

VARIATIONS IN COMMUNITY FISH PRODUCTION AND DIVERSITY ACROSS
THE APPALACHIANS: IMPLICATIONS FOR CLIMATE CHANGE

by

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Thesis submitted to the faculty of the Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

Master of Science
In
Fish and Wildlife Conservation

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January 27, 2014
Blacksburg, VA

Keywords: (secondary annual production, fish assemblages, climate change, Appalachian streams, cold-water fisheries, diversity-production relationship, P/B ratios)

VARIATIONS IN COMMUNITY FISH PRODUCTION AND DIVERSITY ACROSS THE APPALACHIANS: IMPLICATIONS FOR CLIMATE CHANGE

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ABSTRACT

Climate change is considered a major threat to freshwater ecosystems through altering biodiversity, structure, and function. Having a thorough understanding of how diverse ecosystems respond to temperature change is vital to ecosystem management and conservation. During summer 2012, I quantified fish biomass, somatic growth, secondary production, and habitat data for fish communities in 25 Appalachian streams from Vermont to North Carolina. Multiple statistical tests were conducted to determine the relationship between community fish production and air and water temperature, species thermal guild production and air and water temperature, and the relationship between community fish production and diversity. Community fish production estimates ranged from 0.15 to 6.79 g m⁻² yr⁻¹ and community P/B ratios ranged from 0.21 to 1.07. No significant differences existed between mean community production estimates at the cold-water, cool-water, warm-water, and extreme northern sites ($P=0.19$), but P/B ratios in the extreme northern streams were statistically higher than mean community P/B in cold- and cool-water streams in the southern Appalachians ($P=0.002$). Water temperatures had a positive effect on community fish production ($P=0.01$) while air temperatures did not ($P=0.10$). Both air and water temperatures were significant in predicting whether community production would be dominated by cold-water or cool-water fish ($P=0.001$, $P<0.0001$, respectively). Community fish production was

significantly, positively related to species richness ($R^2=0.38$, $P=0.001$) and was one of the highest correlates of community production ($R^2=0.52$). As climate change alters freshwater ecosystems, fish communities may transform by means of shifting fish abundance, biomass, and production among species ultimately affecting ecosystem structure, function, and biodiversity.

ACKNOWLEDGEMENTS

I want to extend my deepest gratitude to Dr. Andy Dolloff and Dr. Andrew Rypel for their constant support, advice, and encouragement throughout the two years of my master's project. I have learned invaluable lessons about fisheries research from both Dr. Rypel and Dr. Dolloff, and I'm so appreciative to have had the opportunity to work closely with them both. Secondly, I want to extend my appreciation to Dr. Jack Webster for always providing relevant and insightful comments concerning my project and wading through drafts of my working plan and thesis.

Furthermore, thank you to the CATT crew at the United States Forest Service Southern Research Station for their assistance during my field season. Special thanks to Joe Cline for his hard work in the field and office and Craig Roghair and Colin Krause for always listening to me recite my conference presentations and providing astute advice on how to improve. Huge thanks to Brandon Fair, who graciously volunteered for me in the lab and then became my lab technician processing endless amounts of fish and otoliths. Thank you to countless graduate and undergraduate students for their field support and/or emotional support throughout this process: Holly Morris, Matt Weberg, Jen Rogers, Shannon White, Brandon Peoples, Caitlin Carey, Alex Silvis, Laci Love, Jian Huang, Mitchell Masser, Thomas Olinger, John Woodward, Christina Bolton, Britney Kreiner, and Shawn Young.

Lastly, without the scientific collection permits from the following agencies this project would not have been possible: Virginia Department of Game and Inland Fisheries, North Carolina Wildlife Resources Commission, Great Smoky Mountains National Park, Tennessee Wildlife Resources Agency, Fernow Experimental Forest, West

Virginia Division of Natural Resources, and Maryland Department of Natural Resources. Keith Nislow at the Forest Service Northern Research Station was instrumental in applying for permits and selecting sites in Vermont and Massachusetts. This project was funded through the United States Forest Service Southern Research Station and Virginia Tech Department of Fish and Wildlife Conservation.

ATTRIBUTION

The three manuscripts will be submitted for publication in three separate journals.

Authors for Manuscript 1 will include myself as the primary author, Dr. C. Andrew Dolloff, Dr. Andrew L. Rypel, Dr. Jackson R. Webster, Dr. Keith Nislow, and Brandon Fair. Dr. Dolloff, Dr. Rypel, and Dr. Webster helped throughout the entire process of Manuscript 1 and were integral parts of developing ideas, methods, and editing the manuscript. Dr. Nislow helped pick and collect data at 5 sites that would not have been possible without his help, and Brandon Fair was vital in processing samples in the lab. Manuscript 2 and 3 will include myself as primary author and my three committee members as they were vital in the development of the ideas, data analysis, and editing of the manuscript.

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THESIS INTRODUCTION

Secondary production rates quantify population success of heterotrophic organisms through time and are directly associated with ecosystem structure and function (Hayes et al. 2007; Valentine-Rose et al. 2007; Dolbeth et al. 2012). Production may be the most sensitive surrogate to evaluate changes in fish populations in response to biotic and abiotic disturbances (Valentine-Rose et al. 2011; Dolbeth et al. 2012). Ricker (1946) and Allen (1951) were some of the first to estimate fish production and revealed the power of production as a powerful metric used to describe a fish population. Since then, fish production studies have been conducted all over the world in a variety of stream, river, and lake ecosystems (e.g., Freeman et al. 1988; Kwak and Waters 1997; Lobón-Cerviá 2003; Mackenzie and Koster 2004; Almodóvar et al. 2006; Valentine-Rose et al. 2007; Valentine-Rose et al. 2011). For example, secondary production rates of fishes have been related to anthropogenic disturbances (Valentine-Rose et al. 2007; Valentine-Rose et al. 2011), water quality and nutrient concentrations (Kwak and Waters 1997; Almodóvar et al. 2006), recruitment rates (Lobón-Cerviá 2005), and habitat diversity (Schlosser 1982). Temperature change can alter fish production through a variety of mechanisms including influencing metabolic rate (Fry 1971), recruitment (Casselman et al. 2002), growth (Nicola and Almodóvar 2004; Rypel 2009), reproduction (Ficke et al. 2007), and range expansion (Chu et al. 2005). With increasing temperatures, secondary production is predicted to change as a consequence of both direct and indirect components of climate change (Dolbeth et al. 2012). Thus, like Dolbeth et al. (2012) suggested, further empirical estimates of secondary production responses to climate change and other stressors will provide invaluable information on ecosystem function and response to threats that biomass and density estimates will not provide alone.

Evaluating community fish production responses to climate change is complex as other factors influence fish production including community biotic factors such as species richness and community evenness (Dolbeth et al. 2012). For example, latitude plays an especially strong role in driving species composition and diversity according to the Latitudinal Diversity Gradient - a widely accepted theory that species richness increases towards the tropics (Hillebrand 2004; Allan and Castillo 2007). While a considerable number of studies have examined diversity-production gradients in terrestrial plant communities (Hector et al. 1999; Tilman et al. 1996; Zak et al. 2003; Tilman et al. 2012) , further research needs to be conducted on the diversity-production relationships in aquatic communities and on freshwater fish (Dolbeth et al. 2012). Fish production studies have documented a positive relationship between species richness and community fish production (Valentine-Rose et al. 2007), a negative trend between species richness and community fish production (Penczak 1981), and no correlation between species richness and fish production (Watson and Balon 1984). However, climate change is expected to have a significant effect on fish assemblages (Chu et al. 2005; Ficke et al. 2007; Lyons et al. 2010); thus, connecting climate change, diversity, and fish production may further increase understanding of the dynamic responses of fish population structure and function to climate change.

Although climate change is predicted to alter structure and function of ecosystems worldwide, some areas are particularly threatened based on species composition and spatial location (Thomas et al. 2004; IPCC 2007). Some freshwater ecosystems like streams in the southern Appalachians are of special concern as they are often hyper-diverse with high levels of endemism (Scott and Helfman 2001). Furthermore, streams at higher latitudes like streams in the Appalachian Mountains are more susceptible to larger temperature changes than tropical and

subtropical streams (ACIA 2004). The three main objectives of my research were to 1) estimate and compare annual production and production to biomass ratios for entire fish assemblages in 25 streams ranging from Vermont to North Carolina, 2) analyze relationships between temperature and community-level annual production and thermal guild production while attempting to account for other potential covariates of production (e.g., habitat complexity, stream size, nutrient availability), and 3) calculate and compare the allocation of production among species in each stream along with relationships between α -diversity (e.g., species richness, Shannon Weiner index, and Pielou's evenness index) and community production, and compare coefficients from diversity-production relationship to similar, previously published relationships for other taxa.

Manuscript 1 Title:
COMMUNITY FISH PRODUCTION DYNAMICS ACROSS A LATITUDINAL GRADIENT
IN EASTERN NORTH AMERICA

ABSTRACT

Climate change is a continuous and significant threat to freshwater ecosystems worldwide. Understanding freshwater fish communities' functional responses to climate change is essential in the conservation of biodiversity and management of economically important species e.g., Brook Trout *Salvelinus fontinalis* in Appalachian streams of Eastern United States. The main goal of this study was to estimate and compare annual community production and community production to biomass ratios for 25 streams in the Appalachian Mountains with varying temperature regimes. I sampled fish communities at 25 low-order, high-elevation streams during June 2012 to September 2012 across a latitudinal gradient from Vermont to North Carolina. Using the instantaneous growth rate method, I calculated annual fish production and community fish production. Community fish production estimates ranged from 0.15 to 6.79 g m⁻² yr⁻¹ and community P/B ratios ranged from 0.21 to 1.07. No significant differences existed between mean community production estimates at the cold-, cool-, warm-water, and extreme northern sites ($P=0.19$), but P/B ratios in the extreme northern streams were statistically higher than mean community P/B in cold- and cool-water streams in the southern Appalachians ($P=0.002$). A high biomass turnover ratio for cold-water streams in the more northern Appalachian Mountain range suggests that these communities may be more productive and perhaps more resilient to disturbances (e.g., some climate change effects) than previously thought, and the lower biomass turnover ratio for the southern Appalachian streams suggests the converse pattern that these communities may potentially require longer amounts of time to recover from disturbances.

INTRODUCTION

Global climate change is a leading threat to biodiversity and ecosystem function in terrestrial and aquatic ecosystems (Walther et al. 2002; Thomas et al. 2004; IPCC 2007). For example, mid-range increases of temperature (1.8-2.0°C) are expected to significantly threaten 15-37% of species and taxa in certain regions (Thomas et al. 2004). Furthermore, a global temperature increase of 2-3°C and increased atmospheric CO₂ levels will substantially alter the structure and function of most ecosystems. The most recent Intergovernmental Panel on Climate Change report (IPCC 2013) predicted increases in the frequency and duration of hot extremes over land masses suggesting an increased threat for streams, rivers, and lakes. Climate change is predicted to especially threaten freshwater ecosystems and temperate freshwater fish through a variety of mechanisms (Ficke et al. 2007).

Fish species will have to adapt to a changing environment or relocate to a more suitable environment as climate change proceeds (Ficke et al. 2007). For example, fish cannot regulate their own body temperatures; thus, as temperatures increase cold-water fish may be forced to shift their range northward (Forister et al. 2010; Walther et al. 2002; Moyle and Cech 2004). Temperature change reduces the availability of suitable habitat (Hunter et al. 2010), which directly limits species niche space (Magnuson et al. 1979) and feeds back positively to increased mortality rates. Under warming conditions fish metabolism generally increases and less energy is expended on growth or reproduction; thus, temperature change further initiates increased mortality and decreased recruitment leading to reduced overall abundance (Pounds 2001; Mayfield and Cech 2002). On the contrary, slight increases in temperature are often associated with increased growth, which suggests increased productivity in a system to a certain point

before temperature increases become detrimental to the population (Kitchell et al. 1977; Myrick and Cech 2000). These consequences affirm that climate change effects can be highly non-linear and non-intuitive and can manifest in variable time periods and inversely across spatial scales (Chu et al. 2005; Ficke et al. 2007).

Freshwater ecosystems are some of the most valuable environments on Earth (Costanza et al. 1997; Ficke et al. 2007). Humans depend on freshwater for irrigation, agriculture, drinking, fisheries, recreation, and industry (Carpenter et al. 1992; Allan et al. 2005; Fischlin 2007). Yet freshwater ecosystems are highly vulnerable to climate and other forms of environmental change (Vitousek et al. 1997; Fischlin 2007; IPCC 2007). Some freshwater ecosystems like streams in the southern Appalachians are of special concern as they are often hyper-diverse with high levels of endemism (Scott and Helfman 2001). Furthermore, streams at higher latitudes like streams in the Appalachian Mountains are more susceptible to larger temperature changes than tropical and subtropical streams (ACIA 2004). These streams contain culturally and recreationally valuable species like Eastern Brook Trout *Salvelinus fontinalis* (Scott and Helfman 2001), which are especially threatened by climate change (Meisner 1990). Thus, empirical data investigating responses of fish communities and individual species to climate change are vital to both the management and conservation of species occurring in Appalachian streams.

Most freshwater climate change studies have focused on species distributional pattern shifts to temperature increases, often using a bioclimatic envelope approach (Chu et al. 2005; Parmesan and Yohe 2003; Perry et al. 2005; Sharma et al. 2011). Although helpful, species distributional patterns do not necessarily provide information on the health, abundance, overall status, or functional responses to stress of populations (Kraft et al. 2008; Lancaster and Downes 2010), including how they might react to a changing climate (Pearson and Dawson 2003). For

example, species presence does not necessitate optimal habitat as individuals can often persist in sub-optimal environments over time, albeit at low levels (Devictor et al. 2011; Rypel 2011).

Thus while predictions exist concerning distributional shifts of species over time (Walther et al. 2002; Chu et al. 2005; Lyons et al. 2010), a more in-depth understanding of how functional metrics (e.g., growth, reproduction, mortality) might respond to changing climate in freshwater ecosystems is needed (Casselman 2002).

Production (i.e., the formation of organism biomass over time) is a foundational concept in ecology (Nicholson and Bailey, 1935; Lindeman 1942; Odum 1960; Odum 1969) and is an especially comprehensive, composite, ecosystem-scale metric that integrates several population-level metrics (e.g., density, biomass, growth, and mortality) in aquatic ecosystems (Hayes et al. 2007; Valentine-Rose 2007). Historically, ecologists have used production rates to quantify energy availability and flows across trophic levels to gain understanding of organismal interactions (Lindeman 1942, Odum 1957; Odum 1969). In what is widely considered one of the foundational studies on food webs, Lindeman (1942) demonstrated how production might be conceptualized and used to estimate energy availability and flow across trophic levels of Cedar Bog Lake, MN. Fish production may also be an ideal metric to use when investigating fish population responses to environmental changes and disturbances and may provide considerably more information relative to static biological measures, e.g., biomass (Hayes et al. 2007; Lobón-Cervía et al. 2011; Dolbeth et al. 2012).

Empirical estimates of community fish production exist for fish species, populations, and regions in the literature (Goodnight and Bjornn 1971; Hopkins 1971; Mann 1971; Penczak 1981; Halyk and Balon 1983; Mazzoni and Lobón-Cervá 2000; Valentine-Rose et al. 2011). Apparently, only one study has quantified community fish production in the southern

Appalachian stream environments at one stream, Guy's Run, Virginia (Neves and Pardue 1983). Thus, more studies and research providing empirical community fish production estimates along varying temperature regimes need to be conducted, since temperature is considered an important factor influencing fish production (Kwak and Waters 1997; Casselman 2002; Almodóvar et al. 2006). In this study, my main objective was to estimate and compare annual community production and community production to biomass ratios for 25 streams in the Appalachian Mountains with varying temperature regimes (i.e., cold, cool, warm, and extreme northern) ranging from Vermont to North Carolina.

METHODS

Study Area.—Study streams were selected from a network of 204 stream sites that were previously identified as potential brook trout habitat by the United States Forest Service Southern Research Station in Blacksburg, VA (USFS SRS). I randomly selected 10% (i.e., 20 sites) from the total 204 sites for quantification of community fish production and five additional “northern” sites selected by the USFS as representative fish production data on streams in more extreme northern latitudes for a total of 25 sampling locations.

The 25 study streams were located in Vermont, Massachusetts, Maryland, West Virginia, Virginia, Tennessee, and North Carolina (Figure 1). Overall, study streams were mostly 2nd and 3rd order streams and were situated across a gradient of latitudes and temperature along the Appalachian Mountain Range. Streams covered a variety of localities and physiographic provinces including the Alleghany Mountains, Great Smokey Mountains, Blue Ridge Mountains, and Piedmont Region in the Southern Appalachian Mountain Range. The five sites in the

extreme northern states, Vermont and Massachusetts, were located in the Green Mountains and Taconic Mountains in the Northeast Appalachians. In Maryland, Virginia, and West Virginia, study streams were located in the Potomac River watershed, James River watershed, and Tennessee River watershed. In Tennessee, the study streams were located in the Upper Tennessee River basin and Nolichucky watershed. The study streams were located in the French Broad River basin, in the Upper Pigeon watershed, in the Upper French broad watershed, Catawba River basin, and Little Tennessee River basin and watershed in North Carolina. In Vermont and Massachusetts, the study sites were located in the Connecticut River Watershed.

Most study streams were characterized by dense canopy cover, were mostly cobble dominated substrate, and had a mean elevation of 540 meters \pm 240 meters (Appendix D). Specific conductance ($\mu\text{S}/\text{cm}$) ranged from 11.3 to 410.0, dissolved oxygen content ranged from medium to high, and pH ranged from 6.5 to 8.0 (Appendix D). Streams contained mostly soft water with average calcium concentrations ranging from 0.62-61.67 mg/L and average magnesium concentrations ranging from 0.21-16.71 mg/L (Appendix D).

Stream Site Temperature Classification.—Using continuous water and air temperature data recorded using HOBO (Bourne, MA, USA) air and water temperature loggers located downstream of each study site and collected by the USFS SRS Coldwater Fisheries Unit, I calculated a variety of temperature metrics for each of the 20 sites located in North Carolina, Tennessee, Virginia, West Virginia, and Maryland including mean annual temperature, annual temperature variability (i.e., standard deviation), minimum summer and winter temperatures, maximum summer and winter temperature, and mean summer temperatures for both the air and water temperature data (Shuter et al. 1980; Casselman 2002; Neuheimer and Taggart 2007). All temperature metrics were calculated based on the year preceding the sampling event (March

2011-March 2012). To *a priori* classify the 20 streams into cold-, cool-, and warm-water streams, I conducted a K-means cluster analysis using a limitation of three clusters. Six temperature metrics were included in the cluster analysis: mean annual air and water temperature (°C), mean summer (June 2012 to August 2012) air and water temperature (°C), and the mean maximum summer air and water temperature (°C) (Wehrly et al. 2003). Extreme northern study streams in Vermont and Massachusetts were *a priori* considered a separate temperature cluster without analysis. Temperature data for the two sites in Vermont were obtained from the nearest USGS temperature logger (USGS 2012), and temperature data for the three sites in Massachusetts was estimated using the Hampshire College Weather Station temperature data from March 2011 to March 2012 (personal communication, Steve Roof).

Fish Sampling.—All 25 sites were sampled during June to September 2012 using a systematic sampling design via backpack electrofishing units. Fish were sampled from two 50 meter stream reaches spaced 50 meters apart until depletion. Block nets with 1/16" mesh were placed downstream and upstream of each 50 meter reach to inhibit immigration and emigration of fish within the sampling area. For all individuals captured, total lengths (mm) were measured and wet weights (g) estimated in situ. A sub-sample of each species captured at each site were euthanized in tricaine methanesulfonate (MS-222) and transported to the lab on ice and frozen for otolith removal, age estimation, and stomach weight determination (g). Following Ketchen (1950) and Devries and Frie (1996) sub-sampling protocol, a fixed stratified sub-sample of 10 individuals per species per length group was collected. To reduce sampling bias, length-group intervals were relatively small (i.e., 30-40mm, 40-50mm, 50-60mm) (Devries and Frie 1996).

Nutrient Sampling.—Duplicate water samples were collected at each stream upstream of the upper reach before sampling started to prevent contamination. Samples were immediately

placed in a cooler with dry ice to ensure fast freezing. The Coweeta Hydrologic Laboratory (Otto, NC, USA) analyzed the water samples for ammonium, nitrite, nitrate, phosphorous, sulfate, potassium, calcium, and magnesium using standard methods (USEPA 1983a; USEPA 1983b). In addition, I used a Yellow Springs Instrument professional probe (Yellow Springs, OH, USA) to obtain a point measurement of water temperature (°C), pH, conductivity ($\mu\text{S}/\text{cm}$), and dissolved oxygen (mg/L).

Habitat Survey.—Habitat data were recorded for the entire 150 meter reach section using a similar estimation method as outlined in the Basinwide Visual Estimation Technique, BVET (Dolloff et al. 1993). In addition to the BVET parameters recorded (e.g., dominant and subdominant substrate, large wood, average and maximum depth, width, habitat units), canopy cover in each habitat unit was recorded using a convex densitometer (Dolloff et al. 1993). Exact length of the sampled reaches and the stream wetted width were measured to the nearest tenth at every 10 meters within the two sampled reaches.

Stream velocity was measured at two transects within the sampling reach using a Marsh-McBirney (Harrisburg, PA, USA) Flo-mate 2000 flow meter. Discharge was measured and calculated using standard methods and the equation expressed by Gore (1996)

$$Q=A \cdot v$$

where Q=discharge, A=area, and v=velocity.

Production calculations.—Otolith sagittae were removed from each retained specimen to estimate age using standard methods (Devries and Frie 1996). Putative annual growth rings were counted under a microscope and interannual growth increments measured by an experienced reader using a computer-based image analysis system interfaced with the microscope. Length-at-

previous ages of all fish were calculated using the Fraser-Lee method (Francis 1990) using the equation

$$L_t = c + (L_c - c) * (O_i / O_c)$$

where L_t =back calculated length at i th annuli, c =intercept constant, L_c =length of fish at capture, O_i =otolith radius at i th annuli, and O_c =otolith radius at capture (Francis 1990; DeVries and Fries 1996). The intercept for each species was determined by plotting fish length as a function of otolith radius length (Francis 1990). Finally, logarithmic or power growth functions were used to predict the age of measured fish from the field using the equation developed from the age-length scatterplots. Mainly logarithmic growth functions were used because the majority of species had relatively low maximum ages.

Secondary production values for each species were estimated using the instantaneous growth rate method (Waters 1977; Hayes et al. 2007). Age-specific growth (G) was calculated using the equation

$$G = \ln(\text{age class}_{x+1} / \text{age class}_x)$$

Age-specific biomass was calculated as the sum of the weights of all individuals sampled within that age class. Age-specific production was then estimated as the production of age-specific biomass and growth (Halyk and Balon 1983; Valentine-Rose et al. 2007, 2011). This method integrates the area under the traditional Allen curve with fish age classes on the x-axis and mean weight on the y-axis (Allen 1949; Hayes et al. 2007). The equation used to calculate production was

$$P = \bar{G} \bar{B}$$

where P =production, \bar{B} =arithmetic mean standing stock, and \bar{G} =instantaneous growth rate.

Annual production ($\text{g m}^{-2} \text{ yr}^{-1}$) was calculated as the sum of production between each age class

(Halyk and Balon 1983). Community fish production was calculated by summing the individual species annual production values (Halyk and Balon 1983). The P/B ratio was calculated as annual production divided by biomass as an estimate of the estimated biomass turnover rate for each species in each stream (Waters 1977; Hayes et al. 2007). Community P/B was calculated by dividing total community production by community biomass.

Fish Species Temperature Classification.—All fish species collected at the 25 study streams were grouped into three temperature groups (i.e., cold-water species, cool-water species, and warm-water species). Using Magnuson et al. (1979) and Lyons et al. (2010) classifications, I assigned each species encountered to the appropriate temperature group. If a species was not included in the Magnuson et al. (1979) or the Lyons et al. (2010) classification, I used published information on the preferred temperature range for the species in question outlined by Jenkins and Burkhead (1993) to determine the appropriate temperature classification for that species.

The amount of production allocated to each species temperature group (i.e., cold-water species, cool-water species, and warm-water species) was determined as the sum of the production values of cold-water species, cool-water species, and warm-water species, separately, of the total community fish production per site. In addition, the percentage of cold-water species, cool-water species, and warm-water species production was determined for each of the four stream temperature groups (i.e., cold-water streams, cool-water streams, warm-water streams, and the extreme northern streams).

Assumptions.—One major assumption of any study relying on the instantaneous growth rate method is that a snapshot estimate of annual production remains relatively consistent over sub-annual time scales. For example, if an investigator captured an abnormally large number of fish during a one-time sample (e.g., during a mass migration event), the abundance and biomass

measures would not be reflective of the true biomass and thus production typically occurring within the ecosystem annually. However, other methods of production calculation that incorporate temporal variations (e.g., the increment summation and size-frequency methods) are laborious and time-consuming, often requiring monthly sampling over long periods (Halyk and Balon 1983). These methods would be impractical in a larger scale analysis of community fish production and would probably preclude the type of study conducted here (Benke 1979; Halyk and Balon 1983). Moreover, most published fish production studies do not rely on empirical measures of production but instead on empirical models that predict production from biomass data alone (Robertson 1979; Mertz and Myers 1998; Randall and Minns 2000). Ultimately, the instantaneous growth method is an *in situ*, empirical, and frequently used method to evaluate fish production, oftentimes using only a one time sample (Halyk and Balon 1983; Valentine-Rose et al. 2007; Lobón-Cerviá 2011; Valentine-Rose et al. 2011).

I also addressed these potential methodological critiques by sampling two reaches per site instead of one, by using block nets upstream and downstream, and by returning a few months later to resample a subset of the sites (n=5 streams) at different locations so as to place my results in an appropriate context. A simple t-test conducted in JMP 10.1 statistical software revealed no significant difference in the mean production per species or total community production values between the summer sample and the fall sample ($P=0.43$, $P=0.24$, respectively). This suggests that community annual production estimates remained statistically the same between the two time periods. Empirical community production estimates were slightly lower in the fall compared to the summer but not significantly, presumably due to natural mortality. Secondly, annual production estimates are considered relatively reliable when more biological metrics are used to calculate the estimate like density, biomass, and growth in this case (Hayes et al. 2007).

Finally and regardless of the limitations of any production calculation method, I used the same protocols for estimating production across all sites. Thus any production estimates in this study were, at a minimum, useful for relative comparisons among the streams used in this study.

RESULTS

Stream Site Temperature Classification.—The K-means cluster analysis grouped the 20 streams in the southern Appalachian range into three clusters. I named the clusters based on their temperature regimes relative to the high elevation Appalachian streams studied. Therefore, the cold-water streams are the coldest of the southern Appalachian streams studied while the cool-water streams are slightly warmer than the cold-water clustered streams, and the last cluster was considered warm-water streams as that cluster had the highest temperatures relative to the other two clusters. Overall, the cluster analysis resulted in three clusters comprised of cold-water streams (8 sites) (i.e., cluster 1), cool-water streams (10 sites) (i.e., cluster 2), and warm-water streams (2 sites) (i.e., cluster 3) (Figure 1, Table 1). Mean summer temperature, maximum summer temperature, and mean annual temperature for the cold-water classified streams were 19°C, 24°C, and 12°C, respectively (Figure 2, Appendix D). Mean summer temperature, maximum summer temperature, and mean annual temperature for the cool-water classified streams were 21°C, 27°C, and 12°C, respectively (Figure 2, Appendix D). Mean summer temperature, maximum summer temperature, and mean annual temperature for the warm-water classified streams were 22°C, 29°C, and 12°C, respectively (Figure 2). Lastly, mean summer temperature, maximum summer temperature, and mean annual temperature for the five extreme northern study streams were 21°C, 23°C, and 11°C, respectively (Appendix D).

Fish Species Temperature Classification.—A total of 40 species were encountered across the 25 study streams with six classified as cold-water species, 20 classified as cool-water species, and 14 classified as warm-water species. Brook Trout, Mottled Sculpin *Cottus bairdii*, and Rainbow Trout *Onchorynchus mykiss* were classified as cold-water species and comprised the highest percentage of total community abundance, biomass, and annual production when present (Appendix A-C). Blacknose Dace *Rhinichthys atratulus*, Rosyside Dace *Clinostomus funduloides*, Mountain Redbelly Dace *Phoxinus oreas*, Longnose Dace *Rhinichthy cataractae*, Bluehead Chub *Nocomis leptocephalus*, and Torrent Sucker *Thorburnia rathoeca* were the most common cool-water species encountered and when present comprised a relatively high percentage of total community abundance, biomass, and production (Appendix A and B). Common warm-water classified species were Central Stonerollers *Campostoma anomalum*, sunfish species *Centrarchus spp.*, and Margined Madtoms *Noturus insignis* (Appendix A and B).

Abundance, Biomass, Production, and P/B.—A total of 6,743 individuals were encountered in the 25 stream sites with biomass estimates and community fish annual production estimates ranging from 0.61 to 10.73 g m⁻² and 0.15 to 6.79 g m⁻² yr⁻¹, respectively (Table 1). Average biomass estimates were highest in the warm-water streams (B=7.21 g m⁻²), lower in cool-water streams (B=3.60 g m⁻²) and extreme northern streams (B=3.03 g m⁻²), and were the smallest in the cold-water streams (B=2.65 g m⁻²) (Table 1, Figure 3). However, mean community biomass estimates from all four stream types were not statistically different ($P=0.39$) (Figure 3).

Conversely, the extreme northern streams had the second highest mean community production estimates (P=2.79 g m⁻² yr⁻¹) with the warm-water streams having the highest mean community production estimates (P=4.96 g m⁻² yr⁻¹) (Table 1, Figure 3). However, only two sites

were classified as warm-water streams; thus, these results may be suspect. The southern Appalachian cold-water classified streams had the smallest mean community production ($P=1.45 \text{ g m}^{-2} \text{ yr}^{-1}$) and cool-water classified streams had the second lowest mean community production ($P=2.25 \text{ g m}^{-2} \text{ yr}^{-1}$) (Table 1, Figure 3). Similarly to mean community biomass, mean community production was not statistically different among the four stream types ($P=0.19$).

Lastly, the average community P/B ratio for the 25 streams was 0.96 with the average community P/B ratio highest in the extreme northern study streams ($P/B=1.40$) and lowest in the cold- and cool-water streams ($P/B=0.73$ and 0.85 , respectively) (Table 1, Figure 3). Mean P/B (0.92) at the warm-water streams was similar, albeit slightly higher than the mean P/B at the cool-water streams. Species richness ranged from 1 to 22 species with an average species richness of 6 (Table 1). Average species richness was highest in the warm-water streams with an average of 21 and smallest in the extreme northern sites with an average of four species (Table 1). Mean community P/B was statistically different among the four stream types ($P=0.002$). Cold-water and cool-water streams P/B were statistically the same while warm-water streams and the extreme northern streams both had unique mean P/B values.

Cold-, Cool-, and Warm-Water Species Production Dynamics.—Cold-water, cool-water, and warm-water species' contribution to total production varied across the four stream types (cold-water streams, cool-water streams, warm-water streams, and extreme northern streams). Community production at the cold-water southern Appalachian streams was dominated by cold-water species production except one stream (i.e., Reed Creek) that had over half the total community production dominated by a single cool-water species (i.e., Blacknose Dace) (Figure 4). All but one of the extreme northern sites had 100% of the production allocated to cold-water fish species (i.e., Brook Trout and Slimy Sculpin *Cottus cognatus*) (Figure 4). Community

production at the cool-water classified streams was mostly allocated to cool-water species; however, one cool-water stream had 100% production allocated to cold-water species (Rainbow Trout and Mottled Sculpin). However, these two species are considered more tolerant to temperature fluctuations than other cold-water species like Brook Trout (Jenkins and Burkhead 1993; Lyons et al. 2010) and thus may be able to persist in more transitional cool-water streams. Warm-water species production was high at one cool-water stream (i.e., Kelso Springs Branch), comprised over half of the community production in the two warm-water streams, and was zero at all five extreme northern streams (Figure 4).

In addition to variations in relative production contribution by species, the percentage of production allocated to cold-water, cool-water, and warm-water species varied across the four stream temperature categories. Cold-water species overwhelmingly dominated community production in the extreme northern sites and the cold-water southern Appalachian stream sites (Figure 3, Figure 5). However, I observed 23% lower cold-water species production of total community production from the cold-water southern Appalachian streams to the extreme northern streams. In addition, percentage of cold-water species production was lower by 40% in streams classified as cold-water than in streams classified as cool-water streams (Figure 5). Cool-water streams had a mean summer temperature 2°C higher and maximum summer temperature 3°C higher than cold-water classified streams. Furthermore, cold-water species production was reduced to only 2% of the total community production in the warm-water southern Appalachian streams, which had 3°C higher mean summer temperatures and 4°C higher mean maximum summer temperatures (Figure 3, Figure 5).

DISCUSSION

Large-scale Comparisons of Community Production and P/B ratios

Community production estimates from this study were within the range of previously published estimates of stream fishes worldwide (Table 2). The range of community fish production in this study was greater than other estimates from an Appalachian stream and similar order tributaries in eastern Kentucky (Lotrich 1973; Neves and Pardue 1983); however, Neves and Pardue (1983) estimated community fish production in one stream while my estimates represent a much larger geographic area. Thus, a larger range of community production values would be expected given the larger spatial extent of this study. Furthermore, the streams (e.g., Whiteoak Creek, Roaring Creek, Scapecat Branch, and Jesse Branch) with lower community fish production had very low concentrations of calcium and magnesium, which is characteristic of soft water streams (Allan and Castillo 2009) (Appendix E). Almodóvar et al. (2006) also found fish biomass and production to have a significant, positive relationship with higher nutrient content, and biomass and production estimates were larger in hard water streams. Soft water streams have long been considered to have lower organism production at all scales; thus, lower fish production at these streams is reasonable (Hynes 1972; Waters 1977; Allan and Castillo 2009). Secondly, the bulk of production in any population usually comes from young-of-the-year fish (Halyk and Balon; 1983; Neves and Pardue 1983; Pajak and Nevers 1987), thus, any increases or decreases in recruitment or young-of-the-year production will significantly alter total community production (Casselman 2002; Lobón-Cerviá et al. 2011). Whiteoak Creek, Roaring Creek, and Scapecat Branch had low abundances of younger age class fish, which is mostly likely contributing to lower overall community fish production.

In contrast, the upper range of my production estimates (i.e., $6.79 \text{ g m}^{-2} \text{ yr}^{-1}$) suggests that southern Appalachian streams and northern Appalachian streams (i.e., streams in Vermont and Massachusetts) can produce relatively high community fish production estimates compared to streams worldwide (Table 2). The upper range of my production estimates were well above the lower range of foothill streams in north New Zealand (Hopkins 1971), tropical rainforest streams in northern Borneo (Watson and Balon 1983), lowland trout streams in southeastern Minnesota (Kwak and Waters 1997), and low altitude neotropical streams in Brazil (Mazzoni and Lobón-Cerviá 2000). An explanation for these relatively high community production estimates could be related to the fact that over 90% of the streams studied were dominated by cold- and cool- water species. Rypel (2014) recently analyzed relationships between body size and temperature for fish species grouped by thermal guild. This study revealed that in general cold-water and cool-water fish species follow Bergmann's rule, i.e., body size increases with increasing latitude and decreasing temperature (Bergman 1847; Rypel (2014). Larger body sizes of individuals for cold-water species at a given age might therefore similarly be associated with increased fish production, since growth of individual fish is one core aspect of production (Allen 1977). Thus, higher community production estimates in the extreme northern sites might be associated with higher cold-water species growth associated with higher latitudes and lower temperatures.

The larger community production estimates in the extreme northern streams (e.g., Adam's Brook, Buffam Brook) and in some of the lower latitude southern Appalachian streams (e.g., Reed Creek, Blizzard Run, Kelso Springs Branch, Swannanoa Creek, Red Fork) could also be influenced by the high abundance of young-of-the-year fish and ecosystem size. Red Fork Creek had a large number of age-0 Rainbow Trout and Mottled Sculpin (both classified as cold-water species) while Reed Creek and Swannanoa Creek contained a large amount of age-0 and

age-1 Blacknose Dace and Bluehead Chub (both classified as cool-water species) (Appendix A and B). Regardless of species, a high abundance and growth of younger age classes (i.e., 0 and 1) corresponds to higher community production estimates, which could be a factor contributing to the higher production estimates in this study (Mathews 1971; Schlosser 1982; Halyk and Balon 1983; Lóbon-Cerviá et al. 2011). The third explanation for the higher production estimates could be attributed to ecosystem size. Production can be sensitive to stream area, since biomass is normalized by stream area (Hayes et al. 2007). Thus, a larger stream may have higher fish abundance (Platts 1979), but smaller streams may have higher fish production per unit area once area is standardized across all samples. Many streams in this study were small, low-order streams; therefore, stream area may also be a factor contributing to the higher production estimates in this study. Although variability in community fish production existed among the 25 streams studied, it was apparent that Appalachian streams in Vermont and Massachusetts and at certain streams across the southern Appalachians have the potential to sustain relatively high levels of community fish production depending on the abiotic and biotic characteristics of the ecosystem (i.e., high abundance of young-of-the-year fish, abundance of cold-water species in higher latitudes, calcium concentrations).

Lastly, annual production-to-biomass ratios, P/B, or turnover ratios are invaluable estimates of how often community biomass is replaced during the year (Waters 1977) and can reveal important ecological relationships (Hayes et al. 2007). However, an increased understanding on the variation in community turnover rates for most types of communities and ecosystems is essential. It is important to note that P/B ratios for salmonid species have been widely cited (Chapman 1978; Kwak and Waters 1997; Lobón-Cerviá et al. 2011). The extreme northern streams had a substantially higher mean community P/B (1.40) compared to the cold-

water streams (0.73), cool-water streams (0.85), and warm-water streams (0.92) in the southern Appalachian range. Similarly, mean community fish P/B of the extreme northern sites was also in the upper range of published fish community P/B values (Table 2) (Mann 1971; Lotrich 1973; Watson and Balon 1983; Penczak 1992). Mean community P/B in cold-, cool-, and warm-water streams from this study were within the range and slightly higher than previously published community P/B values in studies across similar and dissimilar habitats (Neves and Pardue 1983; Hopkins 1971; Mazzoni and Lobón-Cerviá 2000). This trend reveals that the extreme northern streams dominated by cold-water species (94%) had the highest turnover ratio rate and might therefore be more resilient to perturbations than previously thought (Hayhoe et al. 2008; Brooks 2009; Bellard et al. 2013). The converse of this pattern (that replacement rates of southern Appalachian stream fish communities was low), suggests these communities may be less resilient than their more northern analogues and could potentially require longer amounts of time to recover from perturbations.

In this study, production-to-biomass ratios were the most powerful metric used for comparing fish communities in the four stream categories, since the P/B ratios were the only significantly different metric among cold-, cool-, and warm-water streams and the extreme northern streams. Production-to-biomass ratios are tightly linked to year-class recruitment; thus, populations with stronger year-class recruitment are expected to have higher production-to-biomass ratios (Lobón-Cerviá et al. 2011). Still, production-to-biomass ratios exhibit a negative trend with increasing number of age groups in a population or maximum age of a species (longer lived species normally have lower P/B ratios compared to shorter lived species) (Waters et al. 1990; Lobón-Cerviá et al. 2011). A compilation of fish species and the associated P/B ratios summarized by Waters (1977) revealed that cottids and salmonids had the highest P/B ratios

relative to other freshwater fishes. Fish communities in the extreme northern sites were dominated by Brook Trout and Slimy Sculpin, which both had higher on average P/B ratios compared to the same or similar species in the cold-, cool-, and warm-water streams in the more southern Appalachians. Since both species are cold-water species that are sensitive to temperature variations (Lyons et al. 2010), temperature regimes at the extreme northern streams may be driving higher recruitment of these two dominant species because the conditions are more ideal for young-of-the-year survival and growth.

Community Production Dynamics across the Temperature Gradient

Intuitively, cold-water species dominated community production in the cold-water streams, cool-water species dominated in cool-water streams, and warm-water species were dominant in terms of production in the warm-water streams. However, the differences in mean summer temperature and maximum summer temperature among the cold-, cool-, and warm-water streams were not extreme suggesting slight changes in temperature could prompt a shift in the allocation of production of particular fish thermal guilds. Considering cool-water streams had a 2°C higher mean summer temperature than cold-water streams, cold-water fish populations in these more cool-water southern Appalachian streams may be at the edge of their temperature range. The most recent Intergovernmental Panel on Climate Change (IPCC) (2013) models predicted that between 2016 and 2035, global air temperatures will likely increase by 1°C. The prior IPCC (2007) report predicted more conservatively that air temperatures would increase by 0.2°C every decade. Thus, as temperatures continue to increase, the percentage of cold-water fish species production, based on these results, would be predicted to decline, prompting a shift from cold-water species communities to cool- (i.e., Blacknose Dace, Bluehead Chub, Rosyside Dace,

etc.) or warm-water species communities (i.e., catostomids, centrarchids, etc.) (Lyons et al. 2010).

Given these empirical community production estimates, cold-water species production trends in the cold-water, cool-water, and warm-water study streams in the southern Appalachians, the precise temperature estimates at each study stream, and the predicted air temperature increases, it is evident that cold-water fish populations in these historically cold-water streams are at risk of changes in production. The conclusions from this study therefore echo concern over the effects of climate change on cold-water fish community production, especially for more southern Appalachian streams (Clark et al. 2001; Rahel 2002; Chu et al. 2005; Ficke et al. 2007; Sharma et al. 2007; Staudt et al. 2013).

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FIGURES

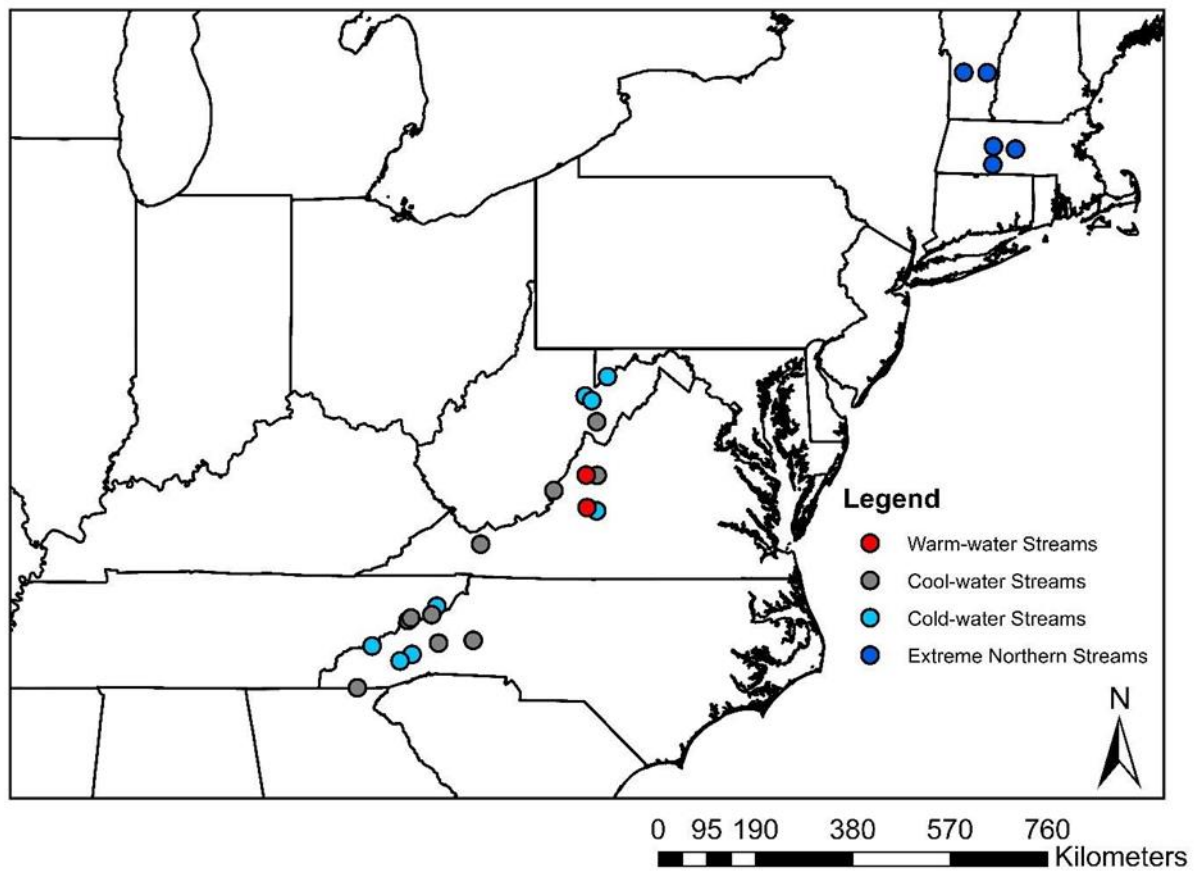


Figure 1. Streams located across the Southern Appalachian Mountain Range sampled for community fish production estimates. Note that Vermont and Massachusetts streams have been slightly offset from their true location for improved clarity. Precise latitude-longitude coordinates for each study stream can be found in Table 1.

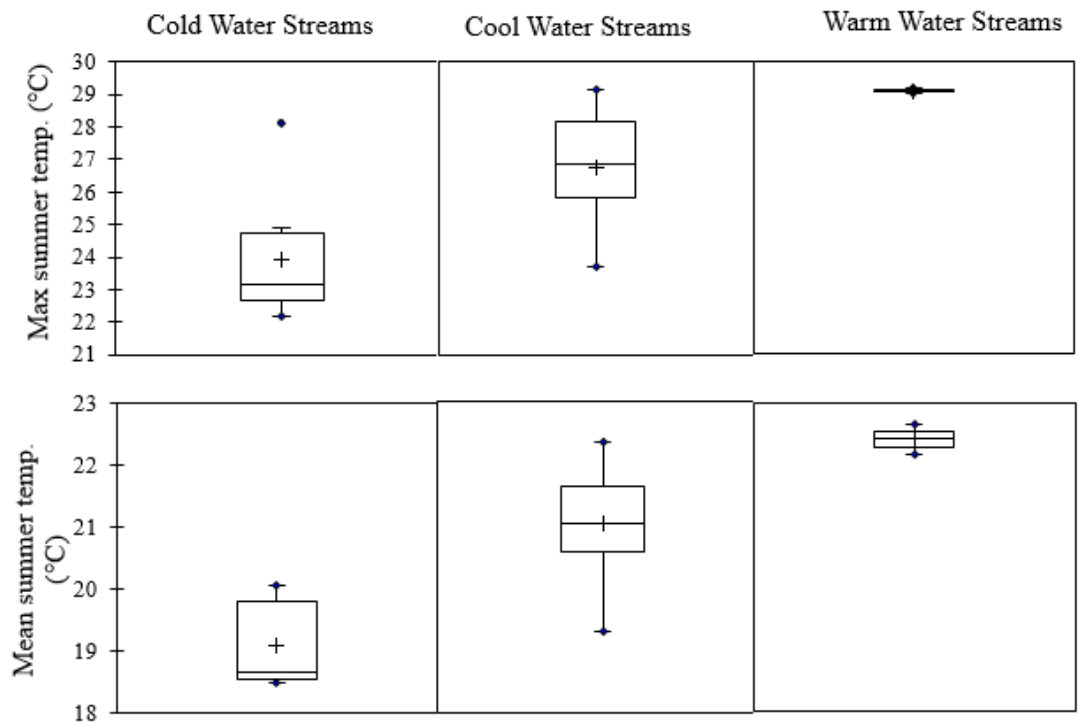


Figure 2: Box plots of the mean maximum summer temperatures (°C) and the mean summer temperatures (°C) for the three stream temperature classifications of the 20 sites across the southern Appalachian Mountains in Maryland, West Virginia, Virginia, North Carolina, and Tennessee.

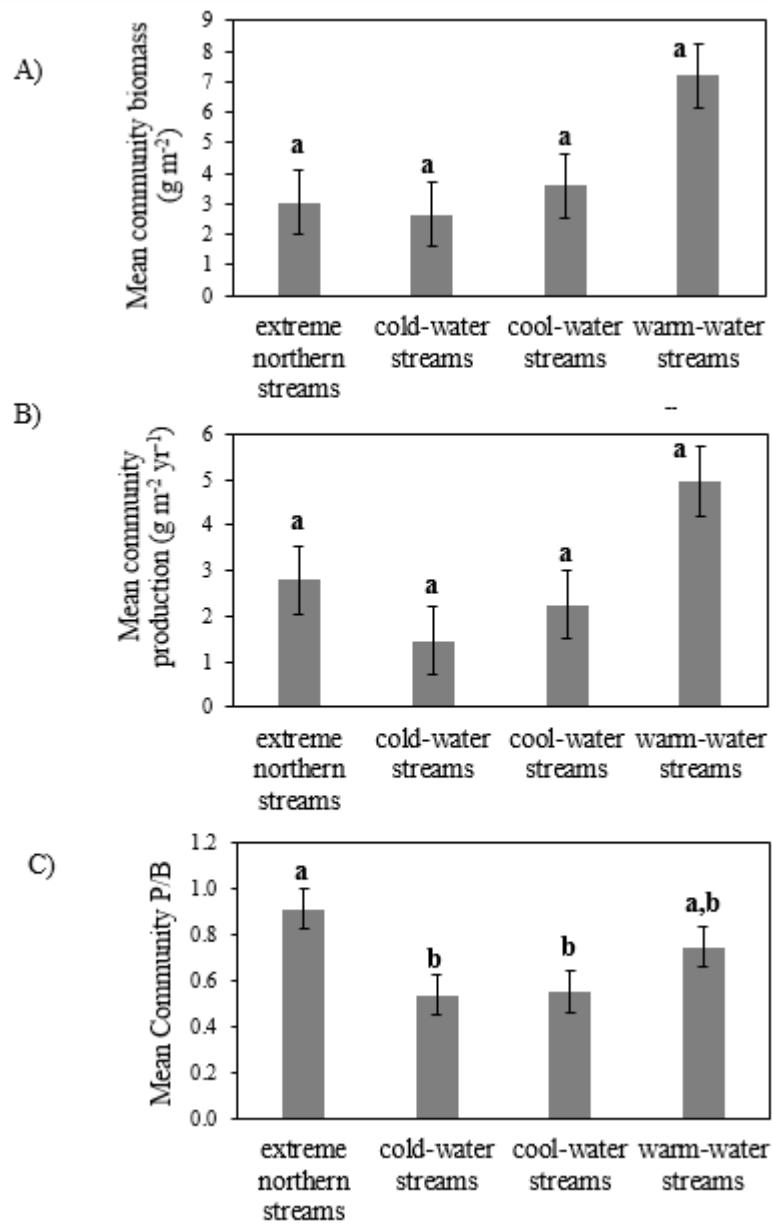


Figure 3. Mean community biomass (A), mean community annual production (B), and mean community P/B ratio (C) of fishes in the 4 stream temperature categories (cold-water southern Appalachian streams, cool-water southern Appalachian streams, warm-water southern Appalachian streams, and the extreme northern streams). Error bars represent the mean ± 1 standard error. Letters denote means that do not statistically differ from one another (Tukey's Post-Hoc $P > 0.05$).

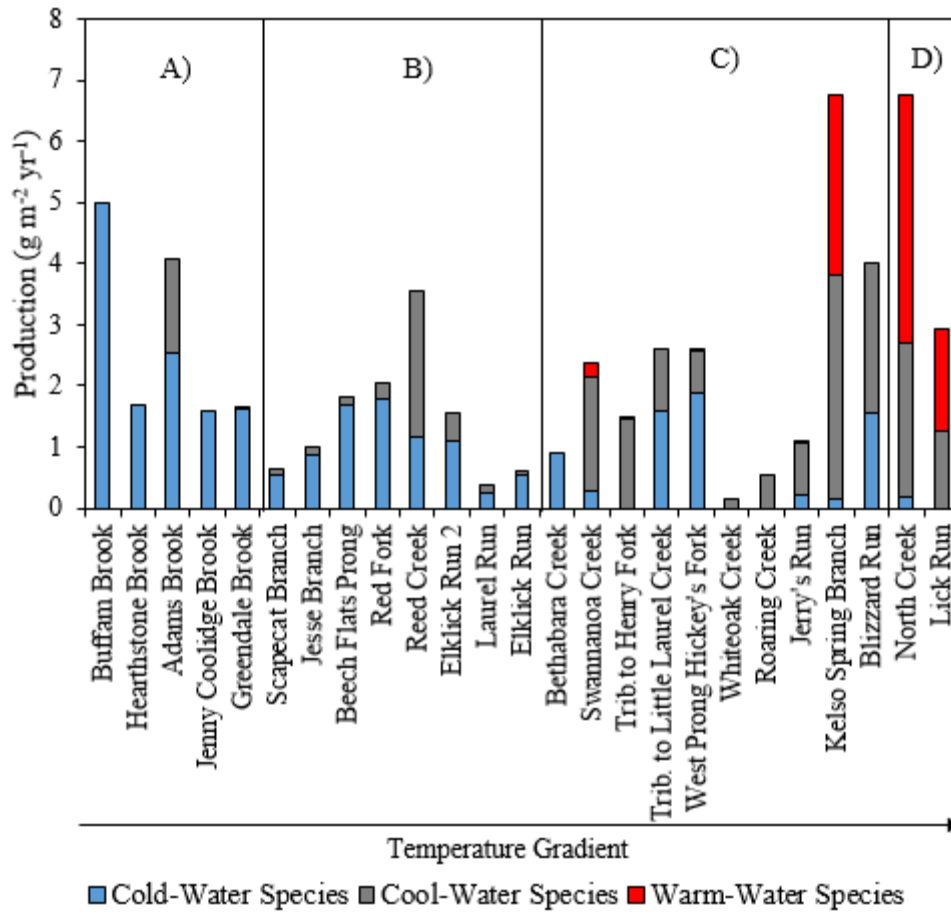
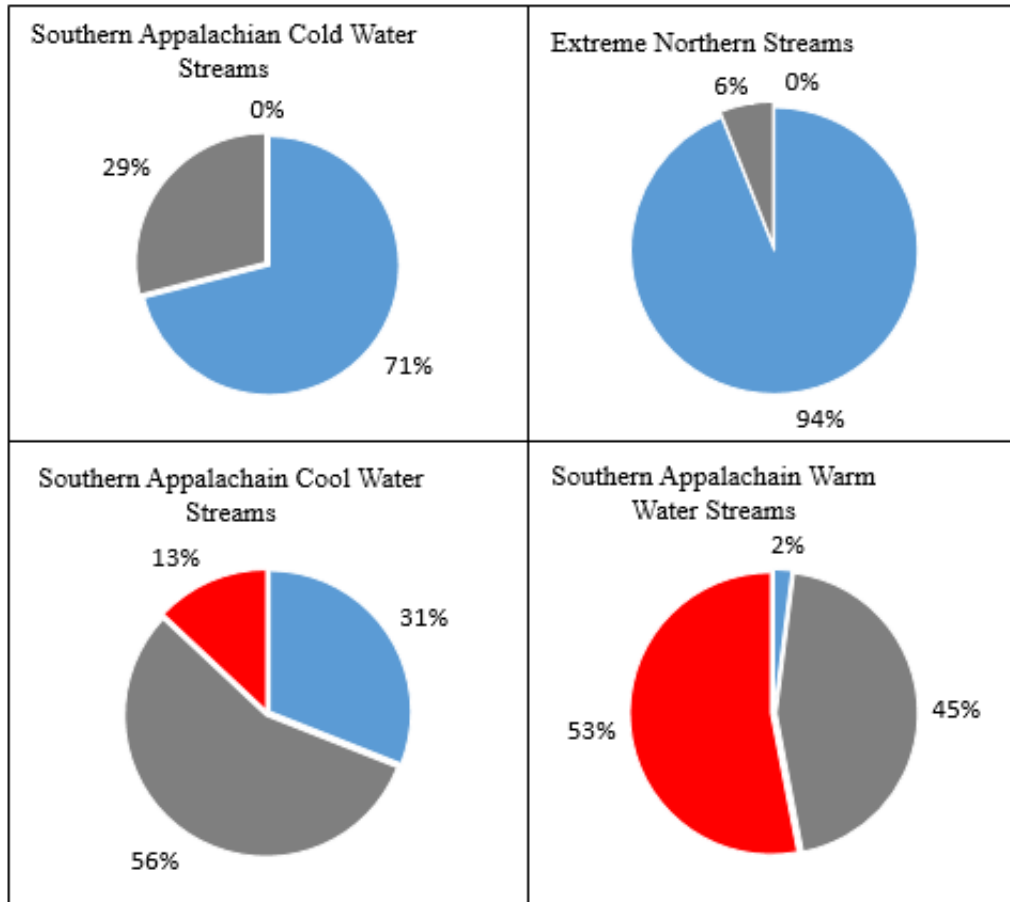


Figure 4. Comparisons of total community annual production ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) and cold-, cool-, and warm-water species production per site arranged according to stream temperature classification A) extreme northern streams, (B) cold-water streams, C) cool-water streams, D) warm-water streams located throughout North Carolina, Tennessee, Virginia, West Virginia, Maryland, and the 5 extreme northern sites in Massachusetts and Vermont sampled during summer 2012.



■ Percentage of Warm-Water Species P
 ■ Percentage of Cool-Water Species P
 ■ Percentage of Cold-Water Species P

Figure 5. Percentage of cold- (blue), cool- (yellow), and warm-water (red) species production at streams classified a priori as cold-water streams (top left) (8 sites), cool-water streams (bottom left) (11 sites), and warm-water streams (bottom right) (2 sites), and the percentage of cold-, cool-, and warm-water species production at the extreme northern sites in Massachusetts and Vermont (5 sites) (top right).

TABLES

Table 1. Community fish abundance, biomass, annual production, and P/B values and selected site characteristics of the study streams sampled during summer 2012. Note that streams are organized from north to south based on latitude.

Stream Name	Site Classification	Fish Community Biological Variable					Site Characteristics		
		N	B (g m ⁻²)	P (g m ⁻² yr ⁻¹)	P/B	Species Richness	Latitude	Longitude	Elevation (m)
Greendale Brook, VT	extreme northern	173	2.00	1.62	1.22	4	43.354	-72.824	534
Jenny Coolidge Brook, VT	extreme northern	150	1.99	1.58	1.81	3	43.340	-72.831	308
Adam's Brook, MA	extreme northern	459	4.89	4.07	1.10	9	42.395	-72.487	71
Hearthstone Brook, MA	extreme northern	81	1.61	1.68	1.47	1	42.385	-72.480	80
Buffam Brook, MA	extreme northern	128	4.66	5.00	1.38	2	42.384	-72.454	158
Laurel Run, MD	cold	164	1.60	0.39	0.63	5	39.343	-79.258	615
Ellick Run #2, WV	cold	314	3.31	1.57	0.56	5	39.078	-79.649	524
Ellick Run, WV	cold	147	0.93	0.60	0.89	2	39.016	-79.532	586
Blizzard Run, WV	cool	606	9.30	4.00	0.73	7	38.728	-79.447	559
Lick Run, VA	warm	531	3.68	3.16	1.08	19	37.993	-79.631	397
Kelso Spring Branch, VA	cool	478	6.81	6.79	1.24	16	37.991	-79.438	422
North Creek, VA	warm	822	10.73	6.77	0.75	22	37.855	-79.616	267
Jerry's Run, VA	cool	351	2.09	1.10	0.79	7	37.784	-80.197	624
Reed Creek, VA	cold	424	6.23	3.56	0.70	11	37.499	-79.449	366
Roaring Creek, VA	cool	95	0.61	0.53	1.02	4	37.035	-81.482	671
Red Fork, TN	cold	258	3.43	2.06	0.82	5	36.159	-82.251	800
Whiteoak Creek, NC	cool	25	0.76	0.15	1.61	3	36.041	-82.338	646
West Prong Hickey's Fork, NC	cool	342	4.78	2.56	0.59	5	35.994	-82.704	670
Trib. to Little Laurel Creek, NC	cool	196	3.79	2.62	0.95	5	35.957	-82.756	572
Trib. to Henry Fork, NC	cool	136	3.15	1.47	0.63	4	35.666	-81.612	362
Swannanoa Creek, NC	cool	553	2.93	2.36	0.93	7	35.635	-82.219	494
Beech Flats Prong, NC	cold	124	2.18	1.81	0.92	3	35.593	-83.387	957
Jesse Branch, NC	cold	117	1.91	1.00	0.75	4	35.477	-82.684	755
Scapecat Branch, NC	cold	30	1.64	0.64	0.59	3	35.382	-82.895	1046
Bethabara Creek, NC	cool	39	1.75	0.91	0.82	2	34.997	-83.644	729

Table 2. Community fish secondary production estimates ($\text{g m}^{-2} \text{yr}^{-1}$) (ranges) and community fish P/B ratios (ranges) organized by increasing community production from previous studies worldwide. Asterisks represent P/B ratios that were not provided and could not be calculated with the available data.

Location	Number of Streams	Water Body Description	Community Production ($\text{g m}^{-2} \text{yr}^{-1}$)	Community P/B	Reference
Eastern Kentucky	3	1st, 2nd, 3rd order tributaries	2.35-3.29	0.58-1.06	Lotrich 1973
Guy's Run, Virginia	1	Appalachian mountain stream	2.86-3.96	0.60-1.60	Neves and Pardue 1983
Appalachian Streams, Eastern U.S.	25	Appalachian mountain streams from Vermont to North Carolina	0.15-6.79	0.20-1.07	present study
Tribs. to Salmon River, Idaho	2	cool water valley tributaries	11.80-13.60	**	Goodnight and Bjornn 1971
North New Zealand	2	small foothill streams	4.28-14.54	0.56-0.62	Hopkins 1971
Warta River, Poland	1	large alluvial river	13.50-16.40	1.58-2.02	Penczak 1992
Jordan Creek, Illinois	1	warm water stream	9.79-17.86	0.13-0.99	Schlosser 1982
Northern Borneo	5	tropical rain forest streams	2.61-26.15	0.70-1.40	Watson and Balon 1983
Southeastern Minnesota	13	lowland to plateau trout streams	3.67-27.96	0.64-1.42	Kwak and Waters 1997
Ubatiba River, Serra do mar, Brazil	1	low altitude neotropical stream	5.15-28.25	1.15-2.73	Mazzoni and Lobón-Cerviá 2000
Southern England Tributaries	4	hard and softwater, small temperate streams	9.10-59.60	0.95-3.14	Mann 1971
Lowland rivers, Poland	2	small lowland rivers	3.07-80.72	0.80-5.30	Penczak 1981
Tidal creeks, Andros Island, Bahamas	8	fragmented and unfragmented tidal creeks	29.00-901.00	**	Valentine-Rose et al. 2011

Manuscript 2 Title:

COMMUNITY FISH PRODUCTION DYNAMICS ACROSS THE SOUTHERN APPALACHIAN MOUNTAIN RANGE: IMPLICATIONS FOR CLIMATE CHANGE

ABSTRACT

Freshwater ecosystems are especially vulnerable to climate change. The main goals of this study were to 1) develop empirical estimates of community fish production at a series of stream sites across the southern Appalachians; 2) to relate community-, thermal guild-, and species-specific production rates to air and water temperature while accounting for potential covariates of production (e.g., habitat complexity, stream size, nutrient availability); 3) to conduct a climate change vulnerability analysis (under a range of climate warming scenarios) on streams across the southern Appalachian range. During summer 2012, I quantified fish biomass, somatic growth, secondary production, and habitat data for fish communities in 25 Appalachian streams from Maryland to North Carolina. Principal components analysis, ordinary least squares multiple regressions, and logistic regression models were developed to determine the relationship between community fish production and air and water temperature and species thermal guild production and temperature. The summer water temperature related factor more strongly predicted community fish production ($\beta=0.14$, $P=0.01$) compared to the summer air temperature related factor ($\beta=0.08$, $P=0.10$). Furthermore, both the summer air temperature related factor and the water temperature related factor were the only environmental factors to significantly predict whether community production would be dominated by cool- or cold-water fish species ($P=0.001$, $P<0.0001$, respectively). Based on future climate change projections, streams in the southern Appalachian range are

vulnerable to mid-level increases (1°C). Since temperature was the strongest environmental variable associated with both community production and thermal guild production, the fish populations in these streams are in a precarious position.

INTRODUCTION

Temperature is often considered the most important abiotic factor influencing the ecology of poikilothermic animals (Christie and Regier 1978; Magnuson et al. 1979; Trudgill et al. 2005; Daufresne and Boët 2007; Sharma et al. 2007). For example, temperature affects the phenology of reproductive activities (Fry, 1971; Stefanescu et al. 2003), developmental schedules (Ward and Stanford 1982; Trudgill et al. 2005), growth (Fry 1971; Rypel 2009), survival (Ficke et al. 2007; Blaustein et al. 2010), and habitat availability. Thermal habitats in aquatic ecosystems, are especially vulnerable to climate change (Casselman 2002). For example, Chu et al. (2005) predicted that the distributional range of an obligate cold-water species (Brook Trout *Salvelinus fontinalis*) would shrink significantly due to increased global temperatures and speculated this could be a general pattern for most cold-water species in similar habitats. Conversely, warm-water fish species are predicted to invade previously cool-water regions and ecosystems as climate warming creates increasing amounts of suitable habitat for these species (Shuter and Post 1990; Chu et al. 2005).

In freshwater fishes, both extreme high and low temperatures drive variability in recruitment, reproduction, mortality, growth, and distribution (Shuter 1980; Jackson et al. 2001; Rypel 2012). General increased temperatures are expected to promote increased rates of growth due to enhanced food availability, increased metabolic rate, reproductive

success, and maintenance of internal homeostasis (Fry 1971; Magnuson et al. 1997). However, extreme temperature increases could also amplify stress by raising metabolic rates, and decreasing oxygen availability thereby affecting growth rates in a variety of complex, non-linear and potentially negative ways (Jackson et al. 2000; Allan and Castillo 2007; Rypel 2009a; Rypel 2012). Similarly convoluted relationships are frequently observed when evaluating and attempting to isolate the effect of temperature variations on other biological rates (Ficke et al. 2007) like recruitment (Pounds 2001; Mayfield and Cech 2002), mortality (Fry 1971; Beitinger et al. 2000), and reproduction (Fry 1971; Ficke et al. 2007). However, all of these factors are directly linked to fish secondary production rates (defined as the amount of tissue elaborated over time by a population) and serves as a composite measure of a fish population's functional responses to environmental variability (Waters and Crawford 1973; Hayes et al. 2007; Dolbeth et al. 2012). Production is linked to physiological processes that are controlled by temperature, and variations in temperature will affect secondary production patterns in both warm- and cold-water species and ecosystems (Allan and Castillo 2007; Hayes et al. 2007).

Production has been widely used to describe the ecology of species at different trophic levels including plants (Tilman et al. 1997), benthic macroinvertebrates (Cross et al. 2006; Benke and Huryn 2010), and both marine (Mackenzie and Foster 2004) and freshwater fishes (Waters 1977; Gerking 1978). However, freshwater fisheries scientists have more infrequently used production to evaluate population functional response to environmental changes (Hayes et al. 2007). Instead, fisheries scientists have more often used surrogate measures and correlates of production (e.g., growth, condition factor,

mortality) in assessing ecosystem responses to anthropogenic and climatic stresses (Hayes et al. 2007; Dolbeth et al. 2012). However, the science of fisheries is in fact chiefly concerned with production rates as this metric explicitly describes the amount of carbon-based material elaborated over time by a population or ecosystem, and thus the amount of carbon available for human consumption and recreation (Lindeman 1942; Waters and Crawford 1973; Neves 1985; Brander 2007). Furthermore, when production is considered, it is usually only approached with “short-cut” methods like empirical models which use e.g., biomass to predict production (Robertson 1979; Mertz and Myers 1998; Randall and Minns 2000).

Empirical estimates of secondary production may be a better measurement for understanding fish population responses to climate change (Dolbeth et al. 2012). In aquatic ecosystems, temperature is known to affect metabolism, growth, and life history cues of aquatic insects (Benke 1984; Tumbiolo and Downing 1994). Casselman (2002) directly evaluated the effects of temperature on year-class production of fishes in the Great Lakes Basin and concluded that year-class production and temperature variations were related for a variety of species thereby, suggesting overall community production is most likely also linked to temperature variations. Richardson et al. (1994) found common New Zealand fish density to be significantly related to temperature; however, this trend was not found in all species evaluated. Furthermore, Rypel (2009) found a significant, positive relationship between Largemouth Bass *Micropterus salmoides* growth and annual temperature variables. Taken together, these studies provide strong evidence for the existence of a relatively unexplored link between temperature and community secondary production. More empirical evidence describing the effects of temperature on

freshwater fish production at larger spatial scales is necessary. Global mean temperatures are expected to increase by up to 4°C by the year 2081-2100 (IPCC 2007), i.e., the maximum width of the thermal niches of many species (Magnuson et al. 1979). Thus climate change has the potential to shift production and sustainability of freshwater fisheries in extreme ways (Sharma et al. 2007), and knowledge of the relationship between temperature and secondary production will help identify communities more or less at risk of collapse due to climate change.

My objectives were 1) to develop empirical estimates of community fish production at a series of stream sites across the southern Appalachians; 2) to relate community-, thermal guild-, and species-specific production rates to air and water temperature while attempting to account for other potential covariates of production (e.g., habitat complexity, stream size, nutrient availability); 3) to conduct a climate change vulnerability analysis (under a range of climate warming scenarios) on streams across the southern Appalachian range.

METHODS

Study Area Description.—Twenty study streams were selected from a network of 204 streams used by the United States Forest Service Southern Research Station (USFS SRS) to monitor stream water temperature (Figure 1). I sampled 10% of the 204 streams (i.e., 20) to estimate community fish production and associated habitat parameters. A cluster analysis was performed on the temperature data of the 204 stream sites containing temperature loggers to create two main stream temperature clusters. Ten sites were then

randomly selected from the two main clusters to encompass the temperature gradient present throughout the larger stream network.

The 20 streams were located in the mountains of Maryland, West Virginia, Virginia, Tennessee, and North Carolina, USA in the southern Appalachians and covered a variety of localities and physiographic provinces (Figure 1). Streams were largely 2nd and 3rd order characterized by dense forest canopy cover, cobble dominated substrate, and elevations ranging from 267-1046 meters (Table 2). Streams were mostly soft water with pH ranging from 6.6-8.0 and calcium and magnesium concentrations ranging from 0.62-61.67 mg/L and 0.21-16.71 mg/L, respectively (Table 2). Calcium and magnesium were used as surrogates of water hardness and alkalinity; thus, high levels of calcium and magnesium were associated with high water hardness and alkalinity (Allan and Castillo 2009).

Data Collection.—Fish sampling at all 20 stream sites occurred during June to August 2012 using a standardized and systematic sampling design. Initial reach starting points were randomly selected upstream of the air and water temperature loggers at each stream. Backpack electrofishing units were used to sample fishes to depletion from two, 50 meter stream reaches spaced 50 meters apart. Block nets with 1/16” mesh were placed downstream and upstream of each 50 meter reach to inhibit immigration and emigration of fishes within the sampling area. For all individuals captured, total lengths were measured to the nearest millimeter and weights estimated to the nearest tenth of a gram using an Ohaus Adventurer Pro Balance (Parsippany, NJ, USA). A sub-sample of each species captured at each site was euthanized in tricaine methanesulfonate (MS-222) and transported to the lab on ice and frozen for otolith removal, age estimation, and stomach

weight determination (g). Following Ketchen (1950) and Devries and Frie (1996) sub-sampling protocol, fixed stratified sub-samples of 10 individuals per species per length group (i.e., approximately 10mm) were collected.

Otolith sagittae were removed from each retained specimen to estimate age using standard methods (Devries and Frie, 1996). Putative annual growth rings were blindly counted under a microscope and interannual growth increments measured by an experienced reader using a computer-based image analysis system interfaced with the microscope. Length-at-previous ages of all fish were calculated using the Fraser-Lee method (Francis, 1990) equation

$$L_t = c + (L_c - c) * (O_i / O_c)$$

where L_t =back calculated length at i th annuli, c =intercept constant, L_c =length of fish at capture, O_i =otolith radius at i th annuli, and O_c =otolith radius at capture (Francis, 1990; DeVries and Fries 1996). The intercept for each species was determined by plotting fish length as a function of otolith radius length (Francis, 1990). Finally, logarithmic or power growth functions were determined for each species' age as a function of length plots and used to predict the age of all fish measured in the field using total length as a predictor. Logarithmic growth functions were used mostly because the majority of species had relatively low maximum ages and because of statistical issues (i.e., sample size) present when using other commonly used growth functions (e.g., the Von Bertalanffy) (Roff 1980; Haag 2009).

Duplicate water samples were collected upstream of the upper reach before commencement of fish sampling. Samples were immediately placed in a cooler with dry ice to ensure fast freezing. Water samples were express shipped to the Coweeta

Hydrologic Laboratory (Otto, NC, USA) and analyzed for concentrations of ammonium, nitrite, nitrate, phosphorous, sulfate, potassium, calcium, and magnesium using standard methods (USEPA 1983a; USEPA 1983b). In addition, point measurements were obtained of water temperature (°C), pH, conductivity (µS/cm), and dissolved oxygen (mg/L) using a Yellow Springs Instrument professional probe (Yellow Springs, OH, USA).

Habitat data were recorded for each 150 meter reach section using a similar estimation method as outlined in the Basinwide Visual Estimation Technique, BVET (Dolloff et al. 1993). In addition to the BVET parameters recorded (e.g., dominant and subdominant substrate, large wood, average and maximum depth, width, habitat units), canopy cover in each habitat unit was estimated using a convex densitometer (Dolloff et al. 1993).

Stream velocity was measured at two transects within the sampling reach using a Marsh-McBirney (Harrisburg, PA, USA) Flo-mate 2000 flow meter. Depth measurements and velocity were recorded at a minimum of 5 points across each transect spaced no more than 3 meters apart (Gore 1996). Discharge was calculated using the equation expressed by Gore (1996)

$$Q=A \cdot v$$

where Q=discharge, A=area, and v=velocity.

Several temperature metrics were calculated at each of the 20 sites using the temperature logger data: mean annual temperature, minimum summer and winter temperatures, maximum summer and winter temperature, mean summer temperatures, and temperature variability (Shuter et al. 1980; Casselman 2002; Neuheimer and Taggart 2007). All temperature metrics were calculated based on the year preceding the sampling

event (i.e., March 2011-March 2012) and these values were considered as relatively characteristic for that site. Multiple annual estimates of temperature variability were not available at any site because temperature loggers were deployed in 2010.

Production calculations.—Secondary production values for each species were estimated using the instantaneous growth rate method (Waters 1977; Hayes et al. 2007). Age-specific growth (G) was calculated using the equation

$$G = \ln(\text{age class}_{x+1} / \text{age class}_x)$$

Age-specific biomass was calculated as the sum of the weights of all individuals sampled within that age class. Age-specific production was then estimated as the production of age-specific biomass and growth (Halyk and Balon 1983; Valentine-Rose et al. 2007; Valentine Rose et al. 2011). This method integrates the area under the traditional Allen curve with fish age classes on the x-axis and mean weight on the y-axis (Allen 1949; Halyk and Balon 1983; Hayes et al. 2007). The equation used to calculate production was

$$P = G\bar{B}$$

where P=production, \bar{B} =arithmetic mean standing stock, and G=instantaneous growth rate. Thus the density, total weight, mean weight, biomass, mean biomass between each age group were calculated along with the instantaneous growth rate from age class x to age class x+1, and annual production ($\text{g m}^{-2} \text{yr}^{-1}$). Community fish production was calculated by summing the individual species annual production values. The P/B ratio was calculated as annual production divided by mean annual biomass as an estimate of the estimated biomass turnover rate for each species in each stream (Waters 1977; Hayes et al. 2007). Community P/B was calculated by dividing total community production by the community biomass.

All fish species collected at the 20 study streams were then grouped into three temperature groups or thermal guilds (i.e., cold-water species, cool-water species, and warm-water species) using the classifications of Magnuson et al. (1979) and Lyons et al. (2010). If a species was not included in the Magnuson et al. (1979) or the Lyons et al. (2010) classification, published information on the preferred temperature range for the species was used (e.g., as outlined in Jenkins and Burkhead 1993) to determine the appropriate temperature classification for that species. The percentage of cold-water, cool-water, and warm-water species production was determined for each stream as the fraction of the total community production represented by the combined production of species in each thermal guild.

Data Analysis.—To evaluate the potential for collinearity among the many biological and environmental independent variables examined, I conducted Spearman correlations on all non-transformed community biological and environmental variables (Appendix F and G). Whereas collinearity was extensive, especially among air and water temperature variables, two principal components analysis (PCA) were performed on the 33 physical and chemical habitat variables collected from the 20 study streams. The first included only air temperature variables plus the additional physical and chemical variables and the second included only water temperature variables plus the same additional physical and chemical variables. Principal components were chosen based on the eigenvalues, scree plot, and variation explained by each component (Fields 2011). A varimax orthogonal rotation was conducted on the final selected principal components to maximize the factor loadings for increased ease of interpretation (Fields 2011). The percent contribution for each variable was calculated by dividing the absolute value of

each factor loading by the sum of the factor loadings. Each principal component factor was classified into categories (i.e., summer air temperature related, habitat related, or water chemistry/winter temperature related) based on the variables with the highest percent contribution to that principal component.

Two multiple regressions were conducted on the log-transformed community production estimates and the three principal components from both principal components analyzes. The three factors in the first multiple regression were represented by a water chemistry (e.g., calcium and magnesium) and winter temperature related factor, summer air temperature factor, and a habitat factor as the independent variables (Pajak and Neves 1987; Almodovar et al. 2006). The three factors in the second multiple regression evaluating the effects of water temperatures were a water hardness (i.e., calcium and magnesium concentrations) and latitude factor, a summer water temperature factor, and a water chemistry factor. Next, two multiple regressions per species temperature guild were conducted for a total six additional models to determine the relationship between the factors from both PCAs and cold-, cool-, and warm-water species production. Production values were log-transformed to adhere to normality assumptions. The relationship between species occurring at greater than five sites were plotted to determine the general trend in specific species relationships with the summer air and water temperature PC factors for the following species: Rainbow Trout *Onchorynchus mykiss*, Mottled Sculpin *Cottus bairdii*, Blacknose Dace *Rhinichthys atratalus*, Longnose Dace *Rhinichthys cataractae*, Bluehead Chub *Nocomis leptocephalus*, Creek Chub *Semotilus atromaculatus*, and Rosyside Dace *Clinostomus funduloides* that occurred at > 5 sites.

The percent of cold-water, cool-water, and warm-water species production at each site were analyzed, because the communities were often mainly dominated by a few species. Thus, I wanted to determine the likelihood of a community being dominated by cold-, cool-, or warm-water species dependent on the environmental factors. Next, a multinomial logistic regression was conducted on the percent production of cold-water species, cool-water species, and warm-water species at each stream and the three independent principal components to determine the effects of temperature on the three fish thermal guilds. Percent production was transformed into a categorical dummy variable based on which species temperature group dominated community production. Based on the Receiver Operating Characteristics (ROC) curve and the goodness of fit test, the multinomial logistic regression model was a good fit confirming that the independent variables accurately predicted thermal guild dominance in the community (Fields 2011).

Lastly, the new Intergovernmental Panel on Climate Change (IPCC) (2013) projections and the temperature data from summer 2012 were used to identify streams in the southern Appalachians that were particularly susceptible to decreases in cold-water fish production and particularly susceptible to an increase in cool-water fish and warm-water fish production. Using the temperature data from the network of streams from the USFS SRS, I determined the areas with the highest susceptibility to shifts in cold-water fish production. Mean summer 2012 temperatures were used as a base point for temperature increases. I conducted a K-means cluster analysis in JMP 10.1 software (SAS Institute, Inc., Cary, NC) on the 20 sites based on mean 2012 summer temperatures. Then the mean summer temperatures for the three clusters were used to classify the

remainder of streams into cold-water streams, cool-water streams, and warm-water streams. Then three separate reclassifications of the sites were conducted based on a mid-level increase of 0.5°C, a one unit increase of 1°C, and a 2°C increase in mean summer temperatures, which is highly unlikely based on IPCC projections (IPCC 2013). All maps were made in ArcGIS 10.1 (ESRI, Redlands, CA).

Assumptions and Limitations.—One major assumption of any study relying on the instantaneous growth method is that a snapshot estimate of annual production remains relatively consistent over sub-annual time scales. However, other methods of production calculation that incorporate temporal variations (e.g., the increment summation and size-frequency methods) are laborious and time-consuming, often requiring monthly sampling over long periods (Halyk and Balon, 1983). These methods would be impractical in a large-scale analysis of community fish production and would probably preclude the type of study conducted here (Benke 1979). Moreover, most published fish production studies do not even rely on empirical measures of production, but instead on empirical models that predict production from biomass data alone (Robertson 1979; Mertz and Myers 1998; Randall and Minns 2000). Ultimately, the instantaneous growth method is an *in situ*, empirical and frequently used method to evaluate fish production, oftentimes using only a one time sample (Halyk and Balon, 1983; Valentine-Rose et al. 2007; Valentine-Rose et al. 2011).

I also addressed these potential methodological critiques by returning a few months later to resample a subset of the sites (n=5 streams) at different locations so as to place my results in an appropriate context. Based on a simple t-test, no significant difference existed between the community production estimates from the summer sample

and fall sample ($P=0.43$). Similarly, no significant difference existed between individual fish production between the two time periods ($P=0.24$). Slight (non-significant) decreases in production were evident in four of the five samples and expected due to natural mortality between sampling events. Finally and regardless of the limitations of any production calculation method, I used the same protocols for estimating production across all sites making any production estimates from this study at a minimum useful for relative comparisons among the streams used in this study.

RESULTS

Community fish production ($\text{g m}^{-2} \text{yr}^{-1}$) ranged from 0.15 to 6.79 with 10 of 20 sites dominated by cold-water species production, eight sites dominated by cool-water species production, and two sites dominated by warm-water species production (Table 1). The most common cold-water species encountered were Brook Trout and Mottled Sculpin, and the most common cool-water species encountered were Blacknose Dace and Longnose Dace. Community production was significantly and positively correlated to mean annual air temperatures ($^{\circ}\text{C}$) (Spearman's $r=0.48$, $P=0.03$), mean annual water temperatures ($^{\circ}\text{C}$) (Spearman's $r=0.54$, $P=0.02$), maximum water temperatures ($^{\circ}\text{C}$) (Spearman's $r=0.55$, $P=0.01$), mean summer air temperatures ($^{\circ}\text{C}$) (Spearman's $r=0.53$, $P=0.02$), and air temperature variation ($^{\circ}\text{C}$) (Spearman's $r=0.53$, $P=0.02$) (Appendix F and G). The only non-temperature related variable that had a significant correlation with community production was elevation (m), which was negatively correlated (Spearman's $r=-0.56$, $P=0.01$). The proportion of cold-water species production showing a relatively strong, negative relationship with mean annual temperatures, mean summer temperatures,

and mean maximum temperatures (Appendix F and G). Conversely, the observed percentages of cool-water and warm-water species production had a relatively strong, positive relationship with temperature variables (Appendix F and G). The percentage of warm-water species production had a stronger positive relationship with temperature variables compared to cool-water species.

Community Production/Temperature Models.—Variations in log-transformed community fish production were significantly explained by a regression using the three main principal component variables as predictors from both the regression model including only air temperatures and the regression model including only water temperatures (Table 5) ($R^2=0.27$, $P=0.04$ and $R^2=0.29$, $P=0.04$, respectively). However factor 3 – the habitat factor from the PCA with air temperatures was the only variable that had a significant effect on community fish production ($\beta=0.08$, $P=0.04$) (Table 5). Secondly, neither the summer air temperature related factor nor the water chemistry/winter temperature related factor had a significant effect on community fish production at the 0.05 alpha level ($P=0.10$, $P=0.16$, respectively). However, factor 3 (summer air temperatures) displayed a positive effect on annual community production that approached significance ($P=0.10$ Table 5, Figure 2). Factor 2 – summer water temperatures was the only variable that had a significant effect on community fish production ($\beta=0.14$, $P=0.01$) (Table 5, Figure 2). Thus, water temperatures had a stronger positive, relationship with community fish production compared to air temperatures.

The thermal guild regression models also highlighted the importance of summer air and water temperatures. The combined cold-water species production was not significant; however, factor 2 (summer air temperatures) had a negative effect on overall

cold-water fish production at the 0.05 alpha level. Thus, cold-water fish production is predicted to decline by $0.08 \text{ g m}^{-2} \text{ yr}^{-1}$ as factor 2 – summer air temperatures increase ($P=0.05$) (Table 7, Figure 4). The combined raw cool-water species production regression model was highly significant ($P=0.0006$, $R^2=0.59$) (Table 6, Figure 4). Factor 2 (summer air temperatures) had a significant positive effect ($\beta=0.13$, $P=0.009$) on cool-water fish production, thus as factor 2-summer air temperatures increase cool-water fish production is expected to increase (Table 7, Figure 4). Conversely, factor 3 (habitat) had a significant, negative effect on cool-water fish production ($\beta=-0.10$, $P=0.005$); thus, increases in dissolved oxygen, canopy cover, and latitude were associated with a decrease in cool-water fish production (Table 7, Figure 4). The regressions for the thermal guilds based on the PCA factors from the summer water temperatures PCA revealed similar but stronger trends. The only significant regression model was for cool-water species production ($P=0.003$), but the cold-water species regression model approached weak significance ($P=0.12$). Factor 2-summer water temperatures had a significant inverse effect on cold-water and cool-water species. Factor 2 – summer water temperatures had a negative effect on cold-water fish production ($\beta=-0.09$, $P=0.03$), and a positive effect on cool-water fish production ($\beta=0.16$, $P=0.0003$) (Table 7, Figure 4). Factor 2 – summer water temperatures was the only significant variable in both the cold-water and cool-water species production models. Both the combined warm-water species production regression model was not significant, and no factor revealed a significant effect on warm-water species production; however, warm-water species were found at only seven stream locations. Therefore, the sample size was smaller in comparison to the cold-water and

cool-water species production regression model, which may be reducing the predictive power of the model (Table 7, Figure 4).

Lastly, species specific trends of the cool-water and cold-water species plotted against summer air and water temperature factors revealed that the cool-water species that occurred at greater than five sites (Blacknose Dace, Rosyside Dace, Longnose Dace, and Creek Chub) had a general positive trend with both summer air temperature factor and the summer water temperature factor (Appendix I). Conversely, Bluehead Chub, a cool-water species, had a negative trend as well with increasing summer temperature factors (Appendix J). Furthermore, the two cold-water species (Rainbow Trout and Mottled Sculpin) that were present at greater than five sites showed a general negative trend with both an increasing summer air and increasing summer water temperature factors (Appendix J).

In the multinomial logistic regression, factor 2 - summer air temperature contributed the most to the overall model's (Table 6) ability to predict proportional production dominance of thermal guilds (Log Likelihood Ratio chi square=14.45, $P=0.001$). Similarly, factor 2 – summer water temperature from the second logistic regression also contributed the most to the model's ability to predict thermal guild dominance (Log Likelihood Ratio chi square=49.57, $P<0.0001$) (Table 6). Thus, both models significantly predicted whether a community would be dominated by cold-water, cool-water, or warm-water species based principally on factor 2 (chi-square ratio=18.87, $P=0.004$, $R^2=0.50$ and chi-square ratio=26.94, $P=0.0001$, $R^2=0.71$) (Table 6). The logistic regression including water temperature in the factors opposed to air temperatures had stronger prediction power and higher R-squared value making it a better fit to the data.

The habitat related factor also contributed significantly (chi-square=7.01, $P=0.03$) to the air temperature logistic regression model's ability to predict thermal guild dominance of production (Table 6). Factor 3 (water chemistry and winter temperature) did not significantly contribute to the model's predictions ($P=0.50$). However, no independent variable could significantly predict a decrease or increase in the log-odds probability of having a fish community dominated by warm-water species compared to a community dominated by cold-water species, which is most likely due to the low amounts of warm-water species percent production (Table 6). At the less strict 0.10 alpha level, an increase in factor 2 – summer air temperatures was associated with a 7.73 increase in the log-odds that a fish community would be dominated by warm-water species compared to cold-water species. However, factor 2 did significantly predict a 2.54 ($P=0.02$) increase in the log-odds that a fish community would be dominated by cool-water fish compared to cold-water fish as the summer air temperature factor increased (Table 6, Figure 3). Similarly, summer water temperature factor from the second logistic regression model almost significantly predicted a 5.10 ($P=0.06$) increase in the log-odds that a fish community would be dominated by cool-water fish compared to cold-water fish as the summer water temperature factor increases.

Climate change vulnerability analysis.—The mean summer temperature of streams in the cold-, cool-, and warm-water clusters were 18.7°C, 20.5°C, 22.2°C, respectively. Based on the most current summer temperatures collected in 2012 from the air and water temperature loggers at each site, 37 of the 204 streams used by the USFS SRS for temperature research were classified as cold-water streams, 95 streams were classified as cool-water streams, and 71 were classified as warmer water streams (Figure

6). Assuming a climate change scenario of 0.5°C rise in summer mean temperatures by 2035, 18 streams were classified as cold-water streams, 99 streams were projected to be cool-water streams, and 87 streams were classified as possible warm-water streams (Figure 5). However, a higher (1°C) rise in mean summer temperatures by 2035 is projected to result in a decrease from 18 streams classified as a cold-water streams to only nine classified as cold-water streams (Figure 5). Furthermore, the number of warm-water streams would be projected to increase from 87 to 110. Lastly a severe, though more unlikely increase of 2°C in mean summer temperatures by 2035 would be predicted to result in a massive downgrade of only two streams remaining classified as cold-water streams and only 23 streams classified as cool-water streams under this scenario (Figure 5). Warm-water streams would progressively increase to dominate with 178 of the 204 classified as warm water (IPCC 2013).

DISCUSSION

Climate change will have unprecedented effects on freshwater species and ecosystems at all scales. For example, a number of empirical models have been generated predicting how Brook Trout and other cold-water species will likely experience range contraction while warm-water species will likely experience large increases in available habitat (Rahel 2002; Chu et al. 2005; Sharma et al. 2007). However these and most other climate change models have overwhelmingly focused on species loss (i.e., presence-absence data), an approach that has long been critiqued for a variety of reasons (Hampe 2004; Heikkinen et al. 2006; Araújo and Peterson 2012). Most notably, the presence of a species does not always indicate optimal habitat as species are often relegated to or

subsist within sub-optimal ecological conditions over time (Lancaster and Downes 2010). For example, metapopulations by definition are agglomerations of spatially segregated sub-populations, some of which can be sources and others sinks (Hanski 1999). Sources can become sinks over time if environmental conditions change and species are maladapted (Eriksson 1996). Production rates are one way of quantifying the capacity of populations and ecosystems to respond to environmental change (Waters 1977; Hayes et al. 2007; Dolbeth et al. 2012). However, species and thermal guild specific responses to climate change will vary based on a number of factors that may change over different spatial and temporal scales prior to species collapse (Magnuson et al. 1979; Chu et al. 2005). For example, cold-water fish survival is associated with mean and maximum summer temperatures (Eaton and Scheller 1996), while warm-water fish growth is limited by mean and maximum winter temperatures (Shuter and Poste 1990). Conversely, low summer and winter temperatures can be associated with increased mortality rates of warm-water fish species (Rahel 2002). As climate change prompts changes to growth and mortality, fish production will also be affected as a result. However, fisheries production response to climate change will be confounded by an assortment of interacting abiotic and biotic factors each contributing in myriad ways to facilitate complex changes to production rates (Watson and Balon 1984; Magnuson et al. 1997).

Complexities in the community production response to climatic variations were clear in this study. For example, community production was only weakly related to summer air temperatures but strongly related to other habitat characteristics (i.e., dissolved oxygen, % canopy cover, latitude, and % riffle habitat). Conversely, community production was strongly related to summer water temperatures and not to

habitat. Significant correlations did exist between air and water temperature and community production, but when other variables (i.e., water chemistry and habitat) were accounted for in the regression models, air temperature did not significantly account for variation in community production. This was most likely due to the complex nature of the relationships between temperature and species growth, survival, and ultimately production (Ficke et al. 2007).

The stronger relationship between water temperatures and fish production compared to the relationship between air temperatures and fish production highlights the importance of groundwater inputs and air/water temperature sensitivity in a changing climate. It is widely accepted that groundwater affects stream water temperatures in high elevation headwater streams and may act as an important cooling function for cold-water species in high elevation streams under climate change stress (Meisner 1990). Groundwater effects on stream water temperatures exhibit a complex relationship and is not entirely understood, and could cause increases or decreases in water temperatures (Lyons et al. 2010). However, groundwater is predicted to follow a similar increase pattern as mean annual air temperatures; thus, as air temperatures increase groundwater temperatures may also increase (Meisner et al. 1988).

The importance of habitat in driving overall production of stream fish communities was highlighted in this study when using air temperature models only. In particular, habitat variables that had the highest percent contribution to the habitat factor (e.g., dissolved oxygen, latitude, and % canopy cover) were especially important in driving community fish production when water temperatures were not included in the model. Lower order, headwater streams further up in the watershed had much lower fish

production than larger higher order streams. For example, Whiteoak creek, a headwater stream in North Carolina had a community fish production value of $0.76 \text{ g m}^{-2} \text{ y}^{-1}$, while West Prong Hickey's Fork, a nearby larger stream had a community fish production estimate of $4.78 \text{ g m}^{-2} \text{ y}^{-1}$. These findings may align with the river continuum concept of streams (Vannote et al. 1980). Headwater streams are generally predicted to be influenced by allochthonous inputs from surrounding upland forests and canopy cover. However, as stream size and order increases, carbon fluxes are predicted to be increasingly autochthonous in origin (Vannote et al. 1980). Thus in this study, community fish production may be more influenced by the river system gradient of physical habitat attributes of each stream (i.e., latitude, dissolved oxygen, and % canopy cover) as well as water temperatures. These factors clearly drive primary and secondary invertebrate production (Benke and Wallace 1980; Hill et al. 1995; Hall et al. 2011), which directly affect food and energy availability for higher trophic levels (Allan and Castillo 2007). Yet total community fish production can be a deceiving metric if looked at in isolation as species- and guild-specific responses to climate change can be highly divergent (Tracy and Christian 1986; Winemiller and Rose 1992; Rypel 2014).

This study revealed a sharp negative relationship between production rates of cold-water species and summer temperatures. Many studies have demonstrated how summer air and water temperature can affect the growth rates, survival, reproduction, abundance, and ultimately production of poikilotherms in freshwater environments (Ward and Stanford 1982; Meisner 1990; Post and Parkinson 2001; Rahel 2002). For example, even small increases in summer air and water temperatures are expected to have major effects on stream fishes in diverse ecosystem types (Casselman 2002; Rahel 2002; Lyons

et al. 2010). In this study, the summer air and water temperature factors were the best variable in predicting dominance of fish production rates by cold-water species (e.g., salmonids and cottids) or cool-water species (e.g., cyprinids and catostomids). The mechanisms by which production could be increased via lower temperatures is unknown and counter to a large body of work on metabolic ecology (Shuter and Meisner 1992; Clark and Fraser 2004); however, some cold-water fish species can be ‘cold-adapted’ and have comparative metabolic rates at lower temperatures than species inhabiting warmer temperatures (Wohlschag 1960). However, several potential explanations for this pattern include increased overall and timing of availability of key food items (Shuter and Meisner 1992), species specific metabolic adaptations to colder temperatures and reduced growing seasons (Devries 1982; Conover and Present 1990; Shuter and Post 1990; Siikavuopio et al. 2010), and decreased interspecific competition with other species and thermal guilds (Fausch 1988; Rodtka and Volpe 2007; McCullough et al. 2009). The mechanisms by which this pattern operates should be a topic of interest for future research. With the most recent IPCC (2013) report predicting more hot temperature extremes compared to cold temperature extremes, these data strongly suggest that fish communities dominated by cold-water species production are at risk of massive production losses as summer temperature extremes intensify. Understanding the mechanisms by which cold-water fish production rates are degraded with increasing temperatures could offer key insights towards improved conservation management of cold-water fisheries in the face of climate change.

Surprisingly, production rates of cool-water fish species increased with increasing summer air and water temperature – an opposite pattern as that observed for cold-water

fishes. Cline et al. (2013) found a similar trend in thermal habitat availability for cold-water species (Siscowet Lake Trout *Salvelinus namaycush*) and cool-water species (Lean Lake Trout and Chinook Salmon *Oncorhynchus tshawytscha*). A decrease in thermal habitat for the cold-water Siscowet Lake Trout but an increase in thermal habitat for the cooler water species, Lean Lake Trout and Chinook Salmon, was observed. However, once temperature increases reach a certain point, cool-water species will also be negatively affected (Cline et al. 2013). Even within temperature guilds of cold-water and cool-water fish species, variations in temperature range and extreme minimum and maximum tolerances and thresholds exist (Magnuson et al. 1979; Lyons et al. 2010); thus, temperatures in the southern Appalachians have not reached these critical values for many of the cool-water species. However, based on IPCC (2013) projections temperatures will likely increase between 0.3-0.7°C by 2035, which could prompt a decline in cool-water species production where cool-water species occur at the edge of their highest temperature range. Climate change will most likely have a continuous and varied effect on southern Appalachian stream fish with increases and decreases in production occurring at varying temporal scales depending on the extent of the temperature increases.

Multinomial regression results suggested that temperature thresholds or ‘tipping points’ (Carpenter and Brock 2006; Scheffer et al. 2009) may exist for entire thermal guilds and thus entire ecological communities in Appalachian streams. For example, production rates of fish communities dominated by cold-water species stand a significant risk of flipping towards other thermal guilds once this temperature threshold is crossed. Critical temperature thresholds have been defined for various marine invertebrates and

marine and freshwater fish species but are known to vary widely (Pörtner 2001; Ficke et al. 2007). Furthermore, critical temperature thresholds for temperate fishes are typically higher for populations occurring in the mid-latitudes where seasonal variations in temperature are higher and lower for populations occurring in extreme high and low latitudes (Pörtner and Peck 2010). For example, even if water temperatures do not reach the lethality limit of a species, numerous other sublethal effects could be manifested that could alter growth, abundance, survival, and ultimately production of that species (Ficke et al. 2007). Thus even slight increases in stream temperatures could initiate shifts in community composition and production, especially if that ecosystem is already near the edge of a thermal threshold (Casselman 2002; Rahel 2002). For example, Jesse Branch, a cold-water stream in North Carolina, was dominated by cold-water fish species, however because its mean annual summer temperature is 19.8 °C, it may be at risk of a dramatic production composition shift in the coming years. Ultimately, the concept of thermal thresholds in streams is an intriguing concept, and the use of production in quantifying and delineating thermal thresholds should be considered fertile grounds for future research.

Cold-water streams throughout the southern Appalachian range are apparently at risk of vast production shifts over time as climate change proceeds. However, the magnitude of production change will depend largely on the magnitude of observed thermal shifts that take place in streams. The most recent IPCC (2013) projections suggest that between 2016 and 2035 global mean surface temperatures will most likely increase by 0.3 to 0.7°C compared to historical levels. For 2081-2100, global mean temperature increases above 2°C relative to 1986-2005 are unlikely (IPCC 2013). Based

on the 204 streams with varying temperature regimes in this study, a potential change of 0.5°C in summer mean temperatures would be predicted to only slightly decrease the number of cold-water and cool-water streams. However, a mid-level increase of 1°C in summer mean temperatures greatly reduced the number of cold-water and cool-water streams in the region suggesting a change in the proportional dominance of fisheries production per thermal guild. Lastly, the worst case scenario based on a 2°C increase in mean summer temperatures resulted in shifting almost all streams to mostly warm-water streams, and most likely their production to warm-water species as well. The streams from the 204 stream network in eastern Virginia and eastern North Carolina appeared to be the most vulnerable to even relatively slight changes in mean summer temperatures (i.e., 0.5 and 1.0°C) as they are already near a thermal threshold for stream type change. These data therefore strongly suggest that streams in the southern Appalachian region are in a precarious position. As temperatures continue to rise, cold-water fish production can be expected to decrease, which will drastically alter biodiversity and ecosystem function as well as cultural and economic interests (e.g., cold-water trout fisheries) (Costanza et al. 1997; Scott and Helfman 2000; Ficke et al. 2007).

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FIGURES

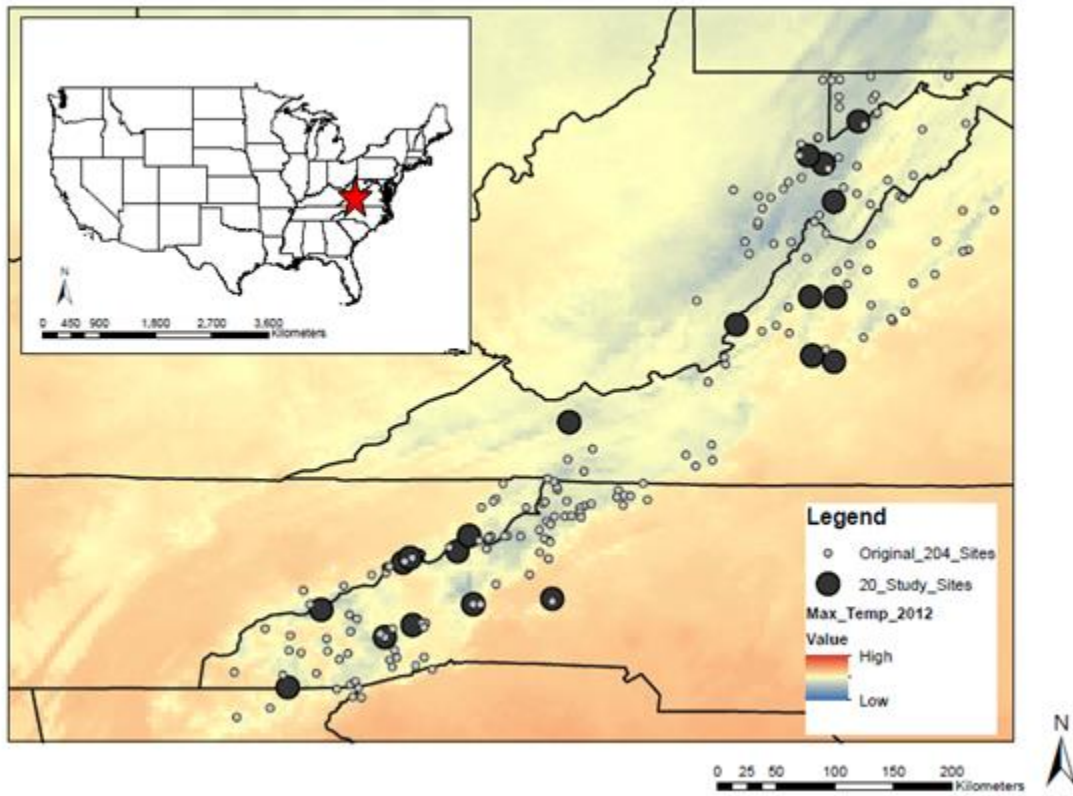


Figure 1. The original 204 temperature sites and the twenty selected study streams located across North Carolina, Tennessee, Virginia, West Virginia, and Maryland sampled during summer 2012. Maximum temperature data from NOAA National Climatic Data Center (www.ncdc.noaa.gov 2013).

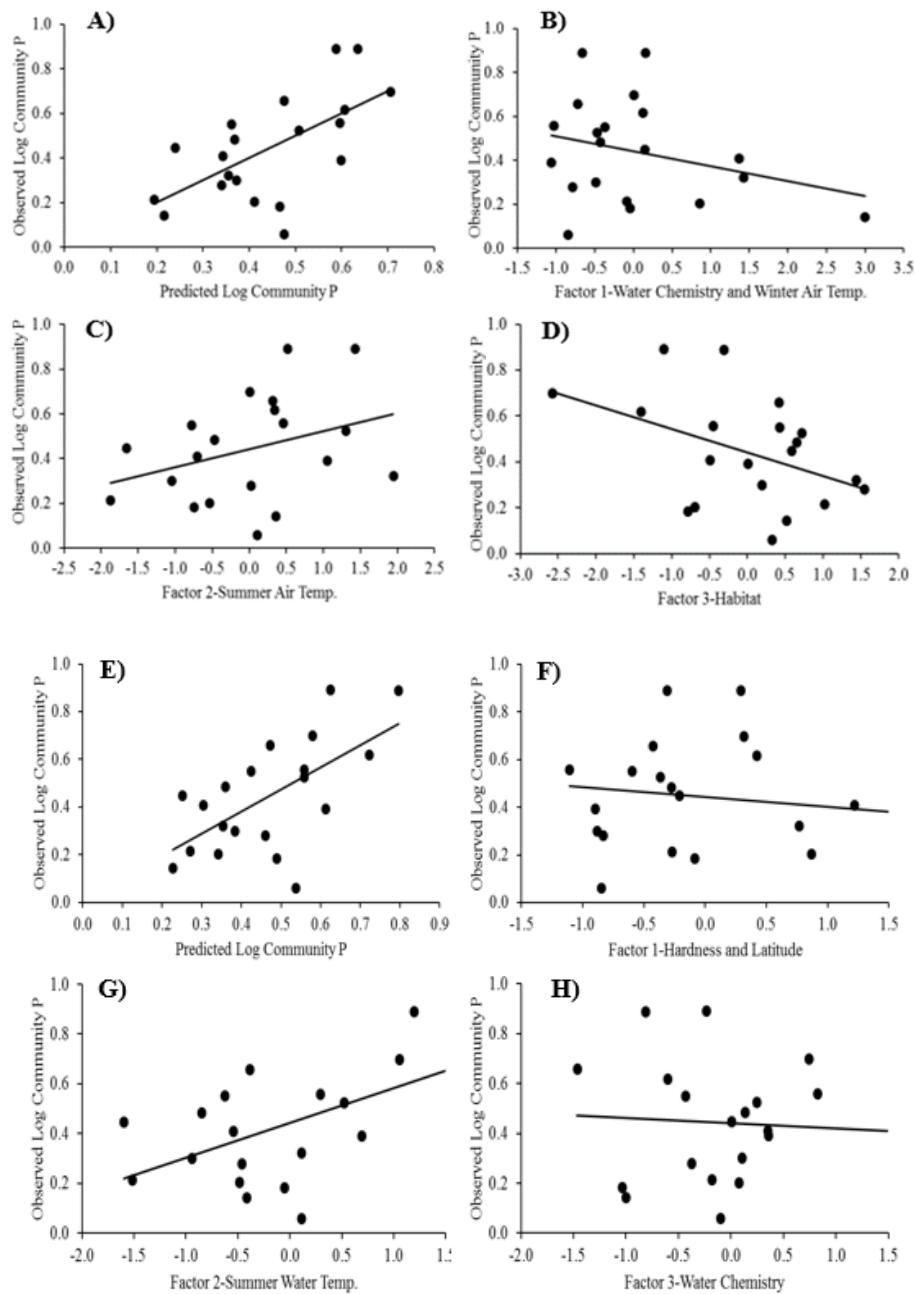


Figure 2. Scatterplots highlighting the relationship between the (A) observed community production and predicted community production based on air temperature model ($R^2=0.39$), (B) observed community production and factor 1 (water chemistry and winter air temperatures) ($R^2=0.08$), (C) observed community production and factor 2 (summer air temperatures) ($R^2=0.12$), and (D) observed community production and factor 3 (habitat) ($R^2=0.19$), (E) observed community production and predicted community production based on the water temperature model ($R^2=0.39$), (F) observed community production and factor 1 (hardness and latitude factor) ($R^2=0.03$), (G) observed community production and factor 2 (summer water temperatures) ($R^2=0.35$), (H) and observed community production and factor 3 (water chemistry) ($R^2=0.01$).

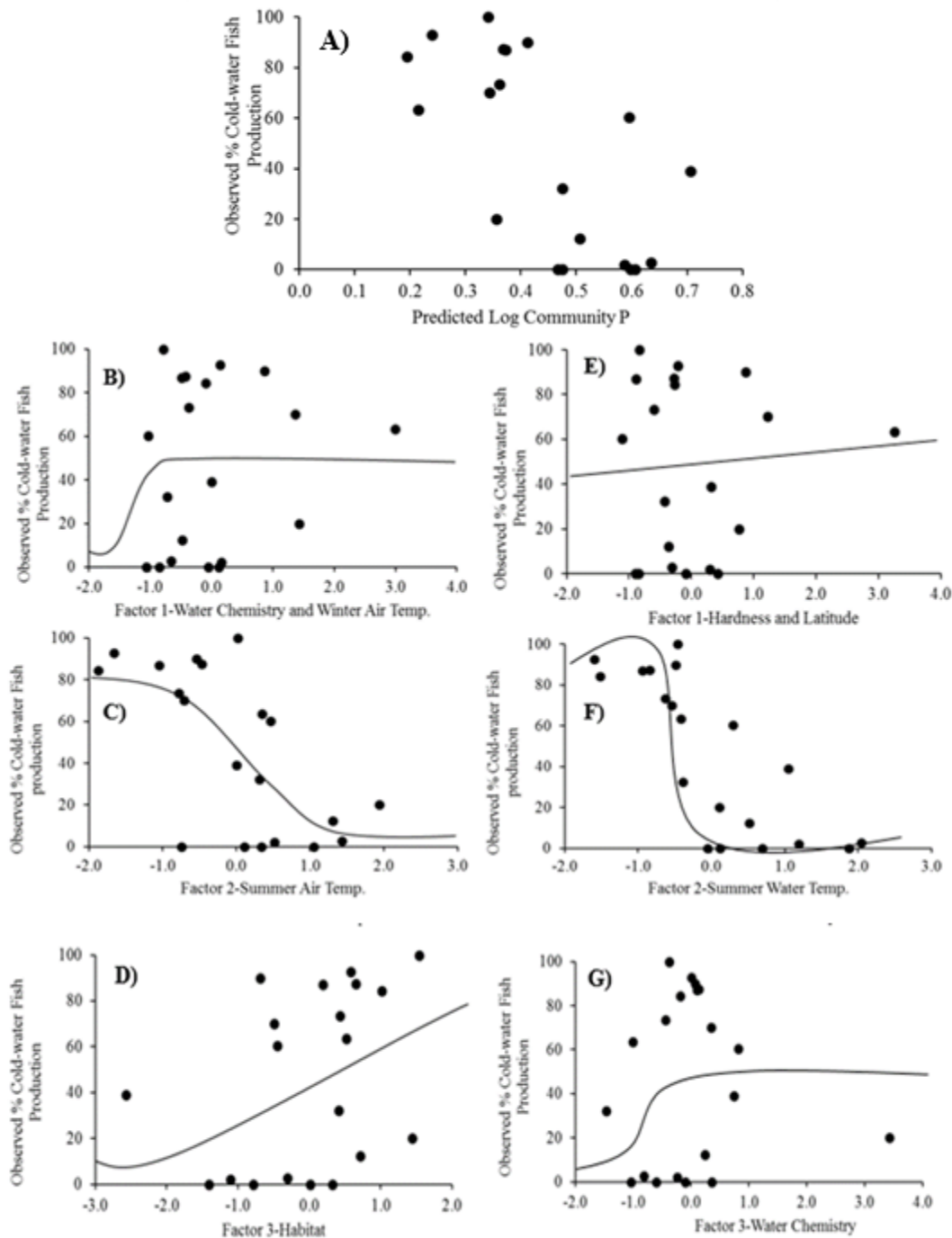


Figure 3. (A) Percent cold-water fish production as a function of the predicted log community production ($R^2=0.46$), (B) percent cold-water fish production as a function of factor 1 (water chemistry and winter air temperatures) ($R^2=0.03$), (C) factor 2 (summer air temperatures) ($R^2=0.45$), and (D) factor 3 (habitat) ($R^2=0.13$) from the Model 1 logistic regression. (E) Percent cold-water fish production as a function of factor 1 (hardness and latitude) ($R^2=0.003$), (F) factor 2 (summer water temperatures) ($R^2=0.77$), and (G) factor 3 (water chemistry) ($R^2=0.006$) from the Model 2 logistic regression.

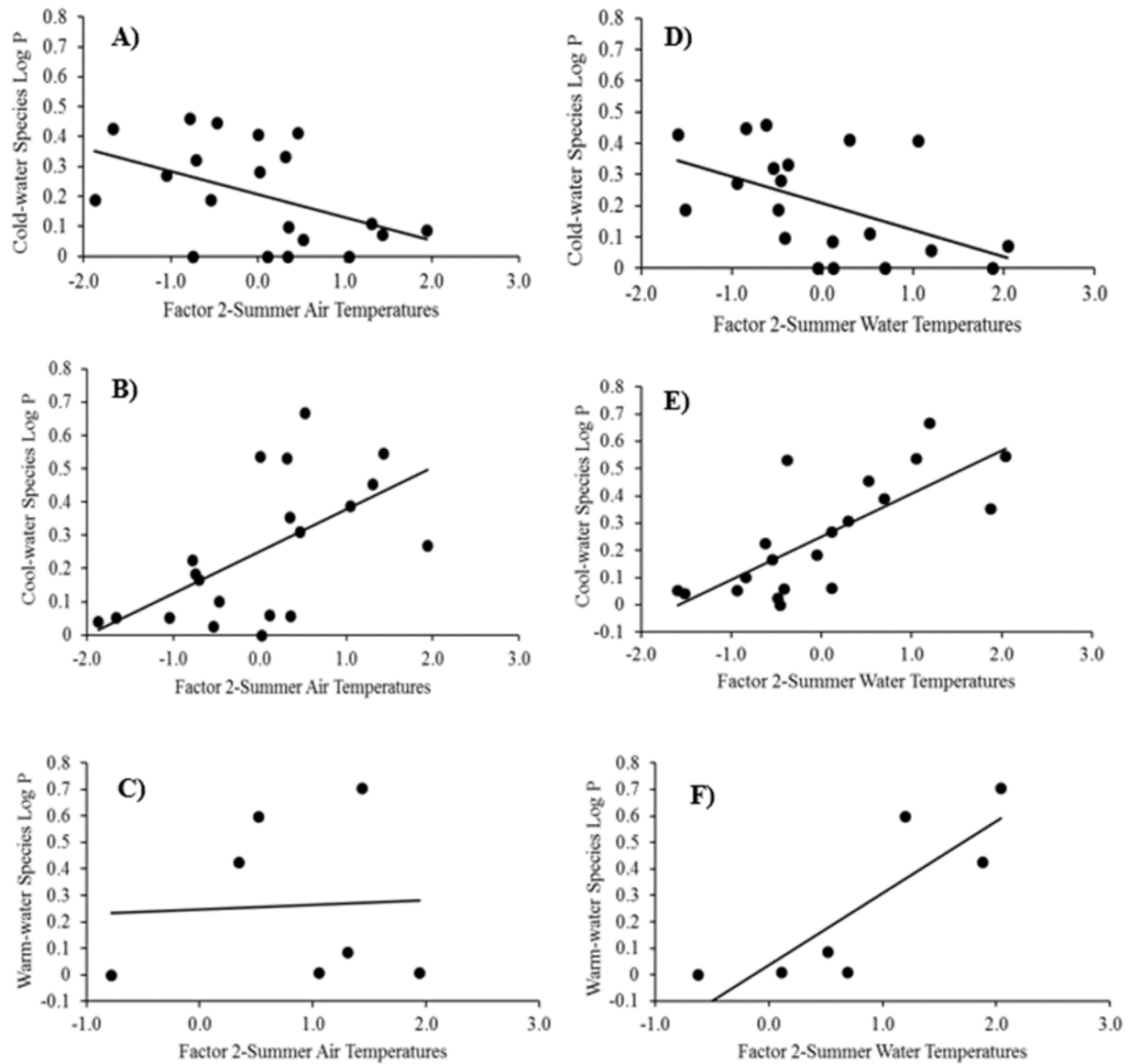


Figure 4. Thermal guild scatterplots of raw cold-water, cool-water, and warm-water species total production (log-transformed) for all 20 sites as a function of the significant variables in the regression models. (A) Cold-water species production, (B) cool-water species production, (C) warm-water species production as a function of factor 2 (Summer Air Temperatures) from the models based on a PCA of habitat and air temperatures. The second column of graphs are (D) cold-water species production, (E) cool-water species production, (F) warm-water species production as a function of factor 2 (Summer Water Temperatures) from the models based on a PCA of habitat and water temperatures. Complete regression results are summarized in Table 7.

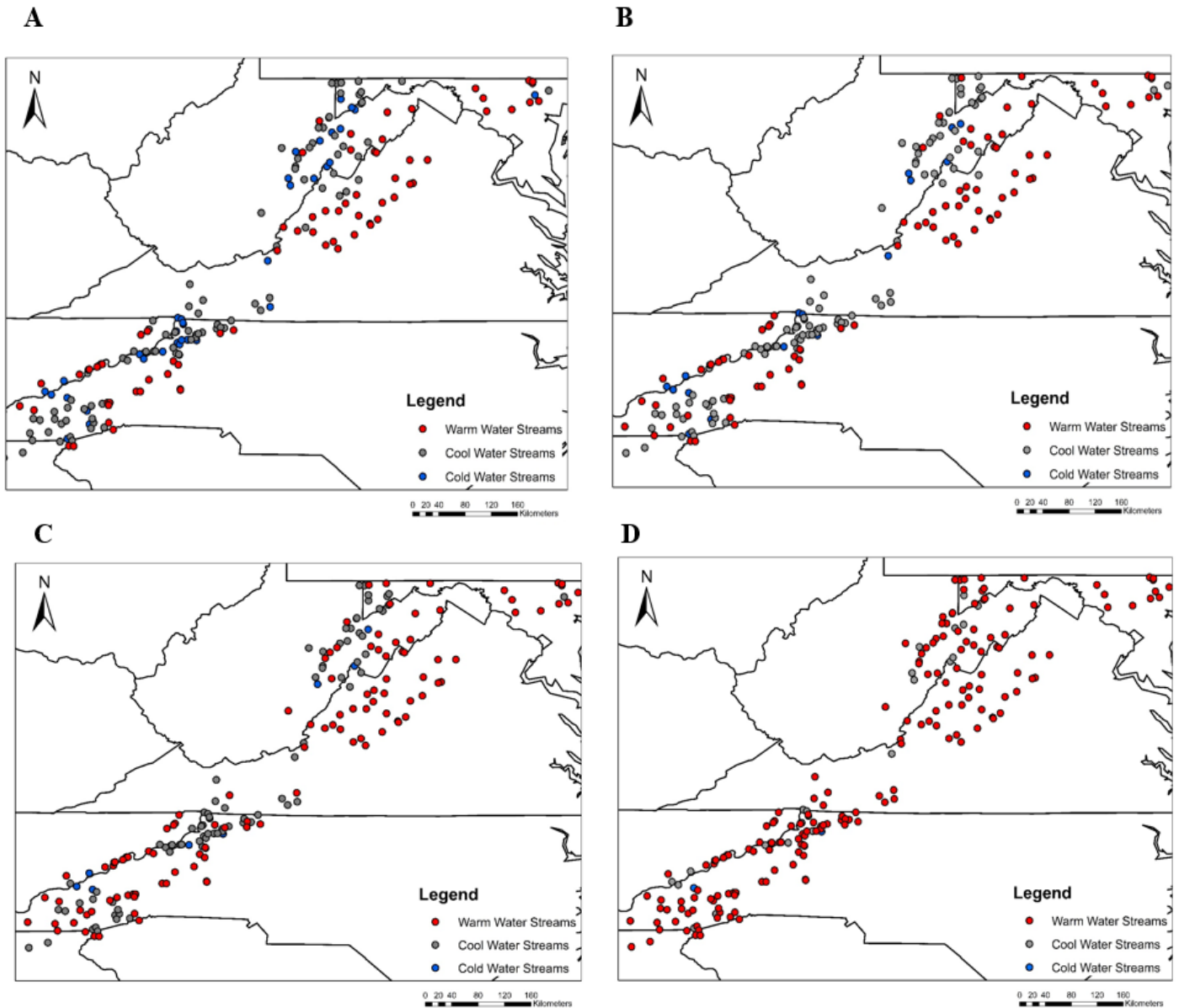


Figure 5. (A) Stream classification based on summer 2012 mean temperatures (n=204). (B) Stream classification based on mid-level increases (0.5°C) of summer mean temperatures (N=204). IPCC (2013) predicted with medium confidence that mean temperatures will likely increase 0.3-0.7°C. (C) Stream classification based on a one-unit increase (1.0°C) in summer mean temperatures (N=204). IPCC (2013) predicted with medium confidence that mean temperatures will likely increase 0.3-0.7°C. (D) Stream classification based on a 2°C increase in summer mean temperatures (n=204). IPCC (2013) predicted that a 2.0°C increase in mean temperatures is unlikely.

TABLES

Table 1. Total number of individuals (N), biomass (B) (g m^{-2}), annual production (P) ($\text{g m}^{-2} \text{ yr}^{-1}$), P/B ratios (P/B), and % production of cold-water, cool-water, and warm-water species for each fish community from the 20 stream locations organized north to south by latitude.

Stream Name	Stream Classification	Number of Individuals	Biomass (g m^{-2})	Annual Production ($\text{g m}^{-2} \text{ yr}^{-1}$)	P/B	% cold water species P	% cool water species P	% warm water species P
Laurel Run	cold	164	1.60	0.39	0.25	63	37	0
Elklick Run #2	cold	314	3.31	1.57	0.47	70	30	0
Elklick Run	cold	147	0.93	0.60	0.65	90	10	0
Blizzard Run	cool	606	9.30	4.00	0.43	39	61	0
Lick Run	warm	531	3.68	3.16	0.86	0	40	53
Kelso Spring Branch	cool	478	6.81	6.79	1.00	2	54	44
North Creek	warm	822	10.73	6.77	0.63	3	37	60
Jerry's Run	cool	351	2.09	1.10	0.53	20	78	2
Reed Creek	cold	424	6.23	3.56	0.57	32	68	0
Roaring Creek	cool	95	0.61	0.53	0.87	0	100	0
Red Fork	cold	258	3.43	2.06	0.60	87	13	0
Whiteoak Creek	cool	25	0.76	0.15	0.20	0	100	0
West Prong Hickey's Fork	cool	342	4.78	2.56	0.54	73	27	0
Trib. to Little Laurel Creek	cool	196	3.79	2.62	0.69	60	40	0
Trib. to Henry Fork	cool	136	3.15	1.47	0.47	0	99	1
Swannanoa Creek	cool	553	2.93	2.36	0.81	12	78	9
Beech Flats Prong	cold	124	2.18	1.81	0.83	93	7	0
Jesse Branch	cold	117	1.91	1.00	0.52	87	13	0
Scapecat Branch	cold	30	1.64	0.64	0.39	84	16	0
Bethabara Creek	cool	39	1.75	0.91	0.52	100	0	0

Table 2. Summary of habitat data of the 20 stream locations organized north to south by latitude. All habitat surveys were conducted during summer 2012 in conjunction with fish sampling.

Stream Name	Latitude	Longitude	Elevation	Watershed Area (km ²)	Average depth (m)	Average Width (m)	Discharge (m ³ s ⁻¹)	Mean Annual Temp. (°C)	Max Summer Temp. (°C)	Temp. Standard Deviation	Conductivity (µS cm ⁻¹)	Dissolved Oxygen (mg L ⁻¹)
Laurel Run	39.343	-79.258	615	22.5	0.30	6.1	0.06	9.9	18.4	6.1	348.9	8.7
Elklick Run 2	39.078	-79.649	524	15.1	0.35	6.8	0.01	10.7	18.1	5.4	91.4	7.5
Elklick Run	39.016	-79.532	586	7.2	0.24	4.3	0.03	10.4	17.5	5.2	134.3	6.0
Blizzard Run	38.728	-79.447	559	6.1	0.13	2.1	0.01	11.2	21.6	6.2	119.7	4.6
Lick Run	37.993	-79.631	397	20.2	0.26	6.5	0.40	12.9	23.8	7.5	67.3	5.0
Kelso Spring Branch	37.991	-79.438	422	4.2	0.20	3.3	0.02	12.6	21.3	6.3	163.4	6.1
North Creek	37.855	-79.616	267	90.5	0.27	6.2	0.09	13.9	24.9	6.5	69.8	7.3
Jerry's Run	37.784	-80.197	624	20.0	0.23	4.7	0.05	11.2	19.6	6.1	168.5	8.9
Reed Creek	37.499	-79.449	366	7.3	0.30	5.1	0.04	10.9	19.3	4.6	21.9	6.3
Roaring Creek	37.035	-81.482	671	25.6	0.17	4.3	0.01	11.1	19.0	5.1	14.1	6.0
Red Fork	36.159	-82.251	800	14.7	0.22	4.7	0.03	10.8	17.7	4.9	15.4	8.6
Whiteoak Creek	36.041	-82.338	646	2.4	0.14	3.6	0.02	11.9	19.5	5.4	22.8	6.8
West Prong Hickey's Fork	35.994	-82.704	670	15.3	0.22	5.2	0.04	12.0	18.8	4.6	27.5	6.0
Trib. to Little Laurel Creek	35.957	-82.756	572	3.6	0.14	2.6	0.03	12.0	19.3	5.6	26.6	7.1
Trib. to Henry Fork	35.666	-81.612	362	2.0	0.13	2.0	0.02	12.9	20.1	5.4	20.3	8.8
Swannanoa Creek	35.635	-82.219	494	6.7	0.10	3.9	0.05	12.8	20.6	5.4	88.1	8.8
Beech Flats Prong	35.593	-83.387	957	11.7	0.34	8.8	0.28	10.7	16.2	4.0	12.0	8.6
Jesse Branch	35.477	-82.684	755	6.8	0.20	3.5	0.08	11.9	17.8	4.2	13.7	8.2
Scapecat Branch	35.382	-82.895	1046	14.3	0.30	15.6	0.26	10.4	16.7	4.7	9.4	9.0
Bethabara Creek	34.997	-83.644	729	2.0	0.18	2.4	0.04	12.6	18.4	4.9	14.9	9.2

Table 3. Principal component factor loadings and percent contribution for each physical and chemical habitat variable included in the principal components analysis with only air temperature included. Variables are organized by decreasing % contribution. Eigenvalues were 9.2, 6.0, and 3.1 for PCs 1, 2, and 3, respectively.

Principal Component 1			Principal Component 2			Principal Component 3		
Physical and Chemical Habitat Variables	Factor Loadings	% Contribution	Physical and Chemical Habitat Variables	Factor Loading	% Contribution	Physical and Chemical Habitat Variables	Factor Loadings	% Contribution
Max winter temp	-0.88	6.1	Temperature variability	0.79	7.2	DO	0.83	9.7
Magnesium	0.85	6.0	Max temp	0.77	7.0	% riffle habitat	0.72	8.4
Conductivity	0.85	5.9	Mean summer temp	0.75	6.9	% run habitat	-0.71	8.3
Calcium	0.81	5.7	Elevation	-0.75	6.8	% canopy cover	0.57	6.7
Mean yearly temp.	-0.80	5.6	Potassium	0.63	5.7	Latitude	-0.54	6.3
Min Temp	-0.80	5.6	Sodium	0.59	5.4	Min winter temp	0.48	5.5
Growing degree days	-0.76	5.3	Average stomach weight	-0.58	5.3	Temperature variability	-0.47	5.4
Sulfate	0.75	5.2	Width to depth ratio	-0.58	5.3	Elevation	0.44	5.1
Potassium	0.72	5.0	Chlorine	0.54	4.9	Average stomach weight	0.36	4.2
Latitude	0.70	4.9	Mean yearly temp.	0.48	4.4	Chlorine	0.36	4.2
Max depth	0.68	4.7	Min Temp	0.46	4.2	Sodium	0.30	3.4
Large wood	-0.54	3.8	Average depth	-0.39	3.5	Max depth	0.25	2.9
Orthophosphate	-0.54	3.8	Conductivity	0.37	3.3	Nitrate	-0.23	2.6
Mean summer temp	-0.53	3.7	pH	0.32	2.9	Calcium	-0.20	2.4
Nitrate	0.52	3.7	Discharge	-0.30	2.7	Width to depth ratio	-0.21	2.4
Max temp	-0.51	3.6	Magnesium	0.27	2.4	Min Temp	0.18	2.1
Min winter temp	-0.52	3.6	Watershed area	0.26	2.3	Orthophosphate	0.18	2.1
Average depth	0.51	3.6	Orthophosphate	0.24	2.2	Max temp	-0.17	2.0
Chlorine	0.33	2.3	Max winter temp	0.23	2.1	Average depth	0.17	2.0
% riffle habitat	-0.30	2.1	Latitude	0.23	2.1	Ammonium	-0.17	2.0
% pool	0.30	2.1	Ammonium	0.23	2.1	Mean summer temp	-0.16	1.9
Sodium	0.26	1.8	Calcium	0.21	1.9	Large wood	-0.15	1.7
Width to depth ratio	-0.14	1.0	Min winter temp	-0.20	1.8	Conductivity	-0.13	1.5
pH	-0.11	0.8	Growing degree days	0.14	1.3	Growing degree days	0.12	1.4
Average stomach weight	-0.10	0.7	% run habitat	0.13	1.2	pH	-0.11	1.3
Temperature variability	0.09	0.7	% canopy cover	-0.14	1.2	Sulfate	0.11	1.3
Watershed area	0.08	0.6	Sulfate	0.13	1.2	% pool	-0.07	0.8
Elevation	0.08	0.6	% riffle habitat	-0.11	1.0	Watershed area	-0.06	0.6
DO	0.08	0.6	Max depth	0.08	0.7	Max winter temp	-0.05	0.6
% run habitat	0.05	0.4	% pool	0.04	0.4	Mean yearly temp.	0.05	0.5
Discharge	0.04	0.3	DO	0.03	0.3	Potassium	0.03	0.4
Ammonium	0.01	0.1	Large wood	0.01	0.1	Magnesium	0.01	0.1
% canopy cover	0.00	0.0	Nitrate	-0.01	0.1	Discharge	0.01	0.1

Table 4. Principal component factor loadings and percent contribution for each physical and chemical habitat variable included in the principal components analysis with only water temperature included. Variables are organized by decreasing % contribution. Eigenvalues were 8.3, 6.1, and 3.0 for PCs 1, 2, and 3, respectively.

Principal Component 1			Principal Component 2			Principal Component 3		
Physical and Chemical Habitat Variables	Factor Loadings	% Contribution	Physical and Chemical Habitat Variables	Factor Loadings	% Contribution	Physical and Chemical Habitat Variables	Factor Loadings	% Contribution
Magnesium	0.90	7.2	Max temp.	0.97	9.1	Sodium	0.81	10.8
Conductivity	0.89	7.1	Mean summer temp.	0.95	8.9	Chlorine	0.80	10.7
Calcium	0.89	7.1	Min summer temp.	0.92	8.6	% pool habitat	-0.58	7.8
Sulfate	0.80	6.4	Temperature Variability	0.86	8.1	Potassium	0.52	7.0
Latitude	0.79	6.3	Elevation	-0.82	7.7	Nitrate	0.44	5.9
Potassium	0.70	5.6	Mean yearly temp.	0.71	6.6	Nitrite	-0.44	5.9
Max winter temp.	-0.70	5.5	DO	-0.47	4.4	Max depth	0.42	5.6
Min winter temp.	-0.67	5.3	% run habitat	0.47	4.4	% run habitat	0.40	5.4
Growing degree days	-0.67	5.3	Nitrite	0.43	4.0	Growing degree days	-0.32	4.3
Large wood	-0.58	4.6	% canopy cover	-0.40	3.8	Large wood	0.25	3.4
Max depth	0.57	4.5	% riffle habitat	-0.39	3.7	DO	0.25	3.4
Mean yearly temp.	-0.53	4.2	pH	0.38	3.6	Average depth	-0.22	3.0
Ammonium	-0.49	3.9	Average depth	-0.37	3.4	% canopy cover	-0.19	2.5
Nitrate	0.49	3.9	Latitude	0.36	3.4	% riffle habitat	-0.18	2.4
Average depth	0.48	3.8	Potassium	0.30	2.8	Sulfate	-0.17	2.3
% pool habitat	0.44	3.5	Width to depth ratio	-0.27	2.6	Ammonium	-0.16	2.1
Temperature Variability	0.40	3.2	Min winter temp.	-0.26	2.4	Discharge	-0.14	1.9
% riffle habitat	-0.37	2.9	Max depth	-0.22	2.1	pH	0.14	1.9
Width to depth ratio	-0.20	1.6	Conductivity	0.20	1.9	Conductivity	0.13	1.7
Chlorine	0.19	1.5	Sodium	0.15	1.4	Elevation	0.12	1.6
Min summer temp.	-0.17	1.4	Calcium	0.15	1.4	Temperature variability	0.11	1.5
Sodium	0.13	1.1	Nitrate	-0.13	1.2	Max winter temp.	0.11	1.4
Nitrite	0.11	0.9	Ammonium	0.11	1.1	Min summer temp.	-0.10	1.4
% canopy cover	-0.08	0.6	Growing degree days	0.08	0.8	Min winter temp.	-0.10	1.3
Elevation	-0.08	0.6	Magnesium	0.07	0.7	Width to depth ratio	-0.10	1.3
% run habitat	0.07	0.5	Chlorine	0.07	0.6	Calcium	-0.08	1.1
Mean summer temp.	-0.04	0.3	Sulfate	-0.06	0.6	Max temp.	-0.08	1.0
Max temp.	-0.03	0.2	Large wood	0.04	0.4	Mean yearly temp.	-0.06	0.8
pH	-0.03	0.2	% pool habitat	0.03	0.3	Mean summer temp.	0.03	0.4
DO	-0.03	0.2	Discharge	-0.01	0.1	Latitude	-0.01	0.1
Discharge	0.02	0.2	Nitrate	-0.01	0.1	Latitude	-0.01	0.1
Ammonium	0.01	0.1	Max winter temp.	0.00	0.0	Magnesium	0.00	0.0
% canopy cover	0.00	0.0	Max winter temp.	0.00	0.0	Magnesium	0.00	0.0

Table 5. Two separate stepwise multiple regression model (n=20) results highlighting effects of covariates (PCs 1-3) for the two PCAs conducted using air temperatures only (Model 1) and the second PCA conducted using water temperatures only (Model 2) on community annual production across the southern Appalachian Mountains.

Independent Variable	Parameter Estimate	<i>P</i>-value	R²
Model 1	3.39	0.04	0.27
Factor 1-Water chemistry and winter air temperatures	-0.08	0.16	0.08
Factor 2-Summer air temperatures	0.08	0.10	0.12
Factor 3-Habitat	-0.10	0.04	0.19
Model 2	3.45	0.04	0.29
Factor 1-Hardness and Latitude	-0.04	0.38	0.03
Factor 2-Summer water temperatures	0.14	0.01	0.35
Factor 3-Water Chemistry	-0.02	0.65	0.01

Table 6. Multinomial logistic regression models (n=20) log likelihood ratio test and parameter estimates with the associated *P*-values highlighting the effects of factor 1 (water chemistry and winter temperature), factor 2 (summer temperatures), and factor 3 (habitat complexity) on the log odds of the dominance of cold-water, cool-water, and warm-water species dominating community production. The first model was based on the three principal component factors determined from air temperatures only, and the second model was based on the three principal component factors determined from water temperatures only.

Independent Variable	Parameter Estimate	<i>P</i> -value	R²
Model 1	18.87	0.004	0.50
Factor 1-Water chemistry and winter air temperatures	-1.07	0.50	**
Factor 2-Summer air temperatures	14.45	0.001	**
Factor 3-Habitat	7.01	0.03	**
Model 2	26.94	0.0001	0.71
Factor 1-Hardness and Latitude	0.001	1.00	**
Factor 2-Summer water temperatures	49.57	<0.0001	**
Factor 3-Water Chemistry	0.41	0.82	**

Table 7. Species and thermal guilds ordinary least squares regression results using production rates as the dependent variable and factors 1, factor 2, and factor 3 as independent variables. Values in bold are significant at the 0.05 alpha level.

	Combined Cold-water Species Production (N=20)			Combined Cool-water Species Production (N=20)			Combined Warm-water Species Production (N=7)		
	Parameter Estimate	<i>P</i> -value	R ²	Parameter Estimate	<i>P</i> -value	R ²	Parameter Estimate	<i>P</i> -value	R ²
Model with air temperatures	F Ratio=1.61	0.23	0.09	F Ratio=9.99	0.001	0.59	F Ratio=1.95	0.30	0.32
Factor 1-Water chemistry and winter air temperatures	-0.02	0.55	0.02	-0.05	0.12	0.06	0.02	0.89	0.55
Factor 2-Summer Air Temperatures	-0.08	0.05	0.21	0.13	0.009	0.36	0.13	0.38	0.08
Factor 3-Habitat	0.01	0.79	0.00	-0.10	0.005	0.24	-0.27	0.10	0.15
Model with water temperatures	F Ratio=2.24	0.12	0.16	F Ratio=7.24	0.003	0.50	F Ratio=4.53	0.12	0.64
Factor 1-Hardness and latitude	-0.03	0.39	0.03	-0.02	0.52	0.01	0.19	0.36	0.07
Factor 2-Summer water temperatures	-0.09	0.03	0.26	0.16	0.0003	0.56	0.18	0.18	0.04
Factor 3-Water chemistry	0.01	0.79	0.00	0.00	0.93	0.00	-0.10	0.29	0.19

Manuscript 3 Title:
DIVERSITY-PRODUCTION RELATIONSHIPS OF FISH COMMUNITIES IN
APPALACHIAN STREAMS

ABSTRACT

Relationships between species richness and ecological production rates are increasingly thought to be pervasive across the globe. Yet diversity-production relationships have not been extensively explored for freshwater fish communities even though fisheries production is a key ecosystem service to humans. The purposes of this study were to 1) evaluate the diversity-production relationship in freshwater stream ecosystems across the Appalachian Mountain range; 2) examine how diversity-production relationships may vary across stream thermal classes; and 3) compare diversity-production relationships of stream fish communities to published relationships for other taxonomic groups. Empirical estimates of annual production rates were derived via field sampling of 25 stream fish communities. Community fish production ranged from 0.15 to 6.79 g m⁻² yr⁻¹ and community fish P/B from 0.21 to 1.07. Species evenness in production differed significantly across cold-water, cool-water, warm-water, and the extreme northern streams when production was used as the variable of interest, and evenness in production declined with stream temperature. Community fish production was significantly and positively related to species richness alone ($R^2=0.38$, $P=0.001$). Furthermore, the relationship increased in strength and significance after accounting for potential covariates of production (e.g., habitat quality, $R^2=0.54$, $P=0.0004$). The diversity-production relationship for stream fish communities was similar to other studies, but demonstrated the strongest relationships. Management of freshwater

fisheries for biomass and production may be more closely linked to conservation of fish diversity than previously thought. Further studies of diversity-production relationships are encouraged for other fish and ecological communities.

INTRODUCTION

The general relationship between biological diversity and production rates is one of the most widespread and intriguing patterns in ecology (Loreau 2000; Mittelbach et al. 2001). Diversity is generally conceptualized as having two main components: species richness and evenness (Whittaker 1972; Worm and Duffy 2003). Yet, ecologists have traditionally only investigated one component of the diversity-production relationship: species richness. Furthermore, diversity-production relationships have been most extensively explored within temperate grassland environments (Tilman et al. 1996; Tilman et al. 2001; Aoki et al. 2003). Thus debate exists over whether these relationships are general across taxa and ecosystems with more complex compositions, biotic interactions, and disturbance regimes (Aoki et al. 2003).

The mechanisms underlying the general diversity-production relationship remains an open and controversial topic (Mittelbach et al. 2001). One hypothesis is that higher species richness increases access to resources (provided there is low niche overlap) thereby increasing overall ecosystem production potential (Nijs and Roy 2000; Tilman et al. 2001). Another is that by having more species, the mathematical probability of having one or two highly productive species in a community increases (Huston 1997; Nijs and Roy 2000). In grassland ecosystems, scientists have documented both positive and uni-

modal relationships between diversity and productivity; however, Aoki (2003) suggested patterns are likely quite variable across taxa and ecosystems. Lake ecosystems have exhibited unimodal diversity-productivity relationships (Dodson et al. 2000).

Relationships between fish species diversity or evenness and community production have not been extensively studied in streams. However, freshwater stream ecosystems and fisheries are extremely valuable natural resources for human cultures and economies (Dalton et al. 1998; Cowx et al. 2010). Valentine-Rose (2007) found strong positive relationships between species richness and community fish production in Caribbean tidal creeks, however Watson and Balon (1984) found no correlation between species richness and production in tropical rain forest streams. Penczak (1981) found higher fish production in areas with lower species richness but pointed out that this relationship was not consistent across all sites sampled. Most importantly, these studies all took place in relatively large, open ecosystems where immigration and emigration effects of highly motile fishes are undoubtedly strong creating the potential for dilution effects. More precise estimates of fish diversity-production relationships are therefore extremely important and should probably first be approached in smaller, more easily studied freshwater environments.

Myriad anthropogenically-mediated environmental disturbances (e.g., climate change, habitat fragmentation, hydrological alteration, pollution, over-fishing) continue to threaten freshwater stream fish biodiversity and ecosystem function (Moyle and Leidy 1992; Dudgeon et al. 2006; Jackson and Mandrak 2002). If traditional diversity-production relationships apply to freshwater stream fisheries, a loss in species richness or evenness due to human impacts could be worrisome as it may precipitate a decline in

overall stream fisheries production. The objectives of this study were to 1) calculate relationships between α -diversity (e.g., species richness, Shannon-Weiner Index of Diversity, and Pielou's evenness index) and community fish production as well as evenness in community abundance, biomass, and production; 2) compare diversity-production relationships across stream thermal classes; and 3) compare coefficients from diversity-production relationships to similar, previously published relationships for other taxa.

METHODS

Study Area.— The 25 study streams were selected across the Appalachian Mountain Range spanning Vermont to North Carolina, USA (Figure 1). The majority (20) of the sites were more southerly located, but five sites were selected for study in the northern Appalachian Mountain range. The 20 southern sites were located in Maryland, West Virginia, Virginia, Tennessee, and North Carolina. These sites were selected from a larger network of 204 southern Appalachian streams used for stream temperature research by the United States Forest Service Southern Research Station (USFS SRS). Each of the 204 stream network sites contained HOBO (Bourne, MA, USA) air and water temperature loggers that were placed at each of the 204 sites by the USFS SRS from 2010-present. Of the 204 sites, 20 (10%) were selected for this study such that a latitude and temperature gradient was represented based on a stratified, random sample. The five extreme northern sites located in Vermont and Massachusetts in the Connecticut River Watershed were selected *a posteriori* by the United States Forest Service Northern

Research Unit to provide a comparison between distinct cold-water streams in the more northern and cold-water streams in the more southern Appalachian Range. Most of the sites were 2nd or 3rd order tributaries characterized by dense canopy cover, relatively high elevation, and dominated by cobble substrate.

Data Collection.—All data collection occurred from June to September 2012 except for field collection of the air and water continuous temperature data, which has been continuously downloaded biannually by the USFS SRS following deployment. A random starting point upstream of the air and temperature loggers was selected for each stream site. Using a systematic sampling design, ETS Electrofishing, LLC ABP-3Q-600 volt backpack electrofishing units were used to sample fish from two 50 meter stream reaches spaced 50 meters apart until depletion. Block nets with 1/16'' mesh were placed downstream and upstream of each 50 meter reach to inhibit immigration and emigration of fishes within the sampling area. For all individuals captured, total lengths (mm) and weights (g) were measured. A sub-sample of each species captured at each site was euthanized in tricaine methanesulfonate (MS-222) and transported to the lab on ice and frozen for otolith removal, age estimation, and stomach weight determination (g). Following Ketchen (1950) and Devries and Frie (1996) sub-sampling protocol, a fixed stratified sub-sample of approximately 10 individuals per species per length group was collected. To reduce sampling bias, length-group intervals were relatively small (i.e., 30-40 mm, 40-50 mm, 50-60 mm) (Devries and Frie 1996).

Replicate water samples were collected at each stream upstream of the upper reach prior to sampling and were immediately placed on dry ice to ensure fast freezing and express shipped to The Coweeta Hydrologic Laboratory (Otto, NC, USA) for

analysis of water concentrations of ammonium, nitrite, nitrate, phosphorous, sulfate, potassium, calcium, and magnesium using standard methods (USEPA 1983a; USEPA 1983b). Habitat data was recorded for the entire 150 meter reach section using similar estimation method as outlined in the Basinwide Visual Estimation Technique, BVET (Dolloff et al. 1993). In addition to the BVET parameters (e.g., dominant and subdominant substrate, large wood density, average and maximum depth, width, habitat units), canopy cover was estimated in each habitat unit using a convex densitometer and stream discharge measured across two transects within the sampling reach using a Marsh-McBirney (Harrisburg, PA, USA) Flo-mate 2000 flow meter following standard procedures (Gore 1996).

Diversity and production calculations.—Species richness was determined for each site, and mean species richness was calculated for the four site temperature classes. An analysis of variance (ANOVA) with Tukey’s post hoc comparisons was conducted to determine if species richness varied significantly across the four temperature classes. In addition, I used the Shannon-Wiener equation to calculate α -diversity as Shannon’s Diversity Index (Kwak and Peterson 2007). Pielou’s evenness index was calculated by dividing the Shannon’s Diversity Index (H) by the maximum value of H (Heip 1964).

Otolith sagittae were extracted from each retained specimen for estimation of age-at-capture and back-calculation of lengths at previous ages (Devries and Frie 1996). Putative annual growth rings were counted under a microscope and interannual growth increments measured by an experienced reader using a computer-based image analysis system interfaced with the microscope. Length-at-previous ages of all fish were calculated using the Fraser-Lee equation (Francis 1990)

$$L_t = c + (L_c - c) * (O_i / O_c)$$

where L_t =back calculated length at i th annuli, c =intercept constant, L_c =length of fish at capture, O_i =otolith radius at i th annuli, and O_c =otolith radius at capture (Francis 1990; DeVries and Fries 1996). The intercept for each species was determined by plotting fish length as a function of otolith radius length (Francis 1990). Finally, logarithmic or power growth functions (depending on the strength of the function fit) were used to predict the ages of all measured fish of unknown age using total length data as a predictor.

Secondary production values for each species were estimated using the instantaneous growth rate method (Waters 1977; Hayes et al. 2007). Age-specific growth (G) was calculated using the equation below.

$$G = \ln(\text{mean weight of age class}_{x+1}) / (\text{mean weight of age class}_x)$$

Age-specific biomass was calculated as the sum of the weights of all individuals sampled within that age class. Age-specific production was then estimated as the production of age-specific biomass and growth (Halyk and Balon 1983; Valentine-Rose et al. 2007; Valentine-Rose et al. 2011). This method integrates the area under the traditional Allen curve with fish age classes on the x-axis and mean weight on the y-axis (Allen 1949; Hayes et al. 2007). The formal equation used to calculate production was

$$P = \bar{B}G$$

where P =production, \bar{B} =arithmetic mean standing stock, and G =instantaneous growth rate. Annual production ($\text{g m}^{-2} \text{ yr}^{-1}$) for each species was calculated in MS EXCEL as the sum of production between each age class (Halyk and Balon 1983), and whole community fish production was calculated by summing all the individual species annual production values for the community (Halyk and Balon 1983). The P/B ratio for each

species was calculated as annual production divided by mean annual biomass as an estimate of the estimated biomass turnover rate for that species in each stream (Waters 1977; Hayes et al. 2007). Community P/B was calculated by dividing total community production by the total community biomass.

Data analysis.— The 20 southern sites were *a priori* clustered into three thermal classes all relative to high elevation Appalachian streams (i.e., cold-water streams, cool-water streams, and warm-water streams) using a K-Means cluster analysis on the mean annual, mean summer, maximum summer, and minimum summer water temperature data, so the warm-water streams still have relatively cool-water temperature regimes. All temperature variables were calculated using the year preceding the sampling event data. Little multiannual temperature data were available yet as HOBO loggers were deployed in 2010. The five extreme northern streams in Vermont and Massachusetts were not included in the cluster analysis and were *a priori* categorized as a separate group.

The potential effect of diversity on community fish production was investigated using three simple linear regressions models with log community fish production as the dependent variable and log species richness as the independent variable in the first model, the Shannon-diversity index in the second model, and Pielou's evenness index in the third model. Three separate ordinary least squares multiple regression models were also performed taking into account potential habitat covariates that were significantly correlated and not multicollinear with the other habitat covariates were included in the models: these included mean summer temperature, dissolved oxygen, and calcium. Lastly, linear regression models were conducted for cold-water and cool-water streams separately to determine the effect of richness and evenness for the stream thermal classes.

Warm-water streams and the extreme northern streams were excluded due to sample size issues and a limited available range of species richness and evenness values. Variables that did not adhere to assumptions of normality were log transformed.

To compare community assemblages, percent similarity was calculated based on individual species relative abundance, relative biomass, and relative production among all 25 sites to create percent similarity matrices. Using these matrices, three separate nonmetric multidimensional scaling models (NMDS) were performed to compare site proximities based on species assemblages across all study locations (Kwak and Peterson 2007). Kruskal's stress value and Shephard's plots were used to determine model fit (Guy and Brown 2007). Sites with greater proximity corresponded to more similar community composition and amount of abundance, biomass, and production allocated to the same species, while sites not clustered in the same area had dissimilar community composition and allocation of abundance, biomass, and production to other species.

To further analyze patterns in community fish abundance, biomass, and production in relation to species diversity and evenness, rank-abundance, rank-biomass, and rank-production curves were generated for each individual site (Whittaker 1972; Clarke 1990; Valentine-Rose et al. 2011). The slope of the rank-curves corresponded to community evenness, thus higher slopes indicated that fewer species dominated community production while shallower slopes indicated a greater sharing of total community production across species. In addition to individual site rank curves, rank curves were averaged by temperature class producing four mean curves (i.e., cold-water streams curve, cool-water streams curve, warm-water streams curve, and extreme northern streams curve). Six analyses of covariance models (ANCOVA) with Tukey's

Post Hoc HSD comparisons were used to determine if significant differences existed among community evenness (assayed as significant differences in slopes, i.e., rank x class interactions) based on species relative abundance, relative biomass, and relative production. The first three ANCOVA models tested statistical significance among community evenness based on rank-abundance, rank-biomass, and rank-production curves, respectively, for the 25 sites individually. Finally, three additional ANCOVA models with Tukey's HSD post hoc comparisons were conducted to test differences in community evenness among the mean cold-water, cool-water, warm-water, and extreme northern streams rank-abundance, -biomass, and -production curves, separately (Valentine-Rose et al. 2011).

Finally, a meta-analysis was performed using any previously quantified and extractable diversity-production relationships occurring at the community level. The slope and strength (i.e., R^2) of the relationship between community fish production and species richness in this study were compared to previous studies on various taxa. However, because production rates can vary inter-specifically to a wide degree based on life-histories, e.g., growth rate and body size (Boudreau and Kerr 1991), diversity-production relationships were standardized by calculating a relative production value for each sample (i.e., ecosystem) in relation to the maximum production estimate found reported for the studied taxonomic group or ecosystem type. Thus for each taxa, percentage of potential maximum production in each study was plotted against species richness in that same ecosystem. As a result, a standardized set of diversity-production relationships was generated for a range of different taxa that could be quantitatively compared.

Assumptions.—One major assumption of any study relying on the instantaneous growth method is that a snapshot estimate of annual production remains relatively consistent over sub-annual time scales. However, other methods of production calculation that incorporate temporal variations (e.g., the increment summation and size-frequency methods) are laborious and time-consuming, often requiring monthly sampling over long periods (Halyk and Balon 1983). These methods would be impractical in a larger scale analysis of community fish production and would probably completely preclude the type of study conducted here (Benke 1979; Halyk and Balon 1983). Moreover, most published fish production studies do not even rely on empirical measures of production, but on empirical models that predict production from biomass alone (Robertson 1979; Mertz and Myers 1998; Randall and Minns 2000). Ultimately, the instantaneous growth method is an *in situ*, empirical and frequently used method to evaluate fish production, oftentimes using only a one-time sample (Halyk and Balon 1983; Valentine-Rose et al. 2007; Lobón-Cerviá 2011; Valentine-Rose et al. 2011).

Potential methodological critiques were also directly addressed in this study by sampling two reaches per stream instead of one such that spatial variability in production estimates could be compared (values were almost uniformly similar across reaches at each site). Furthermore, a subset of five streams were re-sampled several months following initial sampling (during the fall) to evaluate temporal stability in production estimates. A simple t-test conducted in JMP 10.1 statistical software revealed no significant difference in the mean production per species or total community production values between the summer sample and the fall sample ($P=0.43$, $P=0.24$, respectively). Thus community annual production estimates remained statistically similar across time

periods. In fact, follow-up community production estimates were lower, but not significantly so in all cases, which would be predicted *a priori* due to intra-annual natural mortality alone further demonstrating that these production estimates are probably capturing accurately the ecology of fish communities in these streams.

RESULTS

Diversity and allocation of production.— Mean community fish production was $2.32 \text{ g m}^{-2} \text{ yr}^{-1}$ ($\pm 1.84 \text{ SD}$) and ranged from $0.15\text{-}6.79 \text{ g m}^{-2} \text{ yr}^{-1}$ across the 25 streams. Species richness varied across the four stream temperature classes with the extreme northern streams have the lowest species richness (N=5, species richness range=1-9 species) compared to the colder water streams (N=8, species richness range = 2-11 species), cooler water streams (stream N=10, species richness range = 2-16 species), warmer water streams (stream N=2, species richness range = 19-22 species). Warm-water streams had significantly ($P<0.01$) higher species richness compared to the cold-water, cool-water, and extreme northern streams based on post-hoc comparisons of the means, while mean species richness at the cold-water, cool-water, and the extreme northern streams did not differ statistically.

A number of fish species were found consistently across almost all the sites (e.g., Blacknose Dace *Rhinichthys atratulus*, Brook Trout *Salvelinus fontinalis*, Mottled Sculpin *Cottus bairdii*, and Rainbow Trout *Oncorhynchus mykiss*) (Table 1). Species dominance in terms of abundance, biomass, and annual production varied across the streams (Appendix A-C). Blacknose Dace occurred at the most sites (17) but only had the

highest abundance at one site (Table 1). Brook Trout and Mottled Sculpin occurred at the same number of sites (13) and had the second and third overall highest abundance and production excluding Central Stoneroller *Campostoma anomalum*, which had the highest annual production of the top 10 most dominant species across all sites (Table 1).

Bluehead chub *Nocomis leptocephalus*, Brook Trout, and Rainbow Trout had the highest mean annual production rates (0.97, 0.89, and 0.70 g m⁻² yr⁻¹, respectively) compared to the other top 10 most occurring species (Table 1). Additionally, salmonids, cyprinids, or cottids had the highest relative production at each site with all site assemblages dominated by species from one of these three fish families (Figure 2).

Diversity/Production Relationship.—Community fish production was significantly and positively predicted by species richness alone ($R^2=0.38$, $\beta=0.53$, $P=0.001$), Shannon's diversity index alone ($R^2=0.23$, $\beta=1.60$, $P=0.02$), and Pielou's evenness index alone ($R^2=0.22$, $\beta=3.73$, $P=0.01$) (Figure 3). The species richness multiple regression model ($R^2=0.54$, $P=0.0004$), the Shannon's diversity index multiple regression model ($R^2=0.49$, $P=0.001$), and the Pielou's evenness index multiple regression model ($R^2=0.49$, $P=0.001$) with temperature, dissolved oxygen, and a water chemistry variable as covariates accounted for a significant portion of variation in community fish production. Holding the habitat and temperature covariates constant, for every one unit increase in species richness, an increase of 0.52 g m⁻² yr⁻¹ of community fish production is expected ($P=0.004$) (Figure 3). Similarly, controlling for the habitat covariates, a one unit increase in Shannon diversity index is associated with a 2.86 g m⁻² yr⁻¹ increase in community fish production ($P=0.01$) (Figure 3). Lastly, holding the habitat and temperature covariates constant, for every one unit increase in Pielou's evenness index,

an increase of $21.33 \text{ g m}^{-2} \text{ y}^{-1}$ is expected ($P=0.01$). All three diversity and evenness indices had a significant, positive relationship with community fish production and accounted for a significant portion of the variation in community fish production. In addition, species richness had a significant, positive relationship with community production alone at the cool-water streams ($R^2=0.60$, $\beta=0.97$, $P=0.005$) and a near significant relationship with community production of cold-water streams ($R^2=0.39$, $\beta=0.67$, $P=0.06$) (Figure 3). The Shannon diversity index demonstrated a significant, positive relationship with community fish production at the cold-water streams ($R^2=0.53$, $\beta=2.84$, $P=0.02$), and a near significant relationship with community production at the cool-water streams ($R^2=0.24$, $\beta=1.96$, $P=0.08$). Lastly, Pielou's evenness index demonstrated a significant, positive relationship with community production in cold-water streams ($R^2=0.54$, $P=0.02$), and a near significant relationship with community production in cool-water streams ($R^2=0.27$, $P=0.07$). Overall, higher species richness and community evenness were associated with higher annual community fish production (Figure 3).

Non-metric multidimensional scaling ordination.—The NMDS plots for percent similarity of relative abundance and relative biomass showed a similar pattern among streams. Cold-water, cool-water, and extreme northern streams were all situated in a loose cluster suggesting these fish assemblages had similar allocation of abundance and biomass to the same species (Figure 4). However, site temperature classes were more tightly grouped in comparison to the entire cluster. For example, the extreme northern streams tended to be proximally located for all three NMDS plots (Figure 4). The cold-water streams in the southern Appalachians were also tightly clustered together and were

generally closer to the extreme northern streams suggesting high similarity among those fish assemblages. Cool-water streams revealed a more scattered pattern with some sites closer to the extreme northern group and some sites closer to the cold-water southern Appalachian grouping (Figure 4). Site groupings were slightly more distinct based on the NMDS plot of percent similarity of relative production suggesting that similarities and dissimilarities had greater detection when using production; however, the two warm-water classified stream assemblages were clearly different than all the other sampled streams based on the ordination of the percent similarity among relative species abundance at each site (Figure 4). This trend was evident across all three ordinations; however, the ordination of percent similarity of relative biomass and relative production also showed Kelso Springs Branch to be set more distally from the other cool-water streams suggesting dissimilarity (Figure 4). Kelso Springs Branch was only slightly classified as a cool-water stream and had maximum summer temperatures that were considered warm-water, so this site was expected to be an outlier from the cool-water streams. Overall, sites in the same temperature class revealed that fish assemblages and allocation of abundance, biomass, and production to individual species were similar. Although the Kruskal-stress value was slightly higher than the accepted value indicating a good fit (i.e., 0.15) (Kruskal and Wish 1984), inspection of the Shepard's diagram for all three NMDS plots revealed that the three plots were relatively good fits as Shepard's diagrams revealed a relatively smooth, straight line (Shepard 1963).

Rank curves.—Community evenness results varied relative to the fish biological metric used to assess community evenness. Class-level comparisons of mean rank-abundance curves revealed that cold-water streams and cool-water streams had similar

community evenness patterns, the extreme northern streams had similar community evenness based on non-significantly different slopes (Figure 5, Table 2). Warm-water streams were excluded from the analysis because of sample size (only two sites). Site-level comparisons of community evenness based on rank-abundance revealed that technically only two sites (Blizzard Run and Buffam Brook) had significantly different community evenness compared to the other sites. Eight sites, which were comprised of a mix of cold-water, cool-water, and extreme northern streams, were classified as either group A or group B, thus differences were minimal (Table 2). Community evenness results based on mean rank-biomass curves exhibited a similar trend as mean rank-abundance curves (Figure 5, Table 2). No differences existed in community evenness based on the site-level comparisons of the rank-biomass curves (Table 2). Comparisons of the slopes for the rank-production curves were relatively consistent with the pre-determined temperature classifications; however, some sites could be grouped in several groupings (Table 2). Site-level comparisons of rank-production curves revealed more differences among the sites than rank-biomass and rank-abundance comparisons (Table 2). All but one (Buffam Brook) of the extreme northern sites had similar slopes while a subset of the cold-water and cool-water sites did not have significant differences in slopes compared to the extreme northern sites.

Class-level comparisons of mean rank-production curves showed the same results regardless of the metric used (Table 2). Community evenness in production was significantly different among the cold- and cool-water streams and extreme northern streams based on rank-production curves (Figure 5, Table 2). However, cold-water stream mean community evenness was significantly different than the extreme northern

streams but not the cool-water streams. Figure 5 illustrates a shallower slope in cold-water and cool-water streams rank-production curves compared to warm-water and extreme northern streams suggesting species evenness was greater in cold-water and cool-water streams based on relative species production. Overall, production was a more sensitive metric when comparing community evenness among sites but not among thermal classes.

Cross-taxa Literature comparison.—The R^2 was positive for all seven of the diversity-production studies including the present study identified (Table 3), and from these seven studies four studies had extractable data to compare the standardized diversity-production relationships. The present study had a lower R^2 value (0.46) compared to the other study on fish communities in Bahamian tidal creeks ($R^2=0.46$) (Valentine-Rose et al. 2007). The diversity-production relationship in two grassland studies had the highest R^2 value ($R^2=0.52$ and $R^2=0.53$, respectively) with the two studies on the diversity-production relationships of deciduous and desert birds and Arctic tundra to deserts in North America having the lowest R^2 values ($R^2=0.31$, $R^2=0.15$ and $R^2=0.02$, respectively) (Table 3) (Gough et al. 1994; Hurlbert 2004). Lastly, all studies had a positive slope, with the present study and a study conducted in Bahamas tidal creek having the highest slopes from the diversity-production relationship in fishes (3.65 and 3.15, respectively) (Valentine-Rose et al. 2007) (Table 3). The slope from the diversity-production relationship in Minnesota temperate grasslands and sandhills to wetlands in Southeastern U.S. savanna grasslands were 2.88 and 1.47, respectively (Kirkman et al. 2001; Tilman et al. 2001).

DISCUSSION

Improved understanding of diversity-production relationships is fundamental to species and ecosystem conservation (Isbell et al. 2011). This need is especially apparent for freshwater stream ecosystems where biodiversity is increasingly threatened by myriad human activities (Warren and Burr 1994; Duarte et al. 2006). In this study, species richness varied substantially over the spatial scale of the study area thereby providing a unique opportunity to address the potential link between fish diversity and community fish production. Both species richness and diversity indices were strongly and positively correlated with community fish production affirming that fish communities in this context are consistent with the theory that more diverse communities have higher productivity (Tilman et al. 1996; Hector et al. 1999; Tilman et al. 2001). Species richness accounted for a larger portion of explained variation in community fish production compared to Shannon's diversity index; however, Shannon's diversity and Pielou's evenness index had a stronger relationship with community fish production. Additionally, raw species richness and community fish production correlated almost as strongly as the highest correlated temperature variable (maximum summer water temperatures) ($R^2=0.52$, $R^2=0.55$, respectively) (Appendix F). Two prevailing hypotheses currently exist for explaining the mechanisms behind such strong ecological relationships.

Niche complementarity or differentiation is one proposed mechanism for stable species coexistence and increased productivity (Tilman et al. 1997; Lehman and Tilman 2000). For example, interspecific differences in resource requirements by species (e.g., food resource and habitat preferences) are well known drivers of niche differentiation

(Mulder 2001). Thus, a larger number of species would be predicted to increase the efficiency of species energy acquisition (Paine 1966; Loucks 1970; Kaspari et al. 2000). In Appalachian Mountains streams, primary food sources and spatial and temporal habitat preferences of fishes vary distinctly across ecosystems and genera. For example, Central Stonerollers graze algae from boulder and cobble habitats (Fowler and Taber 1985) while Brook Trout are drift feeders on aquatic and terrestrial insects (Allan 1981). Mottled Sculpin are benthic insectivores inhabiting run and riffle habitat (Rohde and Arndt 1981; Jenkins and Burkhead 1993), while Blacknose Dace are generalists that consume a diverse range of prey (Johnson and Johnson 1982). As implied by Tilman et al. (2001), production increases when a particular combination of species that are utilizing all of the resources available in the system are present. Consequently, when fish species combine within communities to utilize a larger variety of resources and habitats, total stream fish production may increase. However, at higher individual (and perhaps species) densities, competition for resources will intensify, which could ultimately limit productive capacity (Huston 1997).

Another potential mechanism for the positive correlation between community fish production and species richness is “chance theory”. That is, increasing species richness increases the probability that one or more highly productive species will colonize a community (Huston 1997; Srivastava and Lawton 1998; Nijss and Roy 2000). In these streams, fish species richness had a stronger correlation with community production and explained a larger amount of the variation in production; however, Shannon’s diversity index and Pielou’s evenness index, which account for both species richness and evenness, had a stronger relationship. Results from production rank-curve analysis revealed that

warm-water streams and the extreme northern streams had the highest slopes (i.e., lower evenness). Warm-water and extreme northern streams also consistently had higher community production but not significantly (Myers et al. unpublished report). Thus, community production at these sites was dominated by a few species rather than all species contributing similar amounts of production. These variations in evenness therefore suggest that the chance theory is also a plausible mechanism in generating a positive correlation between fish diversity and community production. Ultimately, the importance of each potential mechanism to the observed fish diversity-production relationship is beyond the scope of this study. However, multiple mechanisms influencing the diversity-production relationship have been documented in other taxa and is consistent with the concept that diversity-production patterns can be variable across an array of taxa and environments (Waide et al. 1999).

Community fish production was the most sensitive response variable when evaluating the rank-curves used to analyze community differences compared to biomass and abundance. Post-hoc tests revealed more separation in evenness across both site-level and class-level comparisons. Similarly, Valentine-Rose et al. (2011) found rank-production curves had larger differences in community evenness compared to rank-abundance and rank-biomass curves. This suggests that production was the best metric for comparing differences in fish communities across different thermal environments. For example, using abundance or biomass alone would have yielded different conclusions regarding the ecology of these communities. Thus, studies only utilizing abundance and biomass as response variables may yield divergent results and conclusions than if secondary production is used (Dolbeth et al. 2012). In fact, abundance was more aligned

with the results gained from using production compared to the results generated using biomass. At a minimum, these findings strongly suggest that care should be taken when selecting biological metrics for analyzing fish communities as disparate results and conclusions may be produced, which could affect conservation and management strategies (Hayes et al. 2007).

Community production evenness varied significantly across the cold-water, cool-water, and the extreme northern streams. The extreme northern streams had the lowest community production evenness compared to the cold-water streams and the cool-water streams. Several factors are most likely driving differences in community production evenness. Firstly, stream thermal regimes have long been known to influence the diversity and community structure of stream ecosystems (Stoneman and Jones 1996). For example, ecosystem stability is fundamental to the community structure, composition, and productivity in an ecosystem (Loreau 2000). Species adapt to utilize different resources across habitat gradients (e.g., temperature gradient, which was used in this study); thus, as conditions in the gradient become more suitable to more species, alpha-diversity or species richness may increase (Whitaker 1972). Furthermore, increasingly extreme conditions like extreme cold-water streams tend to limit alpha-diversity by restricting the species richness thereby affecting (i.e., reducing) community evenness (Whitaker 1972). Thus more recently disturbed (i.e., pioneer) communities often have reduced levels of species evenness (Pielou 1966; Shafi and Yarranton 1973; Clebsch and Busing 1989). Tilman (1996) suggested that greater diversity in an ecosystem would increase instability in individual populations but increase stability in the overall

community; thus, some species may exhibit higher production while others lower production, which would decrease community evenness.

Fluctuations in disturbance regimes along ecological gradients can also drive ecosystem stability and species turnover (Whitaker 1972; Nilsson and Grelsson 1995; Jackson and Sax 2010). Structure, function, and stability of an ecosystem can be affected by both species richness and community composition (i.e., community evenness) (Worm and Duffy 2003). More diverse communities tend to be more productive but may be less stable (Wardle et al. 2000), but on the other hand, disturbance-prone environments are often characterized by low species richness and stability (Worm and Duffy 2003). Thus, streams in the extreme northern area may have lower species richness and lower evenness and may be more sensitive to temperature disturbances. Concomitantly, latitude plays an especially strong role in driving species composition and diversity as species richness tends to increase towards the tropics (Hillebrand 2004; Allan and Castillo 2007).

Literature comparisons.— Species diversity and ecological productivity are frequently positively correlated with one another but can exhibit significant variations in this relationship (Waide et al. 1999; Tilman et al. 2001; Zak et al. 2003; Valentine-Rose et al. 2011). The stream fish diversity-production relationship in this study was similar compared to that of other taxa. However, this relationship may not be general to other assemblage and habitat types and should therefore be investigated further for other taxa and environments (Nijs and Roy 2000; Tilman et al. 2001; Solimini et al. 2003). Coefficients of determination for the diversity-production relationships in this study were oftentimes greater than other studies demonstrating a similar positive correlation (Table 3). In fact, this Appalachian stream fish diversity-production relationship was similar in

positive correlation and in slope to the diversity-production relationships of Minnesota, U.S. temperate grassland plants (Tilman et al. 1996), Ethiopian desert lake ecosystem (Aoki 2003), sandhills to wetlands savanna grasslands in southeastern U.S. (Kirkman et al. 2001), North American temperate deciduous forest birds and desert/grassland birds (Hurlbert 2004), and coastal marine fish communities (Valentine-Rose et al. 2007) (Table 3). Yet while there was surprising congruence among standardized diversity-production relationships, these trends are by no means definitive and are likely scale-dependent (Aoki 2003). For example, diversity-production relationships can also be characterized by negative or unimodal relationships (Mittelbach et al. 2001). However, it should be of note that the fish diversity-relationship from this study had one of the highest correlation coefficients and slopes compared to that of other taxa (Table 3, Figure 10). Thus, it is suggested that a link exists between fish species richness and fisheries production similar to that found for plant, bird, and coastal marine fish communities (Tilman et al. 1996; Hurlbert 2004; Valentine-Rose et al. 2007; Valentine-Rose et al. 2011). However, debate remains over whether diversity drives productivity or productivity drives diversity (Mittelbach et al. 2001; Gross and Cardinale 2007). Regardless, this study highlights a significant positive link and importance of biodiversity in helping regulate freshwater stream ecosystems and fisheries.

Fisheries science has often been viewed as a separate discipline than ecology, potentially creating neglect in evaluating these patterns in spite of their overall importance. An understanding of the relationship between fish production and diversity may provide complementary insight into fisheries management and conservation. More research needs to be conducted on the diversity-production relationship in aquatic

ecosystems generally and on diverse fish communities. Thus impacts on diversity, though not immediately intuitive, may affect this important resource. For example, Cardinale et al. (2006) found that average species loss altered both ecosystem structure and function. Thus, mitigating effects on diversity may create beneficial effects on fisheries production. For example, reducing or restoring ecosystems and fisheries affected by climate change, habitat fragmentation, pollution, overfishing and invasive species will likely benefit diversity and overall productive capacity of Appalachian stream ecosystems, including valuable cold-water trout fisheries.

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FIGURES

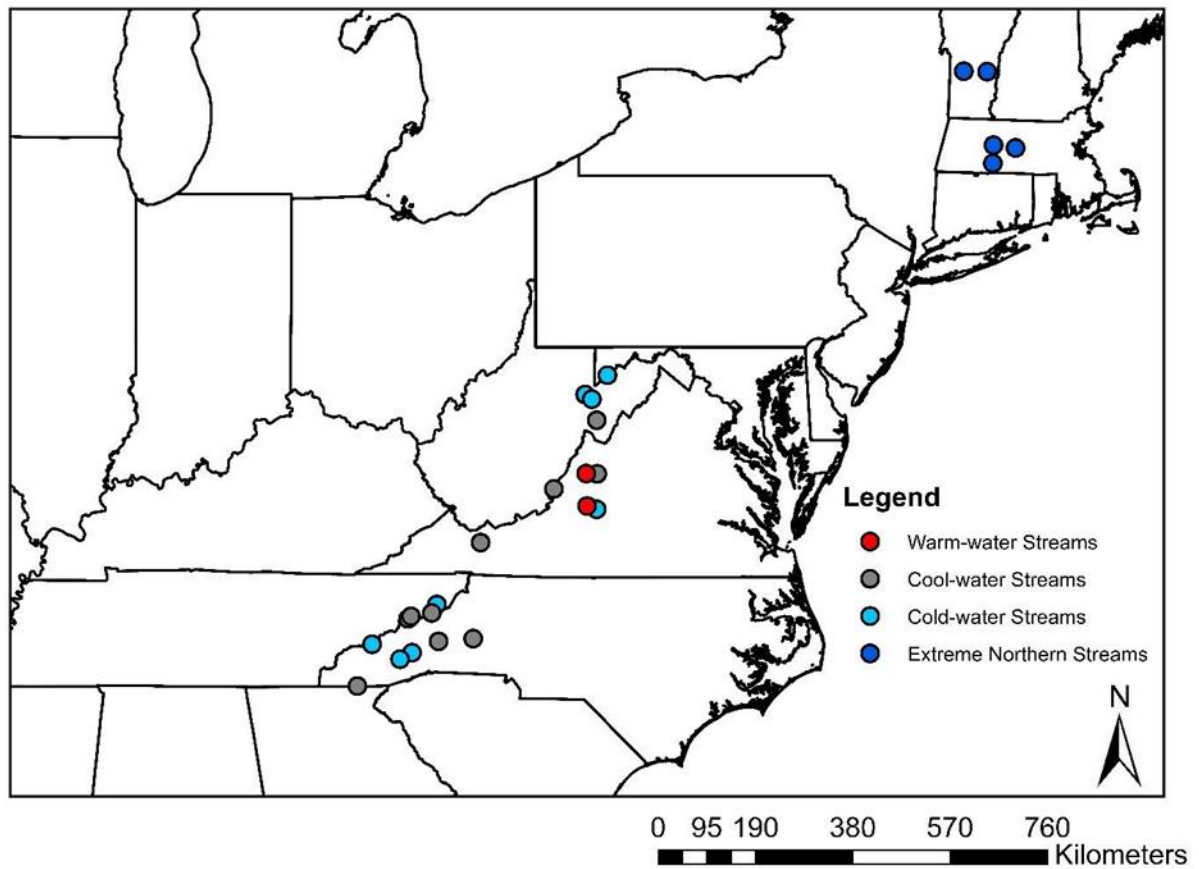


Figure 1. 20 sampling locations classified as cold, cool, and warm water streams located across the Southern Appalachian Mountain Range in North Carolina, Tennessee, Virginia, West Virginia, and Maryland sampled during summer 2012 and 5 extreme northern sampling locations in Vermont and Massachusetts sampled during September 2012. The Vermont and Massachusetts sites have been slightly offset from the true location for better clarity.

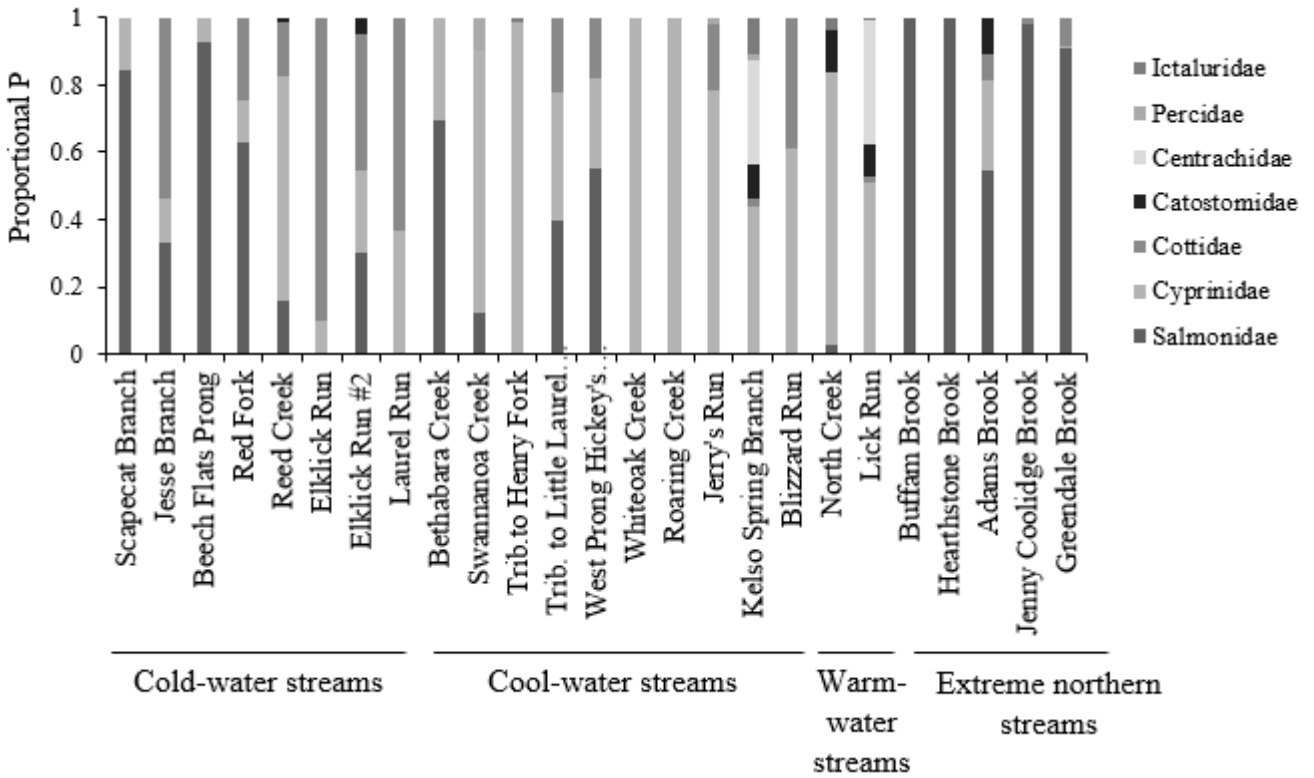


Figure 2. Proportional production (g m⁻² yr⁻¹) per family at the 25 stream locations arranged in increasing latitude from North Carolina to Vermont. Fish family relative production was calculated by summing individual species relative production values.

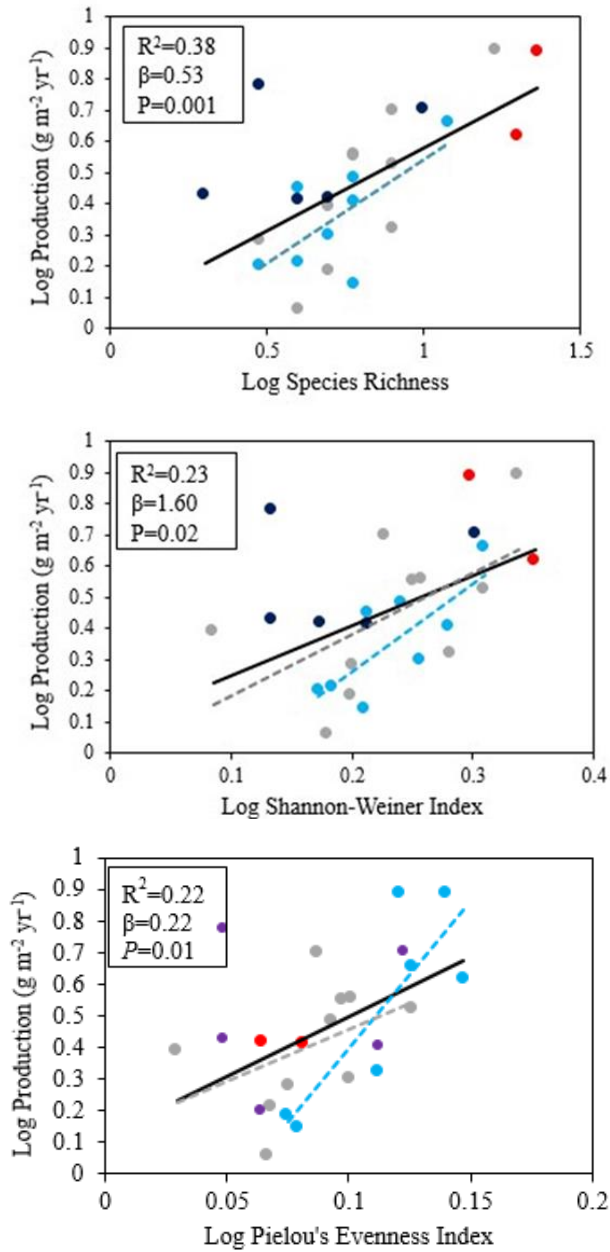


Figure 3. Log community production as a function of log species richness (top graph) and log Shannon Wiener Diversity Index (middle graph), and log Pielou's evenness index. The black solid line represents the overall regression based on 25 sites while the gray dotted line represents the regression of the cool-water streams (10 sites), and the blue dotted line represents the regression for the cold-water streams (8 sites). Site points are color coded based on the thermal groupings (dark blue=extreme northern sites, light blue=cold-water streams, gray=cool-water streams, and red=warm-water streams). Regressions were not conducted for the extreme northern sites and the warm-water streams because the sample size was five or less.

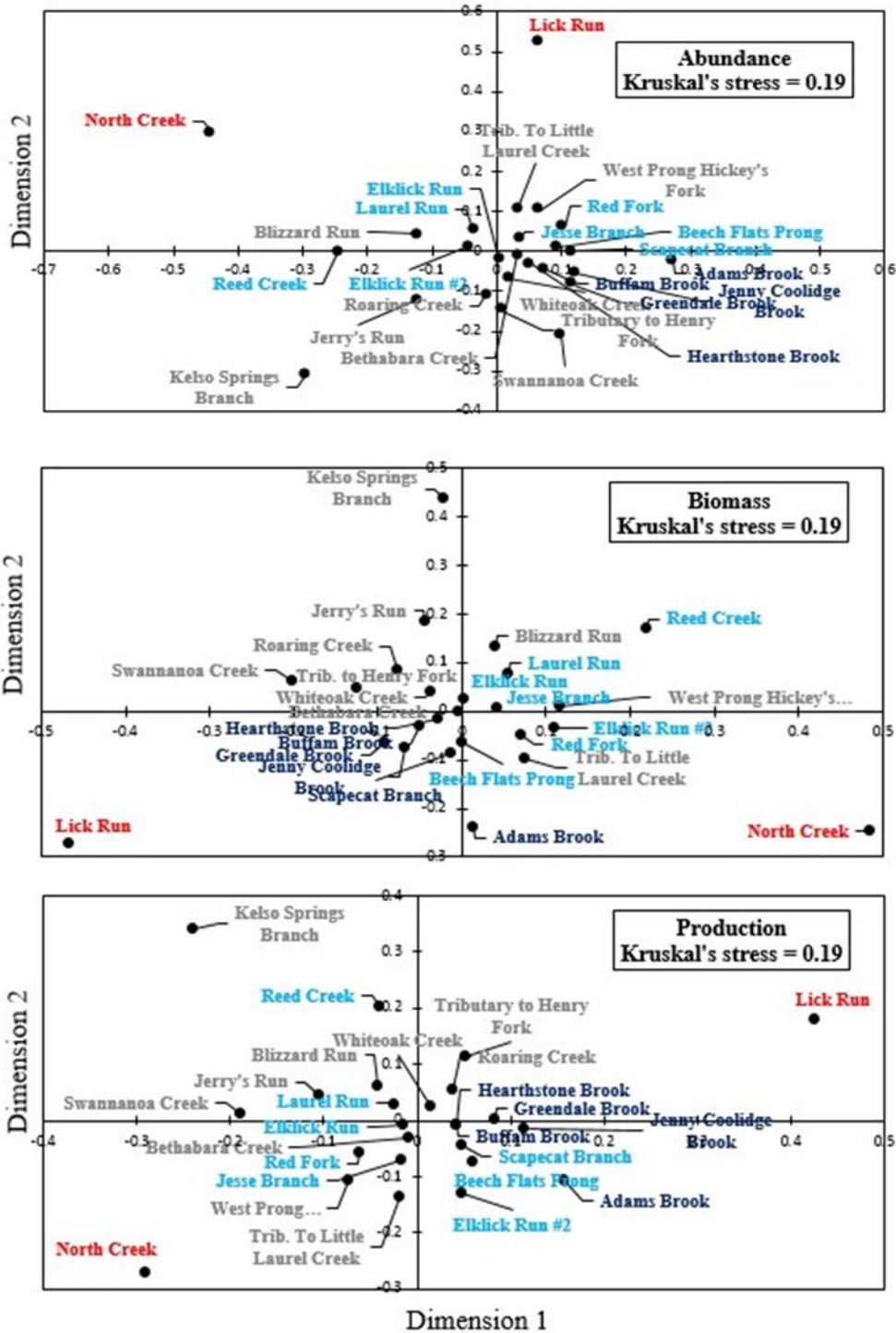


Figure 4. Multidimensional scaling analysis of fish assemblages based on percent similarity of species abundance, biomass, and production among all combinations at the 25 stream locations in the Appalachian Mountains from North Carolina to Vermont. Similar fish assemblages are located more proximally and dissimilar fish assemblages are located more distally. Stream names are colored to represent the temperature category of the stream. Cold-water streams=light blue, cool-water streams=grey, warm-water streams=red, and the extreme northern streams=dark blue.

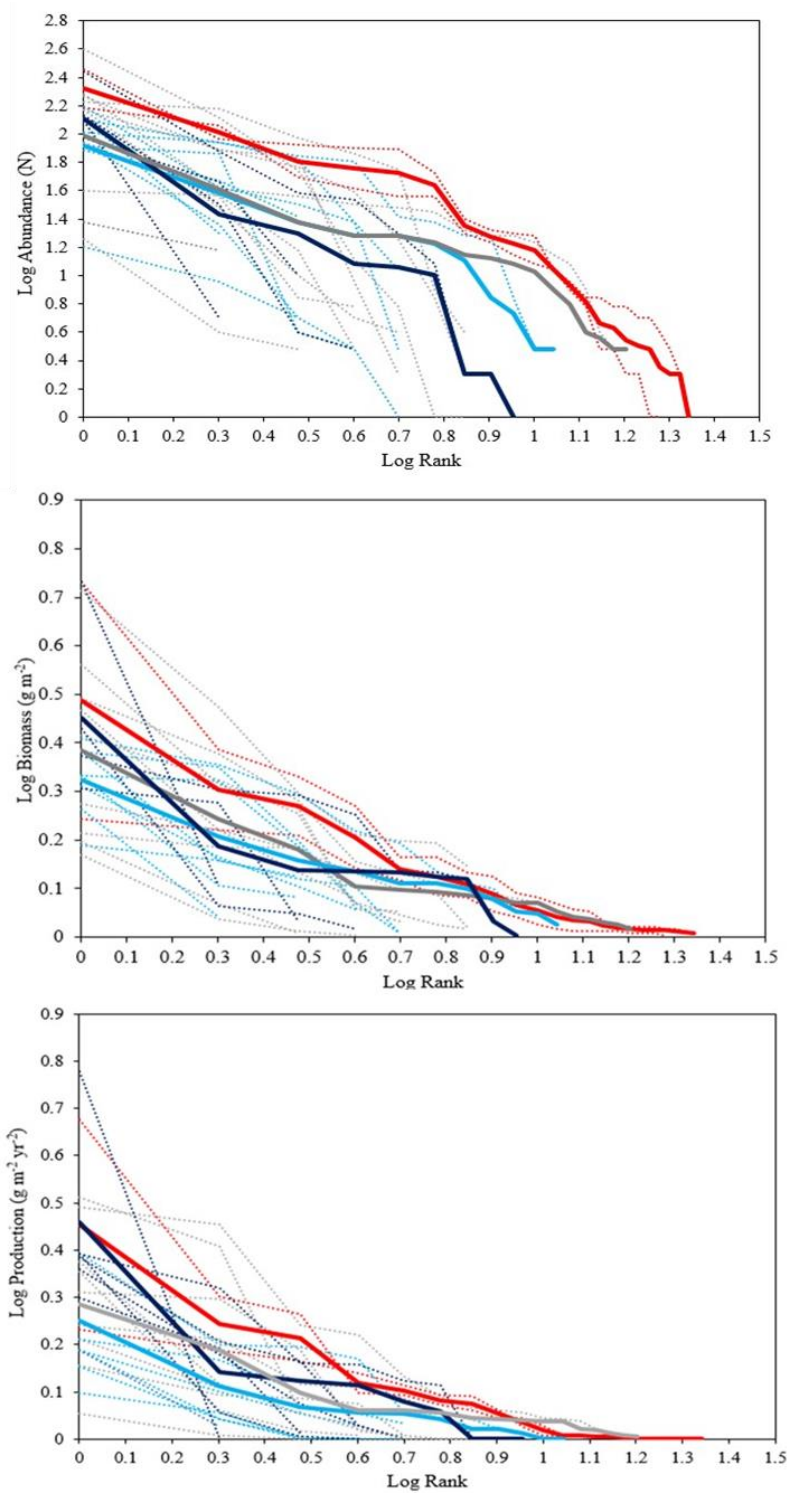


Figure 5. Rank -abundance, -biomass, and -production curves for the 25 streams ranging from Vermont to North Carolina. Cold-water streams are represented by the light blue curves, cool-water streams are represented by the gray curves, warm-water streams are represented by the red curves, and the extreme northern streams are represented by the dark blue curves. Dotted lines are individual sites, and the solid lines represent the mean for the cold-water, cool-water, warm-water, and extreme northern streams.

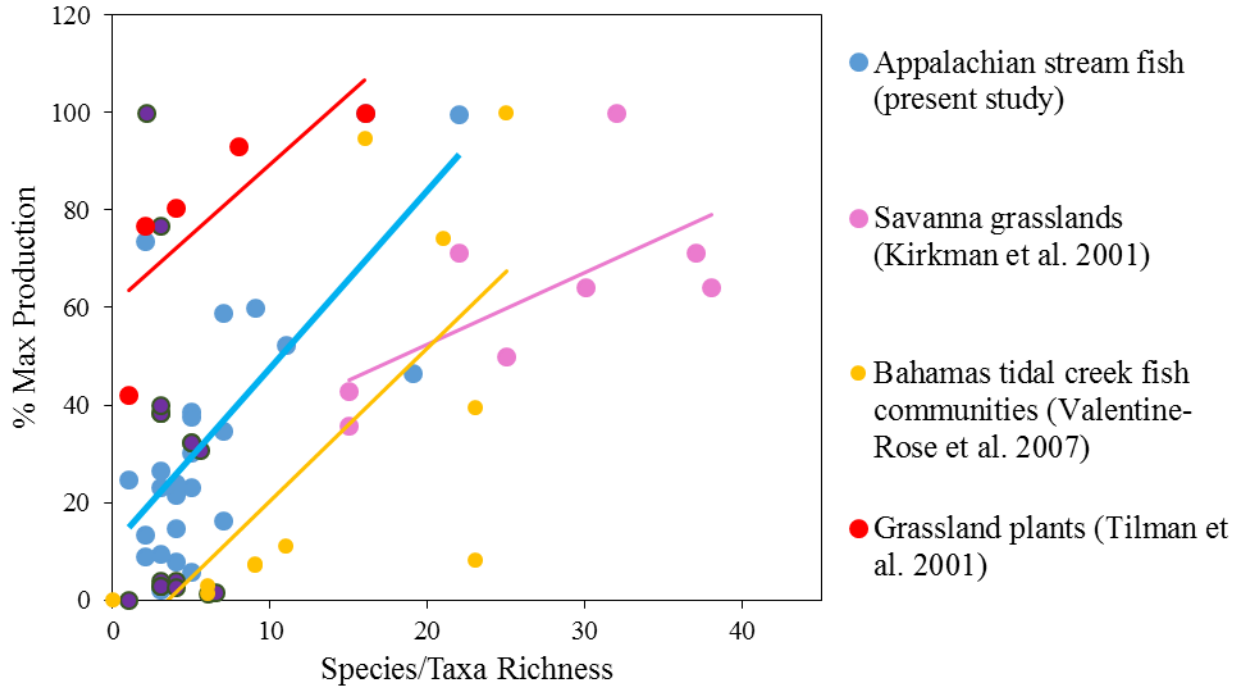


Figure 6. Percentage of maximum community production of samples across each species or taxa group for the published diversity/production relationships listed in Table 5.

TABLES

Table 1. Summary of the ranges and means (in parentheses) for species abundance (number of individuals), biomass (g m^{-2}), annual production ($\text{g m}^{-2} \text{ yr}^{-1}$), P/B ratio, and the # of sites the species occurred for the top 10 most common species encountered across the 25 stream locations ranging from Vermont to North Carolina sampled from June to September 2012. The top 10 most common species were chosen based on the highest relative abundance, biomass, and production out of the 25 fish communities sampled.

Species	Abundance	Biomass	Production	P/B	# of sites present
<i>Rhinichthys atratalus</i> Blacknose Dace	4-400 (66)	0.08-4.18 (0.68)	0.01-2.25 (0.40)	0.34-0.75 (0.79)	17
<i>Salvelinus fontinalis</i> Brook Trout	3-275 (68)	0.02-4.38 (1.05)	0.00-1.68 (0.89)	0.52-1.31 (0.92)	13
<i>Cottus bairdii</i> Mottled Sculpin	6-130 (66)	0.05-1.97 (0.86)	0.003-1.56 (0.48)	0.06-0.75 (0.59)	13
<i>Oncorhynchus mykiss</i> Rainbow Trout	2-185 (77)	0.02-2.65 (1.04)	0.00-1.42 (0.70)	0.002-1.30 (1.10)	9
<i>Nocomis leptcephalus</i> Bluehead Chub	36-154 (96)	0.66-1.56 (1.08)	0.15-1.84 (0.97)	0.45-1.15 (0.94)	6
<i>Clintostomus funduloides</i> Rosyside Dace	2-168 (45)	0.02-0.98 (0.43)	0.00-0.74 (0.18)	0.20-0.80 (0.47)	8
<i>Campostoma anomalum</i> Central Stoneroller	1-285 (68)	0.12-4.38 (1.15)	0.00-3.74 (0.84)	0.03-0.64 (0.45)	5
<i>Semotilus atromaculatus</i> Creek Chub	2-87 (26)	0.04-1.93 (0.56)	0.00-1.26 (0.28)	0.08-1.04 (0.70)	8
<i>Rhinichthys cataractae</i> Longnose Dace	1-64 (21)	0.01-0.65 (0.30)	0.00-0.48 (0.14)	0.14-0.56 (0.57)	9
<i>Thorburnia rathoeca</i> Torrent Sucker	1-84 (26)	0.06-1.14 (0.38)	0.00-0.84 (0.21)	0.51-0.81 (0.53)	6

Table 2. Summary of the Analysis of Covariance (ANCOVA) Tukey’s HSD post-hoc comparison results of the class-level comparisons (cold-water, cool-water, warm-water, and extreme northern streams) and site-level comparisons (25 streams) of the rank-abundance slopes, rank-biomass slopes, and rank–production slopes, separately. Streams not connected by the same letter vertically had significantly different rank curve slopes ($p < 0.05$). All 6 ANCOVA models were significant at the 0.05 alpha level ($P < 0.0001$).

Class/Site	Temperature Category	Slope comparisons for rank-production curves	Slope comparisons for rank-biomass curves	Slope comparisons for rank-abundance curves
Mean cold-water rank curve	**	A	A	A
Mean cool-water rank curve	**	A	A	A
Mean extreme northern rank curve	**	B	B	B
Jerry's Run, VA	cool	A	A	A
Swannanoa Creek, NC	cool	A	A	A
Laurel Run, MD	cold	A	A	A,B
Roaring Creek, VA	cool	A	A	A
Whiteoak Creek, NC	cool	A	A	A
Elklick Run #2, WV	cold	A,B	A	A
Jesse Branch, NC	cold	A,B	A	A,B
Reed Creek, VA	cold	A,B,C	A	A
Bethabara Creek, NC	cool	A,B,C	A	A
Scapecat Branch, NC	cold	A,B,C	A	A
Kelso Spring Branch, VA	cool	B,C	A	A
Adam's Brook, MA	extreme northern	B,C	A	A,B
Red Fork, TN	cold	B,C	A	A
Trib. to Little Laurel Creek, NC	cool	B,C	A	A,B
Elklick Run, WV	cold	B,C	A	A,B
Hearthstone Brook, MA	extreme northern	C	A	A
Jenny Coolidge Brook, VT	extreme northern	C	A	A
Beech Flats Prong, NC	cold	C	A	A
West Prong Hickey's Fork, NC	cool	C	A	A,B
Trib. To Henry Fork, NC	cool	C	A	A,B
Greendale Brook, VT	extreme northern	C	A	A,B
Blizzard Run, WV	cool	C	A	B
Buffam Brook, MA	extreme northern	D	A	B

Table 3. Summary of published diversity/production coefficients of determination (R^2), associated P -value, and the equation of the line for the non-normalized and normalized relationship between diversity and community production for various taxa including the present study. ** denotes information that was unavailable or could not be extracted.

Study Ecosystem and Taxa	N	R^2	P-value	Non-normalized Equation	Normalized Equation	Reference
Appalachian streams from Vermont to North Carolina-stream fish	25	0.38	0.004	log community P=0.53 (log species richness)+0.05	% max production=3.65 (species richness) +11.12	present study
Bahamas tidal creek fish communities	34	0.46	0.02	log community P=0.42 (log species richness)+0.22	% max production=3.15 (species richness)-11.13	Valentine Rose et al. 2007
Ethiopian desert lake habitat-total lake, resevoir, and river ecosystem trophic groups (phytoplankton, zooplankton, and all fish species)	13	0.45	not provided, but significant	**	**	Aoki 2003
Minnesota temperate grassland-vascular plants	147	0.52	<0.001	log community P=0.13 (log species richness)+0.14	% max production=2.88 (species richness)+60.67	Tilman et al. 2001
Sandhills to wetlands-Southeastern U.S. savanna grassland vascular plants	6	0.53	0.03	log community P=0.70 (log species richness)+1.32	% max production=1.47 (species richness)+23.22	Kirkman et al. 2001
Deciduous forests in North American-Birds	1184	0.15	not provided, but significant	**	**	Hurlbert 2004
Desert or grasslands in North America-Birds	658	0.31	not provided, but significant	**	**	Hurlbert 2004
Arctic tundra to deserts in North America-Herbaceous plant communities	36	0.02	p<0.01	**	**	Gough et al. 1994

SUMMARY AND CONCLUSIONS

A total of 6,743 individuals were encountered in the 25 stream sites with biomass estimates and community fish annual production estimates ranging from 0.61 to 10.73 g m⁻² and 0.15 to 6.79 g m⁻² yr⁻¹, respectively. Common species encountered were Brook Trout, Mottled Sculpin *Cottus bairdii*, Blacknose Dace *Rhinichthys atratulus*, Bluehead Chub *Nocomis leptcephalus*, and Longnose Dace *Rhinichthys cataractae*. The extreme northern streams had the second highest mean community production estimates (P=2.79 g m⁻² yr⁻¹) with the warm-water streams having the highest mean community production estimates (P=4.96 g m⁻² yr⁻¹). The southern Appalachian cold-water classified streams had the smallest mean community production (P=1.45 g m⁻² yr⁻¹) and cool-water classified streams had the second lowest mean community production (P=2.25 g m⁻² yr⁻¹). Similarly to mean community biomass, mean community production was not statistically different among the four stream types (P=0.19). Mean community P/B was statistically different among the four stream types (P=0.002) with cold-water and cool-water streams P/B being statistically the same while extreme northern streams both having unique mean P/B values.

The percentage of production allocated to cold-water, cool-water, and warm-water species varied across the four stream temperature categories. Cold-water species overwhelmingly dominated community production in the extreme northern sites and the cold-water southern Appalachian stream sites. However, there was a 23% decrease in cold water species production of total community production from the cold-water southern Appalachian streams to the extreme northern streams. In addition, the percentage of cold-water species production decreased by 40% from streams classified as

cold-water to streams classified as cool-water. Cool-water streams had a mean summer temperature 2°C higher and maximum summer temperature 3°C higher than cold-water classified streams. Furthermore, cold-water species decreased to only 2% of the total community production in the warm-water southern Appalachian streams, which had 3°C higher mean summer temperatures and 4°C higher mean maximum summer temperatures.

My community fish production estimates were within the range of production estimates from previously published studies conducted in similar stream habitats on fish assemblages (Lotrich 1973; Neves and Pardue 1983; and Kwak and Waters 1997). Albeit, the lowest community fish production estimate ($0.15 \text{ g m}^{-2} \text{ yr}^{-1}$) encountered was below all other published estimates, but this is most likely due to the larger spatial scale and number of streams sampled from this study compared to the other studies, which sampled anywhere from 1-13 streams (Lotrich 1973; Neves and Pardue 1983; Kwak and Waters 1997). Furthermore, community P/B ratios were within the range of other published studies and were the most sensitive metric used when comparing differences among community function in cold-water, cool-water, warm-water, and extreme northern streams. Production-to-biomass ratios are tightly linked to year-class recruitment; thus, populations with stronger year-class recruitment are expected to have higher production-to-biomass ratios (Lobón-Cerviá et al. 2011). A compilation of fish species and the associated P/B ratios summarized in Waters (1977) revealed that cottids and salmonids had the highest P/B ratios relative to other freshwater fishes. Fish communities in the extreme northern sites were dominated by Brook Trout and Slimy Sculpin, which both had higher on average P/B ratios compared to the same or similar species in the cold-,

cool-, and warm-water streams in the southern Appalachians. Since both species are cold-water species that are sensitive to temperature (Lyons et al. 2010), the ideal temperature patterns at the extreme northern streams may be a mechanism for higher recruitment of these two dominant species. Ultimately, community fish production allocation to species temperature guilds fluctuated across the study sites in this latitude and temperature gradient highlighting a possible relationship between community fish production and allocation of production and climate change.

Further analysis of these trends revealed a significant relationship between community fish production and water temperature. Community production was significantly and positively correlated to mean annual air temperatures ($^{\circ}\text{C}$) (Spearman's $r=0.48$, $P=0.03$), mean annual water temperatures ($^{\circ}\text{C}$) (Spearman's $r=0.54$, $P=0.02$), maximum water temperatures ($^{\circ}\text{C}$) (Spearman's $r=0.55$, $P=0.01$), mean summer air temperatures ($^{\circ}\text{C}$) (Spearman's $r=0.53$, $P=0.02$), and air temperature variability ($^{\circ}\text{C}$) (Spearman's $r=0.53$, $P=0.02$). The only non-temperature related variable that had a significant correlation with community fish production was elevation (m), which was negatively correlated (Spearman's $r= -0.56$, $P=0.01$). Intuitively, the percentage of cold-water species production had a relatively strong, negative correlation with mean annual temperatures, mean summer temperatures, and mean maximum temperatures. Conversely, the percentage of cool-water and warm-water species production had a relatively strong, positive correlation with the temperature variables. The percentage of warm-water species production had a stronger positive correlation with the temperature variables compared to cool-water species.

Moreover, summer water temperature related principal component factor had a significant positive affect on community fish production ($P < 0.0001$) and was important factor in predicting whether a fish community was dominated by cold-, cool-, or warm-water species production. The summer air and water temperature related factors significantly contributed the most to their respective multinomial logistic regression model's prediction power. The habitat related factor in the air temperature logistic regression also contributed significantly ($\chi^2 = 7.01$, $P = 0.03$) in the model's ability to predict whether cold-water, cool-water, or warm-water species would dominate community production. The summer temperature air and water related factors did significantly predict a 12.74 ($P = 0.02$) and 5.10 ($P = 0.06$), respectively, increase in the odds that a fish community would be dominated by cool-water fish compared to cold-water fish as the summer temperature factor increased.

Although the summer air temperature factor did not account for variation in community production, the summer water temperature factor did. This study revealed a clear functional response of overall community fish production, cold-water, cool-water, and warm-water species production to summer temperatures. Even small increases in summer air and water temperatures are expected to have major effects on stream fishes in other areas (Casselman 2002; Rahel 2002; Lyons et al. 2010). My results added to this trend as the summer air and water temperature factor was the best variable in predicting whether the production of a fish community would be dominated by cold-water species (e.g., salmonids and cottids), cool-water species (e.g., cyprinids and catostomids), or warm-water species (e.g., some percids and centrarchids). With the most recent IPCC (2013) report predicting more hot temperature extremes compared to cold temperature

extremes, the present study suggests communities dominated by cold-water species production are at risk as summer temperature extremes intensify. Even if the thermal regime does not reach the lethal range for a species, sublethal ranges may also negatively affect a fish species by altering growth, abundance, survival, and ultimately production of that species (Ficke et al. 2007). Once that threshold value is reached, the allocation of production may have a higher probability of shifting from one thermal guild to another.

Species richness ranged from 1 to 22 species with an average species richness of six. Average species richness was highest in the warm-water streams with an average of 21 and smallest in the extreme northern sites with an average of four species. Both diversity indices, i.e., species richness and Shannon diversity index, had a significant, positive relationship with community fish production and accounted for a significant portion of the variation in log community fish production ($\beta=0.42$, $P=0.004$, $R^2=0.38$ and $\beta=1.35$, $P=0.01$, $R^2=0.23$, respectively). Higher species richness and community evenness were associated with higher annual community fish production. Production was the most sensitive measure in determining differences among sites compared to biomass and abundance when comparing individual sites.

The significant, positive relationship between species richness and community production may be explained by two theories including the niche complementarity theory (Tilman et al. 1996; Lehman and Tilman 2000) and the theory of the more species present the higher the chance of having one or two productive species (Huston 1997; Nijs and Roy 2000). Furthermore, species richness is considered to significantly alter ecosystem structure and function which could be in the form of altering community production dynamics (Worm and Duffy 2003). Multiple mechanisms influencing the diversity-

production relationship are common in the literature and have been documented across taxa (Waide et al. 1999). Lastly, the diversity-production relationship from this study compared to other taxa was just as strong and in most cases stronger; thus, diversity is an important correlate of community fish production in these Appalachian stream ecosystems. Ultimately, suggesting that diversity may be extremely important when considering management and conservation strategies for Appalachian streams

CONCLUSIONS

- 1) Community fish production varied across the Appalachian range from $0.15 \text{ g m}^{-2} \text{ yr}^{-1}$ to $6.79 \text{ g m}^{-2} \text{ yr}^{-1}$ from Vermont to North Carolina. However, abundance, biomass, and community production did not vary significantly among the four temperature classes.

Community P/B ratios were significantly different among Appalachian streams in this study depending on whether the streams were classified as a cold-water, cool-water, warm-water, or extreme northern streams. These production estimates were aligned with previously published estimates in similar habitats. Lastly, extreme northern streams may have a higher recovery rate compared to cold-water and cool-water streams in the southern Appalachian Mountain range based on the higher P/B ratios.

- 2) Air temperature was not a significant factor in accounting for variations in community fish production; however, water temperatures were a significant factor affecting community fish production. Furthermore, summer air and water

temperature factors were significant in predicting whether the majority of community fish production would be allocated to cold-water, cool-water, or warm-water species.

Habitat complexity was the best predictor of community fish production in the air temperature model, but was not in predicting whether a community would be dominated by cold-water, cool-water, or warm-water species. Water temperatures had a stronger correlation with and effect on community fish production suggesting air/water sensitivity quantification will be extremely important in predicting effects of climate change on fish populations.

Southern Virginia and northern North Carolina and Tennessee were identified as areas with the highest susceptibility to a shift in community fish production allocation to cold-water species to cool- or warm-water species based on summer 2012 temperatures and near 1°C increases in temperature which are likely occur between 2016 and 2035 (IPCC 2013).

- 3) Annual production was usually the best indicator to use in comparing differences in fish assemblage structure and evenness across the 25 streams in the Appalachian Mountains. Fish assemblage structure was similar among sites in the same temperature classes, i.e., cold-water, cool-water, and extreme northern streams. Evenness varied among cold-water, cool-water, and extreme-northern streams with evenness being significantly greater in the cold-water and cool-water streams in the southern Appalachian streams. Lastly, species richness, Shannon's

Diversity, and Pielou's evenness index had a significant positive relationship with community fish production; thus, the greater the diversity and evenness in an ecosystem the higher the community fish production is expected to be. The fish diversity-production relationship was just as strong and in most cases stronger than previously published studies exposing the importance of diversity on ecosystem function in Appalachian streams.

- 4) As climate change affects fish assemblage structure and function in terms of number of species present, types of species present, and the frequency of species occurrence, community and thermal guild production will fluctuate and alter ecosystem function and the amount of resources available for human consumption.
- 5) Climate change continues to be a global problem; however, conservation management is typically focused on local scales (e.g., state, provincial and municipal governments). Thus, management is more of a reactive solution to climate change rather than a proactive solution as management efforts in fisheries will not affect the drivers of climate change. One response of these groups to climate change has been to develop climate change "adaptation strategies and scenarios".

However, the future development of fisheries adaptation and management plans may depend on a firm understanding of how different climate change scenarios affect fisheries production. This study showed that species production in a stream varies across different temperature scenarios. Therefore, state and regional fisheries management organizations throughout the eastern USA may

wish to refer to these models and results to assist in their development of climate change adaptation scenarios and plans and determine areas where management is greatly needed. Furthermore, these and other groups may wish to pursue analogous lines of research on other fisheries and ecosystem types, especially if threshold points of production collapse due to a changing climate are suspected. In the end, fisheries managers and enthusiasts may have to shift management strategies and expectations in the fishery to address the species that are thriving in that ecosystem under that temperature regime during that period of time.

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Appendix C. Number of individuals (N), biomass (B) (g m⁻²), annual production (P) (g m⁻² yr⁻¹), P/B ratio (P/B), and % of total production (%T.P) per species at the 5 most northern sites located in Massachusetts and Vermont sampled during September 2012.

	Adams' Brook					Jenny Coolidge Brook					Extreme Northern Sites Buffam Brook					Hearthstone Brook					Greendale Brook				
	N	B	P	P/B	%T.P	N	B	P	P/B	%T.P	N	B	P	P/B	%T.P	N	B	P	P/B	%T.P	N	B	P	P/B	%T.P
Cold Water Species																									
atlantic salmon	34	0.96	0.30	0.62	7	46	1.02	0.99	1.20	63	5	0.28	0.00	0.00	0	*	*	*	*	*	3	0.12	0	0	0
brooktrout	20	1.36	1.46	1.32	36	94	0.89	0.56	0.97	35	123	4.38	5.00	1.44	100	81	1.61	1.68	1.47	100	134	1.68	1.47	1.25	91
brown trout	12	0.32	0.45	2.8	11	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
rainbow trout	1	0.37	0	0	0	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
mottled sculpin	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
slimy sculpin	75	0.36	0.33	0.65	8	10	0.08	0.03	0.67	2	*	*	*	*	*	*	*	*	*	*	32	0.16	0.14	1.09	9
Cool Water Species																									
banded sculpin	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
blacknose dace	275	1.01	1.09	0.82	27	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	4	0.04	0.01	0.45	1
bluehead chub	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
chain pickerel	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
creek chub	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
crested shiner	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
cutlips minnow	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
fallfish	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
greenhead shiner	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
johnny darter	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
longnose dace	2	0.01	0	0	0	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
mountain redbelly dace	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
blacktip jumprock	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
rosyside dace	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
telescope shiner	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Tennessee shiner	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
torrent sucker	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
warpaint shiner	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
white shiner	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
white sucker	38	0.79	0.44	0.61	11	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Warm Water Species																									
bluntnose minnow	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
brown bullhead	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
central stone roller	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
common shiner	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
fantail darter	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
green sunfish	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
marginated madtom	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
pumpkinseed	2	0.08	0	0	0	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
redbreast sunfish	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
rock bass	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
roselin shiner	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
smallmouth bass	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
striped darter	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
yellow bullhead	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*

Appendix D. Mean (SD) values of physical characteristics for 25 study streams located in North Carolina, Tennessee, Virginia, West Virginia, Maryland, Vermont, and Massachusetts. All habitat surveys were conducted during summer 2012. Temperature variables were calculated from continuous temperature data taken downstream from each site for March 2011 to March 2012. Temperature data for the Massachusetts and Vermont sites was calculated from the closest USGS or weather station temperature logger site (USGS 2012; Roof 2012). Sites are organized from north to south.

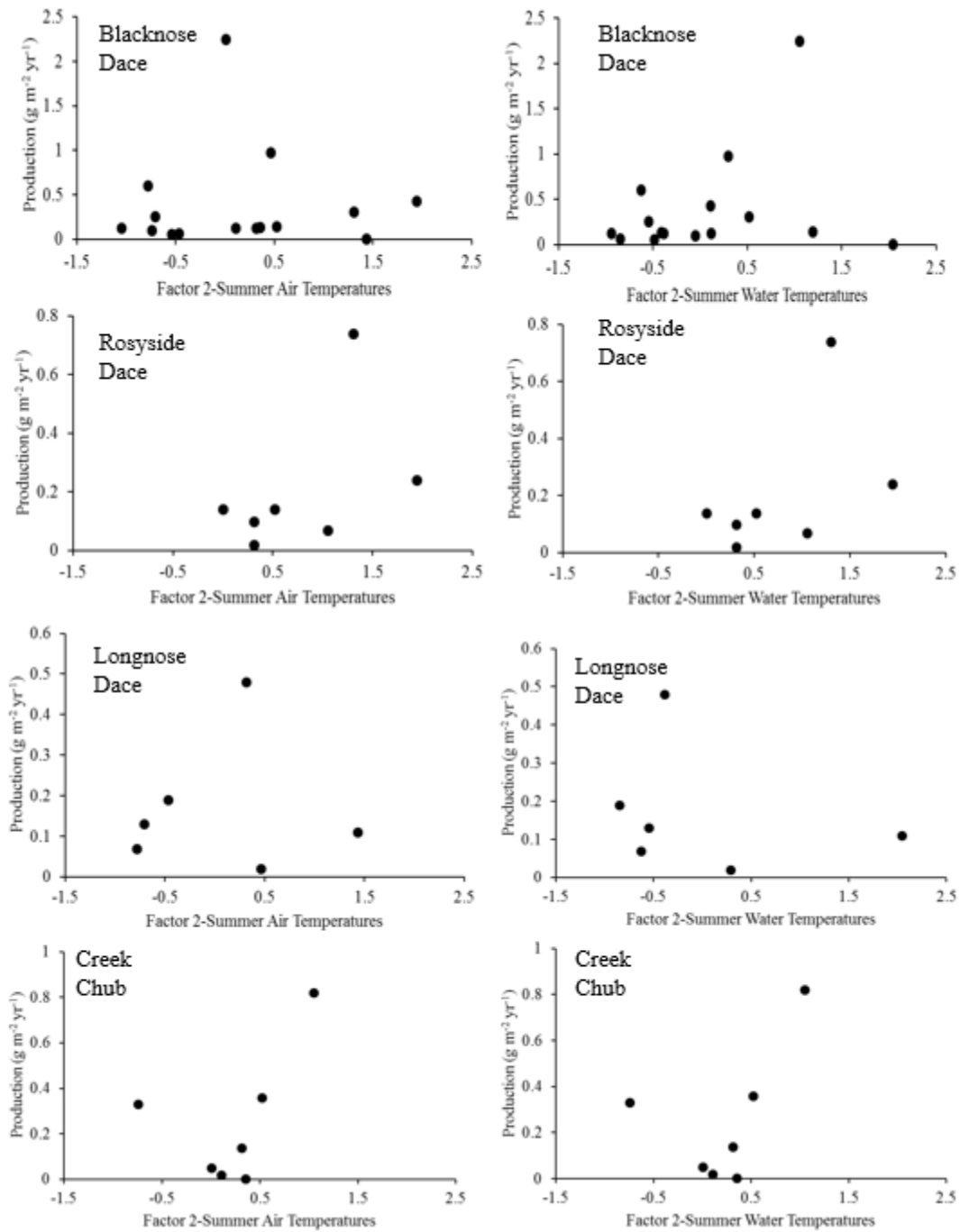
Stream Name	Stream Length (m)	Physical Characteristics						Dominant Substrate
		Width (m)	Depth (cm)	Discharge (m ³ /s)	Mean Yearly Temp. (°C)	Maximum Summer Temp. (°C)	Mean Summer Temp. (°C)	
Greendale Brook	1176	4.4 (1.2)	21.9 (6.9)	0.02	10.0 (9.6)	26.9 (4.3)	20.6 (3.2)	COB
Jenny Coolidge Brook	2002	3.9 (1.5)	20.2 (7.6)	0.01	10.0 (9.6)	26.9 (4.3)	20.6 (3.2)	COB
Adams Brook	2399	4.3 (1.9)	22.8 (9.2)	0.03	11.6 (8.9)	21.5 (3.0)	21.5 (3.0)	COB
Hearthstone Brook	2968	2.3 (0.8)	15 (10.8)	0.01	11.6 (8.9)	21.5 (3.0)	21.5 (3.0)	COB
Buffam Brook	1064	3.0 (1.1)	15.6 (5.4)	0.02	11.6 (8.9)	21.5 (3.0)	21.5 (3.0)	COB
Laurel Run	3255	6.1 (1.7)	29.6 (29.5)	0.06	9.6 (8.5)	23.1 (2.7)	18.5 (2.3)	BED
Elklick Run #2	423	6.8 (5.8)	55.4 (85.2)	0.01	10.4 (7.6)	22.3 (2.0)	18.7 (1.9)	COB
Elklick Run	685	4.3 (1.2)	23.6 (0.3)	0.03	10.5 (7.5)	22.8 (2.4)	18.6 (2.0)	COB
Blizzard Run	1310	2.1 (0.7)	13.4 (9.1)	0.01	12.0 (7.9)	26.7 (3.0)	21.0 (2.4)	COB
Lick Run	1189	6.5 (1.0)	26.3 (11.9)	0.40	12.4 (8.6)	29.0 (3.1)	22.2 (2.5)	COB
Kelso Spring Branch	543	3.3 (1.4)	20.4 (11.8)	0.02	12.2 (8.2)	27.0 (2.7)	21.1 (2.3)	COB
North Creek	749	6.2 (3.2)	27.3 (13.5)	0.09	14.1 (8.0)	29.2 (2.2)	22.7 (1.7)	COB
Jerry's Run	738	4.7 (1.7)	10.9 (3.8)	0.05	11.5 (9.1)	27.0 (2.6)	21.0 (2.2)	COB
Reed Creek	629	5.1 (1.6)	30.0 (15.5)	0.04	11.8 (7.7)	28.1 (4.4)	20.0 (3.5)	BLD
Roaring Creek	520	4.3 (2.3)	16.5 (0.08)	0.01	11.1 (7.4)	23.7 (2.3)	19.3 (1.8)	COB
Red Fork	1930	4.7 (2.7)	21.6 (19.3)	0.03	12.2 (7.2)	24.7 (2.2)	20.1 (1.8)	COB
Whiteoak Creek	799	2.3 (1.1)	14.4 (7.7)	0.02	12.5 (7.3)	26.0 (2.3)	20.4 (1.7)	COB
West Prong Hickey's Fork	480	5.2 (1.8)	21.5 (14.9)	0.04	12.0 (7.2)	24.4 (2.1)	20.1 (1.8)	COB
Trib. to Little Laurel Creek	533	2.7 (0.5)	14.1 (5.7)	0.03	12.9 (7.7)	28.8 (2.4)	21.8 (2.1)	BED
Trib. to Henry Fork	2405	2.0 (0.7)	12.9 (6.2)	0.02	13.8 (7.5)	29.1 (2.7)	22.3 (2.1)	COB
Swannanoa Creek	942	3.9 (0.8)	12.7 (6.6)	0.05	13.4 (7.7)	28.6 (2.1)	22.2 (2.0)	GRV
Beech Flats Prong	853	8.8 (2.1)	33.5 (10.0)	0.28	11.1 (6.7)	22.2 (1.8)	18.5 (1.5)	BLD
Jesse Branch	231	3.5 (0.9)	20.0 (10.0)	0.08	12.0 (7.0)	24.9 (2.1)	19.8 (1.8)	COB
Scapecat Branch	2281	7.1 (1.0)	30.0 (9.4)	0.26	11.4 (6.7)	23.3 (1.9)	18.6 (1.6)	BLD
Bethabara Creek	141	2.4 (0.4)	17.6 (9.0)	0.04	13.4 (7.0)	25.8 (2.0)	21.1 (1.6)	COB

Appendix E. Mean values (mg/L, except as noted) of water quality variables for 25 streams located in North Carolina, Tennessee, Virginia, West Virginia, Maryland, Vermont, and Massachusetts organized from north to south.

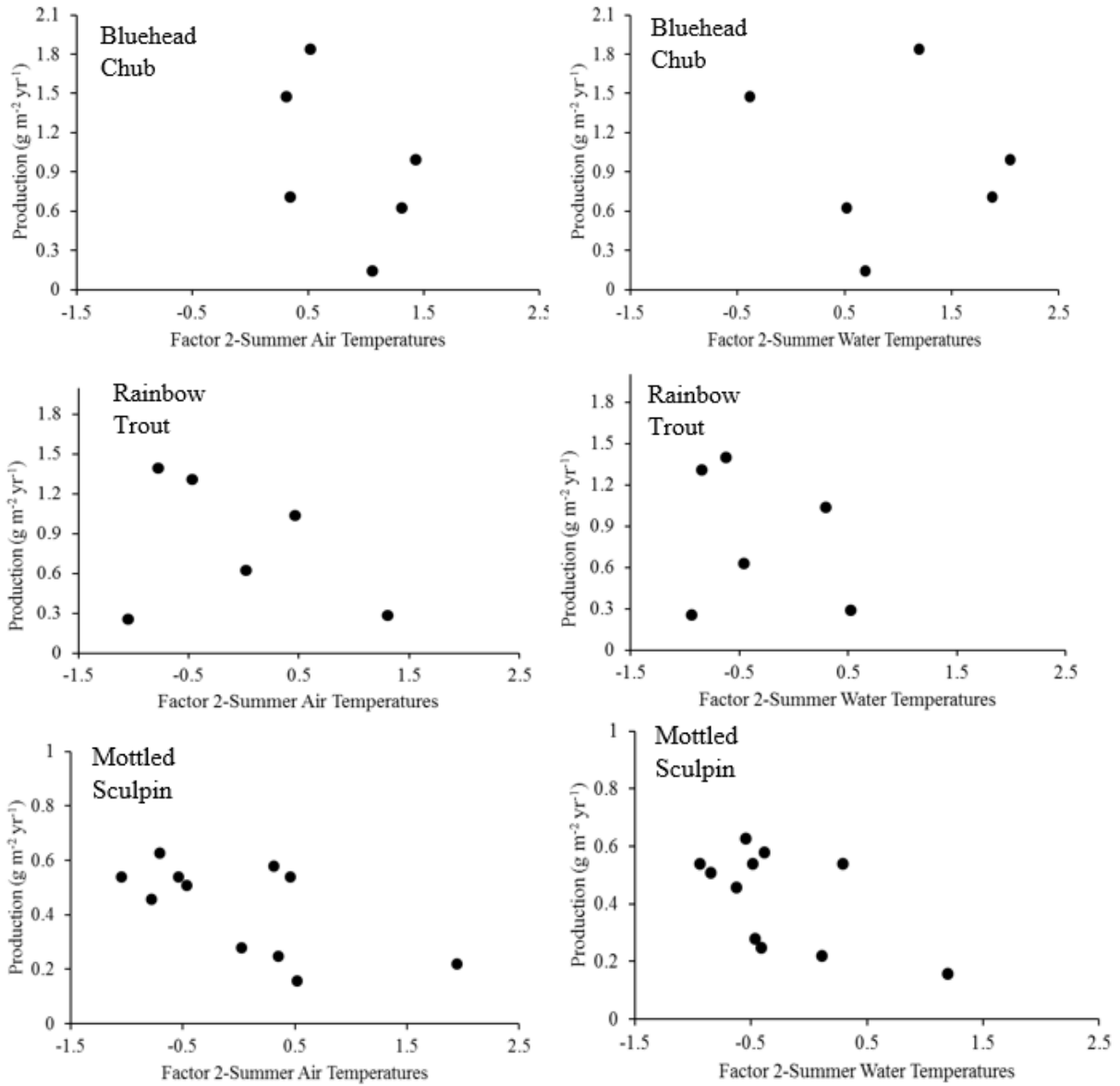
Stream Name	Water Quality Characteristics											
	DO	Conductivity (μ S/cm)	TDS	NH ₄ -N	CL	NO ₃ -N	O-PO ₄	SO ₄	K	NA	CA	MG
Greendale Brook	5.82	25.80	22.80	0.00	0.34	0.08	0.01	3.74	0.90	1.49	3.39	1.18
Jenny Coolidge Brook	4.88	32.40	27.30	0.00	0.57	0.06	0.01	3.22	0.53	1.20	5.13	1.71
Adams Brook	3.79	54.8	39.70	0.02	5.72	0.04	0.01	6.79	0.92	6.09	4.27	1.21
Hearthstone Brook	3.98	30.60	22.10	0.00	1.15	0.01	0.01	8.39	0.63	2.68	2.11	0.82
Buffam Brook	4.33	88.7	65.70	0.00	15.36	0.14	0.01	10.05	0.93	12.27	5.24	1.21
Laurel Run	8.72	348.9	266.50	0.01	2.10	0.28	0.00	153.95	2.23	0.82	61.67	16.71
Elklick Run #2	7.46	91.4	67.60	0.00	0.70	0.61	0.00	5.69	1.37	1.39	17.22	3.03
Elklick Run	6.02	134.3	103.30	0.00	0.84	0.28	0.00	5.30	1.02	1.36	28.62	3.18
Blizzard Run	4.55	119.7	83.80	0.00	1.33	0.54	0.00	5.86	1.15	3.05	15.25	3.10
Lick Run	5.01	67.3	49.40	0.01	0.75	0.12	0.00	7.14	1.09	1.44	9.97	2.45
Kelso Spring Branch	6.07	163.4	115.10	0.01	0.61	0.04	0.00	4.05	0.94	0.76	32.74	2.73
North Creek	7.34	69.8	48.80	0.01	0.92	0.01	0.02	1.93	1.00	2.72	9.12	2.13
Jerry's Run	8.90	168.5	130.00	0.00	35.75	0.37	0.00	13.00	2.46	17.57	11.85	5.15
Reed Creek	6.29	21.9	15.60	0.01	0.84	0.20	0.03	0.89	0.49	1.46	2.09	0.49
Roaring Creek	6.04	14.1	10.40	0.02	0.40	0.04	0.00	3.34	0.46	0.38	1.43	0.40
Red Fork	8.62	15.4	12.30	0.00	0.78	0.16	0.00	1.93	0.53	0.82	1.31	0.38
Whiteoak Creek	6.84	22.8	16.30	0.00	0.57	0.11	0.03	2.08	0.79	1.41	1.83	0.62
West Prong Hickey's Fork	5.96	27.5	19.50	0.00	0.36	0.19	0.00	2.31	0.55	1.04	2.11	1.20
Trib. to Little Laurel Creek	7.09	26.6	19.50	0.00	0.44	0.19	0.03	2.26	0.89	1.50	1.39	0.64
Trib. to Henry Fork	8.76	20.3	15.00	0.00	1.32	0.10	0.01	1.59	0.97	1.28	1.11	0.79
Swannanoa Creek	8.82	88.1	62.20	0.01	8.64	0.27	0.02	9.22	1.49	6.33	11.03	2.04
Beech Flats Prong	8.60	12.0	9.10	0.00	0.38	0.25	0.00	1.44	0.42	0.83	1.07	0.29
Jesse Branch	8.23	13.7	10.40	0.00	0.64	0.05	0.00	0.77	0.52	1.18	0.90	0.39
Scapecat Branch	9.02	9.4	7.80	0.01	0.45	0.13	0.01	0.89	0.48	0.83	0.62	0.21
Bethabara Creek	9.21	14.9	11.70	0.01	0.67	0.04	0.01	1.32	0.48	1.09	1.17	0.52

Appendix H. Summary of species richness, Shannon's diversity index, community abundance (number of total fish), community biomass (g m^{-2}), annual community production ($\text{g m}^{-2} \text{yr}^{-1}$), and P/B ratio at each of the 25 stream sites across the Appalachians.

Stream Name	Stream Class	Species Richness	Shannon's Diversity Index	Community Abundance	Community Biomass	Community Production	Community P/B
Beech Flats Prong	cold	3	0.63	124	2.18	1.81	0.83
Elklick Run	cold	2	0.49	147	0.93	0.60	0.47
Elklick Run #2	cold	5	0.91	314	3.31	1.57	0.52
Jesse Branch	cold	4	0.80	117	1.91	1.00	0.25
Laurel Run	cold	5	0.62	164	1.60	0.39	0.60
Red Fork	cold	5	0.74	258	3.43	2.06	0.57
Reed Creek	cold	11	1.04	424	6.23	3.56	0.39
Scapecat Branch	cold	3	0.53	30	1.64	0.64	0.65
Bethabara Creek	cool	2	0.59	39	1.75	0.91	0.52
Blizzard Run	cool	7	0.69	606	9.30	4.00	0.43
Jerry's Run	cool	7	0.91	351	2.09	1.10	0.53
Kelso Spring Branch	cool	16	1.17	478	6.81	6.79	1.00
Roaring Creek	cool	4	0.58	95	0.61	0.53	0.87
Swannanoa Creek	cool	7	1.04	553	2.93	2.36	0.81
Trib. to Little Laurel Creek	cool	5	0.81	196	3.79	2.62	0.69
Trib. to Henry Fork	cool	4	0.22	136	3.15	1.47	0.47
West Prong Hickey's Fork	cool	5	0.78	342	4.78	2.56	0.54
Whiteoak Creek	cool	3	0.51	25	0.76	0.15	0.20
Adams Brook	extreme northern	9	1.00	459	4.89	4.07	0.83
Buffam Brook	extreme northern	2	0.36	128	4.66	5.00	1.07
Greendale Brook	extreme northern	4	0.49	173	2.00	1.62	0.81
Hearthstone Brook	extreme northern	1	0.36	81	1.61	1.68	1.04
Jenny Coolidge Brook	extreme northern	3	0.63	150	1.99	1.58	0.79
Lick Run	warm	19	1.25	531	3.68	3.16	0.86
North Creek	warm	22	0.99	822	10.73	6.77	0.63



Appendix I. Individual cool-water species production as a function of the air and water summer temperature factors. Only species occurring at greater than 5 sites were graphed.



Appendix J. Individual cool-water species (Bluehead Chub) and cold-water species (Rainbow Trout and Mottled Sculpin) production as a function of the air and water summer temperature factors. Only species occurring at greater than 5 sites were graphed.