

RAINBOW TROUT VERSUS BROOK TROUT BIOMASS AND PRODUCTION UNDER VARIED CLIMATE REGIMES IN SMALL SOUTHERN APPALACHIAN STREAMS

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Abstract—Many Appalachian streams historically dominated by Brook Trout *Salvelinus fontinalis* have experienced shifts towards fish communities dominated by Rainbow Trout *Oncorhynchus mykiss*. We used empirical estimates of biomass and secondary production of trout conspecifics to evaluate species success under varied thermal regimes. Trout populations were sampled in 13 Appalachian streams from Maryland to North Carolina during summer 2012, and biomass and production of trout species were examined in relation to habitat and water temperature data. Rainbow Trout and Brook Trout were found co-occurring at three sites, Rainbow Trout populations were encountered at an additional five sites, and Brook Trout populations were also encountered at an additional five sites. Brook Trout co-occurred at one site with Brown Trout *Salmo trutta*. Biomass estimates for Brook Trout and Rainbow Trout ranged from 0.01 to 1.15 g•m⁻² and 0.35 to 1.60 g•m⁻², respectively. Secondary production estimates for Brook Trout and Rainbow Trout ranged from 0.12 to 1.09 g•m⁻²•yr⁻¹ and from 0.06 to 7.48 g•m⁻²•yr⁻¹, respectively; thus, Rainbow Trout tended to dominate production in study streams where both species co-occurred. Brown Trout biomass where it co-occurred with Brook Trout was 1.14 g•m⁻² and production was 1.20 g•m⁻²•yr⁻¹; thus, it also dominated biomass and production compared to Brook Trout. Logistic regressions revealed percent production of Rainbow Trout had a positive relationship with mean minimum winter air temperature ($P < 0.05$) and, conversely, percent production of Brook Trout had a negative relationship with mean minimum winter temperature ($P < 0.05$). Thus, temperature coupled with interspecific competition could be influencing Brook Trout production in these mixed trout streams. Our results suggest that with increasing winter temperatures Brook Trout production could decrease, further highlighting the need to mitigate the effects of climate change on Brook Trout in their native range.

INTRODUCTION

Brook Trout *Salvelinus fontinalis* are increasingly threatened across their native range by a myriad factors, including increasing temperatures, habitat fragmentation, nonnative species, and other natural and anthropogenic disturbances (Larson and Moore 1985; Meisner 1990; Thieling 2006; Poplar-Jeffers et al. 2009). As a result, Brook Trout biomass, secondary production, and habitat preferences in the southern Appalachians and elsewhere in the eastern United States have been intensely studied and often compared to similar estimates and preferences of nonnative trout species, Rainbow Trout *Oncorhynchus mykiss* and Brown Trout *Salmo trutta* (Neves and Pardue 1983; Whitworth and Strange 1983; Ensign et al. 1990; Flebbe and Dolloff 1995; Kwak and Waters 1997). Rainbow Trout and Brown Trout tend to dominate in areas where Brook Trout co-existed and that once Rainbow Trout establish, they typically usurp Brook

Trout in dominance (Waters 1983; Whitworth and Strange 1983). Yet, continued studies on dynamics and thresholds for species dominance are still needed to understand these patterns in the context of multiple or additive anthropogenic effects, e.g., synergistic effects of species invasions and climate change (Clark et al. 2002; Fausch 2008).

Biomass and secondary production can be used as indicators of biological success to gage the relative success of co-existing species (Waters 1983; Hayes et al. 2007). Secondary production is defined as the formation of living mass of a heterotrophic population or group of populations over some period of time (Waters and Crawford 1973). Secondary production is especially attractive as a response variable due to its integration of other important biological variables (abundance, growth and biomass) into a single dynamic metric. Indeed, rates of secondary production have already served as a strong tool for better

understanding fish populations and for improving conservation management initiatives in the face of environmental change (Waters 1977; Valentine-Rose et al. 2011). Furthermore, the concept of production is strongly aligned with the goals of fisheries science and management more generally (Waters 1977; Waters 1983). The principle reason for the lack of utilization of production as a response variable appears to be mostly related to the time and cost involved in its calculation (Dolbeth et al. 2012). Understanding the production dynamics of co-occurring and competing species may be critical to the future conservation management of coldwater fish populations. Whereas, species possess unique thermal ecologies as a result of different evolutionary trajectories (Magnuson et al. 1979), their biological response to thermal change might be highly divergent (Lyons et al. 2010; Rypel 2013). With increasing temperatures, there could be concomitant shift in fish communities towards species more tolerant of higher temperatures in Appalachian streams (Dunham et al. 2002; Chu et al. 2005). The goal of this study was to use trout biomass and secondary production coupled with continuous air and water temperature and general habitat and water quality data to determine which trout species (i.e., Brook Trout or Rainbow Trout) exhibited increased dominance across a macro-ecological gradient in small southern Appalachian streams.

METHODS

Study sites—Thirteen streams were randomly selected from approximately 100 streams previously identified as potential southern Appalachian Brook Trout habitat by the United States Forest Service, Eastern Brook Trout Joint Venture (EBTJV 2006), and Virginia Tech. The study sites were located in West Virginia, Virginia, Maryland, and North Carolina with one site in Tennessee. Streams covered a variety of localities and physiographic provinces including the Alleghany Mountains, Great Smoky Mountains, Blue Ridge Mountains, and in the Piedmont region of the Appalachian Mountains (Figure 1). Study streams were mostly second and third order streams ranging from elevations of 360 to 1,050 meters and average annual air temperatures of 9.8 to 13.80 °C. Habitat attributes were relatively homogenous across study locations as we selected streams with similar physical

habitat characteristics (e.g., watershed area, stream length, percent forested area, etc.) to decrease the influence of these potential covariates in the analysis.

Data collection—A onetime sampling event at each study stream was conducted from June 2012 to August 2012. We randomly selected a starting point upstream of the HOBO air and water temperature loggers at each study site. Using an Appalachian Aquatics Backpack Electrofishing Unit (Morristown, TN), we sampled fish from two 50-m reaches spaced 50 m apart until depletion. Small mesh block nets were placed upstream and downstream of the reach to prevent fish immigration and emigration during the sampling period. We measured total lengths (mm) and weights (g) of all trout captured, euthanized 15-30 individuals in tricaine methanesulfonate (MS-222) of varying lengths, and immediately placed specimens on ice for transport and otolith removal in the lab.

We used the Basinwide Visual Estimation Technique, BVET, to estimate various independent habitat parameters at each reach (e.g., dominant/subdominant substrate, percent riffle/pool/run habitat, amount of large wood, etc.) (Dolloff et al. 1993). We also collected replicate water samples, which were analyzed at the Coweeta Hydrologic Laboratory for ammonium, nitrite, nitrate, phosphorous, sulfate, potassium, calcium, and magnesium using standard methods (USEPA 1983a; USEPA 1983b). We calculated several temperature variables using the continuous temperature data recorded by the HOBO temperature loggers. We determined the mean annual temperatures, the average daily maximum and minimum summer temperatures, and the average daily maximum and minimum winter temperatures from the year preceding the sampling event.

In the lab, we removed otolith sagittae from all trout collected and weighed the stomach contents of each individual. Ages of each fish were blindly estimated by an experienced reader by viewing each otolith under a stereomicroscope interfaced with image analysis software. Site- and species-specific logarithmic and von Bertalanffy growth functions ($L=L_{\infty}(1-e^{-K(t-t_0)})$) created using EXCEL solver were then used to predict the age of all measured fish (for which no otoliths were taken) using the total length as the predictor (Allen 1966). Biomass was determined by summing the weights of all trout encountered and dividing by the total area sampled. To calculate

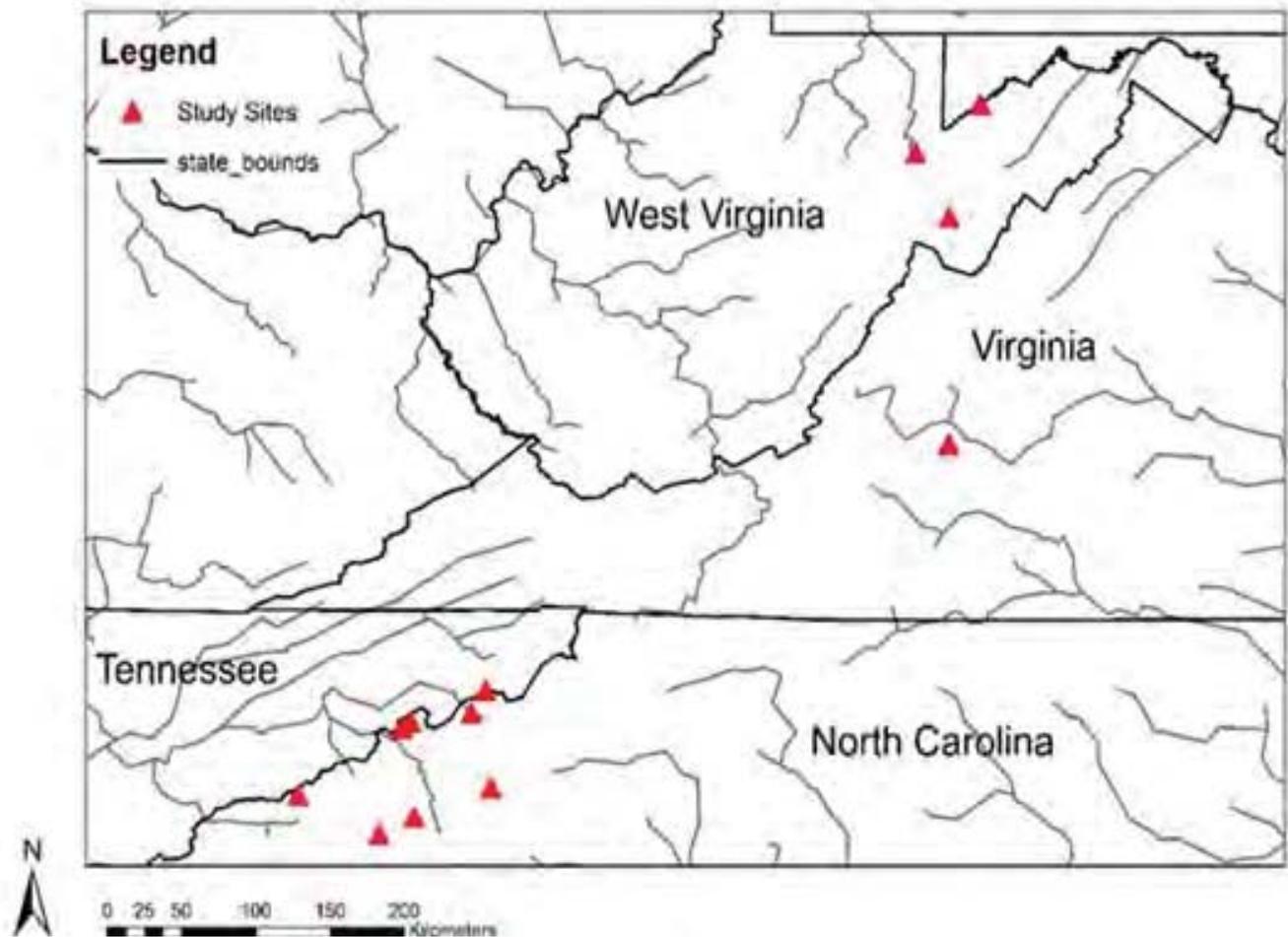


Figure 1. Study stream locations in the southern Appalachian Mountains in Maryland, West Virginia, Virginia, North Carolina and Tennessee sampled during summer 2012.

secondary production we used a modified version of the instantaneous growth rate method (P=GB) (Waters 1977; Hayes et al. 2007), which sums the accumulation of biomass between age classes (B) and is multiplied with the instantaneous growth rate (G) (Valentine-Rose et al. 2007; Valentine Rose et al. 2011). Negative production values were considered to be 0.

Data analysis—Statistical mean comparisons of Brook Trout and Rainbow Trout biological estimates were not conducted due to our limited sample size of streams where both species co-occurred. We calculated total trout biomass and production at each site by taking the sum of the biomass or production estimates for both Brook and Rainbow Trout. With these data, we conducted a multiple linear regression using XLSTAT software on the log-transformed total

production estimate using potential habitat covariates (i.e., $[\text{NO}_3]$, $[\text{Ca}]$, and mean minimum winter temperatures). Non-parametric Spearman r correlations were conducted among the covariates and total trout production, Brook Trout production, and Rainbow Trout production. We then determined the percent biomass and percent production of Brook Trout and Rainbow Trout relative to the total trout values at each site. We conducted a set of multiple multinomial logistic regressions with percent biomass and percent production of the species as the dependent variables, and various temperature and water chemistry variables as potential predictors. We then selected the lowest Akaike Information Criteria (AIC) model to identify the independent variables that accounted for the most variation in percent biomass and percent production for Brook Trout and Rainbow Trout logistic models.

RESULTS

Biomass, production, estimates—Rainbow Trout were encountered at eight streams with number of individuals ranging from 5 to 78, and Brook Trout were encountered at eight streams with number of individuals ranging from 3 to 72. Both Rainbow Trout and Brook Trout occurred together at three sites. One individual Brown Trout occurred at one site with both Rainbow Trout and Brook Trout (Beech Flats Prong), and 16 Brown Trout were encountered at one site where Brook Trout were present (Scapecat Branch). Biomass estimates ranged from 0.01 to 1.15 $\text{g}\cdot\text{m}^{-2}$ and 0.35 to 1.60 $\text{g}\cdot\text{m}^{-2}$ for Brook Trout and Rainbow Trout, respectively. Production estimates ranged from 0.00 to 1.09 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and from 0.00 to 7.48 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for Brook Trout and Rainbow Trout, respectively. Brown

Trout production at Scapecat Branch was 1.20 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. Brook Trout production to biomass (P/B) ratios ranged from 0 to 2.12, and Rainbow Trout production to biomass ratios ranged from 0 to 7.16. Rainbow Trout tended to dominate production, biomass, and P/B across all 13 sites; however, Brook Trout had higher abundances (Figure 2).

Temperature-Production regressions—Log transformed total trout production had a significant, positive relationship with mean minimum winter temperature while controlling for [Ca] and [NO₃] ($P=0.009$) (Figure 3). Holding [Ca] and [NO₃] constant for every one degree increase in the mean minimum winter temperature, log transformed total trout production is expected to increase by 0.1 units. Furthermore, when species-specific production

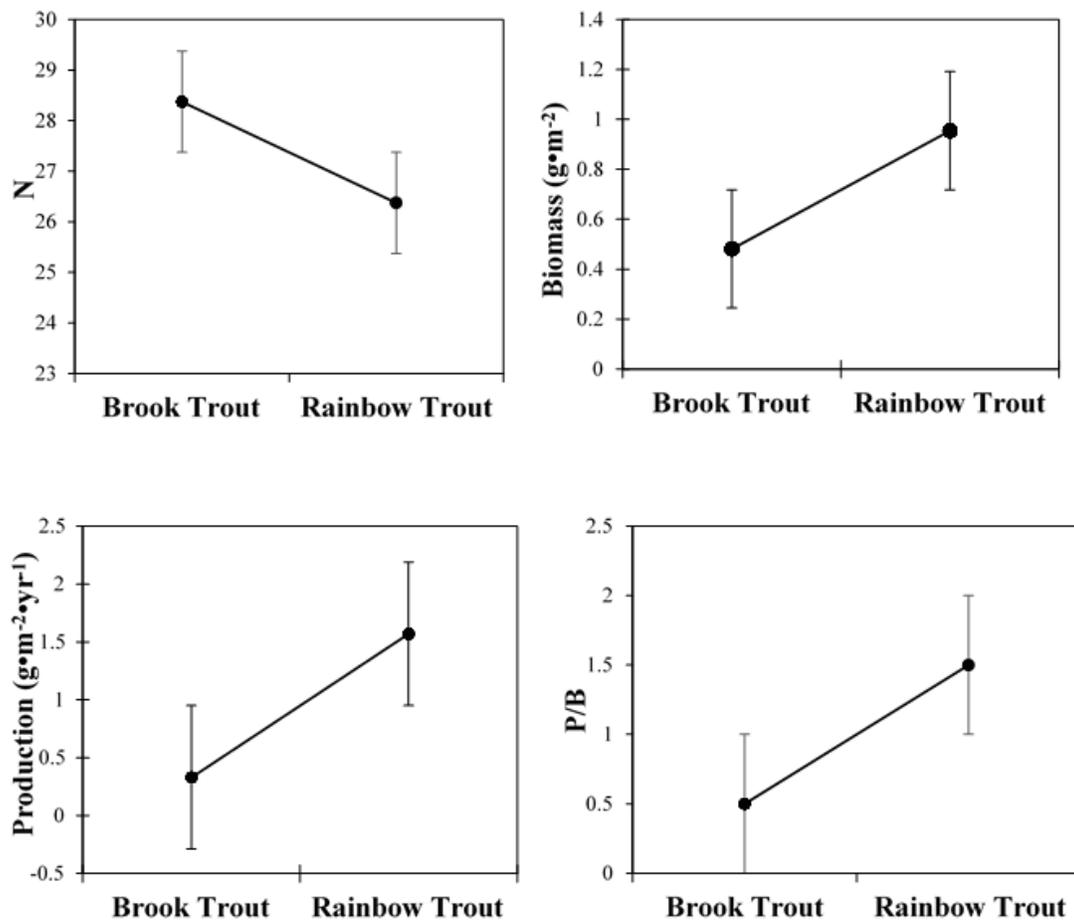


Figure 2. Interspecific comparison of Mean N (number of individuals), biomass ($\text{g}\cdot\text{m}^{-2}$), production ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), and P/B (production/biomass ratio) with standard error bars for Brook Trout versus Rainbow Trout from 13 southern Appalachian streams sampled during summer 2012.

estimates were isolated, Rainbow Trout and Brook Trout production demonstrated opposite responses to mean minimum winter temperature (Figure 3).

A similar relationship between mean minimum winter temperature while controlling for [NO₃] and [Ca] was evident in the logistic regression models of percent biomass and percent production as the dependent variable. Brook Trout and Rainbow Trout had opposite relationships with mean minimum winter temperature. Holding [NO₃] and [Ca] constant, the odds of Brook Trout comprising 100% of the production or biomass of a trout population decreases by 0.002 and 14.8, respectively, for every 1 degree

increase in the mean minimum winter temperature. In contrast, the odds of Rainbow Trout comprising 100% of the production or biomass of a trout population increases by 0.002 and 22.5, respectively, for every one degree increase in mean winter minimum temperature holding [NO₃] and [Ca] constant.

DISCUSSION

Biomass and production—Our results are consistent with previous studies that estimated trout biomass, production, and P/B ratios in similar habitats in Minnesota, USA and other southern Appalachian

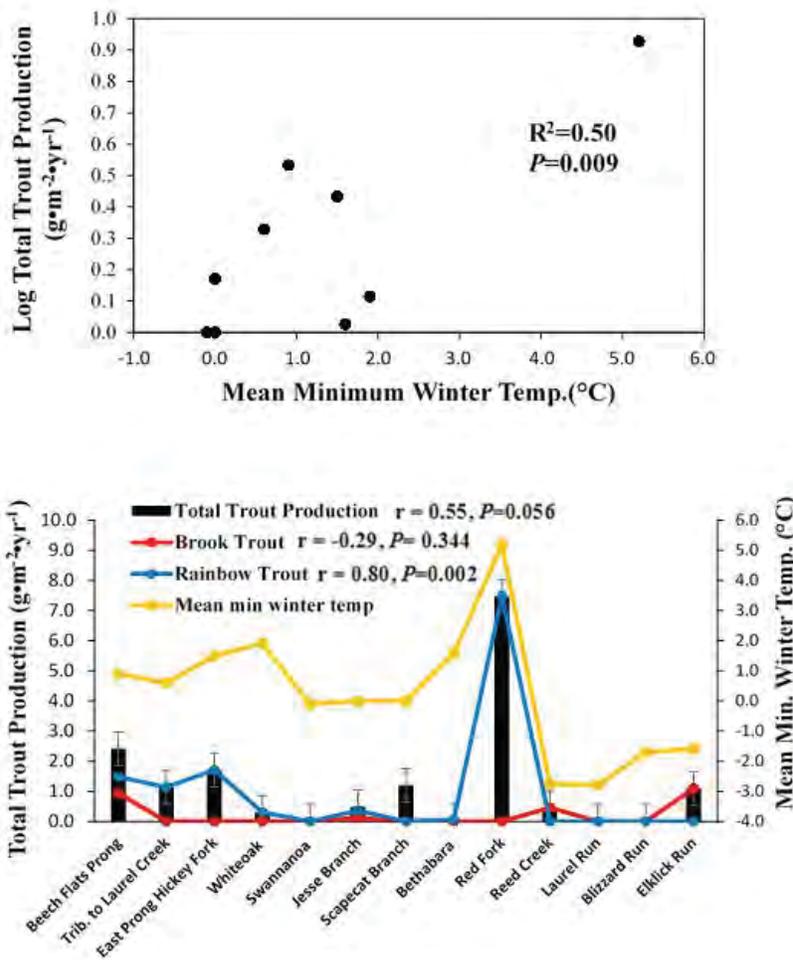


Figure 3. Graph 1-Log total Trout production (g·m⁻²·yr⁻¹) as a function of mean minimum winter air temperature (°C). Adjusted R² and P-value shown on graph. Graph 2-Total Trout production (sum of Trout species production, g·m⁻²·yr⁻¹) (black bars) and the amount of Brook Trout (red line) and Rainbow Trout (blue line) production with the associated mean minimum winter air temperature (°C) (yellow line) at each stream location. Spearman's r values with associated P-values in the legend correspond to correlations between trout production rates and mean minimum winter temperature.

streams (Whitworth and Strange 1983; Kwak and Waters 1997) (Table 1). From this study, Rainbow Trout production and the P/B ratio at one site were both above 7.0, which is slightly higher than other published estimates. This particular site had a large amount of age 0 fish; thus, the production rate increased dramatically compared to streams with older age classes, which is a typical trend, and is still within the range of published data (Waters 1977; Neves and Pardue 1983; Neves et al. 1985). Brook Trout production estimates were similar to those of Brook Trout co-occurring in areas with Rainbow Trout in another Appalachian stream (Whitworth and Strange 1983). Neves et al. (1985) also found Brook Trout production to be lower in areas with Rainbow Trout present, and Rose (1986) concluded that Brook Trout abundance was lower when competitors (e.g., Rainbow Trout) were present. In general, southern Appalachian streams have low densities of Brook Trout due to soft water and reduced stream fertility (Neves and Pardue 1983). Using these empirical estimates, we concluded that Rainbow Trout likely dominate streams compared to Brook Trout when both species co-occur; however, a larger sample size of mixed trout streams require sampling to strengthen these results. With a larger sample size, statistical significance between mean biomass and production of co-occurring Brook Trout and Rainbow Trout could be reached, but we were unable to conclude statistical significance with only 3 streams where Rainbow Trout and Brook Trout coexisted.

Production and temperature—As a group, trout have been classified as coldwater fishes regardless

of species (Magnuson et al. 1979; Lyons et al. 2010). However, Magnuson et al. (1979) highlighted that even species within the same family can exhibit wide variation in thermal niche dimensions. As a result, small differences in thermal niche size may create disproportionate levels of interspecific competition for preferred thermal habitats where biological fitness parameters (e.g., growth) are optimized. Rainbow Trout are considered more tolerant of temperature variations than Brook Trout and have a higher maximum temperature tolerance of 24.0°C compared to 22.4°C for Brook Trout (Neves et al. 1985; Eaton and Scheller 1996). Jenkins and Burkhead (1993) noted that Brook Trout prefer temperatures between 14-16°C and Rainbow Trout prefer temperatures between 12-19°C. Competition between Brook Trout and Rainbow Trout could be influencing the effects of increased temperatures on Brook Trout's temperature threshold in the southern Appalachians. Lohr and West (1992) found Rainbow Trout occupied the middle, deeper sections of the stream while Brook Trout were forced to stay on the margins; however, when Rainbow Trout were removed Brook Trout migrated into deeper water. Brook Trout could be competitively excluded from these areas by Rainbow Trout. With increasing temperatures, margins would likely be unsuitable habitat for Brook Trout. Furthermore, behavioral differences of introduced species could be contributing to disproportionate production rates of Brook Trout in favor of Rainbow Trout. Introduced species are suggested to be more aggressive and adaptable under stress than native species (e.g., Brook Trout) (Waters 1983). This highlights the often convoluted effects temperature has on biological success of fish and

Table 1. Production rates (P) ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) for Trout species in similar streams in the southern Appalachians and elsewhere in the United States.

Stream	Rainbow Trout	Brook Trout	Brown Trout	Source
	P	P	P	
southern Appalachian streams	0.06-7.48	0.84-2.12	1.20	this study
South Fork Holston River, Virginia	3.60	*	*	Neves et al. 1985
Rocky Fork Creek, Tennessee	0.98-1.2	0.77-1.14	*	Whitworth and Strange 1983
Guy's Run, Virginia	*	0.54-1.93	*	Neves and Pardue 1983
Valley Creek, Minnesota	3.30	2.50	13.20	Waters 1983

the need to rigorously manage at-risk Brook Trout populations (Dunham et al. 2002).

Management implications—Mean annual temperatures are projected to increase by approximately 4.5°C in the future in northeastern United States (i.e., where Brook Trout are native). These changes could dramatically shrink the availability of suitable Brook Trout habitat and encourage further population declines (Eaton and Scheller 1996). With 2012 being the hottest year on record in the United States (NCDC 2013), using a robust integrative metric like production to determine the biological responses of Brook Trout to warm temperatures may be essential to documenting the response of this species to climate change. Observed patterns can be contrasted with more temperature tolerant competitors (i.e., Rainbow Trout), in mixed trout streams to intuit appropriate management decisions.

Our study revealed that winter temperature minimums were significantly related to Brook Trout and Rainbow Trout percent biomass and percent production and that analyzing several biological estimates (i.e., abundance, biomass, and production) can produce divergent results at different scales (inter- versus intraspecific). Steps will continuously need to be taken to mitigate effects of Rainbow Trout on Brook Trout in the northeastern U.S. where temperatures (especially winter temperatures) are expected to rise (Eaton and Scheller 1996). For example, Rainbow Trout removal by electrofishing and stocking of Brook Trout could be used as management tools as these methods significantly increased the densities of Brook Trout in a mixed trout stream model (Clark et al. 2002). Ultimately, a multitude of management strategies need to be employed to protect Brook Trout populations in their native range and to diminish the effects of climate change coupled with the presence of nonnative trout species.

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