esa ECOSPHERE

Seasonal streamflow extremes are key drivers of Brook Trout young-of-the-year abundance

Annalise G. Blum[1,2,†] Yoichiro Kanno[3] and Benjamin H. Letcher[4]

[1]Department of Civil and Environmental Engineering, Tufts University, 200 College Avenue, Medford, Massachusetts 02155 USA
[2]U.S. Geological Survey, 12201 Sunrise Valley Drive, Reston, Virginia 20192 USA
[3]Department of Fish, Wildlife, and Conservation Biology, and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523 USA
[4]Leetown Science Center, S. O. Conte Anadromous Fish Research Center, U.S. Geological Survey, One Migratory Way, Turners Falls, Massachusetts 01376 USA

Citation: Blum, A. G., Y. Kanno, and B. H. Letcher. 2018. Seasonal streamflow extremes are key drivers of Brook Trout young-of-the-year abundance. Ecosphere 9(8):e02356. 10.1002/ecs2.2356

Abstract. To manage ecosystems in the context of climate change, we need to understand the relationship between extreme events and population dynamics. Floods and droughts are projected to occur more frequently, but how aquatic species will respond to these extreme events remains uncertain. Based on counts of Brook Trout (*Salvelinus fontinalis*) collected over 28 yr at 115 sites in Shenandoah National Park, we developed mixed-effects models to (1) assess how well extreme streamflow, as compared to mean flows and total precipitation, can explain young-of-the-year (YOY) abundance, (2) identify potential nonlinear relationships between seasonal environmental covariates and abundance using nonlinear generalized additive mixed models, and (3) explore likely impacts of expected future weather and streamflow conditions. We found that (1) using covariates of streamflow extremes improved prediction of YOY abundance compared to use of mean seasonal flow values or precipitation as a proxy, (2) warmer maximum daily spring temperatures were associated with increased YOY abundance up to about 1.5 standard deviations, above which abundance declined, and (3) a strong negative effect of extreme winter streamflow, unlikely to be offset by possibly positive effects from other seasons, is expected to have a detrimental impact on Brook Trout populations given predicted increases in winter precipitation. Because YOY abundance is a strong determinant of population dynamics for these short-lived species, extreme events will have the potential to exert a strong influence on population persistence of Brook Trout in a changing climate. Management actions that maximize resiliency of populations in response to extreme events, such as restoration of habitat connectivity, should be prioritized to buffer negative impacts.

Key words: Brook Trout (*Salvelinus fontinalis;*) climate change; droughts; extreme events; fish ecology; floods; population dynamics.

Received 13 April 2018; revised 27 May 2018; accepted 31 May 2018. Corresponding Editor: Stephanie M. Carlson.

† **E-mail:** annaliseblum@gmail.com

Introduction

To manage ecosystems in the context of climate change, we need to understand the relationship between extreme events and population dynamics. For freshwater populations, predictions that extreme hydrologic events, such as floods and droughts, will increase (Ingram et al. 2013, National Academies of Sciences 2016) are of particular concern. Because streamflow influences the distribution and abundance of aquatic species (Poff et al. 1997), more frequent, longer duration, and/or more extreme high and low streamflow events are likely to have significant consequences for these populations (Nislow et al. 2004, Wenger et al. 2011, Letcher et al. 2015*b*, Ward et al. 2015). We have a limited understanding of how aquatic populations will respond to hydrologic changes (Walters 2016, Wheeler et al. 2017). A number of recent review articles (Clutton-Brock and Sheldon 2010, Warren et al. 2015, Kovach et al. 2016) have highlighted the need to evaluate the impact of climate change on freshwater species using long-term biological datasets which can characterize temporal and nonlinear relationships.

For aquatic as well as terrestrial species, temporal variation in average annual and seasonal weather has been linked to changes in population abundance (Pardikes et al. 2015, Kanno et al. 2017), vital rates (Dybala et al. 2013, Abadi et al. 2017), and population dynamics (Seegrist and Gard 1972, Fernández-Chacón et al. 2011, Grossman et al. 2016, Cleasby et al. 2017). However, responses of animal populations may be more closely related to short-duration, high-magnitude extreme events or disturbances which exceed a biological threshold above or below which animals have reduced fitness (i.e., survival and reproductive success; Resh et al. 1988, Lake 2003, Roland and Matter 2013, Childress and Letcher 2017). Few studies have investigated the effect of extreme weather conditions on long-term population fluctuations and most have focused on terrestrial organisms (Roland and Matter 2013, Bailey and van de Pol 2016). Additionally, nonlinear relationships between abundance and environmental covariates are often hypothesized, but these relationships are rarely modeled (Kovach et al. 2016).

In this study, we use a 28-yr dataset to relate seasonal streamflow extremes to abundance of Brook Trout *(Salvelinus fontinalis)*, a popular cold water species for recreational fishing. Both the timing and magnitude of extreme streamflow events are important to determining impact on Brook Trout young-of-the-year (YOY) abundance (George et al. 2015, Warren et al. 2015, Kovach et al. 2016). Extremely low streamflow can diminish salmonid abundance due to habitat fragmentation, increased competition for food, and greater risk of predation (Bell et al. 2000, Lobón-Cerviá 2009). For fall-spawning Brook Trout, insufficient streamflow in the fall can limit spawning movement or result in dewatering of gravel nests, known as redds (Kanno et al. 2014, Whiteley et al. 2015). Excessive winter and spring flows can also reduce abundance: High streamflow can scour redds during winter and, during spring, large peak streamflow can exceed swimming velocities of fry after emergence (Nislow and Armstrong 2012, Warren et al. 2015).

Native trout across the United States (U.S.) occupy a diminished fraction of their historical habitat (Hudy et al. 2008, Williams et al. 2015), and even greater declines are expected with future climate change (Mantua et al. 2010, Meyers et al. 2010, Wenger et al. 2011, Williams et al. 2015, Bassar et al. 2016). Brook Trout life histories are tightly linked to seasonal environmental conditions (Nislow and Armstrong 2012, Letcher et al. 2015*b*); spawning, incubation, and emergence are regulated by stream flow and temperature, as well as photoperiod (Nislow and Armstrong 2012, Warren et al. 2012). Threshold responses of Brook Trout and other species to water temperature have been identified in laboratory and field studies (Beitinger et al. 2000, Hartman and Cox 2008, Beauchene et al. 2014, Childress and Letcher 2017). However, much of the research on streamflow has been limited to study of a particular flood or low flow event, limiting inference regarding longer-term, nonlinear, and/or temporal relationships (Kovach et al. 2016).

Given a short life span of 2–3 yr and high annual variation in abundance, YOY (fish born within the last year), are a primary driver of Brook Trout population dynamics in small headwater streams (Bassar et al. 2016, Kanno et al. 2016*b*). Focusing on Brook Trout YOY abundance, the aims of this work are to (1) assess how well extreme streamflow, as compared to mean flow and total precipitation, can explain abundance, (2) investigate possible nonlinear relationships between seasonal environmental covariates and abundance, and (3) explore expected impacts of future climate and streamflow conditions.

Methods

Fish, weather, and streamflow data were collected in Shenandoah National Park (SNP), Virginia, USA. By the mid-21st century, this region is expected to experience increases in precipitation in all seasons except summer and increases in temperature across all seasons (Ingram et al. 2013). Building from previous work by Kanno et al. (2015), who used seasonal total precipitation (i.e., average conditions) as a proxy for streamflow, we assessed the benefit of using modeled streamflow covariates which are more closely related to the hypothesized biological mechanisms (such as habitat isolation during low flows or scouring of redds during a flood). Sampling of Brook Trout YOY occurred throughout each summer; thus, we focus on the three seasons preceding summer-time sampling. Furthermore, the effects of summer conditions have been studied extensively; abundance has consistently been found to be positively correlated with summer streamflow and negatively correlated with summer temperature (Nislow et al. 2004, Xu et al. 2010*a*, Warren et al. 2012, Letcher et al. 2015*b*, Kovach et al. 2016, Merriam et al. 2017).

Brook Trout data

Shenandoah National Park encompasses 777 km^2 of mountainous terrain in northern Virginia, USA (Fig. 1) with a mix of deciduous and coniferous forest. Fish study sites were small, shaded headwater streams (1st–3rd order), at elevations ranging from 285 to 802 m and with upstream watershed areas of 1–36 km^2 (Table 1). Streamflow is generally highest in the spring and lowest in summer and fall due to snow melt and rates of evapotranspiration. The most common fish species in SNP other than Brook Trout is the Blacknose Dace, *Rhinichthys atratulus* (Jastram et al. 2013).

The study included 115 sites that were sampled on average nine times (minimum of four) over 1983–2010 by the National Park Service. Brook Trout were sampled annually during June through August using backpack electrofishers at 100-m permanent stream sections. Block nets or cobble dams were set at upstream and downstream site boundaries to minimize fish movement into and out of the site during sampling. Depending on stream width, one to three electrofishing backpack units were used, each accompanied by two individuals to net fish. Forty percent of electrofishing surveys were three-pass depletion surveys, which started in 1995, and the rest of the surveys were single pass. Brook Trout counts were obtained at between five and 64 sites per yr during the 28-yr period.

Streamflow and weather data

Streamflow was predicted based on observed flow at streams gaged by the Shenandoah Watershed Study (SWAS) through the University of Virginia and by the U.S. Geological Survey (USGS). More information about the stream gages, including locations relative to the fish sampling sites, is given in Appendix S1: Fig. S1 and Table S1. Streamflow data were available from four SWAS stream gages located within SNP starting in 1993. Daily streamflow data prior to 1993 were obtained from the USGS National Water Information System from four stream gages neighboring SNP (US Geological Survey 2017) that had not been substantially impacted by humans (Falcone 2011).

Daily streamflow at ungaged fish sampling sites was predicted using the nearest neighbor drainage area ratio method, which assumes that streamflow standardized by watershed drainage area is constant within a region (Hirsch 1979). As is common, standardized streamflow was transferred from the nearest gaged site to each ungaged fish sampling site (Asquith et al. 2006). Given standardized streamflow from a gaged site, daily streamflow at an ungaged site (Q_y) with drainage area (A_y) was predicted:

$$\frac{Q_y}{A_y} = \frac{Q_x}{A_x} \tag{1}$$

where Q_x is a time series of daily streamflow at the gaged site and A_x is the watershed area for the gaged site. For the southeastern United States, this method was found to predict streamflow at ungaged locations comparably to more complex methods (Farmer et al. 2014). To assess the validity of this assumption for SNP, standardized seasonal streamflow extremes for SWAS and USGS sites were compared and found to be similar (Appendix S1: Fig. S2). Using predictions of daily streamflow at trout sampling sites, seasonal average daily streamflow and seasonal streamflow extremes were calculated.

Based on the findings of previous studies (including Kanno et al. 2016*b*: Table 2 and Kovach et al. 2016: Figure 2), hypotheses regarding the impacts of seasonal streamflow and temperature

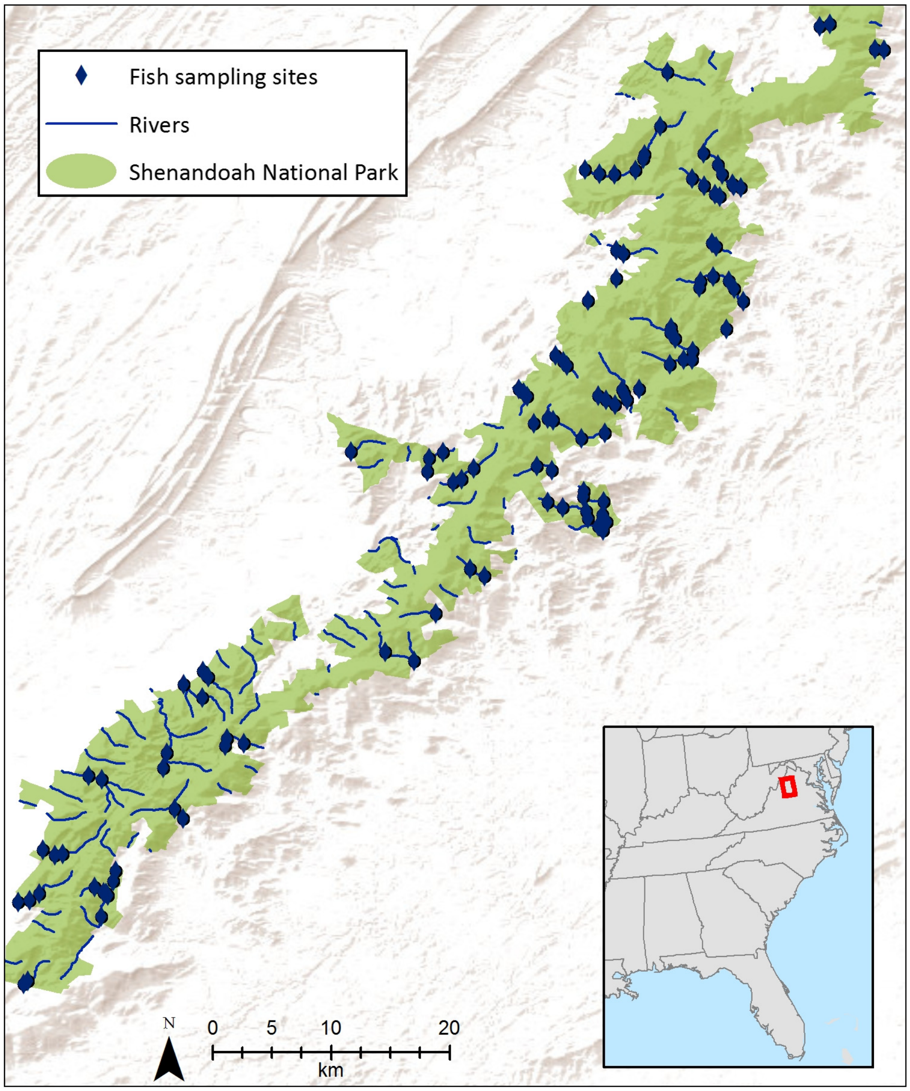

Fig. 1. Map of Shenandoah National Park, streams located within the Park, and 115 fish sampling sites.

on Brook Trout YOY abundance are presented in Table 2. To test proposed seasonal extreme streamflow hypotheses, streamflow extremes were estimated as the 5th percentile (low) streamflow in fall and the 95th percentile (high) flow in winter and spring. Similar metrics for seasonal high and low streamflow have been used previously in studies of population response to hydrologic changes (Visser et al. 2017).

Following Kanno et al. (2015, 2016*b*, 2017), we used air temperature as a proxy for water temperature because heat exchange with air is the major physical driver of stream temperature (Mohseni and Stefan 1999, Morrill et al. 2005, Letcher et al. 2015*a*). We also used seasonal precipitation, often used as a proxy for streamflow, as a benchmark against which we compared mean and extreme streamflow covariates. Daily precipitation (including both snow and rainfall) and daily maximum air temperature at the 1 km^2 resolution were obtained from the Daymet database (http://daymet.ornl.gov) for all fish sampling sites. We summed daily precipitation by season and calculated seasonal means of maximum daily air temperature.

Table 1. Summary of estimated young-of-the-year (YOY) Brook Trout abundance, seasonal weather and streamflow covariates, and study site characteristics.

Variable	Median	Mean	Standard deviation	Min	Max
Estimated YOY abundance	48.8	72.1	76.1	3.5	739.6
Seasonal extremes covariates					
Fall low streamflow† (5th percentile, m^3/s)	0.01	0.02	0.03	0.00	0.32
Winter high streamflow† (95th percentile, m^3/s)	0.31	0.48	0.52	0.01	4.66
Spring high streamflow† (95th percentile, m^3/s)	0.42	0.63	0.62	0.03	5.09
Fall average max daily temperature (°C)	18.0	18.0	1.4	13.7	21.7
Winter average max daily temperature (°C)	6.1	6.0	1.8	1.0	10.6
Spring average max daily temperature (°C)	16.8	16.8	1.5	12.6	20.4
Fall precipitation (mm)	93.2	111.5	126.0	35.8	332.0
Winter precipitation (mm)	75.5	74.5	93.7	22.6	143.0
Spring precipitation (mm)	82.8	84.8	82.6	43.0	168.8
Site characteristics					
Elevation (m)	437	459	115	285	802
Watershed area (km^2)	8.1	9.5	6.6	1.3	36.2

† Estimated from neighboring stream gages.

Table 2. Hypothesized linear and nonlinear effects of fall, winter, and spring streamflow and temperature on Brook Trout young-of-the-year abundance.

Season	Relationship with Streamflow	Relationship with Temperature
Fall (September–November); bioperiod: adult spawning	Positive: Brook Trout need sufficient streamflow to access to small tributaries for spawning (Kanno et al. 2014, Whiteley et al. 2015) and excessively low streamflow can lead to dewatering of eggs. We expect a dome-shaped nonlinear relationship as fall spawning movement and habitat availability have been found to be limited at low streamflows; riffle-pool sequences are typical of Brook Trout streams and drying of riffles can lead to isolated pools (Hakala and Hartman 2004)	Negative relationship: High fall temperatures delay or reduce spawning, as Brook Trout spawning occurs below a temperature threshold (e.g., 11°C; Blanchfield and Ridgway 1997). This sort of thermal cue for spawning would be expected to elicit nonlinear relationships
Winter (December–February); bioperiod: egg incubation	Negative: Peak high flows can wash out redds, the gravel nests in which eggs are deposited (Fausch et al. 2001, Carline and McCullough 2003). An increasing nonlinear relationship is hypothesized as bed scouring increases nonlinearly with stream discharge and egg mortality may increase above a certain threshold of stream discharge (Bull 1979)	Positive: Warmer winters encourage faster hatching of eggs, which leads to longer growing season (Baxter and McPhail 1999)
Spring (March–May); bioperiod: fry rearing	Uncertain: High flow may provide fry with habitat along the bank (Jellyman and Mcintosh 2010, Kaspersson et al. 2012), but excessive flows can result in wash-out after emergence (Jensen and Johnsen 1999, Kanno et al. 2017)	Positive: Warmer temperatures during the fry growing season enhance survival and growth (Coleman and Fausch 2007, Xu et al. 2010*b*)

Abundance modeling

We estimated YOY abundance from Brook Trout count data (one or three pass) using a Poisson binomial N-mixture model (Royle 2004). The Bayesian framework used to estimate abundance is applied from Kanno et al. (2016*b*), with year random effects used to quantify temporal variability. N-mixture models estimate population size from count data while formally accounting for detection probability. Exploiting spatial and temporal replication, site-specific population sizes are assumed to be independent variables distributed according to a selected distribution (such as Poisson, as assumed here), and model parameters (such as detection probability) are estimated from the marginal likelihood of the data. Kéry (2018) showed that parameters are generally identifiable for the Poisson binomial N-mixture models, which were applied here. Abundance estimated by the N-mixture model was used as the response or dependent variable in all models described below.

Linear mixed-effects models were fit with the lme4 package (Bates et al. 2014) in R version 3.4.2 (R Core Team 2017) to estimate the effect of seasonal streamflow, precipitation, and temperature covariates on estimated abundance. In total, analysis included 1164 abundance estimates at 115 sites across 52 stream reaches, which are defined as a continuous piece of a stream with similar hydrologic characteristics (USEPA and USGS 2012). The linear model took the form:

$$\log(N_{i,t}) \sim a_{j[i]} + \beta_1 T_{i,t}^{\mathrm{fall}} + \beta_2 T_{i,t}^{\mathrm{win}} + \beta_3 T_{i,t}^{\mathrm{spr}} + \beta_4 Q_{i,t}^{\mathrm{fall}} + \beta_5 Q_{i,t}^{\mathrm{win}} + \beta_6 Q_{i,t}^{\mathrm{spr}} + \varepsilon_{i,t} \quad (2)$$

where $N_{i,t}$ represents estimated YOY abundance at site i in year t (based on the N-mixture model as described previously), $a_{j[i]}$ is the random intercept of stream reach j within which site i is nested, $\beta_1,\ldots\beta_6$ are fitted regression coefficients representing effect sizes, and $\varepsilon_{i,t}$ is the model error. We assumed $a_{j[i]} \sim N(0, \sigma_a^2)$ and $\varepsilon_{i,t} \sim N(0, \sigma_\varepsilon^2)$. The environmental covariates are given as matrices for site i in year t: $T_{i,t}^{\mathrm{fall}}, T_{i,t}^{\mathrm{win}}, T_{i,t}^{\mathrm{spr}}$ represent the average of daily maximum temperatures for fall, winter, and spring, respectively; $Q_{i,t}^{\mathrm{fall}}, Q_{i,t}^{\mathrm{win}}, Q_{i,t}^{\mathrm{spr}}$ represent the covariates for fall, winter, and spring streamflow, respectively. All covariates were standardized by site to have a mean of zero and a standard deviation of one. Presented effect sizes are thus reported in standard deviations relative to each covariate's mean value at a sampling site. Descriptions and summary statistics for the covariates are shown Table 1. We did not model interactive effects of seasonal covariates because lack of independence between seasons would require a different model structure; thus, we leave these analyses for future work.

To achieve our first aim, three versions of the linear model (Eq. 2) were fit in which $Q_{i,t}^{\mathrm{fall}}, Q_{i,t}^{\mathrm{win}}, Q_{i,t}^{\mathrm{spr}}$ were represented by different seasonal variables: total precipitation, average streamflow, and extreme streamflow (represented by 5th percentile fall streamflow and 95th percentile winter and spring streamflow, selected based on our hypotheses presented in Table 2).

To identify potential nonlinear effects (our second aim), we also fit generalized additive mixed models using the mgcv package for R (Wood 2011). We visually examined partial dependence plots to check for nonlinear relationships between environmental covariates and abundance. For identified nonlinear effects, a mixed model with a quadratic term (calculated by squaring the relevant covariate) was fit. For each of the models, we compared the Akaike information criterion (AIC), root-mean-squared error (RMSE), and percent RMSE (%RMSE, or 100 times the ratio of RMSE relative to average YOY abundance).

As our third aim was to use the selected model to predict future conditions, we conducted a cross-validation to assess the predictive performance of each model. One-third of the observations were randomly selected and omitted ten times; the mean and range of RMSE of predictions from models fit with two-thirds of the observations were compared to assess the predictive performance of each model and check for over-fitting.

Future streamflow and temperature

In the southeastern United States, where SNP is located, mean annual temperature is predicted to increase by 1.5–5.5°C by 2055 (Kunkel et al. 2013). Model forecasts for precipitation are more uncertain, but there is general consensus that precipitation will increase across all seasons except summer (Ingram et al. 2013, Kunkel et al. 2013, Karmalkar and Bradley 2017). Because streamflow, particularly the lowest flows, is controlled by both precipitation and temperature, it is challenging to forecast how streamflow will change in the future. To explore how changes in seasonal temperature, precipitation, and streamflow may impact future Brook Trout YOY abundance under uncertain future climate scenarios, abundance under more extreme scenarios (four standard deviations above and below the mean) of the six covariates was predicted. Partial dependence plots illustrate the marginal effect of each covariate on YOY abundance across the 115 sites.

Results

Model selection and fit

Predicted fall low streamflow ranged from 0 to 0.32 cubic meters per second (m^3/s), compared to winter high streamflow (0.01–4.66 m^3/s) and spring high streamflow (0.03–5.09 m^3/s; Table 1). Within each of the candidate models, none of the covariates were highly correlated: The maximum Pearson correlation between any two covariates included in a given model was between fall and spring temperatures (Pearson's $r = 0.51$).

Linear models with predicted seasonal streamflow covariates (Table 3, Models 2 and 3) had lower AIC compared to the model fit with total seasonal precipitation (Table 3, Model 4). Replacing total seasonal precipitation covariates with seasonal extreme streamflow covariates reduced AIC by 52. Additionally, the linear model with seasonal extreme streamflow covariates had more support compared to the model with seasonal average streamflow covariates (reduction in AIC of 12).

We next refit the top-ranked linear model (Table 3, Model 2), which included seasonal streamflow extremes covariates, as a generalized additive mixed model. Contrary to proposed hypotheses, there did not appear to be strong nonlinear relationships between abundance and most of the covariates. (Appendix S1: Fig. S3 shows partial dependence plots for based on the generalized additive mixed model). The generalized additive formulation of the mixed model did reveal a nonlinear relationship between YOY abundance and spring temperature (Fig. 2). At temperatures above 1.5 standard deviations above the mean, the relationship between spring temperature and abundance reversed from positive to negative. Standardized spring temperatures >1.5 were found at 52 sites over six years, which illustrates that this relationship was not constrained to a small subset of fish sampling sites.

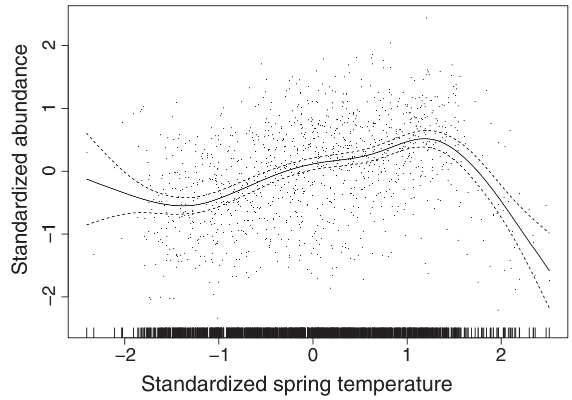

Fig. 2. Partial dependence plot of relative contribution of mean of daily maximum spring temperature to standardized abundance fit with a generalized additive mixed model including random site intercepts. The model fit 6.69 degrees of freedom of the smooth (the number of bends in the curve allowed). The solid line represents model predictions (with random site effects set to zero), dashed lines show 95% confidence intervals, and points illustrate model residuals. Along the lower *y*-axis, a rug plot (vertical lines) indicates frequency of each mean spring daily maximum temperature.

A quadratic mean spring daily temperature term was thus added to the three candidate linear models to capture this nonlinear relationship. Consistent with our findings for linear models, the model including streamflow extremes had the lowest AIC (Table 3, Model 1). The addition

Table 3. Model fit (best to worst) based on Akaike information criterion (AIC), root-mean-squared error (RMSE), RMSE relative to average abundance (%RMSE), 10-fold cross-validation (CV) RMSE mean and range (min–max), and degrees of freedom (df).

Model	AIC	RMSE (%RMSE)	CV RMSE mean (range)	df
1. Extreme streamflow and maximum temperature by season and quadratic term for maximum spring temperature	3038	64.3 (90%)	65.4 (64.6–66.7)	11
2. Extreme streamflow and maximum temperature by season	3073	64.3 (90%)	65.5 (64.5–67.1)	10
3. Average streamflow and maximum temperature by season	3085	64.8 (91%)	66.1 (65.0–67.2)	10
4. Total precipitation and maximum temperature by season	3125	66.7 (93%)	68.0 (67.1–69.1)	10

Note: Seasonal refers to fall, winter, and spring.

of the quadratic mean spring daily temperature term reduced AIC by 35 relative to the streamflow extreme model with only linear terms model.

To select a model to use for prediction, we compared the range of cross-validation RMSE, in which models were refit ten times based on a randomly selected two-thirds of the data. Across the ten replicates, RMSE did not vary substantially for any of the models (Table 3). With the lowest AIC, the model including extreme streamflow covariates and a quadratic term for spring temperature was selected for prediction (Table 3, Model 1). Before using this model for prediction, we confirmed that it was approximately unbiased (47% of model predictions were greater than estimated abundance outcome) and met regression assumptions regarding the distribution of model residuals.

Model predictions match estimated Brook Trout YOY abundance relatively well (Fig. 3). Only in the years in which Brook Trout were sampled at few locations (such as 2007 when Brook Trout were sampled at only five sites) were there notable discrepancies between median estimated abundance and median model-predicted abundance.

Effects of seasonal streamflow and temperature extremes

Fitted model coefficients (Table 4) generally match our hypothesized relationships (see Table 2). Peak winter streamflow had the largest effect (effect = −0.26, SE = 0.03) and was negatively associated with next summer YOY abundance. The effect size of fall streamflow (5th percentile flow) was similar to that of peak winter streamflow but with a positive relationship (effect = 0.25, SE = 0.03). As expected, warmer temperatures in the fall were negatively related to abundance (effect = −0.20, SE = 0.04). Spring high streamflow and winter temperature did not have statistically significant effects on abundance.

Predictions under more extreme conditions

Partial dependence plots for these seasonal covariates illustrate the importance of studying changes in environmental conditions by season (Fig. 4). Under greater fall 5th percentile streamflow (Fig. 4a), increases in Brook Trout YOY abundance would be expected; however, the reverse relationship is expected for increases in 95th percentile winter streamflow (Fig. 4b). For this region, both precipitation and temperature

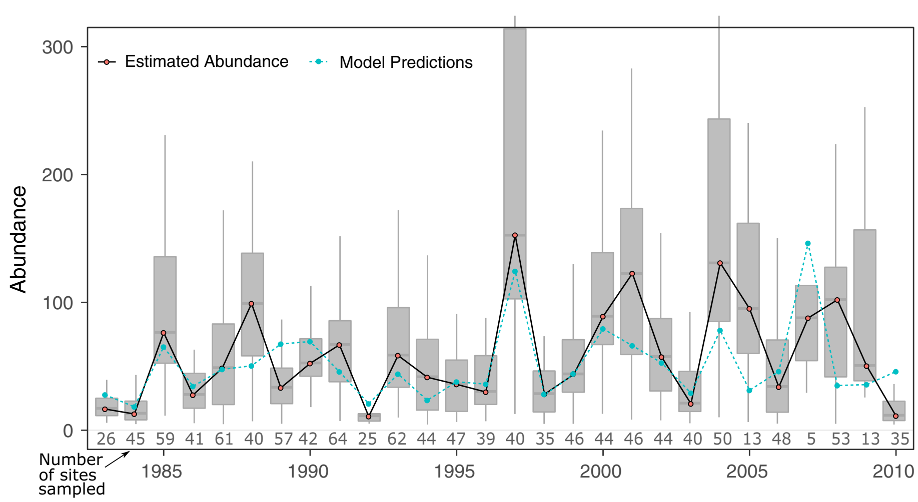

Fig. 3. Estimated annual Brook Trout young-of-the-year (YOY) abundance per 100 m compared to model predictions, $\widehat{N}$. Lines connect points showing median abundance for each year. Numbers along the *x*-axis denote number of stream sites sampled in that year, gray boxplots illustrate the interquartile range (IQR) of YOY abundance across those sites in a given year, and the whiskers extend the boxes to 1.5 of the IQR. (Outliers are omitted for clarity).

Table 4. Effect of seasonal streamflow and temperature extreme on next summer abundance of young-of-the-year Brook Trout based on the selected mixed-effects model fit with random intercepts for each site, nested within stream reach.

Predictor	Coefficient	SE	t	P
Fall low streamflow (5th percentile, ft^3/s)	0.25	0.03	9.18	0.00
Winter high streamflow (95th percentile, ft^3/s)	−0.26	0.03	−8.99	0.00
Spring high streamflow (95th percentile, ft^3/s)	−0.03	0.03	−0.85	0.40
Fall average max daily temperature (°C)	−0.20	0.04	−5.59	0.00
Winter average max daily temperature (°C)	0.01	0.03	0.45	0.65
Spring average max daily temperature (°C)	4.96	0.74	6.69	0.00
(Spring average max daily temperature)^2 (°C^2)	−4.75	0.74	−6.41	0.00

Note: Coefficient is the effect size, SE refers to the standard error, t is the t-statistic, and P is the P-value.

are expected to increase in all three seasons studied here (Ingram et al. 2013). However, the correlation between winter precipitation to winter 95th percentile streamflow (Pearson's r = 0.66) is much higher compared to the correlation of fall precipitation and fall 5th percentile streamflow (Pearson's r = 0.35). This is not surprising as the lowest streamflow during a season occurs

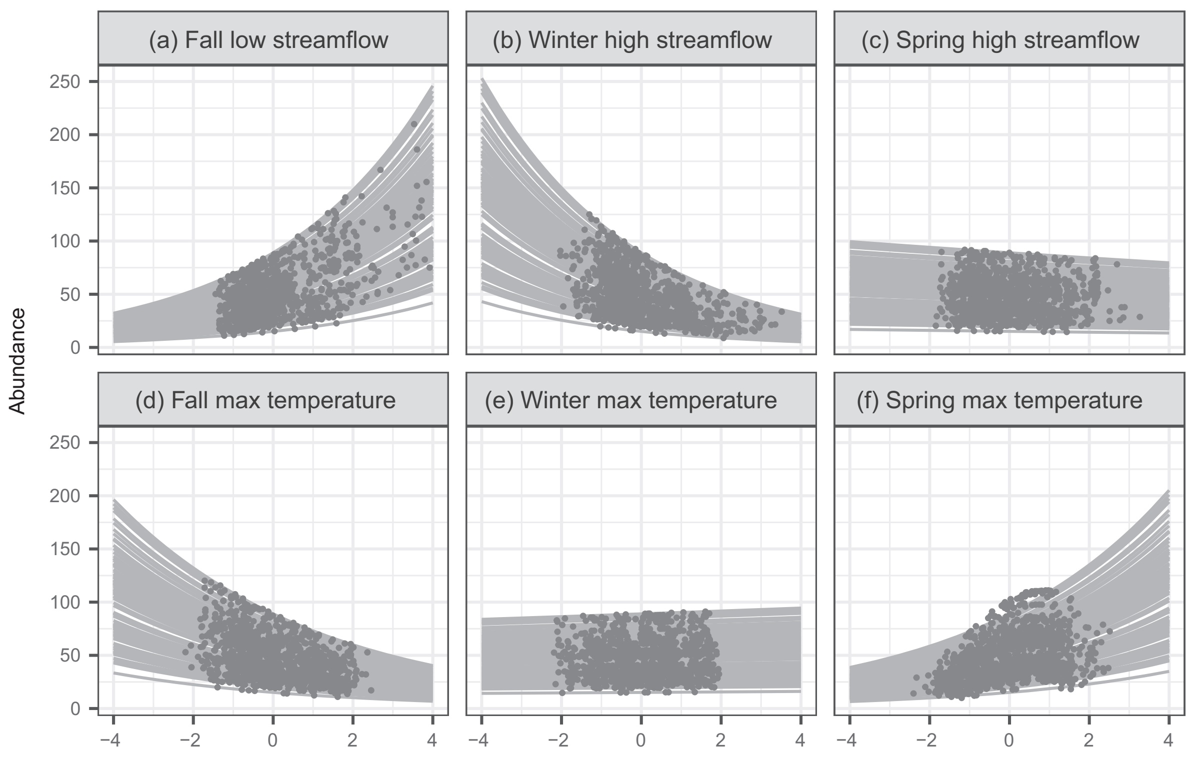

Fig. 4. Partial dependence plots of extreme streamflow and temperature covariates predicted using the selected random intercepts model. (a) Fall 5th percentile streamflow; (b) Winter 95th percentile streamflow; (c) Spring 95th percentile streamflow; (d) Fall mean of daily maximum temperature; (e) Winter mean of daily maximum temperature; (f) Spring mean of daily maximum temperature. Each line represents predicted abundance per 100 m at a fish sampling site, and the observed values of each covariate (the data collection space) are shown as points. As spring temperature represents a combination of a linear and a quadratic term, the points of the sample space do not fall exactly on the prediction lines.

after a period with little precipitation. Even with greater fall precipitation, simultaneous increases in fall temperature and evaporation (Seager et al. 2009) could result in diminished fall streamflow. Thus, predictions are made for both increasing and decreasing fall streamflow, as well as for the other covariates to maintain consistency.

Under a scenario of increasing fall streamflow, the benefits on abundance of these increases are unlikely to offset the strong negative effect of increases in winter peak streamflow (Fig. 5). The most likely future Brook Trout abundances are represented by the top portion of Fig. 5 (above standardized winter peak flows of zero), given expected increases in peak winter streamflow associated with increases in winter precipitation (Kunkel et al. 2013, Karmalkar and Bradley 2017).

Discussion

Seasonal drivers of Brook Trout abundance

Our findings contribute to the growing evidence that extreme hydrologic conditions in the future are likely to have a substantial impact on freshwater species. We found high winter

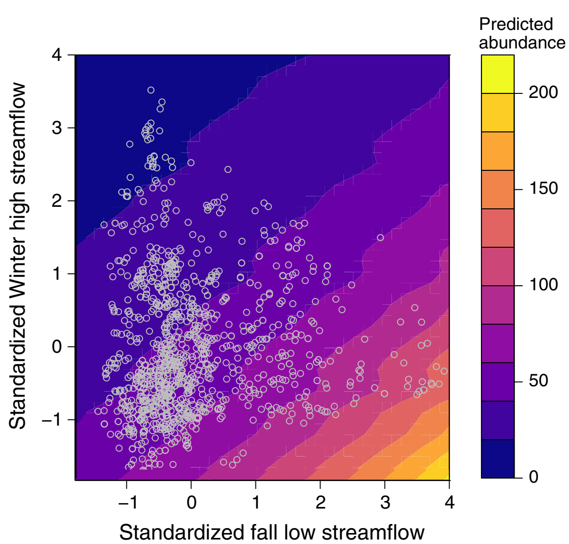

Fig. 5. Predicted young-of-the-year abundance per 100 m compared to low fall streamflow and high winter streamflow. The gray points illustrate the data collection space. Note that axes range from −2 to 4 standard deviations around the mean (represented by 0).

streamflow to be strongly associated with reduced YOY abundance the following summer, similar to other studies of inland trout populations (reviewed by Kovach et al. 2016). This ecological pattern is assumed to result from bed scouring and mortality of early life stages equipped with weak swimming capabilities (Carline and McCullough 2003). Our finding that winter extreme streamflow was a stronger driver of Brook Trout YOY abundance compared to mean flow or total precipitation supports this explanation because bed scouring occurs under short-duration, high-flow events (Cunjak et al. 1998). In fall, excessively low streamflow was found to be associated with reduced YOY abundance. We are less certain of the ecological mechanism that extremely low fall streamflow forces. Low fall streamflow may decrease spawning habitat availability and increase the occurrence of redd superimposition (the reuse of the same spawning locations by different individuals; Essington et al. 1998), result in dewatering of redds, or restrict access to suitable spawning sites, particularly small tributaries that are typically used by Brook Trout (Kanno et al. 2011, Kanno et al. 2015).

Warmer spring temperatures have previously been found to result in greater YOY abundance (Xu et al. 2010*a*, Kanno et al. 2015, 2016*b*, Kovach et al. 2016) and our results based on a linear formulation of our model confirmed these findings. However, a more flexible generalized additive model detected a nonlinear relationship in spring temperature above which YOY abundance declined. This was an unexpected result because spring temperatures are well below the upper thermal threshold of Brook Trout, which can tolerate the temperature up to 20–22°C (Hartman and Cox 2008, Stranko et al. 2008). Possibly, YOY Brook Trout may not be able to obtain sufficient food to compensate for the increased metabolic demand imposed by excessively warm spring temperatures (Hartman and Cox 2008), particularly when a possible mismatch in phenology occurs between trout and their prey (Sato et al. 2016).

Abundance under future conditions

For the southeastern United States, climate models have predicted the largest increases in precipitation in winter (Kunkel et al. 2013, Karmalkar and Bradley 2017). Accordingly, increases in winter peak streamflow are also expected in SNP given the strong correlation between winter precipitation and high flow. Increases in winter high streamflow are expected to have a negative impact on Brook Trout YOY abundance in SNP. This finding is particularly concerning as YOY abundance has been found to be the main factor in driving Brook Trout populations in SNP as well as in Western Massachusetts (Bassar et al. 2016, Kanno et al. 2016*b*). Furthermore, increased winter temperatures are also expected to lead to more frequent rain on snow events and faster melting of snow, both of which could increase the frequency and magnitude of winter floods (Battin et al. 2007, Meyers et al. 2010). Previous work found that detrimental impacts on Brook Trout of changes in streamflow in one season are sometimes offset by changes in another season (Bassar et al. 2016). For this region, increases in fall streamflow could potentially offset the consequences of increasing winter flows; however, it is unclear how expected changes in weather patterns will impact fall streamflow.

Data limitations

One major limitation was the lack of stream gage data, as is frequently the case for headwater streams. A simple statistical method of flow transfer appeared to perform well for this region, but it was not possible to validate the ability of the flow transfer approach at the within-watershed scale. Furthermore, for the early part of the record, the only stream flow data available were from USGS stream gages with much larger basin sizes compared to the fish sampling sites. With higher quality streamflow data, consideration of duration and timing of streamflow extremes would improve understanding of the impacts other aspects of the hydrologic extreme events. As water temperature data were also unavailable, air temperature was used as the best available proxy. For the study region, regression models have been developed to link water to air temperatures, but only for the summer season (Snyder et al. 2015). It is possible that these data limitations obscured identification of hypothesized nonlinear relationships between environmental covariates and Brook Trout YOY abundance. Finally, acid deposition has historically been a concern in this region and we were not able to include water quality in the models due to data limitations. Local bedrock has been found to explain the acid sensitivity of a site (Jastram et al. 2013), which suggests that effects could be relatively constant over time and thus captured by the random site intercepts included in all models. New streamflow, water quality, and water temperature monitoring of these streams, in concert with the fish monitoring, would improve our understanding of the relationship between extreme streamflow, temperature, and Brook Trout populations.

Management implications

Compared to general consensus that temperatures are rising, there is less agreement about how precipitation, streamflow, and extreme hydrologic events in the United States will change in the future (U.S. GCRP 2017). Despite this uncertainty, natural resource managers will have to make decisions about the best strategies to conserve trout and other stream biota. Winter extreme high-flow events, particularly when occurring with high frequency across years, can greatly affect Brook Trout populations given their short life spans (Kanno et al. 2015). Reduced abundance of stream-dwelling salmonids could be partially offset by density-dependent compensatory mechanisms (Letcher and Terrick 1998, Grossman et al. 2009, Bassar et al. 2016), but managers may also need to consider actions to mitigate the impacts of extreme streamflow events. Conservation actions are particularly important for southern Appalachian Brook Trout populations (including those in the study area) because they persist in small, isolated populations that are susceptible to local extirpation due to demographic and environmental stochasticity (Hudy et al. 2008). Several management actions may be feasible to buffer the anticipated increase in frequency and magnitude of extreme flow events.

First, conservation and restoration of stream and riparian habitat should be prioritized to increase local population size and thus likelihood of population persistence. Riparian protection to control sediment load and habitat improvement with complex physical structures (e.g., log jams) are common practices in the southern Appalachian region. Second, management of non-native trout species may counter some of detrimental effects of extreme climate events. Brown Trout (*Salmo trutta*) and Rainbow Trout (*Oncorhynchus mykiss*) typically displace Brook Trout in lower-elevation streams in the southeastern United States, contributing to population fragmentation of Brook Trout in headwaters (Larson and Moore 1985, Hudy et al. 2008). Removal of non-native trout has been used to reintroduce and establish Brook Trout populations (Moore et al. 1986, Kanno et al. 2016*a*). Lastly, restoration of habitat connectivity (e.g., culvert improvement) can facilitate recolonization of fish into more severely flow-affected reaches (Roghair et al. 2002) since not all portions of the dendritic stream network may suffer extreme climate events equally due to spatial heterogeneity in stream size, geomorphology, and extreme microclimates (McCluney et al. 2014). Questions remain regarding to what extent corrective management actions such as these can buffer Brook Trout populations from extreme climate and hydrologic events.

Conclusions

Improved understanding of how freshwater populations respond to extreme hydrologic events can help inform strategies to reduce the negative impacts of climate change. With a long-term dataset, we explored the implications of changes in seasonal extreme streamflow and temperature on Brook Trout YOY abundance in SNP. Management strategies, such as restoration of habitat and connectivity, may serve to minimize the negative effects of future climate change. Extensions of this work to a broader range of streams and aquatic species would inform the development of strategies to manage freshwater ecosystems in the context of future climate change.

Acknowledgments

We are grateful to the Shenandoah Watershed Study (SWAS) based in the Department of Environmental Science at the University of Virginia for sharing their data from four stream gages in Shenandoah National Park. We thank Kyle O'Neil for help accessing the weather data and Nathaniel Hitt, Evan Childress, Rich Vogel, Stacey Archfield, Chuck Kroll, and Ami Risscasi for their helpful suggestions on the manuscript, as well as two anonymous reviewers. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant number DGE-1144081 and Grant number EEC-1444926, as well as U.S. Geological Survey Hurricane Sandy funds. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature Cited

Abadi, F., C. Barbraud, and O. Gimenez. 2017. Integrated population modeling reveals the impact of climate on the survival of juvenile emperor penguins. Global Change Biology 23:1353–1359.

Asquith, W. H., M. C. Roussel, and J. Vrabel. 2006. Statewide analysis of the drainage-area ratio method for 34 Streamflow percentile ranges in Texas. Scientific Investigations Report 2006-5286, USGS, Reston, Virginia, USA.

Bailey, L. D., and M. van de Pol. 2016. Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. Journal of Animal Ecology 85:85–96.

Bassar, R. D., B. H. Letcher, K. H. Nislow, and A. R. Whiteley. 2016. Changes in seasonal climate outpace compensatory density-dependence in eastern brook trout. Global Change Biology 22:577–593.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Battin, J., M. W. Wiley, M. H. Ruckelshaus, R. N. Palmer, E. Korb, K. K. Bartz, and H. Imaki. 2007. Projected impacts of climate change on salmon habitat restoration. Proceedings of the National Academy of Sciences of the United States of America 104: 6720–6725.

Baxter, J. S., and J. D. McPhail. 1999. The influence of redd site selection, groundwater upwelling, and over-winter incubation temperature on survival of bull trout (*Salvelinus confluentus*) from egg to alevin. Canadian Journal of Zoology 77: 1233–1239.

Beauchene, M., M. Becker, C. J. Bellucci, N. Hagstrom, and Y. Kanno. 2014. Summer thermal thresholds of fish community transitions in Connecticut streams. North American Journal of Fisheries Management 34:119–131.

Beitinger, T. L., W. A. Bennett, and R. W. McCauley. 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Environmental Biology of Fishes 58: 237–275.

Bell, V. A., J. M. Elliott, and R. J. Moore. 2000. Modelling the effects of drought on the population of brown trout in Black Brows Beck. Ecological Modelling 127:141–159.

Blanchfield, P. J., and M. S. Ridgway. 1997. Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 54:747–756.

Bull, W. B. 1979. Threshold of critical power in streams threshold of critical power in streams. Geological Society of America Bulletin 90:453–464.

Carline, R. F., and B. J. McCullough. 2003. Effects of floods on brook Trout populations in the Monongahela National Forest, West Virginia. Transactions of the American Fisheries Society 132:1014–1020.

Childress, E. S., and B. H. Letcher. 2017. Estimating thermal performance curves from repeated field observations. Ecology 98:1377–1387.

Cleasby, I. R., T. W. Bodey, F. Vigfusdottir, J. L. McDonald, G. McElwaine, K. Mackie, K. Colhoun, and S. Bearhop. 2017. Climatic conditions produce contrasting influences on demographic traits in a long-distance Arctic migrant. Journal of Animal Ecology 86:285–295.

Clutton-Brock, T., and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution 25:562–573.

Coleman, M. A., and K. D. Fausch. 2007. Cold summer temperature limits recruitment of age-0 cutthroat trout in high-elevation Colorado streams. Transactions of the American Fisheries Society 136:1231–1244.

Cunjak, R. A., T. D. Prowse, and D. L. Parrish. 1998. Atlantic salmon (*Salmo salar*) in winter: “The season of parr discontent”? Canadian Journal of Fisheries and Aquatic Sciences 55:161–180.

Dybala, K. E., J. M. Eadie, T. Gardali, N. E. Seavy, and M. P. Herzog. 2013. Projecting demographic responses to climate change: Adult and juvenile survival respond differently to direct and indirect effects of weather in a passerine population. Global Change Biology 19:2688–2697.

Essington, T. E., P. W. Sorensen, and D. G. Paron. 1998. High rate of red superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. Canadian Journal of Fisheries and Aquatic Sciences 55:2310–2316.

Falcone, J. A. 2011. GAGES II (Geospatial Attributes of Gages for Evaluating Streamflow). USGS. https://water.usgs.gov/GIS/metadata/usgswrd/XML/gagesII_Sept2011.xml

Farmer, W. H., S. A. Archfield, T. M. Over, L. E. Hay, J. H. LaFontaine, and J. E. Kiang. 2014. A comparison of methods to predict historical daily streamflow time series in the Southeastern United States. Scientific Investigations Report 2014-5231. USGS, Reston, Virginia, USA.

Fausch, K. D., Y. Taniguchi, S. Nakano, G. D. Grossman, and C. R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five holartic regions. Ecological Applications 11:1438–1455.

Fernández-Chacón, A., A. Bertolero, A. Amengual, G. Tavecchia, V. Homar, and D. Oro. 2011. Spatial heterogeneity in the effects of climate change on the population dynamics of a Mediterranean tortoise. Global Change Biology 17:3075–3088.

George, S. D., B. P. Baldigo, A. J. Smith, and G. R. Robinson. 2015. Effects of extreme floods on trout populations and fish communities in a Catskill Mountain river. Freshwater Biology 60:2511–2522.

Grossman, G. D., R. E. Ratajczak, C. M. Wagner, and J. Todd. 2009. Dynamics and population regulation of southern brook trout (*Salvelinus fontinalis*) in an Appalachian stream. Freshwater Biology 55:1494–1508.

Grossman, G. D., G. Sundin, and R. E. Ratajczak. 2016. Long-term persistence, density dependence and effects of climate change on rosyside dace (Cyprinidae). Freshwater Biology 61:832–847.

Hakala, J. P., and K. J. Hartman. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. Hydrobiologia 515:203–213.

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

Hirsch, R. M. 1979. An evaluation of some record reconstruction techniques. Water Resources Research 15:1781–1790.

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

Ingram, K. T., K. Dow, L. Carter, and J. Anderson. 2013. Climate of the Southeast United States: variability, change, impacts, and vulnerability. Island Press, Washington, D.C., USA.

Jastram, J. D., C. D. Snyder, N. P. Hitt, and K. C. Rice. 2013. Synthesis and Interpretation of Surface-Water Quality and Aquatic Biota Data Collected in Shenandoah National Park, Virginia, 1979–2009. U.S. Geological Survey Scientific Investigations Report 2013-5157.

Jellyman, P. G., and A. R. Mcintosh. 2010. Recruitment variation in a stream galaxiid fish: multiple influences on fry dynamics in a heterogeneous environment. Freshwater Biology 55:1930–1944.

Jensen, A. J., and B. O. Johnsen. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic Salmon (*Salmo salar*) and Brown Trout (*Salmo trutta*). Functional Ecology 13:778–785.

Kanno, Y., M. A. Kulp, and S. E. Moore. 2016*a*. Recovery of native Brook Trout populations following the eradication of nonnative rainbow Trout in southern Appalachian Mountains streams. North American Journal of Fisheries Management 36:1325–1335.

Kanno, Y., M. A. Kulp, S. E. Moore, and G. D. Grossman. 2017. Native brook trout and invasive rainbow trout respond differently to seasonal weather variation: Spawning timing matters. Freshwater Biology 62:868–879.

Kanno, Y., B. H. Letcher, J. A. Coombs, K. H. Nislow, and A. R. Whiteley. 2014. Linking movement and reproductive history of brook trout to assess habitat connectivity in a heterogeneous stream network. Freshwater Biology 59:142–154.

Kanno, Y., B. H. Letcher, N. P. Hitt, D. A. Boughton, J. E. B. Wofford, and E. F. Zipkin. 2015. Seasonal weather patterns drive population vital rates and persistence in a stream fish. Global Change Biology 21:1856–1870.

Kanno, Y., K. C. Pregler, N. P. Hitt, B. H. Letcher, D. J. Hocking, and J. E. B. Wofford. 2016*b*. Seasonal temperature and precipitation regulate brook trout young-of-the-year abundance and population dynamics. Freshwater Biology 61:88–99.

Kanno, Y., J. C. Vokoun, and B. H. Letcher. 2011. Fine-scale population structure and riverscape genetics of brook trout (*Salvelinus fontinalis*) distributed continuously along headwater channel networks. Molecular Ecology 20:3711–3729.

Karmalkar, A. V., and R. S. Bradley. 2017. Consequences of global warming of 1.5°C and 2°C for regional temperature and precipitation changes in the contiguous United States. PLoS ONE 12:1–17.

Kaspersson, R., J. Höjesjö, and T. Bohlin. 2012. Habitat exclusion and reduced growth: a field experiment on the effects of inter-cohort competition in young-of-the-year brown trout. Oecologia 169: 733–742.

Kéry, M. 2018. Identifiability in N-mixture models: a large-scale screening test with bird data. Ecology 99:281–288.

Kovach, R. P., C. C. Muhlfeld, R. Al-Chokhachy, J. B. Dunham, B. H. Letcher, and J. L. Kershner. 2016. Impacts of climatic variation on trout: a global synthesis and path forward. Reviews in Fish Biology and Fisheries 26:135–151.

Kunkel, K., L. E. Stevens, S. E. Stevens, L. Sun, E. Janssen, D. Wuebbles, and J. G. Dobson 2013. Regional Climate Trends and Scenarios for the U.S. National Climate Assessment Part 9. Climate of the Contiguous United States.

Lake, P. S. 2003. Ecological effects of perturbation by drought in owing waters. Freshwater Biology 48:1161–1172.

Larson, G. L., and S. E. Moore. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian Mountains. Transactions of the American Fisheries Society 114:195–203.

Letcher, B. H., D. J. Hocking, K. O'Neill, A. R. Whiteley, K. H. Nislow, and M. J. O'Donnell. 2015*a*. A robust hierarchical model of daily stream temperature using air-water temperature synchronization, autocorrelation, and time lags. PeerJ PrePrints 3: e1971.

Letcher, B. H., and T. D. Terrick. 1998. Maturation of male age-0 atlantic salmon following a massive, localized flood. Journal of Fish Biology 53:1243–1252.

Letcher, B. H., et al. 2015*b*. Robust estimates of environmental effects on population vital rates: an integrated capture-recapture model of seasonal brook trout growth, survival and movement in a stream network. Journal of Animal Ecology 84:337–352.

Lobón-Cerviá, J. 2009. Why, when and how do fish populations decline, collapse and recover? The example of brown trout (*Salmo trutta*) in Rio Chaballos (northwestern Spain). Freshwater Biology 54:1149–1162.

Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Climatic Change 102:187–223.

McCluney, K. E., N. L. Poff, M. A. Palmer, J. H. Thorp, G. C. Poole, B. S. Williams, M. R. Williams, and J. S. Baron. 2014. Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. Frontiers in Ecology and the Environment 12:48–58.

Merriam, E. R., R. Fernandez, J. T. Petty, and N. Zegre. 2017. Can brook trout survive climate change in large rivers? If it rains. Science of the Total Environment 607–608:1225–1236.

Meyers, E. M., B. Dobrowski, and C. L. Tague. 2010. Climate change impacts on flood frequency, intensity, and timing may affect Trout species in

Sagehen Creek, California. Transactions of the American Fisheries Society 139:1657–1664.

Mohseni, O., and H. G. Stefan. 1999. Stream temperature/air temperature relationship: a physical interpretation. Journal of Hydrology 218:128–141.

Moore, S. E., G. L. Larson, and B. Ridley. 1986. Population control of exotic rainbow trout in streams of a natural area park. Environmental Management 10:215–219.

Morrill, J. C., R. C. Bales, and M. H. Conklin. 2005. Estimating stream temperature from air temperature: implications for future water quality. Journal of Environmental Engineering 131:139–146.

National Academies of Sciences. 2016. Attribution of Extreme Weather Events in the Context of Climate Change. Nap 21852.

Nislow, K. H., and J. D. Armstrong. 2012. Towards a life-history-based management framework for the effects of flow on juvenile salmonids in streams and rivers. Fisheries Management and Ecology 19:451–463.

Nislow, K. H., A. J. Sepulveda, and C. L. Folt. 2004. Mechanistic linkage of hydrologic regime to summer growth of age-0 Atlantic salmon. Transactions of the American Fisheries Society 133:79–88.

Pardikes, N. A., A. M. Shapiro, L. A. Dyer, and M. L. Forister. 2015. Global weather and local butterflies: variable responses to a large-scale climate pattern along an elevational gradient. Ecology 96:2891–2901.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The Natural Flow Regime. BioScience 47:769–784.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433–455.

Roghair, C. N., C. A. Dolloff, and M. K. Underwood. 2002. Response of a brook Trout population and instream habitat to a catastrophic flood and debris flow. Transactions of the American Fisheries Society 131:718–730.

Roland, J., and S. F. Matter. 2013. Variability in winter climate and winter extremes reduces population growth of an alpine butterfly. Ecology 94:190–199.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Sato, T., R. W. El-Sabaawi, K. Campbell, T. Ohta, and J. S. Richardson. 2016. A test of the effects of timing of a pulsed resource subsidy on stream ecosystems. Journal of Animal Ecology 85:1136–1146.

Seager, R., A. Tzanova, and J. Nakamura. 2009. Drought in the Southeastern United States: causes, variability over the last millennium, and the potential for future hydroclimate change. Journal of Climate 22:5021–5045.

Seegrist, D. W., and R. Gard. 1972. Effects of floods on trout in Sagehen Creek, California. Transactions of the American Fisheries Society 101:478–482.

Snyder, C. D., N. P. Hitt, and J. A. Young. 2015. Accounting for groundwater in stream fish thermal habitat responses to climate change. Ecological Applications 25:1397–1419.

Stranko, S. A., R. H. Hilderbrand, R. P. Morgan, M. W. Staley, A. J. Becker, A. Roseberry-Lincoln, E. S. Perry, and P. T. Jacobson. 2008. Brook Trout Declines with land cover and temperature changes in Maryland. North American Journal of Fisheries Management 28:1223–1232.

US Geological Survey. 2017. National Water Information System. Reston, Virginia, USA. http://waterdata.usgs.gov/nwis/

USEPA and USGS. 2012. National Hydrography Dataset Plus - NHDPlus. http://www.horizon-systems.com/NHDPlus/index.php

USGCRP. 2017. Climate science special report: fourth National Climate Assessment, Volume I. Pages 1–470 *in* D. J. Wuebbles, D. W. Fahey, K. A. Hibbard, D. J. Dokken, B. C. Stewart, and T. K. Maycock, editors. U.S. Global Change Research Program, Washington, D.C., USA. https://science2017.globalchange.gov/downloads/CSSR2017_FullReport.pdf

Visser, A., L. Beevers, and S. Patidar. 2017. Macroinvertebrate community response to multi-annual hydrological indicators. River Research and Applications 33:707–717.

Walters, A. W. 2016. The importance of context dependence for understanding the effects of low-flow events on fish. Freshwater Science 35: 216–228.

Ward, E. J., J. H. Anderson, T. J. Beechie, G. R. Pess, and M. J. Ford. 2015. Increasing hydrologic variability threatens depleted anadromous fish populations. Global Change Biology 21:2500–2509.

Warren, M., M. J. Dunbar, and C. Smith. 2015. River flow as a determinant of salmonid distribution and abundance: a review. Environmental Biology of Fishes 98:1695–1717.

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

Wenger, S. J., et al. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences of the United States of America 108:14175–14180.

Wheeler, K., S. J. Wenger, and M. C. Freeman. 2017. States and rates: complementary approaches to developing flow-ecology relationships. Freshwater Biology. https://doi.org/10.1111/fwb.13001

Whiteley, A. R., J. A. Coombs, M. Cembrola, M. J. O'Donnell, M. Hudy, K. H. Nislow, and B. H. Letcher. 2015. Effective number of breeders provides a link between interannual variation in stream flow and individual reproductive contribution in a stream salmonid. Molecular Ecology 24:3585–3602.

Williams, J. E., A. L. Haak, K. Fesenmyer, H. M. Neville, M. Barney, and M. Mayfield. 2015. State of the Trout. Trout Unlimited, Arlington, Virginia, USA.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73:3–36.

Xu, C. L., B. H. Letcher, and K. H. Nislow. 2010*a*. Size-dependent survival of brook trout *Salvelinus fontinalis* in summer: effects of water temperature and stream flow. Journal of Fish Biology 76:2342–2369.

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

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2356/full