Seasonal weather patterns drive population vital rates and persistence in a stream fish

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Abstract

Climate change affects seasonal weather patterns, but little is known about the relative importance of seasonal weather patterns on animal population vital rates. Even when such information exists, data are typically only available from intensive fieldwork (e.g., mark–recapture studies) at a limited spatial extent. Here, we investigated effects of seasonal air temperature and precipitation (fall, winter, and spring) on survival and recruitment of brook trout (*Salvelinus fontinalis*) at a broad spatial scale using a novel stage-structured population model. The data were a 15-year record of brook trout abundance from 72 sites distributed across a 170-km-long mountain range in Shenandoah National Park, Virginia, USA. Population vital rates responded differently to weather and site-specific conditions. Specifically, young-of-year survival was most strongly affected by spring temperature, adult survival by elevation and per-capita recruitment by winter precipitation. Low fall precipitation and high winter precipitation, the latter of which is predicted to increase under climate change for the study region, had the strongest negative effects on trout populations. Simulations show that trout abundance could be greatly reduced under constant high winter precipitation, consistent with the expected effects of gravel-scouring flows on eggs and newly hatched individuals. However, high-elevation sites would be less vulnerable to local extinction because they supported higher adult survival. Furthermore, the majority of brook trout populations are projected to persist if high winter precipitation occurs only intermittently (≤3 of 5 years) due to density-dependent recruitment. Variable drivers of vital rates should be commonly found in animal populations characterized by ontogenetic changes in habitat, and such stage-structured effects may increase population persistence to changing climate by not affecting all life stages simultaneously. Yet, our results also demonstrate that weather patterns during seemingly less consequential seasons (e.g., winter precipitation) can have major impacts on animal population dynamics.

Keywords: air temperature, climate change, count data, *N*-mixture models, precipitation, salmonids, stage-structured populations

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Introduction

Climate change can shift species ranges and affect animal abundance via alterations in local weather conditions (Thomas *et al.*, 2004; Chen *et al.*, 2011). While understanding these biological patterns is important for conservation planning and adaptive management, few studies have investigated the demographic processes that bring about population-scale changes (e.g., Wright *et al.*, 2009; Hegel *et al.*, 2010; Nilsson *et al.*, 2011; Vindenes *et al.*, 2014). Although climate change affects weather patterns during all seasons, the relative

importance of different seasons on population vital rates has rarely been investigated (Dybala *et al.*, 2013), with a vast majority of studies focused on either a single season or annual weather variables (e.g., Hunter *et al.*, 2010; Roland & Matter, 2013; Wenger *et al.*, 2013). Yet, animal populations respond to seasonal weather variations in complex and unexpected ways for a number of reasons.

First, many life history strategies are tightly linked to seasonality, and a consistent change in a weather pattern (e.g., temperature increase) can differentially affect vital rates during different seasons (Wright *et al.*, 2009; Fernández-Chacón *et al.*, 2011; Diamond *et al.*, 2013; Dybala *et al.*, 2013). Second, animal populations are structured by age, size or life stage, and individuals

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require different resources through ontogeny (Werner & Gilliam, 1984). Different individuals are unlikely to respond uniformly to a specific climatic condition, with potentially large differences among life stages (Haslob *et al.*, 2012; Diamond *et al.*, 2013; Dybala *et al.*, 2013). Finally, animal populations are additionally regulated by density-dependent factors, and population density has been shown to influence recruitment and survival across many taxa (Nicola *et al.*, 2008; Diamond *et al.*, 2013; Lok *et al.*, 2013). The magnitude of density dependence can affect population stability and resiliency (Lack, 1954) under changing weather conditions.

Robust inferences on the effect of weather patterns on population vital rates require long-term data sets with rich demographic information. Accordingly, the small number of previous studies that have examined this issue relied primarily on intensively collected field data from a single population or a limited number of populations (e.g., Letcher *et al.*, 2007; Wright *et al.*, 2009; Dybala *et al.*, 2013). Mark–recapture methods are commonly employed to estimate vital rates in intensive field studies conducted at relatively small spatial scales (Williams *et al.*, 2002). However, population vital rates can differ greatly among populations distributed along environmental gradients (Jenouvrier *et al.*, 2009; Fernández-Chacón *et al.*, 2011; Lobøn-Cerviá, 2014; Roth *et al.*, 2014), suggesting that the impact of climate drivers varies not only temporally but also spatially. Current anthropogenic threats to biodiversity, such as climate change and land use, operate at broad spatial scales. We need a fuller understanding of how spatial heterogeneity and seasonal weather affect population vital rates to identify the environmental origins of population vulnerability. This means that long-term data sets must be spatially replicated for robust inferences about effects of seasonal weather on vital rates. Mark–recapture methods cannot easily provide such replication because they are expensive and labor intensive.

Obtaining animal count data without mark–recapture methods is less labor intensive and allows researchers to collect data at broader spatial and temporal scales. Count data have been used less frequently than mark–recapture data in demographic analyses of animal populations (e.g., Gross *et al.*, 2002; Link *et al.*, 2003; Alonso *et al.*, 2011) because the lack of individual histories in count data is assumed to limit inference about vital rates. Recent advances in the analysis of count data provide a promising approach to breaching this limit. Dail & Madsen (2011) proposed a statistical approach that modeled apparent survival and recruitment rates based on count data distributed over space and time. The method was further extended by Zipkin *et al.* (2014a) who demonstrated that demographic heterogeneity among individuals (e.g., age, size, and sex) can be esti-

mated with this framework. This structured population model provides a flexible method for incorporating temporal and spatial heterogeneity in the environment as well as density-dependent processes into the analysis of count data, but its applications to empirical data have been limited to date (Kanno *et al.*, 2014; Zipkin *et al.*, 2014b).

In this study, we use a structured population model to investigate effects of mean air temperature and precipitation during fall, winter, and spring seasons on the survival and recruitment of brook trout (*Salvelinus fontinalis*). We drew on a 15-year count record collected from 72 sites distributed across a 170-km-long mountain range in Shenandoah National Park (SNP), Virginia, USA. Air temperature and precipitation are drivers of stream temperature and flow, which in turn are considered the key physical drivers of population dynamics in lotic ecosystems (Poff *et al.*, 1997; Arismendi *et al.*, 2013). Numerous studies have shown that stream fish populations respond to average and extreme states of these drivers (e.g., Roghair *et al.*, 2002; Perry & Bond, 2009; Xu *et al.*, 2010a). Yet, the relative influence of seasonal weather patterns and spatial heterogeneity on population vital rates of aquatic species is unknown across broad spatial scales. Stream temperature and flow are both expected to respond to climate change via alterations in air temperature and precipitation regimes (Novotny & Stefan, 2007; Huntington *et al.*, 2009). Consequently, there is a critical need for understanding how air temperature and precipitation affect the population dynamics of stream fish, particularly for southern populations of coldwater species such as brook trout for which climate change is of great concern. This is challenging because stream fish tend to be cryptic, elusive, and small bodied, such that individual detection is imperfect. To be useful, methods for inferring vital rates from count data must account for this imperfect detection.

We had two specific objectives. The first was to develop a stage-structured population model to quantify the effects of seasonal mean maximum air temperature and precipitation on vital rates, while accounting for density dependence in recruitment and environmental variation across stages and sampling locations. The majority of previous stream fish studies have focused on the effects of summer conditions on population vital rates (Boss & Richardson, 2002; Xu *et al.*, 2010a), and there exists a critical knowledge gap during other seasons (e.g., Jensen & Johnsen, 1999; Carlson *et al.*, 2008; Berger & Gresswell, 2009). Our second objective was to use the stage-structured model for assessing potential responses of brook trout populations to climate change using climate projections for the study region. Our interest lies in determining whether

certain seasonal weather conditions were more important than others to population persistence and how the frequencies of adverse seasonal weather would affect population persistence.

Materials and methods

Study species

Brook trout are native to eastern North America, ranging from Georgia, USA to Labrador and Quebec, Canada. They inhabit clear and coldwaters. Stream temperature and flow are major factors that determine population dynamics of brook trout. A stream temperature range of 21–22°C causes physiological stress (Hartman & Cox, 2008; Warren *et al.*, 2012) and affect distribution and abundance of wild populations (McKenna & Johnson, 2011). Reduced stream flow has been shown to decrease survival during summer in headwater streams (Xu *et al.*, 2010a), and floods have been related to short-term population declines (Roghair *et al.*, 2002).

Brook trout populations have declined greatly due to a combination of anthropogenic activities, particularly in the southern portion of their range where they currently occur only in high-elevation streams along the Appalachian Mountains (Hudy *et al.*, 2008). Brook trout in headwater streams are typically short-lived (<3–4 years old) (Grossman *et al.*, 2010; Xu *et al.*, 2010b; Kanno *et al.*, 2012), and most body growth takes place during spring months (March–June) in streams located in the northern USA range (Xu *et al.*, 2010b). Brook trout spawn during fall, and females excavate small depressions in gravel substrates called 'redds' in which fertilized eggs develop until hatching in late winter to early spring.

Microhabitat preferences change through ontogeny. Young-of-year (YOY) individuals (<1 year old) are more common at shallower depths, while older trout prefer deeper and slower sections of streams such as pools (Kanno *et al.*, 2012; Anglin & Grossman, 2013). The ontogenetic habitat shifts in brook trout suggest that the same environmental factors probably affect adults and YOY individuals differently. For example, Xu *et al.* (2010a) reported that in headwater streams in Massachusetts, summer drought reduced the survival of large brook trout (>135 mm fork length) but not of smaller individuals. In high-elevation streams in West Virginia, a winter flood decreased YOY abundance more severely than adult abundance because trout redds were scoured during the flood (Carline & McCullough, 2003). However, the generality of these stage-specific impacts of seasonal weather is not known.

Fish data

We used long-term monitoring data collected by the National Park Service (NPS) between 1996 and 2010 at 72 sites distributed across a 170-km-long mountain range in the SNP, Virginia, USA (Fig. 1). The study area lies within the Blue Ridge physiographic region characterized by steep slopes and narrow ridges. Elevation of the study sites ranged from 285 to 802 m (median = 436 m), and this constitutes important changes in aquatic habitats and fish assemblages. Sites were located on small headwater streams (first to third order) that were well shaded by riparian vegetation and were generally characterized as step-pool or cascade habitats (Table 1). Stream flow typically peaked in spring due to snowmelt, followed by low-flow conditions in late summer to fall. Study sites typically harbor few fish species. The most common species other than brook trout were blacknose dace (*Rhinichthys*
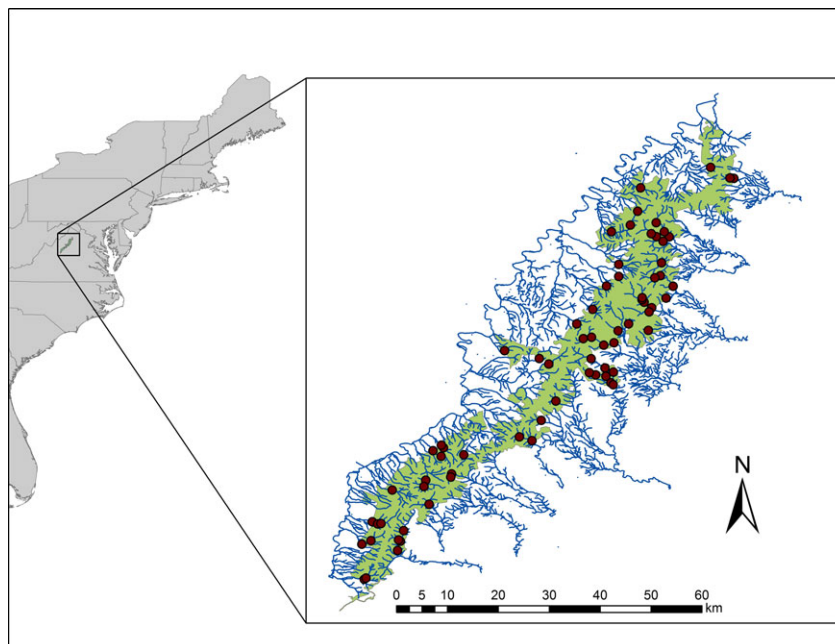
Fig. 1 Map of the Shenandoah National Park (shaded by green) showing fish survey sites (brown circles). Streams are shown in blue lines.

Table 1 Summary of seasonal and site-specific environmental data in the Shenandoah National Park, Virginia, USA, between 1996 and 2010

	Median	Mean	Min.	Max.
Seasonal weather*				
Fall precipitation (mm)	363.3	347.3	117.0	566.9
Winter precipitation (mm)	208.7	245.0	95.2	515.7
Spring precipitation (mm)	316.6	311.1	199.7	420.8
Fall temperature (°C)	18.1	18.3	16.6	20.0
Winter temperature (°C)	6.8	6.4	2.9	9.2
Spring temperature (°C)	17.3	17.2	15.0	19.5
Local sites†				
Latitude	38°4728′N	38°4945′N	38°0970′N	38°8261′N
Longitude	78°4682′W	78°3916′W	78°8118′W	78°1543′W
Elevation (m)	458	436	285	802
Channel slope (%)	7	5	1	21
Catchment area (km²)	9.3	7.6	1.3	36.2
Wetted stream width (m)	5.9	5.5	3.4	10.8
Water depth (m)	0.34	0.33	0.23	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 72 study sites. Summary statistics shown above are median, mean and range across the 15-year study period.
†Elevation, channel slope and catchment 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.

atratulus), mottled sculpin (*Cottus bairdi*), and fantail darter (*Etheostoma flabellare*) (Jastram *et al.*, 2013).

At each site, NPS personnel conducted surveys by first establishing a 100-m stream section by walking within the stream channel with a metered tape. Upstream and downstream ends of sites were typically bounded by natural geomorphic habitat breaks that impeded fish movement (e.g., step pools). Where geomorphic breaks were inadequate to impede movement across site boundaries, cobble dams or block nets were temporarily set up for the survey. Brook trout were surveyed between May and August (mostly June to August). The NPS has maintained a brook trout population monitoring program since 1982 (Jastram *et al.*, 2013), and we used a portion of this long-term data set collected during 1996–2010. This corresponded with a period during which the sampling protocol emphasized visiting the same sites repeatedly across years to the extent possible. The number of yearly surveys ranges from 3 to 15 among sites (mean = 7 surveys per site). Two sites were surveyed annually during the 15-year study period. Of the total potential sampling occasions (72 sites × 15 years = 1080 occasions), data were available on 611 occasions (57%).

Backpack electro-shockers were used to sample fish. In most sampling occasions (81% or 514 of 611 occasions), three-pass depletion surveys were conducted to infer individual detection probabilities. In the remaining occasions, single-pass electrofishing was conducted. We assumed fish populations were closed to movement during surveys because site boundaries coincided with natural geomorphic breaks, cobble dams or block nets. The number of electrofishing backpack units

used 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. YOY individuals can be distinguished from older individuals ('adults' hereafter) based on length–frequency distributions (Xu *et al.*, 2010b; Kanno *et al.*, 2014). A length–frequency histogram was plotted for each site × year combination, and the cutoff size between the two stages was determined individually (see Appendix S1 for example histograms). This generated fish count data by site, year, stage, and sampling replicate (electrofishing pass).

Temperature and precipitation data

We characterized mean seasonal maximum air temperature and total precipitation at each site in each year. Seasons were defined as fall (September–November), winter (December–February) and spring (March–May). Summer temperature and precipitation were not characterized because fish surveys were primarily conducted during summer months. Thus, the definition of summer period would have differed among sites and years, which made interpretation of results challenging. We did not consider that the omission of summer would weaken our analysis greatly because summer is by far the most commonly studied season in population biology of brook trout and other freshwater fish. For example, high summer temperature and drought conditions have been associated with population declines of brook trout (Hakala & Hartman, 2004;

Xu *et al.*, 2010a; Warren *et al.*, 2012). However, relative importance of other seasons on population dynamics is little known for freshwater fish and is the main focus of our study.

Air temperature and precipitation data at the study sites were derived from the Daymet database (http://daymet.ornl.gov). The Daymet model generates daily maximum and minimum air temperature values at the resolution of 1 km^2. We used daily maximum air temperature values 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, although snowfall is commonly recorded during early spring (March and April) and late fall (November) in the study area.

Statistical analysis

We examined the effects of seasonal air temperature and precipitation on population vital rates using a stage-structured open population *N*-mixture model (Zipkin *et al.*, 2014a). Classic *N*-mixture models estimate population abundance at a set of local sites over a time period during which the population is assumed to be closed to births/deaths and immigration/emigration (Royle, 2004). Abundance is inferred by employing a repeated sampling scheme that estimates the detection probability of individuals. Dail & Madsen (2011) extended *N*-mixture models to open populations where population size can change over time due to a survival process and a 'gains' process (recruitment and immigration) in which all individuals contribute equally to population growth. Their approach has been further extended for more realistic situations in which individual heterogeneity, as represented by age, size or sex, is explicitly accounted for (Zipkin *et al.*, 2014a).

Our model uses a stage-structured population framework to provide inferences on abundance and population vital rates in relation to environmental covariates. We assumed an annual population model of brook trout in the SNP comprised of two stages: YOY and adults (Fig. 2). A portion of YOY individuals survive annually and transition into the adult stage
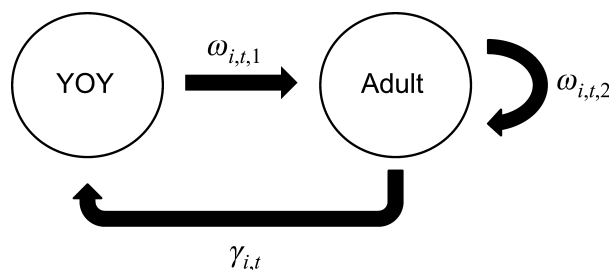
Fig. 2 Annual life cycle of brook trout populations represented by young-of-year (YOY) and adult stages. Vital rates are denoted by $\omega_{i,t,1}$ (YOY survival probability), $\omega_{i,t,2}$ (adult survival probability), and $\gamma_{i,t}$ (per-capita recruitment rate) for site i in year t to indicate that these vital rates were estimated for each site, year, and stage.

within sites. Surviving adults remain in the same adult stage in the following year. YOY and adults typically survive at different annual probabilities (Petty *et al.*, 2005; Letcher *et al.*, 2007), and survival was modeled for each stage. We assumed that only adults were capable of reproducing offspring. While size- and age-at-maturity information does not exist in the SNP brook trout populations, brook trout mature at 100 mm total length in other populations (Hudy *et al.*, 2010; Kanno *et al.*, 2011a) and this body length corresponded well with our YOY–adult cutoff body length in most sites and years (Appendix S1). We assumed that population dynamics were independent across sites. We did not explicitly model immigration and emigration based on the assumption of no net dispersal in and out of a local site. This is a plausible assumption because each site was generally established at a representative section of a stream.

We defined our count data, $y_{i,t,j,k}$, as the observed count of individuals at site i in year t for stage j and electrofishing pass k. Count data ($y_{i,t,j,k}$) represent a portion of true annual abundance ($N_{i,t,j}$) of stage j at site i in year t, due to imperfect detection. Our main interest was to infer annual vital rates that governed the spatial and temporal variation in $N_{i,t,j}$ and to elucidate how these vital rates were affected by environmental covariates. Our approach allowed for establishing a link between annual population dynamics and weather patterns in preceding seasons, as used in other studies (e.g., Diamond *et al.*, 2013; Heisler *et al.*, 2014). Below, we describe our model structure, followed by our model selection approach in relation to the effect of environmental covariates on vital rates.

The population abundance for YOY ($j = 1$) and adults ($j = 1$) in the first year of sampling was assumed to follow a Poisson distribution such that $N_{i,1,j} \sim \text{Poisson}(\lambda_{i,j})$ for all sampling sites $\{i = 1,\dots,72\}$ and stages $\{j = 1,2\}$, where $\lambda_{i,j}$ is the mean abundance of stage j individuals at site i in the first year of sampling. We modeled $\lambda_{i,j}$ as a function of elevation to account for potential variation in abundance among sites:

$$\log(\lambda_{i,j}) \sim a0_j + a1_j * \text{elevation}_i$$

where $a0_j$ represents the intercept and $a1_j$ represents the effect of elevation on the abundance of stage j individuals.

In subsequent years ($t \geq 2$), abundance ($N_{i,t,j}$) was modeled according to the survival and recruitment processes. We assumed that the annual number of surviving individuals followed a binomial process (with parameter $\omega_{i,t,j}$), where total adult abundance was a sum of surviving individuals from both YOY ($j = 1$) and adult ($j = 2$) stages:

$$N_{i,t,2} = \text{Binomial}(N_{i,t-1,1}, \omega_{i,t,1}) + \text{Binomial}(N_{i,t-1,2}, \omega_{i,t,2}).$$

Survival probabilities, $\omega_{i,t,j}$, were modeled for each stage j as a function of seasonal air temperature and precipitation as well as local elevation using the logit link:

$$\text{logit}(\omega_{i,t,j}) = b0_j + \mathbf{B}_j * \mathbf{X}_{i,t}$$

where $b0_j$ is the intercept and the $\mathbf{B}_j$ vector represents regression weights (effect size) for covariates $\mathbf{X}_{i,t}$ (i.e., fall temperature, winter temperature, spring temperature, fall precipitation, winter precipitation, spring precipitation, and elevation) for stage j in site i at year t (but local elevation does not change among years and does not need indexing by year).

Each of the seasonal weather covariates was standardized to have a site-specific mean of zero and a standard deviation of one, and elevation was standardized to have a mean of zero and a standard deviation of one.

We similarly modeled recruitment according to a Markovian process by assuming that local YOY abundance ($N_{i,t,1}$) was a Poisson random variable and depended on adult abundance in the previous year ($N_{i,t-1,2}$):

$$N_{i,t,1} \sim \text{Poisson}(\gamma_{i,t} * N_{i,t-1,2}).$$

The parameter $\gamma_{i,t}$ is the per-capita recruitment probability in site i and year t. We again model $\gamma_{i,t}$ using the seasonal weather covariates and elevation. In addition, we included a density-dependent spawner–recruit function, the Ricker model (Maceina & Pereira, 2007). The Ricker model has frequently been used to describe spawner–recruit relationships in salmonid populations for which spawning habitats are a limiting factor (e.g., Richards et al., 2004; Nicola et al., 2008). Brook trout females are known to spawn over and thus disrupt existing redds (i.e., redd superimposition) (Essington et al., 1998), establishing a mechanism for density dependence at this stage. Spawning habitat is typically limited (Blanchfield & Ridgway, 2005), suggesting that density dependence is more likely to occur at this transition than during subsequent survival. In fact, recruit abundance declined at high spawner abundance in the SNP brook trout populations (see Appendix S2). Accordingly, we modeled $\gamma_{i,t}$ by combining the density-independent (environmental covariates) and density-dependent terms by following Hilborn & Walters (1992):

$$\log(\gamma_{i,t}) = c0 - c1 * N_{i,t,2} + C * X_{\mathbf{i,t}}$$

where $c0$ is the productivity coefficient (per-capita recruitment rate at low spawner abundance), $c1$ is the density-dependent coefficient, and C represents the effects of each environmental covariate represented by $X_{i,t}$. Note that c0 is only interpretable as the productivity coefficient if each covariate in vector X has been centered such that its mean = 0. We note that we had also fit another common density-dependent spawner–recruit function, the Beverton–Holt model. However, the Ricker model fits our data set better than the Beverton–Holt model. For example, the Deviance information criteria (DIC) value of the final model reported in this article was 43 567 (Ricker model) vs. 61 438 (Beverton–Holt model).

Modeling detection probabilities

Individual detection probabilities were estimated from the three-pass depletion data by assuming that the number of individuals subject to detection decreases in successive electrofishing passes. The observed count of individuals at site i in year t for stage j and electrofishing pass k, denoted $y_{i,t,j,k}$, was modeled by assuming that detection probabilities ($p_{i,t,j}$) were constant across passes but could vary by stage and sampling occasion:

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

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

$$y_{i,t,j,3} \sim \text{Binomial}(N_{i,t,j} - y_{i,t,j,1} - y_{i,t,j,2}, p_{i,t,j}).$$

The models above included two covariates that are surrogates of stream flow, which is known to affect electrofishing sampling efficiency, or $p_{i,t,j}$ (Falke et al., 2010; McCargo & Peterson, 2010). Stream flow data were not available in our study sites, and we thus used Julian date and stream width as surrogates for stream flow. 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 (May) to the end (August) observed in the SNP region during 1996–2010 (see Appendix S3 for summer stream discharge patterns). In addition, body growth of YOY during this period can lead to increasing capture rates. Mean stream wetted width represents variation in stream size among sampling locations and was calculated from field measurements taken perpendicular to flow at every 10 m along the sample site on the day that fish sampling occurred. Accordingly, detection probabilities were modeled:

$$\text{logit}(p_{i,t,j}) = d0_j + d1 * (\text{Julian date}_{i,t}) + d2 * (\text{wetted width}_{i,t})$$

where $d0_j$ is the intercept, and $d1$ and $d2$ are the effects of the two covariates at site i in year t. The intercept term is stage specific because electrofishing is size selective (Reynolds & Kolz, 2012). Both Julian date and wetted width were standardized to have a mean of zero and a standard deviation of one.

Selection of covariates

The stage-structured model described thus far can include all environmental variables (i.e., fall temperature, winter temperature, spring temperature, fall precipitation, winter precipitation, spring precipitation, and elevation) as covariates for each survival and recruitment submodel. However, we only used a subset of these covariates in our estimates of survivorship and recruitment to improve parsimony and facilitate ecological interpretation.

Covariate selection involved the following steps. First, we examined correlation of all pairs of seasonal weather covariates. Fall temperature and precipitation were significantly correlated (Pearson's $r = -0.70$), while all other pairs were not highly correlated ($|\text{Pearson's } r| < 0.50$). Thus, we ran a model omitting fall temperature in all submodels and another omitting fall precipitation and then compared the effect size of fall temperature vs. precipitation. For each submodel, we selected the fall weather covariate with a larger effect size in absolute magnitude. This approach allowed us to retain different fall weather covariates for the survival and recruitment processes. Second, we ran a new model using the selected fall weather covariate for each submodel and diagnosed the model output by examining the posterior correlation of parameters. When high posterior correlation was observed between a pair of estimated covariate slopes ($|\text{Pearson's } r| > 0.5$), only the covariate with a larger effect size was retained. Finally, we evaluated the importance of covariates by their estimated coefficient size. Covariates whose 95% credible interval (95% CI) overlapped 0 were dropped from the model. We used DIC

values to confirm model improvement (Spiegelhalter *et al.*, 2002).

Analysis of the models

We analyzed 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, 2013) with the rjags package (Plummer, 2011) (see Appendix S4 for JAGS code). We used Jeffery's priors (mean = 0 and SD = 1.643) for the effect size of survival and detection covariates (uninformative on the logit scale). Intercept terms of survival and detection probabilities were slightly truncated (unif (0.1, 0.9)) based on prior beliefs about the likely range of sampling efficiency and to facilitate model convergence. Posterior distributions of model parameters were estimated by taking every 10th sample from 10 000 iterations of three chains after discarding 10 000 burn-in iterations. Model convergence was checked by visually examining plots of the MCMC chains for good mixture as well as with the R-hat statistic. This statistic compares variance within and between chains, and models are considered to have converged when the value is less than 1.1 for all model parameters (Gelman & Hill, 2007).

As a measure of model goodness of fit, we plotted predicted vs. observed fish count for each stage and electrofishing pass using the selected model. 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).

Demographic analysis

Using mean survivorship and recruitment estimates, we ran elasticity analyses to examine the effect of a proportional change in each vital rate on overall population growth rate, while holding covariates (mean air temperature and precipitation, and elevation) at their mean values. We used three values of local adult abundance in the elasticity analysis (for the density-dependent recruitment portion). These values corresponded to low local abundance (10 individuals per 100 m: 10th percentile of estimated local abundance when pooled over sites and years), median (45 individuals per 100 m: 50th percentile), and high abundance (121 individuals per 100 m: 90th percentile). We calculated the population growth rate and its elasticity to YOY survival, adult survival, and per-capita recruitment rate at each level of local abundance using the 'popbio' package (Stubben & Milligan, 2007) in Program R.

Scenario simulations

To explore model behavior and the potential effects of climate change (alterations in seasonal air temperature and precipitation), we simulated two sets of future environmental scenarios over 30 years (twice the length of the study period). The first set of scenarios assumed temporally constant seasonal weather. To do this, we defined 'high' and 'low' conditions as ±1.5 standard deviations (SD) from the mean value of each seasonal covariate (i.e., fall temperature, winter temperature, spring temperature, fall precipitation, winter precipitation, and spring precipitation), corresponding to uncommon events that occurred in an average of once per 15 years in the historical climate (the study period). We projected mean annual brook trout abundances in our study sites for 12 simulations (six covariates × two conditions) in which the high or low condition for a seasonal covariate persisted for 30 years after the end of our 15-year study period, while the other environmental conditions were held constant at their mean values.

The second set of scenarios represented different frequencies of high winter precipitation. High winter precipitation, along with low fall precipitation, impacted population abundance most negatively (see Results). Winter precipitation is predicted to increase under climate change for the region: In a recent review paper, Ingram *et al.* (2013) summarized that precipitation is projected to increase in the study region for all seasons except summer. Forecasts of precipitation are typically more uncertain than those of air temperature. Even so, a 15% increase in winter precipitation has been predicted for the study region for the period 2041–2070 relative to the period 1971–2000 (Ingram *et al.*, 2013). We changed the frequencies of high winter precipitation (historical mean +1.5*SD) to understand how brook trout populations may respond and how these responses might differ among locations. Four winter precipitation scenarios were considered over the course of 30 years (after the 15-year data period); (i) high winter precipitation occurs once every five years, while the mean winter precipitation condition occurs in other years; (ii) high winter precipitation occurs in three consecutive years, followed by two winters with the mean precipitation condition; (iii) high winter precipitation occurs in four consecutive years, followed by one winter with the mean precipitation condition; and (iv) high winter precipitation occurs every year (i.e., identical to the setting in the first set of simulations earlier). In all four scenarios, other seasonal covariates were held to their mean values. For each of the second set of simulations, we recorded the number of local sites that experienced 'quasi-extinction', defined here as a local site which had ≤5 individuals for each of the two stages (YOY and adult) at the end of the simulation period (i.e., the 45th year).

Results

The selected population model included fall and spring temperature for YOY survival, and fall, winter, and spring precipitation, and elevation for adult survival (Table 2). The recruitment submodel included fall and winter precipitation, and winter and spring temperature, and elevation (Table 2). The R-hat values were less than 1.04 for all parameters in the model. There was a good concordance between predicated and observed trout count for each stage and electrofishing pass, with the goodness-of-fit statistic ranging between 0.36 and 0.76. Model selection details are provided in

Appendix S5, and diagnostics are summarized in Appendix S6.

Detection probabilities and abundance

Adult detection probability [mean = 0.64, 95% credible interval (CI) = (0.63–0.64)] was higher than YOY detection probability [mean = 0.50, 95% CI = (0.49, 0.51)] (Table 2). Julian date had a significantly positive effect on detection probability [mean = 0.17, 95% CI = (0.15, 0.19)] (Table 2), suggesting that detection probability increased from May to August. Stream width had a significant negative effect [mean = −0.17, 95% CI = (−0.19, −0.15)], suggesting that trout capture was more difficult in wider streams.

Annual total abundance estimates summed across 72 sites was generally lower for adults (mean = 4071 individuals) than YOY (mean = 6461) (Fig. 3). YOY abundance fluctuated more widely over time than adult abundance: Coefficient of variation was 59.2 for YOY versus 27.6 for adults. Local abundance of both YOY and adult individuals increased with elevation in the first year of sampling (Table 2).

Population vital rates and demographic analysis

Vital rates were differentially affected by environmental covariates in SNP brook trout populations. Mean annual survival was higher for adults [mean = 0.44, 95% CI = (0.43–0.45)] than for YOY [mean = 0.31, 95% CI = (0.30, 0.32)] (Table 2). Spring air temperature had the greatest impact on YOY survival [effect mean = 0.43, 95% CI = (0.40, 0.46)]. Fall air temperature was the only other covariate retained for YOY survival [effect mean = −0.35, 95% CI = (−0.39, −0.32)]. While higher than average temperatures in the spring had a positive impact on YOY survival, higher temperatures in the fall had a negative effect on YOY survival.

Elevation had the largest effect on adult survival and was positively correlated [effect mean = 0.41, 95% CI = (0.38, 0.43)]. Among seasonal climate covariates, fall precipitation had the strongest effect on adult survival [effect mean = −0.26, 95% CI = (−0.30, −0.23)]. However, winter and spring precipitation was also important, and all three impacted adult survival negatively (Table 2).

Per-capita recruitment was strongly affected by both fall and winter precipitation, but in opposite directions: positive for fall precipitation [mean = 0.40, 95% CI = (0.39, 0.42)] and negative for winter precipitation [mean = −0.42, 95% CI = (−0.44, −0.41)] (Table 2). Estimates of the density-dependent parameters indicated that recruitment was greatly influenced by adult densities. The Ricker stock-recruitment model was

Table 2 Parameter estimates from the model. Parameters for environmental covariates are on the logit scale for survival and detection probability and are on the log scale for initial abundance and recruitment. Intercept terms (in bold) are on the regular scale to facilitate interpretation. JAGS code can be found in Appendix S4

Parameters	Names in JAGS code	Median values (95% CI)
Expected site-specific YOY abundance in the first year of sampling		
Intercept	**exp(a0[1])**	**37 (35, 39)**
Elevation	a1[1]	0.271 (0.222, 0.317)
Expected site-specific adult abundance in the first year of sampling		
Intercept	**exp(a0[2])**	**42 (40, 44)**
Elevation	a1[2]	0.367 (0.330, 0.402)
YOY survival		
Intercept (mean probability)	**b0.mean[1]**	**0.313 (0.306, 0.319)**
Fall temperature	b1[1]	−0.354 (−0.386, −0.323)
Spring temperature	b2[1]	0.429 (0.398, 0.456)
Adult survival		
Intercept (mean probability)	**b0.mean[2]**	**0.444 (0.433, 0.454)**
Fall precipitation	b1[2]	−0.262 (−0.299, −0.227)
Winter precipitation	b2[2]	−0.069 (−0.119, −0.021)
Spring precipitation	b3	−0.244 (−0.283, −0.201)
Elevation	b4	0.406 (0.379, 0.433)
Per-capita recruitment		
Intercept	**c0**	**1.077 (1.045, 1.106)**
Ricker slope	c1	0.0086 (0.0082, 0.0090)
Fall precipitation	c2	0.404 (0.393, 0.415)
Winter precipitation	c3	−0.424 (−0.440, −0.407)
Winter temperature	c4	0.032 (0.020, 0.045)
Spring temperature	c5	−0.207 (−0.218, −0.196)
Elevation	c6	−0.069 (−0.080, −0.058)
Detection probability		
YOY intercept (mean probability)	**d0.mean[1]**	**0.499 (0.491, 0.506)**
Adult intercept (mean probability)	**d0.mean[2]**	**0.635 (0.628, 0.642)**
Julian date	d1	0.170 (0.150, 0.189)
Stream width	d2	−0.169 (−0.188, −0.151)

described as the productivity coefficient of 1.077 [95% CI = (1.045, 1.106)] and the density-dependent coefficient of 0.0086 [95% CI = (0.0082, 0.0090)]. At local sites, YOY abundance increased with adult abundance in the previous year when local adult abundance was less than 50 individuals per 100 m (see Appendix S2). YOY abundance was not sensitive to higher adult abundances in the previous year.

Population growth rate was most sensitive to per-capita recruitment and YOY survival, unless local adult abundance was high (Table 3). At high local adult
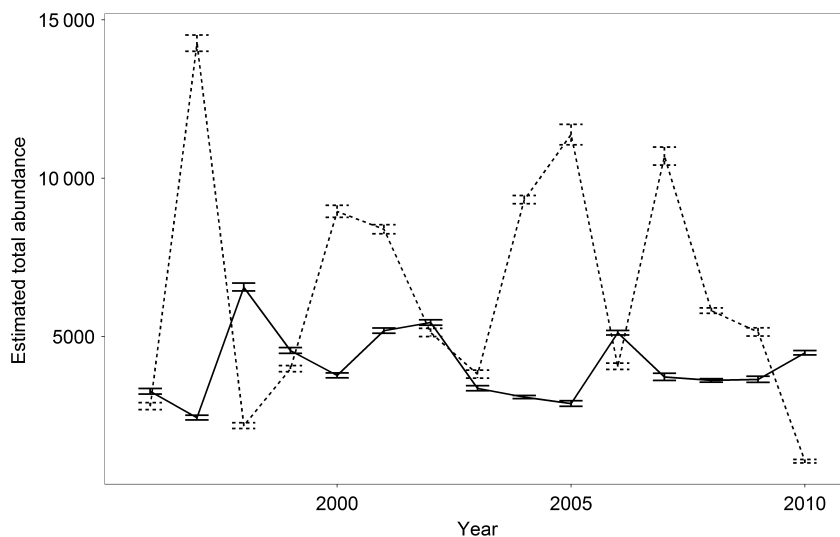
Fig. 3 Mean (+ 95% CI) estimated annual total abundance in the 72 survey sites during 1996–2010. Solid lines indicate adult abundance, and dotted lines indicate YOY abundance.

Table 3 Elasticity of population growth rate to a proportional change in vital rates at three levels of local adult abundance: low (10 individuals per 100 m), median (45 individuals), and high (121 individuals). Elasticity values (values in each column) sum to one (but they do not exactly sum to one due to rounding of each value)

	Local abundance		
	Low	Median	High
Per-capita recruitment	0.382	0.365	0.319
YOY survival	0.382	0.365	0.319
Adult survival	0.235	0.271	0.363

abundance, population growth was most sensitive to adult survival. The population growth rate was 1.17 at low abundance (10 individual per 100 m), 1.04 at median abundance (45 individuals), and 0.83 at high abundance (121 individuals). The population growth rate was one (stable population) when local abundance was 58 individuals.

Simulated scenarios

Scenarios showed that future seasonal weather conditions would strongly impact the persistence of brook trout populations in the SNP. These results were not immediately apparent in the estimated vital rates (Table 2), because vital rates were differentially influenced by seasonal weather covariates. Population abundance in our sites was projected to decline under low fall precipitation, high winter precipitation, and high fall temperature, with the first two weather conditions exerting strong negative effects on abundance (Fig. 4). This pattern emerged because low fall precipitation

and high winter precipitation had a strong negative effect on recruitment (Table 2). Total adult abundance was projected to be lower than or equal to total YOY abundance in all scenarios (Fig. 4), which generally mirrored the observed adult/YOY ratios between 1996 and 2010.

Population persistence depended on the frequencies of high winter precipitation and varied among sites due to the significant positive relationship between elevation and adult survival (Table 2). In the scenario where high winter flow occurred every 5 years, abundance across sites showed a slightly increasing trend (Fig. 5) and none of the local sites experienced quasi-extinction (Fig. 6). Total abundance across sites remained stable, and only one site experienced quasi-extinction when high precipitation occurred for three winters followed by two average winter conditions. However, population decreases were projected at greater frequencies of high winter precipitation; quasi-extinction occurred in 13 sites when four of five winters had high precipitation, and in approximately three quarters of local sites (56 of 72 total sites) when high winter precipitation occurred every year (Figs 5 and 6). Elevation was an important determinant of extinction risk. For example, quasi-extinction was predicted for sites up to 532 m above sea level when high winter precipitation occurred every year, but it was predicted only for sites lower than 408 m when four of five winters were simulated to experience high precipitation.

Discussion

Brook trout populations responded to seasonal weather patterns via complex pathways affecting vital rates.
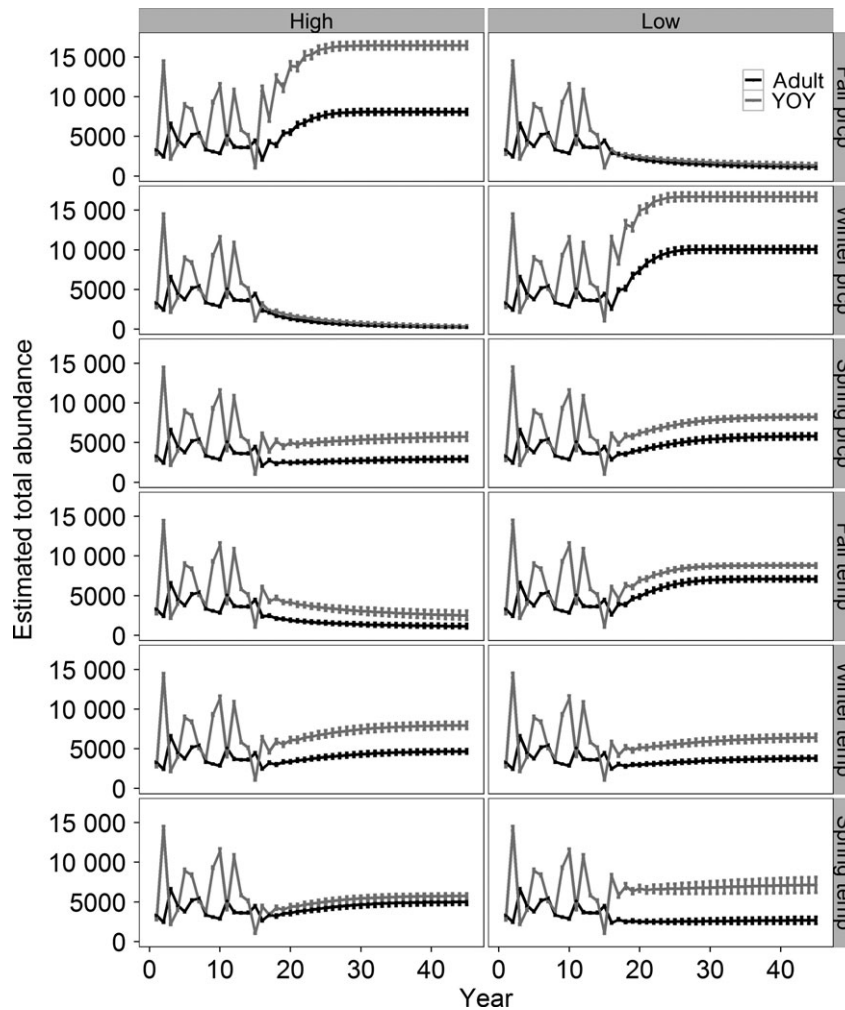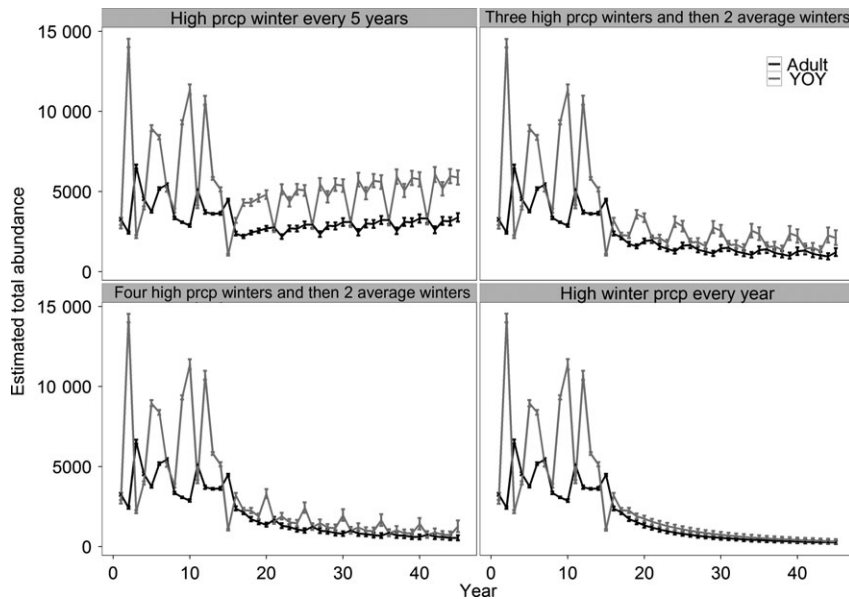
Fig. 4 Estimated (first 15 years) and projected (years 16–45) total abundance in study sites under twelve potential climate scenarios with constant seasonal environmental conditions. Mean and 95% CI are shown.

Most notably, population vital rates were differentially influenced by environmental covariates, with both temperature and precipitation being important only in some seasons and not necessarily for all individuals. YOY survival was influenced most by spring temperature, adult survival was impacted most severely by elevation, and recruitment was influenced most by winter precipitation. Variable responses of population vital rates to environmental conditions have been observed in other studies (e.g., Diamond *et al.*, 2013; Dybala *et al.*, 2013), and this may be a rather common pattern for populations exhibiting ontogenetic shifts in habitat and other resource use. To our knowledge, this is the first study to reveal heterogeneous drivers of different vital rates from a large set of distinct sites based solely on count data.

The heterogeneous impact that climate can have on vital rates has important ecological and conservation implications. Variability in ecological traits and environmental responses among individuals and populations has been identified as a mechanism to buffer species against extinction (i.e., portfolio effect; Schindler *et al.*, 2010; González-Suárez & Revilla, 2013; Moore *et al.*, 2014; Thorson *et al.*, 2014). In essence, different drivers among vital rates indicate that not all life stages may be impacted negatively at the same time. In the case of brook trout, we consider that heterogeneous responses of vital rates, combined with early maturation and high fecundity, may explain why populations are capable of persisting in small and isolated sections of dynamic environments such as headwater streams (Letcher *et al.*, 2007; Kanno *et al.*, 2011b). Climate change is expected to not only alter the mean climate condition but also increase temporal variability in temperature and precipitation (Ingram *et al.*, 2013). While increased climate variability could certainly increase

Fig. 5 Estimated (first 15 years) and projected (years 16–45) total abundance in study sites under four potential high winter precipitation conditions (mean + 1.5*SD) of varying frequencies. Mean and 95% CI are shown.
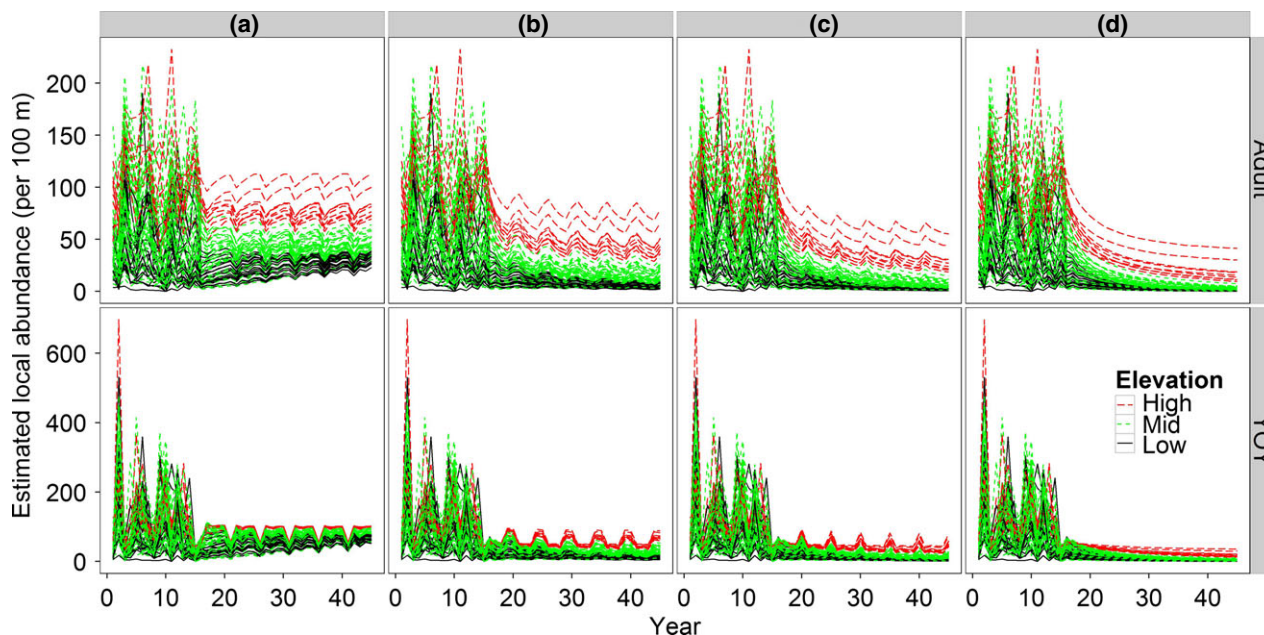
Fig. 6 Local abundance trajectories in 72 survey sites under varying frequencies of high winter precipitation condition (mean + 1.5*SD); (a) high winter precipitation occurs every 5 years, (b) three high precipitation winters followed by two average precipitation winters, (c) four high precipitation winters followed by one average precipitation winter, and (d) high winter precipitation occurs every year. Each line represents mean estimated abundance at each of the 72 sites. For visual clarity, sites were classified as high elevation (>600 m), mid-elevation (400–600 m), and low elevation (<400 m).

temporal fluctuations in population abundance for each life stage and render populations more susceptible to local extirpation (Roland & Matter, 2013), heterogeneous responses among vital rates could also average out individual patterns over a time period. The degree of demographic synchrony and its effect on population persistence should further be investigated for populations structured by age, size, and life stage across many taxa.

Our study showed that the effect of temperature and precipitation on vital rates depends on season. Warm spring had a positive impact on YOY survival, but

warm fall affected YOY survival negatively. Recruitment was influenced positively by fall precipitation, but negatively by winter precipitation. The latter finding indicates that seasonal distributions of precipitation amount can affect brook trout populations even though total precipitation remains unchanged. These results suggest that our examination of population vital rates across seasons provided novel insights of population responses to changing climate, and this knowledge would be required for accurate prediction of population persistence.

High winter precipitation strongly affected the population dynamics of brook trout in our study. Climate change impacts on wild animal populations have been most commonly examined using annual or single-season temperature values (e.g., Roland & Matter, 2013; Wenger *et al.*, 2013; Dueri *et al.*, 2014). For example, potential changes in geographic distributions of cold-water salmonids have been projected based on alterations in annual mean temperature (Flebbe *et al.*, 2006; Zeiger *et al.*, 2012) and summer mean temperature (Roberts *et al.*, 2013; Wenger *et al.*, 2013). Although summer weather is important for a coldwater species such as brook trout and the omission of summer weather patterns is a potential caveat in our study, we found that changes in winter precipitation can also drive local populations to extirpation. We suspect that high winter flow is associated with recruitment failures because fertilized eggs remain in the gravel during this period and are susceptible to bed scouring (Petty *et al.*, 2005; Wenger *et al.*, 2013). The finding that winter weather can potentially be a major driving force in population trajectories was unexpected as stenothermal ectotherm species are typically considered to be regulated by temperature regimes. Interestingly, the winter weather pattern, particularly air temperature, is expected to change more than any other season in many climate change projections (Ingram *et al.*, 2013). Warmer winter would increase the amount of rain, instead of snow, which may exacerbate the winter flow impact on brook trout population dynamics in the future climate.

While high winter precipitation affected trout populations negatively, our simulations indicated that the frequency of such conditions could determine population trajectories. Quasi-extinction was projected to occur at three quarters of survey sites when high winter precipitation conditions were simulated every year, but population abundance did not show a clear sign of decline (only one local site with quasi-extinction) when at least two of five winters were simulated to experience mean winter precipitation conditions. This pattern emerged due partly to density-dependent recruitment. Density-dependent responses of vital rates have been

linked to stability and resiliency in brook trout (Grossman *et al.*, 2010, 2012) and other animal populations (Kruger, 2007; Reed & Slade, 2008). Density-dependent processes can potentially play a major role in population viability under climate change scenarios where climate variability is predicted to increase (Ingram *et al.*, 2013; Rummukainen, 2013) and animals are more likely to experience a combination of favorable and unfavorable conditions across years. A critical question for future work then is: 'Can positive effects of some favorable years on population abundance offset negative impacts of unfavorable years?'

Elevation played an important role in determining variation in the likelihood of population persistence among sites. It was not surprising that brook trout populations were more likely to persist at higher elevation sites under altered climate conditions; similar altitude-mediated effects have been consistently found in animals and plants under climate change projections (Loarie *et al.*, 2009; Chen *et al.*, 2011; Wenger *et al.*, 2013). However, a new perspective offered in the current work is that this pattern resulted from higher adult survival at high-elevation sites, a demographic mechanism that would not have been apparent based solely on analysis of geographic distributions or abundance. Although adult survival was important in explaining heterogeneity among sites, population growth rate was most sensitive to recruitment and YOY survival unless adult abundance was high. The same conclusion has been drawn from other studies of headwater brook trout populations (Marschall & Crowder, 1996; Letcher *et al.*, 2007), and this is common among short-lived freshwater fish species (Vélez-Espino *et al.*, 2006). These complex demographic patterns further suggest a need for understanding how vital rates in stage-structured populations differentially respond to environmental change.

There are few long-term monitoring data sets in animal population ecology. Monitoring designs should be carefully considered when an opportunity exists to collect such data. There remains an important question about the optimal spatial and temporal distributions of sampling effort. While only two of 72 study sites were surveyed every year during the 15-year study period, different sets of additional sites were surveyed in consecutive years throughout the study period. We consider that the judicious inclusion of consecutive years greatly improved our inferences on temporal variation in population vital rates. Zipkin *et al.* (2014a) found that increasing the number of years surveyed resulted in more accurate and precise parameter estimates in simulations of the open population *N*-mixture model; for example, known population vital rates were recovered

accurately with only five sites when data were simulated for 20 years. In addition, a combination of single-pass (16%) and three-pass (84%) depletion surveys allowed us to estimate stage-specific detection probability. Because electrofishing is size selective, accounting for the potential differences in detection probabilities for YOY and adults was necessary for accurate inferences. Our work represented a case study in which a flexible modeling framework was successfully applied to missing or imperfect long-term data to make inferences on key vital rates that differed across space, time, and stages. This modeling framework is a powerful approach because it can incorporate demographic processes at a broad spatial scale and can provide researchers and managers with an innovative tool to link demography to landscape-level conservation efforts.

The current work adds to a growing list of studies that attempt to estimate vital rates in structured populations using count data (Link et al., 2003; Dail & Madsen, 2011; Zipkin et al., 2014a). While we highlighted its strengths in this study, we also recognize the limitations. Importantly, analyses of count data are less capable of making inferences on complex population dynamics compared to traditional mark–recapture methods. Zipkin et al. (2014b) applied a similar state-structured population model to black-throated blue warblers (Setophaga caerulescens) populations, in which survival probabilities were estimated for each life stage and sex. Survival probabilities tended to be underestimated when compared to inferences based on mark–recapture data. Accounting for immigration appears to be another challenge in count data. Zipkin et al. (2014a) used simulated data sets and an empirical data set on a highly immobile stream amphibian (northern dusky salamanders Desmognathus fuscus) and demonstrated that immigration and apparent survival could be estimated simultaneously in stage-structured populations from count data. Such models did not converge or model outputs were sensitive to a slight change in model structures in SNP brook trout data (Y. Kanno & D.A. Boughton, unpublished data). As a result, we could not explicitly account for immigration in this study. Zipkin et al. (2014b) similarly noted that count data may not contain enough demographic information for estimating all parameters in some cases and suggested an integration of mark–recapture and count data as an efficient modeling approach for estimating vital rates (e.g., Schaub & Abadi, 2011; Oppel et al., 2014). In our case, a more structurally complex model than presented here would not be necessary for our goal of identifying key demographic drivers of population responses to seasonal weather patterns. However, if the goal were to understand the relative importance of

immigration versus apparent survival in a meta-population study, a more complex model with additional data sources (e.g., mark–recapture data at a limited number of sites) would be necessary. Our modeling approach is indeed flexible enough to accommodate such additional structures, and future research is much needed to provide a framework in which multiple data sources are integrated for ecological inferences at broader spatial and temporal scales.

Acknowledgements

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Supporting Information

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

Appendix S1. Brook trout length-frequency histograms.
Appendix S2. Spawner-recruit relationship.
Appendix S3. May to August stream flow.
Appendix S4. JAGS code.
Appendix S5. Model selection steps.
Appendix S6. Model diagnostics.