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Seasonal temperature and precipitation regulate brook trout young-of-the-year abundance and population dynamics

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SUMMARY

1. Abundance of the young-of-the-year (YOY) fish can vary greatly among years and it may be driven by several key biological processes (i.e. adult spawning, egg survival and fry survival) that span several months. However, the relative influence of seasonal weather patterns on YOY abundance is poorly understood.
2. We assessed the importance of seasonal air temperature (a surrogate for stream temperature) and precipitation (a surrogate for stream flow) on brook trout (*Salvelinus fontinalis*) YOY summer abundance using a 29-year data set from 115 sites in Shenandoah National Park, Virginia, U.S.A. We used a Bayesian hierarchical model that allowed the effect of seasonal weather covariates to vary among sites and accounted for imperfect detection of individuals.
3. Summer YOY abundance was affected by preceding seasonal air temperature and precipitation, and these regional-scale drivers led to spatial synchrony in YOY abundance dynamics across the 170-km-long study area. Mean winter precipitation had the greatest effect on YOY abundance and the relationship was negative. Mean autumn precipitation, and winter and spring temperature had significantly positive effects on YOY abundance, and mean autumn temperature had a significant negative effect. In addition, the effect of summer precipitation differed along a latitudinal gradient, with YOY abundance at more northern sites being more responsive to inter-annual variation in summer precipitation.
4. Strong YOY years resulted in high abundance of adults (>age 1 + fish) in the subsequent year at more than half of sites. However, higher adult abundance did not result in higher YOY abundance in the subsequent year at any of the study sites (i.e. no positive stock–recruitment relationship).
5. Our results indicate that YOY abundance is a key driver of brook trout population dynamics that is mediated by seasonal weather patterns. A reliable assessment of climate change impacts on brook trout needs to account for how alternations in seasonal weather patterns impact YOY abundance and how such relationships may differ across the range of brook trout distribution.

Keywords: Bayesian hierarchical models, climate change, population dynamics, recruitment, salmonids

Introduction

Abundance of young-of-the-year (YOY) individuals varies widely over time in many teleosts (Allen & Pine, 2000; Jellyman & Mcintosh, 2010; Jenkins, Conron & Morison, 2010). YOY abundance is regulated by abiotic and biotic conditions in freshwater fishes. Spawning success, egg survival and post-hatching survival have been linked to water temperature (Warren *et al.*, 2012; Rolls *et al.*, 2013) and stream flow (Fausch *et al.*, 2001;

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Smith, Odenkirk & Reeser, 2005; Dutterer *et al.*, 2013). This indicates that climate change is a mechanism that will likely affect YOY abundance dynamics. Various forms of stock-recruitment relationships (e.g. linear and nonlinear) have been proposed for fish populations (Ricker, 1975), with differences due to a combination of taxonomy, the strength of environmental factors and the range of fish density investigated (Begg & Marteinsdottir, 2002; Nicola *et al.*, 2008; Grossman *et al.*, 2010; Thorson, Jensen & Zipkin, 2014).

Annual fluctuation in YOY abundance is likely due to several biological processes spanning months. In autumn-spawning salmonids, for example, environmental conditions during pre-spawning, spawning, egg-incubating and fry-rearing periods may affect YOY abundance (Roghair, Dolloff & Underwood, 2002; Carline & McCullough, 2003; Warren *et al.*, 2012; Letcher *et al.*, 2015). However, little is known about the relative importance of seasonal weather conditions on YOY abundance in freshwater fish populations (e.g. Goto *et al.*, 2015; Letcher *et al.*, 2015). Further, the strength of environmental factors affecting YOY abundance may vary among locations (Deschênes & Rodríguez, 2007; McCargo & Peterson, 2010). This is difficult to study because it requires long-term population data collected at multiple locations.

Using a 29-year population data set at 115 stream sites, we investigated the effect of seasonal air temperature and precipitation on temporal and spatial variability in summer YOY abundance of brook trout (*Salvelinus fontinalis*) in Shenandoah National Park (SNP), Virginia, U.S.A. Here, YOY refers to those individuals in their first summer that have attained a body size large enough to be sampled by electrofishing gears (*c.* <90 mm in total length). Air temperature was considered a surrogate for stream temperature, and precipitation was a surrogate for stream flow.

Our objectives were three-fold. The first objective was to identify seasonal weather covariates that affected brook trout YOY abundance. Although summer weather patterns are unquestionably important for coldwater salmonids, recent studies have indicated that brook trout population responses to environmental change are season-specific (Kanno *et al.*, 2015a; Letcher *et al.*, 2015). Second, we examined whether the effect of seasonal weather covariates on YOY abundance differed among stream sites. The study sites differed in watershed areas (range: 1.3–36.2 km^2) and were located in a rugged terrain with elevation ranging from 285 to 802 m above sea level along a 170-km long range running from the north to the south. Therefore, we evaluated how effects of seasonal covariates changed along these environmental gradients. Third, we explored the relationships between YOY abundance in the present year and adult abundance in the following year, and adult abundance in the present year and YOY abundance in the following year, in order to compare the relative importance of the two life stages in driving brook trout population dynamics. To address these objectives, we used a hierarchical model in the Bayesian framework to account for spatial variability in YOY abundance relationships and imperfect detection of individuals.

Methods

Fish data

We analysed a long-term monitoring data set collected by the National Park Service between 1982 and 2010 at 115 sites located throughout the SNP, Virginia, U.S.A. (Fig. 1). The SNP spans across a 170-km long mountain range from south to north. Study sites ranged from 285 to 802 m (median = 437) in elevation, and from 1.3 to 36.2 km^2 (median = 8.1) in watershed area (Table 1). Approximately 40% of the SNP is designated as wilderness, and the study area is predominantly characterised with a mix of deciduous and coniferous forests. Sites were located on small, well-shaded headwater streams (first- to third-order), and many were moderate- to high-gradient streams (median channel slope 6.0%) characterised as step-pool or cascade habitats (Table 1). Stream flow typically peaks in spring, followed by low-flow

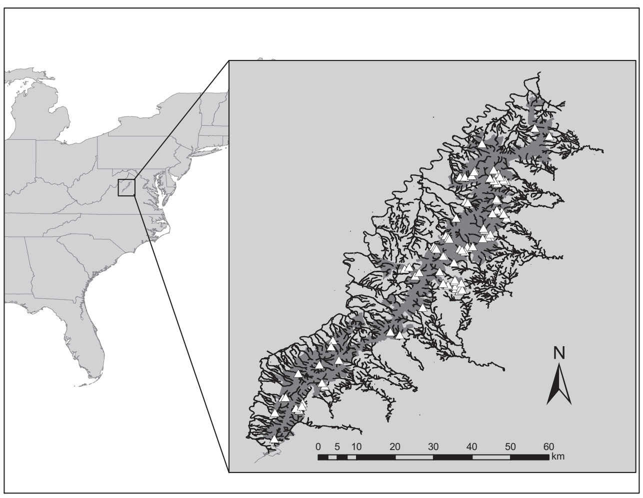

Fig. 1 Map of the Shenandoah National Park (shaded by dark grey) showing 115 fish survey sites (white triangles). Streams are shown in black lines.

Table 1 Summary of seasonal and site-specific environmental data at 115 study sites in the Shenandoah National Park, Virginia, U.S.A., between 1982 and 2010

	Median	Mean	Min.	Max.
Seasonal weather*				
Autumn precipitation (mm)	332.9	325.0	116.4	574.9
Winter precipitation (mm)	242.2	242.2	95.7	514.0
Spring precipitation (mm)	325.0	323.1	177.0	467.0
Summer precipitation (mm)	362.0	343.5	189.8	535.3
Autumn temperature (°C)	18.2	18.2	16.5	20.0
Winter temperature (°C)	6.5	6.1	2.9	9.1
Spring temperature (°C)	17.1	17.0	14.9	19.5
Summer temperature (°C)	27.2	27.4	25.9	28.9
Local sites†				
Latitude	38°52515′N	NA	38°09702′N	38°82609′N
Longitude	78°38048′W	NA	78°81184′W	78°15434′W
Elevation (m)	437	459	285	802
Channel slope (%)	6.0	7.4	0	24.0
Watershed area (km^2)	8.07	9.45	1.31	36.24
Max wetted stream width (m)	5.4	5.8	2.8	10.8
Max water depth (m)	0.39	0.40	0.26	0.54

*Seasonal weather data were based on the Daymet database (http://daymet.ornl.gov). Seasonal precipitation represents total amount of precipitation in each season, and seasonal temperature represents mean daily maximum air temperature in each season. For each year, seasonal precipitation and temperature values were calculated by averaging across 115 study sites, and summary statistics above are median, mean and range across the 29-year study period.

†Elevation, channel slope and watershed area were derived in GIS from the National Elevation Dataset (http://ned.usgs.gov/). Wetted stream width and water depth were based on measurements in the field at ten transects located perpendicular to stream flow and spaced equally across the upstream–downstream length.

conditions in late summer to autumn. Brook trout was one of few fish species in study sites and is typically short-lived (<3–4 years) in headwater streams (Grossman *et al*., 2010; Xu, Letcher & Nislow, 2010). Thus, the study period (29 years) was long enough to include multiple brook trout generations. Other common species were blacknose dace (*Rhinichthys atratulus*), mottled sculpin (*Cottus bairdi*) and fantail darter (*Etheostoma flabellare*; Jastram *et al*., 2013).

Brook trout populations have been surveyed in the SNP since 1982. Backpack electro-shocker units were used to sample brook trout at a 100-m permanent section at each stream site (Jastram *et al*., 2013). Prior to sampling, block nets or cobble dams were set up at upstream and downstream boundaries of sample sections. Block nets or cobble dams were not used when site boundaries coincided with natural geomorphic habitat breaks (e.g. step pools) that impeded fish movement. Single-pass electrofishing surveys were used prior to 1994. Between 1994 and 2010, a combination of single- and three-pass depletion surveys were used (Fig. S1). From the whole data set, we selected 115 sites that were surveyed at least 5 years in the 1982–2010 period (median = 9 years per site, range = 5–22). The number of sites surveyed varies among years (median = 44 sites, range = 5–64; Fig. S1). Surveys were conducted between June and August, and surveys were most common in July (1281 survey occasions in June, 2013 in July, and 1041 in August during the 29-year study period).

The number of electrofishing backpack units ranged between 1 and 3 depending on stream width. Each electrofisher was accompanied by two dip-netters. Sampling crews proceeded upstream by sampling all available habitats. Captured fish were measured for total length (±1 mm) and mass (±0.1 g) and returned to the stream after all passes were completed. A length-frequency histogram was plotted for each sampling occasion, and count of YOY and older individuals ('adults' hereafter) was recorded for each electrofishing pass.

Weather data

We used the Daymet database (http://daymet.ornl.gov) to characterise mean seasonal maximum air temperature and total seasonal precipitation at each site in each year. We defined seasons as summer (June–August), autumn (September–November), winter (December–February) and spring (March–May). The Daymet model generates daily maximum and minimum air temperature values at the resolution of 1 km^2. Daily maximum air temperature values were used to calculate seasonal mean maximum air temperature for each year at each site (hereafter 'seasonal air temperature'). Precipitation represented total amount of precipitation estimated by Daymet in each season at each site (hereafter 'seasonal precipitation'). Winter precipitation includes a mix of snow and rain. Snowfall is also recorded during early spring (March and April) and late autumn (November) in the study area. No pair of seasonal weather covariates was highly correlated with each other (Pearson's $|r| < 0.6$), providing an opportunity to assess relative importance of all seasonal covariates on temporal fluctuation of YOY abundance.

Statistical analysis

Our goal was to examine how seasonal air temperature and precipitation affected temporal variability in YOY abundance in SNP. Based on a literature review on brook trout and other salmonids, we hypothesised how YOY summer abundance might be affected by air temperature and precipitation during preceding seasons (Table 2). We conceived that seasonal weather conditions would influence YOY abundance across 115 study sites although the effect may potentially differ among sites. In addition, capture probability of brook trout may differ among sampling occasions due to environmental conditions (e.g. stream flow); therefore, imperfect detection needed to be incorporated into the model. Accordingly, our analysis is based on the *N*-mixture model (Royle, 2004) with the state process explaining spatial and temporal variation in YOY abundance and the detection process accounting for imperfect detection from three-pass electrofishing data.

Typical of the *N*-mixture modelling approach, our model linked the ecological and detection processes in a hierarchical manner. The ecological process described how true but imperfectly observed YOY summer abundance was affected by seasonal weather covariates during the 29-year study period across 115 sites. Abundance of YOY, $N_{i,t}$, was assumed to follow a Poisson distribution with $N_{i,t} \sim \text{Poisson}(\lambda_{i,t})$, where $\lambda_{i,t}$ is the mean abundance of YOY at site i $\{i = 1, \ldots, 115\}$ during year t $\{t = 1, \ldots, 29\}$. We were primarily interested in the effect of seasonal covariates on YOY abundance, but YOY abundance may also differ among sites. In addition, the timing of sampling between June and August may determine YOY abundance (and detection probability) as individuals grow in body size and recruit to sampling gears. Therefore, we modelled $\lambda_{i,t}$ as a function of eight seasonal weather covariates (Table 2), three site-specific covariates and Julian date on the log-linear scale:

$$\log(\lambda_{i,t}) \sim a + \boldsymbol{\beta_i} \times \boldsymbol{X_{i,t}} + \gamma \times \mathbf{Z_i} + \delta \times (\text{Julian date}_{i,t}) + \varepsilon_{i,t}, \quad (1)$$

where a represents the overall mean abundance per site (intercept), $\boldsymbol{\beta_i}$ represents a vector of the slope (effect size) for eight seasonal weather covariates $\boldsymbol{X_{i,t}}$ at site i in year t, γ is a vector of the slope for site-specific covariates $\boldsymbol{Z_i}$, including elevation, latitude and watershed area, δ is a slope for Julian date on site i in year t, and $\varepsilon_{i,t}$ is an over-dispersion term. Slopes for seasonal weather covariates, $\boldsymbol{\beta_i}$, were modelled as random effects; we considered that the effect of seasonal weather conditions on YOY abundance might differ among sites, although there would also be an overall mean effect characterising study sites. As such, a different regression slope was fit for each site drawn from a normal distribution. Furthermore, we modelled variation in the effect sizes of seasonal covariates among sites as a function of site-specific covariates such that:

$$\begin{aligned}\boldsymbol{\beta_i} = &\boldsymbol{\zeta_0} + \boldsymbol{\zeta_1} \times (\text{elevation}_i) + \boldsymbol{\zeta_2} \times (\text{latitude}_i) \\ &+ \boldsymbol{\zeta_3} \times (\text{watershed area}_i) \\ &+ \eta_i, \eta_i \sim \text{Normal}(0, \boldsymbol{\sigma_\beta^2}),\end{aligned} \quad (2)$$

where $\boldsymbol{\zeta_0}$ is a vector of intercepts corresponding to eight seasonal covariates, $\boldsymbol{\zeta_1}$ is a slope vector for elevation at site i, $\boldsymbol{\zeta_2}$ is a slope vector for latitude, $\boldsymbol{\zeta_3}$ is a slope vector for watershed area, and $\boldsymbol{\varepsilon_i}$ is a vector of residuals that are normally distributed with a mean of 0 and variance of $\boldsymbol{\sigma_\beta}^2$. Three site-specific covariates were not correlated with each other (Pearson's $|r| < 0.53$). We interpreted the intercept $\boldsymbol{\gamma_0}$ as the effect size of seasonal weather covariates after accounting for the site-specific covariates and report these values in evaluating their importance in driving temporal fluctuation in YOY abundance. Seasonal weather covariates were standardised to have a site-specific mean of zero and a standard deviation of one, and site-specific covariates and Julian date were standardised to have a mean of zero and a standard deviation of one.

In the detection process, capture probabilities of individuals per electrofishing pass were estimated from the three-pass depletion data by assuming that fish populations were closed to movement during surveys and an equal amount of sampling effort was expended among electrofishing passes. The imperfectly observed data (i.e. count of individuals) at site i in year t and electrofishing pass k, denoted as $y_{i,t,k}$, were modelled by assuming that detection probabilities ($p_{i,t}$) were constant across passes but could vary among sampling occasions:

Table 2 Hypothetical effects of seasonal weather covariates on young-of-the-year (YOY) abundance in brook trout. YOY sampling took place during summer in this study, and hypotheses refer to the 1-year preceding period that starts with summer of the previous year. Seasons are defined as follows: summer (June–August), autumn (September–November), winter (December–February) and spring (March–May)

Seasonal weather	Bio-periods	Hypotheses
Summer precipitation	Adult pre-spawning	Summer drought reduces adult survival and growth (Letcher *et al*., 2015) with potentially negative effects on energy reserves of autumn-spawning brook trout, similar to negative effects of elevated summer temperature. Thus, lower summer precipitation negatively affects YOY abundance in the following year
Autumn precipitation	Adult spawning	Brook trout exhibit autumn-spawning movement upstream (Kanno, Vokoun & Letcher, 2011). Increased autumn stream flow not only increases potential spawning areas but also helps spawning adults access tributaries (Kanno *et al*., 2014) and results in more successful spawning activities
Winter precipitation	Egg incubation	Incubating eggs are vulnerable to high winter flow events that scour gravel and pebble substrata (Fausch *et al*., 2001; Carline & McCullough, 2003; Petty *et al*., 2005), resulting in a negative relationship between winter precipitation and YOY abundance
Spring precipitation	Fry rearing	Increased spring precipitation results in higher stream habitat volume which reduces competition among individuals (positive effect) (Jellyman & Mcintosh, 2010; Kaspersson *et al*., 2012), but small-bodied fry may also be susceptible to higher stream discharge (negative effect) (Jensen & Johnsen, 1999; Zorn & Nuhfer, 2007). The net effect was challenging to determine prior to analysis.
Summer temperature	Adult pre-spawning	Elevated summer temperature has negative physiological effect on pre-spawning adults, and it delays or reduces spawning (Robinson *et al*., 2010; Warren *et al*., 2012). Thus, high summer temperature results in lower YOY abundance in the following year
Autumn temperature	Adult spawning	Decreasing temperature in autumn is an environmental cue for spawning (Blanchfield & Ridgway, 1997). Cooler autumn temperature triggers brook trout to spawn earlier and help prolong their spawning season (i.e. positive effect)
Winter temperature	Egg incubation	Salmonid eggs hatch faster and more successfully in warmer temperature (Baxter & McPhail, 1999; Baird, Krueger & Josephson, 2002). Earlier hatching also results in longer growing season, and thus, high winter temperature has a positive effect on YOY abundance
Spring temperature	Fry rearing	Warmer temperature during growing season increases fry survival and growth in salmonids (Coleman & Fausch, 2007). Higher spring temperature leads to higher YOY abundance

$$y_{i,t,1} \sim \text{Binomial}(N_{i,t}, p_{i,t}), \quad (3)$$

$$y_{i,t,2} \sim \text{Binomial}(N_{i,t}, (1 - p_{i,t}) \times p_{i,t}), \quad (4)$$

$$y_{i,t,3} \sim \text{Binomial}(N_{i,t}, (1 - p_{i,t}) \times (1 - p_{i,t}) \times p_{i,t}), \quad (5)$$

Similar to the ecological process in which YOY abundance was modelled in relation to covariates, the capture probability was modelled as a function of environmental covariates using a logit link:

$$\begin{aligned}\text{logit}(p_{i,t}) = \theta_0 + \theta_1 \times (\text{Julian date}_{i,t}) + \theta_2 \\ \times (\text{precipitation before survey}_{i,t}) + \theta_3 \\ \times (\text{watershed area}_i), \quad (6)\end{aligned}$$

where θ_0 is the intercept, and θ_1, θ_2 and θ_3 are the effect sizes of the covariates that we assumed important for detection. Julian date was used to approximate the temporal pattern of decreasing stream flow (i.e. higher electrofishing efficiency) from the beginning of the sampling season (June) to the end (August) observed in the SNP (Kanno *et al*., 2015a). We also assumed that YOY individuals would grow in size and become more susceptible to electrofishing over the course of summer. We used the total amount of Daymet-derived precipitation during preceding 7 days of sampling at each site. Precipitation events prior to sampling could lower sampling efficiency by increasing stream discharge and turbidity. Finally, watershed area is a surrogate of stream size and may impact sampling efficiency. All covariates were standardised to have a mean of zero and a standard deviation of one. By analysing single-pass and three-pass electrofishing data jointly and adding environmental covariates for detection, detection probabilities were also inferred for those survey occasions in which only single-pass electrofishing data were available. This resulted in a refined inference of abundance across study sites.

We examined how YOY abundance affected adult abundance in the following year, and how YOY abundance was influenced by adult abundance in the previous year (i.e. stock-recruitment relationship). The *N*-mixture model described above was also fit to the adult count data. This analysis focused on a subset of 40 sites, which had at least six consecutive year intervals of surveys during the study period. We plotted predicted YOY abundance in year t and predicted adult abundance in year $t + 1$ at each site, as well as predicted adult abundance in year t and predicted YOY abundance in year $t + 1$. A simple linear regression was fit to examine relationships between YOY and adult abundance (natural logarithm) at each site. When the regression slope had a positive or negative value with an associated P-value of <0.10, the relationship was considered significantly positive or negative. Otherwise, we considered that there were no statistically significant relationships between abundance of YOY and adults. The conservative P-value (0.10) was used because the analysis was based on a small size of observations at each site [median = 9, range (6–15) across 40 sites]. Furthermore, we examined whether elevation, latitude and watershed area differed among sites with different regression slope categories (positive, negative or not significant) using t-tests. Due to the small sample size, we also assessed whether the number of samples differed among site groups. We do not report effects of seasonal weather covariates on adult abundance because YOY abundance in the previous year was a major driver of adult abundance (see Results) and ecological interpretation of seasonal weather covariates on adult abundance was challenging.

Finally, we plotted predicted YOY and adult abundance for a subset of sites between 1994 and 2010. This was the period when three-pass depletion surveys were common (Supporting Information), and the same sites were revisited across years to the extent possible. We used 34 sites that were revisited at least 10 years during the 15-year sub-period in order to visually examine synchrony in population trends among sites.

We analysed our models with a Bayesian approach using Markov chain Monte Carlo (MCMC) methods in JAGS (Plummer, 2003) called from Program R (R Development Core Team, 2014) with the rjags package (Plummer, 2011). Uninformative priors were used throughout, including Jeffery's priors (mean = 0 and SD = 1.643) for the effect size of detection covariates (uninformative on the logit scale). Posterior distributions of model parameters were estimated by taking every 20th sample from 50 000 iterations of three chains after discarding 100 000 burn-in iterations. Model convergence was checked by visually examining plots of the MCMC chains for good mixture as well as ensuring that the R-hat statistic is <1.1 for all model parameters (Gelman & Hill, 2007). Statistical significance was evaluated based on whether 95% credible interval (95% CI) of the parameter overlapped a value of zero. As a measure of model goodness of fit, we plotted predicted versus observed fish count for each stage and electrofishing pass. We calculated the proportion of predicted values that were above observed values (Gelman, 2003). A perfect model would have a value of 0.5 for this goodness-of-fit statistic, with values closer to zero and one indicative of poor model fit (Gelman, 2003; Kéry & Schaub, 2012).

Results

Our model was valid based on the following criteria. The R-hat values were <1.1 for all parameters in the model. There was no evident posterior correlation of effect size between any pair of seasonal weather covariates (Fig. S2). There was a very good concordance between predicted and observed trout count for YOY and adults, with the goodness-of-fit statistic ranging between 0.37 and 0.63 (Fig. S3).

Of the eight seasonal covariates tested (Table 2), five had statistically significant effects on YOY summer abundance (Fig. 2). Preceding winter precipitation had the greatest effect on YOY abundance, and the relationship was significantly negative [effect mean = −0.36, 95% CI = (−0.44, −0.30)]. Autumn temperature also had a significant negative effect on YOY abundance [effect mean = −0.21, 95% CI = (−0.30, −0.12)]. YOY abundance was positively affected by autumn precipitation [effect mean = 0.19, 95% CI = (0.11, 0.26)], winter temperature [effect mean = 0.10, 95% CI = (0.04, 0.17)] and spring temperature [effect mean = 0.16, 95% CI = (0.08, 0.24)]. Effects of summer precipitation and temperature, and spring precipitation were not statistically significant because their 95% CI overlapped with a

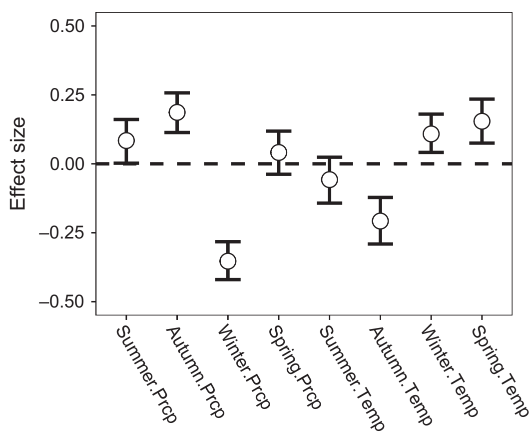

Fig. 2 Effect size (regression slope coefficient) of seasonal weather covariates on variation in young-of-the-year abundance. Open circles indicate posterior means, and error bars indicate 95% credible intervals (CI). Statistical significance was evaluated based on whether 95% CI overlapped with a value of zero (dotted horizontal line).

value of zero (Fig. 2). YOY abundance was also positively influenced by elevation [effect mean = 0.17, 95% CI = (0.11, 0.24)] and watershed area [effect mean = 0.17, 95% CI = (0.10, 0.23)]; it was not significantly affected by latitude [effect mean = 0.05, 95% CI = (−0.11, 0.11)] or Julian date [effect mean = 0.04, 95% CI = (−0.03, 0.10)].

Although summer precipitation did not affect YOY abundance significantly, its impact varied among sites along a latitudinal gradient. There was a statistically significant positive relationship between the effect size of summer precipitation and latitude [$\zeta_2 = 0.09$ (95% CI = (0.02, 0.17)) in eqn 2]. YOY abundance was more responsive to variation in summer precipitation at northern sites, defined here as those located at 38°5′N or north (Fig. 3). Effect sizes of other seasonal covariates did not vary by latitude; in addition, effect sizes of any seasonal covariate did not differ by elevation or watershed area.

Abundance of YOY individuals influenced adult abundance in the following year (Fig. 4). Of 40 sites used in this analysis, 21 sites had statistically positive relationships, and YOY abundance did not affect adult abundance in the following year at the remaining 19 sites. Those 21 positive sites were significantly lower in elevation than the other 19 sites (*t*-value = 2.54, *P*-value = 0.02), but the two groups of sites did not differ in latitude (*t*-value = 0.76, *P*-value = 0.45) or watershed area (*t*-value = −0.93, *P*-value = 0.36). Sample size (number of years with data) did not differ between the two groups (*t*-value = 0.01, *P*-value = 0.99); thus, the observed ecological patterns were not due to statistical artefact due to small sample size. To the contrary, adult abundance was not a good predictor of YOY abundance in the following year (Fig. 4). There was no statistically significant stock–recruitment relationships at 32 of 40 sites, and the relationship was significantly negative at the other eight sites; the latter group of sites was significantly smaller in watershed area than the former group (*t*-value = −3.65, *P*-value = 0.001). Two groups of sites did not differ in elevation (*t*-value = 1.06, *P*-value = 0.32) or latitude (*t*-value = −1.79, *P*-value = 0.10). Again, number of years sampled did not differ between the two groups (*t*-value = 0.82, *P*-value = 0.43).

Because seasonal weather patterns affected YOY abundance and the inter-annual weather patterns varied little among sites (Fig. S4), there was a notable synchrony in

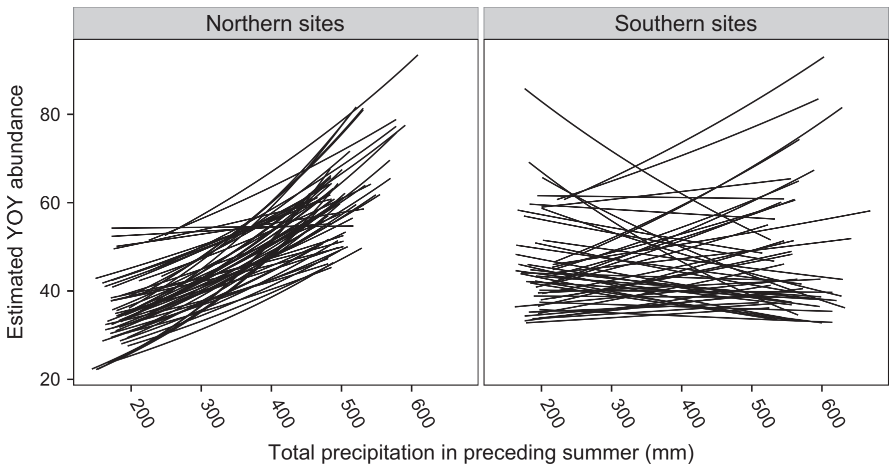

Fig. 3 Predicted mean relationships between summer precipitation and young-of-the-year abundance. Each line represents a study site. Sites were classified as northern (located at 38°5′N or north) or southern sites. Ranges of summer precipitation represent Daymet data at each site.

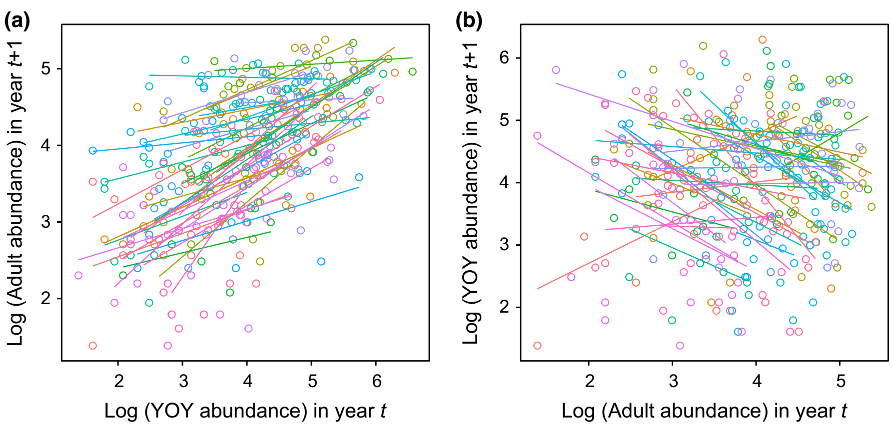

Fig. 4 Predicted relationships between mean young-of-the-year (YOY) abundance in year *t* versus mean adult abundance in year *t* + 1 (a), and mean adult abundance in year *t* versus mean YOY abundance in year *t* + 1 (b). Both YOY and adult abundance are on log scale. Sites were groups by colour.

temporal YOY abundance trends among sites (Fig. 5). For example, YOY abundance was high across sites in some years (e.g. 1997 and 2004) and low across sites in other years (e.g. 1998 and 2010). Spatial synchrony was less evident in adults (Fig. 5).

Accounting for imperfect detection was important because it varied between YOY and adults, and among sampling occasions. Capture probability in a single electrofishing pass was higher for adults [mean = 0.70, 95% CI = (0.69, 0.70)] than YOY [mean = 0.57, 95% CI = (0.56, 0.58)]. Capture probability of YOY was affected strongly by Julian date [effect mean = 0.10, 95% CI = (0.08, 0.13)] and watershed area [effect mean = −0.12, 95% CI = (−0.14, −0.09)], and to a lesser degree by pre-survey precipitation [effect mean = −0.04, 95% CI = (−0.06, −0.02)]. Julian date had a positive effect on YOY capture probability, indicating that YOY brook trout were easier to capture as summer proceeded. For example, the mean capture probability on June 25 (mean Julian sampling date minus 1.5 × SD of sampling dates) was 0.53 [95% CI = (0.52, 0.54)], compared with 0.61 [95% CI = (0.59, 0.62)] on August 4 (mean Julian sampling date plus 1.5 × SD). Watershed area had a negative effect on YOY capture probability; thus, sampling was less efficient at larger streams. The mean capture probability was 0.61 [95% CI = (0.60, 0.62)] when watershed area was 1 km^2 (mean minus 1.5 × SD), and decreased to 0.53 [95% CI = (0.52, 0.54)] when watershed area was 19 km^2 (mean precipitation plus 1.5 × SD). Similar to YOY, capture probability of adults was significantly affected by Julian date [effect mean = 0.07 (95% CI = (0.04, 0.010))] and watershed area [effect mean = −0.10 (95% CI = (−0.13, −0.08))], but not by pre-survey precipitation [effect mean = 0.01 (95% CI = (−0.01, 0.03))].

Discussion

Based on a 29-year data set collected from 115 sites, we demonstrated that (i) seasonal temperature and precipitation affect brook trout YOY abundance, (ii) the effect of seasonal covariates may vary along an environmental gradient (i.e. summer precipitation along a latitudinal gradient), and (iii) YOY abundance, but not adult abundance, was more important in regulating population dynamics in brook trout over a relatively large area (170 km linear range). We consider that season-specific effects (e.g. Letcher *et al.*, 2015), spatial variability in population dynamics (e.g. Petty, Lamothe & Mazik, 2005) and early life history dynamics (e.g. Lobón-Cerviá, 2009a) are among the key lesser-studied areas of research that could improve our understanding of aquatic species responses to anthropogenic environmental changes. This study contributes to these knowledge areas by examining mechanisms of population regulations and complements a series of recent brook trout studies that examined distribution patterns using presence and abundance data over a broad spatial scale without rich temporal coverage (e.g. Hudy *et al.*, 2008; McKenna & Johnson, 2011; DeRolph *et al.*, 2015; DeWeber & Wagner, 2015; Kanno *et al.*, 2015b).

What do our results indicate for climate change impacts in the study region? Abundance of YOY brook trout was significantly influenced by five seasonal covariates, including winter precipitation (negative),

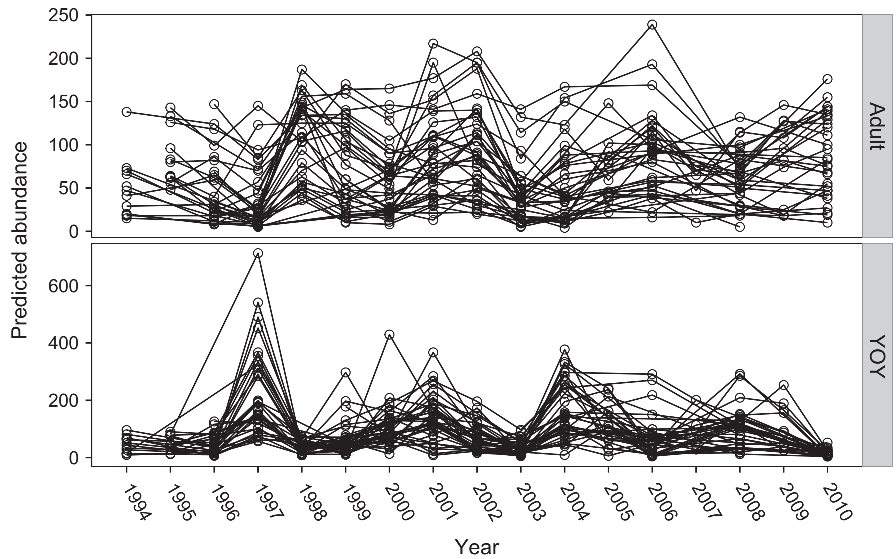

Fig. 5 Predicted mean abundance of adult and young-of-the-year between 1994 and 2010 at 40 sites. Each line represents each site.

autumn temperature (negative), autumn precipitation (positive), winter temperature (positive) and spring temperature (positive). Their effect directions were in agreement with our prior hypotheses (Table 2). Based on a review of existing studies, Ingram *et al.* (2013) summarised that air temperature is projected to increase across all seasons and precipitation is projected to increase for all seasons except summer in the study region. Under this scenario, increased winter precipitation and elevated autumn temperature will have the negative impacts on YOY abundance and population dynamics, but changes in other seasons would have positive or small effects (Fig. 2). Winter precipitation was the strongest seasonal weather factor determining YOY abundance in the SNP. Stream discharge during egg development and hatching has been associated with YOY abundance in Atlantic salmon (Jensen & Johnsen, 1999), brown trout (Daufresne & Renault, 2006) and rainbow trout (*Oncorhynchus mykiss*; Fausch *et al.*, 2001). Although summer conditions have been associated with occupancy, abundance and vital rates of brook trout (McKenna & Johnson, 2011; DeWeber & Wagner, 2015; Letcher *et al.*, 2015), our study suggests that an examination across seasons is critical in understanding climate change impacts on aquatic species (see also Letcher *et al.*, 2015). It is also important to note that our analyses were based on seasonal mean values. Possibly, punctuated extreme events (e.g. floods), which are expected to increase in magnitude and frequency as a result of climate change (Ingram *et al.*, 2013), may have an equal or perhaps greater influence on brook trout population dynamics.

Although summer precipitation did not have a statistically significant overall effect on YOY abundance, its effect differed along a latitudinal gradient. Abundance of YOY was more responsive to variation in summer precipitation at more northern sites in the SNP. We do not offer a definitive explanation for this observation and suggest that more research is warranted to assess whether a similar pattern can be found in other regions and what mechanism (e.g. behaviour and physiology) might be responsible for the observed pattern. On the one hand, our result indicates that environmental change would not affect all sites equally. On the other hand, the effect of other seasonal covariates did not vary by latitude, and none varied along elevation and watershed area gradients. Such a consistent response across sites may be partly responsible for temporal synchrony in YOY abundance across sites. Given that climate operates at the regional scale, it was not surprising that synchrony among sites was observed along the 170-km range within the SNP (e.g. Alonso *et al.*, 2011). For a wide-ranging species such as brook trout, future work is warranted to identify spatial extent of synchronous population dynamics at a broader spatial scale. It should be noted that synchrony in adult abundance seemed less evident in the SNP brook trout populations. This result may be due to relative importance of dispersal (rather than environmental drivers) in regulating local adult abundance (Petty *et al.*, 2005) or density dependence that stabilises variability in YOY abundance (Daufresne & Renault, 2006; Grossman *et al.*, 2012; Dochtermann & Peacock, 2013).

Stock–recruitment relationships were weak with adult abundance generally being a poor predictor of YOY abundance in the following year. This relationship was even negative at eight of 40 sites and these sites were significantly smaller in watershed area, where competition for resources and habitat among adult individuals may be stronger. These findings differ from other Appalachian brook trout populations in which positive stock–recruitment curves were reported (Grossman *et al.*, 2010; Huntsman & Petty, 2014). In our study, abiotic factors (i.e. seasonal weather patterns) exerted a stronger impact on YOY abundance than a biotic factor (i.e. spawner abundance). Abiotic influence on YOY abundance has been commonly observed in stream salmonids (Lobón-Cerviá, 2014; Letcher *et al.*, 2015). The climate-driven variability in YOY abundance was carried over in adult abundance in the subsequent year in this study, and the importance of recruitment to early life stages has been reported in population dynamics of other salmonid populations (Milner *et al.*, 2003; Lobón-Cerviá, 2009b) as well as coral reef fishes (Chesson, 1998; Armsworth, 2002). In the SNP, YOY abundance was the major driver of brook trout population dynamics, particularly at lower-elevation sites. It indicates that brook trout populations, at least YOY individuals, were typically maintained below carrying capacity at these sites. However, this conclusion is incomplete because other aspects of population vital rates such as individual body growth are frequently density dependent in YOY salmonids (Utz & Hartman, 2009; Grossman *et al.*, 2010; Imre, Grant & Cunjak, 2010), and these aspects were not examined in the current study.

The finding that brook trout YOY abundance drives population dynamics has important management implications. Brook trout is a popular recreational fish and fishing regulations are set on harvestable individuals (i.e. adults), but management actions targeted at YOY individuals may often be effective in regulating and conserving brook trout populations (Marschall & Crowder, 1996; Kanno *et al.*, 2015a). It means, for example, that improving egg to fry survival by reducing sedimentation may be as important for population size as promoting adult survival by implementing more strict fishing regulations. Because the strength of YOY year class is a reliable indicator of adult population size in the following year, managers would also be able to anticipate adult population size (i.e. fishing success) based on YOY abundance. Spatial synchrony in YOY trends indicates that monitoring a small number of stream sites may be adequate to describe abundance patterns in a relatively expansive area (e.g. SNP). From the conservation perspective, our results demonstrate that seasonal weather patterns affect brook trout population dynamics through YOY abundance and population dynamics, and climate change impacts will manifest based on cumulative seasonal effects.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Number of sites surveyed between 1982 and 2010.

Figure S2. Posterior correlation of effect size of seasonal weather covariates.

Figure S3. Predicted versus observed count for each stage and electrofishing pass.

Figure S4. Temporal trends of seasonal weather patterns across 115 sites between 1982 and 2010.

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