

ARTICLE

Strong variation in Brook Trout trends across geology, elevation, and stream size in Shenandoah National Park

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Abstract

Objective: Landscape context structures fish abundance and dynamics, and understanding trends in fish abundance across the landscape is often prerequisite for effective conservation. In this study, we evaluated the status and trends of Brook Trout *Salvelinus fontinalis* in Shenandoah National Park to understand how these are structured across bedrock geology, elevation, and stream size.

Methods: We used long-term monitoring data from 94 sites in Shenandoah National Park to evaluate trends in Brook Trout abundance over a 27-year period (1996–2022) and assess the importance of local environmental covariates using a hierarchical Bayesian N-mixture model based on depletion sampling. Focal covariates were chosen for their demonstrated importance in structuring fish populations in Shenandoah National Park and elsewhere. Bedrock geology controls sensitivity to acid deposition, watershed area is related to stream habitat features such as complexity and flow variability, and elevation creates gradients in temperature.

Result: Models revealed significant decreases in adult Brook Trout abundance over time (95% credible intervals < 0) for 31 of 94 sites (33%), and at least three sites exhibited apparent extirpations over the study period. Estimated Brook Trout abundance declined by 50% or more in approximately 70% of streams across the park over the study period. Sites with the warmest water temperatures exhibited the fastest declines in abundance. However, large watersheds on poorly buffered bedrock exhibited significant gains in abundance over time, suggesting some recovery from acid deposition due to improvements in air quality.

Conclusion: Our analysis revealed large and divergent changes in Brook Trout abundance over recent decades and suggests the importance of local water temperature and acid sensitivity as probable causal mechanisms. These results highlight the importance of considering local factors when evaluating long-term trends in stream fish populations. Results of this study can assist the development of targeted conservation actions within Shenandoah National Park and elsewhere.

KEYWORDS

acid deposition, Brook Trout, climate change, population trends

INTRODUCTION

A central challenge for fish conservation is to understand how local context mediates the influence of broadscale environmental conditions (McCluney et al. 2014). Attributes such as watershed size, elevation, geology, and land cover can influence stream fish population responses to stressors, resulting in divergent trends across the landscape. For example, bedrock geology types can vary in their buffering capacity, governing stream susceptibility to acidic deposition and leading to variable responses across the landscape (Baldigo and Lawrence 2000). Understanding the relationships between population trends and such landscape attributes is essential for prioritizing locations and tailoring conservation actions for species threatened by climate change, land-use change, and other large-scale changes.

Land-use changes (Stranko et al. 2008), nonnative species (Kirk et al. 2018; Zorn et al. 2020), acidic deposition (Baker et al. 1996), and other factors have led to widespread declines in the distribution of Brook Trout *Salvelinus fontinalis* across the southern and central Appalachian mountains in North America (Hudy et al. 2008). Ongoing land-use conversion of forested habitats continues to threaten Brook Trout populations, and many studies have predicted further declines as anthropogenic climate change progresses (Flebbe et al. 2006; Snyder et al. 2015; Bassar et al. 2016; Carlson et al. 2017). Although protected areas largely prevent land-use conversion with their boundaries, climate change, acidic deposition, and other processes that operate at regional or global scales may pervade protected area boundaries (Hansen and DeFries 2007).

Brook Trout populations across the eastern United States have been exposed to high levels of acidic deposition, especially before the 1994 Clean Air Amendments, but the effects varied across the landscape (Bailey et al. 1987; Baker et al. 1996; Robison et al. 2013). Streams within poorly buffered watersheds have exhibited low fish diversity and suppressed Brook Trout abundance, while fish communities in other streams were not obviously affected (Baldigo and Lawrence 2000; Harmon et al. 2021). This local heterogeneity in response to a regional stressor demonstrates the importance of evaluating the variation across the landscape, particularly as the effects of climate change become more pronounced.

Stream and air temperatures have risen in the eastern United States in recent decades due to climate change (Rice and Jastram 2015; Yao et al. 2021), but the local manifestation of climate change effects in streams is also likely to be mediated by landscape variables, such as elevation, stream size, and groundwater inputs (Snyder et al. 2015; Hitt et al. 2023). Air temperatures tend to decrease with

Impact statement

Brook Trout are an iconic fish that are threatened by climate change because they rely on cold water and sufficient flow. Brook Trout populations across much of Shenandoah National Park declined sharply in recent decades, especially in smaller, lower-elevation streams with warmer water temperatures. However, populations in acid-sensitive streams appear to be recovering from prior effects of acid deposition.

increasing elevation, which likely means that salmonid populations at higher elevations are less likely to be exposed to thermal stress (Stull 1988; Isaak et al. 2015). Also, streams with larger watersheds tend to be more resilient to summer drying and can offer additional opportunities for fish to move to seek refuge from stressful conditions (Childress et al. 2019). Along with underlying geology, these factors are likely to create substantial variability in the status and trends of Brook Trout across the landscape.

We used 27 years of monitoring data to examine how Brook Trout abundance and trends vary across bedrock geology, watershed area, and elevation within Shenandoah National Park. Our objectives were to (1) assess population status and trends across Shenandoah National Park and (2) understand associations between landscape characteristics and Brook Trout status and trends within the park. We focused on bedrock geology, watershed area, and elevation because of their high potential for structuring responses to changes in broadscale environmental changes based on the strong links between bedrock geology and susceptibility to acidification (Robison et al. 2013), watershed area and stream habitat (Stearman et al. 2019), and elevation and air temperature (Stull 1988). Similar landscape features are likely to mediate responses to regional stressors in other parts of the species' range, and understanding how abundance and responses to stressors vary across the landscape may assist development of location-specific conservation actions elsewhere.

METHODS

Study area

Shenandoah National Park encompasses approximately 81,000 ha within the northern Blue Ridge Mountains in Virginia, ranging from 171 to 1235 m in elevation. The park is long and narrow, following the spine of the mountain range (Figure 1). Due to its landscape position,

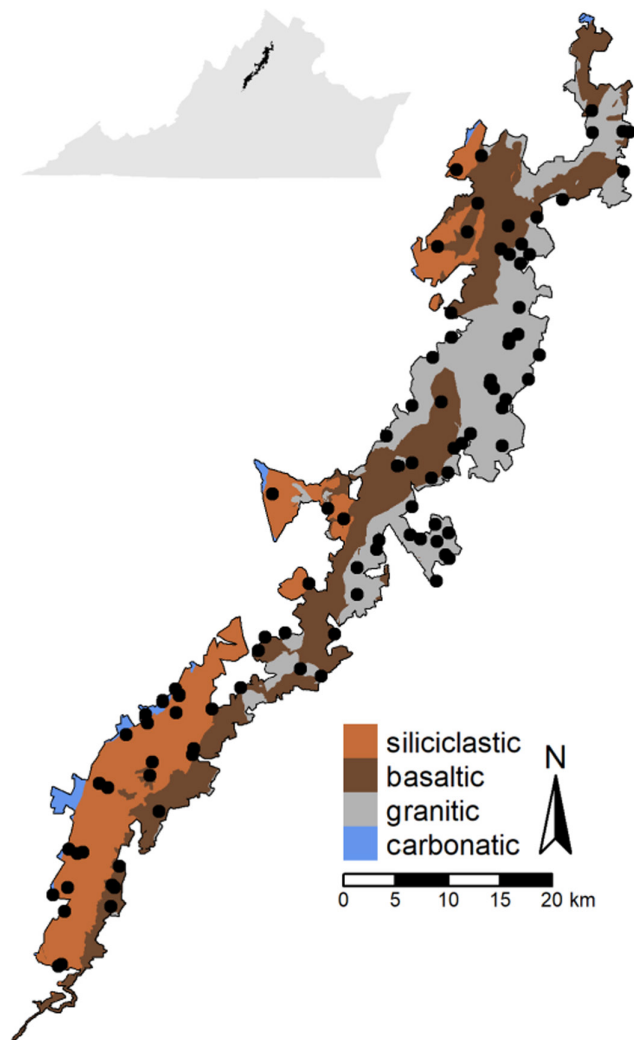


FIGURE 1 Bedrock geology within the boundaries of Shenandoah National Park, Virginia (from Southworth et al. 2009), with black dots showing fish sample sites used in this study.

Shenandoah National Park largely protects headwater systems, and there are a few places where streams flow from private land into the park. Shenandoah National Park is over 97% forested with broadleaf deciduous, mixed, and some conifer forests. Dominant tree species include oak *Quercus* spp., hickory *Carya* spp., pine *Pinus* spp., tulip tree *Liriodendron tulipifera*, maple *Acer* spp., and basswood *Tilia americana* (Cass et al. 2012). Study sites ranged from 243 to 951 m in elevation and 1.3 to 36.2 km² in watershed area and were located on first- to fourth-order streams characterized by step-pool or cascade morphology. There are approximately 330 km of streams with a watershed area of at least 1.3 km² within Shenandoah National Park.

Underlying geology varies across Shenandoah National Park, with siliciclastic, granitic, and basaltic bedrock types each comprising roughly one-third of the park area (Southworth et al. 2009; Figure 1), with varying capacity to

buffer the effects of acidic deposition (Robison et al. 2013). Streams draining siliciclastic watersheds tend to have very low acid-neutralizing capacity and lower pH, particularly during high-flow conditions (Riscassi et al. 2019; Scanlon et al. 2021). Granitic bedrock has intermediate base cation content, and basaltic bedrock contains high levels of base cations, which gives streams in watersheds with these bedrock types higher acid-neutralizing capacity and pH. Quarterly sampling from 14 streams across the study period yielded a mean pH of 5.8 for siliciclastic geology, 6.6 for granitic, and 6.9 for basaltic (Riscassi et al. 2021), and higher resolution data from one siliciclastic watershed indicates that pH typically approaches 5.0 at the highest streamflows (Riscassi et al. 2019). Carbonate geology (e.g., limestone) is also present in the park but only exists in a few low-elevation areas near the park boundary. Carbonate geology does not comprise more than 5% of the watershed of any site used in this study.

Brook Trout, Blacknose Dace *Rhinichthys atratulus*, and Blue Ridge Sculpin *Cottus caeruleomentum* are the most widespread and abundant fishes in Shenandoah National Park (E. S. Childress, unpublished data), and at least 33 fish species have been repeatedly observed within Shenandoah National Park over time (Jastram et al. 2013). Reproducing populations of Brown Trout *Salmo trutta* are currently present in one stream (two sites) included in this study and were extirpated from an additional stream during the study period. Brown Trout are removed annually from the stream with a reproducing population by National Park Service personnel via electrofishing. When Brown Trout were present in study sites, mean abundance was estimated to be 6.6 fish/100 m (Childress, unpublished data). Abundances of American Eel *Anguilla rostrata* have been increasing within one major watershed (Rappahannock River) within Shenandoah National Park due to removal of a fish passage barrier outside the park boundary in 2004 (Hitt et al. 2012).

Fish sampling

Fish populations have been surveyed in Shenandoah National Park since 1982 using backpack electrofishing with dip nets at established approximately 100-m reaches (Wofford and Demarest 2018). Cobble dams, block nets, or natural habitat breaks were used to minimize emigration during sampling. Prior to 1994 single-pass electrofishing was used, between 1994 and 2008 a combination of single-pass and three-pass depletion sampling was used, and between 2009 and 2022 all sampling was conducted using three passes. For this study, we used data from 1996 to 2022 because consistent three-pass surveys began in that year and a major flood in a few watersheds in 1995

caused severe short-term declines in Brook Trout abundance (Roghair and Dolloff 2005). We included all sites that had at least two sampling visits during the study period. Surveys used in this study were conducted between May 22 and September 27, with 96% of surveys occurring in June through August. A total of 94 sites were included, with an average of 10.4 visits per site (range = 2–21). Three passes were completed during 88.6% of surveys, and at least one three-pass survey was conducted at every site. The N-mixture models assume presence; to avoid violating this assumption due to local extirpations, data from three sites where zero Brook Trout were captured for multiple years at the end of the time series were truncated after the first zero catch.

The number of electrofishing backpack units used varied from one to three among surveys depending on stream width, and each electrofisher was accompanied by two netters. All captured Brook Trout were measured for total length (± 1 mm) and mass (± 1 g), and age-class was determined for each fish by plotting length-frequency histograms for each sampling occasion and visually determining the breakpoint between young-of-year (age-0) and older (age ≥ 1 , hereafter “adult”) Brook Trout.

Modeling

We used an N-mixture model to estimate mean abundance, trends in abundance, and their variability across site characteristics while accounting for imperfect detection (Royle 2004). Models were fit to age-0 and adult data separately due to the strong interannual variation in age-0 fish related to annual weather patterns (Kanno et al. 2016). Abundance was assumed to follow a Poisson distribution with overdispersion. We modeled mean abundance at site i in year t on the log scale with fixed effects for watershed area ($wsArea$, β_{wsArea}), elevation ($elev$, β_{elev}), and dominant geology (bedrock type comprising $>50\%$ of the watershed area, μ_{geol}), two-way interactions among these variables, and a binary variable indicating whether catastrophic flooding and debris flows occurred at the site in 1995 (β_{flood} ; equation 1). The subscript $geol$ is a placeholder for the site-specific dominant geology ($sili$ = siliciclastic, $basa$ = basaltic, and $gran$ = granitic), indicating that separate parameters were fit for each geology type. We included random intercepts at the site level ($ranSite$) and HUC14 watershed level ($ranWs$), and an overdispersion term (i.e., a random site/year term; ϵ) was also included to account for additional stochastic variation beyond that captured by the Poisson distribution and the other random effects. All random effects were assumed to be normally distributed on the log scale with mean zero and a term-specific variance. An offset term was included to

account for slight variation in site length from the 100-m target; site length was measured during each survey, and the offset was standardized to 100 m (i.e., site length/100).

$$\ln(\lambda_{i,t}) \sim \mu_{geol} + \beta_{elev-geol} \times elev_i + \beta_{wsArea-geol} \times wsArea_i + \beta_{elev-wsArea} \times elev_i \times wsArea_i + \beta_{flood} \times flood_i + \beta_{year,i} \times year_t + ranSite_i + ranWs_{w_i} + siteLength_{i,t} + \epsilon_{i,t} \quad (1)$$

Two watersheds, Staunton River and Moormans River, experienced approximately 500-year floods in 1995 that initiated debris flows eliminating Brook Trout and completely removing riparian forest in the lower reaches within the park (Wieczorek et al. 2000). Populations in these watersheds later increased as lower reaches were recolonized from upstream reaches and riparian forest and stream morphology recovered (Roghair et al. 2002). The binary flood term was included as a predictor to account for this isolated, but strong, effect on a small subset of sites ($N=7$) within these watersheds immediately preceding the study period.

Temporal trends in abundance (β_{year}) were also modeled using fixed effects of watershed area (γ_{wsArea}), elevation (γ_{elev}), dominant geology (γ_{geol}), binary flood indicator (γ_{flood}), and two-way interactions between dominant geology and watershed area and elevation (equation 2). Again, $geol$ is a placeholder for site-specific dominant geology as above. We included random slopes for year at the site and watershed level.

$$\beta_{year,i} = \gamma_{geol} + \gamma_{elev-geol} \times elev_i + \gamma_{wsArea-geol} \times wsArea_i + \gamma_{elev-wsArea} \times elev_i \times wsArea_i + \gamma_{flood} \times flood_i + ranSiteTrend_i + ranWsTrend_{w_i} \quad (2)$$

To account for detection probability, we modeled captures during each electrofishing pass as a binomial draw from a latent abundance variable (equation 3). The number captured during each pass (y) was subtracted from latent abundance prior to subsequent binomial draws representing additional passes. Capture probability of Brook Trout is likely to vary among locations and sampling occasions based on site conditions during sampling (e.g., streamflow, habitat characteristics). Therefore, we included wetted stream width, which was measured at 11 transects (every 10 m) at each site after electrofishing, as a covariate and a random site effect, and capture probability was assumed to be constant across all electrofishing passes during a sampling event.

$$\begin{aligned} y_{i,j,1} &\sim \text{Binomial}(N_{i,j}, p_{i,j}) \\ y_{i,j,2} &\sim \text{Binomial}(N_{i,j} - y_{i,j,1}, p_{i,j}) \\ y_{i,j,3} &\sim \text{Binomial}(N_{i,j} - y_{i,j,1} - y_{i,j,2}, p_{i,j}) \end{aligned} \quad (3)$$

The model was fit in a Bayesian framework in R (R Core Team 2022) and JAGS (Plummer 2003). Diffuse priors were used for all parameters. The model was fit with three Markov chains, and the first 20,000 iterations were discarded, then every 200th sample from the next 200,000 iterations was retained. Model convergence and chain mixing were evaluated by visually inspecting posterior chains and using scale-reduction factors, which are typically interpreted as indicating poor mixing when they are greater than 1.1 (Brooks and Gelman 1998). We used posterior predictive checks for each age-class and electrofishing pass to evaluate model goodness of fit. Predicted captures were generated during parameter estimation and used to estimate Bayesian *p*-values, which are the proportion of the predicted data that are greater than the observed data. We included an overall Bayesian *p*-value for each age-class below, and values for each electrofishing pass can be found in the Supplemental Materials available in the online version of this article. Values near 0.5 indicate a lack of bias (Gelman et al. 2013).

Post hoc temperature analysis

The primary goals of this study were to identify the variation in Brook Trout abundance and trends across the park and understand associations between landscape characteristics and the observed status and trends. Thus, we used landscape predictors in the primary analysis. However, to begin to interpret why trends in Brook Trout abundance may vary across the landscape, we explored whether differences in thermal conditions were associated with variation in trends and whether air temperatures changed across the study period.

We used instantaneous temperature data collected at the study sites during fish sampling to characterize stream temperatures at each study site. Although instantaneous temperatures are noisier than long-term means, they have been shown to be valuable indicators of spatial and temporal variation (Rice and Jastram 2015). We restricted the data set to temperatures collected in June–September between 1996 and 2022 to characterize summer temperatures but included sites that were not included in the Brook Trout trend analysis to improve estimation of among-site variance, which resulted in a data set containing 1093 temperature measurements across 154 sites.

To account for diel and seasonal effects, we first fit a linear mixed-effects model to the temperature data with day of the year, day of the year squared, and time of day (decimal hour; range = 7.4–16.9) as fixed effects and site-level random intercepts. Covariates were *z*-score standardized; thus, the random intercepts represent the predicted average temperature at the average sampling date and time. This provides a metric reflecting the relative

thermal environment across the sites (i.e., “colder” versus “warmer” sites) corrected for seasonal and diel fluctuations in stream temperature, with some shrinkage toward the mean for sites without substantial data.

Next, we fit a linear regression between site elevation and relative stream temperature because the influence of elevation on air temperature and subsequently water temperature is the most likely explanation for elevation effects on Brook Trout populations. In contrast, though watershed area could affect stream temperature, area was not included here because it also likely influences Brook Trout populations via other mechanisms, such as influencing the habitat volume, presence of refuge during dry periods, and vulnerability to predation.

Then, we fit a linear regression with the estimated site-specific age-0 or adult Brook Trout trend as the response variable and relative stream temperature, geology type, watershed area, and interactions between geology type and the other covariates as predictors to understand whether Brook Trout trends differed by stream temperature and whether that relationship varied across geology types.

Finally, we evaluated whether air temperatures changed across the study period using two data sources: a Clean Air Status and Trends Network monitoring station at Big Meadows located centrally in the park (SHN418; U.S. Environmental Protection Agency 2023) and the NClimGrid monthly gridded climate data set (Vose et al. 2014). The NClimGrid data contained 43 locations within the park for which monthly averages were modeled from historical weather data; we averaged data from these locations within time periods to evaluate average patterns across the park. Temperature data from the Big Meadows weather station were largely complete, but data from 2007 were excluded because there was a gap of several months; other years in the study period were 97% complete on average. The precipitation data from the Big Meadows weather station site had many large gaps and were not used. We used simple linear regression to evaluate trends in mean July temperature, mean annual temperature, and annual precipitation (NClimGrid only).

Parkwide predictions

To explore management implications for unsampled locations in the park, we used the fitted parameters from the adult model to predict abundance and trends in stream segments parkwide. We chose the adult model because adult fish are the focus of management and because the parametric uncertainty and random variation were lower than in the age-0 model, making it more reliable for out of sample prediction. We derived the stream network from a digital elevation model (U.S. Geological

Survey 2020) and split into reaches between each confluence, then split any reaches longer than 500 m into sections that were less than 500 m long to minimize variability in watershed area and elevation within reaches; mean reach length was 390 m. We used fixed effects, excluding the flood effect, plus watershed-level (HUC14) random effects to predict Brook Trout abundance and trends across the entire stream network. We excluded the flood effect during prediction because the focus of the study is on long-term changes rather than recovery from catastrophic flooding, which has been well documented for these events (Roghair et al. 2002). The implications of this are discussed below. Because the predicted 2022 abundance does not include the random year effect, the predictions represent abundance in an average year occurring at the same time as 2022.

RESULTS

Abundance and trend model

Inspection of scale-reduction factors and Bayesian p -values indicated model convergence and the ability to reproduce the sample data without bias (scale-reduction factors < 1.01 ; Bayesian p -value = 0.43 adult model, 0.44 age-0 model; Figure S1 available in the Supplemental Materials in the online version on this article).

Brook Trout mean abundance and trends varied strongly across geology type, elevation, watershed area, and flood history (Figures 2 and 3; Figure S2). In general, parameters from models fit only to age-0 fish or adults were similar with a few exceptions (Figure 4), which are described below. Trends at individual sites were also very similar between models fit to adults and age-0 fish; however, the credible intervals for site-level age-0 trends were much more likely to overlap with zero (Figure 5).

Overall, mean abundance increased with elevation and watershed area, and there was a significant positive interaction between the two (Figure 4). Estimated mean abundances across the sampled parameter space (Figure 2) were within the range of observed values for age-0 and adult age-classes (Figure S2). The slight differences in mean abundance among geology types were not statistically significant at the 95% level. Catastrophic flooding did not have a significant effect on mean abundance at the 95% level, but posterior means were positive. At sites that experienced catastrophic flooding, the posterior mean estimate was an increase of 72% for age-0 fish (posterior 85% positive) and 41% for adults (posterior 74% positive). Elevation and watershed area effects were strong and associated with high variability in estimated abundance across sites (Figure 2).

Trends in Brook Trout abundance varied substantially across the 94 study sites, and credible intervals tended to be narrower for adults than age-0 fish, leading to a higher proportion of statistically significant results (Figure 5). Age-0 fish exhibited negative trends at the 95% confidence level for 21% of sites, and adult fish showed negative trends at 33% of sites; 41% of sites showed negative adult trends at the 90% confidence level. Positive trends were evident at a smaller proportion of sites, with age-0 fish exhibiting increases at 3% of sites and adults at 14% of sites at the 95% confidence level (Figure 5).

In contrast to mean abundance, trends in abundance varied strongly by bedrock geology type, with no significant trends in siliciclastic watersheds (age-0 fish: posterior mean = -0.9% annually, 95% CI = -5.6% to 4.0% ; adult: 1.4% , -1.6% to 4.9%) but strong negative trends in basaltic watersheds (age-0 fish: -5.5% , -9.9% to -0.9% ; adult: -5.1% , -8.1% to -1.9%) and marginally significant negative trends in granitic watersheds (age-0 fish: -4.3% , -8.8% to 0.3% ; adult: -2.8% , -5.7% to 0.3%) at mean elevation and watershed area. High elevation and larger watershed sites had more positive trends in abundance in basaltic and granitic watersheds, whereas abundance trends in siliciclastic watersheds increased with watershed area but were less affected by elevation (Figure 4). Together, these effects created strong variation in trends across site characteristics (Figure 3). Siliciclastic sites were estimated to have no significant trend in smaller watersheds but significant positive trends in large watersheds. In contrast, basaltic and granitic sites were estimated to have strong negative trends in small watersheds at low elevations and no significant trend in high elevation and/or large watershed locations. Sites that experienced catastrophic flooding just prior to the start of the study period had significantly higher trends, reflecting the recovery of the populations after the major disturbance.

Overall patterns of mean abundance and temporal trends were very similar between age-0 and adult fish (Figure 5). However, the magnitude of the variance was higher for the overdispersion parameter and marginally higher for the year random effect from the model fit to the age-0 data than the model fit to the adult data. Other variance parameters were similar between the two life stages. Detection probability was higher for adults (0.69; 95% CI = 0.68–0.71) than age-0 fish (0.56; 95% CI = 0.54–0.57) and declined significantly with increasing stream width for both life stages (Figure S3).

Post hoc temperature analysis

Point temperature measurements were significantly related to day of the year, day of the year squared, and time

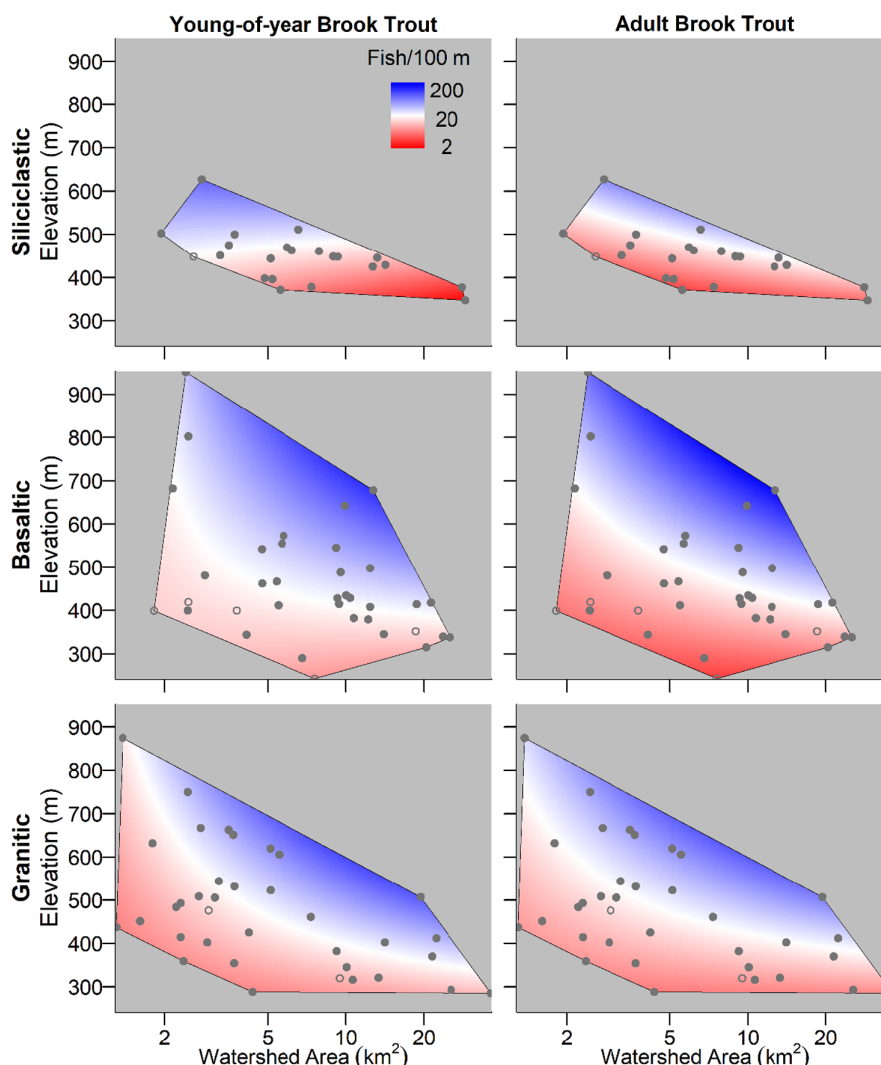


FIGURE 2 Brook Trout young-of-year (left panels) and adult (right panels) estimated mean abundance (posterior mean) across bedrock geology type (rows), watershed area, and elevation from a model driven by 94 sites in Shenandoah National Park from 1996 to 2022. Points show the covariate values of individual sampling sites. Open symbols are sites where Brook Trout were not detected during the final sampling visit.

of day in the linear mixed-effects model, and site-specific random intercepts had a standard deviation of 1.2°C. Site-specific intercepts, which estimate the average temperature on the mean sample date and time, were correlated with site elevation (slope = $-5.5^{\circ}\text{C}/\text{km}$, $p < 0.001$, $R^2 = 0.48$; Figure S4). Brook Trout abundance trend models lacked a significant interaction between temperature and geology for age-0 fish ($F_{2,78} = 1.6$, $p = 0.21$) or adults ($F_{2,78} = 2.0$, $p = 0.14$). Moreover, a model without the interaction term explained most of the variation in abundance trends for both age-0 ($F_{6,80} = 20.74$, $p < 0.001$, $R^2 = 0.61$) and adult fish ($F_{6,80} = 35.7$, $p < 0.001$, $R^2 = 0.73$). The regression indicated a negative relationship between abundance trends and temperature for both age-0 (slope = -0.14 , $p < 0.001$) and adult fish (slope = -0.13 , $p < 0.001$).

Mean annual and July air temperatures increased significantly (Figure S5) for both the Big Meadows weather

station (annual: slope = $0.039^{\circ}\text{C}/\text{year}$, $p = 0.03$; July: slope = $0.058^{\circ}\text{C}/\text{year}$, $p = 0.04$) and parkwide average NClimGrid data (annual: slope = $0.038^{\circ}\text{C}/\text{year}$, $p = 0.01$; July: slope = $0.064^{\circ}\text{C}/\text{year}$, $p = 0.03$). In contrast, there was no significant trend in NClimGrid annual precipitation across the study period ($p = 0.75$).

Parkwide predictions

Across all stream reaches with a watershed area of at least 1.3 km², 12% of stream length was predicted to have very low adult Brook Trout abundance (<2 individuals per 100 m), and 36% of stream length was predicted to support fewer than five adult fish per 100 m on average. Despite having increasing trends, siliciclastic watersheds were only predicted to have high abundance (i.e., >50

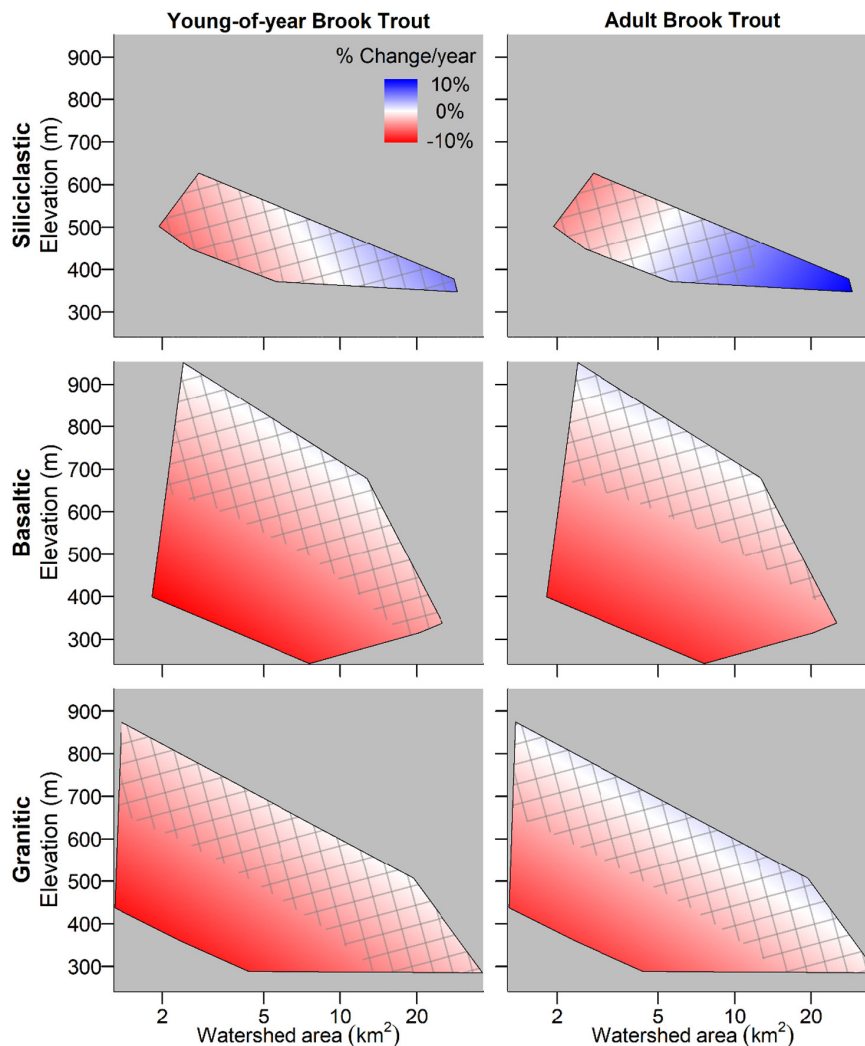


FIGURE 3 Heat maps showing estimated (posterior mean) 27-year trends (colors) in young-of-year (left panels) and adult (right panels) Brook Trout abundance across different bedrock geology (rows), watershed area, and elevation based on 94 sites in Shenandoah National Park. Estimates are only shown within polygons surrounding the combinations of geology, watershed area, and elevation that were sampled. Cross-hatching indicates areas where the 95% credible interval for the trend overlapped zero.

adults per 100 m) in a very small percent of park streams (1.3 km, 0.3%). The highest present-day abundances were predicted within the central part of the park, where larger watershed areas occurred at higher elevations on the eastern slope of the Blue Ridge (Figure 6).

Adult Brook Trout abundance was predicted to be declining by at least 2.5% annually (i.e., 50% over 27 years) in more than 70% of the total stream length within the park, and only 11% of stream length was predicted to have a trend greater than or equal to zero (Figure 6). Streams with predicted increasing trends were largely located in the southwestern part of the park, where siliciclastic bedrock dominates (Figures 1 and 6). However, a few sections of streams in granitic and basaltic watersheds were predicted to have positive trends, and these occurred in larger watersheds at higher elevations in many of the same locations with high predicted abundance.

Overall, the predictions mirrored the estimated trends closely (Figure S6). However, because the flood effect on mean abundance and temporal trend was excluded for these predictions, the trends were consistently underpredicted at sites that experienced catastrophic flooding and associated debris flows (Figure S6). Mean abundance was also underpredicted at five of these flood sites, consistent with the potential positive effect of the flood on mean abundance at these sites described above.

DISCUSSION

Our results indicate that there have been strong and divergent trends in Brook Trout abundance across Shenandoah National Park streams over recent decades. The park has not been subject to land-use changes associated with reduced

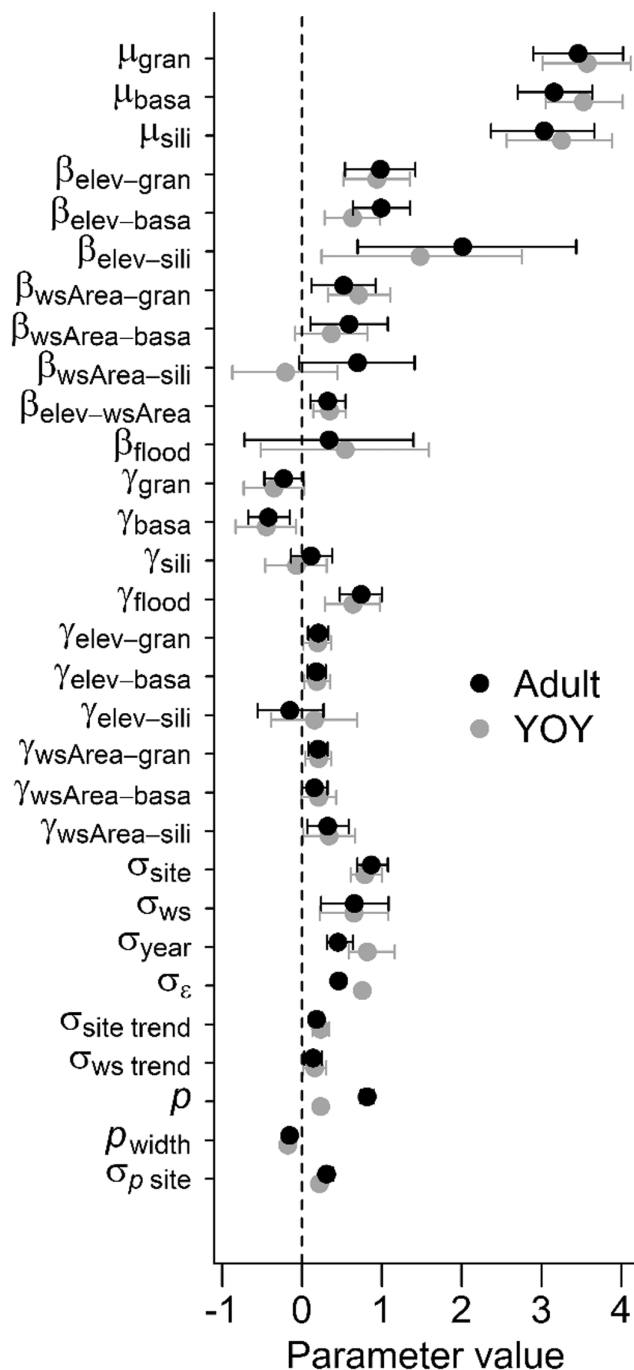


FIGURE 4 Estimated parameter values for models predicting young-of-year (YOY; gray) and adult (black) Brook Trout abundance at 94 sites across Shenandoah National Park from 1996 to 2022. Points represent the posterior mean, and whiskers display the 95% credible interval. Symbols indicate the following: μ represents geology-specific intercepts, β represents fixed effects on mean abundance, γ shows interactions with year (i.e., fixed effects on trend), σ shows standard deviations for random effects, and ρ indicates terms in the detection model (see Methods for full equations).

occupancy and declines in abundance elsewhere (Hudy et al. 2008; Stranko et al. 2008), nonnative salmonids are very rare within the park, and fisheries management has

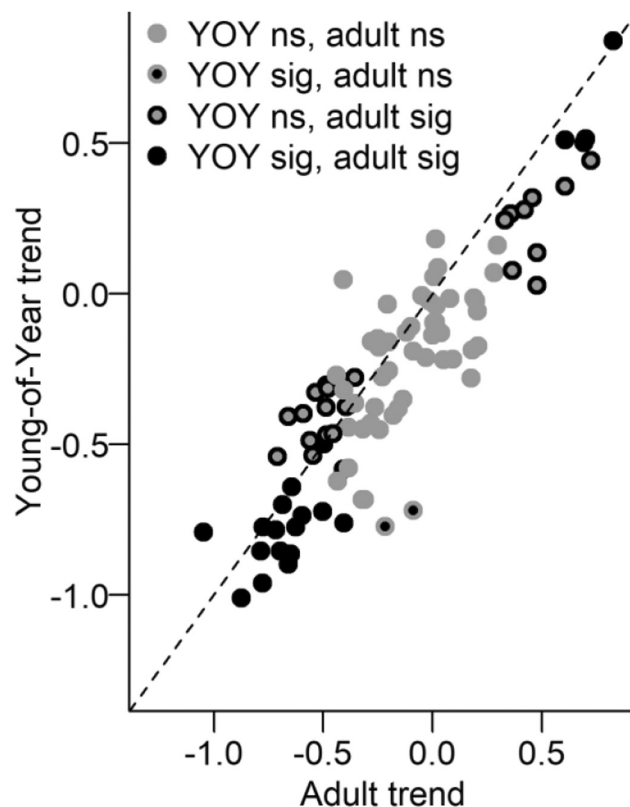


FIGURE 5 Independently estimated trends for young-of-year (YOY) and adult Brook Trout from 1996 to 2022 for sites across Shenandoah National Park. The dashed line is the 1:1 line. Color combinations indicate whether 95% credible intervals for the trend of each life stage overlapped zero (“ns”) or not (“sig”).

not changed substantially (E. D. Demarest, personal communication), and yet, most Brook Trout populations within Shenandoah National Park have declined dramatically over recent decades. Thus, regional- or global-scale changes that operate across protected area boundaries, including climate change and recovery from acid deposition, are most likely at the root of these declines. However, the trends were highly variable across landscape characteristics, highlighting the role of local (i.e., watershed and subwatershed) factors in mediating the effects of regional or global processes. Managers can apply our results to consider where conservation efforts could be targeted based on where populations appear to be most and least resilient.

The strong effects of bedrock geology on Brook Trout abundance and trends likely stem from its central role in mediating stream morphology, chemistry, and hydrology. Siliciclastic streams with larger watersheds had estimated increases in adult Brook Trout abundance of two- to five-fold over the study period, whereas most populations in basaltic and granitic watersheds exhibited sharp declines. Of particular relevance within Shenandoah National Park, underlying geology mediates the response of stream chemistry and

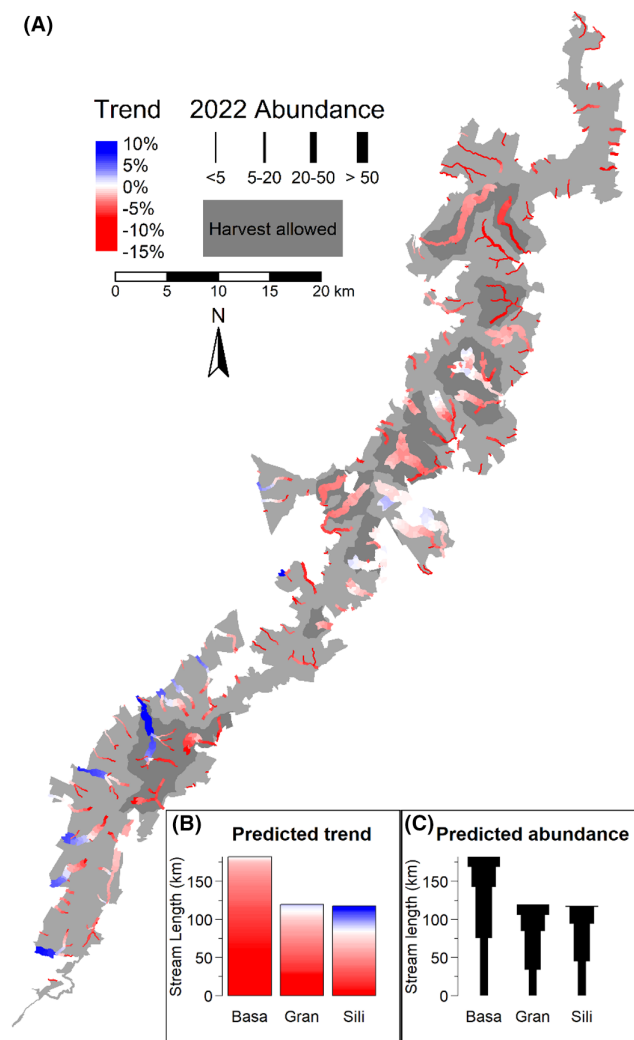


FIGURE 6 (A) Predicted adult Brook Trout trends (line color) and 2022 abundance (line width, fish per 100 m) across streams in Shenandoah National Park. Dark-gray areas show watersheds where recreational harvest of Brook Trout is legal within the park. The bar charts show (B) stream length within each geology type colored by predicted trend and (C) stream length within each geology type with bar width reflecting the abundance categories shown on the map (i.e., <5, 5–20, 20–50, and >50 adults per 100 m in order of increasing width).

biota to acidic deposition. The poorly buffered siliciclastic watersheds within Shenandoah National Park have lower acid-neutralizing capacity and pH than those draining other geology types (Robison et al. 2013), which is associated with reduced fish species richness within Shenandoah National Park's siliciclastic streams (Harmon et al. 2021) and has been implicated in declines and extirpations of Brook Trout in the park and elsewhere (Bulger et al. 1995). Although the 1990 Clean Air Act amendments greatly reduced acidic emissions (LaCount et al. 2021), Shenandoah National Park's siliciclastic watersheds have been slow to recover due to the large quantities of sulfate stored in their soils (Scanlon

et al. 2021). Streams in siliciclastic watersheds tend to have low pH at base flow, but the most physiologically stressful conditions for fish occur during high-flow events, when sulfate is flushed from shallow soils and pH can decrease sharply (Baker et al. 1996). Although base flow pH changed little over the study period in siliciclastic streams in Shenandoah National Park, the decreases associated with flood events have become less severe since the mid-1990s (Riscassi et al. 2019; Scanlon et al. 2021). Surprisingly, this modest recovery from acidic deposition in siliciclastic watersheds appeared to override the negative trends observed within other geology types during the study period.

Bedrock geology also influenced how Brook Trout trends varied across elevation and watershed area, which may reflect differences in hydrology or stream morphology or spatial variation in recovery from acidification. Elevation and watershed area were both associated with variation in abundance trends in basaltic and granitic watersheds, but only watershed area was important in siliciclastic watersheds. This difference may be partly driven by the narrower elevation range within siliciclastic watersheds in the park and could also reflect differences in hydrology or stream morphology, but larger watersheds also tend to have more stable and higher pH because they integrate the more variable inputs from their subwatersheds (Povak et al. 2013; Snyder et al. 2013). Although high-resolution, long-term temperature data were not available for this study, point temperature measurements taken during fish surveys were associated with elevation, and posterior means of trends in Brook Trout abundance were also correlated directly with estimates of stream temperature derived from point temperature measurements. Variability in groundwater inputs also creates heterogeneity in thermal regimes within Shenandoah National Park (Snyder et al. 2015; Johnson et al. 2017; Briggs et al. 2018); however, elevation had a clear effect on stream temperature, likely driven by the negative relationship between elevation and air temperature. Indeed, the slope of the water temperature–elevation regression closely matched the slope of air temperature–elevation relationships expected from boundary-layer meteorology (Stull 1988). The association between elevation and temperature, the lack of alternative hypotheses for the mechanism underlying the effect of elevation, and the correlation between abundance trends and temperature all indicate that sites with higher stream temperatures were more likely to decline during the study, which is consistent with a large literature describing the influence of temperature on Brook Trout distribution and demography (Wehrly et al. 2007; DeWeber and Wagner 2014; Childress and Letcher 2017). Further, the increasing air temperatures

in the park during the study period create a plausible link between temporal changes in temperature and trends in Brook Trout abundance. Streams with higher average temperatures likely also have higher frequencies of stressful high temperatures in response to recent increases in regional temperatures due to climate change (Rice and Jastram 2015; Yao et al. 2021). However, the association between abundance trends and temperature could also reflect increased vulnerability of higher temperature sites to other stressors (e.g., Hitt et al. 2017). In either case, continued warming due to climate change would be expected to extend or exacerbate these trends (Snyder et al. 2015).

The importance of watershed area for both trends and average abundance was largely consistent across the study sites. Larger streams tend to provide more refuge during low-flow, high-temperature periods (Petty et al. 2012; Childress et al. 2019), perhaps related to increased mobility or the presence of deeper pools. Thus, it is likely that stream size mediates the effects of changing precipitation or air temperature regimes, but the specific mechanism behind the relationship between watershed area and Brook Trout trends is less certain. Still, the influence of watershed area provides important information about where to focus conservation efforts.

Brook Trout populations often exhibit high among-year variability, which has been shown to limit power to detect trends and create differences in power to detect trends between age-0 fish and adults in simulation studies (Wagner et al. 2014; Hilderbrand and Kazyak 2017; Pregler et al. 2019). Our empirical results confirm these predictions with the lower among-year variance in adult populations reflected in a higher proportion of significant trends in adult than age-0 Brook Trout abundance for both positive and negative trends. Brook Trout reproductive success and age-0 abundance are strongly influenced by interannual variation in weather (Kanno et al. 2016; Blum et al. 2018), which is reflected in the higher among-year variance identified in our models. Detection probabilities were also lower for age-0 fish than adults. Both factors contribute to uncertainty in parameter estimates, which were higher for trend-related parameters in the age-0 model than in the adult model, reducing the power to detect population trends in age-0 fish. Previous research has demonstrated that including temporal covariates did not substantially increase the power to detect trends in Brook Trout (Pregler et al. 2019). However, our result that trends across Shenandoah National Park were highly variable and strongly structured by landscape attributes indicates that including relevant spatial covariates is likely to have large implications for overall trend detection.

The catastrophic flooding in two watersheds within Shenandoah National Park in 1995 reduced Brook Trout

populations several fold, but as indicated by our results and reported elsewhere, populations rebounded (Roghair et al. 2002; Roghair and Dolloff 2005). Our results suggest that catastrophic flooding may have increased mean abundance as well, with higher confidence in the effect for age-0 Brook Trout. There are few analogs in the literature of salmonid responses to floods of this scale given their rarity, but several studies have demonstrated positive effects of flooding on salmonid spawning success and habitat quality (Ortlepp and Mürle 2003; Harrison et al. 2017). Thus, it is possible that despite short-term population declines, the floods increased abundance on a longer timescale by improving habitat quality.

Conservation implications

Because conservation actions are inherently location-specific, addressing the impacts of climate change, acid deposition, and other large-scale stressors requires understanding the variation in system responses across the landscape to be able to prioritize conservation actions. Thus, understanding the variation in Brook Trout populations across Shenandoah National Park can help target conservation efforts to maximize benefits. Although most streams within Shenandoah National Park have become less suitable for Brook Trout and exhibited low and declining abundance, populations in relatively large watersheds situated at high elevations and populations in large siliciclastic watersheds appear to have been more resilient over the study period. These populations may benefit from additional protection, for example by targeting forest pest treatments to ensure stable and persistent riparian forest. The positive trends in siliciclastic watersheds suggest that increasing the rate or magnitude of recovery from the effects of acidic deposition may further bolster these populations. Additionally, populations that have declined precipitously may no longer be robust to the effects of recreational harvest, and changes to fishing regulations may help slow declines.

Given the association with stream temperature, negative trends may continue as temperatures continue to warm. The retraction of populations upstream as low-elevation populations decline further increases isolation, which is already significant in Appalachian Brook Trout populations and has increased extirpation risk and led to genetically depauperate populations (Kazyak et al. 2022). A more detailed understanding of the mechanisms behind the landscape variation in Brook Trout trends found in this study will be important for inference about future changes. For example, the recovery of depressed populations in acid-sensitive watersheds may mask declining habitat quality from other stressors that

could cause declines on longer time scales. However, it is also possible that these watersheds may be more resilient, and a better understanding of how flow regimes, stream temperature regimes, sedimentation, and other possible stressors have changed and vary across the landscape is necessary to tease apart the underlying causes.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available upon request.

ETHICS STATEMENT

Handling of fish was carried out in accordance with American Fisheries Society *Guidelines for the Use of Fishes in Research* (Use of Fishes in Research Committee 2014).

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SUPPORTING INFORMATION

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