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**Temporal trends in consumption, growth, and successful feeding traits of a
central Appalachian brook trout population at the watershed scale**

Ryan Michael Utz

A Thesis

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in

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Keywords: brook trout, bioenergetics, feeding strategy, distribution, trophic ecology

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Abstract

Temporal trends in consumption, growth, and successful feeding traits of a central Appalachian brook trout population at the watershed scale

Ryan Michael Utz

Brook trout (*Salvelinus fontinalis*) in Appalachia frequently experience limitations in food availability. In order to determine temporal variation in consumption, successful feeding, and corresponding population patterns and growth, the feeding dynamics of a population of brook trout were monitored throughout a headwater watershed over the course of two years. The Middle Fork River brook trout experienced food limitation throughout summer and fall, however, mean consumption estimates fell below maintenance ration only during the winter seasons. Consumption estimates were significantly related to watershed position, as fish in low density, downstream reaches consistently consumed significantly more energy than fish upstream during warm months. During the summer, when fish were most energetically stressed, a significant negative relationship existed between large fish density and mean consumption estimates. Brook trout exhibited generalist feeding throughout the year and consumed a high diversity of organisms. During each season, fish observed feeding above maintenance ration consumed significantly different proportions of certain prey taxa than fish feeding below maintenance ration. Specifically, some terrestrial organisms appeared to be most important during spring, summer, and fall. The population of brook trout in the Middle Fork River watershed did not appear to be evenly distributed with respect to food resources, suggesting that the full potential of resource availability is not being exploited by the population. Alternatively, brook trout may not distribute on a food resource scale, and/or the energetic costs of movement do not equal the benefit of increased feeding. Furthermore, terrestrial organisms appear to outweigh aquatic prey in terms of prey importance to Middle Fork brook trout, implying that active riparian zone management may have consequences to central Appalachian salmonids.

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Dedicated to Mom

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Chapter 1: Literature Review

Quantitative surveys of fish diets allow insight into the ecological processes of fishes. Measurement of dietary trends may provide insight into trophic cascades (Vander Zanden et al. 2000), niche specialization of individuals within a species (Bridcut and Giller 1995, Beaudoin et al. 1999), and help explain the causal mechanisms governing the distribution of organisms at the watershed scale (Nakano et al. 1999). Examining how seasonal change influences prey availability can indicate when fish experience feeding related stress or population change (Ensign et al. 1990). Such stressful feeding conditions may be affected by environmental variables, such as watershed position, annual variations in prey availability, prey and predator density, specific habitat features, and water temperature. Temporal changes in diet composition and how they relate to other physical conditions may be particularly important in species where food resources are consistently limited during certain seasons.

Appalachian brook trout (*Salvelinus fontinalis*) represent one such species where food resources are often limited. Multiple studies of salmonid feeding patterns in southern and central Appalachia have revealed that feeding during the summer months may be particularly low (Cada et al. 1987, Ensign et al. 1990, Sweka 2003), although food limitation may not be limited to summer alone (Sweka and Hartman 2001). Brook trout populations in Appalachia have been reduced due to historic and recent human activity, such as uncontrolled logging, acidic precipitation, acid mine drainage, introduced species, and overfishing (Marscall and Crowder 1996). As a result, the effects of natural periodic episodes of food resource depletion may be compounded due to local anthropogenic impacts. This review focuses on the quantitative and qualitative lotic

salmonid feeding ecology that likely governs Appalachian brook trout populations with an emphasis on processes that affect feeding rates at the watershed scale.

Seasonal Change

Among the most important variables that affect feeding rates of lotic salmonids is temporal change. The warmer seasons are considered the most productive seasons for stream dwelling salmonids, as temperatures are conducive to efficient gastric evacuation and insect activity is high (Power 1980, Neveu 1999). However, the summer months may present poor feeding conditions for lotic salmonids, as flow decreases and insect activity drops (Cada et al. 1987, Ensign et al. 1990). During particularly dry summers, habitat related stressors may compound the effects of low feeding rates (Hakala and Hartman 2004). Salmonids employ a range of strategies in order to survive summer, such as exploiting disproportionately productive habitat units (de Crespin de Billy 2002) and targeting terrestrial invertebrate prey (Kawaguchi and Nakano 2001, Sweka 2003). Nevertheless, food limitation may not be limited to summer alone, and lotic salmonids may utilize other strategies and environmental variables to survive sparse prey availability during colder seasons.

Feeding conditions for lotic salmonids during the winter may be poor, particularly for brook trout (Cunjak and Power 1987, Sweka and Hartman 2001). The brook trout life history strategy poses a problem for fish surviving winter, as this species spawns in the fall and consequentially enters the winter season with reduced energy stores (Hutchings 1994, Hutchings et al. 1999). Trout and salmon continue to feed and exploit disproportionately productive habitats during the winter (Cunjak 1987, LeHane et al. 2001). However, colder water temperatures during the winter reduce metabolic demands

(Elliot 1976). Consequently, multiple surveys of different salmonid species have observed fish feeding below maintenance ration for extended periods without substantial population mortality (Cunjak 1987, Steinhart and Wurtsbaugh 2003). Brook trout do experience low feeding rates during fall and winter (Sweka and Hartman 2001). Yet winter induced physiological stress appears to be caused by acclimatization to cold temperatures near the onset of winter, and, following acclimatization, severe loss of energy reserves due to winter conditions becomes less severe (Cunjak 1988).

Watershed Position

One environmental feature that may affect feeding conditions independent of seasonal change is the position of fish in the watershed. An extensive case study of this concept involves Arctic grayling (*Thymallus arcticus*) in Alaska. As position in the watershed moves upstream, mean Arctic grayling size increases (Hughes and Reynolds 1994). The relationship between fish size and watershed position was found to be driven by a dominance hierarchy, where larger, more competitively dominant fish defended upstream positions and excluded smaller fish driving them into downstream reaches (Hughes 1992, Hughes 1999, Hughes 2000). The upstream positions occupied by large fish were found to be more profitable in terms of foraging and temperature quality (Hughes 2000). While this case study represents the most detailed examination relating habitat quality in terms of foraging and fish distribution in salmonids, contrasting relationships between salmonid population distribution and watershed position have been observed or suggested in other species.

All organisms, including stream-dwelling salmonids, generally distribute spatially according to one of two ways as proposed by Fretwell and Lucas (1970). One

distribution pattern is termed ideal-free, where organisms distribute equally along a resource gradient. Here, higher densities of organisms are found where resources are abundant, and fewer organisms in areas of low resource availability. The other pattern, competitive-dominant, theorizes that dominant organisms acquire and defend territories of higher quality and competitively exclude less dominant organisms to areas of low resource availability. While the Arctic grayling example may suggest that lotic salmonids distribute according to the competitive-dominant principle, others have observed salmonids distributed according to the ideal-free theory. Bohlin et al. (1994) found a relationship between body size and watershed position in Scandinavian brown trout (*Salmo trutta*), where trophic resources were divided evenly along the watershed gradient. Fish were therefore considered to be distributed under ideal-free mechanisms. In a prey manipulation experiment of a headwater watershed, Nakano et al. (1999) found that the removal of an important resource (terrestrial organisms) caused lotic salmonid populations to spatially redistribute according to available resources, again suggesting an ideal-free distribution. Therefore, both distributional patterns as proposed by Fretwell and Lucas (1970) have been observed in lotic salmonid populations. Few similar studies on Appalachian brook trout have been conducted. However, increased levels of energy intake, particularly due to higher rates of piscivory, have been observed in brook trout occupying large reaches of streams at the periphery of their typical habitat (Thorne 2004). Furthermore, movement in a downstream direction has been suggested to improve foraging conditions in general (Schlosser 1995). An understanding of how brook trout employ different reaches of watersheds to obtain energy could help determine which habitats are necessary to grow and maintain populations.

Terrestrial Organisms

Recent research suggests that in some cases terrestrial organisms may exceed aquatic prey in importance. Allan (1951) first suggested that terrestrial organisms may allow streams to carry salmonid populations greater in biomass than what aquatic prey could provide. Multiple studies in headwater watersheds in Japan have revealed that terrestrial prey organisms consistently provide more energy to trout than aquatic prey sources (Nakano et al. 1999, Kawaguchi and Nakano 2001). Further, salmonids were found to be spatially distributed based on the availability of terrestrial organisms in these systems (Nakano et al. 1999). Fish in watersheds considered largely dependent on salmon carcass nutrients in Alaska have been shown to acquire substantial energy both directly (Wipfli 1997) and indirectly (Wipfli and Gregovich 2002) from insects with no obligate aquatic phase.

Despite these findings, most diet studies of lotic salmonids have focused on aquatic prey taxonomy and compile all terrestrial organisms into one broad category (Cada et al. 1987, Forrester et al. 1994, Bridcut and Giller 1995, Mookerji et al. 2004). In some (Forrester et al. 1994, Bridcut and Giller 1995), terrestrial organisms were found to be of particular importance, yet little to no attention was given to the taxonomic detail of such organisms. When terrestrial taxonomic detail is considered, findings show that some taxa provide a disproportionate amount of energy to aquatic systems, while others may be negligible (Wipfli and Gregovich 2002). Such findings have implications for stream management, as active manipulation of the riparian zone may affect terrestrial insect communities and consequentially affect the aquatic community and stream fishes (Nakano and Kawaguchi 2001, Wipfli and Gregovich 2002, Allan et al. 2003).

The importance of terrestrial organisms to salmonids in Appalachia has received little attention until recently, though such prey items may be of particular importance. Sweka (2003) found that terrestrial organisms may play a large role in shaping Appalachian brook trout growth rates throughout certain times of the year. Others have concurred with this finding, suggesting terrestrial organisms act as important energy sources for salmonids in the Appalachians (Cada et al. 1987, Ensign et al. 1991, Thorne 2004). In these studies, the taxonomic specifics of terrestrial organisms were not reported. Yet in a study of central Appalachian brook trout, Webster and Hartman (2005) found differing levels of importance for various terrestrial prey organisms. Watersheds containing brook trout in central Appalachia are low in productivity, as they are typically headwater systems dependent on allochthonous energy input from the surrounding forest ecosystems (Vannote et al. 1980, Schlosser 1991, Schlosser 1995). Therefore, the conditions for stream fishes in Appalachia are likely similar to other systems of low productivity, such as streams in Japan and Alaska, where terrestrial energy sources have received much research attention.

Feeding Strategy and Prey Diversity

Lotic salmonids employ a diverse range of feeding strategies across the environments in which they occur. In some watersheds, lotic salmonids may use a small number of prey organisms over the course of the year. For instance, different species of trout may exploit as few as three to five genera of prey organisms over the course of a year in tailwater reaches of rivers (McKinney and Speas 1991, Odenkirk and Estes 1991) or Arctic environments (Steingrímsson and Gislason 2002). More commonly, however, lotic salmonids employ a highly generalist strategy and exploit a large number of prey

taxa (Allen 1981, Hubert and Rhodes 1989, Angradi and Griffith 1990, Nielsen 1992, Forrester et al. 1994, Bridcut and Giller 1995, Amundsen et al. 1996, Mookerji et al. 2004). Due to this commonly observed generalist strategy, some diet studies have placed emphasis on prey diversity (Bridcut and Giller 1995), though defining ‘high’ diversity to allow comparison among studies has yet to be resolved (Chipps and Garvey *in press*).

Brook trout in eastern North America seem to employ a generalist feeding strategy. Sweka (2003) and Forrester et al. (1994) both reported a broad range of taxa in brook trout stomachs during the warmer seasons. However, during the summer, multiple studies of Appalachian salmonids have shown that prey availability of particular taxa decreases and stomach content consequentially declines during this time of year (Cada et al. 1987, Ensign et al. 1990, Sweka 2003). Despite cold temperatures during the winter, active feeding on multiple taxa has been observed in brook trout during this season (Cunjak and Power 1987, Sweka and Hartman 2001). Due to the broad environmental variability in seasons experienced by brook trout and generalist feeding pattern they employ, a detailed understanding of what specific prey taxa are important and when could help improve management and ecological understanding of the species.

Objectives

The current study aimed to quantitatively and descriptively assess brook trout diet across a range of seasons and watershed positions in a central Appalachian watershed. Salmonid diets may be influenced by a host of variables as described above, and the current study attempted to address as many as possible. An understanding of the multiple factors influencing the amount of energy brook trout are capable of deriving from the environment could help influence future management decisions and thus assist in

protecting the species. Specifically, goals of this study included: (1) determining the seasonal patterns in brook trout consumption and how it relates to maintenance ration and growth rates, (2) discerning if population density or watershed position plays a role in energy intake, (3) describing brook trout feeding strategy with an emphasis on aquatic and terrestrial resource use, and (4) identifying any disproportionately important food items that may be necessary in carrying brook trout populations through periods of stress.

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Chapter 2: Temporal variation in the energy intake of Appalachian brook trout at the watershed scale.

Abstract- Salmonids often experience prolonged periods of poor feeding conditions with consequences at the individual and population level. Feeding intensity may be related to seasonal change, habitat and watershed variables, or fish density. This study examined the consumption and growth rates of Appalachian brook trout (*Salvelinus fontinalis*) across a range of seasons and stream sizes within the same watershed. Consumption varied significantly with seasonal change. Energy intake was highest during the spring and late summer, reduced from mid-summer to fall, and lowest during winter. Estimates of maintenance ration provided insight into whether or not brook trout were obtaining sufficient energy to maintain weight; consumption significantly exceeded maintenance ration during the spring, early summer, and fall. Growth rates were significantly positively correlated with consumption estimates, with positive growth observed only when the time interval ended during a spring or early summer sampling period. Population change was significantly positively correlated with corresponding consumption estimates. Significant differences in consumption between stream sizes were observed, with fish in downstream reaches obtaining more energy than fish upstream. During the summer and fall months, the population density of large fish was negatively correlated with mean consumption in a given site. Findings in this study concur with others that Appalachian brook trout are energetically stressed through the summer, though mean consumption was significantly lower than maintenance ration only during the winter. Downstream habitat appeared to be underutilized for energy exploitation by the total population. Further, the negative relationship between trout

density and consumption during the summer suggests that Middle Fork brook trout do not distribute with resource availability at the watershed scale.

Introduction

Salmonids commonly occur in watersheds of low productivity, often with ecological consequences at the individual and population level. In temperate mountainous regions, trout typically occupy headwater reaches of watersheds. These streams derive nearly all energy from allochthonous input from the surrounding terrestrial ecosystem and are naturally low in productivity (Vannote et al. 1980). As a result, sparse food resources may often be capable of shaping population dynamics through emigration of fish in search of food resources (Petty et al. 2005). Energy intake also determines how an individual fish grows (Elliot 1976, Filbert and Hawkins 1995). Within low productivity headwater systems, growth has been correlated with energy intake at the reach scale due to differences in the quality and quantity of food at different reaches (Kawaguchi and Nakano 2001, Thorne 2004). Despite the obvious importance of energy intake in fish populations, little attention has been paid to temporal and spatial trends in consumption rates of wild salmonids (Neveu 1999). Those that have, found salmonids endure sustained periods of energy intake below maintenance ration (Cada et al. 1987, Cunjak and Power 1987, McKinney and Speas 2001, Sweka 2003).

Due to the sparse availability of food resources, the distributional trends of lotic salmonids at the watershed scale may play a role in how energy is obtained and allocated. Hughes and Reynolds (1994) and Hughes (1999) observed distributional patterns of arctic grayling (*Thymallus arcticus*) where fish size increased as the position in the

watershed moved upstream. Competitive dominance of larger individuals was the driving force in this pattern, as larger individuals assumed upstream positions where both temperature and concentrations of food were optimal (Hughes 2000). As a result, both body size and energy intake was correlated with position in the watershed. Similar trends have been observed in other salmonids, such as the brown trout (*Salmo salar*) (Bohlin et al. 1994). Although some studies show that feeding varies at the microhabitat scale (De Crespín de Billy et al. 2002), the current study was concerned with variation at the watershed scale.

Appalachian brook trout (*Salvelinus fontinalis*) occupy low productivity headwater systems (Schlosser 1995) and are considered vulnerable to anthropogenic impacts (Marscall and Crowder 1996). Similar to salmonids in other regions, Appalachian brook trout likely experience severe limitations in food availability during certain seasons. Multiple studies have either suggested (Cada et al. 1987) or shown (Ensign et al. 1990, Sweka 2003, Thorne 2004) that Appalachian salmonid populations experience limitations in energy intake. Specifically, these fish may spend a significant proportion of the summer months obtaining daily rations less than what is required to maintain a constant body weight (Cada et al. 1987, Sweka 2003). Brook trout energy intake in central Appalachia may be related to watershed position, as piscivory rates increase in larger order reaches of streams (Thorne 2004). Appalachian brook trout have been subjected to multiple historic and ongoing anthropogenic effects, such as uncontrolled logging, acidic precipitation, introduced species, overfishing, and acid mine drainage (Marscall and Crowder 1996, Clark and Rose 1997). Such detrimental effects

may compound the consequences of poor feeding conditions during certain seasons to create population instability and/or decline.

A detailed understanding of how temporal and spatial change affects the amount of energy consumed by brook trout at the watershed scale could help determine how brook trout populations react to variations in feeding conditions. Temporal variation in consumption likely affects the growth of individual fish, recruitment of fish into larger size classes, and mortality when food limitation is coupled with environmental extremes. Further, position in the watershed may affect how much energy a fish derives from the environment. Identifying how seasonal change and watershed position interact to affect energetic input could help managers prioritize specific habitat units and foresee periods of feeding related stress. Objectives of this study were to: (1) determine the seasonal patterns in brook trout consumption and how it relates to maintenance ration, (2) establish how growth relates to energy intake over the course of a year and (3) discern if population density or watershed position plays a role in energy intake.

Methods

Study Area

The study was conducted within the Middle Fork watershed, a north flowing tributary of the Tygart River in the central Appalachian Mountains of Randolph County, West Virginia. The majority of land cover within the watershed is that of secondary growth hardwood deciduous forest. All sites in the study are located in the southernmost extent of the watershed (Figure 1) and are of low order and high gradient (see Table 1 for descriptions of each site). Nine-200 m sites were selected to encompass a range of stream sizes and were based on a number of criteria: each site contained a resident brook

trout population, consistently held age-0 brook trout (indicating water quality was sufficient for spawning) and was devoid of fish barriers between other sites. Temperature regimens in these reaches are suitable for trout; temperature rarely exceeded 20°C through the duration of the study. The West Virginia Division of Natural Resources and the West Virginia Department of Environmental Protection have actively added limestone sand to riparian areas of streams within the watershed to remediate the effects of acid precipitation and acid mine drainage in the Middle Fork since the 1990's (WVDNR 2001). This process is commonly used in the region and successfully increases pH, restores fish communities, and increases invertebrate abundance (Clayton et al 1998), though invertebrate productivity and diversity may not reach pre-acidification levels following treatment (McClurg 2004). Some sites selected in this study were not actively treated with lime (Table 1); however, each site without a limestone treatment retained the ability to support brook trout spawning and carry fish populations. In order to quantify water quality in each site, a sample of water was taken in February, May, July, and October 2004 and tested at a laboratory for pH and alkalinity. The means of both measurements were calculated for each site based on the four seasonal measurements (Table1); this calculation provided an estimate of mean water quality across seasons.

Fish diversity differed across sites, but was typical of Appalachian headwater systems. The number of species encountered increased with stream size. In nearly all sites fish fauna was dominated by brook trout and mottled sculpin (*Cottus bairdi*). Other fish sampled include blacknose dace (*Rhynchichthys obtusis*), longnose dace (*R. cataractae*), creek chub (*Semotilus atromaculatus*), white sucker (*Catostomus*

commersoni), northern hogsucker (*Hypentelium nigricans*), and fantail darter (*Etheostoma flabellare*).

Fish and Habitat Sampling

Fish sampling occurred eleven times over the course of two years (Table 2). Sampling was conducted between 0800 and 1600 hours and the order of sites to sample was randomly chosen during each day. A three-pass depletion electrofishing procedure (Platts and Nelson 1988) was used in order to estimate fish populations within the 200 m section. Before sampling, block nets were placed at the top and bottom of each section to restrict fish movement in or out of sections during sampling. Sampling teams used an electrofishing unit (Smith-Root, DC, 60 hz, 500-750 V, Vancouver, WA) and dip nets to capture fish.

Following collection, fish were processed at a streamside station. All fish were immobilized with a clove oil and 95% ethanol solution. Brook trout were weighed to the nearest 0.5 g, and total length was taken to the nearest mm. A subset of 10 brook trout per site per month was chosen for stomach content removal. Only fish >110 mm fork length were considered eligible for gut content removal due to gear restrictions; the gape of fish below this size was usually about the same size of the flushing tube diameter (7 mm). This size class generally represented age-1 and older fish as is apparent in length frequency histograms (Figure 2). An attempt was made to collect an equal range of fish sizes to analyze for gut content at each site. Stomach contents were removed by directing a constant flow of stream water into the foregut until all items had been apparently collected (Twomey and Giller 1990). Gut items were filtered with a 250 μ m sieve and transferred to 95% ethanol. This process of collecting stomach contents has proven

effective (Light et al. 1983) and analysis with the gear used in this study has found that the technique is acceptably efficient (Sweka 2003).

During May 2004, each fish over 100 mm fork length was given a unique color-coded mark using Visible Implanted Fluorescent Elastomer (Northwest Marine Technology, Shaw Island, WA) tags for subsequent identification and growth estimation. Following an analysis of recapture success, tagging was carried out every sampling period starting in December 2004 and ending in June 2005. Marks of up to seven colored tags were injected into the caudal and dorsal fins of trout, allowing the identification of individual fish in subsequent months. All fish other than trout were counted and weighed. Each fish was allowed to recover from the clove oil treatment and returned to the stream reach within two hours. A sample of 10 trout were randomly collected from sites, frozen, and kept for analysis of dry weight during select sampling periods (see Table 3). Estimates of brook trout dry weights were needed in order to estimate fish energy density, a necessary component of bioenergetics modeling.

In order to determine if habitat or fish density variables were related to consumption at the watershed scale, habitat variables were calculated at each site. Habitat sampling was conducted during base flow on August 17th, 2005 according to a modified version of Dolloff et al. (1997). Variables were directly measured, rather than estimated, on each 200 m reach of stream. Reaches within each site were classified as riffle or pool and the length of each unit was measured. Within each habitat unit, specific measurements were taken along a linear transect perpendicular to the stream, including wetted width, bankful width, and depth (3 points per transect). The number of times a transect was measured within a habitat unit depended on the length of the unit, with

measurements made approximately every 20 m in riffles and every 2 m in pools. The basin area (km²) of each site was determined using coordinates derived from a global positioning system at the midpoint of each site and calculated using GIS.

Laboratory Procedures

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

Estimates of Consumption and Daily Ration

Estimates of consumption and maintenance ration were calculated in order to determine seasonal and spatial variation in energy intake. Comparing estimated consumption to maintenance ration suggests whether or not fish are obtaining enough energy to maintain body weight. Estimated maintenance rations (EMR, in Joules per

gram fish wet weight per day) were calculated based on a bioenergetics model for brook trout (Hartman and Sweka 2001) and used fish weight, fish energy density, and observed water temperature as variables. Maintenance ration was determined by calculating the energy required to maintain zero growth over the course of a day. Energy densities were calculated from either observed mean energy density in collected fish using a dry weight-energy equation for Salmonidae (Hartman and Brandt 1995) or interpolated from energy densities taken before and after a given collection period (see Table 3 for observed trout energy densities). Mean fish energy density was assumed to be equal across sites during a given month. Consumption estimates were calculated based on a model proposed by Eggers (1977). Each prey item was converted to energy using published dry weight-energy equations (Table 4, Cummins and Wuycheck 1971), and the total energy in the gut was summarized for each fish.

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

assumption that a measurement of diet during daylight hours provided sufficient data to calculate mean feeding conditions for the corresponding season.

Growth Rates

Growth estimates were calculated in order to quantify temporal trends and compare growth to consumption variables. Mark-recapture analysis of tagged individuals provided estimates of growth over the course of the study. Growth was calculated from the following equation (from Jensen 1990):

$$G = 100 * (\ln X_t - \ln X_0) / \Delta t$$

where G is daily growth, X_t is the final weight at time t , X_0 is the initial weight, and Δt is the amount of time elapsed between capture events in days. Size-adjusted growth (G_i):

$$G_i = G / \ln X_0$$

was also analyzed to determine if fish size affected growth rates. All fish obviously missing an individual mark were removed from growth analyses to prevent inaccurate growth increments from distorting patterns. Growth intervals were considered between consecutive sampling events only for the purpose of simplification. For example, if a fish was caught in June 2004 and August 2004, but not July 2004, growth rates were not calculated for that particular fish.

Statistical Analyses

Consumption estimates were square-root transformed to approximate normality and were analyzed using repeated measures analysis of variance (ANOVA) to test for differences between months. Duncan's multiple range test was used to determine specific differences once overall differences had been established. A two-way pairwise t-

test was performed on mean maintenance ration and observed consumption for each month to determine if fish were meeting maintenance requirements. Differences in growth rates between months were tested for using repeated measures ANOVA and Duncan's multiple range post-hoc test. Early analyses showed that each month could be classified into one of three broad seasons based on similarities in temperature and consumption (Table 5).

Population estimates were calculated in order to determine population change, estimate fish density, and allow comparison of consumption and population variables. Population estimates of all fish, and fish eligible for gastric lavage, were calculated for each stream using the Zippin model in program CAPTURE (White et al. 1982). Estimates of the population of all reaches combined were calculated by adding the populations and standard errors of each reach (Mood et al. 1974). If less than 30 fish were captured then the actual number of fish caught was substituted for an estimate (Riley and Fausch 1992). Fish density per site was calculated as the population estimate divided by the wetted area (m^2) of base flow. For analysis of consumption by site, each site was placed into one of three classes (upstream, midstream or downstream) based on similarities in basin area, trout density, wetted width, and fish species present (see Table 2). Differences in mean square-root transformed consumption across stream classes within each season were tested using ANOVA and Duncan's repeated measures test post-hoc. Fish size and temperature were included in the ANOVA model; thus site type and temperature were considered when exploring differences in consumption between site classes. If site class did influence consumption, stepwise multiple regression was performed on mean consumption per site by habitat and density variables to determine if

any variables were significantly correlated. Non-linear relationships were also explored to test for best-fit during these analyses by plotting both original and log-transformed variables. Further, Chi-square analysis was performed on diet composition by site class within each season to determine if differences in resource exploitation existed between site classes. For this analysis, prey organisms were organized into nine categories based on taxonomy. Site types with no significant differences within a season were treated as groups.

Results

Consumption and Seasonal Change

Brook trout consumption ($\text{J g}^{-1} \text{ fish d}^{-1}$) varied significantly throughout the year. Consumption estimates were linked to seasonal change with significant differences among months (F-value 23.84, $\text{df}=10$, $p<0.0001$, Table 5). Mean consumption was significantly highest during the spring (May/June 2004 and 2005), lowest during late winter (March 2004 and 2005), and intermediate during the summer and fall months (Figure 3). Differences in mean consumption values between winter and summer/fall months were occasionally statistically significant. Within a designated season, significant differences occurred between June and May of both years (Table 5).

During certain months, mean consumption differed significantly from the corresponding mean estimated maintenance ration (Figure 3 and Table 6). Whether or not a significant difference was observed was linked to seasonal change. Mean consumption during all spring months was significantly higher than maintenance ration. Only one significant difference was observed between consumption and maintenance ration during the summer or fall (September 2004); means of EMR and consumption

were not significantly different during all other months within these seasons.

Maintenance ration estimates were significantly higher than mean observed consumptions for both March samples.

Although comparisons between consumption and maintenance ration suggested that fish were meeting metabolic demands, <50% of fish were observed feeding above maintenance ration throughout a majority of sampling periods (Figure 4). The proportion of fish eating above maintenance ration exceeded 0.5 only during spring months. The distribution of consumption values during each season was skewed to the right, where a minority of individuals consumed a disproportionately large amount of energy relative to the mode (Figure 5).

Growth

Mean growth rates varied significantly with time ($F=23.13$, $df=8$, $p<0.0001$, Table 7 and Figure 6). Positive growth was recorded only when the period of observation ended during a spring month. During any interval of time ending in summer, fall or winter, observed growth was either negative or near zero. No statistically significant differences between growth rates were observed between periods of time when the time interval ended in the mid to late summer, fall, or winter (Table 7). Patterns in size-corrected growth (G_i) were similar to overall growth (Table 7). Growth rates were significantly positively correlated with mean estimated consumption between months ($F=6.95$, $n=9$, $p=0.0336$, Figure 7) and estimated consumption at t_n ($F=26.14$, $n=9$, $p=.0014$, Figure 7).

Population Change

Estimates of brook trout populations across all sites varied with seasonal change (Figure 8 and Table 8). Population change was positive between late winter and early summer during both years, stable between summer and fall 2004, and negative between September 2004 and December 2004. Change in populations between December 2004 and March 2005 (over winter) was small. Shifts in population estimates were similar between all fish and fish eligible for gastric lavage (Figure 8). Fish density was significantly related to basin area during all seasons. Trout density was negatively correlated with basin area at the log-log scale for fish over 110 mm fork length ($F=23.48$, $n=26$, $p<0.0001$, Figure 9) and all fish ($F=51.14$, $n=26$, $p<0.0001$ Figure 9). Mean consumption during the corresponding months was significantly positively correlated with population change of all fish ($F=16.14$, $n=10$, $p=0.0039$, Figure 10) but not fish eligible for gastric lavage ($F=0.77$, $n=10$ $p=0.4045$, Figure 10).

Consumption by Site and Population Density

During each of the three seasons, significant differences in consumption were apparent between site classes (Table 9). Fish in upstream locations consumed significantly less energy than fish occupying downstream and midstream reaches during spring and summer (Table 10). During winter, the trend shifted, with upstream consumption significantly greater than mid-order reaches, but not downstream reaches (Table 10). Because weight and temperature significantly differed across sites, these variables were included in the model. Neither negated the effects of site type during any season (Table 9). During the summer/fall season, a significant negative $\log(y)-x$

relationship existed between mean consumption and large fish density ($F=19.44$, $n=9$, $p=0.0031$, Figure 11).

Significant differences in prey exploitation were detected across sites without significant differences in mean consumption within each season (Table 11 and Figure 12). One prey type dominated energetic input during each season: Coleoptera during the spring, Lepidoptera during the summer and fall, and aquatic insect taxa during the winter. In the reach classes where mean consumption was significantly higher, the respective seasonal dominant prey types were exploited more than in reaches with lower mean consumption during each season. For example, fish in midstream and downstream reaches (where fish had significantly higher mean consumption estimates) exploited Lepidoptera larvae more heavily than those in upstream reaches during the summer and fall (Figure 12).

Discussion

Temporal Consumption and Implications

Trends inherent in this data suggest that brook trout in the upper Middle Fork River watershed experience food limitation throughout most of the year. Mean estimated daily ration fell below maintenance ration only during the winter months. Though mean consumption did not significantly differ from the corresponding maintenance ration throughout the summer and fall, less than half of the population was eating above maintenance ration during these months. The mean consumption value was elevated by a minority of particularly successful fish which were observed feeding at high rates when resources were low. Therefore, though brook trout experienced stressful feeding conditions during the summer and fall, the mean consumption of the population matched

or exceeded maintenance ration, and coincidentally the population appeared to experience low mortality over the course of the summer. The ability of the Middle Fork River brook trout to obtain sufficient energy contrasts findings of brook trout diet studies.

Similar limitations in summer food intake have previously been inferred or observed in Appalachian salmonids, though the implications of such conditions vary from the current study. Cada et al. (1987), Ensign et al. (1990), and Thorne (2004) observed a substantial drop in the number of items and/or mean stomach content weight found in brook trout stomachs from spring to summer in populations of Appalachian salmonids. In Ensign et al. (1990), the ensuing drop in brook trout consumption was calculated as below maintenance ration. Such inefficient food resources were not observed in either summers of the current study. Sweka (2003) observed an occasional mean summer consumption estimate below maintenance ration in the same watershed as the current study; however, his study was limited to two sites and one sampling event per summer season. Thus the summer consumption values in the current study may more accurately reflect typical summer conditions for brook trout at the watershed scale.

The current study suggests that either brook trout in central Appalachia experience less severe food limitation than in southern Appalachia, or consumption is subject to annual variation. Environmental conditions for brook trout in the region may be highly variable between years due to periodic drought and flooding (Carline and McCullough 2001, Hakala and Hartman 2004). The summer seasons in the current study were not particularly severe, and it is likely that consumption values during drought years would drop below those observed in this study. Observations of a minority of fish feeding on particularly large or abundant organisms during the summer increased the

mean consumption estimate. Thus, it is likely that central Appalachian brook trout rely on a highly generalist strategy during the summer (*Chapter 3*) which allows for feeding well above maintenance ration on occasion during periods of low resource availability. However, during other potentially stressful times of the year, brook trout observed in this study appeared to use temperature to survive rather than opportunistic events.

While the lowest rates of energy intake were observed during the winter, water temperatures during this time probably buffered detrimental effects of low feeding. Low water temperatures decrease the metabolic demand of salmonids (Elliot 1976). Acclimitization to decreasing water temperatures with the onset of winter may stress brook trout, particularly those fish exhausted from fall spawning (Cunjak 1988). However, once fish adjust to low temperatures, low metabolic rates decrease energetic demand and the physical consequences of low feeding may be reduced for the remainder of winter, even when fish feed below maintenance ration during such periods (Cunjak and Power 1987, Steinhart and Wurtsbaugh 2003). Results in this study concur, as the largest drop in estimated population and growth rates occurred with the onset of winter (between September and December 2004). Although this observed population drop could have been attributed to post-spawning emigration, sites less suitable for spawning (mid and downstream reaches) did not experience an increase in population. Regardless, both consumption and population estimates changed very little between December 2004 and March 2005. Therefore, the low consumption during these months did not seem to induce mortality once the apparent post-spawning mortality occurred.

Despite an apparent lack of mortality during periods of stressful feeding conditions, consumption seemed to affect changes in brook trout populations at the

watershed scale. Mean consumption was positively correlated with total population change, but not population change of larger individuals. Changes in population estimates could have occurred via movement or mortality. The lack of a relationship between consumption and large fish population changes could have been attributed to movement of larger fish. In central Appalachia, adult brook trout are capable of moving large distances (Logan 2003, Thorne 2004, Petty et al. 2005) and may move in order to improve spawning or foraging conditions (Lamothe 2002). Therefore, the lack of a relationship between adult populations and consumption may be caused by an inability to accurately assess 110mm+ fish populations due to movement. The relationship between total fish population and mean consumption implies that temporal feeding conditions are similar between fish sampled for gut contents and fish considered too small for gastric lavage. Though larger fish tend to defend more productive territories and exclude smaller individuals (Persson 1985, Grant and Kramer 1990, Nakano 1995), resource availability is linked to seasonal change. Therefore, though smaller individuals may inhabit territories of poor quality, temporal variations in resource availability likely affect all fish. Thus correlations between total population change and observed consumption of one size class of fish should be expected.

Growth rates varied predictably with temporal change and followed trends similar to changes in consumption, though variables other than consumption were likely influential. Only two significantly different periods of growth were recorded; those ending in the spring (positive growth) and those ending in all other months. Though fish size may significantly affect growth rates of salmonids (Elliot 1976, McKinney and Speas 2001), trends in size-corrected growth differed only slightly from patterns in

overall growth. Temperature may also play an important role in growth rates of lotic salmonids (Jensen 1990). Although this study was not designed to examine the effects of temperature on brook trout growth, the effects of temperature were indirectly considered when calculating gastric evacuation and maintenance metabolism. Thus comparisons between growth and consumption contain temperature variables. Factors other than those mentioned likely affected growth rates as well, such as gamete hydrolysis during the fall (Power 1980); this process probably influenced the growth rate between August 2004 and September 2004 in this study (fish were gravid during the September sampling). Nevertheless, growth rates were significantly correlated with consumption, and variations in growth rates were highly influenced by temporal change.

The sometimes erratic change in growth rates during the course of the study may have important implications. The change in growth rates between late spring and early summer was particularly dramatic, shifting from positive and high between May and June to negative between June and July during both years. The importance of sampling frequency when studying growth rates is highlighted. For instance, if the June 2004 sample is omitted, growth rates between May 2004 and July 2004 would have been calculated as $0.294\%d^{-1}$. From this observation, one may conclude that summer offers favorable conditions for growth up until mid July. However, data in the current study shows that growth during the mid to late summer is consistently poor. Other studies have examined brook trout growth rates using longer intervals of time (Cada et al. 1987, Lamothe 2003, Thorne 2004) with various results. Specifically, Cada et al. (1987) reported that the highest growth rates in adult southern Appalachian salmonids occurred over the winter, while Thorne (2004) and Lamothe (2002) reported positive mean growth

rates over summer. Growth rates in the current study did not concur with either of these findings; however, the intervals between sampling events were shorter in the current study. Therefore, conclusions previously made about Appalachian salmonid growth rates could have been distorted due to the growth fluctuations that may occur seasonally. However, despite the detailed report of temporal growth rates, intensive shocking regimens may pose problems in assessing growth.

Electrofishing has been shown to significantly decrease growth rates in salmonids (Gatz et al. 1986, Dwyer and White 1995, Dwyer and White 1997 Hughes 1998), and the frequency of electrofishing in the current study may have affected growth rates.

Reductions in growth rates may be caused by internal injury, which has been documented in wild brook trout populations in streams similar to those in the current study (Hollender and Carline 1994). Nevertheless, the growth rates recorded during intervals in 2005, after a year of study, were not significantly different from the same intervals recorded in 2004 when the brook trout population had been exposed to fewer electrofishing events.

Further, growth rates were significantly correlated with corresponding consumption estimates (though consumption estimates were not derived from tagged fish only). Injury as a result of electrofishing is more common in larger fish (Hollender and Carline 1994), and the fish observed in this study were much smaller than fish used in the laboratory experiments examining the effects of electrofishing mentioned above. Larger fish that are more susceptible to injury typically grow less under normal conditions (Whitworth and Strange 1983, Cada et al. 1987). Therefore, while growth values may be underestimated, overall trends in growth in the observed brook trout population are likely accurate. Minimal effects of electrofishing at the population level aside from growth (i.e.

mortality and movement) have been observed (Habera et al. 1996, Carline 2001, Dunham et al. 2002), suggesting that while individuals may be damaged by electrofishing induced injury, population level processes may be affected little by electrofishing. Those studies which have reported Appalachian salmonid growth rates contrasting those found in the current study (Cada et al. 1987, Lamothe 2002, Thorne 2004) sampled fish multiple times over the course of a year using DC pulsed electrofishing. Therefore, injuries sustained by fish in the current study would have been similar in fish sampled in other mentioned studies, likely rendering growth rates comparable between the current study and others.

Fish Density and Consumption

Across all seasons, trout density was negatively correlated with stream size for all fish and fish eligible for gastric lavage. Similar trends have been observed in nearby watersheds (Petty et al. 2005) and likely has to do with life history strategy. Brook trout utilize different locations in the watershed for foraging, feeding or refugia; upstream reaches of streams are most often used for spawning (Power 1980, Curry et al 2002). The exploitation of foraging habitat (downstream) may require long-distance movement from natal stream areas and such movements may be energetically costly (Schlosser 1991, 1995). As a result, stream fish densities may be directly related to size-specific habitat requirements, as seen in this study. However, the trends in fish density at the watershed scale did not result in fish distribution patterns based on resource availability.

Mean consumption seemed to be influenced by watershed position and trout density throughout the year. Specifically, during both spring and summer, fish in downstream and midstream reaches derived a significantly higher amount of energy from their environments than fish occupying upstream reaches. This finding concurs with

others that have found movement in a downstream direction improves foraging conditions (Schlosser 1991, 1995). The trend reversed during winter, with significantly higher energy intake occurring in upstream reaches; however, this period of time is associated with low growth due to low temperatures as seen in this study. Therefore the most consequential seasons concerning consumption rates occur during warmer months. Consumption was negatively correlated with large fish density during the summer and fall months.

One mechanism allowing increased feeding in downstream reaches may be territoriality. Stream-dwelling salmonids defend territories from invaders and benefit from increased foraging and growth rates in higher quality territories (Hughes 1992, Nakano 1995). In downstream reaches, an increased amount of space and decreased number of fish could ease territory defense and size, potentially resulting in increased growth through increased foraging rates or lower metabolic costs. Larger fish have been found to defend high-quality territories (Grant and Kramer 1990, Nakano 1995), and fish in downstream reaches were more capable of exploiting particularly important prey taxa (*Chapter 3*) during the corresponding seasons, such as Coleoptera during the spring and Lepidoptera during summer. Additionally, the occupation of downstream territories may increase growth rates. Salmonids physically defend territories from other fish, and such acts require the expenditure of energy that could otherwise be used for growth or metabolism (Metcalf 1986). Growth rates were not comparable between sites in this study due to low recapture rates in some reaches. However, the trends observed in consumption may suggest that fish in down and midstream reaches may have spent less time defending territory and more time foraging, potentially resulting in a greater

capacity for growth than fish upstream. Thorne (2004) found increased growth rates in larger order systems, as the spatial scale used was similar the finding concurs with the current study. This disproportionate rate of resource exploitation may have implications for brook trout distributional ecology.

Organisms tend to distribute via one of two mechanisms: ideal-free distribution, which states that organisms distribute based on resource availability, or competitive dominant, where organisms distribute by competitive interactions (Fretwell and Lucas 1970). In the current study, brook trout that moved away from natal upstream reaches were rewarded with an increased rate of energy intake. This observation points to competitive-dominant distribution in brook trout, as fish choosing to move downstream assumed a competitive advantage over those that stayed in upstream reaches. As a result, fish were apparently disproportionately distributed according to resources at the watershed scale due to the competitive nature of migrating individuals. Other studies, however, have observed ideal-free mechanisms in stream salmonids, both at the local (Kawaguchi et al 2003) and watershed (Bohlin et al 1994, Hughes and Reynolds 1994) scale. Factors other than food resources, such as territoriality, may be driving ideal-free distribution in salmonids.

Salmonids defend contiguous territories, and the defense of such territories coupled with food availability may affect the abundance of stream salmonids. Studies of salmonid territoriality show that territory size is related to fish size, but not food availability except when food resources are abnormally high (Keeley 2000, Imre et al. 2004). Therefore, when food resources limit growth (as is often the case), lotic salmonid populations will be subject to emigration as subordinate individuals are forced to cope

with the exclusion of resources (Grant et al. 1998, Imre et al. 2004). As a result, lotic salmonids become dispersed throughout the watershed as territories and food resources become evenly distributed among fish throughout the watershed. The current study did not directly quantify brook trout territory or total food abundance. Regardless, food abundance has been shown to explain approximately 84% of the variation in salmonid abundance (Imre et al. 2004). The significant differences in energy acquisition observed in the current study between reaches suggest that the Middle Fork River brook trout population most likely did not redistribute on a territory and resource scale.

If brook trout truly operate under ideal-free distribution, it is unclear why consumption rates were not proportionally distributed with density in this study. The high density of fish in small, upper reaches of streams was likely related to reproductive success at these sites, yet some movement from these sites by adult fish should be expected (Petty et al. 2005). One causal mechanism may be fishing pressure, which tends to remove larger individuals (Marscall and Crowder 1996) and may be influential in structuring populations in the system studied (Webster 2004). Though all sites included in the current study are on private land and road access is limited due to locked gates on logging roads, most downstream and some midstream sections in this study are close (approximately <1 km or less) to public roadways, and may be affected by angling pressure. If angling mortality was the cause of reduced populations in downstream and midstream sections, population decline would be expected in these reaches during seasons of high angling activity, such as spring and summer. Yet large fish populations remained relatively stable during these seasons. Therefore, it remains unclear if angling mortality reduced the ability of Middle Fork River brook trout to exploit downstream

resources. Multiple studies (Logan 2003, Petty et al. 2005) show that brook trout are highly capable of long distance movements in the Middle Fork watershed, and the current study illustrates that downstream reaches offer favorable foraging conditions. Future research examining the cause of low population density in downstream reaches could help define what management decisions could be made in order to improve brook trout populations in central Appalachian watersheds.

Management Implications

Findings in this study highlight important temporal and qualitative details of brook trout feeding ecology over the course of the year. This study and others (Cada et al 1987, Ensign et al 1990, Sweka 2003, Thorne 2004) note the importance of mid-summer as a stressful period of energy intake for brook trout. Brook trout may rely on a generalist feeding pattern and occasional successful feeding periods to survive typical summer seasons. Further, this study underscores the importance of carefully considering temporal change when examining growth. Growth rates changed significantly over a short period of time, and positive growth was only realized during the spring and early summer.

Location appears to be an important factor in determining the level of energy intake in a brook trout population. While attention must be paid to upstream reaches of streams and brook trout spawning success to ensure population persistence (Petty et al. 2005), foraging habitat may play a disproportionately important role in providing areas to promote fish growth. The population in this study did not appear to be distributed evenly in relation to resources. If improvements are made which enhance the suitability of downstream reaches to brook trout, such as the removal of barriers or reductions in

angling mortality, headwater brook trout populations may improve in quantity and fish size.

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Tables

Table 1. Physical features and number of fish species encountered for each site in the Middle Fork River watershed. The column titled ‘Limed’ refers to whether or not an active limestone treatment site existed above the site reach. If the site was not limed, water quality in the study reach retained the ability to hold young-of-the-year brook trout.

Site Name	Stream	Limed (Y/N)	Stream Class	Basin Area (km ²)	Mean Wetted Width (m)	Mean Bankful Width (m)	Mean pH	Mean Alkalinity (mg/l)	Observed Fish Species
Brush	Brush Run	N	Upstream	0.83	1.46	3.97	5.17	1.38	1
KittleLOW	Kittle Creek	Y	Downstream	15.38	4.77	9.36	6.27	6.30	8
KittleMID	Kittle Creek	Y	Midstream	5.26	2.44	5.89	6.30	5.33	4
KittleUP	Kittle Creek	Y	Upstream	2.05	2.19	3.98	6.73	15.78	2
Light	Light Run	N	Midstream	5.24	3.13	7.07	6.04	3.60	4
Mitchell	Mitchell Lick Fork	Y	Upstream	1.78	2.08	5.02	6.25	6.25	1
RockyLOW	Rocky Run	Y	Downstream	9.94	4.36	7.98	5.51	2.08	7
RockyUP	Rocky Run	Y	Midstream	6.44	3.76	9.14	5.42	1.68	1
Sugar	Sugar Drain	N	Upstream	1.64	2.42	5.36	6.47	8.05	2

Table 2. Dates of fish sampling in the Middle Fork River designated by month.

Sampling Period	Start date	End date
March 2004	3/13	3/20
May 2004	5/10	5/12
June 2004	6/13	6/16
July 2004	7/16	7/19
August 2004	8/16	8/18
September 2004	9/24	9/26
December 2004	12/2	12/5
March 2005	3/12	3/18
May 2005	5/9	5/11
June 2005	6/9	6/11
July 2005	7/12	7/13

Table 3. Energy densities by wet weight (WW) of brook trout removed from random sites during selected sampling periods. A subset of brook trout were removed in order to estimate energy density, a component of bioenergetics models.

Month	Energy Density (J g ⁻¹ WW)	SE
September04	4042	220
December04	4784	174
March05	4631	181
May05	3429	193
July05	4461	242

Table 4. Energy densities by dry weight (DW) of prey types encountered in brook trout stomachs (from Cummins and Wuycheck 1971).

Order	Stage	Energy Density (J g ⁻¹ DW)
Acarina	Adult	24318.1
Anura	Adult	6858.3
Aranae	Adult	20202.3
Blatteria	Adult	22835.9
Caudata	Adult	6858.3
Coleoptera	Adult	23263.0
Coleoptera	Larval	25721.2
Collembola	Adult	23263.0
Cypriniformes	Adult	30502.3
Decapoda	Adult	22249.7
Diplopoda	Adult	22145.0
Diptera	Adult	24213.4
Diptera	Larval	24818.3
Diptera	Pupa	24818.3
Ephemeroptera	Adult	22898.7
Ephemeroptera	Larval	22898.7
Gastropoda	Adult	8474.5
Hemiptera	Adult	23606.3
Homoptera	Adult	23606.3
Hymenoptera	Adult	19381.6
Hymenoptera	Larval	19381.6
Isopoda	Adult	18586.1
Lepidoptera	Adult	22835.9
Lepidoptera	Larval	22835.9
Mecoptera	Adult	22195.6
Megaloptera	Adult	22835.9
Megaloptera	Larval	22835.9
Neuroptera	Adult	22835.9
Odonata	Adult	21424.9
Odonata	Larval	21424.9
Oligochaetae	Adult	23342.5
Opiliones	Adult	22145.0
Orthoptera	Adult	22835.9
Plecoptera	Adult	20193.9
Plecoptera	Larval	22717.8
Psocoptera	Adult	22835.9
Salmiformes	Adult	19343.9
Scorpioniformes	Adult	16547.0
Thysanoptera	Adult	22835.9
Trichoptera	Adult	20930.8
Trichoptera	Larval	21040.0
Zoraptera	Adult	22835.9

Table 5. Designations of sampling periods into season for analyses of consumption estimates. Classifications were based on feeding intensity and temperature. Means within a column with different letters are significantly different following a square root transformation in order to approximate normality. Consumption estimates are in joules per gram wet weight of fish per day.

Season	Sampling Periods	Mean Temperature (°C)	Mean Consumption (J g ⁻¹ d ⁻¹)
Spring	May 2004	11.04	57.19 ^A
	June 2004	15.88	49.73 ^A
	May 2005	12.49	59.79 ^B
	June 2005	15.40	38.66 ^C
Summer/Fall	July 2004	16.20	16.91 ^{D,E}
	August 2004	18.02	18.62 ^{E,F}
	September 2004	14.37	20.99 ^D
	July 2005	16.87	22.95 ^D
Winter	March 2004	5.33	6.99 ^F
	December 2004	5.19	11.51 ^{E,F}
	March 2005	2.61	7.92 ^F

Table 6. Mean estimated consumption and maintenance ration (EMR) per month. T-test results of differences between square-root transformed EMR and consumption for each month are provided. The number of fish encountered with no food items present in the gut per month is provided (# empty).

Month	n	# Empty	EMR		Consumption		t	df	P
			Mean	SE	Mean	SE			
March04	76	2	12.03	0.14	6.99	0.84	-5.80	75	<0.0001
May04	87	0	10.75	0.16	57.19	8.08	5.74	86	<0.0001
June04	85	1	12.97	0.17	49.73	4.71	7.79	84	<0.0001
July04	88	7	18.32	0.65	16.91	2.59	-0.54	87	0.5910
August04	83	10	18.59	0.28	18.62	4.25	<0.01	82	0.9960
September04	84	3	15.09	0.45	20.99	2.69	2.19	83	0.0314
December04	77	4	11.59	0.14	11.51	1.19	-0.06	76	0.9499
March05	89	3	10.34	0.15	7.92	1.11	-2.21	88	0.0294
May05	90	0	11.86	0.18	59.79	4.11	11.60	89	<0.0001
June05	90	0	13.34	0.17	38.66	3.95	6.40	89	<0.0001
July05	90	4	19.22	0.28	22.95	4.03	0.93	89	0.3526

Table 7. Mean growth (G) and size-adjusted growth (Gi) across all elapsed time periods eligible for growth analysis. Means within each column with different letters are significantly different from each other.

Period of Elapsed Time	n	G (% d ⁻¹)	Gi (% d ⁻¹)
May04 to June04	77	0.419 ^A	0.1289 ^A
June04 to July04	41	-0.125 ^{B,C}	-0.0318 ^B
July04 to August04	26	-0.036 ^{B,C}	-0.0129 ^B
August04 to September04	23	0.003 ^{B,C}	0.0003 ^B
September04 to December04	23	-0.190 ^C	-0.0524 ^B
December04 to March05	84	0.022 ^B	0.0116 ^B
March05 to May05	88	0.382 ^A	0.1502 ^A
May05 to June05	110	0.330 ^A	0.1244 ^A
June05 to July05	122	-0.136 ^{B,C}	-0.0420 ^B

Table 8. Population estimates $\pm$ standard error (SE) of all fish and fish large enough to sample gut contents (110+ mm FL). Estimates for each 200 m stream section are combined across all sites per month.

Month	All Fish		110+ mm FL	
	Population	SE	Population	SE
August04	526	26.36	177	0.25
December04	345	6.56	133	0.00
July04	541	6.64	199	0.15
July05	549	6.32	234	4.29
June04	522	21.88	194	0.63
June05	513	13.75	257	2.66
March04	333	5.05	123	0.00
March05	353	10.71	163	0.16
May04	400	5.42	193	0.25
May05	385	5.18	192	1.21
September04	497	7.78	164	2.56

Table 9. ANOVA results table of square-root transformed consumption by site type with weight and temperature included as covariates.

Season	Effect	df	F-value	p
Spring	Overall model	4	6.39	<0.0001
	Site type	2	9.39	0.0001
	Weight	1	0.22	0.6364
	Temperature	1	4.35	0.0378
Summer/Fall	Overall model	4	8.31	<0.0001
	Site type	2	14.11	<0.0001
	Weight	1	3.57	0.0596
	Temperature	1	3.11	0.0786
Winter	Overall model	4	8.20	<0.0001
	Site type	2	8.50	0.0003
	Weight	1	3.63	0.0579
	Temperature	1	6.24	0.0131

Table 10. Mean consumption by site type for each season. Means with different letters within each season are significantly different from each other following a square-root transformation of consumption.

Season	Stream Classification	Mean Consumption (J g ⁻¹ d ⁻¹)	Standard Error
Spring	Downstream	58.03 ^A	5.47
	Midstream	62.95 ^A	6.01
	Upstream	39.42 ^B	3.01
Summer/Fall	Downstream	24.88 ^A	2.60
	Midstream	25.74 ^A	3.50
	Upstream	13.13 ^B	2.43
Winter	Downstream	8.89 ^A	1.38
	Midstream	5.61 ^B	0.79
	Upstream	11.12 ^A	1.03

Table 11. Results of Chi-Square analysis of variation in diet composition by energy. Comparisons were made based on significant differences in mean consumption by site type (see Table 10).

Season	Site Type Comparison	df	Likelihood Ratio	
			Chi-Square	p
Spring	Upstream * Midstream/Downstream	8	48300	<0.0001
Summer/Fall	Upstream * Midstream/Downstream	8	27741	<0.0001
Spring	Midstream * Upstream/Downstream	8	12120	<0.0001

Figures

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

Figure 2. Distribution of fish size by total length across seasons. The arrow highlights the point at which fish were considered large enough to sample gut contents.

Figure 3. Mean ($\pm 95\%$ confidence intervals) monthly estimated maintenance ration (EMR) and observed consumption values across all sites.

Figure 4. Proportions of fish eating above and below maintenance ration during each period of sampling.

Figure 5. Frequency histograms of fish consumption estimates for each season.

Figure 6. Mean ($\pm 95\%$ confidence intervals) total growth (G) and size-adjusted growth (G_i) observed during the duration of the study. Note that not all intervals of time are equal in duration.

Figure 7. Results of linear regression between monthly growth and mean consumption between corresponding growth intervals (top graph) and consumption at t_n (bottom graph).

Figure 8. Population ($\pm$ standard error) estimates of all fish and fish eligible for gut content analysis across all sampling periods. Estimates represent the population of all 200 m sites combined.

Figure 9. Fish densities as a function of basin area across all seasons. The upper graph illustrates fish eligible for gastric lavage (110mm+ FL); the bottom graph depicts all fish.

Figure 10. Results of linear regression analysis between monthly brook trout population change and mean consumption. The upper graph represents the size class of fish suitable for gastric lavage, the bottom graph represents all fish.

Figure 11. Mean consumption as a function of mean fish density during the summer and fall. Each point represents a site.

Figure 12. Distribution of energy sources by taxa between site types during each season. Comparisons were made based on significant differences in mean consumptions between site types (EPT=Ephemeroptera, Plecoptera, Trichoptera). Site types with black bars represent sites with significantly higher consumption rates.

Chapter 3: Temporal change in successful feeding of an Appalachian brook trout population.

Abstract- Salmonids in headwater systems exploit a variety of prey items during different seasons. During some periods of the year, brook trout (*Salvelinus fontinalis*) in Appalachia may experience stressful feeding conditions due to high temperatures and low food availability. Feeding parameters of a population of brook trout in central Appalachia were monitored over the course of two years in order to quantify overall feeding trends and to identify the importance of various prey items. Brook trout exhibited generalist feeding during all seasons. Prey diversity was lowest during the winter and peaked in the spring, though significant differences in diversity measures were observed within seasons and with months across years. Fish feeding above maintenance ration exploited a greater diversity of prey items than fish feeding below maintenance ration, suggesting that employing a generalist feeding pattern helps sustain individuals. Within each season specific prey taxa were exploited at significantly different rates by fish feeding above maintenance ration compared to those feeding below maintenance ration. Specifically, some terrestrial insect taxa contributed more energy to fish eating above maintenance ration during spring and summer. During fall and winter, large organisms, such as crayfish and vertebrate prey, contributed disproportionately more energy in fish feeding above maintenance ration. Findings in this study imply that terrestrial organisms are more important than aquatic organisms in sustaining brook trout populations during warmer months. Further, specific terrestrial taxa may be more important than others, and future examinations of headwater salmonid diets should consider taxonomic detail in terrestrial organisms and the relationship between terrestrial organisms and the riparian vegetation state.

Introduction

Lotic salmonids frequently inhabit environments of low productivity, such as headwater streams. Consequently, the quality and quantity of food intake may play an important role in shaping salmonid populations. The most frequently cited source of energy for salmonids in such ecosystems is the aquatic macroinvertebrate community (Allan 1980, Neveu 1999), which derives most energy from allochthonous sources in the surrounding watershed (Vannote et al. 1980). Such sources of energy often result in stream communities low in productivity and thus offer limited resources to higher trophic levels, such as stream fish (Cada et al. 1987). However, recent surveys in Japanese streams have indicated that terrestrial invertebrates may play a dominant role over aquatic sources in providing energy to salmonids (Nakano et al. 1999, Kawaguchi and Nakano 2001). This idea is not new to stream fish ecology, as Allan (1951) noted that terrestrial input to streams often allowed fish biomass to persist above the capacity provided by the aquatic prey community. Nevertheless, studies which examine the specific importance of individual prey taxa (either terrestrial or aquatic) to lotic salmonids during episodes of low prey availability are rare.

Brook trout (*Salvelinus fontinalis*) in Appalachia occupy environments of low productivity and populations may be shaped by feeding dynamics (Cada et al. 1987, Ensign et al. 1990). Particularly, feeding rates drop from spring to summer and brook trout may be subjected to prolonged periods of feeding at or below maintenance ration (Ensign et al. 1990, Sweka 2003, *Chapter 2* of this thesis). Studies of stream salmonids have concluded that drops in feeding rates during stressful times are caused by decreasing rates of drift (Ensign et al. 1990, de Crespín de Billy 2002). These periods have been

shown to affect brook trout population dynamics. Such episodes of low feeding rates may affect emigration, recruitment of fish into larger size classes, and mean growth rates (*Chapter 2*).

Bioenergetics models may be employed to elucidate details in feeding patterns. With a bioenergetics model, one may use variables such as fish size, temperature, and prey and predator energy densities to determine the minimal amount of energy required to maintain body weight (Elliot 1976, Sweka and Hartman 2001). This value is termed maintenance ration (C_{main}) and may be compared to an observed rate of daily ration (C_{24}), which is calculated using observed stomach contents and the gastric evacuation rate (Eggers 1977). Comparing C_{24} to C_{main} allows individual fish to be classified as eating either above or below maintenance ration (Hayward and Margraf 1987, McKinney and Speas 2001). Such comparisons allow analyses of dietary trends in fish eating above and below maintenance ration to make inferences on successful feeding strategy.

A detailed understanding of the feeding strategy of brook trout could improve our understanding of stream salmonid ecology. Particular prey organisms may be important in supporting fish during periods of low productivity or driving growth rates during periods of abundant food resources. Although considerable literature exists examining brook trout diet patterns, many examined only particular seasons and most categorized all terrestrial prey taxa into one group (Cada et al. 1987, Thonney and Gibson 1989, Ensign et al. 1990, Forrester et al. 1994, Bridcut and Giller 1995, Mookerji et al. 2004). However, when the taxonomic detail of terrestrial organisms is considered, studies have found that some taxa may be of particular importance while others negligible as energetic input to aquatic ecosystems (Wipfli and Gregovich 2002) or fish diet (Webster and

Hartman 2005). Objectives in this study were to: (1) determine the overall feeding strategy of brook trout over the course of the year in a central Appalachian watershed, (2) quantify the temporal differences in aquatic and terrestrial prey consumption, and (3) identify if the feeding patterns of fish feeding above maintenance ration differ from fish feeding less successfully.

Methods

Study Area

The study was conducted within the Middle Fork watershed, a north flowing tributary of the Tygart River in the central Appalachian Mountains of Randolph County, West Virginia. The majority of land cover within the watershed is that of secondary growth hardwood deciduous forest. All sites in the study are located in the southernmost extent of the watershed (Figure 1) and are of low order and high gradient. Nine-200 m sites were selected based on a number of criteria: each site contained a resident brook trout population, consistently supported age-0 brook trout (suggesting chemical conditions were suitable enough for spawning), and was devoid of fish barriers between other sites. Temperature regimens in these reaches are suitable for trout; temperature rarely exceeded 20°C through the duration of the study. The West Virginia Division of Natural Resources and the West Virginia Department of Environmental Protection have actively added limestone sand to riparian areas of streams within the watershed to remediate the effects of acid precipitation and acid mine drainage in the Middle Fork since the 1990's (WVDNR 2001). This process is commonly used in the region and successfully increases pH, restores fish communities, and increases invertebrate abundance (Clayton et al. 1998). Some sites selected in this study were not actively

treated with lime (Sugar Drain, Light Run and Brushy Run). However, each site without a limestone treatment retained the ability to support brook trout spawning and carry fish populations.

Fish diversity differed across sites but was typical of Appalachian headwater systems. The number of species encountered increased with stream size; however, in nearly all sites fish fauna was dominated by brook trout and mottled sculpin (*Cottus bairdi*). Other fish sampled include blacknose dace (*Rhynchithys obtusis*), longnose dace (*R. cataractae*), creek chub (*Semotilus atromaculatus*), white sucker (*Catostomus commersoni*), northern hogsucker (*Hypentelium nigricans*), and fantail darter (*Etheostoma flabellare*).

Fish and Habitat Sampling

Fish sampling occurred eleven times over the course of two years (Table 1). All sampling events were divided into four seasons based on similarities in mean consumption estimates and temperature for some statistical analyses (Table 2). Sampling was conducted between 0800 and 1600-hr and the order of sites to sample were randomly chosen during each day. A three-pass electrofishing procedure (Platts and Nelson 1988) was used to estimate fish populations within the 200 m section. Before sampling, block nets were placed at the top and bottom of each section to restrict fish movement in or out of sections during sampling. Sampling teams used an electrofishing unit (Smith-Root, DC, 60 hz, 500-750 V, Vancouver, WA) and dip nets to capture fish.

Following collection, fish were processed at a streamside station. All fish were immobilized with a clove oil and 95% ethanol solution. Brook trout were weighed to the nearest 0.5 g, and total length was taken to the nearest mm. A subset of 10 brook trout

per site per month was chosen for stomach content removal. Only fish >110 mm fork length were considered eligible for gut content removal due to gear restrictions; the tube used in flushing water into the gut was usually larger than the gape of fish below this size (7 mm diameter). However, the fish that were analyzed generally represented age 1-and older fish as is apparent in length frequency histograms (Figure 2). An attempt was made to collect an equal range of fish sizes to analyze for gut content at each site. Stomach contents were removed by directing a constant flow of stream water into the foregut until all items had been apparently collected (Twomey and Giller 1990). Gut items were filtered with a 250 μ m sieve and transferred to 95% ethanol. This process of collecting stomach contents has proven very effective in removing gut contents (Light et al. 1983) and analysis with the gear used in this study has found that the technique is acceptably efficient (Sweka 2003). A sample of 10 trout was randomly selected from sites, frozen, and kept for analysis of fish dry weight during select sampling periods. Dry weight estimates were needed in order to calculate an estimate of fish energy density, a necessary component of bioenergetics analyses conducted in this study (described below).

Laboratory Procedures

All prey items were identified to the Family level or the lowest taxonomic classification possible (Merritt and Cummins 1996, Borror et al. 1989). Extremely small organisms (<0.5 mm length) or organisms partially destroyed beyond identification to Family were classified to Order. The lengths of prey items were measured via an ocular micrometer to the nearest 0.1 mm; when lengths were unavailable head capsules widths were measured to the nearest 0.1 mm. Crayfish (*Cambarus bartonii*) carapace lengths

were measured rather than head capsule width or body length. The dry mass of each organism was estimated using published length- or head width-dry mass equations, with the exception of crayfish where a carapace-dry mass equation was used (Sample et al. 1993, Benke et al 1999, Johnston and Cunjak 1999, Sabo et al. 2002). Vertebrate food items, such as frogs, salamanders, and fish were dried at a temperature of 60° C for 48-hr to calculate dry weight. Each prey item was further classified as either aquatic or terrestrial, with aquatic organisms possessing a life stage with an obligate aquatic phase. Therefore, adult aquatic insects, such as Ephemeroptera, were classified as aquatic (Sweka 2003). Frozen brook trout were thawed, weighed to the nearest 0.1 g, and dried at a temperature of 60° C for 72-hr for dry weight and energy density analysis.

Estimates of Consumption and Daily Ration

Calculations were made to approximate brook trout maintenance ration and observed consumption. Both variables allowed analyses of trends in consumption and the comparison of feeding habits of fish eating above and below maintenance ration. Maintenance rations (in Joules per gram of fish wet weight per day) were calculated based on a bioenergetics model for brook trout (Hartman and Sweka 2001) and used fish weight, fish and prey energy densities, and observed water temperature as variables. Energy densities were calculated from either observed mean energy density in collected fish using dry weight-energy equation for Salmonidae (Hartman and Brandt 1995) or interpolated from energy densities taken before and after a given collection period. Mean fish energy density was assumed to be equal across sites during a given month (see Chapter 2 for fish energy density and temperature variables). Such variables were applied to the brook trout bioenergetics model and maintenance ration was calculated by

determining the energy required to maintain zero growth over the course of one day.

Each prey item was converted to energy using dry weight-energy equations (Cummins and Wuycheck 1971), and the total energy in the gut was summarized for each fish.

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

Statistical Analyses

In order to determine the overall feeding strategy of all fish during each season, a graphical method first proposed by Costello (1990) and later modified by Amundsen et al. (1996) was employed. With this analysis, percent frequency of occurrence ($\%F_i$) of a given prey item is calculated with the following equation:

$$\%F_i = (N_i / N) * 100$$

where N_i is the number of trout with prey i in their stomach and N is the total number of fish with food present in stomachs. This value is placed on the x-axis and plotted against prey-specific abundance ($\%P_i$):

$$\%P_i = (\sum S_i / \sum S_t) * 100$$

Where S_i is the energy of prey i in a stomach and S_t is the total energy content of stomachs that contain prey i . With a graph of all prey categories, inferences may be made on prey importance and variation in feeding strategy. All prey items were classified first into source (aquatic or terrestrial) and then taxonomic order. Prey categories that comprised simultaneously $<5\%$ by frequency of occurrence and $<5\%$ by prey-specific abundance were placed into an aquatic or terrestrial 'rare item' category. This graphical analysis was conducted for each season in order to quantify temporal trends in feeding strategy.

Measures of prey diversity within each fish were calculated in order to further quantify feeding strategy. While measures of diversity in diet studies have been criticized for failing to define 'high' diversity (Chipps and Garvey *in press*), diversity variables have been successfully employed in defining feeding strategies within a population (Bridcut and Giller 1995). Two diversity measures (each using family as the lowest taxa) were calculated for each stomach with food items present: total number of families and Shannon's reciprocal index ($1/D$, Krebs 1994). Means of both measures were calculated for each month and tested for differences between months using repeated measures analysis of variance (ANOVA) and Duncan's repeated measures post-hoc.

Consumption estimates by origin (aquatic or terrestrial) were calculated separately in order to determine if fish were deriving a majority of energy from either

source. Mean consumption values were calculated for both prey categories. A t-test was run on the means between aquatic and terrestrial consumption for each month to determine if one category was significantly higher than the other.

In order to determine if specific feeding strategies affected whether or not a fish was eating above or below maintenance ration, all fish with stomach contents present were classified as either above or below maintenance ration for use in several analyses. Fish were placed into the 'above maintenance ration' category if the observed consumption exceeded maintenance ration. The means of both diversity indices were calculated for both groups and tested for significant differences using a t-test within each season. Differences in consumption of specific prey items were tested between fish eating above and below maintenance ration. For this analysis, prey categories were derived by classifying all organisms first by origin (aquatic or terrestrial) and then by taxonomic Order. Because of the high diversity of prey exploited by brook trout, further categorization of prey items was necessary for analysis. Within each season, the highest four orders by count and the highest four by energy were selected for analysis. All remaining prey items that did not fall into the first eight prey categories were placed into a broad aquatic or terrestrial 'other' category. As a result, each prey item consumed by brook trout fell into one of ten categories defined by order and origin. The first eight prey categories selected (those not classified as 'other') represented between 80-95% of prey by count and energy within a season. While differences likely existed in the exploitation rates of different prey organisms between sites (*Chapter 2*), this study was concerned with the general nature of successfully feeding fish throughout the watershed. Therefore, differences in feeding rates between sites were not considered.

Statistical analyses were performed on proportional prey values as suggested by Somerton (1991). The proportional energy derived from each of the ten prey categories was calculated for each fish within a season. These proportions were first square-root and then arcsine transformed to approximate normality. A multivariate analysis of variance (MANOVA) was performed on the transformed proportions to test for differences in proportional prey exploitation between fish eating above and below maintenance ration. Because two groups were being compared, Hotelling's T^2 statistic was to determine if a statistical difference in exploitation existed between fish eating above and below maintenance ration. If such an overall significant difference existed, differences in exploitation rates of specific prey were tested. An empirical probability distribution was computed by randomly sorting all transformed proportions of a given prey item into equal sized samples as the original data and computing a t-statistic with 5000 repetitions. Following the randomization procedure, a t-test was performed on the transformed proportions of fish above and below maintenance ration. The t-statistic was then compared to the empirical probability distribution to determine significance. Because these tests were performed *a posteriori*, the α -level was adjusted using the Bonferroni correction. Ten prey categories per season were tested, consequentially, differences were considered significant at $\alpha=0.005$.

Results

Overall Feeding Strategy

The brook trout population typically exhibited a generalist feeding pattern with little variation between seasons (Figures 3 and 4). Most prey types fell on the low end of the prey-specific abundance scale. However, a few rare taxa dominated content when

consumed and consequentially scored high in prey-abundance for the particular fish that contained them. These were large food items, such as fish (cyprinids, cottids, and juvenile brook trout), salamanders (Caudata: Plethodontidae) and cockroaches (Blattaria). During each season a number of taxa were observed at high frequencies but did not consistently score high in abundance, such as beetles (Coleoptera) during the spring and caddisfly larvae (Trichoptera) during the winter. No single dominant taxa (high in both frequency and prey-specific abundance) emerged during any season. See Appendix A for detailed information of consumption by taxa.

Prey diversity varied significantly between and within seasons by both mean number of families ($df=10$, $F=66.5$, $p<0.0001$) and the reciprocal of Shannon's diversity index ($df=10$, $F=18.09$, $p<0.0001$, Table 3 and Figure 5). Diversity by both variables was highest during spring and lowest during winter. Both measures of diversity were occasionally significantly variable within seasons, and occasional significant differences existed between the same months of different years.

Consumption estimates by origin of prey varied significantly with seasonal change. Terrestrial prey consumption significantly exceeded aquatic prey consumption during all months aside from winter (Table 4 and Figure 6). Specifically, terrestrial prey consumption peaked in May and declined with the arrival of summer. During the winter months, terrestrial prey consumption fell to near zero and aquatic prey significantly exceeded terrestrial energy input. Over the course of the study, terrestrial prey consumption varied on a greater scale than aquatic prey consumption.

Strategy and Consumption in Relation to Maintenance Ration

Whether or not a fish consumed energy above maintenance ration was related to seasonal change and prey diversity variables. Fish feeding above maintenance ration represented the minority of individuals during all seasons except spring (Table 5). Measures of prey diversity per fish were significantly different between individuals eating above and below maintenance ration. Specifically, mean prey families per individual fish was significantly higher in fish eating above maintenance ration during all seasons (Table 6) while the reciprocal of Simpson's diversity index was significantly higher in fish eating above maintenance ration during the summer (Table 7).

The results of a MANOVA test on proportional prey by energy showed that during each season whether or not a fish was feeding above or below maintenance ration was significantly related to exploitation of particular prey taxa (Table 8). Differences between fish feeding above and below maintenance ration in particular prey exploitation rates varied with seasonal change (Table 9). Throughout spring, fish feeding above maintenance ration fed on a significantly higher proportion of terrestrial Coleoptera and significantly less terrestrial Hemiptera/Homoptera and aquatic Trichoptera. Fish feeding above maintenance ration through the summer fed on a significantly higher proportion of terrestrial Coleoptera and Lepidoptera. During fall, fish feeding above maintenance ration exploited terrestrial Lepidoptera at a significantly higher proportion. All fish that fed on crayfish were calculated as feeding above maintenance ration during the fall, preventing a statistical comparison of crayfish proportions between groups of fish. Vertebrate taxa (fish and salamanders) during the winter were consumed at a significantly higher proportion by fish eating above maintenance ration. Trichoptera dominated winter

consumption, contributing >50% of energetic input for both groups of fish, though no significant difference in Trichoptera exploitation existed between groups of fish.

Discussion

Temporal Strategy

Brook trout in the upper Middle Fork River exhibited generalist feeding across all sampled seasons despite a drop in available prey items during the winter. This contrasts observed strategies of other salmonid populations (Odenkirk and Estes 1991, Bridcut and Giller 1995, Wipfli 1997, Steingrimsson and Gislason 2002) including brook trout (Forrester et al. 1994), where a single or small number of prey taxa dominated diet by count and/or abundance. Other dietary studies have detected a more generalized feeding strategy (Allan 1981, Thonney and Gibson 1989). However, in most studies where terrestrial items appeared important, all such prey items were placed into a single category (Thonney and Gibson 1989, Forrester et al. 1994, Bridcut and Giller 1995). By categorizing all prey taxa with equivalent detail and observing diet shifts multiple times over the course of the year, observations in the current study suggest that the Middle Fork River brook trout population does not disproportionately feed on one particular prey order by weight and number during any season.

The examination of diversity in the current study allows limited, but potentially meaningful, comparisons to other studies. Prey diversity measures have received little attention in fish diet literature (Chipps and Garvey *in press*). While several papers have employed diversity to quantify diet (Tokeshi 1991, Bridcut and Giller 1995), the majority of dietary studies have reported varying levels of taxonomic detail. Salmonids may

exploit as few as three to five genera in a particular season (McKinney and Speas 1991, Odenkirk and Estes 1991, Steingrimsson and Gislason 2002, Steinhart and Wurtsbaugh 2003). Others have reported a greater number of prey taxa in salmonid diets (Allan 1980, Thonney and Gibson 1989, Ensign et al. 1991, Forrester et al. 1994, Bridcut and Giller 1995, Wipfli 1997, Mookerji 2004). Direct comparison of findings in the current study to these studies is difficult, as differences in taxonomic detail exist. However, those that did identify taxa beyond Order could quantify the majority of diet by seven to twelve families (Allan 1981, Hubert and Rhodes 1989, Bridcut and Giller 1995). Considering that Middle Fork River brook trout exploited a mean of fifteen families in one season, fish observed in the current study likely exploit a higher diversity of prey taxa than most observed salmonid populations.

Variation in diet patterns between years may distort conclusions made about salmonid feeding trends. While the majority of salmonid diet studies observed one season or multiple seasons across one year, few have examined diets over the course of more than one year (but see Sweka 2003 and Thorne 2004). In the current study, significant differences were observed in diversity variables during the same month between 2004 and 2005. Limiting the study to one year would have led to less detailed conclusions on variation in diversity. Such variation between years suggests that Appalachian brook trout dietary components may not be annually consistent and may be linked to yearly variations in insect activity.

Terrestrial prey seems to be more heavily exploited by Middle Fork River brook trout than aquatic prey throughout a majority of the year. Several dietary studies have found terrestrial food items to be important (Allan 1981, Forrester 1994, Bridcut and

Giller 1995), but studies showing terrestrial insects may significantly exceed aquatic prey sources in importance have been limited to Japanese streams (Kawaguchi and Nakano 2001, Kawaguchi et al. 2003) and one in central Appalachia (Sweka 2003). Findings in the current study show that terrestrial energy input consistently exceeds aquatic input during all but the winter months. Contrary to Japanese streams where terrestrial consumption peaked in summer (Kawaguchi et al. 2003), brook trout in the Middle Fork River consumed the largest amount of terrestrial energy during the spring and terrestrial insect consumption decreased as summer progressed yet remained greater than aquatic energy input.

Components of Successful Feeding

The dietary pattern employed by brook trout feeding above maintenance ration may explain why brook trout exhibit a generalist pattern. Fish feeding above maintenance ration contained a higher mean number of prey families per gut than those feeding below maintenance ration during each season. Therefore, exploiting a variety of prey types increased the chances of maintaining body weight during stressful times (summer) and increased the chances of growing during opportunistic conditions (spring). Exploitation of a range of prey organisms may increase the chances that one of the prey organisms is disproportionately large in size and therefore offers more energy. Considering the findings related to mean familial number, it is unclear why the diversity index was significantly different between fish eating above and below maintenance ration only during the summer. The summer months may be the most stressful to brook trout due to high temperatures and low food availability (Ensign et al. 1990, Sweka 2003,

Chapter 2). Consequently, adopting a strategy of high generalization may be particularly important during these months.

The significantly different energetic proportions of taxa found between fish eating above and below maintenance ration may highlight disproportionately important prey items. During warmer months, terrestrial organisms (terrestrial Coleoptera during both seasons and terrestrial Lepidoptera during the summer and fall) were exploited at higher rates by successful fish than by fish eating below maintenance ration. However, most other terrestrial organisms were not significantly different between both classes of fish and one terrestrial prey class (Hemiptera and Homoptera during the spring) were exploited at a higher rate in fish feeding below maintenance ration. Therefore, while terrestrial organisms exceed aquatic prey in terms of energetic input for brook trout, particular terrestrial organisms may play a dominant role in sustaining fish populations, while others offer comparatively little energetic benefit. This suggests that classifying all terrestrial insects into one group as in other salmonid taxonomic diet studies (Forrester et al. 1994, Bridcut and Giller 1995, Mookerji et al. 2004) may distort the true values of prey importance. One study that did consider terrestrial taxonomic detail is Webster and Hartman (2005), which found that certain terrestrial organisms may score higher in the index of relative importance (IRI) than others. Another study with terrestrial taxonomic detail (Allan 1981) found that non-native brook trout may specifically target Coleoptera in Colorado. Terrestrial Coleoptera were also considered the largest contributor of energy among terrestrial organisms to Alaskan streams (Wipfli and Gregovich 2002). The findings of the current study concur that particular terrestrial organisms, such as

Coleoptera and Lepidoptera, may be of disproportionate importance relative to all other prey items.

While brook trout consuming very large organisms (fish, salamanders, and crayfish) were usually found to be feeding above maintenance ration, these prey organisms were detected as significantly important only during the fall (where all fish consuming crayfish were feeding above maintenance ration) and winter (Vertebrata). This likely occurred due to the low rate at which these organisms were encountered. Therefore, while these organisms offer a substantial energy to brook trout capable of capturing them, such captures occur at such a low rate that the statistical method employed in the current study did not consistently detect them as exploited more significantly by fish feeding above maintenance ration during spring and summer. Such a finding may suggest that large organisms play a limited role in sustaining the over all population during some seasons. These findings contrast those of Thorne (2004), which found that vertebrate and crayfish prey dominated brook trout diet by weight. Differences between Thorne (2004) and the current study could have been attributed to a number of factors: energetic values were calculated differently between the studies, the current study sampled a larger number of fish, and Thorne (2004) included two large (30 and 41.7 km² basin area) mainstem reaches of a stream where brook trout consumed a disproportionate number of fish relative to smaller reaches. Nevertheless, in the current study crayfish and vertebrate prey were detected at higher proportions in fish eating above maintenance ration during fall and winter. Therefore, these large prey organisms may become increasingly important as terrestrial organisms become scarce during colder temperatures.

Despite taxonomic prey differences between fish eating above and below maintenance ration, other taxa (those not exploited at significantly different rates between groups of fish) did appear to be important prey to the Middle Fork brook trout population. For example, during the winter months, Trichoptera were exploited at very high rates by a majority of the fish. High rates of Trichoptera exploitation during the winter are common in lotic salmonids (Cunjak and Power 1987, Lehane et al. 2001, Sweka and Hartman 2001). While differences in Trichoptera exploitation were not significant between groups of fish, the high energetic contribution by Trichoptera implies that this particular taxa constitutes an important part of the diet during winter. Therefore, prey items that were not found to be exploited at significantly different rates between groups of fish should not be discarded as unimportant. Rather, items found in significantly higher rates in fish feeding above maintenance ration should be considered a component of successful feeding strategy along with a generalist pattern.

Over the course of the study, aquatic insects never emerged as contributing a greater amount of energy in fish feeding above maintenance ration. During spring, specialization on aquatic taxa seemed correlated with daily ration estimates below maintenance, as fish feeding above maintenance ration fed on significantly less Trichoptera (an aquatic insect). While aquatic insects provided a majority of energy during the winter, brook trout grow little and experience low rates of mortality once acclimated to cold water temperatures (Cunjak and Power 1987, *Chapter 2*). Therefore aquatic insects seem to play a minor role relative to terrestrial insects in shaping and sustaining brook trout populations in this Appalachian watershed. Most dietary studies of lotic salmonids focus taxonomic detail on aquatic insects and group all terrestrials into

one broad category (Cada et al. 1987, Forrester et al. 1994, Bridcut and Giller 1995, Mookerji et al. 2004). Findings in this study and others (Kawaguchi and Nakano 2001, Sweka 2003) imply that future diet studies of headwater stream salmonids should focus more attention on terrestrial organisms.

Management Implications

Findings in this study provide details on what constitutes successful feeding for an Appalachian headwater salmonid. Brook trout in the Middle Fork River appear to rely on terrestrial organisms for survival during stressful periods and growth during productive periods. Managers controlling brook trout populations may consider such organisms are disproportionately more important than aquatic insects. Such a concept implies that manipulating riparian zones to control terrestrial insects may have substantial effects on salmonid populations, as demonstrated in Nakano et al. (1999) and Kawaguchi and Nakano (2001). Select organisms in the terrestrial fauna may play a dominant role in sustaining or growing populations. Further, maintaining access to a broad range of prey items, both terrestrial and aquatic, seems to be important in providing necessary feeding conditions for brook trout.

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Tables

Table 1. Dates of fish sampling in the Middle Fork watershed designated by month.

Sampling Period	Start date	End date
March 2004	3/13	3/20
May 2004	5/10	5/12
June 2004	6/13	6/16
July 2004	7/16	7/19
August 2004	8/16	8/18
September 2004	9/24	9/26
December 2004	12/2	12/5
March 2005	3/12	3/18
May 2005	5/9	5/11
June 2005	6/9	6/11
July 2005	7/12	7/13

Table 2. Designations of sampling periods into seasonal categories for analyses of consumption estimates. Classifications into season were based on feeding intensity and temperature.

Season	Sampling Periods	Mean Temperature (°C)	Mean Consumption (J g ⁻¹ d ⁻¹)
Spring	May 2004	11.04	57.19
	June 2004	15.88	49.73
	May 2005	12.49	59.79
	June 2005	15.40	38.66
Summer	July 2004	16.20	16.91
	August 2004	18.02	18.62
	July 2005	16.87	22.95
Fall	September 2004	14.37	20.99
Winter	March 2004	5.33	6.99
	December 2004	5.19	11.51
	March 2005	2.61	7.92

Table 3. Mean and standard error (SE) of the reciprocal Shannon's diversity index (1/D) and the number of families observed per stomach for each month. Means with different letters within a column are significantly different following a square-root transformation.

	1/D		Families per stomach	
	Mean	SE	Mean	SE
March 04	6.26 ^{A,B}	1.28	5.19 ^A	0.39
May 04	8.43 ^C	0.90	9.44 ^B	0.50
June 04	17.63 ^D	1.93	9.86 ^B	0.62
July 04	9.37 ^C	1.36	4.65 ^{A,C,D}	0.31
August 04	5.75 ^{A,B}	0.80	4.28 ^{C,D}	0.35
September 04	5.52 ^{A,B}	0.60	5.60 ^A	0.35
December 04	4.17 ^B	0.55	3.85 ^D	0.23
March 05	3.90 ^B	0.39	3.76 ^D	0.21
May 05	11.84 ^E	1.30	14.73 ^E	0.57
June 05	12.07 ^E	1.34	9.52 ^B	0.50
July 05	8.15 ^{A,C}	0.95	5.69 ^C	0.39

Table 4. Mean and standard error (SE) of prey consumption ($\text{J g}^{-1} \text{d}^{-1}$) by source of prey for each month. Results of t-tests between mean aquatic and terrestrial consumption are provided.

Month	Aquatic		Terrestrial		df	t	p-value
	Mean	SE	Mean	SE			
March04	7.09	0.85	0.27	0.06	94	4.36	<0.0001
May04	9.72	1.42	51.10	8.00	165	-5.24	<0.0001
June04	11.46	1.63	40.59	4.64	161	-5.95	<0.0001
July04	4.34	0.92	16.51	3.07	139	-3.73	0.0003
August04	7.06	1.96	20.07	5.68	110	-2.10	0.0377
September04	4.58	1.34	19.23	2.70	140	-4.64	<0.0001
December04	11.55	1.18	2.06	0.83	92	4.21	<0.0001
March05	8.14	1.13	0.28	0.14	99	2.88	0.0048
May05	19.29	1.73	40.92	4.19	176	-4.74	<0.0001
June05	7.74	1.47	31.97	3.85	172	-5.84	<0.0001
July05	6.41	1.28	20.68	4.48	151	-3.08	0.0024

Table 5. Number of fish consuming energy above and below maintenance ration by count and percentage during each month.

Season	Month	n	Above Maintenance Ration		Below Maintenance ration	
			n	%	n	%
Spring	May 2004	87	67	77.01	20	22.99
	June 2004	84	67	79.76	17	20.24
	May 2005	90	87	96.67	3	3.33
	June 2005	90	62	68.89	28	31.11
Summer	July 2004	81	28	34.57	53	65.43
	August 2004	73	26	35.82	47	64.18
	July 2005	86	33	38.37	53	61.63
Fall	September 2004	81	37	45.68	44	54.32
Winter	March 2004	74	14	18.92	60	81.08
	December 2004	73	33	45.21	40	54.79
	March 2005	86	22	25.58	64	74.42

Table 6. Mean and standard error (SE) for number of prey families observed per fish for fish eating above and below maintenance ration during each season. Results of t-tests between means within a season are provided.

Season	Above		Below		df	T	p
	Mean	SE	Mean	SE			
Spring	12.01	0.33	6.41	0.40	349	8.03	<0.0001
Summer	6.55	0.39	3.99	0.20	232	6.50	<0.0001
Winter	5.30	0.38	3.79	0.17	231	4.23	<0.0001
Fall	6.41	0.58	4.93	0.41	79	2.14	0.0358

Table 7. Mean and standard error (SE) of the reciprocal Shannon's diversity index (1/D) for fish eating above and below maintenance ration during each season. Results of t-tests between means within a season are provided.

Season	Above		Below		df	T	p
	Mean	SE	Mean	SE			
Spring	12.52	0.78	12.09	1.82	349	0.23	0.8155
Summer	9.81	1.19	6.79	0.72	232	2.32	0.0215
Winter	4.38	0.77	4.88	0.58	231	-0.49	0.6241
Fall	5.56	0.79	5.49	0.89	79	0.06	0.9546

Table 8. Results of MANOVA tests of differences in prey proportion (by energy) between fish eating above and below maintenance ration.

Season	Categorical df	Den df	Hotelling's T	p-value
Spring	10	340	0.4104	<0.0001
Summer	10	223	0.2480	<0.0001
Fall	10	70	0.3609	0.0117
Winter	10	222	0.1416	0.0009

Table 9. Mean proportion of prey taxa in fish feeding above and below maintenance ration. Results of t-tests between mean proportions per taxa are provided. P-values with an asterisk denote a significant difference at the $\alpha=0.005$ level.

Season	Order	Origin (A/T)	Above		Below		df	T	p
			Mean	SE	Mean	SE			
Spring	Diptera	A	0.1197	0.0112	0.1392	0.0247	349	-0.30	0.7580
	Trichoptera	A	0.0192	0.0023	0.1249	0.0287	349	-6.07	<0.0001*
	Ephemeroptera	A	0.0327	0.0048	0.0543	0.0129	349	-1.44	0.1452
	Hemiptera/Homoptera	T	0.0059	0.0007	0.0393	0.0133	349	-3.98	<0.0001*
	Coleoptera	T	0.4327	0.0197	0.1816	0.0335	349	6.53	<0.0001*
	Diptera	T	0.0970	0.0088	0.1306	0.0283	349	-0.12	0.8968
	Hymenoptera	T	0.0523	0.0072	0.0617	0.0194	349	0.16	0.8660
	Plecoptera	A	0.0594	0.0083	0.0913	0.0202	349	-1.58	0.1108
	Other	A	0.0573	0.0098	0.1093	0.0268	349	-1.79	0.0178
	Other	T	0.1238	0.0141	0.0678	0.0217	349	2.38	0.0188
Summer	Coleoptera	T	0.2122	0.0332	0.1039	0.0186	232	3.45	0.0006*
	Diptera	A	0.0517	0.0158	0.0963	0.0174	232	-2.08	0.0382
	Diptera	T	0.1246	0.0255	0.1718	0.0241	232	-1.10	0.2668
	Hymenoptera	T	0.0802	0.0202	0.0709	0.0165	232	0.87	0.3944
	Trichoptera	A	0.0100	0.0041	0.0548	0.0143	232	-2.16	0.0266
	Lepidoptera	T	0.1923	0.0332	0.1033	0.0200	232	3.24	0.0020*
	Decapoda	A	0.1069	0.0300	0.0554	0.0160	232	1.70	0.0888
	Vertebrata	A	0.0436	0.0193	0.0358	0.0140	232	0.44	0.6538
	Other	A	0.0635	0.0156	0.1581	0.0240	232	-2.26	0.0224
	Other	T	0.1151	0.0256	0.1499	0.0218	232	-0.84	0.4032
Fall	Hemiptera/Homoptera	T	0.0662	0.0280	0.1697	0.0360	79	-2.51	0.0136
	Hymenoptera	T	0.0474	0.0170	0.1490	0.0347	79	-2.51	0.0122
	Lepidoptera	T	0.5496	0.0580	0.2833	0.0509	79	3.55	0.0006*
	Diptera	A	0.0186	0.0068	0.0290	0.0076	79	-0.81	0.4196
	Orthoptera	T	0.0514	0.0245	0.0432	0.0276	79	0.50	0.6260
	Vertebrata	A	0.0448	0.0319	0.0326	0.0237	79	0.17	0.8623
	Decapoda	A	0.0506	0.0339	0.0000	0.0000	79	-	-
	Coleoptera	T	0.0560	0.0279	0.0396	0.0205	79	0.74	0.4602
	Other	A	0.0409	0.0148	0.1065	0.0367	79	-1.33	0.1916
	Other	T	0.0747	0.0308	0.1470	0.0352	79	-1.75	0.0852
Winter	Trichoptera	A	0.5300	0.0400	0.6335	0.0270	231	-1.84	0.0678
	Ephemeroptera	A	0.0931	0.0216	0.1373	0.0189	231	-1.05	0.2906
	Plecoptera	A	0.1581	0.0354	0.0982	0.0162	231	1.68	0.0962
	Diptera	A	0.0570	0.0142	0.0547	0.0129	231	0.85	0.3718
	Vertebrata	A	0.0544	0.0239	0.0064	0.0049	231	2.95	0.0032*
	Coleoptera	A	0.0517	0.0160	0.0276	0.0094	231	1.94	0.0476
	Decapoda	A	0.0099	0.0077	0.0101	0.0051	231	0.09	0.9352
	Non-insect Arthropoda	T	0.0108	0.0072	0.0111	0.0056	231	0.46	0.6238
	Other	A	0.0194	0.0133	0.0081	0.0055	231	1.35	0.1687
	Other	T	0.0156	0.0073	0.0130	0.0037	231	0.85	0.8614

Figures

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

Figure 2. Length-frequency histogram of all fish captured in the Middle Fork watershed by season. The arrow indicates the size considered large enough to sample gut contents.

Figure 3. Feeding strategy of the Middle Fork brook trout population during spring and summer. Each point represents a prey type based on taxonomic order and origin (terrestrial or aquatic) for brook trout in the Middle Fork Watershed, West Virginia.

Figure 4. Feeding strategy of the Middle Fork brook trout population during fall and winter. Each point represents a prey type based on taxonomic order and origin (terrestrial or aquatic) for brook trout in the Middle Fork Watershed, West Virginia.

Figure 5. Mean ($\pm$ 95% CI) familial prey diversity (D^{-1}) and number of observed families in brook trout stomachs across all months.

Figure 6. Mean consumption ($\pm 95\%$ CI) by source of prey during each month.

Appendix A (Stomach contents): Summary of all food items recorded in brook trout diets by count and energy.

Season	Order	Family	Stage	Combined energy (J)	% of total energy	Count	% of total count
Summer/Fall	Aranae	spp.	adult	11893.02	1.7787	65	1.918
	Blattaria	Cryptoceridae	adult	5561.81	0.8318	1	0.030
	Caudata	Plethodontidae	adult	11158.46	1.6688	9	0.266
	Coleoptera	Bruchidae	adult	3.92	0.0006	1	0.030
		Buprestidae	adult	2176.86	0.3256	3	0.089
		Cantharidae	adult	1401.58	0.2096	23	0.679
		Carabidae	adult	18516.36	2.7693	25	0.738
		Cerambycidae	adult	4629.00	0.6923	8	0.236
		Chrysomelidae	adult	5804.58	0.8681	24	0.708
		Coccinellidae	adult	2898.14	0.4334	7	0.207
		Curculionidae	adult	977.66	0.1462	26	0.767
		Dytiscidae	adult	631.84	0.0945	6	0.177
		Dytiscidae	larvae	935.87	0.1400	5	0.148
		Elateridae	adult	6153.35	0.9203	18	0.531
		Elmidae	larvae	52.21	0.0078	4	0.118
		Gyrinidae	adult	7125.16	1.0656	5	0.148
		Gyrinidae	larvae	1302.46	0.1948	3	0.089
		Hydrophilidae	adult	253.79	0.0380	1	0.030
		Lycidae	adult	807.00	0.1207	4	0.118
		Mordellidae	adult	26.89	0.0040	1	0.030
		Mycetophagidae	adult	10.37	0.0016	2	0.059
		Noteridae	adult	5.09	0.0008	1	0.030
		Oedemeridae	adult	166.19	0.0249	1	0.030
		Pedilidae	adult	96.04	0.0144	1	0.030
		Pselaphidae	adult	3.40	0.0005	1	0.030
		Psephenidae	adult	8.02	0.0012	1	0.030
		Scarabaeidae	adult	19990.05	2.9897	17	0.502
		Scolytidae	adult	69.95	0.0105	8	0.236
		spp.	adult	4230.30	0.6327	41	1.210
		Staphylinidae	adult	595.85	0.0891	17	0.502
	Collembola	Isotomidae	adult	66.67	0.0100	3	0.089
		Sminthuridae	adult	3.24	0.0005	3	0.089
	Decapoda	Cambaridae	adult	59567.49	8.9089	35	1.033
	Diplopoda	spp.	adult	8260.38	1.2354	13	0.384
	Diptera	Anisopodidae	adult	63.15	0.0094	1	0.030
		Asilidae	adult	22490.50	3.3637	20	0.590
		Bombyliidae	adult	908.23	0.1358	6	0.177
		Ceratopogonidae	adult	341.99	0.0511	10	0.295
		Chironomidae	adult	9.54	0.0014	10	0.295
		Chironomidae	larvae	29.55	0.0044	18	0.531
		Dolichopodidae	adult	818.41	0.1224	30	0.885
		Drosophilidae	adult	475.72	0.0711	23	0.679
		Empididae	adult	8743.60	1.3077	276	8.144
		Empididae	larvae	6.02	0.0009	1	0.030
		Muscidae	adult	566.65	0.0847	12	0.354
		Mycetophilidae	adult	178.21	0.0267	9	0.266
		Ottidae	adult	47.22	0.0071	1	0.030
		Phoridae	adult	58.06	0.0087	8	0.236
		Pipunculidae	adult	82.71	0.0124	3	0.089

Appendix A continued

Season	Order	Family	Stage	Combined energy (J)	% of total energy	Count	% of total count
Summer/Fall	Diptera	Rhagionidae	adult	125.99	0.0188	1	0.030
		Scatopsidae	adult	25.31	0.0038	1	0.030
		Sciaridae	adult	88.09	0.0132	7	0.207
		Sciomyzidae	adult	22.78	0.0034	1	0.030
		Simuliidae	adult	9.14	0.0014	12	0.354
		Simuliidae	larvae	4.79	0.0007	1	0.030
		spp.	adult	16226.21	2.4268	190	5.606
		spp.	larvae	2947.43	0.4408	560	16.524
		spp.	pupae	80.68	0.0121	31	0.915
		Syrphidae	adult	180.35	0.0270	2	0.059
		Tachnidae	adult	380.36	0.0569	3	0.089
		Tephritidae	adult	114.89	0.0172	3	0.089
		Tipulidae	adult	7101.84	1.0621	20	0.590
		Tipulidae	larvae	754.28	0.1128	4	0.118
	Ephemeroptera	Ameletidae	larvae	198.34	0.0297	4	0.118
		Baetidae	adult	124.40	0.0186	10	0.295
		Baetidae	larvae	78.10	0.0117	9	0.266
		Ephemerellidae	larvae	522.83	0.0782	11	0.325
		Heptageniidae	adult	1236.23	0.1849	4	0.118
		Heptageniidae	larvae	2780.82	0.4159	18	0.531
		Potamanthidae	larvae	40.78	0.0061	3	0.089
		spp.	adult	806.57	0.1206	10	0.295
		spp.	larvae	1038.58	0.1553	14	0.413
	Hemiptera	Cydnidae	adult	156.28	0.0234	49	1.446
		Gerridae	adult	3160.88	0.4727	25	0.738
		Hydrometridae	adult	467.46	0.0699	4	0.118
		Lygaeidae	adult	27.86	0.0042	1	0.030
		Miridae	adult	1906.95	0.2852	8	0.236
		Pentatomidae	adult	3961.49	0.5925	4	0.118
		Reduviidae	adult	229.46	0.0343	2	0.059
		spp.	adult	11655.89	1.7432	23	0.679
		Achilidae	adult	294.82	0.0441	12	0.354
		Aphididae	adult	3015.87	0.4510	355	10.475
		Cercopidae	adult	348.74	0.0522	5	0.148
		Cicadellidae	adult	4402.63	0.6585	36	1.062
		Cixiidae	adult	274.52	0.0411	6	0.177
		Eriosomatidae	adult	67.05	0.0100	4	0.118
		Membracidae	adult	2144.72	0.3208	5	0.148
		spp.	adult	2432.65	0.3638	11	0.325
	Hymenoptera	Braconidae	adult	1993.67	0.2982	192	5.665
		Chrysidae	adult	12.00	0.0018	1	0.030
		Colletidae	adult	304.16	0.0455	1	0.030
		Diapriidae	adult	34.59	0.0052	6	0.177
		Eulophidae	adult	6.82	0.0010	2	0.059
		Formicidae	adult	14341.75	2.1449	243	7.170
		Halictidae	adult	515.97	0.0772	5	0.148
		Ichneumonidae	adult	579.75	0.0867	14	0.413
		Mymaridae	adult	1.14	0.0002	2	0.059
		Pompilidae	adult	47.39	0.0071	2	0.059

Appendix A continued

Season	Order	Family	Stage	Combined energy (J)	% of total energy	Count	% of total count
Summer/Fall	Hymenoptera	Pteromalidae	adult	4.60	0.0007	3	0.089
		spp.	adult	7080.60	1.0590	38	1.121
		spp.	larvae	4204.90	0.6289	2	0.059
		Tenthredinidae	adult	3082.01	0.4609	3	0.089
		Tiphiidae	adult	76.11	0.0114	2	0.059
		Vespidae	adult	9603.58	1.4363	6	0.177
	Isopoda	spp.	adult	11.48	0.0017	2	0.059
		Hepialidae	adult	1406.47	0.2103	1	0.030
		Oecophoridae	adult	10233.90	1.5306	1	0.030
		Pyralidae	adult	1854.53	0.2774	5	0.148
		spp.	adult	61357.07	9.1765	21	0.620
	Mecoptera	spp.	larvae	183440.14	27.4351	291	8.587
		Bittacidae	adult	382.32	0.0572	2	0.059
		Panorpidae	adult	3731.48	0.5581	12	0.354
	Megaloptera	Corylophidae	adult	55.65	0.0083	1	0.030
	Odonata	Petaluridae	larvae	309.30	0.0463	1	0.030
	Oligochaeta	spp.	adult	702.82	0.1051	1	0.030
	Opiliones	spp.	adult	708.42	0.1059	36	1.062
	Orthoptera	Acrididae	adult	3295.67	0.4929	3	0.089
		Gryllacrididae	adult	14925.45	2.2322	6	0.177
		spp.	adult	7974.34	1.1926	2	0.059
	Plecoptera	Tetrigidae	adult	617.46	0.0923	2	0.059
		Capniidae	adult	108.46	0.0162	1	0.030
		Capniidae	larvae	61.22	0.0092	1	0.030
		Chloroperlidae	adult	368.91	0.0552	2	0.059
		Chloroperlidae	larvae	109.60	0.0164	5	0.148
		Leuctridae	adult	1322.61	0.1978	15	0.443
		Leuctridae	larvae	127.93	0.0191	25	0.738
		Nemouridae	adult	378.59	0.0566	5	0.148
		Nemouridae	larvae	36.75	0.0055	10	0.295
		Peltoperlidae	larvae	132.36	0.0198	2	0.059
		Perlodidae	larvae	41.04	0.0061	2	0.059
		Pteronarcyidae	adult	693.89	0.1038	1	0.030
		Pteronarcyidae	larvae	2280.72	0.3411	4	0.118
		spp.	adult	72.35	0.0108	3	0.089
		spp.	larvae	64.02	0.0096	4	0.118
	Psocoptera	Psocidae	adult	40.70	0.0061	1	0.030
	Scorpaeniformes	Cottidae	adult	44451.93	6.6482	10	0.295
	Thysanoptera	spp.	adult	1.40	0.0002	1	0.030
	Trichoptera	Glossosomatidae	larvae	313.27	0.0469	8	0.236
		Hydropsychidae	adult	1004.85	0.1503	14	0.413
		Hydropsychidae	larvae	699.19	0.1046	19	0.561
		Lepidosomatidae	larvae	31.81	0.0048	2	0.059
		Limnephilidae	adult	1297.62	0.1941	12	0.354
		Limnephilidae	larvae	777.03	0.1162	12	0.354
		Philopotamidae	adult	34.26	0.0051	1	0.030
		Philopotamidae	larvae	683.06	0.1022	28	0.826
		Rhyacophilidae	larvae	691.53	0.1034	7	0.207
		spp.	adult	168.78	0.0252	3	0.089

Appendix A continued

Season	Order	Family	Stage	Combined energy (J)	% of total energy	Count	% of total count
Summer/Fall	Trichoptera	spp.	larvae	104.65	0.0157	2	0.059
	Total			668632.70		3389	
Spring	Anura	Hylidae	adult	3687.03	0.2042	1	0.011
	Aranae	spp.	adult	10726.88	0.5941	116	1.289
	Blattaria	Cryptocercidae	adult	40212.55	2.2272	6	0.067
	Caudata	Plethodontidae	adult	5876.88	0.3255	12	0.133
	Coleoptera	Anobiidae	adult	13.98	0.0008	1	0.011
		Buprestidae	adult	1713.59	0.0949	4	0.044
		Byrrhidae	adult	117.73	0.0065	8	0.089
		Cantharidae	adult	5204.88	0.2883	47	0.522
		Carabidae	adult	82606.26	4.5751	135	1.501
		Cerambycidae	adult	16369.75	0.9066	41	0.456
		Cerylonidae	adult	3.39	0.0002	1	0.011
		Chrysomelidae	adult	63348.27	3.5085	249	2.768
		Ciidae	adult	6.83	0.0004	2	0.022
		Cleridae	adult	559.89	0.0310	4	0.044
		Coccinellidae	adult	6932.82	0.3840	22	0.245
		Corylophidae	adult	27.90	0.0015	4	0.044
		Cucujidae	adult	226.07	0.0125	10	0.111
		Curculionidae	adult	5363.33	0.2970	169	1.879
		Dermestidae	adult	36.31	0.0020	1	0.011
		Dytiscidae	adult	719.39	0.0398	4	0.044
		Dytiscidae	larvae	609.98	0.0338	8	0.089
		Elateridae	adult	26548.85	1.4704	138	1.534
		Elmidae	adult	92.37	0.0051	1	0.011
		Elmidae	larvae	395.50	0.0219	4	0.044
		Eucnemidae	adult	366.53	0.0203	4	0.044
		Gyrinidae	adult	417.02	0.0231	1	0.011
		Gyrinidae	larvae	349.28	0.0193	1	0.011
		Helodidae	adult	7.18	0.0004	2	0.022
		Hydrophilidae	adult	703.77	0.0390	12	0.133
		Lathridiidae	adult	34.78	0.0019	6	0.067
		Lucanidae	adult	11002.09	0.6093	30	0.333
		Lyctidae	adult	2004.36	0.1110	1	0.011
		Melandryidae	adult	121.30	0.0067	2	0.022
		Mordellidae	adult	34.30	0.0019	1	0.011
		Mycetophagidae	adult	88.76	0.0049	5	0.056
		Nosodendridae	adult	25.20	0.0014	1	0.011
		Noteridae	adult	810.16	0.0449	8	0.089
		Phalacridae	adult	57.75	0.0032	1	0.011
		Pselaphidae	adult	247.63	0.0137	16	0.178
		Ptiliidae	adult	6.00	0.0003	2	0.022
		Rhizophagidae	adult	145.95	0.0081	18	0.200
		Rhysodidae	adult	161.12	0.0089	1	0.011
		Salpingidae	adult	12.85	0.0007	2	0.022
		Scarabaeidae	adult	726166.24	40.2186	286	3.179
		Scolytidae	adult	5081.52	0.2814	268	2.979
		spp.	adult	16168.87	0.8955	143	1.590
		Staphylinidae	adult	13780.46	0.7632	208	2.312

Appendix A continued

Season	Order	Family	Stage	Combined energy (J)	% of total energy	Count	% of total count
Spring	Coleoptera	Tenebrionidae	adult	1577.71	0.0874	3	0.033
		Collembola	adult	115.49	0.0064	21	0.233
	Collembola	Sminthuridae	adult	209.25	0.0116	29	0.322
		spp.	adult	30.16	0.0017	3	0.033
		Cypriniformes	adult	131.16	0.0073	1	0.011
	Decapoda	Cambaridae	adult	42304.91	2.3431	52	0.578
	Diplopoda	spp.	adult	68274.55	3.7814	32	0.356
	Diptera	Anisopodidae	adult	99.82	0.0055	2	0.022
		Anthomyzidae	adult	49.08	0.0027	1	0.011
		Asilidae	adult	20744.84	1.1490	28	0.311
		Bibionidae	adult	3620.97	0.2005	29	0.322
		Bombyliidae	adult	82.49	0.0046	1	0.011
		Cecidomyiidae	adult	78.70	0.0044	3	0.033
		Ceratopogonidae	adult	1874.84	0.1038	42	0.467
		Chironomidae	adult	21.58	0.0012	39	0.434
		Chironomidae	larvae	97.65	0.0054	45	0.500
		Dolichopodidae	adult	1700.37	0.0942	58	0.645
		Drosophilidae	adult	168.57	0.0093	13	0.145
		Empididae	adult	90432.84	5.0086	1802	20.031
		Empididae	larvae	277.39	0.0154	34	0.378
		Heleomyzidae	adult	63.48	0.0035	4	0.044
		Muscidae	adult	943.31	0.0522	29	0.322
		Mycetophilidae	adult	1900.10	0.1052	110	1.223
		Phoridae	adult	202.37	0.0112	26	0.289
		Pipunculidae	adult	93.61	0.0052	4	0.044
		Rhagionidae	adult	9647.20	0.5343	38	0.422
		Scatopsidae	adult	79.59	0.0044	2	0.022
		Sciaridae	adult	1752.53	0.0971	92	1.023
		Sciomyzidae	adult	2701.04	0.1496	28	0.311
		Simuliidae	adult	67.00	0.0037	53	0.589
		Simuliidae	larvae	66.54	0.0037	20	0.222
		spp.	adult	88542.46	4.9039	649	7.214
		spp.	larvae	982.62	0.0544	826	9.182
		spp.	pupae	852.97	0.0472	73	0.811
		Stratiomyidae	adult	268.67	0.0149	2	0.022
		Syrphidae	adult	6377.50	0.3532	31	0.345
		Tabanidae	adult	194.60	0.0108	3	0.033
		Tephritidae	adult	167.98	0.0093	5	0.056
		Therevidae	adult	85.41	0.0047	1	0.011
		Tipulidae	adult	20922.66	1.1588	167	1.856
		Tipulidae	larvae	14832.53	0.8215	24	0.267
		Xylophagidae	adult	386.14	0.0214	5	0.056
	Ephemeroptera	Ameletidae	larvae	1118.54	0.0620	20	0.222
		Baetidae	adult	639.21	0.0354	33	0.367
		Baetidae	larvae	962.77	0.0533	78	0.867
		Ephemerellidae	adult	104.53	0.0058	3	0.033
		Ephemerellidae	larvae	2393.63	0.1326	43	0.478
		Heptageniidae	adult	340.31	0.0188	2	0.022
		Heptageniidae	larvae	15048.76	0.8335	121	1.345

Appendix A continued

Season	Order	Family	Stage	Combined energy (J)	% of total energy	Count	% of total count
Spring	Ephemeroptera	Potamanthidae	larvae	178.15	0.0099	6	0.067
		spp.	adult	3971.15	0.2199	42	0.467
		spp.	larvae	5022.06	0.2781	35	0.389
	Gastropoda	spp.	adult	1.13	0.0001	4	0.044
	Hemiptera	Acanthosomatidae	adult	132.36	0.0073	1	0.011
		Cydnidae	adult	2288.00	0.1267	278	3.090
		Gerridae	adult	5422.35	0.3003	25	0.278
		Lygaeidae	adult	85.32	0.0047	4	0.044
		Miridae	adult	85.10	0.0047	3	0.033
		Pentatomidae	adult	19882.72	1.1012	8	0.089
		Reduviidae	adult	36.93	0.0020	3	0.033
		spp.	adult	745.04	0.0413	10	0.111
		Veliidae	adult	8.46	0.0005	3	0.033
	Homoptera	Aphididae	adult	245.87	0.0136	50	0.556
		Cercopidae	adult	103.06	0.0057	3	0.033
		Cicadellidae	adult	4010.48	0.2221	112	1.245
		Cixiidae	adult	255.52	0.0142	9	0.100
		Delphacidae	adult	21.18	0.0012	1	0.011
		Eriosomatidae	adult	1.72	0.0001	1	0.011
		spp.	adult	508.11	0.0281	21	0.233
	Hymenoptera	Andrenidae	adult	217.05	0.0120	1	0.011
		Anthophoridae	adult	416.03	0.0230	3	0.033
		Apidae	adult	4938.41	0.2735	3	0.033
		Braconidae	adult	1070.98	0.0593	80	0.889
		Colletidae	adult	9291.29	0.5146	11	0.122
		Cynipidae	adult	26.06	0.0014	5	0.056
		Diapriidae	adult	74.61	0.0041	19	0.211
		Encyrtidae	adult	2.53	0.0001	1	0.011
		Eucoilidae	adult	126.35	0.0070	5	0.056
		Eulophidae	adult	231.25	0.0128	9	0.100
		Eurytomidae	adult	3.89	0.0002	1	0.011
		Formicidae	adult	18081.36	1.0014	251	2.790
		Heloridae	adult	2.68	0.0001	1	0.011
		Ichneumonidae	adult	1553.81	0.0861	28	0.311
		Megachilidae	adult	468.42	0.0259	3	0.033
		Mymaridae	adult	39.64	0.0022	15	0.167
		Pompilidae	adult	366.19	0.0203	1	0.011
		Pteromalidae	adult	23.42	0.0013	11	0.122
		Sphecidae	adult	55.79	0.0031	1	0.011
		spp.	adult	49419.44	2.7371	95	1.056
		Tenthredinidae	adult	564.78	0.0313	15	0.167
		Tiphiidae	adult	402.42	0.0223	4	0.044
		Vespidae	adult	472.43	0.0262	3	0.033
	Isopoda	spp.	adult	30.45	0.0017	1	0.011
	Lepidoptera	Psychidae	adult	692.48	0.0384	1	0.011
		Pyalidae	adult	6037.78	0.3344	19	0.211
		spp.	adult	4238.50	0.2347	9	0.100
		spp.	larvae	62554.73	3.4646	151	1.679
	Mecoptera	Bittacidae	adult	238.89	0.0132	1	0.011

Appendix A continued

Season	Order	Family	Stage	Combined energy (J)	% of total energy	Count	% of total count
Spring	Mecoptera	Panorpidae	adult	1193.22	0.0661	6	0.067
	Neuroptera	Coniopterygidae	adult	2.36	0.0001	10	0.111
	Odonata	Gomphidae	adult	4704.41	0.2606	1	0.011
		Gomphidae	larvae	2210.57	0.1224	3	0.033
		spp.	larvae	281.19	0.0156	1	0.011
	Oligochaeta	spp.	adult	761.10	0.0422	3	0.033
	Opiliones	spp.	adult	169.34	0.0094	15	0.167
	Orthoptera	Acrididae	adult	11538.96	0.6391	10	0.111
		Gryllacrididae	adult	201.25	0.0111	1	0.011
		spp.	adult	5407.36	0.2995	2	0.022
	Plecoptera	Tetrigidae	adult	371.08	0.0206	1	0.011
		Capniidae	larvae	306.92	0.0170	3	0.033
		Chloroperlidae	adult	2109.41	0.1168	10	0.111
		Chloroperlidae	larvae	1158.50	0.0642	36	0.400
		Leuctridae	adult	10457.40	0.5792	74	0.823
		Leuctridae	larvae	409.01	0.0227	41	0.456
		Nemouridae	adult	2262.57	0.1253	17	0.189
		Nemouridae	larvae	327.91	0.0182	63	0.700
		Peltoperlidae	adult	219.27	0.0121	1	0.011
		Peltoperlidae	larvae	1479.31	0.0819	14	0.156
		Perlidae	adult	815.59	0.0452	1	0.011
		Perlidae	larvae	902.25	0.0500	5	0.056
		Perlodidae	adult	1030.94	0.0571	3	0.033
		Perlodidae	larvae	2487.95	0.1378	28	0.311
		Pteronarcyidae	adult	32237.31	1.7855	25	0.278
		Pteronarcyidae	larvae	21280.42	1.1786	16	0.178
		spp.	adult	644.43	0.0357	12	0.133
		spp.	larvae	1414.37	0.0783	34	0.378
		Taeniopterygidae	adult	505.51	0.0280	3	0.033
		Taeniopterygidae	larvae	151.01	0.0084	15	0.167
	Scorpaeniformes	Cottidae	adult	18650.15	1.0329	6	0.067
	Thysanoptera	Heterothripidae	adult	4.34	0.0002	1	0.011
		Phlaeothripidae	adult	2.63	0.0001	1	0.011
	Trichoptera	Brachycentridae	adult	12.98	0.0007	1	0.011
		Georyssidae	adult	109.74	0.0061	3	0.033
		Georyssidae	larvae	42.14	0.0023	1	0.011
		Glossosomatidae	adult	41.56	0.0023	1	0.011
		Glossosomatidae	larvae	30.10	0.0017	3	0.033
		Hydropsychidae	adult	955.10	0.0529	17	0.189
		Hydropsychidae	larvae	4800.32	0.2659	78	0.867
		Lepidosomatidae	larvae	70.54	0.0039	4	0.044
		Limnephilidae	adult	2281.36	0.1264	46	0.511
		Limnephilidae	larvae	5527.02	0.3061	141	1.567
		Philopotamidae	adult	277.21	0.0154	4	0.044
		Philopotamidae	larvae	1091.23	0.0604	64	0.711
		Phryganeidae	adult	380.15	0.0211	1	0.011
		Phryganeidae	larvae	414.60	0.0230	4	0.044
		Polycentropodidae	larvae	15.05	0.0008	1	0.011
		Rhyacophilidae	adult	182.31	0.0101	2	0.022

Appendix A continued

Season	Order	Family	Stage	Combined energy (J)	% of total energy	Count	% of total count
Spring	Trichoptera	Rhyacophilidae	larvae	1984.79	0.1099	17	0.189
		spp.	adult	3578.04	0.1982	30	0.333
		spp.	larvae	481.24	0.0267	8	0.089
		Uenoidae	larvae	102.24	0.0057	3	0.033
	Zoraptera	Zorotypidae	adult	0.25	0.0000	1	0.011
Winter	Total			1805546.37		8996	
	Acarina	spp.	adult	3.18	0.0014	1	0.054
	Aranae	spp.	adult	802.32	0.3611	21	1.133
	Caudata	Plethodontidae	adult	3729.55	1.6787	5	0.270
	Coleoptera	Carabidae	adult	22.22	0.0100	1	0.054
		Curculionidae	adult	47.18	0.0212	2	0.108
		Dytiscidae	larvae	7330.89	3.2997	15	0.809
		Erotylidae	adult	34.29	0.0154	1	0.054
		Georyssidae	larvae	114.38	0.0515	1	0.054
		Gyrinidae	larvae	1192.04	0.5365	1	0.054
		Pselaphidae	adult	8.88	0.0040	1	0.054
		Scolytidae	adult	17.07	0.0077	1	0.054
		spp.	adult	648.34	0.2918	6	0.324
		Staphylinidae	adult	202.56	0.0912	7	0.378
		Isotomidae	adult	30.99	0.0140	11	0.593
		Sminthuridae	adult	29.64	0.0133	7	0.378
	Decapoda	Cambaridae	adult	1995.95	0.8984	7	0.378
	Diptera	Cecidomyiidae	adult	51.66	0.0233	2	0.108
		Ceratopogonidae	adult	195.70	0.0881	8	0.431
		Chironomidae	adult	4.73	0.0021	6	0.324
		Chironomidae	larvae	66.86	0.0301	40	2.157
		Drosophilidae	adult	5.18	0.0023	1	0.054
		Empididae	larvae	4.46	0.0020	1	0.054
		Mycetophilidae	adult	52.90	0.0238	1	0.054
		Phoridae	adult	6.34	0.0029	1	0.054
		Sciaridae	adult	44.52	0.0200	3	0.162
		Simuliidae	adult	1.20	0.0005	1	0.054
		Simuliidae	larvae	107.25	0.0483	13	0.701
		spp.	adult	15.75	0.0071	2	0.108
		spp.	larvae	97.46	0.0439	3	0.162
		spp.	pupae	0.64	0.0003	1	0.054
		Tipulidae	larvae	8776.12	3.9502	25	1.348
		Xiphocentronidae	adult	33.79	0.0152	1	0.054
	Ephemeroptera	Ameletidae	larvae	388.21	0.1747	13	0.701
		Baetidae	larvae	403.62	0.1817	29	1.564
		Ephemerellidae	larvae	2928.06	1.3179	25	1.348
		Heptageniidae	larvae	15595.84	7.0198	88	4.746
		Isotomidae	larvae	32.80	0.0148	3	0.162
		Leptophlebiidae	larvae	17.46	0.0079	1	0.054
		Potamanthidae	larvae	834.18	0.3755	2	0.108
		spp.	larvae	240.80	0.1084	5	0.270
	Hemiptera	Gerridae	adult	1094.03	0.4924	6	0.324
		spp.	adult	3.95	0.0018	1	0.054
	Homoptera	Aphididae	adult	2.72	0.0012	1	0.054

Appendix A continued

Season	Order	Family	Stage	Combined energy (J)	% of total energy	Count	% of total count
Winter	Homoptera	Cicadellidae	adult	20.91	0.0094	1	0.054
		Psyllidae	adult	5.86	0.0026	1	0.054
	Hymenoptera	Andrenidae	adult	361.52	0.1627	1	0.054
		Formicidae	adult	71.47	0.0322	3	0.162
		Ichneumonidae	adult	17.36	0.0078	1	0.054
	Lepidoptera	spp.	larvae	22.87	0.0103	3	0.162
	Megaloptera	Corylophidae	larvae	1681.11	0.7567	1	0.054
	Odonata	Gomphidae	larvae	845.36	0.3805	3	0.162
	Oligochaeta	spp.	adult	470.27	0.2117	2	0.108
	Plecoptera	Capniidae	adult	2462.36	1.1083	29	1.564
		Capniidae	larvae	393.43	0.1771	7	0.378
		Chloroperlidae	larvae	96.70	0.0435	5	0.270
		Leuctridae	adult	120.96	0.0544	1	0.054
		Leuctridae	larvae	269.14	0.1211	39	2.104
		Nemouridae	adult	1126.62	0.5071	9	0.485
		Nemouridae	larvae	169.56	0.0763	21	1.133
		Peltoperlidae	larvae	371.16	0.1671	8	0.431
		Perlodidae	larvae	2521.49	1.1349	34	1.834
		Pteronarcyidae	larvae	29635.01	13.3389	11	0.593
		spp.	adult	473.56	0.2132	18	0.971
		spp.	larvae	265.33	0.1194	14	0.755
		Taeniopterygidae	adult	348.57	0.1569	3	0.162
		Taeniopterygidae	larvae	373.12	0.1679	21	1.133
	Salmoniformes	Salmonidae	adult	25077.48	11.2875	2	0.108
	Scorpaeniformes	Cottidae	adult	3600.47	1.6206	2	0.108
	Trichoptera	Brachycentridae	adult	338.29	0.1523	3	0.162
		Brachycentridae	larvae	1878.82	0.8457	15	0.809
		Georyssidae	larvae	218.79	0.0985	4	0.216
		Glossosomatidae	larvae	26.47	0.0119	1	0.054
		Helicopsychidae	adult	31.75	0.0143	1	0.054
		Helicopsychidae	larvae	318.18	0.1432	1	0.054
		Hydropsychidae	larvae	2061.85	0.9281	41	2.211
		Lepidosomatidae	larvae	1297.10	0.5838	25	1.348
		Limnephilidae	adult	5902.11	2.6566	136	7.335
		Limnephilidae	larvae	58821.67	26.4759	524	28.263
		Philopotamidae	adult	12432.07	5.5957	202	10.895
		Philopotamidae	larvae	498.07	0.2242	18	0.971
		Phryganeidae	larvae	2995.20	1.3482	8	0.431
		Polycentropodidae	larvae	62.85	0.0283	3	0.162
		Rhyacophilidae	larvae	250.09	0.1126	7	0.378
		spp.	adult	8433.75	3.7961	165	8.900
		spp.	larvae	8585.83	3.8645	89	4.800
	Total			222170.31		1854	

Appendix B (Fish species in each site): Fish species captured in each site over the course of the study. All sites contained brook trout; if brook trout was the only fish species encountered it is noted on the table. Scientific and common names are provided.

Site name	Scientific name	Common name
Brushy Run	Brook trout only	-
KittleLOW	<i>Catostomus commersoni</i>	White sucker
	<i>Cottus bairdi</i>	Mottled Sculpin
	<i>Etheostoma flabellare</i>	Fantail darter
	<i>Hypentelium nigricans</i>	Northern hogsucker
	<i>Rhinichthys cataractae</i>	Longnose dace
	<i>Rhinichthys obtusis</i>	Blacknose dace
	<i>Semotilus atromaculatus</i>	Creek chub
KittleMID	<i>Cottus bairdi</i>	Mottled Sculpin
	<i>Rhinichthys cataractae</i>	Longnose dace
KittleUP Light	<i>Cottus bairdi</i>	Mottled Sculpin
	<i>Cottus bairdi</i>	Mottled Sculpin
	<i>Rhinichthys cataractae</i>	Longnose dace
	<i>Rhinichthys obtusis</i>	Blacknose dace
	<i>Semotilus atromaculatus</i>	Creek chub
Mitchell	<i>Cottus bairdi</i>	Mottled Sculpin
RockyLOW	<i>Catostomus commersoni</i>	White sucker
	<i>Cottus bairdi</i>	Mottled Sculpin
	<i>Hypentelium nigricans</i>	Northern hogsucker
	<i>Rhinichthys cataractae</i>	Longnose dace
	<i>Rhinichthys obtusis</i>	Blacknose dace
	<i>Semotilus atromaculatus</i>	Creek chub
RockyUP	Brook trout only	-
Sugar	<i>Cottus bairdi</i>	Mottled Sculpin

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Curriculum vitae

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Education

West Virginia University (WVU), Morgantown, WV: M.S. in Fisheries Resources,
graduation date: December 2005

- Master's Thesis: Temporal trends in consumption, growth and successful feeding traits of a central Appalachian brook trout population at the watershed scale

Advisor: Dr. Kyle Hartman

Pertinent Coursework: Fisheries Management, Statistics (x2), Fish Ecology, GIS, Fish Physiology, Advanced Ichthyology, Quantitative Ecology, Limnology

Total Credits: 40 currently, 52 expected (semester system), current GPA 4.00

University of Miami (UM), Coral Gables, FL: B.S. in Biology

Pertinent Coursework: Ecology, Genetics, Tropical Field Biology, Chemical Oceanography, Biometrics, Aquaculture, Marine Biology, Organic Chemistry (x2), Calculus (x2)

Total Credits: 116 (semester system), final GPA: 3.80

Professional Experience

Graduate Research Assistant, WVU, Morgantown, WV May '04-Present

- Included personal research, research for collaborative long-term project, and assisting other graduate students with field work.

Duties involved: backpack electrofishing, BVET habitat analysis, stomach lavage (brook trout), elastomer tagging, insect identification, sediment analysis, larval fish trapping, organizing & leading field crew, data entry and analysis

Work Load: Minimum 20 hrs/week, usually 40+. Salary of ~\$820/month

Supervisor: Dr. Kyle Hartman

Graduate Teaching Assistant, WVU, Morgantown, WV Aug '03-May'04

- Included overseeing four introductory biology labs.

Duties Involved: Preparation of teaching material, lecturing, instruction and assistance with basic lab techniques (microscopy, bacteria culture, etc.), evaluation of student work

Work Load: Minimum 20hrs/week, usually ~30. Salary of ~\$960/month

Supervisor: Dr. Jane Caldwell

Undergraduate Research Assistant/Intern, UM, Turrialba, Costa Rica June-Aug '02

- Included assisting doctoral candidate with her research at the Centro Agronomo Tropical de Investigación y Enseñanza (CATIE)

Duties Involved: Assisting with experimental design/implementation, soil collection, plant maintenance, mycorrhizal fungus identification (in lab)

Work Load: ~40 hours/week. No paid salary (housing and meals provided)

Supervisors: Drs. Michelle Schroeder and Dave Janos

Volunteer Experience

Earthwatch Volunteer, Mindo, Ecuador July 2000

- Involved assisting with field work for several projects

Duties Involved: Mist netting (birds), vegetation surveys

Supervisor: Dr. Dusty Becker (Kansas State University)

Earthwatch Volunteer, Tanjung Puting National Park, Indonesia July 1999

- Involved assisting with field work for several projects

Duties Involved: DBH on forest trees, primate surveys

Supervisor: Dr. Carey Yeager (University of Florida)

Skills and Qualifications

Computer Skills

Familiar with the following software: SAS, SPSS, NTSys, MARK, CAPTURE, ArcGIS, Fish Bioenergetics, ProCite, Microsoft Access, Excel, Word, and Powerpoint

Written and Oral Communication

Public research presentations, poster presentations, formal seminar presentations

SCUBA-Advanced Certified

Certified CPR and First Aid

Professional Affiliations

American Fisheries Society

Member of national chapter since 2003

Member of WV chapter since 2003

Member WVU student chapter since 2003

American Institute of Fishery Research Biologists

Member since 2005

Honors and Awards

Best Student Presenter- February 2005 Joint Meeting of American Fisheries Society, Society of American Foresters, and The Wildlife Society (West Virginia State Chapters)

Graduated with General Honors- UM May 2003

- Awarded to students graduating after completing at least 20 credits of honors level classes and with a cumulative GPA of 3.6 or higher

Graduated Cum Laude- UM May 2003

Various Academic Lists- UM (August 1999 to May 2003)

- President's List (1/7 semesters)
- Provost's List (4/7 semesters)
- Dean's List (6/7 semesters)

George Merrick Scholarship- August 1999 to May 2003

- Awarded to students entering UM with academic achievement, continued through degree pending GPA

Public Presentations

Utz, R. M. and K. J. Hartman. 2005. Patterns of spatial and temporal feeding ecology of a mid-Appalachian brook trout population. East Coast Trout Management and Culture Workshop IV. Lock Haven, PA. June 7, 2005.

Utz, R.M., and K. J. Hartman. 2005. Patterns of spatial and temporal feeding ecology of a mid-Appalachian brook trout population. Davis College of Agriculture, Forestry, and Consumer Science Ninth Annual Graduate Student Research Conference (WVU). Morgantown, WV. April 14, 2005.

Hartman, K. J., Niles, J., Utz, R. M., Webster, J. W., and B. Moore. 2005. Assessment of spatial and temporal variability in stream habitat and its influence on brook trout population dynamics. **Poster**. Annual meeting of Mead-Westvaco Research Forest supporters. Charleston, WV. February 17, 2005.

Utz, R.M., and K. J. Hartman. 2005. Temporal trends in energy storage, consumption, and growth in a population of central Appalachian brook trout. Joint meeting of the WV Society of Foresters, Wildlife Society, and American Fisheries Society. Flatwoods, WV. February 5, 2005.

Utz, R.M., and K. J. Hartman. 2005. Temporal trends in energy storage, consumption, and growth in a population of central Appalachian brook trout. Southern Division American Fisheries Society spring meeting. Virginia Beach, VA. February 12, 2005.

Utz, R.M., and K. J. Hartman. 2004. Dynamic patterns of energy storage in a central Appalachian brook trout population with respect to seasonal change, food availability, and growth. American Fisheries Society Southern Division 4th Annual Student Colloquium. St. Augustine, FL. November 6, 2004

References

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