49	36	37	26
SEPT				
mean	0.96	1.07	1.03	0.98
SE	0.0118	0.0136	0.0197	0.0141
range	0.81 - 1.15	0.83 - 1.35	0.86 - 1.27	0.81 - 1.08
n	41	54	28	28

Table 18. Biomass (kg/ha) and number (no/ha) of brook trout populations in four streams of Shenandoah National Park.

Month/ Trout size	Piney		White oak		Madison		Hawksbill	
	kg/ha	no/ha	kg/ha	no/ha	kg/ha	no/ha	kg/ha	no/ha
MAY								
Age 1	12.0	842	17.5	1485	8.8	418	12.0	925
Age 2 ⁺	21.3	385	8.3	186	9.7	117	13.3	293
Monthly total	33.3	1227	25.8	1671	18.5	535	25.3	1218
JULY								
Age 0	13.4	4091	2.1 ^a	784	1.9	441	10.5	3105
Age 1	55.5	2601	12.4 ^a	670	22.8	927	33.2	1846
Age 2 ⁺	93.3	1435	26.6 ^a	439	27.2	345	6.6	124
Monthly total	162.2	8127	41.0	1893	51.9	1713	50.3	5075
SEPT								
Age 0	12.7	2870	3.3	829	2.4	490	9.2	2123
Age 1	37.0	1714	18.5	915	9.8	392	27.7	1663
Age 2 ⁺	40.6	662	27.2	464	7.8	88	10.4	207
Monthly total	90.3	5246	49.0	2208	20.0	970	47.4	3993

^aBiomass estimate extrapolated from the first run and percent captured at White Oak in the first run in September.

Table 19. Numbers of fish caught when estimating population sizes with the two catch method. N is the population estimate for the study section. The area sampled is presented in Table 2.

Trout size/ Stream	1st pass	2nd pass	N and 95% CI
MAY			
Age 1			
Piney	21	7	31 ±7
White oak	14	12	98 ±420
Madison	8	6	32 ±88
Hawksbill	32	5	38 ±3
Age 2+			
Piney	12	2	14 ±2
White oak	7	3	12 ±8
Madison	3	2	9 ±26
Hawksbill	6	3	12 ±12
JULY			
Age 0			
Piney	51	24	96 ±28
White oak	12	8 ^a	36 ±53
Madison	16	2	18 ±1
Hawksbill	63	10	75 ±4
Age 1			
Piney	35	15	61 ±18
White oak	20	7 ^a	31 ±8
Madison	31	6	38 ±4
Hawksbill	32	9	45 ±7
Age 2+			
Piney	26	6	34 ±4
White oak	11	5 ^a	20 ±12
Madison	10	3	14 ±4
Hawksbill	3	0	3 ±0
SEPT			
Age 0			
Piney	57	13	74 ±6
White oak	12	8	36 ±53
Madison	17	4	22 ±4
Hawksbill	32	12	51 ±12
Age 1			
Piney	21	11	44 ±26
White oak	26	9	40 ±9
Madison	14	3	18 ±3
Hawksbill	19	10	40 ±25
Age 2+			
Piney	12	3	16 ±3
White oak	11	5	20 ±12
Madison	4	0	4 ±0
Hawksbill	5	0	5 ±0

^aI did not make a second pass in White Oak in July. I estimated this value by finding the capture efficiency ($\frac{\text{number in second pass}}{\text{number in first pass}}$)

for White Oak in September and multiplying it by the number captured in the first pass in July.

Appendix II

Stomach contents by time of day and estimations of daily ration in four streams of Shenandoah National Park.

Table 20. Average stomach contents (mg dry wt/gm wet wt) at different times during the day in four streams in Shenandoah National Park. The number of fish sampled are in parentheses.

Month/ Stream	Morning 0900	Midday 1500	Evening 2100	Night 0300
MAY				
1 ⁺				
Piney ^a	2.42(5)	2.54(5)	0.92(6)	0.42(5)
White Oak	1.16(9)	0.75(6)	1.24(10)	1.00(13)
Madison	1.72(9)	2.11(12)	2.60(12)	3.51(12)
Hawksbill	2.43(11)	2.09(11)	2.89(10)	1.25(10)
2 ⁺				
Piney ^a	2.64(5)	1.48(6)	1.37(4)	1.39(8)
White Oak	1.82(6)	3.65(4)	3.20(6)	1.12(2)
Madison	2.48(6)	3.13(3)	1.63(3)	1.13(4)
Hawksbill	2.23(5)	3.75(5)	1.50(5)	3.34(5)
JULY				
0 ⁺				
Piney	0.72(10)	2.01(10)	2.26(10)	0.93(11)
White Oak	2.63(11)	2.18(10)	3.02(9)	0.94(11)
Madison	1.05(10)	1.04(10)	0.80(10)	0.78(10)
Hawksbill ^b	1.44(12)	3.59(10)	3.15(11)	1.55(9)
1 ⁺				
Piney	1.23(10)	0.79(10)	1.16(10)	1.87(10)
White Oak	1.67(9)	1.87(11)	0.88(12)	2.27(12)
Madison	0.37(13)	0.44(13)	0.19(12)	0.87(11)
Hawksbill ^b	2.57(10)	2.48(15)	2.61(9)	3.77(10)
2 ⁺				
Piney	1.72(6)	0.60(6)	2.15(5)	1.25(6)
White Oak	3.05(5)	2.39(5)	1.34(5)	3.15(3)
Madison	0.32(5)	0.09(5)	0.09(5)	0.84(5)
Hawksbill ^b	3.63(8)	2.33(4)	3.05(8)	2.14(5)
SEPT				
0 ⁺				
Piney	0.91(11)	1.05(10)	1.82(14)	0.69(12)
White Oak	0.71(11)	1.33(11)	2.93(9)	0.64(11)
Madison	0.92(11)	2.20(13)	2.43(11)	2.83(13)
Hawksbill	2.73(12)	3.50(11)	1.33(12)	1.42(13)
1 ⁺				
Piney	0.66(11)	1.07(10)	0.83(10)	0.59(11)
White Oak	0.62(11)	0.40(9)	0.86(11)	0.65(10)
Madison	1.54(13)	0.63(14)	0.30(12)	1.59(13)
Hawksbill	1.18(12)	1.27(11)	1.47(11)	1.65(10)
2 ⁺				
Piney	0.13(6)	0.77(6)	0.28(5)	0.31(7)
White Oak	0.31(9)	0.42(8)	0.73(7)	0.83(5)
Madison	0.39(6)	0.57(3)	0.27(5)	1.40(5)
Hawksbill	3.43(5)	0.43(5)	1.44(5)	1.46(10)

^aHeavy rains fell at 1500 hours.

^bHeavy rains fell at 2100 hours.

Table 21. Comparison of Elliott and Persson's (1978) and Egger's (1977) methods of estimating daily ration (g dry wt/g dry wt * 100). Difference is Elliott and Persson's estimate of daily ration minus Egger's estimate.

Trout size/ Stream	Elliott and Persson ration(%)	Eggers ration(%)	Difference ration(%)
MAY			
Age 1			
Piney	2.20	2.20	0.00
White Oak	1.22	1.22	0.00
Madison	4.34	4.34	0.00
Hawksbill	3.11	3.11	0.00
Average	2.72	2.72	0.00
Age 2+			
Piney	2.40	2.40	0.00
White Oak	2.92	2.88	-0.04
Madison	3.65	3.65	0.00
Hawksbill	3.88	3.88	0.00
Average	3.21	3.20	-0.01
JULY			
Age 0			
Piney	5.68	5.66	0.02
White Oak	7.52	7.49	0.03
Madison	3.22	3.22	0.00
Hawksbill	7.49	7.48	0.01
Average	5.98	5.96	0.02
Age 1			
Piney	4.84	4.82	0.02
White Oak	5.68	5.71	-0.03
Madison	1.63	1.72	-0.09
Hawksbill	8.78	8.79	-0.01
Average	5.23	5.26	-0.03
Age 2+			
Piney	5.50	5.47	0.03
White Oak	8.41	8.48	-0.07
Madison	1.17	1.14	0.03
Hawksbill	8.51	8.49	0.02
Average	5.90	5.90	0.00
SEPTEMBER			
Age 0			
Piney	3.34	3.32	0.02
White Oak	3.90	3.83	0.07
Madison	6.64	6.64	0.00
Hawksbill	7.06	7.04	0.02
Average	5.98	5.96	0.02
Age 1			
Piney	2.33	2.34	-0.01
White Oak	1.75	1.72	0.03
Madison	3.21	3.21	0.00
Hawksbill	4.42	4.38	0.04
Average	2.93	2.91	0.02
Age 2+			
Piney	1.10	1.10	0.00
White Oak	1.58	1.56	0.02
Madison	2.08	2.08	0.00
Hawksbill	5.30	5.31	-0.01
Average	2.51	2.51	0.00

Appendix III

Source of energy during the summer for brook trout populations in four streams of Shenandoah National Park.

Table 22. Summer food habits by percent (dry wt /dry wt x 100) of brook trout in four streams in the Shenandoah National Park. TE is terrestrial invertebrates from terrestrial sources, TA is terrestrial invertebrates from aquatic sources, TT is the total of terrestrial invertebrates, AQ is aquatic invertebrates, CR is crayfish, and VE is vertebrates.

Trout size/ Stream	TE	TA	TT	AQ	CR	VE
MAY						
1+						
Piney	4.7	0.0	4.7	90.9	3.5	0.9
White oak	7.6	0.0	7.6	90.3	2.1	0.0
Madison	52.8	0.0	52.8	32.2	1.1	14.0
Hawksbill	15.1	1.5	16.5	81.3	0.3	1.7
average	20.0	0.4	20.4	73.9	1.7	4.1
2+						
Piney	6.7	0.0	6.7	92.1	0.8	0.3
White oak	4.2	0.0	4.2	64.8	11.0	20.1
Madison	77.9	0.0	77.9	8.4	2.0	11.6
Hawksbill	25.5	2.5	28.0	68.1	3.2	0.6
average	28.6	0.6	29.2	58.3	4.2	8.2
JULY						
0+						
Piney	48.9	2.0	50.9	49.0	0.0	0.0
White oak	37.6	11.5	49.1	49.3	0.0	1.6
Madison	87.9	2.2	90.1	9.9	0.0	0.0
Hawksbill	73.9	5.6	79.5	20.5	0.0	0.0
average	62.1	5.3	67.4	32.2	0.0	0.4
1+						
Piney	85.0	2.0	87.0	10.1	3.0	0.2
White oak	69.1	7.0	76.1	22.3	10.6	1.5
Madison	67.3	0.0	67.3	7.2	24.7	0.8
Hawksbill	67.7	3.4	71.1	26.2	2.4	0.2
average	72.3	3.0	75.3	16.5	7.6	0.7
2+						
Piney	70.9	0.4	71.3	3.7	1.3	23.8
White oak	81.2	2.0	83.2	2.7	0.4	13.7
Madison	34.1	0.4	34.5	3.3	62.2	0.0
Hawksbill	62.8	0.7	63.5	14.7	14.1	7.6
average	62.3	0.9	63.1	6.1	19.5	11.3
SEPT						
0+						
Piney	69.9	7.7	77.6	17.0	0.0	5.4
White oak	25.7	1.1	26.8	71.6	0.0	1.5
Madison	83.4	1.9	85.3	6.7	0.1	7.8
Hawksbill	82.9	3.2	86.1	12.8	0.3	0.7
average	65.5	3.5	69.0	27.0	0.1	3.9
1+						
Piney	61.8	3.7	65.5	11.7	13.2	9.6
White oak	30.2	15.4	45.6	40.8	10.6	3.0
Madison	77.9	1.1	79.0	6.8	1.9	12.4
Hawksbill	85.9	1.6	87.5	3.0	9.5	Tr
average	63.9	5.4	69.4	15.6	8.8	6.3
2+						
Piney	80.6	6.2	86.8	5.8	7.4	0.0
White oak	45.8	2.8	48.6	20.7	29.1	1.4
Madison	96.7	0.5	97.2	0.9	1.8	0.0
Hawksbill	73.5	0.8	74.3	1.4	24.2	0.0
average	74.2	2.6	76.8	7.2	15.7	0.4

Vita

Kelly J. Meyer was born in Riverton Wyoming on October 24, 1961 and graduated from Riverton High in 1980. Kelly then attended Utah State University in Logan Utah and graduated with a BS in Fisheries and Wildlife (Fisheries option) in June 1984. After graduation, Kelly spent two and a half years as a Peace Corps Volunteer in Lesotho, southern Africa. Kelly was attached to the National Park Section and studied trout and an endangered cyprinid. Kelly was admitted to graduate school in February 1988 and will graduate with a MS in Fisheries and Wildlife in December 1990. After graduation, Kelly plans to return to the western US to look for work.

A handwritten signature in cursive script that reads "Kelly Meyer".