


Fish assemblage production estimates in Appalachian streams across a latitudinal and temperature gradient

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Abstract

Production of biomass is central to the ecology and sustainability of fish assemblages. The goal of this study was to empirically estimate and compare fish assemblage production, production-to-biomass (P/B) ratios and species composition for 25 second- to third-order streams spanning the Appalachian Mountains (from Vermont to North Carolina) that vary in their temperature regimes. Fish assemblage production estimates ranged from 0.15 to 6.79 g m⁻² year⁻¹, and P/B ratios ranged from 0.20 to 1.07. There were no significant differences in mean assemblage production across northern cold-water, southern cold-water and southern cool-water streams ($p = .35$). Two warm-water streams, not included in these comparisons, had the highest mean production and biomass values. Mean assemblage P/B was significantly higher in northern cold-water streams relative to southern cold-water and cool-water streams ($p = .01$). Species evenness in production declined with stream temperature and differed significantly across the lower latitude cold-water, cool-water and warm-water streams and the higher latitude (i.e. more northern) cold-water streams. Our fish assemblage production estimates and P/B ratios were both lower and higher compared to previously published estimates for similar stream habitats. This study provides empirical fish assemblage production estimates to inform future research on southern Appalachian streams and on the potential impacts of varying temperature regimes on cold-water, cool-water and warm-water fish production in the coming decades as climate change continues to threaten fish assemblages.

KEYWORDS

assemblage composition, assemblage evenness, biomass, P/B ratios, secondary production

1 | INTRODUCTION

Secondary production (i.e. production of organisms other than primary producers) is a foundational principle in ecology and fisheries (Downing, 1984; Lindeman, 1942; Waters, 1977) and is defined as the creation of heterotrophic biomass over time scaled to the population or community level (Allen, 1951; Huryn & Benke, 2007). Production integrates several vital population-level metrics (most notably—density, biomass, population growth and mortality) (Downing, 1984;

Hayes, Bence, Kwak, & Thompson, 2007; Huryn & Benke, 2007; Valentine-Rose, Layman, Arrington, & Rypel, 2007). Fish secondary production is a useful metric for understanding aquatic ecosystems and fisheries in a general sense but can be a useful tool for evaluating the response of fisheries to environmental perturbation or change (Dolbeth, Cusson, Sousa, & Pardal, 2012; Hayes et al., 2007; Lobón-Cerviá, Gonzalez, & Budy, 2011; Rypel, Goto, Sass, & Vander Zanden, 2015). However, in the few cases where fish secondary production has served as the response variable to environmental change or gradients,

the focus has almost exclusively been on calculation of population-level production estimates for a single species (Almodóvar, Nicola, & Elvira, 2006; Lobón-Cerviá et al., 2011; Neves, Brayton, & Helfrich, 1985; Rypel et al., 2015). Recent evidence suggests that the influence of environmental degradation on fish assemblage production (also termed community production) can be greater compared to analyses of single species production (Valentine-Rose, Rypel, & Layman, 2011).

Stream ecosystems in the southern Appalachians are particularly vulnerable to the effects of climate change and other anthropogenic stressors, yet only a few studies have quantified fish assemblage production in southern Appalachian streams (e.g. Freeman et al., 1988; Neves & Pardue, 1983), which can provide valuable information about fish assemblage responses to anthropogenic and environmental impacts (Valentine-Rose et al., 2011). Some streams in this region are characterised by hyperdiverse communities and high levels of endemism (Warren, Angermeier, Burr, & Haag, 1997); while others in the higher elevations are characterised by one or two cold-water species, such as the culturally and recreationally valuable eastern Brook Trout *Salvelinus fontinalis* (Scott & Helfman, 2001). Invasive Rainbow Trout *Oncorhynchus mykiss* and Brown Trout *Salmo trutta* are also present throughout the southern Appalachian range (Whitworth & Strange, 1983; Larson & Moore, 1985). Having baseline information on fish assemblage production in highly sensitive streams, such as what is provided in this study, will be essential for informed future management strategies.

Having this baseline information on fish assemblages can also be useful to sustainable management of fish populations in the face of a changing environment, which will depend strongly on improved predictions of the impacts of climate change on the functional ecology of diverse aquatic ecosystems and assemblages (McGowan, Cayan, & Dorman, 1998; Tonn, 1990). Climate change is one of the largest and most pervasive threats to the integrity of aquatic ecosystems and fish populations at all scales (Beamish, 1995; Brander, 2007). Bioclimatic envelope models strongly suggest that the geographic ranges of many cool- and cold-water adapted species will shift northward as climate change progresses (Forister et al., 2010; Hein, Öhlund, & Englund, 2014; Moyle & Cech, 2004; Walther et al., 2002). In head-water mountain stream habitats, as temperatures rise, the likelihood of long-term persistence of resident cold- and cool-water fish species will be influenced by the capacity for adaptation to novel temperature regimes or immigration to more favourable habitats (Wenger et al., 2011). Local adaptation mechanisms include modifications to habitat usage (Magnuson, 1979), physiological accommodation (Parmesan, 2006; Rijnsdorp, Peck, Engelhard, Möllmann, & Pinnegar, 2009) and phenological modifications such as timing of reproduction (Farmer, Marschall, Dabrowski, & Ludsins, 2015; Lyons et al., 2015; Parmesan & Yohe, 2003; Schneider, Newman, Card, Weisberg, & Pereira, 2010). Because many individuals and species will be less capable of rapid adaptation, temperature change will undoubtedly alter mortality and production rates of myriad freshwater fish assemblages. Some species, notably those which tolerate both a broad range and warmer temperatures, may benefit from increased average temperatures via enhanced growth and ostensibly increased production (Black, Boehlert,

& Yoklavich, 2005; Cline, Bennington, & Kitchell, 2013; Rypel, 2012). Of particular concern are species and populations that might respond to climate change in highly nonlinear ways (Chu, Mandrak, & Minns, 2005; Ficke, Myrick, & Hansen, 2007), whereby a small change in temperature may yield a disproportionately large effect on key vital rates like recruitment (Farmer et al., 2015; Hansen, Carpenter, Gaeta, Hennessy, & Vander Zanden, 2015). Thus, in addition to empirical estimates, an initial, snapshot understanding of the extent to which production may vary across thermal regimes could yield useful information on the vulnerability of Appalachian fish assemblages to climate change and other anthropogenic and environmental disturbances.

To compare baseline production estimates in the Appalachians using temperature data from 2012 and to inform future studies, our primary objective was to empirically estimate and compare annual fish assemblage production, assemblage production-to-biomass ratios and assemblage composition for 25 streams in the Appalachian Mountains with differing temperature regimes (i.e. northern/higher latitude cold-water streams, southern cold-, cool- and warm-water streams) ranging from Vermont to North Carolina.

2 | MATERIALS AND METHODS

2.1 | Site selection and classification

Twenty streams were selected from a network of 204 stream sites previously identified as potential Brook Trout habitat by the United States Forest Service Southern Research Station in Blacksburg, Virginia, USA (USFS SRS). An additional five “northern” (New England) streams were also included in this study for 25 total study streams (Figure 1). Study sites were mostly second- to fourth-order streams situated across diverse settings including the Alleghany Mountains, Great Smoky Mountains, Blue Ridge Mountains and Piedmont Region in the southern Appalachian Mountains and the Green and Taconic Mountains in the north-east Appalachians. Study streams were almost always characterised by dense canopy cover, cobble-dominated substrate and had a mean elevation of 540 ± 240 m.

Each stream, excluding the five northern cold-water sites, was instrumented with a data logger to record both water and air temperature (Onset HOBO, Bourne, MA, USA) at 30-min intervals. We focused on the following thermal metrics (for both air and water) as being critical to the ecology of fishes in these streams: mean annual temperature, annual temperature variability (i.e. standard deviation), minimum summer and winter temperatures, maximum summer and winter temperatures, and mean summer temperatures (Casselman, 2002; Neuheimer & Taggart, 2007; Shuter, MacLean, Fry, & Regier, 1980). All temperature metrics were calculated based on the year preceding sampling (March 2011 to March 2012).

To a priori classify the 20 more southern streams into cold-, cool- and warm-water streams, we conducted a K-means cluster analysis constrained to a maximum of three clusters. Six temperature metrics were included in the cluster analysis: mean annual air and water temperatures (°C), mean summer (June 2012 to August 2012) air and water temperatures (°C), and the mean maximum summer air and

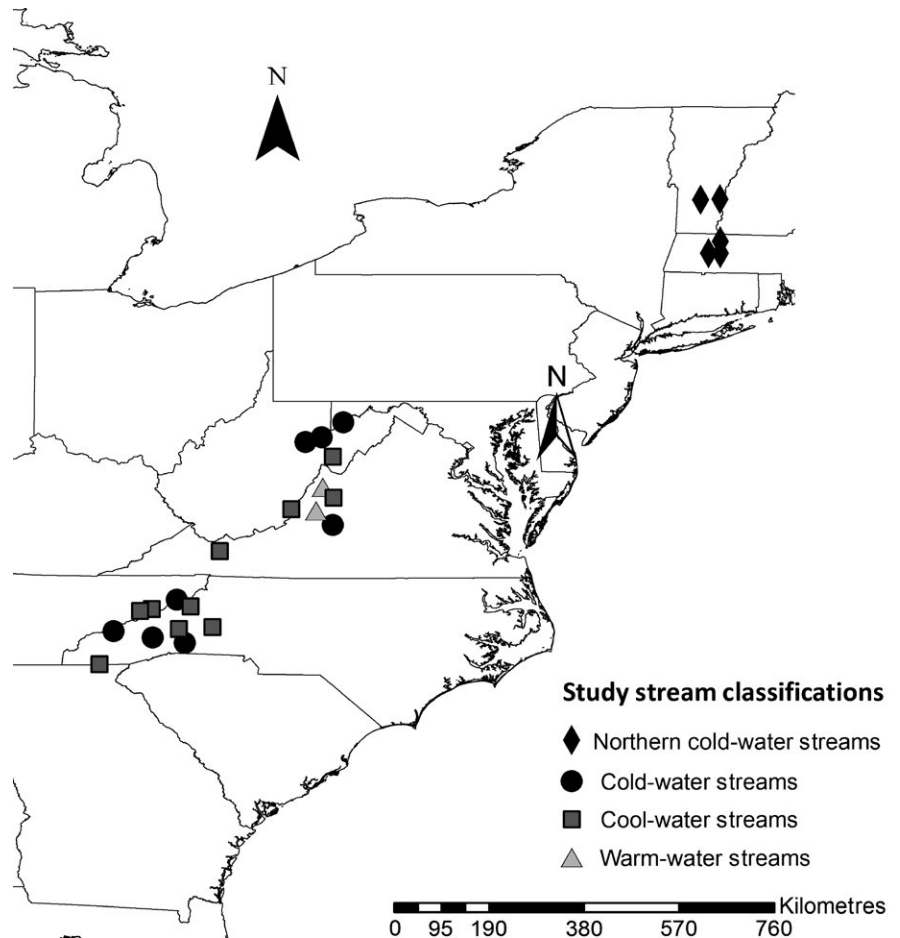


FIGURE 1 Study streams located across the Appalachian Mountain range sampled for fish assemblage production estimates. Some Vermont and Massachusetts streams (i.e. northern cold-water streams) have been slightly offset from their true location for improved readability. Precise latitude–longitude coordinates for each study stream can be found in Table 1

water temperatures (°C) (Wehrly, Wiley, & Seelbach, 2003). The more northern study streams in Vermont and Massachusetts were a priori considered a separate temperature cluster without analysis (i.e. northern cold-water streams).

2.2 | Sampling and production calculations

All 25 sites were sampled June–September 2012 using backpack electrofishing units and block nets. Block nets with 1.6 mm mesh were placed downstream and upstream of each of two 50-m reaches spaced 50 m apart. An average of four to five electrofishing passes were conducted to deplete fish in each reach until we were catching approximately 10 fish or less. For all individuals captured, total lengths (mm) and wet weights (0.1 g) were measured in situ. A subsample of each species captured at each site was euthanised in concentrated tricaine methanesulphonate (MS-222) solution and transported to a Virginia Tech laboratory on ice and frozen for otolith removal and age estimation. Following Ketchen (1950) and DeVries and Frie (1996) subsampling protocols, a fixed stratified subsample 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 & Frie, 1996).

We sampled five of the study streams a second time (but without collecting individuals for age-determination) approximately 5 months

after the initial sampling to assess the temporal stability of our instantaneous production estimates. These streams were selected to maximise the time between sampling, as they were the first five streams sampled in the study.

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

$$L_t = c + (L_c - c) \times (O_i \div O_c)$$

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 (DeVries & Frie, 1996; Francis, 1990). 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 best goodness of fit) were used to predict the ages of fish measured in the field using the equation developed from the age-length scatterplots.

Fish secondary production values for each species were estimated using the instantaneous growth rate method (Hayes et al., 2007;

Waters, 1977). The equation used to calculate production between each age class was

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

where P = production, \bar{B} = mean biomass between age class x and $x + 1$ and G = instantaneous growth rate (equation below). Production from age class _{x} and age class _{$x+1$} was calculated as the product of growth (G) and mean biomass (\bar{B}) (Halyk & Balon, 1983; Valentine-Rose et al., 2007, 2011). After calculating production (P) between each age class, we summed these values to get total annual production ($\text{g m}^{-2} \text{ year}^{-1}$) per species (Halyk & Balon, 1983). Fish assemblage production was calculated by summing the individual species annual production values (Halyk & Balon, 1983) for each reach. Age-specific growth (G) in the equation above was calculated using the equation

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

Mean biomass (\bar{B}) was calculated by averaging the biomass of age class _{x} and age class _{$x+1$} (Hayes et al., 2007). We calculated biomass (g m^{-2}) of each age class by dividing the total weight (g) by the area (m^2) sampled using stream-wetted width and average depth. The P/B ratio for each species in each stream was then calculated by dividing the annual production by total biomass (sum of biomass for each age class) (Hayes et al., 2007; Waters, 1977) (see Appendix A for example calculations). Assemblage P/B was calculated by dividing total assemblage production by total assemblage biomass.

All fish species collected at the 25 study streams were classified a priori as cold-water species, cool-water species and warm-water species. Our assignments of species to thermal categories follow those used by Magnuson, Crowder, and Medvick (1979), Lyons et al. (2009), and Lyons, Stewart, and Mitro (2010) classification, which were based on laboratory studies and previous published literature. If a species was not included in the Magnuson et al. (1979) or the Lyons et al. (2010) classification, we used published information on the preferred temperature range for the species in question outlined by Jenkins and Burkhead (1994) to determine the appropriate thermal niche for that species. We summed production values across species classified as cold-water, cool-water and warm-water fishes at each site and calculated the percentage contribution of each thermal group to total production for the four stream types (i.e. northern cold-water streams, southern cold-, cool- and warm-water streams).

Duplicate water samples were collected at each stream upstream of the upper reach before sampling started. Samples were immediately placed in a cooler with dry ice to ensure fast freezing. The Coweeta Hydrologic Laboratory (Otto, NC, USA) analysed the water samples for ammonium, nitrite, nitrate, phosphorous, sulphate, potassium, calcium and magnesium using standard methods (EPA 1983). In addition, we used a Yellow Springs Instrument professional probe (Yellow Springs, OH, USA) to obtain a point measurement of water temperature ($^{\circ}\text{C}$), pH, conductivity ($\mu\text{S}/\text{cm}$) and dissolved oxygen (mg/L).

Habitat data were recorded for the entire 150 m reach section using a similar estimation method as outlined in the Basinwide Visual Estimation Technique, BVET (Dolloff, Hankin, & Reeves, 1993). In addition to the BVET parameters recorded (e.g. dominant and sub-dominant 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 m 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 = water-column cross-sectional area and v = average water-column velocity.

2.3 | Statistical analyses

We used analysis of variance (ANOVA) with Tukey's post hoc HSD comparisons to compare mean assemblage biomass, production and P/B ratios among the northern cold-water and more southern cold-water and cool-water streams. Warm-water streams were excluded from this analysis because of an inherently low number of streams to gain reliable statistical power in ANOVA ($N = 2$). We estimated annual assemblage production at five of the study streams (see fish sampling section above) using samples collected in June and October 2012 to evaluate variation in production estimated in different seasons. We conducted a paired t test in JMP 10.1 statistical software to test for a significant difference in total assemblage production estimated using the July compared to October samples at these five sites.

Rank-abundance, rank-biomass and rank-production curves were generated using species-specific values for each of the 25 fish assemblages (Clarke, 1990; Valentine-Rose et al., 2011; Whittaker, 1972). Slopes of each rank curve (\log_{10} - \log_{10} -transformed) were considered to approximate relative assemblage evenness. Thus, a higher slope in a log-transformed rank-production curve indicated that fewer species dominated total assemblage-wide production compared to an assemblage curve with a shallower slope. Rank curves were created for each individual stream community and also for each combined stream temperature class by averaging the rank-abundance, biomass or production values of the same species across streams of the same class (i.e. separate curves for cold-water, cool-water, warm-water and northern cold-water streams) to determine the average evenness by thermal class.

We used analyses of covariance (ANCOVAs) on the \log_{10} - \log_{10} -transformed curves with Tukey's post hoc HSD to assess significant differences in assemblage evenness. In the models, \log_{10} (abundance, biomass or production) was the dependent variable, \log_{10} (Species Rank) was the independent variable, and stream or stream thermal class were categorical variables. Significant differences in slope (i.e.

evenness) were assessed via the rank \times class or rank \times site interaction terms. All statistics were considered significant at $\alpha < 0.05$. The first three ANCOVA models tested statistical significance among assemblage evenness based on rank-abundance, rank-biomass and rank-production curves respectively, for the 25 sites individually. 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 northern cold-water streams rank-abundance, -biomass and -production curves, separately.

3 | RESULTS

3.1 | Site classification

Based on the K-means cluster analysis, the 20 southern Appalachian streams clustered into three basic groups: (i) cold-water (eight sites), (ii) cool-water (10 sites) and (iii) warm-water (two sites) (Table 1). The more southern cold-water, cool-water and warm-water classified streams had an mean annual air temperature of 11.92°C (standard deviation [SD] = 1.37), 12.09°C (SD = 1.19) and 11.91°C (SD = 0.14), mean maximum summer (June to August) air temperature of 23.92°C (SD = 1.96), 26.72°C (SD = 1.81) and 29.08°C (SD = 0.12), and mean summer air temperature of 19.09°C (SD = 0.70), 21.04°C (SD = 0.94) and 22.41°C (SD = 0.35) respectively (Figure 2). The northern streams that were a priori classified as having a different thermal regime had a mean annual air temperature of 10.86°C (SD = 1.06), a mean summer air temperature of 21.12°C (SD = 0.48) and a mean maximum summer air temperature of 23.40°C (SD = 3.29). Note that we labelled these clusters based on their prevailing temperature regimes relative to one another; thus, our use of cold-, cool- and warm-water differs from more absolute definitions commonly used to describe the optimum temperature range for cold-, cool- and warm-water freshwater fish species (Armantrout, 1998).

3.2 | Fish assemblage abundance, biomass and production

We captured 6,743 fish representing 40 species across the 25 study sites. Based on Lyons et al. (2010) fish classifications, six species were classified as cold-water species, 20 as cool-water species and 14 as warm-water species. Species richness ranged from 1 to 22; however, richness was typically higher in warm-water streams and lower in northern cold-water sites (Table 1).

Fish assemblage biomass and annual production ranged from 0.61 to 10.73 g m⁻² and 0.15 to 6.79 g m⁻² year⁻¹ respectively (Table 1). Blacknose Dace *Rhinichthys atratulus*, rosyside dace *Clinostomus funduloides*, Longnose Dace *Rhinichthys cataractae* and Bluehead Chub *Nocomis biguttatus* were the most common cool-water species encountered and when present comprised a relatively high percentage of total assemblage abundance, biomass and production (Appendix B). At sites where they were present, cold-water species (i.e. Brook Trout, Sculpin *Cottus* spp. and Rainbow Trout) tended to comprise a high percentage of total assemblage abundance, biomass and annual

production (Appendix B). Common warm-water species encountered were Central Stonerollers *Camptostoma anomalum* and Sunfishes *Lepomis* spp. (Appendix B).

Assemblage fish biomass was higher in warm-water streams ($B = 7.21$ g m⁻²), than in cool-water ($B = 3.60$ g m⁻²), northern cold-water ($B = 3.03$ g m⁻²) and southern cold-water streams ($B = 2.65$ g m⁻²) (Figure 3). Similarly, fish production was highest ($P = 4.96$ g m⁻² year⁻¹) in the warm-water streams but did not differ significantly ($p = .35$) among the southern cold-water ($P = 1.45$ g m⁻² year⁻¹), southern cool-water ($P = 2.25$ g m⁻² year⁻¹) and northern cold-water streams ($P = 2.79$ g m⁻² year⁻¹) (Figure 3). Mean fish assemblage P/B for all 25 streams combined was 0.65; thus on average, assemblage fish biomass in Appalachian streams turned over more than half of the total biomass annually. A significant ANOVA ($p = .01$) revealed that differences in turnover rate existed across thermal classes. Mean assemblage P/B was significantly higher in the northern cold-water streams compared to all other stream temperature classes, excluding the warm-water streams (both Tukey's $p < .05$). However, there was no difference in fish assemblage P/B between southern cold-water and southern cool-water streams (Tukey's $p > .05$).

Fish assemblage production at all but one of the northern cold-water sites was mostly allocated to cold-water fish species (i.e. Brook Trout and Slimy Sculpin *Cottus cognatus*) (Appendix B). Similarly, assemblage production at the southern cold-water sites was dominated by cold-water species with the exception of Reed Creek, where over half the total assemblage production was attributed to a single cool-water species, Blacknose Dace (Figure 4). Assemblage production at the cool-water sites was mostly allocated to cool-water species; however, one cool-water stream had 100% production allocated to two cold-water species (Rainbow Trout and Mottled Sculpin *Cottus bairdii*) (Figure 4). Production attributable to warm-water species made up over half of the assemblage production in the two warm-water streams, comprised about 40% of production at one cool-water stream, Kelso Springs Branch, and was zero at all five northern cold-water sites.

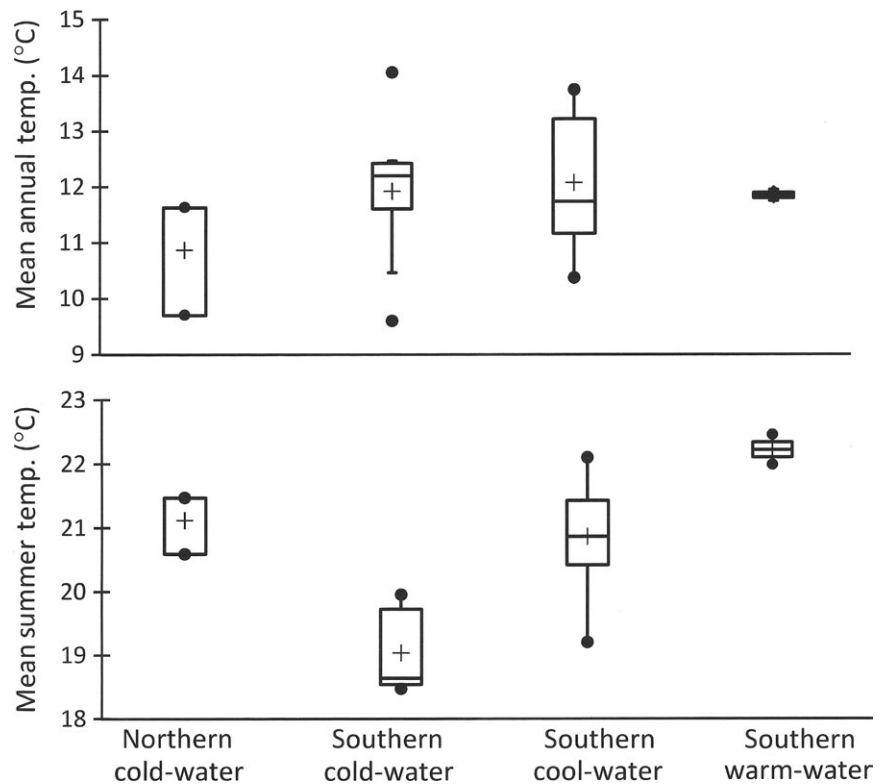
The proportion of cold-water species production was 40% lower in streams classified as cool-water streams compared to the southern cold-water streams (Figure 4). Cool-water streams had a mean summer temperature 2°C higher and maximum summer temperature 3°C higher than southern cold-water streams. Furthermore, cold-water species production was reduced to only 2% of the total assemblage production in the warm-water streams, where mean summer and mean maximum summer temperatures were 3°C and 4°C higher respectively (Figure 4).

Based on the paired t test of the July and October sample of the five sites that were sampled twice, no significant difference existed between total assemblage production between the two sampling dates ($p = .14$). Excluding one site, assemblage production estimates were slightly lower in the fall compared to the summer sample but not significantly, presumably due to natural mortality. The mean difference between the samples ranged from an increase of 0.57 and decrease ranging from -1.69 to -0.49. Fall estimates at the four streams with

TABLE 1 Fish assemblage abundance, biomass, annual production, and P/B values and selected site characteristics of the study streams sampled during summer 2012. Note that sites are organised from north to south based on latitude

Fish assemblage biological variable						Site characteristics				
Stream name	Site classification	N	B (g m ⁻²)	P (g m ⁻² year ⁻¹)	P/B	Species richness	Latitude	Longitude	Elevation (m)	Mean annual air temp. (°C)
Greendale Brook, VT	Northern cold-water	173	2.00	1.62	0.81	4	43.354	-72.824	534	10.0
Jenny Coolidge Brook, VT	Northern cold-water	150	1.99	1.58	0.79	3	43.340	-72.831	308	10.0
Adam's Brook, MA	Northern cold-water	459	4.89	4.07	0.83	9	42.395	-72.487	71	11.6
Hearthstone Brook, MA	Northern cold-water	81	1.61	1.68	1.04	1	42.385	-72.480	80	11.6
Buffam Brook, MA	Northern cold-water	128	4.66	5.00	1.07	2	42.384	-72.454	158	11.6
Laurel Run, MD	Cold-water	164	1.60	0.39	0.25	5	39.343	-79.258	615	9.6
Elklick Run #2, WV	Cold-water	314	3.31	1.57	0.47	5	39.078	-79.649	524	10.4
Elklick Run, WV	Cold-water	147	0.93	0.60	0.65	2	39.016	-79.532	586	10.5
Blizzard Run, WV	Cool-water	606	9.30	4.00	0.43	7	38.728	-79.447	559	12.0
Lick Run, VA	Warm-water	531	3.68	3.16	0.86	19	37.993	-79.631	397	12.4
Kelso Spring Branch, VA	Cool-water	478	6.81	6.79	1.00	16	37.991	-79.438	422	12.2
North Creek, VA	Warm-water	822	10.73	6.77	0.63	22	37.855	-79.616	267	14.1
Jerry's Run, VA	Cool-water	351	2.09	1.10	0.53	7	37.784	-80.197	624	11.5
Reed Creek, VA	Cold-water	424	6.23	3.56	0.57	11	37.499	-79.449	366	11.8
Roaring Creek, VA	Cool-water	95	0.61	0.53	0.87	4	37.035	-81.482	671	11.1
Red Fork, TN	Cold-water	258	3.43	2.06	0.60	5	36.159	-82.251	800	12.2
Whiteoak Creek, NC	Cool-water	25	0.76	0.15	0.20	3	36.041	-82.338	646	12.5
West Prong Hickey's Fork, NC	Cool-water	342	4.78	2.56	0.54	5	35.994	-82.704	670	12.0
Trib. to Little Laurel Creek, NC	Cool-water	196	3.79	2.62	0.69	5	35.957	-82.756	572	12.9
Trib.to Henry Fork, NC	Cool-water	136	3.15	1.47	0.47	4	35.666	-81.612	362	13.8
Swannanoa Creek, NC	Cool-water	553	2.93	2.36	0.81	7	35.635	-82.219	494	13.4
Beech Flats Prong, NC	Cold-water	124	2.18	1.81	0.83	3	35.593	-83.387	957	11.1
Jesse Branch, NC	Cold-water	117	1.91	1.00	0.52	4	35.477	-82.684	755	12.0
Scapecat Branch, NC	Cold-water	30	1.64	0.64	0.39	3	35.382	-82.895	1046	11.4
Bethabara Creek, NC	Cool-water	39	1.75	0.91	0.52	2	34.997	-83.644	729	13.4

FIGURE 2 Box plots of mean annual air temperatures (°C) and mean summer air temperatures (°C) for the northern cold-water streams ($N = 5$), southern cold-water streams ($N = 8$), southern cool-water streams ($N = 10$) and southern warm-water streams ($N = 2$) of the 25 sites across the Appalachian Mountains in Vermont, Massachusetts, Maryland, West Virginia, Virginia, North Carolina and Tennessee



lower values were 62%–77% lower than spring estimates. However, the values were not significantly different, thus; this suggests that assemblage production estimates remained statistically the same between the two time periods.

3.3 | Rank curves

Temperature class-level comparisons of mean rank-production curves showed the same results regardless of the metric used (Table 2). Assemblage 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 assemblage 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 assemblage evenness among sites but not among thermal classes.

Evenness varied in relation to both stream thermal class and the selected response metric (i.e. abundance, biomass, or production). For example, while cold-water streams and cool-water streams had similar levels of evenness in assemblage abundance (ANCOVA $p = .50$), northern cold-water streams had a significantly higher slope (ANCOVA, $p < .05$ for all, Figure 5). Assemblage evenness results based on mean rank-biomass curves exhibited the same trend as mean rank-abundance curves: cold-water and cool-water streams did not differ in biomass evenness (ANCOVA $p = .83$); however, northern cold-water

streams were significantly less even based on biomass compared to the other two classes (ANCOVA, $p < .05$ for all, Figure 5). Rank-production curves revealed the highest number of statistical differences in evenness compared to the other response metrics examined (Table 2). There were significant differences in assemblage evenness based on production for all three stream thermal classes ($p < .01$ for all) except for cold-water and cool-water classes ($p = .86$) (Figure 5, Table 2). In general, evenness in production declined with temperature; thus, cold-water streams were less even in production compared to cool-water and warm-water streams. Overall, rank-production provided different results when used as the response metric when comparing evenness among sites but not among thermal classes.

4 | DISCUSSION

4.1 | Assemblage production, P/B and evenness

Our snapshot view of fish assemblage production for 2012 may vary widely in subsequent years so care should be taken in comparing these values with previously published estimates; however, our estimates provide additional insight into potential production for Appalachian streams across a temperature gradient. Some of the fish assemblage production estimates from this study were within the range of other previously published estimates from stream fish assemblages (Table 3), but some streams from this study had both lower and greater assemblage production than similar stream habitats in Virginia, eastern Kentucky and North Carolina (Freeman et al., 1988; Lotrich, 1973; Neves & Pardue, 1983) (Table 3). This suggests some of the streams had higher and some lower production potential compared to

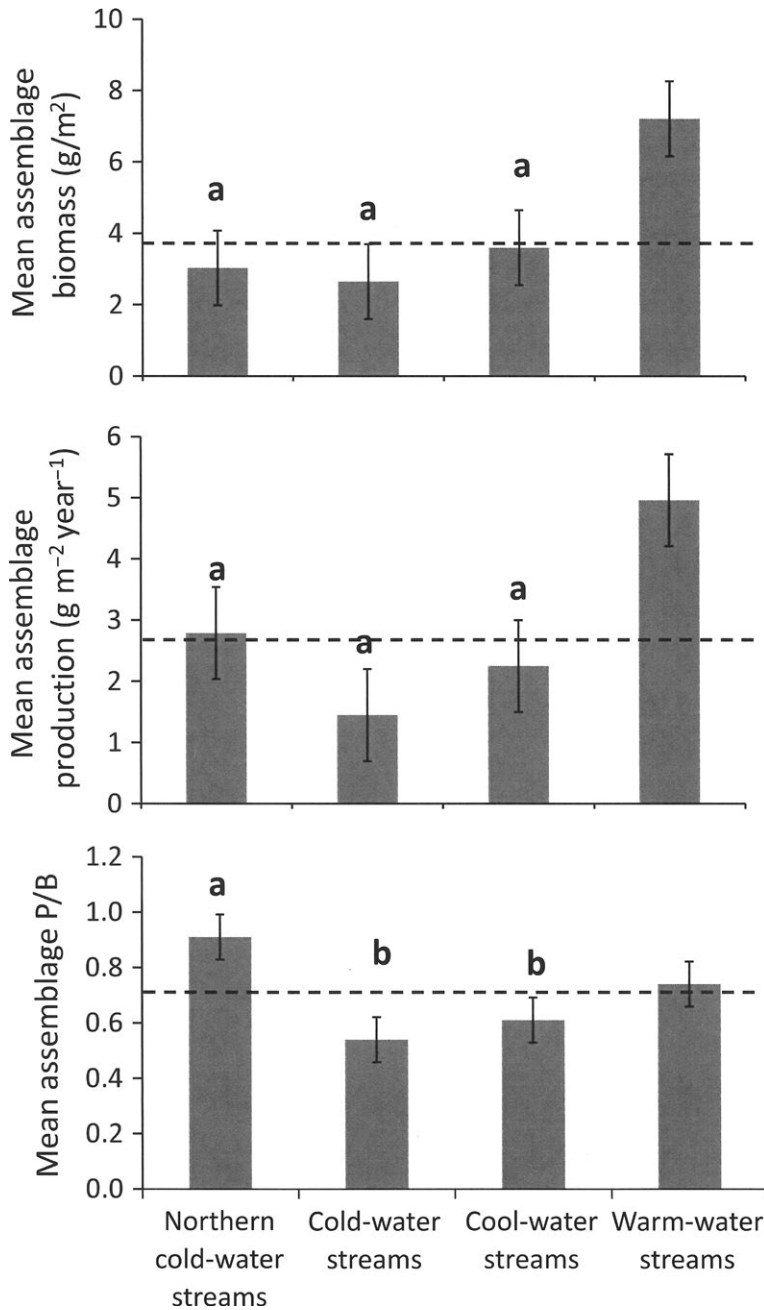


FIGURE 3 Mean assemblage biomass, mean assemblage annual production and mean assemblage P/B ratio for fishes in the four stream temperature categories (cold-water southern Appalachian streams, cool-water southern Appalachian streams, warm-water southern Appalachian streams and northern cold-water streams). Warm-water streams were excluded from statistical comparisons because of the low sample size. Error bars represent the mean \pm 1 standard error. Corresponding letters denote means that do not statistically differ from one another (Tukey's post hoc $p > .05$)

others, potentially due to recruitment success during that year, higher mortality prior to sampling, or better fish habitat and temperatures prior to sampling.

The bulk of production in any population usually originates from young-of-the-year fish (Halyk & Balon, 1983; Neves & Pardue, 1983; Pajak & Neves, 1987); thus, any increases or decreases in recruitment or young-of-the-year production may alter total assemblage production (Casselman, 2002; Lobón-Cerviá et al., 2011). Whiteoak Creek ($P = 0.15 \text{ g m}^{-2} \text{ year}^{-1}$), Roaring Creek ($P = 0.53 \text{ g m}^{-2} \text{ year}^{-1}$) and Scapecat Branch ($P = 0.64 \text{ g m}^{-2} \text{ year}^{-1}$) had low abundances of younger age class fish, which is also most likely contributing to lower overall fish assemblage production at these sites. Low recruitment success during this year could account for the lower production estimates at these particular streams and a high recruitment year could be

accounting for the higher production estimates in some streams in the present study compared to the published literature.

The upper range of our production estimates (i.e. $6.79 \text{ g m}^{-2} \text{ year}^{-1}$) was above that of other streams in similar habitats in the United States and, in some cases, worldwide (Table 3; see also Rypel & David, 2017). For example, the upper range of our production estimates were also above estimates for foothill streams in north New Zealand (Hopkins, 1971), tropical rainforest streams in northern Borneo (Watson & Balon, 1984), lowland trout streams in south-eastern Minnesota (Kwak & Waters, 1997) and low altitude neotropical streams in Brazil (Mazzoni & Lobón-Cerviá, 2000). An explanation for these high assemblage 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) analysed relationships between

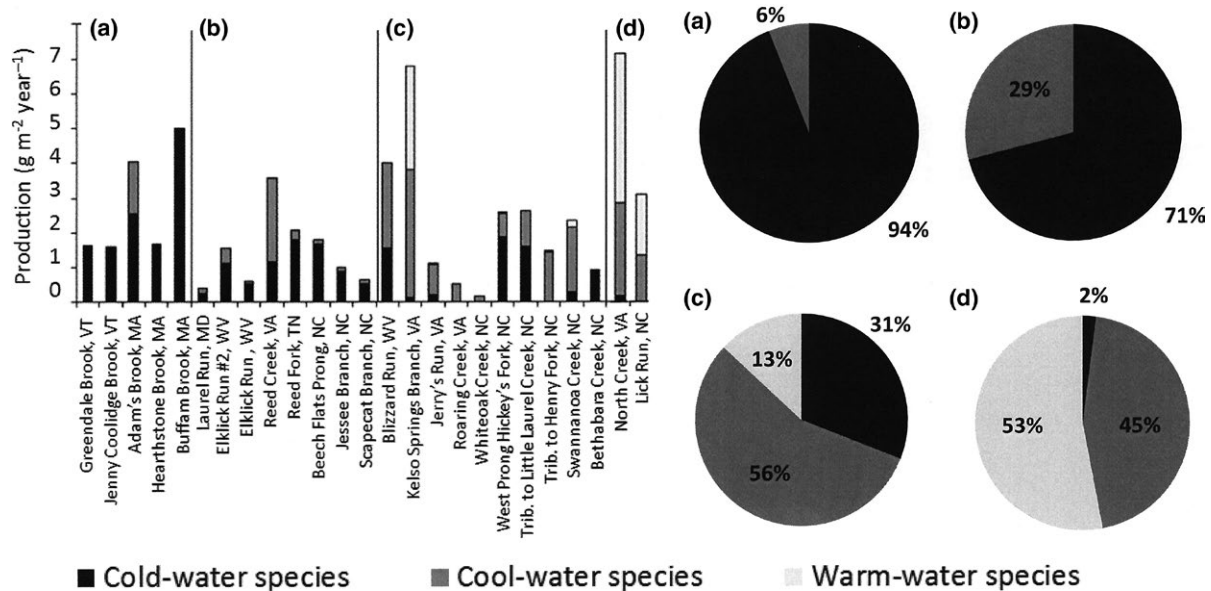


FIGURE 4 Comparisons of total assemblage annual production (g m⁻² year⁻¹) of cold-, cool- and warm-water species per site (left panel) and percentage of total production of cold-, cool- and warm-water species production (right panel) at streams classified a priori as northern cold-water streams (a) (five sites), southern cold-water streams (b) (eight sites), cool-water streams (c) (10 sites) and warm-water streams (d) (two sites) located throughout North Carolina, Tennessee, Virginia, West Virginia and Maryland, and the five northern sites in Massachusetts and Vermont sampled during summer 2012

body size and temperature for fish species grouped by thermal guild and showed that in general cold-water and cool-water fish species follow Bergmann's rule, that is, body size increases with increasing latitude and decreasing temperature (Bergmann, 1847; Rypel, 2014). Larger body sizes and growth in individuals of cold-water species at a given age might therefore similarly be associated with enhanced fish production, as growth of individual fish is one important aspect of production and is directly related to the P/B ratio (Allen, 1971). Thus, higher assemblage production estimates in the northern cold-water sites might be associated with enhanced cold-water species growth at lower temperatures; however, more analysis needs to be conducted to confirm this trend.

In this study, high assemblage production, like those encountered in the two warmwater streams and some of the cool-water and northern cold-water streams, was frequently driven by high standing stock biomass levels (e.g. in Kelso Springs Branch, Lick Run, Adam's Brook, Buffam Brook, Reed Creek, Blizzard Run, Swannanoa Creek, Red Fork). Fish biomass has frequently been used as a predictor in empirical models of fish production (Downing, Plante, & Lalonde, 1990). High biomass levels often corresponded to elevated abundances of young-of-the-year fish (i.e. recruitment), which in turn increased production. 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 number of age-0 and age-1 blacknose dace and bluehead chub (both classified as cool-water species). High abundances of younger age classes (i.e. age-0 and age-1) for multiple species, regardless of the thermal regime in the stream, will typically yield high assemblage production estimates (Halyk & Balon, 1983; Lobón-Cerviá et al., 2011; Mathews, 1971; Schlosser, 1982). Therefore,

factors that engender positive recruitment of diverse Appalachian stream fish species may positively affect fish assemblage production.

In addition to high biomass, relatively high P/B ratios were encountered at some of the study sites. The biomass turnover rate for a given community is directly related to growth (Anderson, Darring, & Benke, 1998). For example, northern cold-water streams had a significantly higher mean assemblage P/B (0.91) compared to the more southern cold-water (0.54), cool-water (0.60) and warm-water streams (0.74). Similarly, mean fish assemblage P/B of the northern cold-water sites was in the upper range of published fish assemblage P/B values (Table 3) (Lotrich, 1973; Mann, 1971; Penczak, 1992; Watson & Balon, 1984). Mean assemblage P/B in the southern cold-, cool- and warm-water streams from this study were comparable to previously published assemblage P/B values in studies across similar habitats (Hopkins, 1971; Neves & Pardue, 1983) and lower than some studies in dissimilar habitats, such as neotropical streams in Brazil (Mazzoni & Lobón-Cerviá, 2000). A high or low assemblage P/B is an important observation that carries potential fisheries management implications in terms of conservation of fish biomass and enhanced growth in vulnerable stream ecosystems.

Post hoc tests revealed more separation in evenness across comparisons of production than biomass or abundance. Valentine-Rose et al. (2011) also found rank-production curves had larger differences in community evenness compared to rank-abundance and rank-biomass curves. Combined, these two studies provide compelling evidence that production could provide unique results when comparing differences in fish assemblages along major environmental gradients. For example, using abundance or biomass alone would have yielded different, albeit still useful conclusions regarding the ecology of these

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 northern cold-water 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 six ANCOVA models were significant at the 0.05 alpha level ($p < .0001$).

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 northern cold-water 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	Northern cold-water	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	Northern cold-water	C	A	A
Jenny Coolidge Brook, VT	Northern cold-water	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	Northern cold-water	C	A	A,B
Blizzard Run, WV	Cool	C	A	B
Buffam Brook, MA	Northern cold-water	D	A	B

**The temperature category for the class-level mean comparisons is denoted in the first column.

assemblages. Thus, studies utilising only abundance and biomass as response variables may yield divergent results and conclusions than if fish production is used (Dolbeth et al., 2012). At a minimum, these findings suggest the importance of carefully selecting appropriate biological metrics depending on the research question posed for analysing fish assemblages as disparate results and conclusions may be produced, which could influence important conservation and management strategies (Hayes et al., 2007). For example, climate change management or adaptation strategies based on abundance or biomass, disregarding growth, recruitment and/or production may not fully address fish assemblages' needs. Fish respond to climate change and other stressors via changes in abundance, biomass, growth, recruitment, phenological changes and assemblage dynamics (Lynch

et al., 2016). Understanding potential changes in fish production to anthropogenic and environmental stressors would aid in identifying areas with high or low production potential to focus conservation and management efforts.

4.2 | Assumptions

Empirically based instantaneous growth rate methods are frequently used to evaluate fish production, sometimes with a single sample based on a revised version of the instantaneous growth rate method (Halyk & Balon, 1983; Lobón-Cerviá et al., 2011; Rypel et al., 2015; Valentine-Rose et al., 2007, 2011). The primary assumptions of any study relying on a single sample to estimate production are that

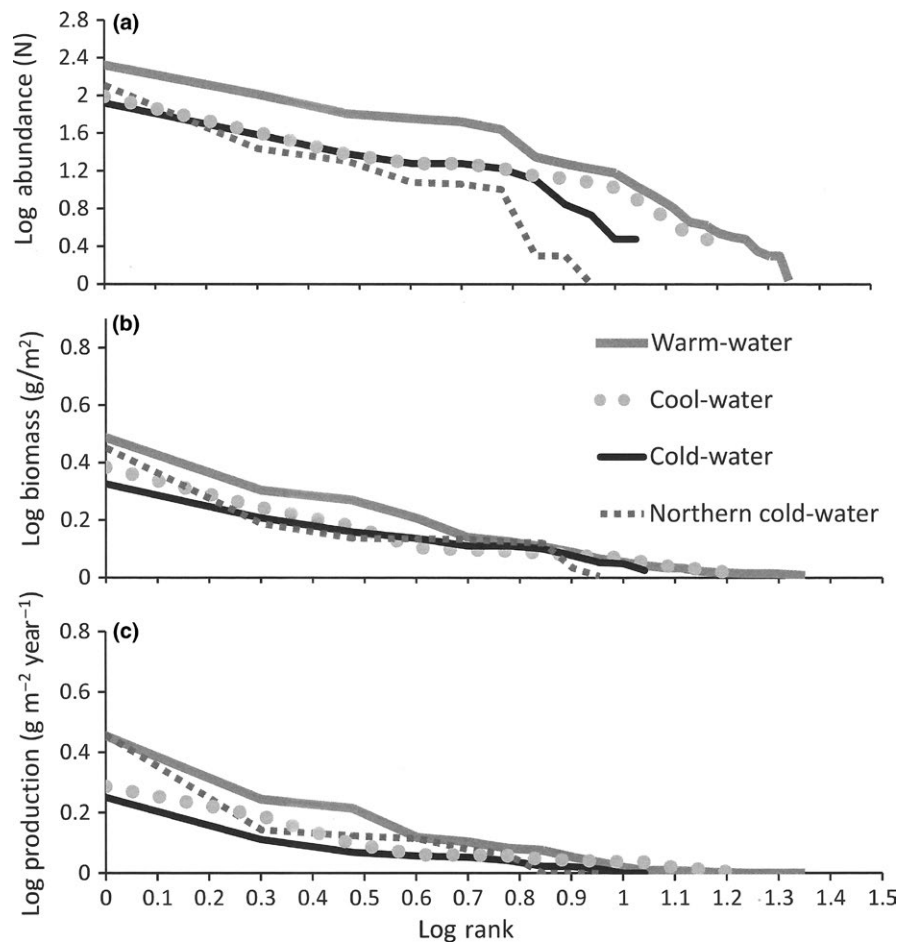


FIGURE 5 Fish assemblage rank-abundance (a), -biomass (b) and -production (c) curves for the northern cold-water streams ($N = 5$), southern cold-water streams ($N = 8$), southern cool-water streams ($N = 10$) and southern warm-water streams ($N = 2$) located across the Appalachian Mountain range

age-specific survival and growth are constant, resulting in a stable population age-structure. Other methods exist to estimate production through time (e.g. instantaneous growth, the increment summation and size-frequency methods) but require frequent re-sampling (Halyk & Balon, 1983). These methods are ultimately impractical for estimating fish assemblage production among multiple watersheds and sites separated by long distances, as in the present study (Benke, 1979; Halyk & Balon, 1983). Finally, the production estimates from this study are useful for relative comparisons among the study streams during this year and provide, in some cases, the first production estimates available in the literature for these streams, which can be used to compare production estimates in future studies. Lastly, temperature classification of the streams was based on the year prior to sampling, and we did not analyse whether this year was typical or atypical in comparison with other years. Thus, this is a snapshot view of temperature and fish assemblage production for a single point in time.

5 | CONCLUSIONS

Unsurprisingly, cold-water species dominated assemblage production in cold-water streams, cool-water species dominated production in cool-water streams, and warm-water species were dominant in warm-water streams. However, differences in mean and maximum summer

temperatures among stream thermal classes were not large. These patterns suggest that only slight changes in temperature could promote large shifts in the allocation of production across fish species. Considering that cool-water streams had a 2°C higher mean summer temperature than cold-water streams, cold-water fish populations in cool-water southern Appalachian streams may currently rest at the edge of their temperature thresholds.

These empirical fish assemblage production estimates across a thermal and latitudinal gradient contribute to current research needs highlighted in the literature calling for increased research on climate change impacts on fish assemblages (Comte, Buisson, Daufresne, & Grenouillet, 2013; Daufresne & Boët, 2007). In addition, this study provides empirical fish assemblage production estimates to inform future research on southern Appalachian stream ecosystems and provides initial numbers to prompt more research to determine the potential impacts of changing temperature regimes or other stressors on cold-water fish production in the Appalachians (Chu et al., 2005; Clark, Rose, Levine, & Hargrove, 2001; Ficke et al., 2007; Sharma, Jackson, Minns, & Shuter, 2007; Staudt et al., 2013).

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TABLE 3 A noncomprehensive list of fish assemblage secondary production estimates ($\text{g m}^{-2} \text{ year}^{-1}$) (ranges) and assemblage fish P/B ratios (ranges) organised by increasing assemblage production from the literature identified as potentially relevant to the present study. 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	Assemblage production ($\text{g m}^{-2} \text{ year}^{-1}$)	Assemblage P/B	References
Eastern Kentucky	3	First-, second-, third-order tributaries	2.35–3.29	0.58–1.06	Lotrich (1973)
Coweeta Creek, North Carolina	3	Third- and fourth-order Appalachian streams	1.35–3.59	**	Freeman et al. (1988)
Speed River, Ontario	3	Sixth-order stream, tributary to Grand River	1.03–3.60	1.24–1.93	Mahon, Balon, and Noakes (1979)
Guy's Run, Virginia	1	Appalachian mountain stream Appalachian mountain	2.86–3.96	0.60–1.60	Neves and Pardue (1983)
Appalachian Streams, Eastern U.S.	25	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)
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 (1984)
South-eastern 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)

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APPENDIX A

Annual production and P/B example calculations for using hypothetical fish data to demonstrate our production calculation methods.

Pred. Age	#age group	Density (no./m ²)	Total weight/age(g)	Mean Weight (g)	Biomass(g/m ²)	Bbar	G	Production (P)
0	275	0.005248763	2115.88	7.69	0.040384528		2.32273431650714	0.3583995
						0.154301		
1	179	0.003416467	14052.77	78.51	0.268216845		0.942687808826817	0.211628906
						0.224495		
2	47	0.000897061	9471.33	201.52	0.180773593		0.577713231869961	0.159125815
						0.275441		
3	54	0.001030666	19391.18	359.10	0.370108075		0.409895679630917	0.132995101
						0.324461		
4	27	0.000515333	14607.97	541.04	0.278813628		0.374621172730638	0.097236758
						0.25956		
5	16	0.000305383	12590.47	786.90	0.240306835		0.215762153818959	0.058091942
						0.269241		
6	16	0.000305383	15622.34	976.40	0.298174457			

Production Calculation Steps:

$$P_{\text{age } 0\text{-age } 1} = G \cdot \bar{B}$$

$$P_{\text{age } 0\text{-age } 1} = ((\text{LN}(\text{mean weight}_{\text{age } 1}) - \text{LN}(\text{mean weight}_{\text{age } 0})) * ((\text{Biomass}_{\text{age } 0} + \text{Biomass}_{\text{age } 1})/2))$$

$$P_{\text{age } 0\text{-age } 1} = ((\text{LN}(78.51) - \text{LN}(7.69)) * ((0.04 + 0.27)/2))$$

$$P_{\text{age } 0\text{-age } 1} = (2.32) * (0.15)$$

$$P_{\text{age } 0\text{-age } 1} = 0.36 \text{ g m}^{-2} \text{ y}^{-1}$$

$$P_{\text{age } 1\text{-age } 2} = G \cdot \bar{B}$$

$$P_{\text{age } 1\text{-age } 2} = ((\text{LN}(\text{mean weight}_{\text{age } 2}) - \text{LN}(\text{mean weight}_{\text{age } 1})) * ((\text{Biomass}_{\text{age } 1} + \text{Biomass}_{\text{age } 2})/2))$$

$$P_{\text{age } 1\text{-age } 2} = ((\text{LN}(201.52) - \text{LN}(78.51)) * ((0.18 + 0.27)/2))$$

$$P_{\text{age } 1\text{-age } 2} = (0.94) * (0.22)$$

$$P_{\text{age } 1\text{-age } 2} = 0.21 \text{ g m}^{-2} \text{ y}^{-1}$$

Population Estimates	Calculation	Value
Total Annual Biomass	Sum of Biomass Values for each age class (0-6)	1.67
Annual Production	Sum of P Values between age classes (last column)	1.02
P/B	=1.02/1.67	0.61

APPENDIX B

Number of individuals (N), biomass (B) (g m⁻²), annual production (P) (g m⁻² year⁻¹), P/B ratio (P/B) and % of total production (%T.P) per species at the 25 northern cold-water (five sites), southern cold-water (eight sites), southern cool-water (10 sites) and southern warm-water (two sites) streams from Vermont to North Carolina.

	Cool Water Stream Sites																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																						
	Roaring Creek				Bethesda Creek				Jerry's Run				Swanoma Creek				Kelso Springs Branch				Tributary to Henry Fork				Blizard Run				Trib. To Little Laurel Creek				West Prong Hickory's Fork				Whitewalk Creek																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																		
	N	B	P	PB	%T.P.	N	B	P	PB	%T.P.	N	B	P	PB	%T.P.	N	B	P	PB	%T.P.	N	B	P	PB	%T.P.	N	B	P	PB	%T.P.	N	B	P	PB	%T.P.	N	B	P	PB	%T.P.																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																															
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