

# Native brook trout and invasive rainbow trout respond differently to seasonal weather variation: Spawning timing matters

Yoichiro Kanno<sup>1</sup>  | Matt A. Kulp<sup>2</sup> | Stephen E. Moore<sup>2\*</sup> | Gary D. Grossman<sup>3</sup> 

<sup>1</sup>Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC, U.S.A.

<sup>2</sup>Great Smoky Mountains National Park, National Park Service, Gatlinburg, TN, U.S.A.

<sup>3</sup>Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, U.S.A.

## Correspondence

Yoichiro Kanno, Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC, U.S.A.  
Email: ykanno@clemson.edu

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## Abstract

1. Salmonids have been introduced globally, and native and invasive salmonids co-exist in many regions. However, their responses to seasonal weather variation and global climate change are poorly known.
2. The aim of this study was to compare effects of inter-annual variation in seasonal weather patterns on native brook trout (BKT) (*Salvelinus fontinalis*) versus invasive rainbow trout (RBT) (*Oncorhynchus mykiss*) abundance using summer electrofishing data (May through September) spanning 28 years in the Great Smoky Mountains National Park, U.S.A. (c. 200 stream sites per species). In particular, we tested if different spawning timing between BKT (autumn) and RBT (late winter) would result in heterogeneous population responses to high seasonal precipitation, which would negatively affect early life stages with impaired swimming ability.
3. As predicted, young-of-the-year (YOY) abundance of autumn-spawning BKT was most strongly impacted by total precipitation between February and March, and RBT YOY abundance was most strongly impacted by peak precipitation between April and May. Despite the presence of these different key seasonal drivers, inter-annual variation in YOY density of these two species was positively correlated because precipitation in April and May also impacted the abundance of BKT YOY.
4. Adult abundance was less responsive to weather variation than YOY abundance, and was most strongly correlated with YOY abundance in the previous year, indicating the importance of flow-driven population control influences on early life stages affecting population sizes into subsequent years. Adult BKT densities were not affected by any weather covariate, whereas adult RBT densities were correlated with four weather covariates in competing models. As a result, there was no correlation in the inter-annual variation in adult density in these two species.
5. The differing responses of BKT and RBT to long-term seasonal weather patterns suggest that they will likely respond differently to global climate change. In particular, winter precipitation will likely be the key environmental driver of differences in their population responses.

## KEYWORDS

climate change, early life stage, invasive species, recruitment, stream flow

\*Supervisory Fishery Biologist, retired.

## 1 | INTRODUCTION

Global climate change (GCC) will produce varying responses in aquatic species because species respond differently to the same environmental drivers (Buisson & Grenouillet, 2009; Chessman, 2013; Lyons, Stewart, & Mitro, 2010). Stream temperature and flow patterns are important factors that will change with GCC (Arismendi, Safeeq, Johnson, Dunham, & Haggerty, 2013; Kaushal et al., 2010; Wenger et al., 2011), and altered thermal and flow regimes will affect population dynamics and assemblage structure of stream fishes (Grossman, Moyle, & Whitaker, 1982; Piffady, Souchon, Capra, & Parent, 2010; Wenger et al., 2011). Nonetheless, our ability to predict how species and assemblages will respond to GCC is limited by a lack of long-term data at the local and regional scales and a lack of mechanistic understanding of climatic processes affecting biota. In addition, predicting GCC effects on stream fish assemblages and populations are complicated because native and invasive species may respond differently to climate variation.

Salmonids, a group of coldwater fishes, are prized as sport fishes and likely to be affected by GCC. Members of this family have been introduced world-wide for increased angling opportunities (Gozlan, Britton, Cowx, & Copp, 2010), and invasive salmonids often negatively affect native salmonids (Baxter, Fausch, Murakami, & Chapman, 2007; Fausch, 1988). In North America, for example introduced rainbow trout (RBT; *Oncorhynchus mykiss*) have displaced many populations of native brook trout (BKT; *Salvelinus fontinalis*) in the east, whereas the latter species is an invader in the west with strong negative consequences for native cutthroat trout (*Oncorhynchus clarkii*) (Fausch, 2008). In both cases, the invaders occupy stream habitat downstream, whereas the natives occur upstream, sometimes only above physical barriers that block upstream immigration by invaders (Fausch, Rieman, Dunham, Young, & Peterson, 2009; Moore, Larson, & Ridley, 1986). Given these patterns, the management of invasive salmonids is necessarily an important aspect of native salmonid conservation. Consequently, quantifying the responses of native and invasive salmonids to GCC is essential for scientific management of native trout and prediction of how these species will respond to environmental change (Clark, Rose, Levine, & Hargrove, 2001; Eaton & Scheller, 1996; Lyons et al., 2010).

Projecting salmonid responses to GCC has focused on their upper thermal limits and potential increase in stream temperature during summer (Eaton & Scheller, 1996; Lyons et al., 2010; Wenger et al., 2013). This is a reasonable approach for coldwater species, but recent studies show that thermal and flow patterns during other seasons also affect stream salmonid populations and impacts differ by life stage (Kanno et al., 2015; Letcher et al., 2015). Aside from summer stream temperature effects, a consistent and strong pattern reported is negative impacts of high stream flows on young-of-the-year (YOY) abundance (Kovach et al., 2016). Salmonids deposit their eggs in gravel ("redds"), and eggs and fry are susceptible to high flow events via scouring mortality (Carline & McCullough, 2003; Jensen & Johnsen, 1999; Lobon-Cervia, 2004). If high flows indeed affect the strength of the YOY abundance, differences in timing of spawning among native and

invasive species may provide an environmental origin of differential responses to GCC. For example members of the genus *Oncorhynchus* are late winter/spring spawners, whereas members of the *Salvelinus* spawn in autumn and early winter (Fausch, 2008). Thus, high flows in late spring would affect the former more strongly, whereas winter high flows would affect the latter more negatively, potentially leading to an asynchronous pattern of inter-annual variation in abundance between two species. We posited that this flow-driven mechanism (i.e. abiotic control) would be probable because recruitment to the YOY stage is a key driver of population dynamics in stream fishes with a short life span such as headwater salmonids (Vélez-Espino, Fox, & McLaughlin, 2006), and local adult abundance (i.e. biotic control) in stream salmonids is not always a reliable predictor of YOY abundance in the following year (Kanno et al., 2015; Lobon-Cervia, 2014). Indeed, positive stock–recruitment relationships (i.e. relationships between current adult abundance and YOY abundance in the subsequent year) have been documented in some stream salmonid populations (Grossman, Ratajczak, Wagner, & Petty, 2010; Huntsman & Petty, 2014), but not in others (Kanno et al., 2016; Milner et al., 2003).

In this paper, we examined the effects of seasonal precipitation and air temperature (i.e. surrogates for stream flow and temperature) on summer density estimates of YOY and adult native BKT and invasive RBT in the Great Smoky Mountains National Park (GRSM), U.S.A. Our data set is unusual because of its extensive spatial (the entire GRSM: 2,047 km<sup>2</sup>) and temporal (28 years) coverage of trout sampling data. We tested three hypotheses. First, spawning periods differ and periods of early life-history stages only partially overlap between BKT (autumn–spring) and RBT (late winter–spring). Because timing of high stream flow events can dictate success of early life-history stages, we hypothesised that YOY abundance of the two species would not covary among years and this pattern would also result in weak temporal covariance of adult abundance. Our second hypothesis was that variation in precipitation during those egg incubation and fry rearing periods would affect YOY abundance of both species more strongly than other seasonal weather covariates and stock size (adult abundance) in the previous year. We considered that precipitation would be more important than air temperature in affecting YOY abundance because stream temperature does not approach trout's upper thermal limits from autumn to spring, and stock–recruitment relationships can vary greatly among sites in stream salmonids (Grossman et al., 2010; Kanno et al., 2016; Milner et al., 2003). Finally, we hypothesised that high precipitation during egg and fry development would affect YOY abundance more strongly than adult abundance because adult fish have stronger swimming abilities and are capable of coping with higher stream discharge. Adult abundance would then be less sensitive to weather variation in these seasons.

## 2 | METHODS

### 2.1 | Study area

The Great Smoky Mountains National Park is located in eastern Tennessee and western North Carolina. It was established in 1934 and

currently encompasses 2,047 km<sup>2</sup> of southern Appalachian hardwood forests (Van Miegroet, Moore, Tewksbury, & Nicholas, 2007) and 4,640 km of 1st to 5th order streams. The dominant vegetation types in the GRSM include montane oak-hickory (31%), high-elevation hardwood (17%), yellow pine species (16%), cove hardwood (12%) and spruce-fir forest (8%) (Jenkins, 2007; Whittaker, 1956). Park watersheds are sensitive to acidic deposition due to high-elevation topographic features coupled with highly weathered, unglaciated, base-poor soils, shallow hydrological flowpaths and mature forests (Cai, Johnson, Schwartz, Moore, & Kulp, 2012; Johnson & Lindberg, 1992; Neff, Schwartz, Moore, & Kulp, 2013; Robinson et al., 2008). Atmospheric sulphur and nitrogen depositions have resulted in acidification of the soil and the stream water in GRSM (Cook et al., 1994; Deyton et al., 2009; Nodvin, Van Miegroet, Lindberg, Nicholas, & Johnson, 1995). Base stream flow pH values typically range from <5.0 to 6.5 throughout much of GRSM and specific conductivity is typically <30 µS/cm (Robinson et al., 2008). Streams in GRSM are considered extremely unproductive compared to other trout streams (Kulp & Moore, 2005), given the geographical location, poor buffering capacity of underlying geology, relatively high rainfall (roughly 100–254 cm/year) and some of the highest acid deposition rates in North America (Cai, Johnson, Schwartz, Moore, & Kulp, 2011; Powers, 1929; Silsbee & Larson, 1982).

Brook trout are the only salmonid native to the Southern Appalachian region and were once widely distributed in streams at elevations higher than 400 m throughout GRSM (King, 1938). Brown trout (*Salmo trutta*: Salmonidae) and RBT were introduced in area streams soon after 1900 for recreational angling and the latter has established many populations in GRSM (King, 1938). Habitat degradation and the introduction of RBT have been attributed to extirpation of BKT populations in approximately 75% of the historical range within GRSM (Larson & Moore, 1985). Due to historical stocking effort (1935–75), current BKT populations in GRSM are represented by pure southern populations with no hatchery introgression, with a limited number of populations with some hatchery stock introgression (Kulp & Moore, 2005). In GRSM, BKT spawn in autumn, whereas RBT spawn in late winter. YOY fish of both species reach similar body size by mid-summer, indicating that body growth is slower in BKT than in RBT.

This study is based on streams that have been surveyed as part of the ongoing GRSM long-term monitoring programme. Subsets of sites differed among analyses (see below), but a total of 214 sites in 59 BKT streams and 191 sites in 62 RBT streams were used. Study streams varied with respect to accessibility ranging from within 100 m to >4 km from a trailhead or road. BKT typically occupy headwater streams and RBT downstream in the GRSM (Table 1). For example median stream width was 4.6 m and stream discharge was 0.08 m<sup>3</sup>/s among BKT sites, whereas RBT sites were wider (median = 6.3 m) and had a higher median discharge (0.15 m<sup>3</sup>/s) (Table 1). BKT sites tended to be steeper than RBT sites (median stream gradient: 7.9% versus 6.4%) (Table 1). Substrate consisted of cobble, gravel and boulders, with smaller amounts of sand, silt and bedrock in some pools.

**TABLE 1** Median values (95th quantile range) of chemical and physical characteristics of brook and rainbow trout monitoring sites sampled between 1993 and 2015 within Great Smoky Mountains National Park. Measurements were taken at the time of electrofishing surveys during summer (June–August)

	Brook trout	Rainbow trout
Number of sites	214	191
Stream order	2 (1–4)	3 (2–5)
Specific conductivity (µS/cm)	14.2 (7.8–27.6)	14.5 (7.9–45.4)
Water temperature (°C)	15.0 (11.7–18.0)	15.2 (12.0–19.1)
Discharge (m <sup>3</sup> /s)	0.08 (0.01–0.50)	0.15 (0.02–1.21)
Width (m)	4.6 (3.0–9.8)	6.3 (3.3–18.3)
Stream gradient (%)	7.9 (2.8–16.0)	6.4 (1.3–13.2)

## 2.2 | Sampling

Study sites were 100 m in length and were sampled between May and September 1987–2014 using backpack electrofishing units (Habera, Strange, Carter, & Moore, 1996). Annual samples from streams were typically collected during the same period (within a 2–3 weeks time window) from year to year to minimise sampling bias, and among-month variability in trout density was low relative to spatial and among-year variability (see Section 3). Fish population size was inferred with the three-pass depletion technique using block nets to account for variation in sampling efficiency among surveys (Trout Committee SDAFS, 1992). Fishes collected in each pass were held in holding cages outside of the sampling area until all sampling was completed. We let 30 min elapse between passes to ensure that assumptions of the depletion estimator were met (Trout Committee SDAFS, 1992). Total length (mm) and mass (g) were measured for each fish. Abundance was estimated using Microfish 3.0, which utilises the Burnham maximum-likelihood estimate model (van Deventer & Platts, 1989). This method estimates capture probabilities of individuals during each survey and corrects abundance accordingly. Sampling efficiency is high and consistent in our sampling. Habera, Kulp, Moore, and Henry (2010) reported from a subset of our study streams that first-pass capture efficiency was 0.74 for adult RBT (95% CI: 0.69–0.79) and 0.46 for YOY (95% CI: 0.37–0.55), indicating that 98% of adult individuals and 84% of YOY individuals, on average, were captured after three electrofishing passes. Density (number fish per 100 m<sup>2</sup>) of YOY and adults was inferred by dividing the population size estimate by the area (mean wetted stream width [m] × total site length) and multiplying by 100. Length frequency histograms were plotted for each survey and gaps in distributions were used to separate YOY from adults (Figure S1). This visual technique is commonly used to identify the two life stages in BKT (Kanno et al., 2015; Letcher et al., 2015).

## 2.3 | Weather data

We characterised seasonal weather conditions at each site using Daymet (Thornton et al., 2016), which estimates daily air

temperature and precipitation at the 1 km<sup>2</sup> scale. Daily air temperature values are predicted in Daymet with a mean absolute error of c. 1°C and daily precipitation occurrence is predicted with 83% accuracy (Thornton, Running, & White, 1997). We used Daymet for environmental data due to lack of stream temperature and flow data at the extensive spatial scale of this study. We defined three time periods (hereafter “seasons”) based on the timing of key early life-history stages that could have been affected by variation in weather patterns. Peak spawning of BKT occurs in October and spawning has been documented as early as September in GRSM (M. Kulp, unpublished data). The October–January (“Oct–Jan”) period thus covers BKT spawning, egg incubation and hatching. BKT fry are present during the February–March (“Feb–Mar”) period and it corresponds with RBT spawning and egg incubation period in GRSM. YOY individuals of both species (<50 mm TL) are present during the April–May (“Apr–May”) period. We did not characterise weather conditions during the May–September period because this coincided with fish collections, and our analyses dealt with variation in flow and temperature prior to fish sampling. In addition, the focus of our paper was to examine the effect of weather variation during seasons that affect spawning and egg/fry development.

We estimated total seasonal precipitation for each site using Daymet (hereafter “total precipitation”), whereas peak precipitation for each season was defined as the highest value of consecutive 3-day total precipitation measurements (Table S1). Previous research has shown that high flow events during egg incubation and fry rearing periods were related to low YOY abundance in stream salmonids (Jensen & Johnsen, 1999; Roghair, Dolloff, & Underwood, 2002). Both total and peak precipitation were characterised because the negative impacts of high flow on early life stages could be linear or nonlinear (e.g. a threshold above which gravel scouring occurs). Thus, peak precipitation was considered to represent low-frequency, but high-magnitude flow events. Total and peak precipitation in each season were moderately to highly correlated (Pearson's  $r = .53$ – $.72$ ). Thus, only one precipitation covariate was used in statistical analysis (see “Section 2.4” below). Stream flow correlates strongly with precipitation in GRSM. We compared Daymet precipitation and USGS streamflow gage data at a study site in Cataloochee River, which was the only site with long-term streamflow gage data in the study area (Figure S2). Precipitation and streamflow were highly correlated with each other in all seasons (Pearson  $r = .64$ – $.82$ ).

Seasonal mean temperature was calculated as the arithmetic mean of daily mean temperature for each season and site (Table S1). We did not include peak temperatures because they never reached values that would produce negative physiological effects in BKT or RBT during the three seasons defined above (i.e. “Oct–Jan,” “Feb–Mar” and “Apr–May”). In addition, mean and peak temperature were moderately to highly correlated with each other (Pearson's  $r = .33$ – $.70$ ). Seasonal mean temperature was not correlated with total or peak precipitation in any season (Pearson's  $|r| \leq .36$ ). Unlike precipitation, a long-term stream temperature data set was not available at any of the study sites to validate correlation between stream and air temperature. Responses of stream temperature to increased

air temperature can vary by site due to the influence of ground water (Kanno, Vokoun, & Letcher, 2014a; Snyder, Hitt, & Young, 2015). Although the rate of change in stream temperature can differ among sites, inter-annual variation in air temperature should still be a key driver of stream temperature variation because heat exchange with air is the major mechanism affecting stream temperature (Mohseni & Stefan, 1999; Morrill, Bales, & Conklin, 2005).

## 2.4 | Statistical analysis

### 2.4.1 | Inter-annual synchrony in density between species

We quantified inter-annual synchrony in YOY and adult densities between BKT and RBT using linear mixed-effects models and the *lmer* function in package “lme4” (Bates, Maechler, Bolker, & Walker, 2015) in Program R (R Core Team, 2015). Models were constructed to quantify spatial and temporal variation in both response variables, i.e. YOY and adult density. We considered survey year and month to be random effects representing temporal variation, and our primary interest was to quantify inter-annual variation in density averaged across study sites. Because sites were nested within streams, we also treated both among- and within- stream differences as random effects. A total of 1,052 samples were available at 214 sites in 59 streams between 1987 and 2014 for BKT, and a total of 819 samples were available at 191 sites in 62 streams for RBT. Correlation in year random effects between BKT and RBT was examined for each life stage using Pearson's  $r$ . All analyses employed an alpha of .05 for statistical significance.

### 2.4.2 | Seasonal weather effects on density

We examined relationships between summer trout density, and temperature and precipitation in seasons prior to sampling by including seasonal covariates in the mixed-effects models described above. We evaluated competing models using an information theoretic approach. The density of each life stage (YOY or adult) was modelled using the same random-effects structure (i.e. years, months, streams and sites nested within streams). In addition, we included air temperature and precipitation in the Oct–Jan, Feb–Mar and Apr–May periods, as well as density of the other life stage in a previous year, as fixed-effects predictors. Our primary focus of this paper was to examine the effects of seasonal weather variation on abundance, but spawning adult density can affect YOY density in the following year (i.e. stock–recruitment relationships: Grossman et al., 2006, 2010; Huntsman & Petty, 2014), and alternatively adult density can be positively related to YOY density in the previous year (Kanno et al., 2016). Accordingly, our analysis was based on data from consecutive years. A total of 592 samples collected between 1988 and 2014 were available from 48 sites nested within 19 streams for BKT, and 376 samples from 45 sites in 21 streams for RBT. Weather and density predictors were modelled as fixed effects because we were interested in understanding the overall effects of the predictors averaged across sites. In this analysis, sites with a greater number of



samples made a greater contribution to the overall effect than those with a smaller number of annual samples. Predictor variables were standardised to have a site-specific mean of zero and a standard deviation of one (Table S1).

We developed a set of candidate models using a top-down approach informed by values of Akaike's Information Criteria corrected (AICc) for small sample size. We began with saturated models that included temperature and precipitation during the Oct–Jan, Feb–Mar and Apr–May periods, and density of the non-response life-history stage. Because total and peak precipitation were moderately to highly correlated in all three seasons (see above), two saturated models were developed with one model containing mean temperature and total precipitation during the three seasons and the other containing mean temperature and peak precipitation. We compared effect sizes (i.e. regression coefficients) between total and peak precipitation, and an additional saturated model was developed by selecting the one with a larger effect size for each season. From this model, we sequentially removed the least significant predictor based on the effect size until a new model did not decrease in the AICc value.

Effect size of predictor variables on trout density was inferred by accounting for model uncertainties. An Akaike weight (i.e.  $w_i$  value) of each model was calculated based on  $\Delta\text{AICc}$  value, which was the difference in AICc values between the top-ranked model and the model of interest. We interpreted models with  $w_i$  values that were  $\geq 10\%$  of the value of the top-ranked model (Burnham & Anderson, 2002; Grossman, Nuhfer, Zorn, Sundin, & Alexander, 2012). Akaike weights then were used to evaluate the relative support of competing models to infer effect size of predictor variables. We simulated 1,000 sets of regression coefficients to account for correlation among predictor variables, in which the number of sets was proportional to the Akaike weight of a model (Wenger et al., 2013). For example if there are two models under consideration with Akaike weights of 0.7 and 0.3, then 700 draws of regression coefficients derived from the better supported model and 300 draws came from the less supported model. These sets of regression coefficients were used to quantify trout density responses (mean and 95% confidence interval) in relation to the observed range of each seasonal weather covariate retained in the top-ranked model.

### 2.4.3 | Stock–recruitment and recruitment–stock relationships

We tested for the presence of stock–recruitment relationships by examining the effect of YOY density on adult density in the following year, and the effect of adult density on YOY density in the following year for BKT and RBT. This analysis was based on 45 sites in BKT and 31 sites in RBT, for which at least 6 consecutive-year surveys were available. Density was log-transformed prior to analysis and density of one life stage at year  $t$  was plotted against that of the other life stage at year  $t + 1$ . A simple linear regression was fit for each site and we counted the number of sites with positive and negative relationships.

## 3 | RESULTS

### 3.1 | Inter-annual synchrony in density between species

Contrary to our prediction of asynchrony in inter-annual abundance between BKT and RBT due to different spawning periods, annual densities (i.e. year effects) of YOY were positively correlated between the two species (Pearson's  $r = .78$ ,  $p < .001$ ,  $df = 26$ ) (Figure 1). In other words, years of abundant summer YOY individuals of BKT were typically years in which YOY abundance was also high in RBT. However, annual densities of BKT and RBT adults were not significantly correlated (Pearson's  $r = -.28$ ,  $p = .143$ ,  $df = 26$ ) (Figure 1), indicating that demographic processes and environmental responses of the two species differ after the YOY life stage.

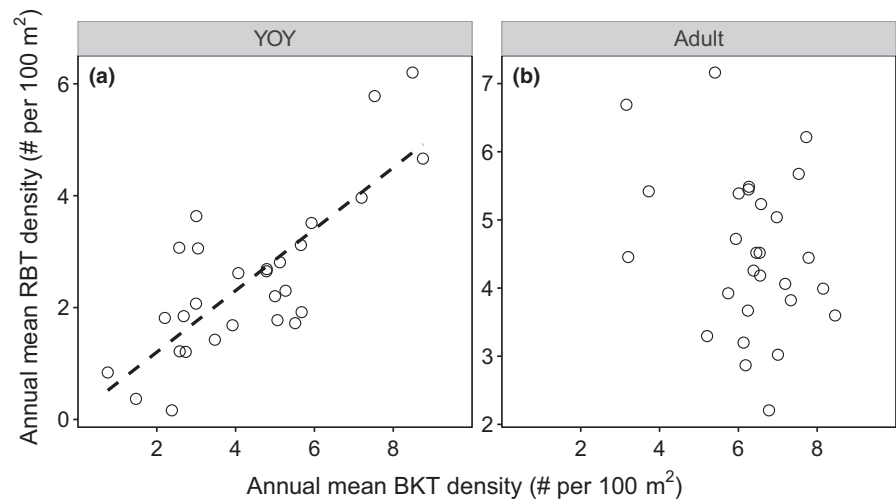
Densities of both BKT and RBT varied most among streams, except among-year variation was the largest source of variation for RBT YOY density (Table 2). Among-stream variance was greater than within-stream variance for both YOY and adult densities of both species. Among-month variance typically was low relative to other sources of variance, suggesting our use of data collected between May and September had little effect on results (Table 2).

### 3.2 | Seasonal weather effects

The mixed-effects analyses identified three interpretable models for BKT YOY and four interpretable models for BKT adult (Table 3). The Akaike weights for the best fitting model were similar for YOY (0.53) and adult (0.49) in BKT. Precipitation had the strongest impacts on YOY abundance, and adult density had a positive effect in all three interpretable models (Tables 3 & S2, Figure 2). As we predicted, total precipitation in the Feb–Mar period (i.e. fry development period for BKT) had the strongest effect on BKT YOY density in the top-ranked model (effect size =  $-2.15$ ,  $p < .001$ ) (Table 4, Figure 2). High precipitation values during this season resulted in the 95% CI for predicted BKT YOY density overlapping zero, indicating that high flow during fry development led to major declines in YOY density (Figure 2). BKT YOY density also was negatively affected by Apr–May total precipitation (effect =  $-1.48$ ,  $p = .001$ ) and Oct–Jan mean temperature (effect =  $-0.82$ ,  $p = .04$ ), and positively by Feb–Mar mean temperature (effect =  $0.74$ ,  $p = .08$ ) in the top-ranked model (Figure 2, Table 4). Adult density in the preceding year had a positive effect on BKT YOY density (Tables 3 & S2), indicating the existence of a positive stock–recruitment relationship (see below). Results for adult BKT density were less complex, and the best fitting model only contained a positive effect of YOY density (effect =  $2.37$ ,  $p < .001$ , Tables 4 & S3). The three remaining interpretable models contained negative effects of Oct–Jan temperature, a positive effect of Feb–Mar temperature, and positive effects of Oct–Jan peak precipitation (Tables 3 & S3). As we predicted, adult density was less responsive than YOY density to seasonal weather variation in BKT.

In RBT, YOY and adults had four and three interpretable models respectively (Table 3, Figures 3–4). As we predicted, RBT YOY

**FIGURE 1** Annual synchrony in (a) young-of-the-year (YOY) and (b) adult density (# fish per 100 m<sup>2</sup>) between brook trout (BKT) and rainbow trout (RBT). Values indicate annual mean densities (i.e. year effect) in linear mixed-effects models. Dotted line is based on least squares regression in YOY ( $r = .78$ ,  $p < .001$ ), but there was no statistically significant relationship in adult ( $r = -.28$ ,  $p = .143$ )



**TABLE 2** Variance of random effects for density of each life-history stage of brook trout and rainbow based on linear mixed-effects models without any covariate. YOY, young-of-the-year

Random effects	Brook trout		Rainbow trout	
	YOY	Adult	YOY	Adult
Among streams	8.88	27.27	1.72	4.32
Among sites within streams	2.61	7.87	1.41	1.46
Among years	4.77	2.15	3.06	1.93
Among months	0.34	0.67	1.44	0.03
Residual	18.26	15.20	7.29	6.71

density was negatively affected by Apr–May peak precipitation (i.e. fry development period), and it was the only predictor in the top-ranked model (effect =  $-0.88$ ,  $p = .005$ ; Tables 4 & S4, Figure 3). Similar to BKT YOY, the density of RBT YOY was severely diminished when Apr–May peak precipitation was high (Figure 3). As with BKT, environmental variables displayed differential effects depending on the season, and Apr–May peak precipitation had a negative effect on YOY density, whereas Feb–Mar total precipitation had a positive impact (Tables 3 & 4). As predicted and similar to BKT, abundance of adult RBT was most strongly affected by YOY density in the previous year (Tables 3 & 4). However, adult RBT was also positively influenced by peak precipitation in Oct–Jan (effect =  $0.68$ ;  $p < .001$ ) and Feb–Mar (effect =  $0.58$ ,  $p = .004$ ) in the top-ranked model (Table 4, Figure 4), and negatively affected by Apr–May peak precipitation and temperature in competing models (Tables 3 & S5).

### 3.2.1 | Stock–recruitment and recruitment–stock relationships

Positive stock–recruitment relationships were more common in BKT than RBT (Figure 5). Stock–recruitment curves were positive at approximately half of BKT sites (25 out of 45 sites), but RBT displayed positive responses at only 10 of 31 sites. In contrast, the density of YOY was a reliable predictor of adult density in the following year for both BKT and RBT (Figure 6). The relationship was

positive at 41 out of 45 BKT sites, and at 28 out of 31 RBT sites, suggesting that strengths of the YOY year class translate into subsequent years.

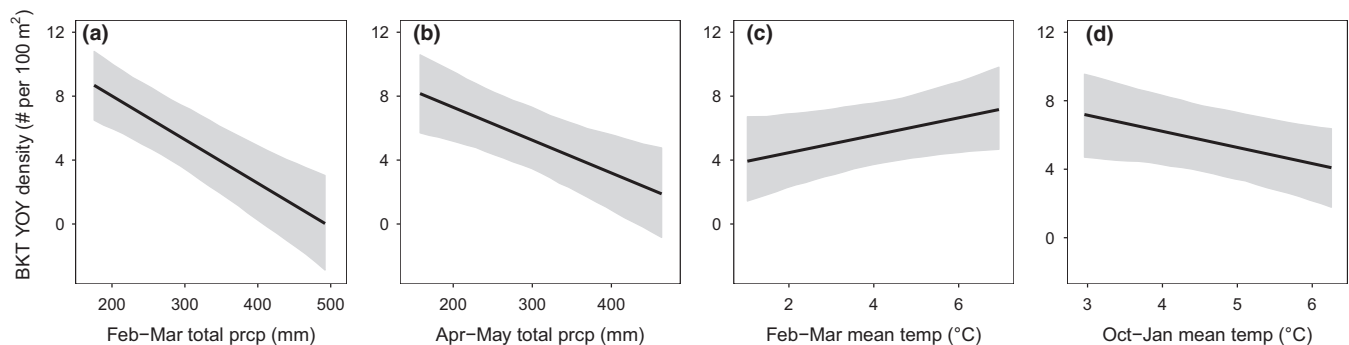
## 4 | DISCUSSION

Results provided support for two of our three hypotheses, but not for the first hypothesis. As predicted, winter precipitation (February–March for BKT) and spring precipitation (April–May for RBT) were the strongest drivers of summer YOY density, which confirmed negative effects of high stream flow on early life stages through stress or mortality associated with bed scouring flow events (hypothesis 2). Similarly, high precipitation affected YOY density negatively, but not adult density, to reflect adults' stronger abilities to withstand high stream flow (hypothesis 3). However, inter-annual variation in YOY density of the two species was correlated, contrary to our first hypothesis that differences in spawning timing would lead to asynchrony in temporal YOY density patterns between the two species. Our first prediction did not hold true despite the finding that YOY density was best predicted by high precipitation during early life stages that differed between BKT (February–March) and RBT (April–May). We reason that lack of support for the first prediction was because YOY abundance of BKT was also strongly affected by April–May total precipitation. Thus, high precipitation in April and May negatively affected both species, which was responsible for covariance in YOY density between the two species. Although BKT spawn in autumn and earlier than RBT, body size of YOY BKT in April and May is still not large enough (<50 mm total length) to be effectively sampled by electrofishing. Thus, it is plausible that high stream flow during these months can negatively affect survival of YOY individuals of both species.

Native BKT and invasive RBT showed similar and different population responses to seasonal climate variation. YOY abundance was driven by precipitation patterns after fry emergence, similar to previous studies of stream salmonids (Cattaneo, Huguency, & Lamouroux, 2003; Fausch, Taniguchi, Nakano, Grossman, & Townsend, 2001;

**TABLE 3** Candidate models (Akaike weight  $\geq 10\%$  of the top-ranked model) for each life stage of brook trout and rainbow trout. Seasons are October–January (OctJan), February–March (FebMar) and April–May (AprMay). Capital letter “T” refers to temperature and “P” refers to precipitation. Precipitation includes either total or peak value in each model. Adult density (“ADTDens”) and YOY density (“YOYDens”) are also included. Positive (+) and negative (–) signs in parentheses indicate direction of regression coefficients. YOY, young-of-the-year; BKT, brook trout; RBT, rainbow trout; AICc, Akaike’s Information Criteria corrected

	Candidate model	AICc	$\Delta$ AICc	Akaike weight
BKT YOY	OctJanT(–), FebMarT(+), FebMarTotalP(–), AprMayTotalP(–), ADTDens(+)	3,598.25	0.00	0.53
	OctJanT(–), FebMarT(+), AprMayT(–), FebMarTotalP(–), AprMayTotalP(–), ADTDens(+)	3,599.46	1.21	0.29
	OctJanT(–), FebMarT(+), AprMayT(–), OctJanTotalP(+), FebMarTotalP(–), AprMayTotalP(–), ADTDens(+)	3,600.41	2.15	0.18
BKT Adult	YOYDens(+)	3,407.10	0.00	0.49
	OctJanT(–), YOYDens(+)	3,408.01	0.91	0.31
	OctJanT(–), OctJanPeakP(+), YOYDens(+)	3,410.05	2.95	0.11
	OctJanT(–), FebMarT(+), OctJanPeakP(+), YOYDens(+)	3,411.21	4.11	0.06
RBT YOY	AprMayPeakP(–)	1,959.23	0.00	0.43
	FebMarTotalP(+), AprMayPeakP(–)	1,960.22	0.99	0.26
	OctJanT(+), FebMarTotalP(+), AprMayPeakP(–)	1,960.64	1.41	0.21
	OctJanT(+), AprMayT(+), FebMarTotalP(+), AprMayPeakP(–)	1,962.85	3.62	0.07
RBT Adult	OctJanPeakP(+), FebMarPeakP(+), YOYDens(+)	1,730.33	0.00	0.46
	AprMayT(–), OctJanPeakP(+), FebMarPeakP(+), YOYDens(+)	1,730.54	0.21	0.41
	AprMayT(–), OctJanPeakP(+), FebMarPeakP(+), AprMayPeakP(–), YOYDens(+)	1,733.43	3.09	0.10



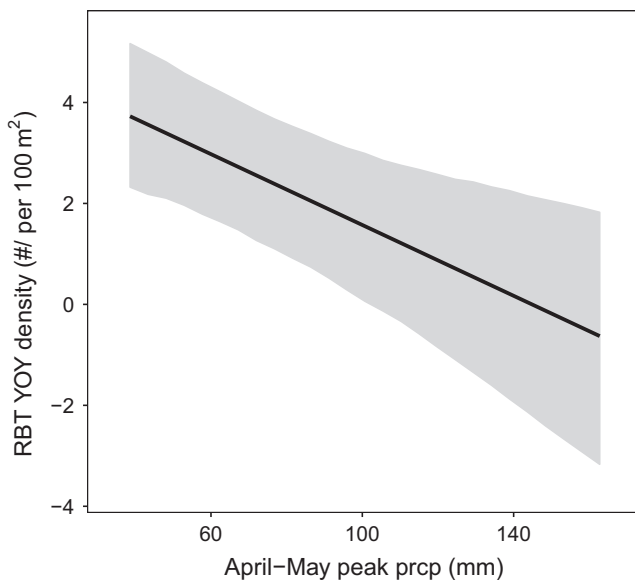
**FIGURE 2** Model-averaged effects of seasonal weather covariates retained in the top-ranked model for brook trout young-of-the-year (YOY) density (# fish per 100 m<sup>2</sup>): (a) total precipitation in February and March (mm), (b) total precipitation in April and May (mm), (c) mean air temperature in February and March (°C) and (d) mean air temperature between October and January (°C). Mean responses are shown in black lines and 95% confidence intervals are shown in grey shade. The observed range of each covariate is shown and represents annual mean values averaged across sites (Table S1)

Zorn & Nuhfer, 2007a). The strength of the YOY year class was a good predictor of adult abundance in both species. In addition, seasonal weather variation affected YOY abundance more strongly than adult abundance in both species. These findings suggest a flow-driven mechanism of trout population control that acts during the early life stages and translates into subsequent stages. However, BKT and RBT differed in the timing of high precipitation events to which each species is most susceptible, and adult RBT abundance was more responsive to seasonal weather variation than adult BKT abundance (Table 3). Accordingly, year-to-year adult density did not co-vary between the two species, despite the presence of covariance in YOY density.

Different population responses to seasonal weather variation between BKT and RBT suggest that GCC will affect native and invasive trout differently in the southern United States and possibly elsewhere. Based on our findings, it is reasonable to suggest that spring high flow would affect both species negatively, but winter (February–March) high flow would be the key environmental factor affecting population responses between BKT and RBT. Years with wet winter would affect BKT negatively via their negative effects on early life stages, but RBT would not spawn until late winter and high winter flow would not negatively affect early life stages of RBT. In fact, the February–March precipitation positively affected RBT YOY density. Increased stream flow in this season may have provided

**TABLE 4** Effect size (regression coefficient) of fixed-effects predictors retained in the top-ranked mixed-effects model for each life-history stage of brook and rainbow trout. Seasons are October–January (OctJan), February–March (FebMar) and April–May (AprMay). Precipitation is either total or peak value. Effect size of competing models is reported in online Supporting Information appendices (Tables S2–S5). YOY, young-of-the-year

Species	Life stage (response)	Predictor	Coefficient	t	p
Brook trout	YOY	OctJanTemp	−0.82	−2.15	.040
		FebMarTemp	0.74	1.85	.079
		FebMarTotalPrpc	−2.15	−5.18	<.001
		AprMayTotalPrpc	−1.48	−3.76	.001
		Adult density	0.91	2.43	.015
	Adults	YOY density	2.37	10.07	<.001
Rainbow trout	YOY	AprMayPeakPrpc	−0.88	−2.99	.005
	Adult	OctJanPeakPrpc	0.68	3.55	<.001
		FebMarPeakPrpc	0.58	3.16	.004
		YOY density	1.04	7.80	<.001



**FIGURE 3** A model-averaged effect of April–May peak precipitation (the highest value of consecutive 3-day total precipitation during the period in mm) on rainbow trout young-of-the-year (YOY) density (# fish per 100 m<sup>2</sup>). The top-ranked model for rainbow trout YOY density included only April–May peak precipitation. Mean responses is shown in black line and 95% confidence interval is shown in grey shade. The observed range of the April–May peak precipitation is shown and represents annual mean values averaged across sites (Table S1)

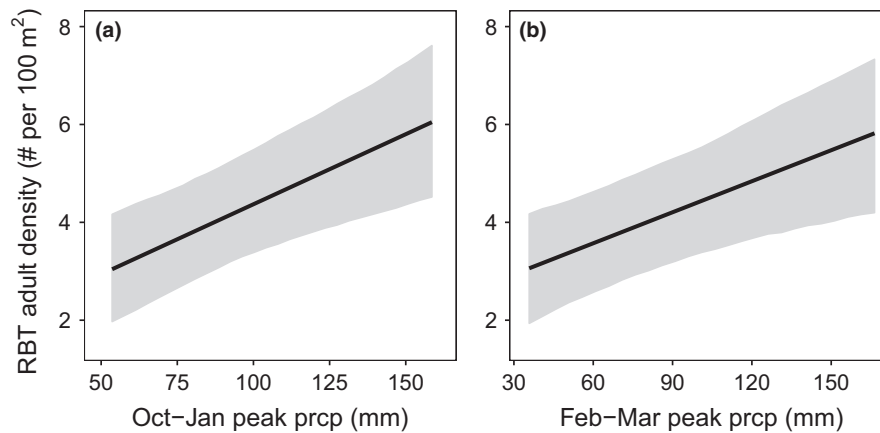
better access to spawning areas for RBT, similar to a finding by Kanno, Letcher, Coombs, Nislow, and Whiteley (2014b) of the importance of increased early autumn flow for BKT spawning access. Precipitation is projected to increase in all seasons except summer and extreme flow events (e.g. floods) are expected to increase in frequency and magnitude under GCC in the study area (Ingram, Dow, Carter, & Anderson, 2013). Flow-driven control of trout populations will thus become more important under such climate conditions. For the Southern Appalachian Region, there is increasing evidence that variation in precipitation (Angert et al., 2005; Groisman et al., 2004; Laseter, Ford, Vose, & Swift, 2012), stream flow (Grossman, Sundin, & Ratajczak, 2016) and air temperatures is increasing (Ford, Laseter,

Swank, & Vose, 2011), as are mean air temperatures (Ford et al., 2011). We also found that adult abundance of RBT is more responsive to seasonal weather variation than BKT adults. We cannot offer mechanistic reasons for the differences between two species, but they differ in thermal and preferences. BKT prefer colder water temperatures than RBT (Eaton et al., 1995). Adult BKT preferentially occupy pools (Anglin & Grossman, 2013) and adult RBT prefer riffles and runs (Baltz, Vondracek, Brown, & Moyle, 1991; Grossman & Ratajczak, 1998). These ecological differences could also interact with GCC to produce varying population responses between native and invasive species. More research is warranted to understand if and how native and invasive aquatic species respond to GCC at broad spatial scales like this study, as well as local spatial scales especially in areas of sympatry.

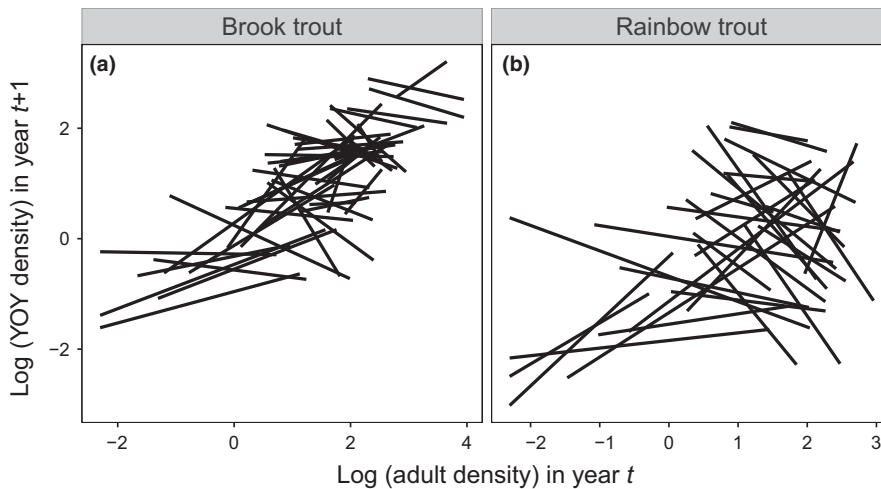
Interpretable models for both adult BKT and RBT density demonstrated the positive effects of YOY density in the previous year. In other words, high YOY abundance in the current year was followed by high adult abundance in the subsequent year, which is typical of populations that exhibit short maximum lifespans such as headwater salmonids (Grossman et al., 2010; Xu, Letcher, & Nislow, 2010). Stock–recruitment relationships varied among sites in both species, although the frequency of positive stock–recruitment relationships was higher for BKT than RBT. Many stream salmonid populations do not show positive stock–recruitment relationships (Kanno et al., 2016; Milner et al., 2003), but positive relationships have been detected for BKT in both the Southern and Middle Appalachians and Michigan (Grossman et al., 2012; Petty, Lamothe, & Mazik, 2005; Zorn & Nuhfer, 2007b).

Although we observed interpretable relationships between environmental variables and trout population dynamics, we were unable to obtain stream temperature and flow data from our study streams. Instead, we used air temperature and precipitation data. Nonetheless, we believe these values are representative of inter-annual variability in stream temperature and flow experienced by our study streams (Figure S2). Instrumenting over hundreds of sites would have been logistically prohibitive and inordinately expensive. However, stream temperature and flow data would be essential for identifying threshold values at which populations respond to temperature and flow alterations. An additional problem we faced

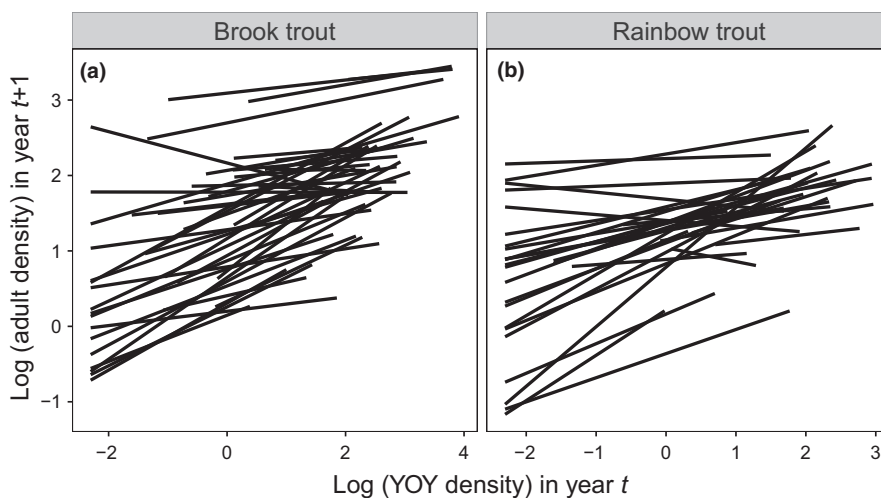




**FIGURE 4** Model-averaged effects of seasonal weather covariates retained in the top-ranked model for rainbow trout adult density (# fish per 100 m<sup>2</sup>): (a) peak precipitation from October through January (the highest value of consecutive 3-day total precipitation during the period in mm), and (b) peak precipitation in February and March (mm). Mean responses are shown in black lines and 95% confidence intervals are shown in grey shade. The observed range of each covariate is shown and represents annual mean values averaged across sites (Table S1)



**FIGURE 5** Log-transformed relationships between adult density in year  $t$  versus young-of-the-year (YOY) density in year  $t + 1$  in (a) brook trout and (b) rainbow trout (i.e. stock–recruitment relationships). The unit of original density values is # fish per 100 m<sup>2</sup>. Each line represents a site and is based on least squares regression



**FIGURE 6** Log-transformed relationships between young-of-the-year (YOY) density in year  $t$  versus adult density in year  $t + 1$  in (a) brook trout and (b) rainbow trout (i.e. recruitment–stock relationships). The unit of original density values is # fish per 100 m<sup>2</sup>. Each line represents a site and is based on least squares regression

using indirect sources for environmental data was a decreased ability to separate the effects of extreme (i.e. floods) from mean conditions.

Grossman et al. (2016) provided a graphical model that predicted GCC could tip Southern Appalachian stream fish populations from

density-dependent regulation to density-independent control if the frequency of extreme events increases. The increases in variability and magnitude already are occurring (Grossman et al., 2016), and may ultimately lead to reduced compensatory responses by populations to deleterious environmental variation (e.g. floods and

droughts) (Bassar, Letcher, Nislow, & Whiteley, 2016). Long-term studies of stream fish populations in the Southern Appalachians show that density-dependent regulation is common in these fishes including Southern BKT (Grossman et al., 2006, 2010, 2016), although density-independent influences such as flow variation also are present. Consequently, a shift in population control, and ultimately assemblage structure, produced by GCC is not an unlikely possibility. Such a situation would greatly reduce the ability of fisheries biologists to manage wild populations of stream fishes including stream salmonids.

Our results have other important implications for trout management. Besides the direct negative impacts on habitat suitability for trout (i.e. increasing flow variability and temperature), different trout species likely will respond differently to environmental change (Fausch, 2008). From a manager's perspective, this may have the positive aspect of preserving a trout fishery because it could be viewed as an inter-specific "portfolio effect" (Schindler et al., 2010) and trout resources as a whole may fluctuate less over time than the trend of a single species. On the negative side, if GCC favours invasive species such as RBT, then this may inhibit efforts to remove this species and restore BKT to streams they formerly occupied. Finally, sensitivity of YOY density and trout populations to flow variation indicates that flow management could be a viable option for conservation of coldwater fishery in certain areas (i.e. tail-water habitats) particularly when more than one trout species with different spawning seasons co-exist.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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