Hydrobiologia (2014) 727:151–166
DOI 10.1007/s10750-013-1794-0

PRIMARY RESEARCH PAPER

The temperature–productivity squeeze: constraints on brook trout growth along an Appalachian river continuum

J. Todd Petty · David Thorne ·
Brock M. Huntsman ·
Patricia M. Mazik

Received: 10 July 2013 / Revised: 17 December 2013 / Accepted: 18 December 2013 / Published online: 31 December 2013
© Springer Science+Business Media Dordrecht 2013

Abstract We tested the hypothesis that brook trout growth rates are controlled by a complex interaction of food availability, water temperature, and competitor density. We quantified trout diet, growth, and consumption in small headwater tributaries characterized as cold with low food and high trout density, larger tributaries characterized as cold with moderate food and moderate trout density, and large main stems characterized as warm with high food and low trout density. Brook trout consumption was highest in the main stem where diets shifted from insects in headwaters to fishes and crayfish in larger streams. Despite high water temperatures, trout growth rates also were consistently highest in the main stem, likely due to competitively dominant trout monopolizing thermal refugia. Temporal changes in trout density had a direct negative effect on brook trout growth rates. Our results suggest that competition for food constrains brook trout growth in small streams, but access to thermal refugia in productive main stem habitats enables dominant trout to supplement growth at a watershed scale. Brook trout conservation in this region should seek to relieve the "temperature–productivity squeeze," whereby brook trout productivity is constrained by access to habitats that provide both suitable water temperature and sufficient prey.

Keywords Brook trout · Growth and consumption · Diet · Watershed scale · Density dependence · Competition · Thermal refugia

Introduction

Evidence of climate change and its effects on coldwater fishes continues to mount (Daufresne & Boet, 2007; Rieman et al., 2007; Bates et al., 2008; Isaak et al., 2010; Wenger et al., 2011; Warren et al., 2012). Brook trout life history attributes that are affected by stream temperature (growth, consumption rates, and mobility) have been well documented (Hilderbrand & Kershner, 2004; Sotiropoulos et al., 2006; Hartman & Cox, 2008; Xu et al., 2010; Petty et al., 2012). For example, optimal growth temperatures for brook trout (*Salvelinus fontinalis*) range from 10 to 19 °C (Hartman & Sweka, 2001). Consequently, distributions of several salmonid species, including brook trout, are expected to become highly restricted within

---

Handling editor: M. Power

J. T. Petty (✉) · D. Thorne · B. M. Huntsman
Division of Forestry and Natural Resources, West
Virginia University, Morgantown, WV 26506, USA
e-mail: jtpetty@mail.wvu.edu

Present Address:
D. Thorne
West Virginia Division of Natural Resources, Elkins,
WV 26241, USA

P. M. Mazik
U.S. Geological Survey, WV Cooperative Fish and
Wildlife Research Unit, West Virginia University,
Morgantown, WV 26506, USA

small, isolated cold-water streams as a result of long-term changes in water temperature and flow (Flebbe et al., 2006; Haak et al., 2010; Isaak et al., 2010; Rieman & Isaak, 2010; Wenger et al., 2011).

Models predicting fish response to ambient warming have generally assumed that warming will have consistent bioenergetics consequences across all streams. In other words, incremental increases in water temperature are expected to produce consistent incremental declines in trout growth potential, especially during warmer summer months under the assumption of constant consumption rates (Hill & Magnuson, 1990; Ries & Perry, 1995). However, species such as brook trout often inhabit complex riverscapes (sensu Fausch et al., 2002) comprised of stream networks that differ with regard to thermal regime, underlying productivity, and competitor densities, all of which have been shown to influence fish growth and consumption. For example, recent studies have shown significant density-dependent controls on brook trout population dynamics (Grossman et al., 2010; Grossman et al., 2012; Petty et al., 2012) and growth (Utz & Hartman, 2009; Xu et al., 2010). Furthermore, spatial variation in food availability may be as important as temperature in determining fish growth potential (Hughes, 1998). These mechanisms may be further complicated with the addition of exotic competitors, such as brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*). Consequently, fish bioenergetic response to climate change may be more complicated than what is assumed in current modeling approaches.

For the past several years, we have studied brook trout dynamics in an Appalachian river network, and this system provides a good opportunity for quantifying the potential for complex trout response to climate change. Brook trout distributions within the upper Shavers Fork watershed in West Virginia are controlled simultaneously by mechanisms that affect recruitment and survival within headwater streams (e.g., water quality and competition for food) and mechanisms that affect dispersal among tributaries and larger main stem habitats (e.g., isolation due to barriers) (Petty & Thorne, 2005; Petty et al., 2005; Poplar-Jeffers et al., 2009). Petty et al. (2012) also demonstrated that high rates of brook trout mobility in larger streams could be attributed to individuals searching for thermal refugia within their optimal energetic range during prolonged periods of warm temperatures and low flows. The need to access cold-water refugia in larger streams, however, creates a dilemma for brook trout seeking to maximize growth potential. Prey productivity in the upper Shavers Fork watershed increases with stream size (Petty et al., 2012), which suggests that the growth potential for brook trout in this watershed may be higher at larger main stem sites. However, when temperatures exceed thermal tolerance ranges for brook trout, brook trout tends to aggregate near cold-water sources (Petty et al., 2012). Increased densities at these cold-water sources could then increase the potential for density-dependent mechanisms in influencing the energetics of the brook trout population. Specifically, growth rates may decrease due to fish density, even though prey productivity is high, and temperature is at an optimal range (Utz & Hartman, 2006). Alternatively,

Table 1 *A priori* expectation for brook trout energetics within the upper Shavers Fork watershed in Pocahontas and Randolph counties WV

	Small adults	Large adults
Diet	Shift from aquatic and terrestrial insects in headwaters to fish and crayfish in mainstem	Same as small adults but with a more distinct shift toward fish
Growth	Highest growth in large tributaries where temperatures remain cool and trout densities are low. Seasonally variable growth in mainstem due to highly variable water temperature	Equal growth across all habitats, because large adults are better able to adjust distributions to maximize individual growth potential
Consumption	Increasing consumption from small tributaries to mainstem associated with reduced trout density and increased food availability	Same as small adults
Growth efficiency	Declining growth efficiencies in larger tributaries and mainstem habitats due to increased metabolic costs of mobility and high water temperatures	Same as small adults

reduced temperatures could increase the amount of exploitable habitat on the landscape, reducing aggregation of brook trout near thermal refugia and increase growth potential through alleviated density effects.

Our understanding of present-day growth dynamics and bioenergetics is essential to our understanding of how brook trout populations may respond to climate change in Appalachian watersheds over time. Consequently, we conducted a watershed scale study of brook trout diet, growth, and consumption within the upper Shavers Fork watershed over a period from April 2002 to November 2003. Our objectives were to (1) quantify spatial and temporal variation in brook trout diet, growth, and consumption across a gradient of habitat types ranging from small, cold, headwater tributaries to larger, warmer main stems; and (2) quantify the extent to which trout density affects brook trout growth and consumption. In order to address these objectives, we generated a series of a prior expectation (Table 1) based on known biology of brook trout within the upper Shavers Fork watershed (Petty et al., 2005, 2012) and other watersheds within the region (Utz & Hartman, 2009), as well as guiding principles of density-dependent habitat selection theory (Hughes, 1998; Petty & Grossman, 2010).

Study area

This study was conducted in the upper Shavers Fork watershed, a large (i.e., >150 km^2 basin area), high elevation (originates at 1500 m) watershed located in the Central Appalachian Plateau physiographic province of east central West Virginia (Fig. 1). The study area was located entirely within the Monongahela National Forest in eastern West Virginia, and land cover is dominated by a mixed deciduous–coniferous forest. Natural variation in bedrock geology and stream size produces a high degree of variability in physical, chemical, and biological characteristics of streams (Petty et al., 2001; Petty & Thorne, 2005; Petty et al., 2005; Utz & Hartman, 2006; Petty & Grossman, 2010; Petty et al., 2012) (Table 2). Six study reaches in the upper Shavers Fork drainage were selected to represent the wide variability in drainage area, elevation, temperature, and potential food availability and diversity (Fig. 1; Table 2). Sites consisted of two small headwater tributaries characterized by narrow widths, cold-water, relatively open canopies, low invertebrate biomass, and low fish species richness (Table 2). Larger tributaries were wider but still cold due to dense canopy cover. Large tributaries also had relatively low aquatic invertebrate biomass but possessed much higher fish species richness (Table 2). Lower Second Fork in particular showed lower macroinvertebrate productivity, which has been linked to episodically reduced pH (Bopp, 2002). Main stem sites were much wider and warmer and possessed high aquatic invertebrate biomass and fish species richness (Table 2). Fish assemblages in the upper Shavers Fork are typical for Appalachian streams and include: brook trout, invasive brown trout (*S. trutta*) and rainbow trout (*Onchorynchus mykiss*), rosyface shiner (*Notropis rubellus*), rosyside dace (*Clinostomus funduloides*), blacknose dace (*Rhinicthys obtusus*), longnose dace (*Rhinichthys cataractae*), central stoneroller (*Campostoma anomalum*), fantail darter (*Etheostoma flabellare*), mottled sculpin (*Cottus bairdi*), Northern hog sucker (*Hypentelium nigricans*), and creek chub (*Semotilus atromaculatus*) (Petty et al., 2005).

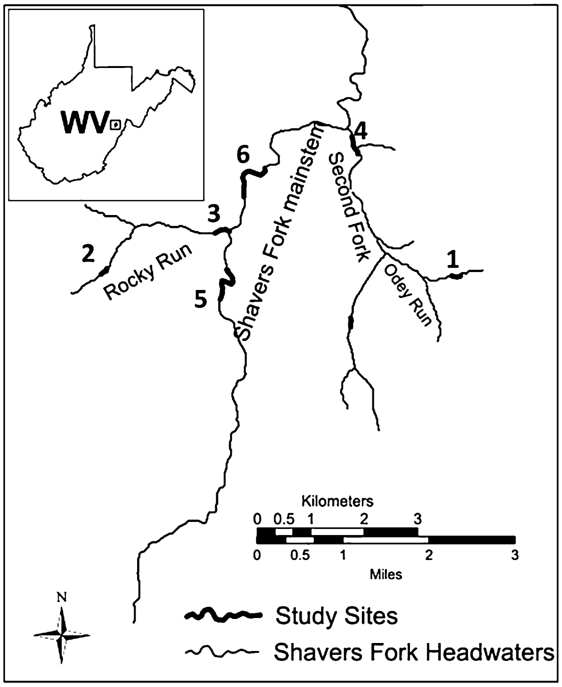

Fig. 1 Map of upper Shavers Fork study area in eastern West Virginia, USA. Also illustrated are six study sites, the numbers of which correspond to sites listed in Table 1. Sites are numbered in order of drainage area from smallest to largest

Table 2 Characteristics of study sites

Site name/map #	Site type	Drainage area (km^2)	Wetted width (m)	Canopy cover (%)	Max average temperature		Fish species richness	Aq invert biomass (mg/m^2)
					2002 (°C)	2003 (°C)		
Little Odey Run/1	Small Trib	1.3	2.6	35	18.73	17.76	1	150
Upper Rocky Run/2	Small Trib	1.8	2.2	25	22.61	22.11	2	165
Lower Rocky Run/3	Large Trib	6.8	3.5	95	18.68	18.13	13	185
Lower Second Fork/4	Large Trib	15.5	5.7	90	19.53	18.87	13	110
Upper Shavers Fork/5	Mainstem	30	13.1	50	26.03	23.61	17	705
Lower Shavers Fork/6	Mainstem	41.7	15.1	25	25.12	23.88	17	610

"Map #" refers to site numbers on map in Fig. 1. "Max Avg Temp" is the maximum average daily water temperature recorded at each site over the course of the year

Methods

Temperature monitoring

Temperature recording monitors (Optic StowAway® and Hobo WaterTemp Pro® data loggers, Onset Computer Corporation, Bourne, MA) were anchored to the bottom of the thalweg, where they were least likely to be susceptible to desiccation, to collect hourly water temperature data (±0.1°C) from April 1 until November 1 in 2002 and 2003. Mean daily temperature (MDT) and maximum weekly average temperature (MWAT) were calculated from continuous data to quantify variability among seasons and sites. Weekly average temperature was calculated as the moving average of the daily mean for each seven-day cycle for each site. The maximum value was then identified as the MWAT, signifying the peak water temperature week of the annual thermal regime within each site.

Brook trout abundance and size structure

Each study reach was sampled to quantify brook trout abundance and size/age structure in each of seven sampling periods (June, August, and October 2002; April, June, August, and October 2003). Early spring, spring, summer, and fall sampling refer to data collected in April, June, August, and October, respectively. Reach length equaled 30 times the mean stream width with a minimum length of 100 m and a maximum length of 300 m (Freund & Petty, 2007). Three-pass depletion methods were used to collect all brook trout and estimate population size (Petty et al., 2005). Electrofishing units (Model 15A, 200–800 V pulsed DC, ~60 Hz, Smith-Root, Inc., Vancouver, WA) were used in conjunction with a combination of dipnets and a collection seine. One unit was used in tributary sites, whereas two were employed in main stem sites to maintain efficiency in the wider channel and deeper pools (Hense et al., 2010). Electrofishing was begun at the downstream end of each stream reach employing a seine and dipnets to capture stunned fish. Upstream reach boundaries were established to coincide with natural stream features (e.g., base of a high gradient riffle or a bedrock ledge) to reduce fish dispersal opportunities. All captured fish were measured for standard length (SL) (±1 mm) and wet weight (±0.1 g). Fish were sorted by SL each season, and a relative age structure was derived from length–frequency histograms of the distribution (Petty et al., 2005). Juveniles were clearly distinguishable from adults based on size. Stock size of brook trout (115 mm SL, Anderson & Neumann, 1996) was used to define the boundary between small and large adults. Juvenile size class breaks in this study correspond with those identified by Petty et al. (2005, 2012).

Brook trout diet

Gut contents were collected on a subset of adult brook trout in each reach for each sampling period. A uniform sample of smaller and larger fish was sought for the diet study to take 50% of diets from small adults and the other 50% from large adults. Because of difficulty with gastric lavage in smaller individuals, we did not quantify diets of juvenile trout. Ten fish per reach were sampled each season, resulting in a total of 360 diet samples over the entire study period from brook trout ranging in size from 96 to 221 mm. Stream water forced into the gut through a tube inserted through the mouth flushed stomach contents out through the esophagus and mouth into a collection container (Wipfli, 1997). Contents flushed out were sieved with a 250 µm screen, labeled, stored in 95% ethanol, and returned to the lab for analysis.

Prey items in stomach samples were identified to family level whenever possible. Some groups were uncommon, and keying beyond class or order was not feasible with standard laboratory microscopes (e.g., Nematoda). If a head capsule was present, then the prey item was identified and counted. Identification of aquatic and terrestrial invertebrates was completed using Borror et al. (1989), Merritt and Cummins (1996), McCafferty and Provonsha (1998), and Thorp and Covich (2001). Head capsule widths and body length were measured with an ocular micrometer to the nearest 0.1 mm, and dry mass of insects was estimated from published equations (Smock, 1980; Sample et al., 1993; Benke et al., 1999; Sabo et al., 2002). Dry mass of fish, amphibians, crayfish, and insects with unpublished relational data was estimated by drying individual prey items or a subsample of prey items at 80°C for 24 h and weighing to the nearest 0.1 mg on an analytical balance (Model SWA-200-DR, Sargent-Welch, Inc., Buffalo Grove, IL) after cooling to room temperature. Subsample weight was then divided by the number in the subsample to get a mean individual mass for all like individuals. All individual weights are best estimates with no correction for loss of mass due to digestion or preservation in ethanol. Sample volume was determined to the nearest 0.1 ml both for the total volume of stomach contents and for the identified prey items.

All prey items were categorized into one of six categories for analysis: fish (FIS), amphibians (AMP), crayfish (CRA), obligate aquatic invertebrates (OAI), non-obligate invertebrates (NOI), and obligate terrestrial invertebrates (OTI). Fish species in the trout diets included minnows, sculpin, and darters. Amphibians included both salamanders (only Plethodontidae were identified in diets) and frogs (a single Ranidae was identified). Crayfish were separated from other invertebrates because of the size and mass difference relative to other aquatic invertebrate prey. Only one family of crayfish (Cambaridae) was observed in trout diets. Categorization of prey types OAI, NOI, and OTI was based on life history information in Borror et al. (1989), Merritt and Cummins (1996), McCafferty and Provonsha (1998) and Thorp and Covich (2001). Obligate aquatic invertebrates (non-crayfish) were defined as those organisms or life stages that must use the aquatic environment for the completion of its current life stage (e.g., caddisfly larvae, stonefly nymphs, riffle beetles) (Merritt & Cummins, 1996; McCafferty & Provonsha, 1998; Thorp & Covich, 2001). Obligate terrestrial invertebrates were organisms that do not require the aquatic environment for completion of the life cycle, but may at times find themselves in the aquatic environment as prey by chance (e.g., ants, grasshoppers). Terrestrial/aquatic invertebrates were those organisms that do not fall neatly as aquatic or terrestrial. Any combination of three reasons for being in the aquatic environment allowed an organism to be placed in this category: (a) a terrestrial or airborne adult stage (e.g., mayfly adult) of an organism that is obligate aquatic at other life stage(s), (b) a predominantly terrestrial organism that spends much of its life on or around the water's edge or on aquatic vegetation (e.g., Coleoptera: Chrysomelidae, Hemiptera: Saldidae), or (c) a predominantly terrestrial organism that utilizes aquatic organisms as prey or as a host to a parasitic larval stage of the organism (e.g., Hymenoptera: Braconidae and Ichneumonidae) (Merritt & Cummins, 1996).

Brook trout growth and consumption

Individual growth was measured at repeated intervals by mark-recapture of brook trout within the study reaches. All brook trout greater than 60 mm SL ($n = 933$) were given unique marks upon initial capture using Visible Implanted Fluorescent Elastomer (Northwest Marine Technology, Shaw Island, WA) tags for identification upon subsequent recapture. Marks of up to six fluorescent and non-fluorescent colors were injected via hypodermic syringe into multiple fin and body locations. Fish under 60 mm were not marked to reduce stress-related mortality. All fish were returned to their initial capture location.

Mean daily growth (henceforth "daily growth") for individuals captured at ~2 month intervals (range 51–88 days, mean 61.7 days) was calculated from the equation:

$$G = (\ln X_t - \ln X_0)/\Delta t, \tag{1}$$

where G is the mean daily growth, X_t is the final weight at time t, X_0 is the initial weight, and Δt is the growth period in days between recaptures (Jensen, 1990). Size-adjusted instantaneous growth rate (henceforth “specific growth”) was calculated by the equation:

$$G_i = G/\ln X_0. \tag{2}$$

This adjustment standardizes growth to a unit of growth per unit body size per day (g/g/day).

Seasonal interval consumption was estimated from bioenergetics simulations run with Fish Bioenergetics 3.0 software using the brook trout model developed by Hartman and Cox (2008). Continuous (hourly) data from temperature loggers (°C) were averaged into four-hour-time periods to estimate consumption for six equal intervals each day. Other input parameters were seasonal mean predator energy density (j/g wet weight, Sweka, 2003), mean prey energy density (j/g wet weight, Cummins & Wuycheck, 1971), diet composition (% of each prey item type in seasonal diet) from diet samples, initial wet weight (g), final wet weight (g), and number of days between weight measurements. Within the bioenergetics model, the value for RA (the intercept of the allometric mass function) was divided by six (K. Hartman, personal communication) to correct for the change from daily estimates of consumption to the 4-hour estimates. Also, all measurements of days in each input parameter had to be multiplied by six, since each day had six intervals in the 4-hour simulations.

Simulations were run on 216 observations of fish recaptured in the sampling season following the previous observation to estimate gross consumption (C) during the time interval and the proportion of maximum consumption (Pr$C_{\max}$) necessary over the interval to produce the growth results. Mean instantaneous consumption (henceforth “consumption rate”) in g/g/day was calculated by the equation:

$$C_i = C/W_0/\Delta t, \tag{3}$$

where C_i is the mean instantaneous consumption rate, C is consumption in grams of prey consumed over the time interval, W_0 is the initial weight of the individual fish in grams, and Δt is the measured time interval in days. As with the growth rate, the instantaneous consumption rate is adjusted to the initial weight of the fish to standardize consumption to a unit of body mass per day. Growth efficiency was calculated by dividing specific growth by consumption rate. Growth efficiency can be interpreted as the proportion of the total mass of food consumed over a time interval that was converted to trout biomass.

Statistical analyses

Chi square analysis was used to test for differences in diet composition of prey types (FIS, AMP, CRA, OAI, NOI, OTI) among seasons, size classes (small vs. large adults), and site types (small tributaries, large tributaries, and main stem). Bonferroni corrections were made to avoid inflation of experiment-wide error resulting from multiple comparisons of the same data. We used repeated measures ANOVA to test for effects of season and site type on brook trout growth and consumption. Tests were run on small and large adult trout separately. Each sampling season was treated as a repeated measure with tests for effects of season, site type, and the season × site type interaction. We used correlation analysis to assess effects of brook trout density on specific growth and consumption. These analyses were conducted separately within each season. Due to high variability in diet and growth estimates and relatively low sample sizes, an alpha = 0.10 significance criterion was used for all statistical tests.

Results

Stream flow and water temperature

Over the course of the study from April 2002 to November 2003, flow and temperature conditions followed a typical seasonal pattern for this system (Fig. 2). Water temperatures tended to peak in July and August during periods of prolonged low flow conditions. Nevertheless, summer 2002 was a much warmer and drier season than summer 2003 (Table 2; Fig. 2). In 2002, mean weekly temperatures exceeded 15°C in the Shavers Fork main stem as early as June 1, whereas this threshold was not reached in 2003 until mid July (Fig. 2). Water temperatures in small and large tributaries also were notably cooler in 2003 (Table 2).

Brook trout populations

Brook trout densities were highest in the small tributaries, intermediate in large tributaries, and lowest in the Shavers Fork main stem (Fig. 3). All brook trout size classes tended to follow this trend. However, large adults were proportionately more

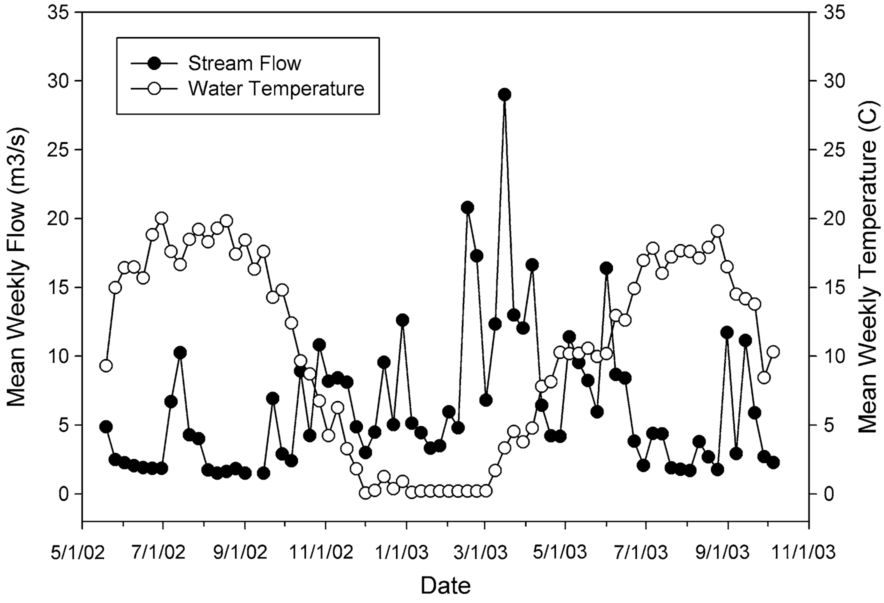

Fig. 2 Temporal variation in stream flow and water temperature within the upper Shavers Fork mainstem over the course of the study (early May 2002–late October 2003)

abundant in the main stem, whereas tributary populations tended to be dominated by small adults and juveniles. Small adult densities underwent a sharp reduction in fall 2002 within small and large tributary sites, and reduced small adult densities persisted throughout the 2003 sampling seasons. Large adult densities also declined in fall 2002 but had recovered in late summer 2003 (Fig. 3).

Diet composition

We observed significant variation in brook trout diet composition among seasons (spring vs. summer vs. fall; Chi-sq. = 1,750, d.f. = 25, $P < 0.01$), among site types (small tributary vs. large tributary vs. main stem; Chi-sq. = 523, d.f. = 10, $P < 0.01$), and between size classes (small vs. large adults; Chi-sq. = 90, d.f. = 5, $P < 0.01$) (Table 3). Seasonally, there was an overall increase from spring to fall in the contribution of terrestrial insects to brook trout diets, especially for small adults in all site types and for large adults in small tributaries (Table 3). For example, the contribution of terrestrial insects to large adults inhabiting small tributaries increased from 0% in spring to 63% in fall.

As expected, there was an overall increase in the contribution of fish and crayfish, and a decline in the contribution of aquatic and terrestrial insects to brook trout diets from small headwater tributaries downstream to larger main stem habitats (Table 3). For example, fish were rarely consumed by tributary brook trout across seasons. However, fishes comprised 40–50% of the summer diets of brook trout residing in the main stem (Table 3). In contrast, the diets of small adult brook trout residing in small tributaries were always dominated by aquatic and terrestrial insects (Table 3). Overall, seasonal and spatial variation in diet composition was similar between small and large adult brook trout. The most notable difference was that crayfish were generally more important to large adult diets and increased in contribution from spring to fall (Table 3), whereas terrestrial insects were more important to small adult diets, especially in large tributary and main stem sites (Table 3). Small adult brook trout residing in large tributaries did deviate away from the spatial patterns observed in consumption for both % crayfish and terrestrial insect, where crayfish contributions were lower than expected, while terrestrial insects were higher (Table 3).

Growth and consumption

We observed a significant direct effect of season ($F = 8.0$; d.f. = 4,135; $P < 0.01$) and a significant interactive effect of season and site type ($F = 1.7$; d.f. = 8, 135; $P = 0.10$) on specific growth rates of small adult brook trout (Fig. 4A). Growth rates of small adults were highly variable and were maximized

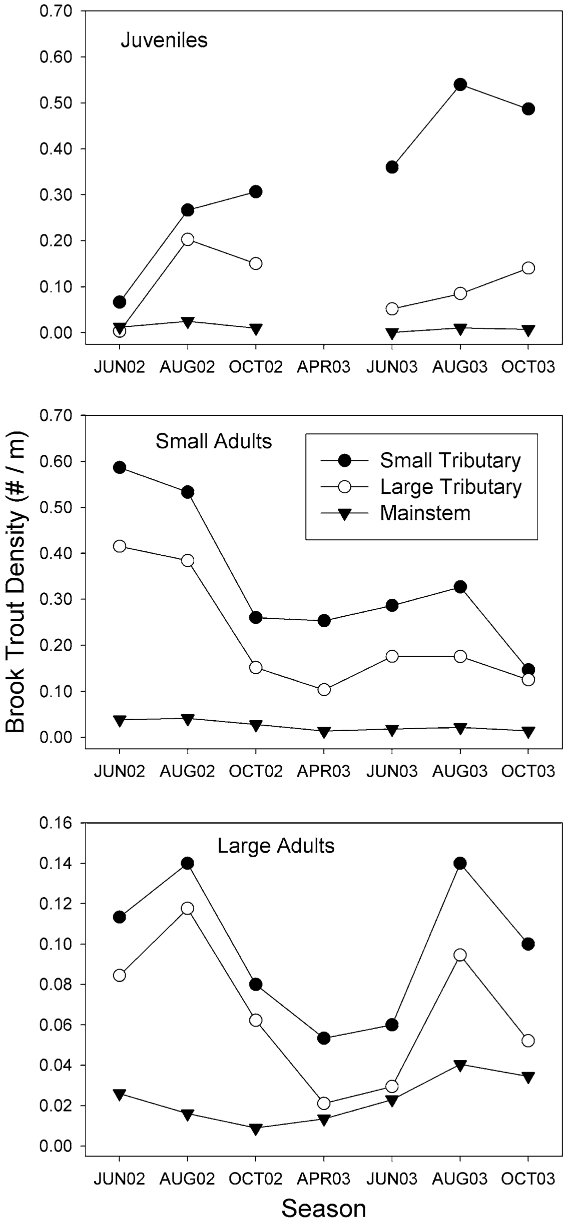

Fig. 3 Seasonal variation in brook trout density within small tributaries, large tributaries, and main stem habitats over the course of the study from spring 2002–fall 2003. Data are presented separately for juvenile, small adult, and large adult brook trout

in spring at the small tributary and mainstem sites (Fig. 4A). Growth rates for small adults in large tributaries showed less variability and a modest peak during the summer (Fig. 4A). Cumulative annual growth rates of small adults were 1.5 times higher in the main stem (0.057 g/g/day) than in small tributaries (0.039 g/g/day) (Fig. 5). We also observed significant seasonal effects ($F = 4.1$; d.f. = 2, 135; $P = 0.01$) and season x site type interactive effects ($F = 2.21$; d.f. = 8, 135; $P = 0.04$) on specific growth rates of large adult brook trout (Fig. 4D). Adult growth rates in the tributary tended to be lowest in fall and highest in spring (Fig. 4D). Growth of large adult brook trout in small tributaries was more variable than in the main stem over time (Fig. 4D), and ultimately resulted in significantly higher large tributary and main stem growth rates over time (Fig. 5). Cumulative annual large adult growth rates were 2.6 times higher in main stem habitats (0.008 g/g/day) and 2.5 times higher in large tributaries (0.007 g/g/day) than in small tributaries (0.003 g/g/day).

Small adult consumption rates varied significantly among seasons ($F = 9.1$; d.f. = 4, 135; $P < 0.01$) and among site types ($F = 4.3$; d.f. = 2, 135; $P = 0.02$). Consumption rates of small adults were highest in summer 2002 and tended to be higher in the mainstem than in small or large tributaries regardless of season (Fig. 4B). Cumulative annual consumption rates of small adults were also 1.5 times higher in the mainstem (0.015 g/g/day) than in small tributaries (0.010 g/g/day) (Fig. 5). Large adult consumption rates varied significantly among seasons ($F = 4.8$; d.f. = 4, 135; $P < 0.01$) and among site types ($F = 14.6$; d.f. = 2, 135; $P < 0.01$). Consumption rates were most variable within small tributaries, whereas consumption was relatively constant in large tributaries and main stem habitats (Fig. 4E). Most notably, consumption rates of large adults increased markedly as a function of stream size (Figs. 4E, 5). Cumulative annual estimates of large adult consumption rates were 2.2 times higher in main stems (0.011 g/g/day) and 1.3 times higher in large tributaries (0.007 g/g/day) than in small tributaries (0.005 g/g/day).

Growth efficiency of small adults (i.e., growth rate relative to consumption rate) was highly variable over time, especially in main stem habitats (Fig. 4C). Our expectation that growth efficiency would be lowest in main stem habitats was not supported by the data (Figs. 4C, 5). In fact, the highest growth efficiencies for small adults were observed in main stem habitats in spring (Fig. 4C). Cumulative annual estimates suggest that small adult growth efficiencies were similar across all habitat types (Fig. 5). Growth efficiencies of large adults were highly variable over time and

Table 3 Percent contributions by number of fish (FIS), amphibians (AMP), crayfish (CRA), obligate aquatic insects (OAI), non-obligate aquatic insects (NAI), and obligate terrestrial insects (OTI) to small and large adult brook trout diets across seasons and site types

	Small adults						Large adults					
	FIS	AMP	CRA	OAI	NOI	OTI	FIS	AMP	CRA	OAI	NOI	OTI
Spring												
ST	0	19	0	60	21	0	0	27	0	53	20	0
LT	37	0	4	47	11	1	0	3	0	50	32	15
MS	0	0	34	62	1	2	0	0	14	36	49	1
Summer												
ST	0	0	2	32	24	41	5	13	9	26	23	24
LT	0	0	0	28	23	48	10	1	2	26	31	31
MS	46	0	16	9	6	23	38	0	0	5	6	52
Fall												
ST	0	0	2	41	7	50	0	0	13	9	15	63
LT	8	0	0	9	14	69	1	2	52	19	9	16
MS	27	0	0	12	12	49	31	0	59	7	1	2

ST small tributaries, *LT* large tributaries and *MS* mainstem

interestingly were not synchronized with small adults (Fig. 4F). Large adult growth efficiencies were extremely low in fall in small tributaries and relatively constant over time in large tributaries and the main stem (Fig. 4F). Contrary to expectations, overall growth efficiencies of large adults were constant across habitat types (Fig. 5).

Effects of trout density

The spatial pattern of adult brook trout densities was positively correlated over time (Fig. 6A). Sites with low trout density in 2002 remained relatively low in 2003, and sites with high density remained relatively high. Nevertheless, there was a dramatic reduction in brook trout density from 2002 to 2003, especially within sites of high trout density in 2002 (Fig. 6A).

Significant (i.e., $P < 0.10$) negative correlations between brook trout density and consumption rates were observed in summer 2002 ($r = -0.76$), fall 2002 ($r = -0.84$) and spring 2003 ($r = -0.57$). A significant negative correlation between density and growth rates was observed in summer 2002 ($r = -0.50$) only (Fig. 6A). Contrary to expectations, we observed a strong positive correlation ($r = 0.96$) between brook trout density and growth rates in summer 2003, which is the year that brook trout densities declined so precipitously (Fig. 6A). Interestingly, we observed a significant relationship between the relative change in brook trout growth from 2002 to 2003 and the relative change in brook trout density (Fig. 6B). Sites where we observed the greatest declines in brook trout density were characterized by the highest relative increases in brook trout growth (Fig. 6B).

Discussion

Our results indicate that brook trout diet, growth, and consumption within the Upper Shavers Fork riverscape are influenced by a complex interaction of intraspecific competition, water temperature, and food availability. Despite ideal summer water temperatures, brook trout growth in small headwater tributaries was constrained by food availability and competitor density. In contrast, adult brook trout growth and consumption were maximized in main stem habitats, despite elevated summer water temperatures. These results support the hypothesis that linkages between small headwater tributaries where reproduction occurs and productive main stem habitats are needed to maximize brook trout growth potential at the watershed scale.

Higher levels of brook trout growth and consumption in large tributaries and main stem habitats can largely be attributed to a more productive and diverse prey base (Petty et al., 2012) and a shift in diet from

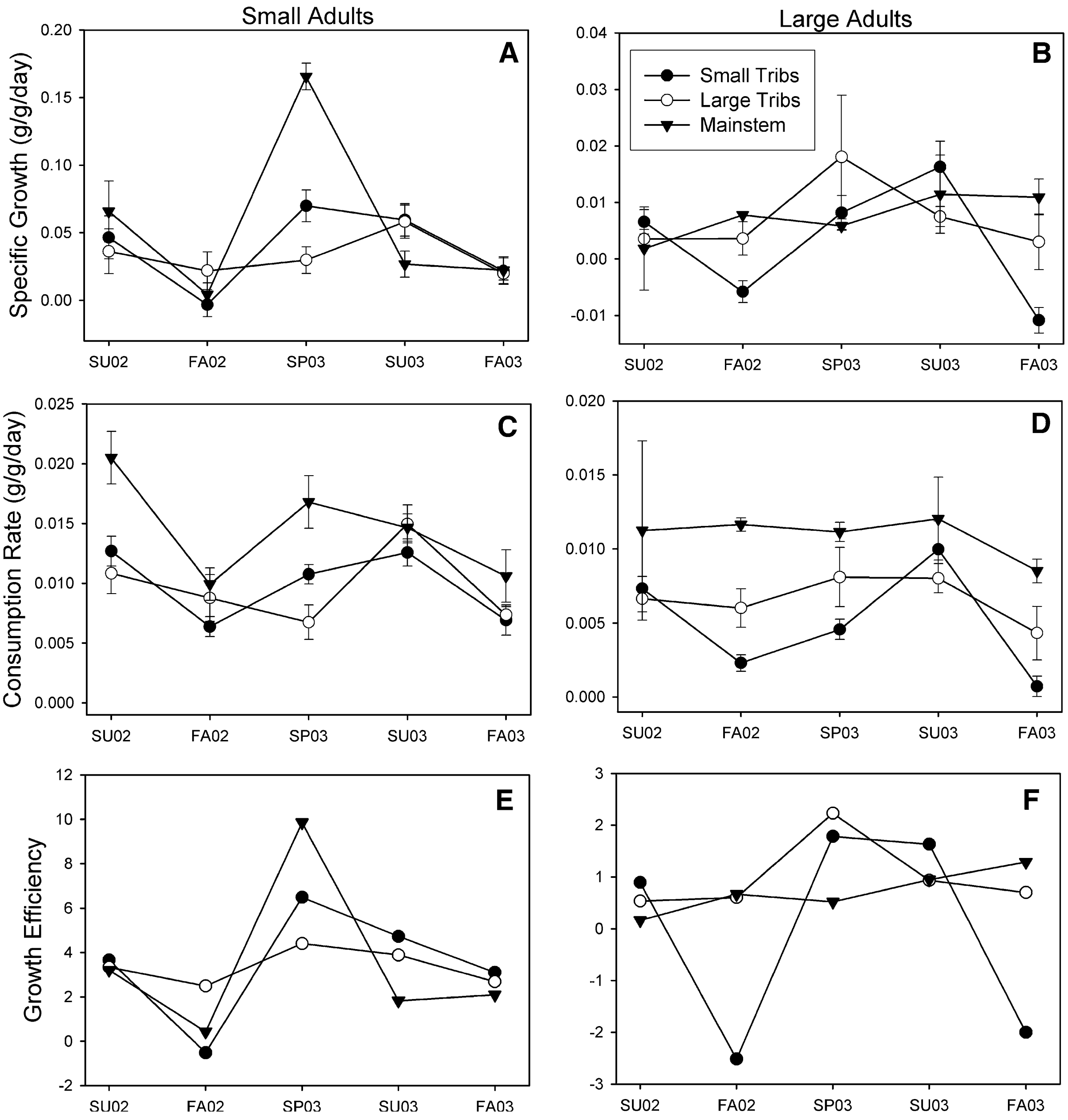

Fig. 4 Seasonal variation in small and large adult brook trout specific growth rates (**A**, **D**), consumption rates (**B**, **E**), and growth efficiency (**C**, **F**) within small tributaries, large tributaries, and main stem habitats. *Error bars* are ±1 SE

invertebrates to fish. As expected, brook trout diets varied consistently along the continuum from small tributaries, where prey is limited to aquatic and terrestrial invertebrates, to the larger main stem, where the prey base is characterized by a greater availability of small fish. Interestingly, terrestrial insects were an important prey item for small adult brook trout across all habitat types. Given that fishes are a higher quality food source than invertebrates (fish = 5086 calories per gram, aquatic invertebrates = 4229 calories per gram, Cummins & Wuycheck, 1971), it makes sense that brook trout diets shift to a greater dependence on fish when they are available. Our results on brook trout diets in small headwater streams are consistent with

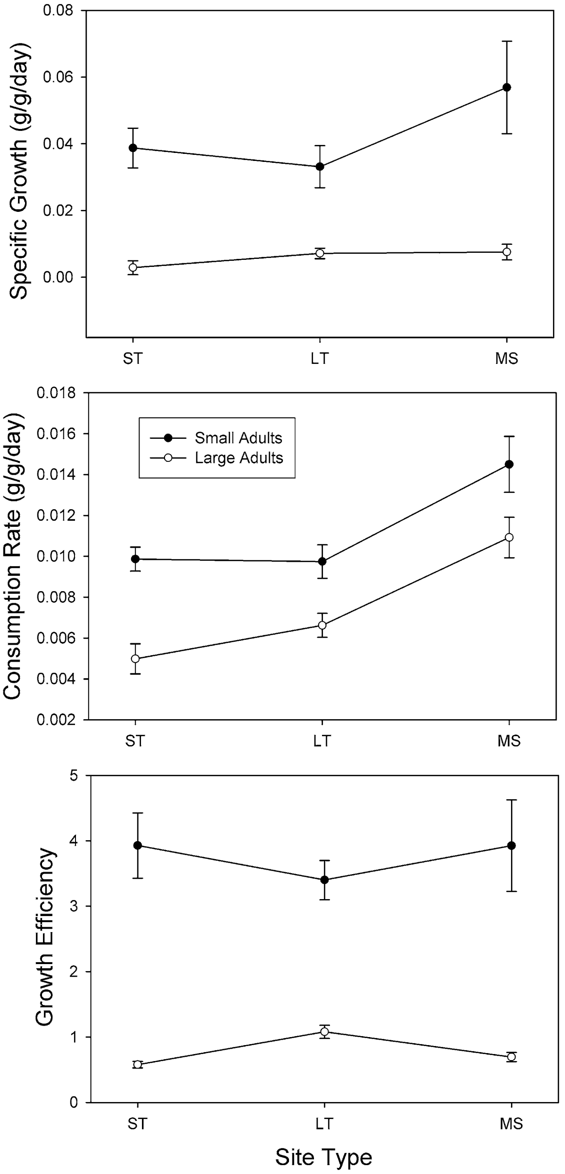

Fig. 5 Annualized mean growth, consumption, and growth efficiency of small adult and large adult brook trout in small tributaries (ST), large tributaries (LT), and main stem habitats (MS)

previous research in this region, which has documented a strong dependence of headwater brook trout populations on terrestrial inputs (Webster & Hartman, 2005; Utz & Hartman, 2007; Sweka & Hartman, 2008).

Studies of brook trout diets in larger waterbodies are surprisingly rare, and to our knowledge, ours is the first study to quantify brook trout diet and growth in a

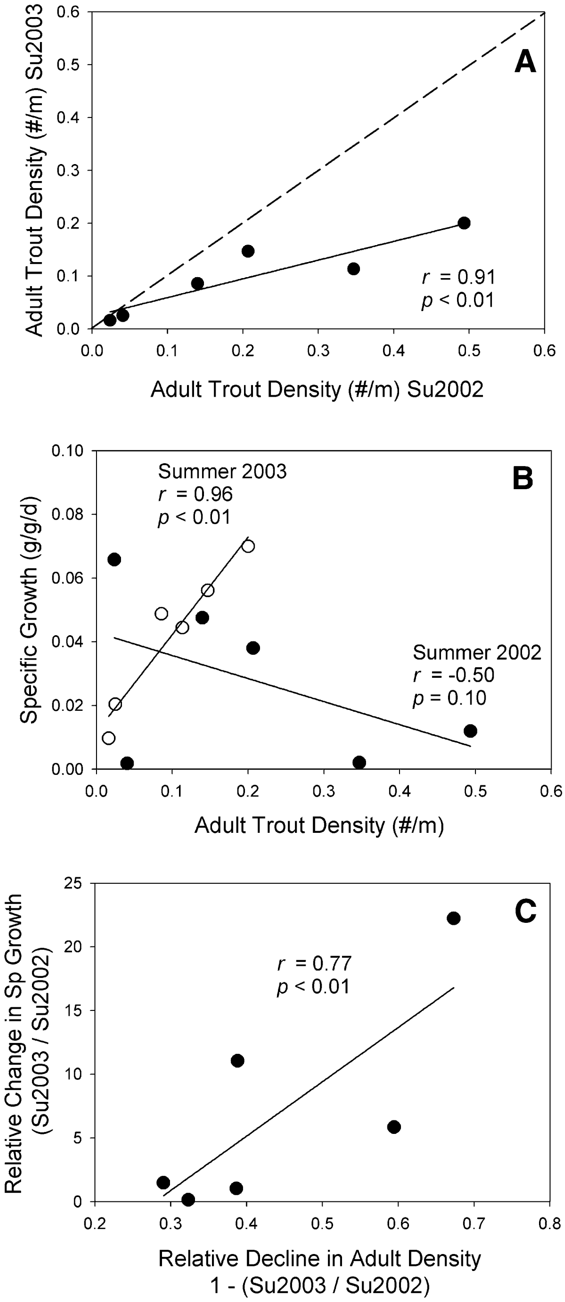

Fig. 6 Spatial and annual variation in brook trout growth and its relation to trout density. **A** Relationship between adult brook trout density in summer 2002 and summer 2003 across six study sites. *Dashed line* is a 1:1 line. Statistics represent the correlation between summer 2002 and summer 2003 densities. **B** Relationship between adult brook trout growth rates and trout density in summer 2002 and summer 2003. **C** Relationship between the proportional change in brook trout density from summer 2002 to summer 2003 (all sites declined in density over this time period) and proportional change in brook trout growth rate over the same time period

large Appalachian river main stem. Studies in the northwestern US have demonstrated that salmonids adopt a highly migratory life history strategy so as to maximize growth potential from marine-derived nutrients (Gross et al., 1988; Chaloner et al., 2002; Wipfli et al., 2003). In addition, Robillard et al. (2011) found that brook trout growth supported by Lake Superior prey were significantly larger than individuals supported by productivity from the smaller natal tributaries. Additional studies are needed in the central Appalachian region to determine the extent to which brook trout diets vary along river continua and the consequences that diet shifts may have for brook trout growth and consumption.

Differences in brook trout growth and consumption between tributary and main stem habitats in the upper Shavers Fork also may be explained by density-dependence and intraspecific competition. Previous research has shown that fish density can have a negative impact on fish size through intraspecific (Utz & Hartman, 2009; Grossman et al., 2010; Petty et al., 2012), and interspecific competition (Dunham & Vinyard, 1997; Carlson et al., 2007; Amundsen & Gabler, 2008), and negatively affect consumption rates (Amundsen & Gabler, 2008; Utz & Hartman, 2009). Our data suggest significant density-dependent effects on growth and consumption, especially in the summer. During summer months, aquatic invertebrate biomass in headwater streams may decline dramatically as most species transition into terrestrial adults during late summer (Poff & Huryn, 1998; Gowan & Fausch, 2002; Sotiropoulos et al., 2006). The reduction of available prey biomass is not only observed in lower prey consumption during the summer but also in lower growth rates and body condition of many aquatic predators (Ensign et al., 1990; Sotiropoulos et al., 2006). The decline in prey density, therefore, can result in strong intraspecific competitive interactions, especially in small streams where brook trout densities are high.

Unfortunately, brook trout density and overall food availability are highly correlated along the stream size continuum in many Appalachian watersheds, including the upper Shavers Fork. Consequently, it can be difficult to separate competitor effects from the effects of prey availability. However, the dramatic change in brook trout densities from 2002 to 2003 provided an opportunity to test for direct competition effects on brook trout growth and consumption (Fig. 6). Sites that experienced the greatest decline in brook trout density also experienced the greatest increase in growth. This finding provides evidence of a direct effect of competitor density on brook trout growth.

Perhaps the most interesting result of this study was the complex inter-relationships between summer water temperatures, brook trout distributions, and habitat dependent brook trout growth and consumption. We observed higher brook trout densities in tributaries during 2002, an especially warm year, than in 2003, an especially cool year. In contrast, brook trout densities in the main stem were higher in the cooler year than in the warmer year, although main stem densities remained low relative to tributaries (Fig. 3). Numerous studies have shown that water temperature is one of the most important factors influencing habitat selection by cold-water fishes (Hughes, 1998; Keefer et al., 2009; Young et al., 2010; Petty et al., 2012), and consequently it is not surprising that brook trout avoided extremely warm conditions in the main stem. Interestingly however, when brook trout concentrated within the cold tributaries to avoid extreme main stem conditions, a strongly negative density-dependent response of brook trout growth was observed (Fig. 6). By staying in the high density, low prey productivity tributaries during the warm year, both growth and consumption rates were substantially lowered. In contrast, cooler conditions during 2003 appeared to allow brook trout to expand their use of the main stem and simultaneously relieve strong negative density-dependent effects on tributary brook trout growth rates.

Contrary to expectations, our results indicate that using main stem habitats consistently maximized brook trout growth rates. We expected energy consumption and perhaps spring growth rates to be higher in the larger waterbodies. However, we also expected main stem growth efficiencies to be low due to higher metabolic costs of movement and high water temperatures resulting in relatively constant growth across habitat types (Morinville & Rasmussen, 2003). Nevertheless, we found that energy consumption in the main stem was high enough to counteract higher energetic costs of using the main stem. The heterogeneous nature of main stem temperatures may partially explain these patterns. Hughes (1998) demonstrated the importance of considering heterogeneous temperature profiles within larger waterbodies when modeling salmonid habitat selection. For this study, temperature loggers were anchored to stakes driven into the stream benthos to measure ambient temperatures. During warm summer months, brook trout are more likely to use thermal refugia (i.e., deep pools, tributary confluences, seeps, groundwater upwellings) to alleviate thermal stress (Petty et al., 2012). If the ambient temperatures used in bioenergetics modeling were higher than actually experienced by individual brook trout, then actual consumption estimates would be lower than predicted based on our growth estimates. This would be especially true in the summer, when temperatures often exceeded optimal ranges for brook trout. Higher growth rates in main stem habitats were likely the result of a combination of higher prey consumption coupled with use of thermal refugia.

If growth rates in the main stem are consistently high, and growth rates in the tributaries are constrained by density, then why are brook trout densities in the main stem so low? Optimal foraging and density-dependent habitat selection theory (Fretwell & Lucas, 1970; Pullium & Danielson, 1991; Petty & Grossman, 2010) suggest that mobile foragers should adjust densities through movement in a manner that would lead to relatively equal growth across habitat types. Stream fishes, in particular, have consistently been shown to adhere to predictions of habitat selection theory at both the individual (Hughes & Dill, 1990; Hill & Grossman, 1993; Gowan & Fausch, 2002; Petty & Grossman, 2010) and population level (Hughes, 1998; Thompson et al., 2001; Gowan & Fausch, 2002). Consequently, given that brook trout are highly mobile in this system (Petty et al., 2012), we would expect individuals to move from high density tributaries to larger main stem habitats to such a level where growth rates would be relatively equal throughout the watershed.

The simplest explanation for this finding is that brook trout may compete for and are limited by the availability of thermal refugia in the main stem. Petty et al. (2012) found that brook trout commonly aggregate near cold-water sources in the Shavers Fork main stem, especially when ambient stream temperature exceeds 20°C. This pattern has been observed in many other salmonid species (Torgersen et al., 1999; Goniea et al., 2006; Breau et al., 2007; Keefer et al., 2009; Young et al., 2010). Limited access to thermal refugia explains why fewer individuals leave a large cold-water source (tributaries) during hot years, because less thermal refuge may be available in the main stem. Competition for thermal refugia also may explain why brook trout size distributions in the main stem are highly skewed toward larger individuals (Hughes, 1998). Our hypothesis is that main stem habitats represent the highest quality foraging habitats for individuals able to compete for and maintain access to thermal refugia. Smaller, subdominant individuals, in contrast, may be forced to remain in the cooler tributaries where high densities and low food availability constrain growth. Similar justification was given by Hughes (1998) to explain why large Arctic grayling (*Thymallus arcticus*) orients themselves upstream where the most profitable feeding microhabitats are located. Within the upper Shavers Fork watershed, those individuals able to access and defend thermal refuge in the main stem are then capable of experiencing elevated growth potential compared to brook trout inhabiting other positions within the watershed.

Other explanations for low brook trout density in the main stem despite higher growth rates include: higher predation or harvest risk, competition with brown and rainbow trout, and unmeasured costs, such as missed opportunity costs, associated with moving from spawning areas to the main stem. An important direction for future research must seek to explain how food, temperature, density, interspecific competition, predation, harvest, and missed opportunity costs interact to affect brook trout use of larger Appalachian rivers.

Management implications

Over the past 100 years, brook trout have experienced extensive declines throughout their native range (Hudy et al., 2008), and consequently, population and habitat restoration are important components of range-wide brook trout conservation strategies (Petty & Merriam, 2012). Previous research has emphasized the combined importance of restoring brook trout reproductive processes in headwater tributaries through treatment of acid precipitation (Petty & Thorne, 2005; Petty et al., 2005; McClurg et al., 2007) as well as restoring dispersal processes through culvert removal (Poplar-Jeffers et al., 2009). The results of our current study emphasize the importance of main stem habitats and thermal refugia to brook trout growth potential in this system (Petty et al., 2012). Given the potential negative consequences of climate change on brook trout (Flebbe et al., 2006), population restoration in this system will require provision of thermal refugia within the main stem (Petty et al., 2012), and perhaps removal of exotic brown trout that may be competing with brook trout for access to these refugia (Wenger et al., 2011). Because of the negative effects of brook trout density on growth, the colder tributaries themselves cannot provide both thermal refugia and access to food resources. We refer to this problem as the "temperature–productivity squeeze." This concept recognizes that overall brook trout growth potential is constrained by the availability of habitats that combine both suitable water temperatures and access to sufficient prey. We believe that loss of and competition with brown trout for thermal refugia in productive main stems may contribute to the isolation of brook trout populations in small headwater tributaries (Letcher et al., 2007) and may explain the loss of large-bodied brook trout throughout much of the central and southern Appalachian region.

Acknowledgments We thank the U.S. Geological Survey and the U.S. Fish and Wildlife Service for financial support for this study. Comments from Kyle Hartman greatly improved earlier versions of this manuscript. We also thank Mike Shingleton and Steve Brown from the WVDNR for sharing their expertise and ideas. As always, we are grateful to Becky Nestor for her administrative support of this project. Use of trade names does not imply endorsement by the U.S. Government.

References

Amundsen, P. A. & H. M. Gabler, 2008. Food consumption and growth of Atlantic salmon *Salmo salar* parr in sub-Arctic rivers: empirical support for food limitation and competition. Journal of Fish Biology 73: 250–261.

Anderson, R. O. & R. M. Neumann, 1996. Length, weight, and associated structural indices. In Murphy, B. R. & D. W. Willis (eds), Fisheries Techniques, 2nd ed. American Fisheries Society, Bethesda, MD: 447–482.

Bates, B. C., Z. Q. Kundzewicz, S. Wu & J. P. Palutikof (eds), 2008. Climate Change and Water. Technical Paper of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva.

Benke, A. C., A. D. Huryn, L. A. Smock & J. B. Wallace, 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18: 308–343.

Bopp, J., 2002. The Combined Effects of Water Chemistry, Canopy Cover, and Basin Area on Benthic Macroinvertebrates along a Central Appalachian Stream Continuum. West Virginia University, Morgantown.

Borror, D. J., C. A. Triplehorn & N. F. Johnson, 1989. An Introduction to the Study of Insects, 6th ed. Saunders College Publishers, Ft. Worth, TX.

Breau, C., R. A. Cunjak & G. Bremset, 2007. Age-specific aggregation of wild juvenile Atlantic salmon *Salmo salar* at cool water sources during high temperature events. Journal of Fish Biology 71: 1179–1191.

Carlson, S. M., A. P. Hendry & B. H. Letcher, 2007. Growth rate differences between resident native brook trout and non-native brown trout. Journal of Fish Biology 71: 1430–1447.

Chaloner, D. T., M. S. Wipfli & J. P. Caouette, 2002. Mass loss and macroinvertebrate colonisation of Pacific salmon carcasses in southeastern Alaskan streams. Freshwater Biology 47: 263–273.

Cummins, K. W. & J. C. Wuycheck, 1971. Caloric equivalents for investigations in ecological energetics. International Association of Theoretical and Applied Limnology 18: 1–158.

Daufresne, M. & P. Boet, 2007. Climate change impacts on structure and diversity of fish communities in rivers. Global Change Biology 13: 2467–2478.

Dunham, J. B. & G. L. Vinyard, 1997. Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids. Canadian Journal of Fisheries and Aquatic Sciences 54: 1025–1030.

Ensign, W. E., R. J. Strange & S. E. Moore, 1990. Summer food limitation reduced brook and rainbow trout biomass in a southern Appalachian stream. Transactions of the American Fisheries Society 119: 894–901.

Fausch, K. D., C. E. Torgersen, C. V. Baxter & H. W. Li, 2002. Landscape to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience 52: 483–498.

Flebbe, P. A., L. D. Roghair & J. L. Bruggink, 2006. Spatial modeling to project Southern Appalachian trout distribution in a warmer climate. Transactions of the American Fisheries Society 135: 1371–1382.

Fretwell, S. D. & H. L. Lucas Jr, 1970. On territorial behavior and other factors influencing habitat distribution in birds. 1. Theoretical development. Acta Biotheoretica 1970: 16–36.

Freund, J. G. & J. T. Petty, 2007. Response of fish and macroinvertebrate bioassessment indices to water chemistry in a mined Appalachian watershed. Environmental Management 39: 707–720.

Goniea, T. M., M. L. Keefer, T. C. Bjornn, C. A. Peery, D. H. Bennet & L. C. Stuehrenberg, 2006. Behavioral thermoregulations and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. Transactions of the American Fisheries Society 135: 408–419.

Gowan, C. & K. D. Fausch, 2002. Why do foraging stream salmonids move during summer? Environmental Biology of Fishes 64: 139–153.

Gross, M. R., R. M. Coleman & R. M. McDowall, 1988. Aquatic productivity and the evolution of diadromous fish migration. Science 239: 1291–1293.

Grossman, G. D., R. E. Ratajczak, C. M. Wagner & J. T. Petty, 2010. Dynamics and regulation of the southern brook trout (*Salvelinus fontinalis*) population in an Appalachian stream. Freshwater Biology 55: 1494–1508.

Grossman, G. D., A. Nuhfer, T. Zorn, G. Sundin & G. Alexander, 2012. Population regulation of brook trout (*Salvelinus fontinalis*) in Hunt Creek, Michigan: a 50-year study. Freshwater Biology 57: 1434–1448.

Haak, A. L., J. E. Williams, H. M. Neville, D. C. Dauwalter & W. T. Colyer, 2010. Conserving peripheral trout populations: the values and risks of life on the edge. Fisheries 35: 530–549.

Hartman, K. J. & K. M. Cox, 2008. Refinement and testing of a brook trout bioenergetics model. Transactions of the American Fisheries Society 137: 357–363.

Hartman, K. J. & J. A. Sweka, 2001. Development of a bioenergetics model for Appalachian brook trout. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 55: 38–51.

Hense, Z., R. W. Martin & J. T. Petty, 2010. Electrofishing capture efficiencies for common stream fish species to support watershed-scale studies in the central Appalachians. North American Journal of Fisheries Management 30: 1041–1050.

Hilderbrand, R. H. & J. L. Kershner, 2004. Are there differences in growth and condition between mobile and resident cutthroat trout? Transactions of the American Fisheries Society 133: 1042–1046.

Hill, D. K. & J. J. Magnuson, 1990. Potential effects of global climate warming on the growth and prey consumption of great lakes fish. Transactions of the American Fisheries Society 119: 265–275.

Hill, J. & G. D. Grossman, 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology 74: 685–698.

Hudy, M., T. M. Theiling, N. Gillespie & E. P. Smith, 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. North American Journal of Fisheries Management 28: 1069–1085.

Hughes, N. F., 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology 79: 281–294.

Hughes, N. F. & L. M. Dill, 1990. Position choice by drift-feeding salmonids: model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47: 2039–2047.

Isaak, D. J., C. H. Luce, B. E. Rieman, D. E. Nagel, E. E. Peterson, D. L. Horan, S. Parkes & G. L. Chandler, 2010. Effect of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. Ecological Applications 20: 1350–1371.

Jensen, A. J., 1990. Growth of young migratory brown trout *Salmo trutta* correlated with water temperature in Norwegian rivers. Journal of Animal Ecology 59: 603–614.

Keefer, M. L., C. A. Peery & B. High, 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. Canadian Journal of Fisheries and Aquatic Sciences 66: 1734–1747.

Letcher, B. H., K. H. Nislow, J. A. Coombs, M. J. O'Donnell & T. L. Dubreuil, 2007. Population response to habitat fragmentation in a stream-dwelling brook trout population. PLoS One 2(11): e1139.

McCafferty, W. P. & A. V. Provonsha, 1998. Aquatic Entomology: The Fisherman's and Ecologist's Illustrated Guide to Insects and Their Relatives. Jones and Bartlett, Boston.

McClurg, S. E., J. T. Petty, P. M. Mazik & J. L. Clayton, 2007. Stream ecosystem response to limestone treatment in acid impacted watersheds of the Allegheny Plateau. Ecological Applications 17: 1087–1104.

Merritt, R. W. & K. W. Cummins, 1996. An Introduction to the Aquatic Insects of North America, 3rd ed. Kendall and Hunt, Dubuque, IA.

Morinville, G. R. & J. B. Rasmussen, 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 60: 401–410.

Petty, J. T. & G. D. Grossman, 2010. Giving-up densities and ideal pre-emptive patch use in a predatory benthic stream fish. Freshwater Biology 55: 780–793.

Petty, J. T. & E. P. Merriam, 2012. Brook trout restoration. Nature Education Knowledge 3:17. http://www.nature.com/scitable/knowledge/library/brook-trout-restoration-83031062.

Petty, J. T. & D. Thorne, 2005. An ecologically based approach to identifying restoration priorities in an acid impacted watershed. Restoration Ecology 13: 348–357.

Petty, J. T., J. Freund, P. Lamothe & P. Mazik, 2001. Quantifying instream habitat in the upper Shavers Fork basin at multiple spatial scales. Proceedings of the Southeastern association of Fish and Wildlife Agencies 55: 81–94.

Petty, J. T., P. J. Lamothe & P. M. Mazik, 2005. Spatial and seasonal dynamics of brook trout populations inhabiting a central Appalachian watershed. Transactions of the American Fisheries Society 134: 572–587.

Petty, J. T., J. L. Hansbarger, B. M. Huntsman & P. M. Mazik, 2012. Brook trout movement in response to temperature, flow, and thermal refugia within a complex Appalachian riverscape. Transactions of the American Fisheries Society 141: 1060–1073.

Poff, N. L. & A. D. Huryn, 1998. Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. Canadian Journal of Fisheries and Aquatic Sciences 55: 201–217.

Poplar-Jeffers, I. O., J. T. Petty, J. T. Anderson, S. J. Kite, M. P. Strager & R. H. Fortney, 2009. Culvert replacement and stream habitat restoration: Implications from brook trout management in an Appalachian watershed, U.S.A. Restoration Ecology 17: 404–413.

Pullium, R. H. & B. J. Danielson, 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist 137: S50–S66.

Rieman, B. & D. Isaak, 2010. Climate Change, Aquatic Ecosystems and Fishes in the Rocky Mountain West: Implications and Alternatives for Management. USDA Forest Service, Rocky Mountain Research Station, GTR-RMRS-250, Fort Collins, CO.

Rieman, B. E., D. Isaak, S. Adams, D. Horan, D. Nagel, C. Luce & D. Myers, 2007. Anticipated climate warming effects on bull trout habitats and populations across the interior Columbia River basin. Transactions of the American Fisheries Society 136: 1552–1565.

Ries, R. D. & S. A. Perry, 1995. Potential effects of global climate warming on brook trout growth and prey consumption in central Appalachian streams, USA. Climate Research 5: 197–206.

Robillard, M. M., R. L. McLaughlin & R. W. Mackereth, 2011. Diversity in habitat use and trophic ecology of brook trout in Lake Superior and tributary streams revealed through stable isotopes. Transactions of the American Fisheries Society 140: 943–953.

Sabo, J. L., J. L. Bastow & M. E. Power, 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21: 336–343.

Sample, B. E., R. J. Cooper, R. D. Greer & R. C. Whitmore, 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129: 234–240.

Smock, L. A., 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10: 375–383.

Sotiropoulos, J. C., K. H. Nislow & M. R. Ross, 2006. Brook trout, *Salvelinus fontinalis*, microhabitat selection and diet under low summer stream flows. Fisheries Management and Ecology 13: 149–155.

Sweka, J. A., 2003. Aquatic-Terrestrial Linkages in Appalachian Streams: Influence of Riparian Inputs on Stream Habitat, Brook Trout Populations, and Trophic Dynamics. West Virginia University, Morgantown.

Sweka, J. A. & K. J. Hartman, 2008. Contribution of terrestrial invertebrates to yearly brook trout prey consumption and growth. Transactions of the American Fisheries Society 137: 224–235.

Thompson, A. R., J. T. Petty & G. D. Grossman, 2001. Multiscale effects of resource patchiness on foraging behaviour and habitat use by longnose dace, *Rhinichthys cataractae*. Freshwater Biology 46: 145–160.

Thorp, J. H. & A. P. Covich, 2001. Ecology and Classification of North American Freshwater Invertebrates, 2nd ed. Academic Press, San Diego, CA.

Torgersen, C. E., D. M. Price, H. W. Li & B. A. McIntosh, 1999. Multiscale thermal refugia and stream habitat associations of Chinook salmon in northeastern Oregon. Ecological Applications 9: 301–319.

Utz, R. M. & K. J. Hartman, 2006. Temporal and spatial variation in the energy intake of a brook trout (*Salvelinus fontinalis*) population in an Appalachian watershed. Canadian Journal of Fisheries and Aquatic Sciences 63: 2675–2686.

Utz, R. M. & K. J. Hartman, 2007. Identification of critical prey items to Appalachian brook trout (*Salvelinus fontinalis*) with emphasis on terrestrial organisms. Hydrobiologica 575: 259–270.

Utz, R. M. & K. J. Hartman, 2009. Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 66: 1072–1080.

Warren, D. R., J. M. Robinson, D. C. Josephson, D. R. Sheldon & C. E. Kraft, 2012. Elevated summer temperatures delay spawning and reduce redd construction for resident brook trout (*Salvelinus fontinalis*). Global Change Biology 18: 1804–1811.

Webster, J. J. & K. J. Hartman, 2005. The role of terrestrial invertebrates in allopatric brook trout headwater streams in the central Appalachian mountains. Journal of Freshwater Ecology 20: 101–107.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet & J. E. Williams, 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change PNAS 108: 14175–14180.

Wipfli, M. S., 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 54: 1259–1269.

Wipfli, M. S., J. Hudson & J. Caouette, 2003. Marine subsidies in freshwater ecosystems: *Salmon carcasses* increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society 132: 371–381.

Xu, C. L., B. H. Letcher & K. H. Nislow, 2010. Context-specific influence of water temperature on brook trout growth rates in the field. Freshwater Biology 55: 2253–2264.

Young, R. G., J. Wilkinson, J. Hay & J. W. Hayes, 2010. Movement and mortality of adult brown trout in the Motupiko River, New Zealand: effects of water temperature, flow, and flooding. Transactions of the American Fisheries Society 139: 137–146.