

# Changes in seasonal climate outpace compensatory density-dependence in eastern brook trout

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## Abstract

Understanding how multiple extrinsic (density-independent) factors and intrinsic (density-dependent) mechanisms influence population dynamics has become increasingly urgent in the face of rapidly changing climates. It is particularly unclear how multiple extrinsic factors with contrasting effects among seasons are related to declines in population numbers and changes in mean body size and whether there is a strong role for density-dependence. The primary goal of this study was to identify the roles of seasonal variation in climate driven environmental direct effects (mean stream flow and temperature) vs. density-dependence on population size and mean body size in eastern brook trout (*Salvelinus fontinalis*). We use data from a 10-year capture-mark-recapture study of eastern brook trout in four streams in Western Massachusetts, USA to parameterize a discrete-time population projection model. The model integrates matrix modeling techniques used to characterize discrete population structures (age, habitat type, and season) with integral projection models (IPMs) that characterize demographic rates as continuous functions of organismal traits (in this case body size). Using both stochastic and deterministic analyses we show that decreases in population size are due to changes in stream flow and temperature and that these changes are larger than what can be compensated for through density-dependent responses. We also show that the declines are due mostly to increasing mean stream temperatures decreasing the survival of the youngest age class. In contrast, increases in mean body size over the same period are the result of indirect changes in density with a lesser direct role of climate-driven environmental change.

**Keywords:** climate change, density-dependence, integral projection models, metapopulations, salmonids, size-structure

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## Introduction

Extrinsic environmental factors, such as climate, can influence population dynamics by directly altering demographic rates (e.g. survival). These effects on vital rates can yield little overall change in population size if they are buffered by intrinsic density-dependent compensatory mechanisms (Cappuccino & Price, 1995). These types of dynamics are challenging to understand in natural, complex environments when multiple environmental variables and seasonal changes produce contrasting effects on demographic rates (Breitburg *et al.*, 1998; Letcher *et al.*, 2002; Stenseth *et al.*, 2002; Xu *et al.*, 2010a). Moreover, in structured populations, environmental change may directly alter the demographic rates of subclasses of the population differently and the compensatory effects of density-dependence rarely affect these groups in the same way (Coulson *et al.*, 2001; Einum & Nislow, 2005; Einum *et al.*, 2006; Bassar *et al.*,

2010, 2013; van de Pol *et al.*, 2010). Combining the complex structure of the environment and the population leads to the possibility of cross-season effects whereby changes in population size due to environmental change in a previous season can trigger density-dependent compensation in the current season (Reed *et al.*, 2013).

In structured populations, age- and size-structure may also be influenced by changes in seasonal environmental drivers. However, surprisingly little is known about how changes in climate will alter mean body size within populations in aquatic ecosystems (Millien *et al.*, 2006), though it has been suggested that body sizes should decrease with changes in warming due to temperature-size rules (Daufresne *et al.*, 2009; but see Vindenes *et al.*, 2014). These additional characters of the population are of particular concern in harvested populations (such as in forestry or fisheries), where economic value is strongly influenced by individual body size, or in populations where reproductive value is strongly size-dependent.

An additional challenge in understanding the combined action of multiple extrinsic (density-indepen-

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dent) factors and intrinsic (density-dependent) mechanisms on population dynamics is that often we do not have a way to connect changes in field measurements of age- and/or size-specific demographic rates (survival, somatic growth, reproduction, etc.) with population dynamic quantities. Consequentially, we rarely have the ability to weigh the influence of various extrinsic factors against each other in their impact of population dynamics and characteristics. This limitation seriously constrains our ability to both make robust predictions and understand important mechanisms, both of which are essential in providing science support to management and conservation in the context of a changing climate.

Discrete time matrix population models offer one way to understand the relative influence of multiple extrinsic factors on population dynamics and characters, but are often insufficient or cumbersome when much of the demography of the organism is determined by traits like body size that change throughout life. In this context, matrix models require numerous parameters to account for differences among stages in the response to environmental changes. Integral projection models (IPM's) offer a solution to this problem by treating continuous traits as continuous variables in statistical fitting of the demographic rates (Easterling *et al.*, 2000). In doing so, they often require far fewer parameters, but yield better, more natural fits to data than would be used in similar matrix models (Easterling *et al.*, 2000). They can also be combined with categorical descriptors of the life history to yield age and size models (Ellner & Rees, 2006), can be density-dependent (Bassar *et al.*, 2013), and can be analyzed using any of the analytical tools available to matrix population models (Childs *et al.*, 2004; Ellner & Rees, 2007). To our knowledge, they have yet to be applied to structured (age-, size-, -space) populations that live in strongly seasonal environments. Because most populations are structured in some way and live in spatially structured habitats, the development of methods that allow us to connect field measurements of demographic rates with population dynamics under these scenarios should be a valuable tool in understanding how changes in climate have influenced population characters in a wide range of systems.

Here, we investigate how changes in two climate-driven environmental factors (stream flow and temperature) over the last 10 years have influenced the population size and mean body size of declining populations of eastern brook trout (*Salvelinus fontinalis*). We addressed the following questions: (1) What were the relative effects of seasonal variation in climate driven environmental direct effects (mean stream flow and temperature) vs. climate induced density-dependence

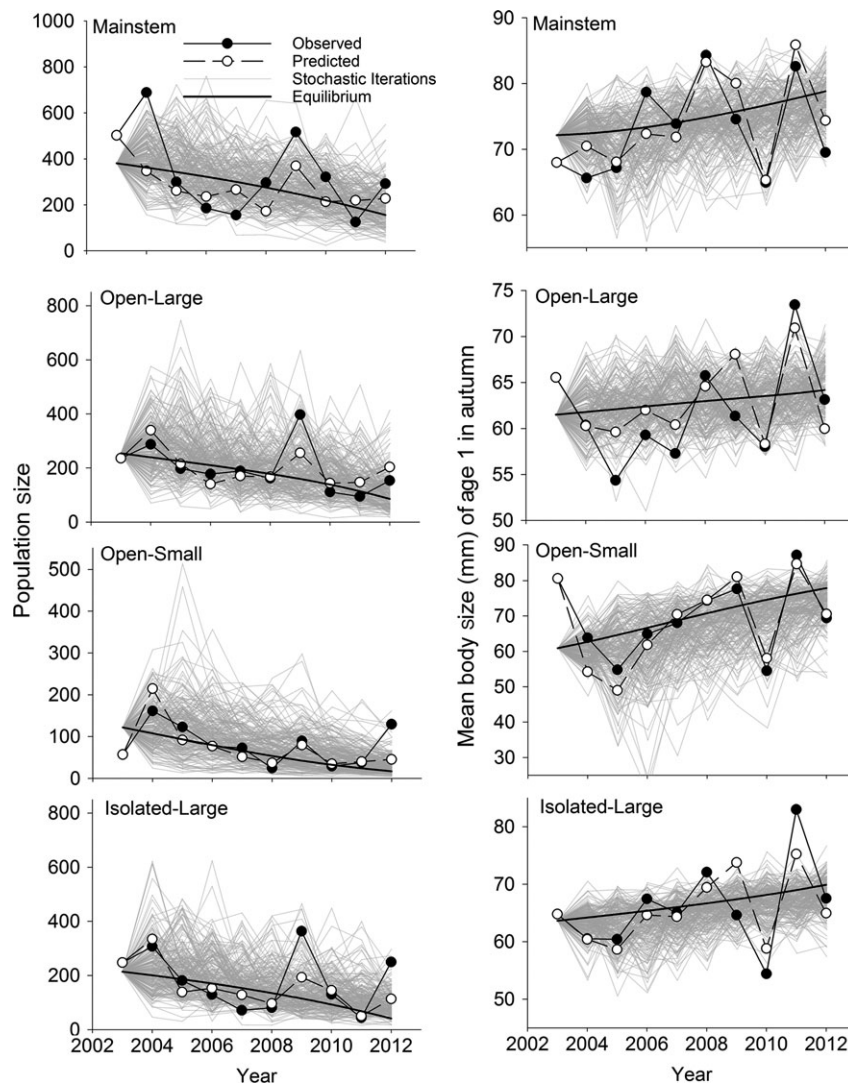
effects on population characteristics? (2) Which season (s) and which environmental variables had the largest influence on population characteristics? (3) Through which demographic parameters of which age groups did changes in climate driven environmental effects produce the largest effects on population characteristics? To answer these questions, we developed a discrete-time population projection model that integrates matrix modeling techniques used to characterize discrete population structures (age and habitat type) with distinct seasonal effects (Caswell & Trevisan, 1994; Caswell, 2001; Hunter & Caswell, 2005) and body size-dependent demographic rates (Easterling *et al.*, 2000; Ellner & Rees, 2006). The model is parameterized using capture-mark-recapture data from a 10-year study of brook trout in four adjacent streams in Western Massachusetts, USA. The populations experience marked seasonality in stream flow and temperature and have been declining in abundance over the last 10-years (Fig. 1). We examine each question in relation to both the equilibrium population size and mean body size within each age group by expanding analytical sensitivity analyses of nonlinear matrix models (Caswell, 2008) to include those that simultaneously consider discrete and continuous characteristics in seasonal environments.

## Materials and methods

### *Study site and measurement of environmental variables*

The study streams are located in Whately, Massachusetts, USA. The study area is comprised of a 1-km long mainstem (West Brook) and three-second order ~300 m tributaries (Jimmy, Mitchell, and O'Bear). All streams directly flow into the West Brook (hereafter: Mainstem), but differ in their degree of connection and size (Table S1). Jimmy Brook (hereafter: Open-Large, OL) flows unimpeded into the Mainstem, is the largest of the tributaries and always contains uninterrupted flowing water. Mitchell Brook (hereafter: Open-Small, OS) is the smallest tributary, is separated from the Mainstem by a small culvert which does not preclude movement between it and the Mainstem and occasionally has low flow rates. O'Bear Brook (hereafter: Isolated-Large, IL) is near the size of Jimmy brook, but trout cannot move from the Mainstem into the IL brook because of a 2.2 m high barrier waterfall.

The watershed is an 11.8 km<sup>2</sup> mixed hardwood forest. The streams all consist of a closed canopy with the streambed comprised mainly of cobbles with occasional boulders. The streams are mostly riffles with occasional pools and glides (see Letcher *et al.*, 2002). The upper boundary of each stream is blocked by waterfalls and the downstream boundary of the Mainstem also has a waterfall. In addition to brook trout, the Mainstem, and 'Open' streams also contain blacknose dace (*Rhinichthys atratulus*) and naturalized populations of brown trout (*Salmo trutta*). Atlantic salmon were stocked as 25 mm



**Fig. 1** Observed (closed symbols), predicted (open symbols), stochastic iterations (gray lines), and equilibrium population size (left panels) and mean body size of the age 1 cohort (right panels) (solid lines) in each of the four streams in the autumn of each year. Equilibrium population size and mean body size were calculated for each year and stream using the predicted seasonal stream flow and temperature values of that year. The projection model is a discrete-time model, but we fit spline curves through the equilibria of each year for illustration.

fry into the Mainstem in the early years of the study (2002–2004), but do not occur in the study area on their own. Hatchery trout are not stocked in the study streams.

Four times a year (approximately corresponding to the winter and summer solstice and spring and autumn equinox) from 2002 to 2012, brook trout were captured in each stream using standard electrofishing techniques (300 V DC, unpulsed) (Letcher *et al.*, 2007). Captured brook trout were anesthetized, measured for fork length (FL), and untagged fish >60 mm FL were tagged with 12 mm passive integrated transponder tags (PIT tags; Digital Angel, St. Paul, MN, USA). Fish that were large enough to be captured, but less than 60 mm FL were anesthetized, measured and an anal fin was clipped for identification of individuals that had already been captured. Mortality from sampling was rare and

tagging has minimal long-term effects on growth or survival (Gries & Letcher, 2002; Sigourney *et al.*, 2005). Two stationary PIT tag detecting antennas were placed at the lower boundary of the Mainstem to detect fish permanently leaving the study area [91% average detection efficiency (Zydlewski *et al.*, 2006)]. Each stream is split into 20 m sections and in the tributaries we captured fish using a single-pass. In the Mainstem, we used double-pass and blocked the upper and lower barriers of each 20 m section to increase our ability to capture fish. Fish were returned to the same 20 m sections where they were captured. Overall, the data consists of 20 089 observations of 10 458 individual brook trout. Sampling was conducted in accordance with the USGS Conte Anadromous Fish Research Center's animal care and use protocols.

Water temperature ( $\pm 0.01$  °C) in the streams was measured every 2 h using temperature data loggers (Onset Computer Corporation, Pocasset, MA, USA) attached to a submerged rock. Stream depth was measured every 2 h using data loggers (Onset Computer Corporation) in the downstream end of the Mainstem. Stream flow was estimated using a flow extension model (Nielsen, 1999) and was based on data from a nearby USGS stream gage (Mill River, Northampton, MA, USA) (for details, see Xu *et al.*, 2010a). Mean stream flow and temperature over each seasonal sampling period (interval between sampling dates) and year of the study were calculated from these data.

### Projection model construction

We describe the model following the life cycle of female brook trout. We begin with the equations used to describe the recruitment of new individuals into the population. We then present the integro-difference equations that describe the size, age, and river specific transitions from one season to the next after recruitment and show how these seasonal projection equations are combined to result in a yearly projection equation. Finally we describe how stream temperature, stream flow rate and density can alter the vital rates and describe the statistical methods used to parameterize the model. Summaries and descriptions of the functions, variables and parameters are provided in Table 1. The variable  $z$  is the fork length (FL) of the fish in season  $q$ ,  $a$  is the age (in years) of the fish, and  $r$  is the river the fish resides in. Apostrophes on  $z$ ,  $q$ , and  $r$  denote the size or river the fish is predicted to be in the following season (i.e. the within year, between season changes).  $T$  is the mean seasonal water temperature (°C),  $F$  is the seasonal mean flow rate ( $\text{m}^3 \text{s}^{-1}$ ),  $D$  is the numerical density (estimated abundance,  $\text{N m}^{-2}$ ) and  $B$  is the biomass density ( $\text{g m}^{-2}$ ) (Table 1). Subscripts denote where a parameter or function depends on a categorical variable and parentheses denote where a parameter or function depends on a continuous variable.

**Brook trout life history and model structure. Recruitment**—The model follows the life cycle of female brook trout and begins with reproduction by adult (age 2+) females in autumn immediately following the autumn census (Fig. 2). All adult females lay eggs and the number of eggs they lay  $C(z)$  is a function of body length. The model is female only and so the number of eggs laid is divided by two to represent only new females. The number of eggs laid in fish is generally a power function of length and for brook trout was estimated in a previous study (Letcher *et al.*, 2007) (Table 1). Age 1 (new recruits) individuals have never been observed to produce eggs. The eggs remain in a prerecruit stage (age 0) until just before the autumn census, when they recruit into the population (age 1). We assume that there is no movement between rivers at this age because we currently lack reliable data on movement for this life stage. The production of new recruits is described by:

$$n(z)_{a=1,r,\text{Aut},t+1} = R(z, F_{\text{All}}, T_{\text{All}}, D_{\text{Aut}}, B_{\text{Sum}})_{r,\text{Sum}} \int_0^{300} C(z)n(z)_{a=2+,r,\text{Aut},t} dz. \quad (1)$$

The function  $n(z)_{a=2+,r,\text{Aut},t}$  is the number of size  $z$  (continuous) individuals of age 2+ in river  $r$  in the autumn in year  $t$ . Multiplying this function by the size-specific number of eggs laid,  $C(z)$  yields the total number of eggs laid across all individuals of each size. Integrating with respect to size then yields the total number of eggs laid in the population in the autumn. The limits of integration (0 to 300) mean that the function is considered over the fork length values of 0 to 300 mm. The upper limit of 300 was chosen to cover the full observed size range (about 30 mm more than the largest trout ever caught in the streams).

The total number of eggs laid in the stream is then multiplied by a recruitment function which describes the survival of the eggs from laying to recruitment at size  $z'$ . Importantly, the recruitment function does not depend on the size of the parent females,  $z$ . This is because we currently do not have a way to connect the size of the recruiting offspring with parent size, though future parentage assignment via genetic techniques may allow this to be included. The recruitment function,  $R$ , is a composite of two functions describing the probability of surviving from laying to recruitment,  $S(F_{\text{All}}, T_{\text{All}}, D_{\text{Aut}})_{a=0,r}$ , and the probability of recruiting at size  $z$ ,  $O(z', F_{\text{All}}, T_{\text{All}}, B_{\text{Sum}})_r$  (Table 1). Survival from laying to recruitment is a function of mean flow and mean temperature in each season and on the numerical density ( $D_{\text{Aut}}$ ) of adults (age 2+) in each stream in the autumn. Adult density in the autumn can influence the probability of recruitment the following autumn (Egglshaw & Shackley, 1977) because suitable breeding sites are limited in the streams and increased adult density can either lead to failure of some fish to breed, reduces the survival of eggs that are laid in unsuitable locations, or reduces individual survival of prerecruitment fry via increased intracohort competition (Elliott & Hurley, 1998; Einum & Nislow, 2005).

Size at recruitment is a probability density function describing the distribution of sizes among new recruits. In the model, this distribution is assumed to be Gaussian with mean  $\mu_O(F_{\text{All}}, T_{\text{All}}, B_{\text{Sum}})_r$  and variance  $\sigma_O^2$  (Table 1). The mean size at recruitment is assumed to be a function of mean flow and mean temperature in each season and on biomass density ( $B_{\text{Sum}}$ ) of age 1 and 2+ fish in each stream in the summer (Egglshaw & Shackley, 1977). The biological interpretation of this parameter is that increased numbers of older, larger fish can alter the mean size at recruitment by outcompeting the incipient recruits for resources. Biomass density here is used instead of numerical density because these types of interactions should also be a function of the size distribution of the adults and biomass density allows a simple way for the size distribution of adults to be included without additional and more complex terms (Bassar *et al.*, 2013).

**Table 1** Description of variables, functions, and parameters in brook trout projection model. Parameter estimates can be found in the Table S1–S9

Variable/Function/ Parameter	Description	Values/Formula
$z, z'$	Fork length (FL) at beginning/end of season. Measured in millimeters	Continuous with values from 0 to 300.
$a, a'$	Age at beginning/end of season	0, 1, 2+
$r, r'$	River at beginning/end of season	Mainstem, Open-Large, Open-Small, Isolated
$q$	Season	Autumn, winter, spring, summer
$E$	Generic notation for abiotic environmental variables ( $T$ and $F$ )	
$T$	Mean water temperature. Standardized to mean of 0 and standard deviation 1	
$F$	Mean flow rate. Standardized to mean of 0 and standard deviation 1	
$n(z)_{a,r,q,t}$	Continuous population size distribution of age $a$ fish in river $r$ in season $q$ in year $t$	
$N_{a,r,q,t}$	Total population size of age $a$ fish in river $r$ in season $q$	$\int n(z)_{a,r,q,t} dz$
$D_{a,r,q,t}$	Total population numerical density of age $a$ fish in river $r$ in season $q$	$\int n(z)_{a,r,q,t} dz / \text{area}_{r,q}$
$B_{a,r,q,t}$	Total population biomass density of age $a$ fish in river $r$ in season $q$ . The relationship between mass (grams) and length (mm) is $m(z) = 0.000009z^{3.03}$ and was estimated using all the length and mass data from the recaptures. $P$ -values for both parameters $<0.0001$	$\int m(z)n(z)_{a,r,q,t} dz / \text{area}_{r,q}$
$p(z)_{a,r,q,t}$	Mean fork length of age $a$ fish in river $r$ in season $q$	$\int zn(z)_{a,r,q,t} dz / \int n(z)_{a,r,q,t} dz$
$\psi_{r',r,q}$	Probability of moving from river $r$ to river $r'$ in season $q$	
$K(z'   z, T, F, N)_{a',a,r,q}$	Projection kernel describing the transition and recruitment functions	$G(z'   z, T, F)_{a,r,q} S(z, T, F)_{a,r,q}$
$C(z)$	Number of eggs laid by female of size $z$ . Only age 2+ females reproduce (Letcher <i>et al.</i> , 2007). Number of eggs is divided by two because this is a female only model	$0.00187z^{2.19} / 2$
$R(z, F_{All}, T_{All}, B_{Sum})_{a',a,r,Sum}$	Recruitment function describing the survival from eggs (beginning of autumn) to recruitment and the size at recruitment	$O(z', F_{All}, T_{All}, B_{Sum})_r S(F_{All}, T_{All}, D_{Aut})_{a=0,r}$
$O(z, F_{All}, T_{All}, B_{Sum})_r$	Size at recruitment function describing the distribution of body sizes of new recruits at the beginning of the autumn census	$(2\pi\sigma_O^2)^{-0.5} e^{-\frac{(z' - \mu_O(F_{All}, T_{All}, B_{Sum}))^2}{2\sigma_O^2}}$
$S(F_{All}, T_{All}, D_{Aut})_{a=0,r}$	Survival function of age 0 individuals describing the survival from eggs (beginning of autumn) to recruitment just before the autumn census the following year	$\text{logit}^{-1} \left( \Phi_r + \sum_{E=T}^F \sum_q \Phi_{E,q,r} E_q + \Phi_{D,r} D_{r,Aut} \right)$
$S(z, T, F)_{a,r,q}$	Survival of size $z$ fish of age $a$ (1 or 2+) in river $r$ from start of season $q$ to start of season $q + 1$	$\text{logit}^{-1} (\Phi_{a,r,q} + \Phi_{z,a,r,q} z + \Phi_{F,a,r,q} F + \Phi_{T,a,r,q} T + \Phi_{FT,a,r,q} FT)$
$G(z'   z, T, F)_{a,r,q}$	Probability of age $a$ (1 or 2+) fish in river $r$ in season $q$ growing to size $z'$ given fish was size $z$ at beginning of the season	$(2\pi\sigma_{Ga,r,q}^2)^{-0.5} e^{-\frac{(z' - \mu_{Ga,r,q}(z,T)) ^2}{2\sigma_{Ga,r,q}^2}}$
$\mu_O(F_{All}, T_{All}, B_{Sum})_r$	Mean fork length at recruitment	$Y_r + \sum_{E=T}^F \sum_q Y_{E,q,r} E_q + Y_{D,r} B_{Sum}$
$\sigma_O^2$	Variance in size at recruitment. Depends only on stream	

Table 1 (continued)

Variable/Function/ Parameter	Description	Values/Formula
$\mu_G(z, F, T)_{a,r,q}$	Mean somatic growth of age $a$ fish in river $r$ in season $q$ given fish was size $z$ at beginning of the season	$\Gamma_{a,r,q} + \Gamma_{z,a,r,q}z + \Gamma_{F,a,r,q}F + \Gamma_{T,a,r,q}T + \Gamma_{FT,a,r,q}FT$
$\sigma_{G_{a,r,q}}^2$	Variance in somatic growth of age $a$ fish in river $r$ in season $q$	
$\rho(z)_{a,r,q}$	Probability of capture of age $a$ fish of size $z$ in river $r$ in season $q$	
$\Phi$	Effect of stream, environmental variable (T or F), or numerical density on logit transformed survival. For prerecruitment survival only, $\beta_{PC_i}$ is the regression coefficient between principle component $i$ and logit transformed survival	$\sum_{i=1}^5 \beta_{PC_i} \text{cor}(PC_i, E_q)$
$\Gamma$	Effect of stream or environmental variable (T or F) on growth increment	
$\gamma$	Effect of stream, environmental variable (T or F), or numerical density on mean size at recruitment. $\beta_{PC_i}$ is the regression coefficient between principle component $i$ and mean size at recruitment	$\sum_{i=1}^5 \beta_{PC_i} \text{cor}(PC_i, E_q)$

Effectively it weights numerical density in such a way that when there are more, larger individuals in the population, the outcome of competitive interactions are increasingly asymmetric. For simplicity, the variance in size at recruitment is not a function of environmental variables or density.

*Survival, growth, and movement of age 1 and 2+*—After recruitment in the autumn, the age 1 fish survive and grow through the autumn, winter, and spring according to their sizes and stream of residency at the beginning of each season. They then move to a different stream or stay in their current stream immediately before the next seasonal census. These transitions are described by a set of integro-difference equations. For any given season, the number of fish of size  $z'$ , age  $a$  in river  $r'$  in the next season ( $q'$ ) is described by the generic integro-difference equation:

$$n(z')_{a,r',q',t} = \sum_r \psi_{r'|r,q} \int_0^{300} K(z'|z, T, F)_{a,r,q} n(z)_{a,r,q,t} dz. \quad (2)$$

The function  $n(z)_{a,r,q,t}$  describes the number of size  $z$  (continuous) individuals of age  $a$  in river  $r$  in season  $q$  in year  $t$ . The variable  $\psi_{r'|r,q}$  is the probability of moving from river  $r$  into river  $r'$  in season  $q$ . The function  $K(z'|z, T, F)_{a,r,q}$  is the demographic projection kernel describing the size, age, river, and season specific survival and size transitions and how these change as a function of the mean water temperature ( $T$ ) and mean flow rate ( $F$ ).

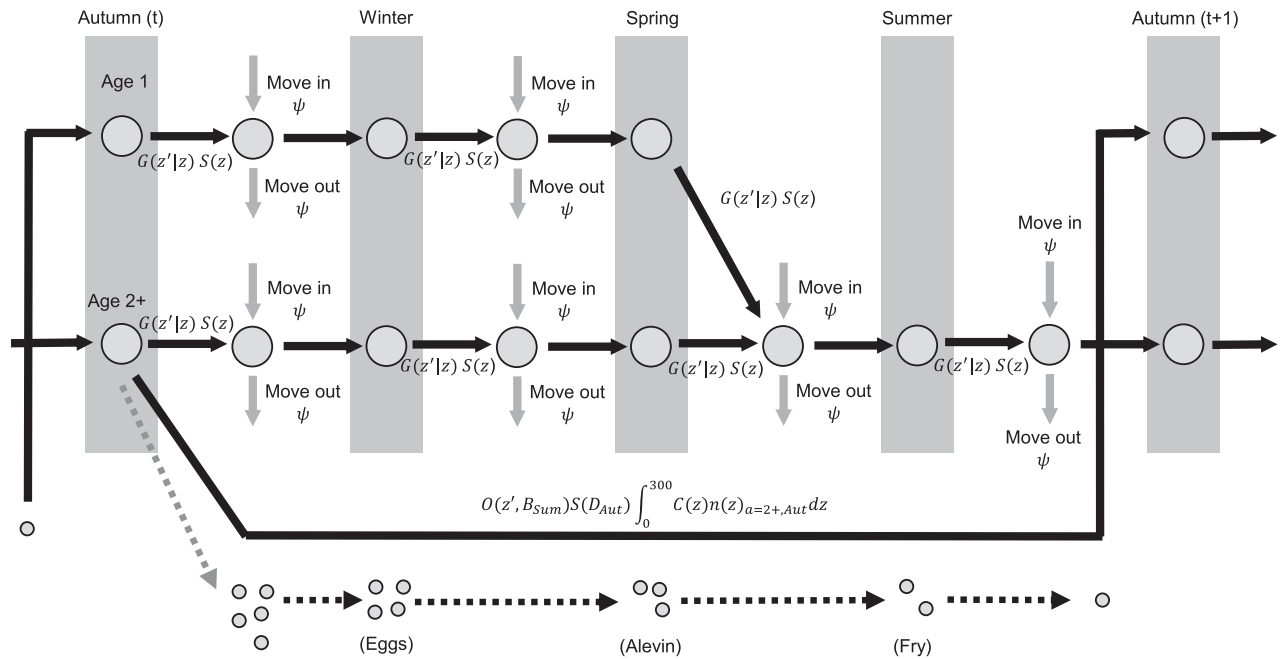
To project across all four seasons (starting from the autumn), and thus have a projection for a whole year, we simply create projection equations for each season:

$$\begin{aligned} n(z')_{a,r',\text{Win},t} &= \sum_r \psi_{r'|r,\text{Aut}} \int_0^{300} K(z'|z, T, F)_{a,r,\text{Aut}} n(z)_{a,r,\text{Aut},t} dz, \\ n(z'')_{a,r'',\text{Spr},t} &= \sum_r \psi_{r''|r',\text{Win}} \int_0^{300} K(z''|z', T, F)_{a,r',\text{Win}} n(z')_{a,r',\text{Win},t} dz', \\ n(z''')_{a,r''',\text{Sum},t} &= \sum_r \psi_{r'''|r'',\text{Spr}} \int_0^{300} K(z'''|z'', T, F)_{a,r'',\text{Spr}} n(z'')_{a,r'',\text{Spr},t} dz'', \\ n(z)_{a+1,r,\text{Aut},t+1} &= \sum_r \psi_{r|r''',\text{Sum}} \int_0^{300} K(z|z''', T, F)_{a,r''',\text{Sum}} n(z''')_{a,r''',\text{Sum},t} dz''', \end{aligned} \quad (3)$$

and then substitute the appropriate projected population abundance function (e.g.  $n(z')_{a,r',\text{Win},t}$ ) into each equation for the subsequent season (not shown due to space constraints). Importantly, age transitions occur at the end of the summer immediately prior to the autumn census. The demographic kernel in each season is a function that describes the somatic growth and survival as a function of body size, temperature, flow, age, river, and season. The kernel for each season is:

$$K(z'|z, T, F)_{a=1,r,q} = G(z'|z, T, F)_{a=1,r,q} S(z, T, F)_{a=1,r,q}, \quad (4)$$

where  $G$  is a probability density function that describes the probability of growing to size  $z'$  given size  $z$  at the beginning of the season. It is assumed to be Gaussian with mean  $\mu_G(z, F, T)_{a,r,q}$  and variance  $\sigma_{G_{a,r,q}}^2$  (Table 1). Stream flow and temperature influence the mean growth but for simplicity



**Fig. 2** Graphical representation of brook trout life cycle and structure of the population dynamic model for a given stream in the metapopulation. Solid black arrows represent demographic transitions that are functions of mean stream flow and temperature, solid gray arrows represent between stream movement probabilities that are independent of mean stream flow and temperature. Adult females (age 2+) lay eggs in redds (nests) immediately following the autumn census. The eggs transition through multiple, unobserved life stages (eggs, alevin, fry) and recruit into the juvenile population (age 1) immediately prior to the next autumn census. At this point the fish can be tagged and represent the observable portion of the population (denoted by the large gray, vertical bars). These fish then survive to the winter census with a probability determined by their current stream, mean stream flow, mean stream temperature, and body size ( $z$ ) at the autumn census. Surviving fish can then grow (in length) and move to other streams with probabilities given by  $\psi$ . The same thing happens from winter to spring. In the spring, the juvenile fish (age 1) transition to adults immediately following surviving and growing and immediately prior to moving between streams. Since the movement probabilities are not age specific, the choice of whether they transition between ages and or river first does not matter. These fish along with the all other adults from previous years reproduce, survive, grow and then move between streams according to the season-specific adult (age 2+ probabilities) for the rest of their lives.

do not affect the variance. The function  $S$  describes the probability of a size  $z$  individual surviving the season. The survival function also depends on mean stream flow and temperature in each season (Robinson *et al.*, 2010; Xu *et al.*, 2010a; Letcher *et al.*, 2015).

After joining the adult population in the autumn, these new adults and other adults survive, grow, and move between streams throughout the remainder of their lives according to the seasonal transitions:

$$K(z'|z, T, F)_{a=2+,r,q} = G(z'|z, T, F)_{a=2+,r,q} S(z, T, F)_{a=2+,r,q} \quad (5)$$

As in age 1 survival and growth, the survival and growth of age 2+ fish depends on mean temperature and flow. Effects of density on age 1 and 2+ demographic rates were not considered because density-dependence in stream salmonids is often strongest in the early juvenile stages (Sinclair, 1989; Elliott, 1994) and preliminary analyses in this system show that density effects through survival and growth of older fish have a very small influence on the model outcome (see Table S4 and Fig. S2). Including age 1 and 2+ density dependence in the

analysis of the model fit of the overall projection model did not improve the fit for the Westbrook metapopulation (without:  $r^2 = 0.83$ , with:  $r^2 = 0.82$ ) or the Isolated Large population (without:  $r^2 = 0.86$ , with:  $r^2 = 0.84$ ). Including density dependence in age 1 and 2+ also did not dramatically alter the slope of changes in the equilibrium population size or mean body size through time (Fig. S2).

*Demographic rate equations and parameter estimation. Recruitment*—The probability of surviving from eggs to recruitment for each stream and year of the study were calculated by first calculating the probability of capture adjusted number of recruits entering each population in the autumn census and dividing this value by the expected number of eggs entering the system (i.e.  $\int_0^{300} n(z)_{a=1,Aut,t+1} dz / \int_0^{300} C(z)n(z)_{a=2+,Aut,t} dz$ ) in the previous autumn. The number of adults in the previous autumn was also based on probability of capture adjusted estimates of the number of adult females in each population (Letcher *et al.*, 2015). Population sizes were adjusted for

probability of capture by dividing the observed number of individuals by the probability of capture statistic ( $\rho$ ) obtained from a Bayesian Markov chain Monte Carlo (MCMC) model for that season, age, and size (see below).

The effects of seasonal stream flow, stream temperature, and numerical density on survival was then estimated in a linear regression framework. Because we have relatively few numbers of years in the study, we used principal components analysis (PCA) to reduce the number of environmental variables. The PCA included stream, season and year specific mean flow and temperature values (see Table S7 for eigenvalues, loadings, and proportion of variance explained). The linear model included *logit*-transformed observed survival probabilities as the dependent variable and river as a fixed categorical effect, the first five of eight principal components as covariates and the interaction between river and the principal components. We included the first five principal components because our aim was to use principal components as a variable reduction technique and the first five accounted for greater than 95 percent of the total variance in the environmental drivers (Table S7). Using the five of the eight left enough residual degrees of freedom to meet statistical assumptions (eight for full model, Table S9). Numerical density of adult brook trout and its interaction with mean body length and river were entered as covariates. Prior to analysis, environmental variables were standardized to mean of zero and standard deviation of 1 and numerical density was centered on the mean for each stream. We then selected the best model using the small sample size version of Akaike's Information Criteria (AICc). We considered all possible combinations of environment and density variables (Table S8). Since there was no clear best model, we used model averaging techniques to average all the models with delta AICc scores less than four (Table S8). The structure of the final model is shown in Table 1.

Because the statistical parameter estimation was done with principal components and not directly with seasonal stream flow and temperature variables, the parameters describing the effects of the environmental variables,  $\Phi_{E^q}$ , are linear combinations of multiple PC's each with its own estimated parameter,  $\beta_{PC_i}$ , from the statistical model. These linear combinations are calculated as:

$$\Phi_{E^q} = \sum_{i=1}^5 \beta_{PC_i} \text{cor}(PC_i, E^q), \quad (6)$$

where  $\beta_{PC_i}$  is the parameter estimate from the linear model for the  $i$ th PC and  $\text{cor}(PC_i, E^q)$  is the pairwise correlation between standardized scores of the  $i$ th PC and the standardized environmental variable (seasonal flow or temperature). Note that the  $\beta_{PC_i}$  values are the regression coefficients where the scores of the  $i$ th PC have a variance equal to the eigenvalue for that PC (see Table S5).

The body size of recruiting fish was measured at the autumn census. The sizes of all new recruits were measured in the autumn census and included all fish smaller than a size threshold that marks the boundary between age zero and one based on size distributions. We used a general linear model to estimate the mean recruit size for each river as a function of

environmental drivers and biomass density in the summer census. As in the model for prerecruitment survival, stream was entered as a fixed effect, PC's and their interactions with stream were entered as covariates, and biomass density and its interaction with stream were entered as covariates. We used the same principal components that were used in the model of prerecruitment survival as covariates. Model selection procedures were the same as those used for the recruit survival. The variance in size at recruitment was taken from residual variance of the linear model. Parameter estimates are given in Tables S5 and S6.

*Survival, growth, and movement of age 1 and 2+*—Survival, growth, and movement of age 1 and 2+ fish were estimated in a Bayesian Markov chain Monte Carlo (MCMC) framework. Details of the estimation procedure can be found in Letcher *et al.* (2015). We briefly describe the salient details below. The effect of stream flow and temperature on the survival of age 1 and 2+ fish was estimated using a state-space formulation of Cormack-Jolly-Seber survival model and consisted of a process model (survival) and an observational model (probability of capture) (Gimenez *et al.*, 2007; Royle, 2008; Letcher *et al.*, 2015). Survival was a Bernoulli variable with *logit*-transformation. Stream was entered as a categorical effect and individual fork length at the beginning of each season, mean seasonal stream flow and temperature were entered as covariates. We also included interactions between stream, size, stream flow, and temperature. Year was included as a random effect on the intercept. Probability of capture was assumed to vary as a function of age, size, and stream, but did not vary as a function of environmental variables.

The mean somatic growth of age 1 and 2+ fish in any given age, river, and season was calculated as the simple change in individual length from one season to the next. Stream was entered as a categorical effect and fork length at the beginning of each season, mean seasonal stream flow, and temperature were entered as covariates. We also included interactions between stream, size, stream flow, and temperature. Year was included as a random effect on the intercept. The variance in growth among individuals was modeled as a function of stream and season.

The location of individuals was taken directly from their observed locations at each capture event. Movement between streams was modeled as a multistate process with the likelihood of an individual's location at the next sampling occasion being drawn from a categorical distribution (Calvert *et al.*, 2009; Letcher *et al.*, 2015). Movement between streams was assumed to vary only as a function of stream and season.

### Model analyses

We performed a few different analyses of the model. The first is simply a test of the ability of the model to replicate the observed year to year dynamics in the system. This was evaluated by comparing the observed yearly population growth estimates ( $\log \lambda_O$ ) with the population growth rates obtained



from the model ( $\log \lambda_p$ ) using the observed combinations of season mean stream flow and temperature values.

Second, we asked whether density-dependence is strong enough to keep the populations from extirpation. To answer this we performed a stochastic projection of 200 iterations over a 30 year period. For each year, stream flow and temperature values for each season and stream were drawn from multivariate normal distributions that includes the within year between season covariance among the environmental variables (e.g. for example wet springs may be followed by dry summers, etc.). The mean for each environmental variable changed with year according to the observed trends. A population in any iteration was considered to be extirpated if it crossed the quasi-extinction threshold of 10 individuals in the population. From these quasi-extinctions, we calculated the cumulative probability of quasi-extinction under two scenarios. The first scenario is when we assume there are no density-dependent effects in the model. This effectively means turning all the density-dependent parameters to zero. The second scenario is with the density-dependent parameters at their estimated values. The difference in these two curves is the influence of density-dependence in the system on extinction probabilities.

The stochastic analysis answers the question of whether or not density-dependence can decrease the probability of extinction, but it cannot tell us, at least in a very tractable way, how these declining trends in the populations are caused through the multiple demographic pathways. Nor can the stochastic analysis inform much about the changes in body size of recruits during this period. To answer these questions, we conducted an analysis of the equilibrium dynamics of the population to understand how the linear change in the environmental variables interacts with population density and body size to potentially buffer the impacts of environmental change. We define the equilibrium population size for any population as  $\hat{N}$ . Likewise, the mean body size of new recruits in the autumn is taken as the mean body size at equilibrium,  $\hat{p}$ . This approach is justified because although natural populations will rarely if ever be at equilibrium, if the equilibrium is an attractor, it defines the state toward which the population is pulled (Otto & Day, 2007). Hence the equilibrium is a property of the population regardless of the current state of the population and changes in the equilibrium caused by the environmental trends will be manifested in the population dynamics. The temporal change in the equilibrium population size and mean body size and the stochastic trends across iterations are clearly related in this system (Fig. 1). Details on the calculations necessary to perform these calculations are provided in the Supporting Information and we provide a brief overview below.

How changes in the equilibrium population size or mean body size through time are influenced by environmental variables that also change with time can be calculated using the chain rule of calculus. This simply means multiplying the observed change in each of the environmental variables in each of the seasons by the effect that such a change has on the equilibrium population size and summing across all season and environmental variables. For changes in total population size with time as a function of environmental

effects in each of the seasons, we write (using autumn as an example):

$$\frac{d\hat{N}_{\text{Aut}}}{dt} = \sum_q \frac{d\hat{N}_{\text{Aut}}}{dF_q} \frac{dF_q}{dt} + \sum_q \frac{d\hat{N}_{\text{Aut}}}{dT_q} \frac{dT_q}{dt}. \quad (7)$$

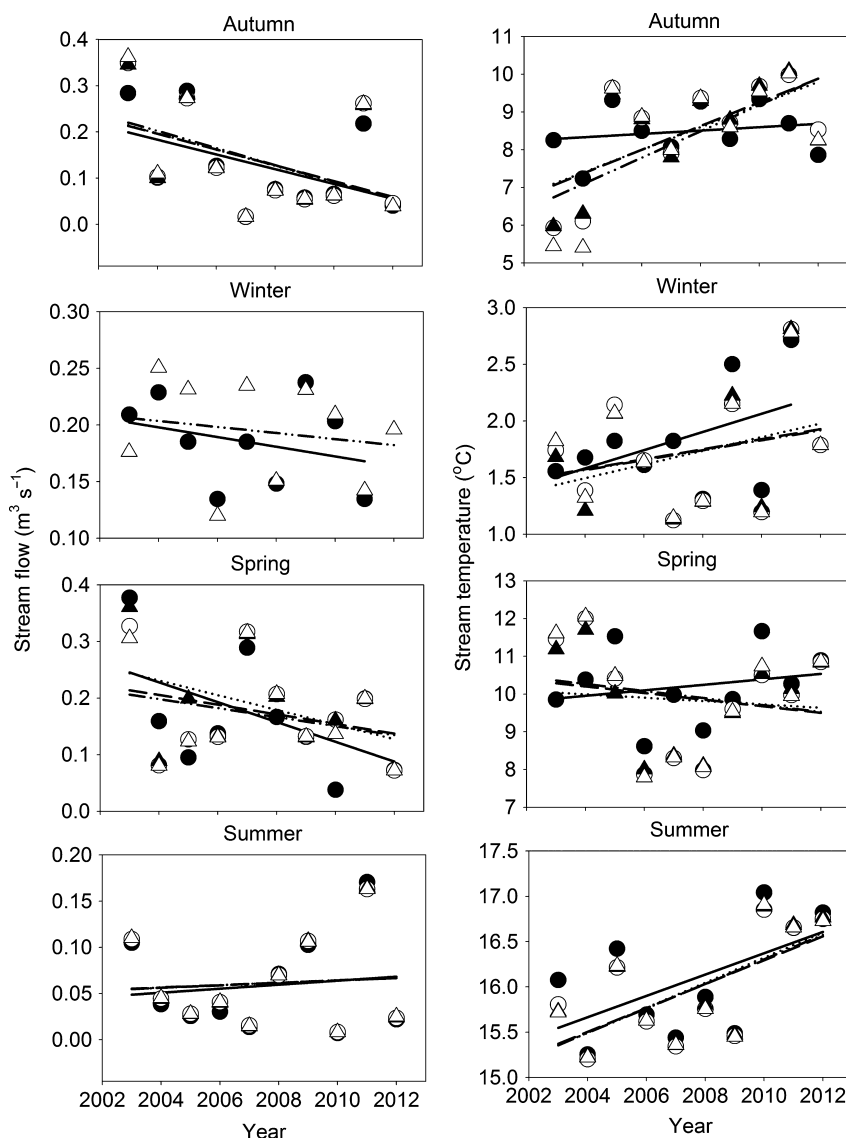
Because we must choose one season in which to measure changes in population size, we used population size in the autumn, but this choice does not influence any of the results presented. The total derivative  $\frac{d\hat{N}_{\text{Aut}}}{dE_q}$  in each term in Eqn 7 describes how the environmental effect ( $E = \text{Flow}$  or  $E = \text{Temperature}$ ) influences population size through all demographic pathways (density-independent and density dependent) and are evaluated at the seasonal flow and temperature values for that year,  $\left. \frac{d\hat{N}_{\text{Aut}}}{dE_q} \right|_{E_t}$ . The total derivative  $\frac{dE_q}{dt}$  in each term ( $E = \text{Flow}$  or  $E = \text{Temperature}$ ) describes how the environmental effect changes through time. This derivative is the slope of the regression line of the environmental variable (seasonal flow or temperature) against time (Fig. 3). Analogous calculations for mean body size are given in the Supporting Information.

Each of the derivatives in Eqn 7 describing the change in population size as a function of the environment variables ( $\frac{d\hat{N}_{\text{Aut}}}{dE_q}$ ) are composed of a direct effect which changes population size through the density-independent parameters of the demographic rates and through the density-dependent parameters. These density-independent (direct) and density-dependent (indirect) influence of changes in the environment on population size can be separated into:

$$\frac{d\hat{N}_{\text{Aut}}}{dE_q} = \frac{\partial \hat{N}_{\text{Aut}}}{\partial E_q} + \frac{\partial \hat{N}_{\text{Aut}}}{\partial N_{\text{Sum}}} \frac{d\hat{N}_{\text{Sum}}}{dE_q} + \frac{\partial \hat{N}_{\text{Aut}}}{\partial N_{\text{Aut}}} \frac{d\hat{N}_{\text{Aut}}}{dE_q}. \quad (8)$$

The first term gives the change in the equilibrium population size resulting directly from the environmental change (density-independent term) in season  $q$ . The second and third terms describe how changes in the density-independent term change population size in the summer and the autumn and then how these changes further affect the population size through the density-dependent parameters.

The influence of environmental variables on the equilibrium population size (e.g. the derivative  $\frac{\partial \hat{N}_{\text{Aut}}}{\partial E_q}$ ) and mean body size (e.g. the derivative  $\frac{\partial \hat{p}}{\partial E_q}$ ) were calculated using sensitivity analysis modified from Caswell (2008). The methods were modified to accommodate the seasonal and metapopulation structure of the projection model (Caswell & Trevisan, 1994; Hunter & Caswell, 2005). In all analyses, the Mainstem, OL and OS populations are analyzed as a single metapopulation and the IL population is analyzed separately. Prior to all of the analyses, we approximate the continuous portions of the model using a high dimensional matrix approximation of the kernel (Easterling *et al.*, 2000). The result of doing so is that the overall model can be placed within a matrix population model framework for analysis. Details of how this was done can be found in the Supporting Information. Equilibrium population size and mean body size for each population were



**Fig. 3** Trends in seasonal stream flow and temperature over the 10 year in the Mainstem (closed circles, solid lines), Open-Large (open circles, dashed lines), Open-Small (closed triangles, dotted lines), and Isolated-Large (open triangles, dash-dot lines) study streams.

found by numerical iteration through 300 yearly time-steps, which was more than sufficient to reach the equilibrium population size and structure.

## Results

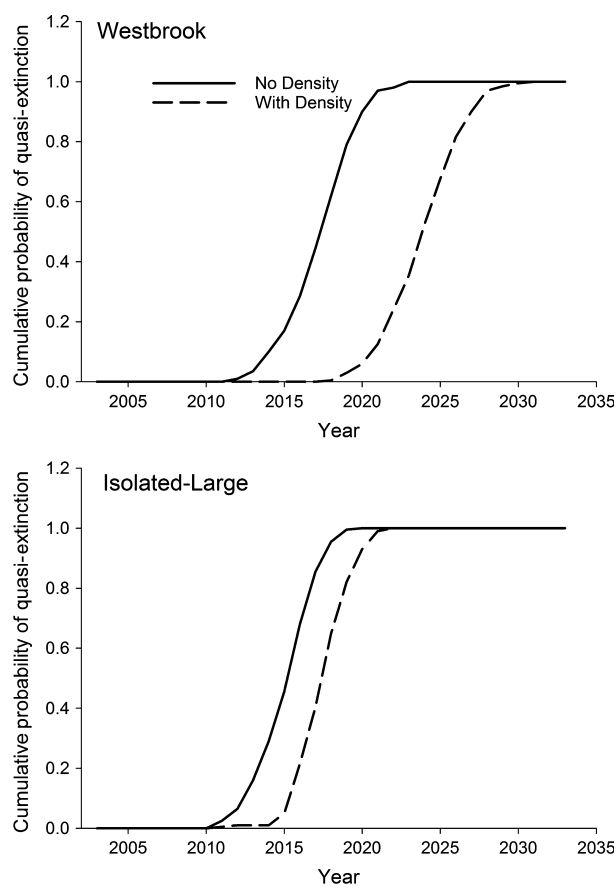
### *Environmental trends*

Stream flow rates have significantly declined in the autumn (GLM:  $t_{35} = -3.11$ ,  $P = 0.004$ ) and in the spring (GLM:  $t_{35} = -2.4$ ,  $P = 0.020$ ). In both cases, the declines have resulted in approximately 50% reduction in the mean flow (Fig. 3). Stream temperatures have significantly increased in all streams except the Mainstem in

the autumn (GLM: OL:  $t_{32} = 2.23$ ,  $P = 0.033$ ; OS:  $t_{32} = 2.26$ ,  $P = 0.031$ ; IL:  $t_{32} = 2.26$ ,  $P = 0.031$ ) and in all streams in the summer (GLM:  $t_{35} = 4.94$ ,  $P < 0.001$ ). Mean autumn stream temperatures in the tributary populations have increased by about 3 °C and summer mean temperatures have increased by about 1 °C in all streams (Fig. 3).

### *Observed trends in population size and size at recruitment*

The population sizes of all streams have decreased over the course of the study (ANCOVA: year:  $F_{1,28} = 6.13$ ,  $P = 0.020$ ; stream · year:  $F_{1,28} = 0.43$ ,  $P = 0.732$ ; Fig. 1).



**Fig. 4** Cumulative probabilities of quasi-extinction in the Westbrook metapopulation and the Isolated-Large population. The probabilities are based on using 200 independent iterations and the seasonal environmental conditions. Within each year, the seasonal conditions are assumed to have a covariance structure estimated from the data. Each population was assumed to go extinct upon crossing the quasi-extinction threshold of 10 individuals.

Over the course of the study, the mean body size of age 1 fish in the autumn (new recruits) has increased at an average rate of  $1.2 (\pm 0.50\text{SE}) \text{ mm yr}^{-1}$  across all streams (ANCOVA: year:  $F_{1,28} = 5.45, P = 0.027$ ; stream  $\times$  year:  $F_{1,28} = 0.24, P = 0.865$ ).

#### *Fit of the model to observed annual growth rates*

To understand how these environmental trends are influencing the population size and size of recruits we constructed and analyzed a demographic projection model. The predicted yearly population growth rates from the projection model using the observed time series of seasonal environmental variables accounted for a significant amount of variation in observed population growth rates in the metapopulation ( $r^2 = 0.83, df = 7,$

$P = 0.001$ ; Fig. S1) and in the Isolated-Large (IL) stream ( $r^2 = 0.86, df = 7, P < 0.001$ ; Fig. S1). In both the metapopulation and the IL population the predicted slope did not differ from unity (GLM: Metapopulation:  $t_7 = 0.43, P = 0.68$ ; IL:  $t_7 = 1.52, P = 0.17$ ; Fig. S1).

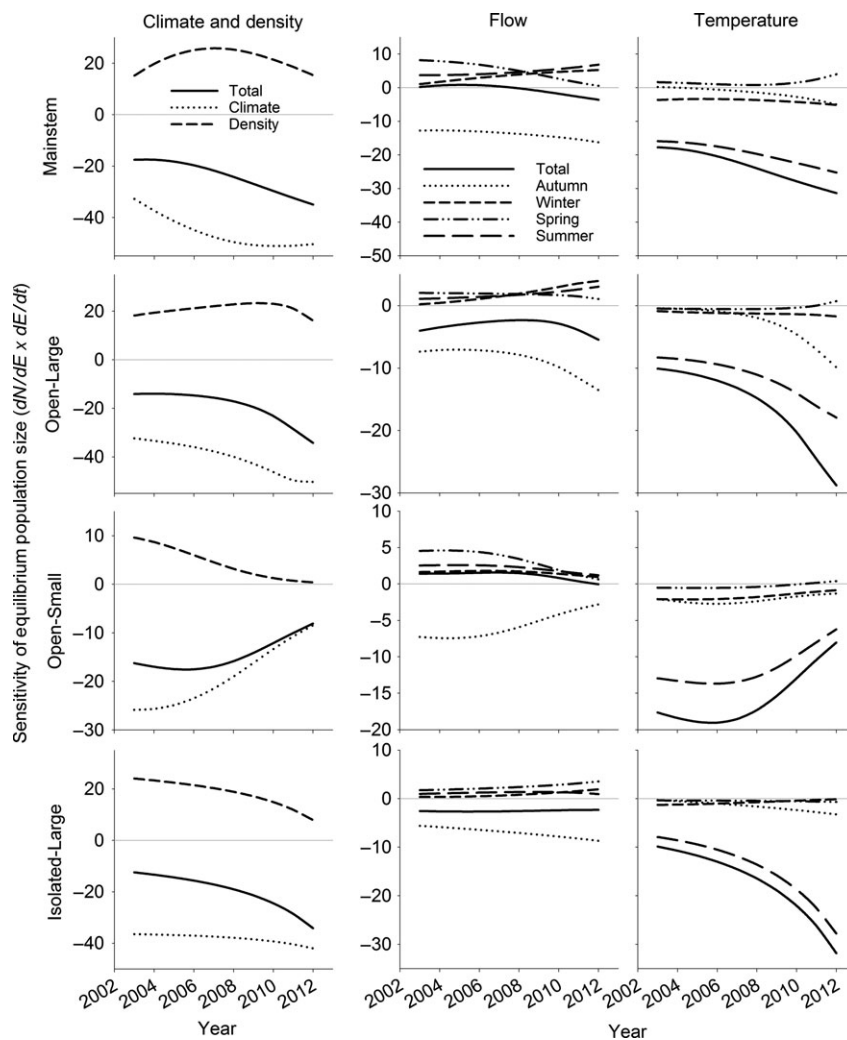
#### *Population size and extinction probabilities*

To ask whether the environmental trends are driving the populations toward extinction and whether density-dependence in this system can buffer this process, we used the model to calculate the cumulative probability of quasi-extinction assuming a scenario with no density dependence and with the observed density dependence. In both cases, the model predicts the populations to go extinct within the next 15 years if the current environmental trends continue (Fig. 4). In both the Westbrook metapopulation and Isolated-Large population, assuming density-dependence did not operate in the system would have given much earlier predictions of extinction, although the buffering ability of density appears to be stronger in the Westbrook (Fig. 4).

To answer which environmental trends are causing the decline and through which demographic rates, we analyzed the influence of each of these seasonal trends on the equilibrium population size. The equilibrium population sizes at each time step calculated using the model also decreased through time (Fig. 1). These declines in the predicted equilibria population sizes were caused by negative direct effects of changes in the climate that were larger in magnitude than the effect of density-dependence in every year (Fig. 5). The declines in the population sizes of the Mainstem, Open-Large, and Isolated-Large populations showed a slight increase in the rates of decline with time. This change in the rate of decline in these streams resulted from a slight decrease in the influence of density-dependence with time. The rate of decline in the Open-Small population was initially steep and has slightly decreased through time.

Observed changes in temperature in all streams and in all seasons (with the exception of spring temperature in the Mainstem) decreased the equilibrium population sizes, with the largest component of the effect deriving from temperature changes in the summer (Fig. 5). Changes in stream flow in all seasons except autumn increased the equilibrium population size, but because the effect of stream flow in the autumn was large and negative, the overall annual effect of changes in stream flow was very small (Fig. 5).

The decreases in the equilibrium population sizes of all populations due to environmental change were primarily driven by large negative direct effects on survival from eggs to recruitment (Fig. 6). In the



**Fig. 5** Slope of the line between equilibrium population size and time (derivative). *Left Panels:* The total derivative is split into direct (climate) and indirect (density) derivatives. *Center and Right Panels:* Decomposition of the slope of the line between equilibrium population size and time (derivative) into effects of seasonal flow and temperature in each stream. Negative or positive values indicate that the equilibrium population size is either decreasing or increasing through time respectively. Changes in climate variables generally directly decrease the equilibrium while density-dependence generally tends to increase the equilibrium. Positive values of the derivatives of density-dependence indicate they are buffering the decline in equilibrium population size.

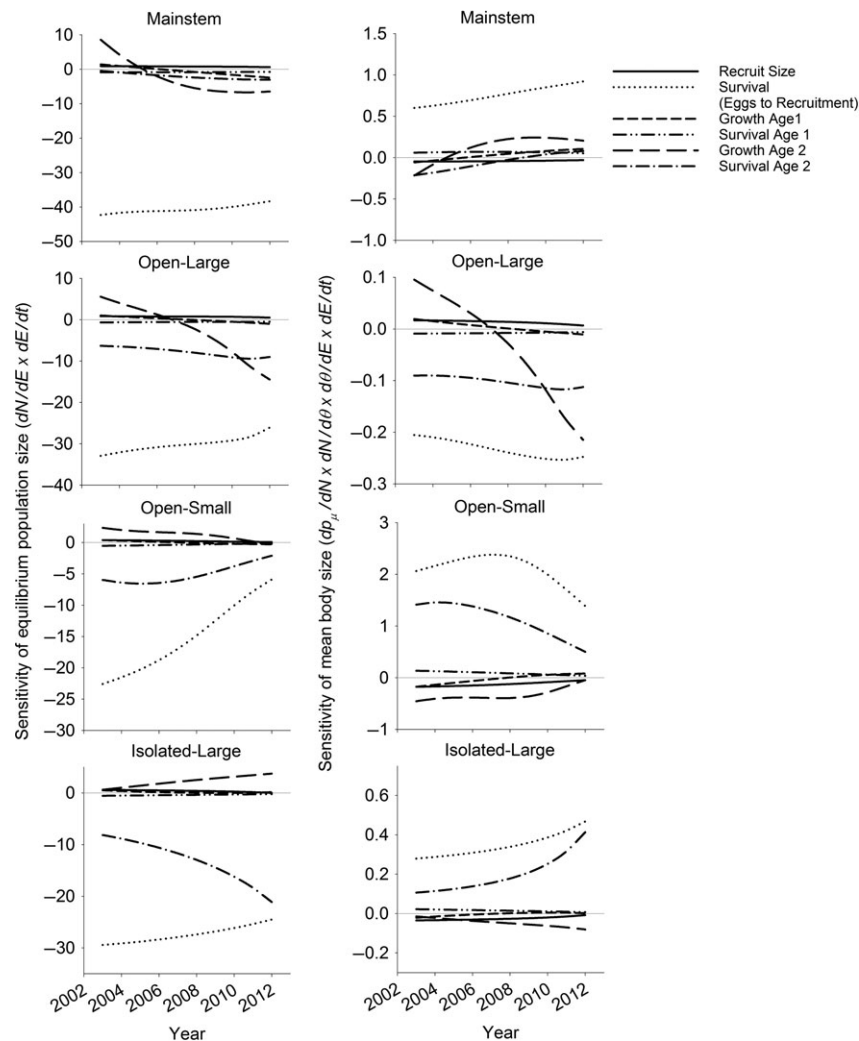
Open-Small (OS) and Isolated-Large (IL) tributary populations, survival of age 2+ fish also contributed to the effects, but to a much smaller degree (Fig. 6). Effects acting via the other demographic rates were comparatively smaller and varied in direction.

#### *Size at recruitment*

In agreement with the observed trends in body size at recruitment the model revealed that the equilibrium mean body size of age 1 fish has also increased through time (Fig. 1) with the largest increase in the Open-Small (OS) population (average rate: 3.2 mm yr<sup>-1</sup>) and the smallest increase in the Open-Large (OL) population

(average rate: 0.2 mm yr<sup>-1</sup>). However, in contrast with the relative effects of climate-driven environmental variation on population size, it was the indirect effect of climate through changing population density that was primarily responsible for the increases in mean size of age 1 fish in all streams except the Open-Large population (Fig. 7).

The seasonal environmental variables responsible for the majority of effects on equilibrium mean body size were more varied than in the analysis with population size. The total effect of changes in mean stream flow tended to increase mean body size (Fig. 7). The total effect of changes in mean stream temperature likewise had tended to increase mean body size in all streams



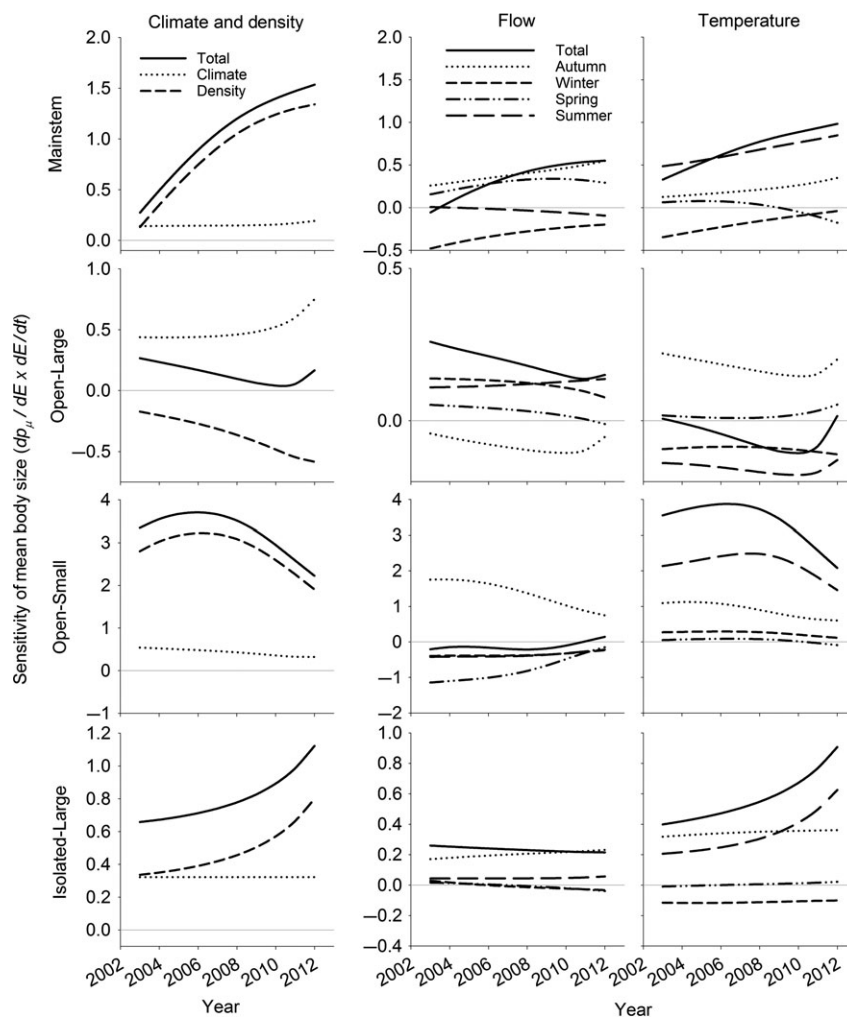
**Fig. 6** *Left Panels:* Direct effect of environmental change (stream flow plus stream temperature in all seasons) on equilibrium population size in each stream through each of the demographic rates. *Right Panels:* Indirect effect of environmental change (stream flow plus stream temperature in all seasons) on equilibrium mean body size in each stream through each demographic rate and its influence on the population size. Negative or positive values indicate that the equilibrium population size is either decreasing or increasing through time respectively.

except the Open-Large population (Fig. 7), which showed no overall change. In the Mainstem, Open-Small, and Isolated-Large populations, increases in mean summer and autumn temperatures tended to be the largest effects and together offset any smaller opposing effects in other seasons. Similarly to equilibrium population size, survival of the youngest age class had the largest effect on the mean body size at equilibrium and determines the overall direction of the effect (Fig. 6).

## Discussion

Understanding how multiple climate-driven factors across seasonal environments influences population characteristics (population size, body size, and other

trait-distributions) is a major challenge. The research we present here meets this challenge by showing how changes in two such factors (stream flow and temperature) over a 10 year period has caused changes in population size and mean body size in populations of eastern brook trout. Our main results are that (1) declines in population size and increases in mean size of age 1 fish (new recruits) over the last 10 years were driven by environmental changes (Figs 1 and 3), (2) the direct negative effect of high mean summer temperature on the survival of new recruits (fish in the youngest age-class) is the main climate-driven environmental factor causing the decline in population size (Fig. 5), (3) density-dependent compensation did not overcome negative effects of environmental change on population



**Fig. 7** Sensitivity of equilibrium mean body size of age 1 fish in the autumn. *Left Panels:* The total derivative is split into direct (climate) and indirect (density) derivatives. *Center and Right Panels:* Decomposition of the slope of the line between equilibrium mean body size of age 1 and time (derivative) into effects of seasonal flow and temperature in each stream. Negative or positive values indicate that the equilibrium mean body size of age 1 fish in the autumn is either decreasing or increasing through time respectively.

size, but did slow down the rate of decline (Figs 4–6), and (4) In contrast with the direct, negative effects of high summer temperatures on survival of recruits, warm summers were associated with increases in mean body size in three of the four streams and density-dependence was the dominant mechanism (via increased growth rates at low densities), (Figs 6 and 7).

Our modeling framework was critical to surmounting some of the major challenges in forecasting population trajectories in the context of a changing climate. For example, environmentally driven changes in a population in one season may decrease population size while changes in another may increase population size with the implication that demographic rates derived from a single season may not do very well in predicting how the population might change in response to overall

changes (Reed *et al.*, 2013). For example in the brook trout populations, decreasing flow in the autumn (Fig. 3) has led to a decline in the population size (Fig. 5), but this effect is completely offset by changes in flow in the other seasons, such that there has been almost no change in population size due to changes in stream flow over the 10 years. In contrast with the offsetting effects of changes in stream flow, changes in stream temperature in all seasons have decreased population size. Stream temperature (especially in the summer) has long been thought to be an important environmental variable that can adversely influence population size in salmonids through its effect on survival (Carlson & Letcher, 2003; Schrank *et al.*, 2003), growth (Meeuwig *et al.*, 2004; Xu *et al.*, 2010a,b), and general health (Powers, 1929; Maether *et al.*, 2008).

Others have suggested that temperature in the winter (Huusko *et al.*, 2007) is important in determining brook trout numbers. The research presented here is consistent with the observation that the effects of summer temperatures on population size are potentially large and changes in summer temperatures are driving population declines. However, while most studies have examined these effects on larger, older trout, the results here reveal that population declines are caused by decreased survival of the youngest, smallest fish.

Our results are also consistent with the general importance of climate-driven recruitment dynamics, particularly prerecruitment survival, on population trajectories for a potentially wide range of species. It is important to keep in mind that our definition of prerecruitment survival is actually a composite of several demographic rates—including the probability of a female of a given age and size actually reproducing in a given year. The composite nature of this parameter reflects the lack of information of demographic parameters from eggs to recruitment. Despite the composite nature of the prerecruit parameter, we can infer the life stage that is most affected by the seasonal effects—because prerecruitment stages (eggs, alevin, juveniles) occur approximately in different seasons. For example, any environmental effects on the prerecruitment survival that occur in the autumn can be assumed to be due to nesting success (probability of reproduction or survival during the egg stage). Likewise, any environmental effects in the summer can be assumed to be affecting age 0 fish directly. These results further suggest that understanding the extent to which populations are recruitment-limited, either currently or in the future, may help to increase our understanding of likely population responses to climate change.

In this system, density-dependence does not change the result that changes in climate-driven environmental effects have decreased population size—but it has slowed the decline. The results of the stochastic analysis show that this buffering capacity through density-dependence is stronger in the metapopulation (Fig. 4) compared to the isolated population. However, density-dependence did not fully buffer these populations from these changes because density-dependence was always a weaker force on the equilibrium population size than changes in climate-driven environmental effects in this system (Fig. 5). Initial models that also include density dependence on age 1 and 2+ growth and survival do not change this result (Table S4 and Fig. S2).

While a slowed decline has important management implications, changes in climate-driven environmental variables that have a negative impact on population size are likely driving the populations to extinction

despite some compensatory density-dependent effects. The majority of research examining the potential compensatory scope of density-dependence with climate change consider how density-dependence influences the variance in population size through time drawing on ideas of stochastic boundedness (Chesson, 1978). Comparisons of stochastic projections predicting the probability of population persistence with and without density-dependence typically then show that including density-dependence increases population persistence (Morris & Doak, 2002; Henle *et al.*, 2004; Mugabo *et al.*, 2013). The increased persistence can arise simply due to the decrease in the variance without being related to any environmental trends. Our analysis shows that density-dependence can do more than bound the year-to-year fluctuations and can influence the temporal trends themselves.

Density-dependence alters how mean body size of age 1 fish has changed with the changing environmental effects and we found that decreased population size over the course of the study has resulted in increasing size at recruitment. This result is in contrast with other studies that predict that mean body size of aquatic organisms should get smaller with increasing temperatures based on temperature-size relationships (e.g. Daufresne *et al.*, 2009), and also is in contrast with predictions based on increased energy allocation to metabolism in ectotherms as a function of increasing temperature. Increasing temperatures in the summer alone in the brook trout decreases body size of recruits (as predicted by energetics Table S5), but this effect is completely swamped by the opposing effect of decreased densities increasing body size. Density-dependent growth and size of salmonid fish (particularly young juveniles) in streams has been demonstrated in multiple systems (Imre *et al.*, 2010). This highlights that predictions that do not account for the multiple demographic effects of climate changes will not likely accurately predict the direction of changes to populations. These results are for a single life stage. Whether the positive effects of density also occur over multiple life stages is an open question. Nevertheless, it points to the importance of explicitly incorporating density-dependent dynamics in assessing climate effects that directly influence population size.

Our analysis here is based on changes in the seasonal mean stream flow and temperatures. Within each season, flow or temperature can vary considerably and metrics beyond simply the mean may be better indicators of climate change. In principle one could find parameters for each of the demographic rates for the variance or some measure of skewness in temperatures in each season in addition to the mean. This would then

rely on having enough observations to fit the statistical model (with many environmental parameters) and some reasonable level of independence among these predictors such that they are individually interpretable (e.g. little or no covariance among the mean and the other predictors). With the brook trout studied here, using only the seasonal means resulted in explaining 88% of the variance in annual population growth rates. Thus at least for brook trout, the seasonal means appear to be excellent integrators of how seasonal flow and temperatures influenced the vital rates, population size, and size at recruitment.

In the Westbrook metapopulation, eastern brook trout also coexist with naturalized brown trout (*Salmo trutta*) and these streams have also historically contained Atlantic salmon (*Salmo salar*). Preliminary analyses in this system have shown that brown trout are also declining in numbers (B. Letcher and R. Bassar unpublished data) and that the causes for these declines are also climate related. What is unknown is how competitive interactions among brook trout and brown trout are influencing the rate of decline for either species. Although answering this question is beyond the scope of this paper, future analyses employing two species models similar to the single species model we develop here may be able to address questions such as these in this and other similar systems.

Overall, the results of the model show that continued changes in the climate-driven environmental effects of stream flow and temperature will decrease population size and at the same time increase the body size of individuals in the populations. Whether the changes will continue depends upon whether the environmental changes continue and whether the populations are able to adapt to them. The types of environmental changes observed here are expected to exert strong natural selection on traits. There are a growing number of studies that show fitness related traits are changing with changes in climate and that some of this change has an evolutionary basis (Ferriere & Legendre, 2013; Gonzalez *et al.*, 2013). Part of the reason why survival of early recruits was responsible for the declines in population size is that the equilibrium population size is most sensitive to changes in this demographic rate. A high sensitivity also means that traits underlying this demographic parameter should be under the strong natural selection. Local adaptation of early life-history traits to thermal regimes has been shown in brown trout (Jensen *et al.*, 2008). Whether such evolutionary changes are able to promote population persistence in populations of brook trout remains unknown, but the analytical framework here provides a basis for understanding the potential for these effects.

## Acknowledgments

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## Supporting Information

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

**Appendix S1.** Materials and methods.

**Table S1.** Estimated benthic area ( $m^2$ ) of each of the streams in each season.

**Table S2.** Probability of moving between streams for each season ( $\psi_{r,y}^q$ )\*.

**Table S3.** Table of survival and growth parameters. For both survival and growth, parameters are based on standardized predictors. For survival, parameters are on the logit scale.

**Table S4.** The parameter estimates of density in each of the seasons on adult somatic growth and survival.

**Table S5.** Parameter estimates ( $\gamma$  and  $\Phi$ ) calculated from estimates in Table S9.

**Table S6.** Variance in size at recruitment and growth for each age, season and stream.

**Table S7.** Principle component loadings, eigenvalues and proportion of variance explained by each principle component for the early life models.

**Table S8.** Model selection results of top ten pre-recruitment survival and size at recruitment models.

**Table S9.** Parameter estimates ( $\beta$ 's) and standard errors for model averaged early life models.

**Figure S1.** Plot of the relationship between the observed and predicted population growth rates and mean body size predicted from the model based on the observed seasonal stream flows and temperatures and population sizes and distributions in that year.

**Figure S2.** Reproduction of deterministic components of Fig. 1 with the predicted equilibrium population size and mean body size when a density dependent effect on adult growth and survival is included in the model.