Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2015, **84,** 337–352 doi: 10.1111/1365-2656.12308

Robust estimates of environmental effects on population vital rates: an integrated capture–recapture model of seasonal brook trout growth, survival and movement in a stream network

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Summary

1. Modelling the effects of environmental change on populations is a key challenge for ecologists, particularly as the pace of change increases. Currently, modelling efforts are limited by difficulties in establishing robust relationships between environmental drivers and population responses.

2. We developed an integrated capture–recapture state-space model to estimate the effects of two key environmental drivers (stream flow and temperature) on demographic rates (body growth, movement and survival) using a long-term (11 years), high-resolution (individually tagged, sampled seasonally) data set of brook trout (*Salvelinus fontinalis*) from four sites in a stream network. Our integrated model provides an effective context within which to estimate environmental driver effects because it takes full advantage of data by estimating (latent) state values for missing observations, because it propagates uncertainty among model components and because it accounts for the major demographic rates and interactions that contribute to annual survival.

3. We found that stream flow and temperature had strong effects on brook trout demography. Some effects, such as reduction in survival associated with low stream flow and high temperature during the summer season, were consistent across sites and age classes, suggesting that they may serve as robust indicators of vulnerability to environmental change. Other survival effects varied across ages, sites and seasons, indicating that flow and temperature may not be the primary drivers of survival in those cases. Flow and temperature also affected body growth rates; these responses were consistent across sites but differed dramatically between age classes and seasons. Finally, we found that tributary and mainstem sites responded differently to variation in flow and temperature.

4. Annual survival (combination of survival and body growth across seasons) was insensitive to body growth and was most sensitive to flow (positive) and temperature (negative) in the summer and fall.

5. These observations, combined with our ability to estimate the occurrence, magnitude and direction of fish movement between these habitat types, indicated that heterogeneity in response may provide a mechanism providing potential resilience to environmental change.

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Given that the challenges we faced in our study are likely to be common to many intensive data sets, the integrated modelling approach could be generally applicable and useful.

Key-words: annual survival, Bayesian modelling, capture–mark–recapture, integrated model, movement, sensitivity, stream fish, stream network, survival

Introduction

Environmental variation can be a key driver of population dynamics, but sorting out how environmental variation affects population dynamics is challenging. First, multiple aspects of environmental variation can each independently influence population dynamics through complex pathways (Ozgul *et al.* 2009; Coulson *et al.* 2011; Pelletier *et al.* 2012). Furthermore, except in some extreme events, environmental drivers rarely act alone and likely interact (Mysterud *et al.* 2001; Stenseth *et al.* 2004; Bakker *et al.* 2009). Secondly, patterns of environmental variation almost always vary across space and, depending on the extent of local adaptation, the demographic response to environmental variation itself may also vary across space (Angilletta, Steury & Sears 2004). Thirdly, the various environmental drivers can influence population growth via any one of a combination of the five basic demographic processes: development, survival, reproduction, inheritance and movement (Coulson & Tuljapurkar 2008). Fourthly, the environmental drivers likely have different effects in different seasons as both environmental change and the demographic response to change vary seasonally (Caswell & Shyu 2012). Finally, the strength and direction of environmental effects may vary over ontogeny (Bonner, Morgan & King 2010). The challenges in establishing robust relationships between environment and population processes may be a major factor in the generally poor forecasting performance of many current population projection models (Coulson *et al.* 2001, 2011; Crone *et al.* 2013).

A clear understanding of environmental driver effects on population dynamics is particularly important as the pace of environmental change quickens (Karl & Trenberth 2003; Dawson *et al.* 2011). The relative importance of environmental drivers that are directly or indirectly altered by changes in climate is likely to increase. For example, in temperate streams, water flow and water temperature are strongly related to variation in precipitation and air temperature which in turn affect demographic processes in stream fishes (Xu, Letcher & Nislow 2010). A thorough understanding of the effects of these environmental drivers on population dynamics and local population persistence is critical for effective forecasting and management. For example, the inability to appropriately incorporate these dynamics is suggested to strongly limit the applicability of species distribution models to adequately forecast the effects of a changing climate (Guisan & Thuiller 2005).

The development of this understanding consists of two essential components: (i) data with sufficient duration and resolution and (ii) models with appropriate structure to accommodate the challenges involved in estimating effects of environmental drivers. Long-term data allow estimation of independent and interactive environmental effects on vital rates because multiple years are likely to encompass a wide range of environmental variation (Clutton-Brock & Sheldon 2010). Additionally, data of sufficient temporal resolution, particularly in highly seasonal regions, are necessary to capture seasonal effects of environmental drivers. Finally, tracking performance and fates of known individuals is required to fully characterize the influence of environmental drivers on demographic processes such as body growth, movement and survival. Similarly, to take full advantage of high-resolution, long-term data, we need to build a model that can estimate key demographic rates and how the rates respond to environmental variation.

For small-bodied species that are hard to observe and track in the field, the recent increase in the use of passive integrated transponder (PIT) tags has generated a wealth of individual-based field data. This is especially true for stream fishes that are often abundant in stream networks, are spatially constrained to essentially one dimension by the stream network and are therefore relatively easy to capture and recapture. Combined with in-stream PIT tag antennas that allow estimation of movements past fixed locations in stream networks (Zydlewski *et al.* 2006), these data provide the necessary information for estimating survival, growth and movement rates. If complete data were available for all individuals in a population, these rates could be measured directly, but capture and recapture rates of stream fishes (and most animals) are always <1, leading to missing observations. Well-established capture–recapture models exist (Lebreton *et al.* 1992) to account for missing observations when estimating survival alone, but in stream fishes (and other animals and plants) survival and detection commonly depend on time-varying characteristics (states) of individuals such as body size or location. In this case, more complex models are needed to model state-dependent survival effectively (Bonner, Morgan & King 2010). One way to do this is to integrate models for the states with the survival model (King, Brooks & Coulson 2008; Royle 2009; Bonner, Morgan & King 2010). This model integration generates a full 'feedback' loop between process models (e.g. survival, growth, movement) and latent states, providing the basis for robust parameter estimates and propagation of uncertainty among model components. The combination of long-term high-resolution data and the potential for flexible, integrated model formulation provides the foundation for the development of robust estimates of environmental effects on key demographic rates.

We collected high-resolution (seasonal), long-term data (11 years, approximately seven generations) on individually tagged brook trout (*Salvelinus fontinalis*) at four sites in a stream network. We also developed and applied an integrated state-space capture–recapture model (Royle 2008) that estimates key processes (body growth, survival and movement) as a function of steam flow and temperature. The combination of (i) process integration, (ii) the ability to estimate latent variables for missing data, (iii) the explicit estimation of covariance structure among all model components and (iv) the propagation of uncertainty through the model makes this a useful contribution. This flexible modelling structure allows us to generate robust seasonal and site-specific estimates of environmental effects on body growth and survival. Further, these estimates and their uncertainties can form the basis of estimates of annual size- and location-dependent survival or of a population projection model (Ellner & Rees 2006; Rees & Ellner 2009), which can generate projections under future climates and can identify sensitivities of key population dynamic pathways to environmental change.

Materials and methods

DATA

Study site

Our study site is the West Brook (WB) and three tributaries, located in western Massachusetts, USA (Fig. S1, Supporting information). The stream network is situated in a mixed hardwood forest with a dense canopy, a few local residences and some small farms. The focal study area consists of a 1-km long reach of the WB and 300-m long reaches of three tributaries (open large, OL; open small, OS; isolated, IS). The bottom of the study area on the WB contains a small, but passable, waterfall while the top is unobstructed. A waterfall (2·3 m) blocks access to IS from the WB, and large (>4 m, OL, OS) or small (1 m, IS) waterfalls delimit the upstream ends of the tributary study areas. Average stream width is 4·5 m for the WB, 3 m for OL, 2 m for IS and 1 m for OS.

Naturally reproducing populations of brook trout (*S. fontinalis*) and brown trout (*Salmo trutta*) inhabit the WB, OL and OS (minimal numbers of brown trout in OS). Only brook trout have been found in IS. Atlantic salmon (*Salmo salar*) fry were stocked into the WB during early years of the study (2002–2004). The only other species consistently found in the WB is blacknose dace (*Rhinichthys atratulus*), but densities are generally low. There is no trout stocking in the study area, and fishing pressure is very low.

We conducted seasonal sampling (spring = late March, summer = June, autumn = late September, winter = early December) of the WB and three tributaries since 2002 and report data collected from summer 2002 to spring 2012 for a total of 43 sampling occasions (Table S1, Supporting information). Sampling consisted of collecting fish from 20-m sections sequentially from downstream to upstream in each reach (47 sections in the WB and 15 sections in each of the tributaries). In the WB, we used temporary block nets to isolate each section and ran two electrofishing passes (200–300 V unpulsed DC). In the tributaries where capture rates were high, we did not use block nets and conducted one pass surveys. On capture, we measured the fork length (±1 mm) and recorded the section of capture of each fish. We also recorded the tag number of tagged fish and tagged any untagged fish larger than 60-mm fork length (Gries & Letcher 2002). Tags were 12-mm PIT (Digital Angel, St. Paul, MN, USA) tags, which provide unique alphanumeric codes for each fish. Following workup, fish were returned to capture sections.

Passive integrated transponder tag antennas (Zydlewski *et al.* 2006) at the top and bottom of the study area identified fish that left the study area. The wire antennas are housed in PVC piping. The bottom side of the rectangular antennas is buried in the stream substrate and the antenna surrounds the stream. A detailed description of the PIT tag antennas can be found in Horton, Dubreuil & Letcher (2007) and Horton & Letcher (2008).

Stream temperature was recorded every 2 h with data loggers (Onset Corp., Bourne, MA, USA) placed at the downstream end of the study area in the WB and just upstream of the confluence of each tributary. Stream depth was also recorded every two hr (Onset Corp.) at the downstream end of the WB study area and reflects an index of among-year seasonal variation across the study area. Depth was converted to stream flow (m^3 s^{-1}) using a stage-discharge relationship.

Field data summary

We present data from 43 sampling occasions (Table S1, Supporting information). Ice build-up in the stream during four winter sampling occasions precluded sampling all sections in the WB (2002, 2005, 2007, 2012) and all sections in the tributaries during 2002 and led to incomplete sampling in the WB in 2003 (30 of 47 sections) and 2004 (three of 47). Overall, we recorded 20 089 observations of 10 458 individual trout. Average seasonal stream discharge was much more variable among years compared to seasonal steam temperature (Fig. 1). Discharge was most variable in the spring and least variable in the winter.

Brook trout life history

Brook trout spawn in the late autumn, depositing eggs into small depressions in the stream substrate. Developing embryos spend the winter in the substrate and ‘fry’ emerge in late winter/early spring. Age at first reproduction is typically 1 year. Maximum age is four in our system, although there are typically few three- and very few 4-year-old fish (Letcher *et al.* 2007). Trout are polygynous and can be highly fecund (100’s of eggs), with an exponential distribution of family sizes of surviving fry (Kanno *et al.* 2014). When found in small stream habitats (such as our study system), brook trout establish and defend feeding territories, from which they feed mainly on invertebrates carried by the stream current past their territory(Allan 1981).

Definition of first growth year

Preliminary analyses indicated strong differences in size-dependent survival between young and older fish, suggesting the need to separate fish by an age-based metric. Age in fish is typically increased on January 1 (e.g. age-0+ for fish in their first year

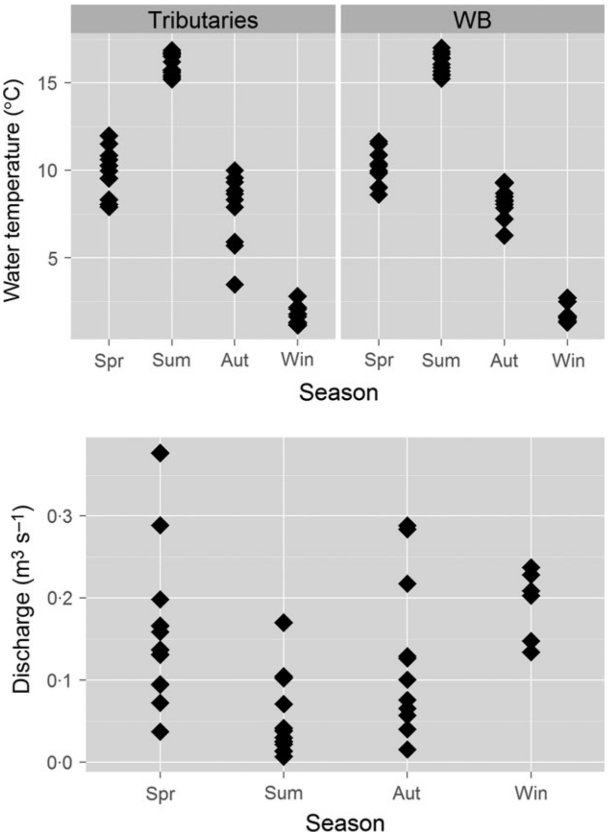

Fig. 1. Average seasonal discharge (above) and temperature (below). Individual points represent 1 year. Stream temperatures are combined across tributaries.

before January 1). Based on the marked seasonal variation in brook trout growth (very high 'spring' growth, Xu, Letcher & Nislow 2010) and the resulting size difference before and after spring, we chose to identify growth years based on size differences rather than the calendar. Growth year '0/1' included fish from age-0+ in the fall to age-1+ fish in the spring (before the age-1+ spring growth spurt). Growth year '1+' included all samples older than age-1+ spring (after the age-1+ spring growth spurt).

MODEL DEVELOPMENT

Our goal is to develop a modelling framework that simultaneously estimates the effects of environmental variation on interacting components of the population. Our integrated model consists of four modules – survival, body growth, movement and detection (Fig. 2). The body growth and movement models estimate latent states (body size and location) for missing observations. Modelling values integrating over uncertainty for the missing observations with latent states allows estimation of state-dependent survival and growth using continuous state values. Our integrated approach also incorporates uncertainty in the state estimates into the estimates of state-dependent survival and growth.

Model selection

We did not conduct model selection within our integrated model because (i) application of model selection techniques for complex integrated models is an area of active research and (ii) the long run times make running multiple alternate models challenging. Instead, we conducted external model selection with simpler models for each model component – growth, survival and detection. We did not conduct model selection for movement because the limited number of movements in the raw data suggested a very simple structure for the movement component. For growth, survival and detection, we were interested in determining appropriate structure for the independent variables season, river, year, growth year, stream temperature, stream flow and body length.

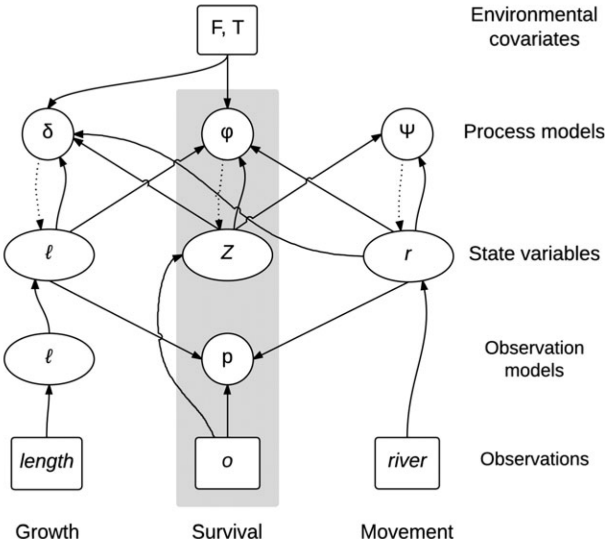

Fig. 2. Diagram of the model structure. The three model modules are arranged in columns. Symbols are defined in the text. Data are in boxes, models are in circles and state variables are in ovals. For simplicity, description of priors and indexing are omitted. Indexing for the state variables and models is $i[r,g]_{s,y}$, where i represents individual, r = river, g = growth year, s = season and y = year. r and g are dynamic characteristics of individuals, and s and y are common among individuals for any time step t. Arrows show dependencies. Dashed arrows represent dependencies at time step $t + 1$. The grey box identifies the model structure for a simple Cormack–Jolly–Seber model, which forms the basis of the integrated model.

For growth and survival, we assessed AIC from generalized linear models of increasing complexity using the glm() function in program R (family = 'gaussian' for growth and 'binomial' for survival) (R Core Team 2014). Growth was estimated as the change in length (mm day^{-1}) of individuals caught on consecutive sampling occasions. Individuals caught on consecutive occasions represented 34% of all captures. Survival was estimated based on subsequent captures; if a fish was captured in a later occasion, the fish was coded as alive, otherwise it was coded as dead. This approach is commonly used in selection analyses (Hendry, Letcher & Gries 2003) in evolutionary studies, but it underestimates survival because it does not account for imperfect detection.

For detection probability model selection, our goal was to determine first if we needed separate estimates for growth years 0/1 and 1+ and secondly whether we needed size structure within growth years. As we were not interested in effects of the other covariates on detection, we ran a simple multistate version of the Cormack–Jolly–Seber (CJS) model in Program MARK (White & Burnham 1999). We defined five evenly divided (numerically) body size (mm)-based states (state 1, ≤ 90; state 2, 91–105; state 3, 106–120; state 4, 121–135; state 5 > 135) and tested for variation in probability of capture with and without variation among states. We did not use this CJS model for survival model selection (or as the overall integrated model) because inclusion of all the covariates (flow, temperature, river, season, year) led to a model that did not converge in MARK.

INTEGRATED MODULAR PARAMETER ESTIMATION MODEL

Survival module

We used a state-space formulation of the standard CJS survival model (Gimenez *et al.* 2007; Royle 2008). The state-space model consisted of a process model (survival) and an observation model (capture). The CJS model estimates the alive state ($z_{i,t}$, 1 = alive, 0 = dead) and the probability of capture ($p_{i,t}$) for each individual (i) and sampling occasion (t) based on an encounter history of individual captures ($o_{i,t}$, 1 = captured, 0 = not captured for each t). In a CJS model, estimation is conditioned on first capture (f_i) of each individual such that $z_{i,f_i} = 1$. Following the first capture, $z_{i,t+1}$ is estimated as a Bernoulli trial with probability equal to the product of survival over the interval t to $t + 1$ ($\varphi_{i,t}$) and the latent alive state at time t:

$$z_{i,t+1} = \mathrm{bernoulli}(\varphi_{i,t} \cdot z_{i,t});\, t > f_i \qquad \text{eqn 1}$$

To account for the unequal number of days between observations of individuals, $\varphi_{i,t}$ was raised to the power of ($d_{i,t}/D_{s,r}$), where ($d_{i,t}$) equalled the actual number of days between observations for fish caught on consecutive occasions or the number of days between an actual capture and the median date of the sampling occasion for fish not caught on consecutive occasions. $D_{s,r}$ was defined as the mean number of interval days for each sampling interval across all individuals categorized by season (s) and river (r).

We modelled survival ($\varphi_{i,t}$) as a linear function of individual body length ($\ell_{i,t}$; mm), averaged seasonal stream flow ($F_{i,t}$; $\mathrm{m}^3\ \mathrm{s}^{-1}$), averaged seasonal stream temperature ($T_{i,t}$; °C) and the interaction between flow and temperature. The intercept (β_0) and slopes ($\beta_{1:4}$) of the linear model were indexed by season (spring, summer, autumn, winter), river (WB, OL, OS, IS) and whether an individual was in growth year 0/1 at time t or older (g):

$$\begin{aligned} \mathrm{log}it(\varphi_{i,t}) = \beta_{0,s,r,g} + \beta_{1,s,r,g} \cdot \ell_{i,t} + \beta_{2,s,r,g} \cdot F_{i,t} \\ + \beta_{3,s,r,g} \cdot T_{i,t} + \beta_{4,s,r,g} \cdot F_{i,t} \cdot T_{i,t} \end{aligned} \qquad \text{eqn 2}$$

At each sampling occasion (t), when an individual was observed, season, g, river and length were known. At sampling occasions, when an individual was not observed, river and length were estimated from the movement and growth models (see below). g was determined by comparing $\ell_{i,t}$ to occasion- and river-specific size distribution cut-offs in the fall, winter and spring that clearly distinguished first-growth-year fish from older fish (Fig. S2, Supporting information). $F_{i,t}$ and $T_{i,t}$ were observed mean temperature or flow between dates of capture (t:$t + 1$, where t represented actual date of capture for individuals captured on an occasion or the median date of the sampling occasion for individuals that were not captured). The three independent variables were standardized to a mean 0 and SD 1 within the inference model. We used independent, weakly informative on the probability scale, truncated priors for the intercept: $\beta_{0,s,r,g} \sim N(0,\ 0{\cdot}44)\ T(-3{\cdot}5,\ 3{\cdot}5)$. The truncated prior kept estimates out of the very flat (and unlikely) portions of the logit likelihood (Standard deviations defined in the normal distributions throughout the model description were converted from precisions (1 SD^{-2}) that are used by JAGS). Our model for betas 1 : 4 included random effects across season and river:

$$\beta_{1:4,s,r,g} \sim N(\mathrm{muPhi}_{1:4,g}, \mathrm{sigmaPhi}_{1:4,g}) \qquad \text{eqn 3}$$

with weakly informative priors for $\mathrm{muPhi}_{1:4,g} \sim N(0,\ 1{\cdot}22)$ and $\mathrm{sigmaPhi}_{1:4,g} \sim \mathrm{gamma}(2,\ 0{\cdot}1)$.

Capture module

The probability of capture (p) was the probability of detection given that an individual is alive at time t ($z_{i,t} = 1$) and available for capture ($1-\eta_{i,t}$), where $\eta_{i,t}$ was an indicator of observed permanent emigration based on the PIT tag antenna data. $\eta_{i,t}$ equalled 1 for occasions after which fish were last observed on the PIT tag antenna at the top or bottom of the study area and equalled 0 for fish that were not observed for the last time on the antennas (not known to have emigrated permanently). We scaled capture probability by the proportion sampling sections completed for each s, y, r ($\omega_{s,y,r}$). $\omega_{s,y,r}$ equalled 1 for the majority of samples, except for the incomplete winter samples (Table S1, Supporting information). In the capture likelihood, the individual encounter histories ($o_{i,t}$) are modelled as the result of a Bernoulli trial:

$$o_{i,t} \sim \mathrm{bernoulli}(p_{i,t} \cdot z_{i,t} \cdot (1 - \eta_{i,t}) \cdot \omega_{s,y,r}) \qquad \text{eqn 4}$$

We modelled p as a function of body size for each s, y, r, g combination. We included y in the intercept and slope to account for yearly variation in p without explicitly modelling effects of stream flow and temperature on p.

$$\mathrm{log}it(p_{i,t}) = \beta_{0,s,y,r,g} + \beta_{1,s,r,y,g} \cdot \ell_{i,t} \qquad \text{eqn 5}$$

Priors for the intercept were independent and weakly informative $\beta_{0,s,r,y,g} \sim N(0,\ 1{\cdot}22)$. For the slope, we used a random effects structure across s, r, y:

$$\beta_{1,s,r,y,g} \sim N(\mathrm{mu}P_g, \mathrm{sigma}P_g) \qquad \text{eqn 6}$$

with weakly informative priors on the mean; $\mathrm{mu}P_g \sim N(0,\ 1{\cdot}22)$, and SD; $\mathrm{sigma}P_g \sim \mathrm{gamma}(2,\ 0{\cdot}1)$.

Growth module

We modelled body size using a growth model to integrate over uncertainty in body size observations. When length was observed ($\mathrm{length}_{i,t}$), the source of uncertainty was measurement error. When length was not observed (individual not captured), uncertainty in $\ell_{i,t}$ was derived from the growth model. Length was modelled as a linear change in body length ($\delta_{i,t}$) between consecutive sampling occasions:

$$\ell_{i,t+1} = \ell_{i,t} + \delta_{i,t} \qquad \text{eqn 7}$$

Linear growth in length is a reasonable assumption for salmonids over relatively short seasonal growth periods (Sigourney *et al.* 2008). We accounted for measurement (observation) error in length (Sigourney, Munch & Letcher 2012), by allowing a small SD in the observed lengths (length):

$$\text{length}_{i,t} \sim N(\ell_{i,t}, 0{\cdot}01) \qquad \text{eqn 8}$$

Body growth was estimated as:

$$\delta_{i,t} \sim N(\epsilon\delta_{i,t}, \text{sigma}\epsilon\delta_{s,r,y,g}) \qquad \text{eqn 9}$$

where $\epsilon\delta_{i,t}$ was mean expected seasonal growth and sigma $\epsilon\delta_{s,r}$ was the SD in expected seasonal growth rate. We divided $\epsilon\delta_{i,t}$ by $d_{i,t}{\cdot}D_{s,r}$ to account for unequal sample intervals among individuals. The model for $\epsilon\delta_{i,t}$ was similar to the model for $\varphi_{i,t}$:

$$\begin{aligned}\epsilon\delta_{i,t} = {} & \beta_{0,s,r,y,g} + \beta_{1,s,r,g} \cdot \ell_{i,t} \\ & + \beta_{2,s,r,g} \cdot F_{i,t} + \beta_{3,s,r,g} \cdot T_{i,t} + \beta_{4,s,r,g} \cdot F_{i,t} \cdot T_{i,t}\end{aligned} \qquad \text{eqn 10}$$

except for additionally indexing β_0 by year and using a random error structure across years for the intercept:

$$\beta_{0,s,r,y,g} \sim N(\text{muGrInt}_{s,r,g}, \text{sigmaGrInt}_{s,r,g}) \qquad \text{eqn 11}$$

We used slightly informative prior means on $\text{muGrInt}_{s,r,g} \sim N(g_s, 10)$, where $g_s = (25, 10, 8, 4)$, reflecting plausible seasonal values (Letcher *et al.* 2007) and a wide distribution (SD = 10). Incorporation of g_s improved run times compared with uninformative prior means. We used non-informative priors for $\text{sigmaGrInt}_{s,r,g} \sim U(0, 100)$.

For the slopes, we used a random effects structure across seasons and rivers:

$$\beta_{1:4,s,r,g} \sim N(\text{muGr}_{1:4,g}, \text{sigmaGr}_{1:4,g}) \qquad \text{eqn 12}$$

with $\text{muGr}_{1:4,g} \sim N(0, 32)$ and $\text{sigmaGr}_{1:4,g} \,\tilde{}\, U(0, 100)$. We further constrained $\beta_{1:4,2,r,1} \sim U(-0{\cdot}001, 0{\cdot}001)$ to reflect the lack of data (impossible condition) for $g = 1$ in the summer.

Our model for sigma $\epsilon\delta_{s,r,y,f}$ included random effects across years:

$$\text{sigma}\,\epsilon\delta_{s,r,y,g} \sim N(\text{muSigma}\,\epsilon\delta_{s,r,g}, \text{sigmaSigma}\,\epsilon\delta_{s,r,g}) \qquad \text{eqn 13}$$

with non-informative priors for muSigma $\epsilon\delta_{s,r,g} \sim N(0, 32)T(0,)$ and $\text{sigmaSigmaGr}_{s,r,g} \sim U(0, 100)$.

Movement module

The movement module estimates the state location (river) of each individual at each sampling occasion based on observed locations (river_t) and movements of all fish. When river_t was observed ($o_{i,t} = 1$), it was treated as known without error, otherwise it was modelled as a latent variable (r_t). Discrete movement between rivers was modelled as a multistate process (Calvert *et al.* 2009). The likelihood of an individual's location at the next sampling occasion (r_{t+1}) was drawn from a categorical distribution:

$$\text{river}_{t+1} = \text{cat}(\psi_{i,t,r_t}) \qquad \text{eqn 14}$$

$$r_t = \text{river}_t \cdot z_{i,t} + 1 \qquad \text{eqn 15}$$

where $\psi_{i,t,r_{t+1}}$ represents a vector of normalized transition probabilities given the occasion (t) and all possible destination rivers (r) at the next occasion, and $z_{i,t}$ represents an individual's alive/dead state. By multiplying the categorical outcome by $z_{i,t}$ and adding one, all dead individuals are considered to be in category one and all alive individuals can be in categories two through five (WB, OL, OS, IS). The normalized transition probabilities come from a multinomial process. We begin with $\beta_{s,r_{j,t},r_{k,t+1}}$, which is a parameter specific to season, beginning location (i.e. river j at time t) and ending location (i.e. river k at time $t + 1$) that is normally distributed on the logistic scale. Then, a multinomial back transformation (generalized logit link) is used, so that all transition probabilities sum to one given the season and an individual's current location. An individual's current location is used as the baseline category; therefore, the multinomial back transformation for the probability of moving is:

$$\psi_{i,t,r_{t+1}} = \frac{e^{\beta_{s,r_{j,t},r_{k,t+1}}}}{1 + \sum_{k \neq j} e^{\beta_{s,r_{j,t},r_{k,t+1}}}} \qquad \text{eqn 16}$$

And the probability of staying at the current location is:

$$\psi_{i,t,r_{t+1}} = \frac{1}{1 + \sum_{k \neq j} e^{\beta_{s,r_{j,t},r_{k,t+1}}}} \qquad \text{eqn 17}$$

We used independent weakly informative priors, $\beta_{s,r_{j,t},r_{k,t+1}} \sim N(0, 1{\cdot}5)$. Estimated movement rates are minimum estimates because our sampling could not detect movements (particularly spawning) that occurred between sampling occasions.

PARAMETER ESTIMATION

We used JAGS (http://mcmc-jags.sourceforge.net/) to code the model and to draw posterior samples of the parameters. We called JAGS from R using the R package 'rjags'. We set initial values for z to 1 from the first to the last observation for each individual and NA for all other observations. We used overdispersed initial values (relative to the posteriors, checked with initial runs) for the remaining parameters. We specified 500 adaptive phase iterations and 50 000 estimation iterations with a thin rate of 5. We ran five chains and checked convergence using the 'potential scale reduction factor' (Brooks & Gelman 1998) in the R 'coda' package (diagnostic values <1·1 indicate good chain mixing). We also checked chains visually for lack of autocorrelation.

The model was very large, with *c.* 15 million nodes in JAGS. We ran five chains on different threads using the R package 'parallel' which improved run times, but required substantial RAM (10·6 GBytes per chain). A single run took 25 h to adapt and 26 days for estimation on an IBM System x3650 M3 with 96 GB of RAM (IMB Corporation, Armonk, NY, USA).

GOODNESS-OF-FIT

We conducted posterior predictive checks (Rubin 1984; Gelman *et al.* 2004) to assess model goodness-of-fit. Posterior predictive checks involve comparing simulated data based on model parameter estimates to observed data. We developed a simulation that replicated dynamics in our brook trout system and based the posterior predictive checks on three state variables calculated for each sampling occasion in each river: average body size, abundance of observed individuals and the proportion of individuals observed in each river. These state variables represent outcomes of the three key processes in the model: body growth, survival and movement.

The simulation projected body sizes, abundances and locations (rivers) for fish from eight cohorts (2004–2011). Initial size distributions and locations for each cohort were sampled with replacement from each cohort's fall age-0 data that included all tagged fish plus fish that were too small to tag. We needed to include the untagged fish in the simulation because initial and subsequent size distributions and abundances in the simulation would be biased low without them. The number of initial fish sampled equalled the total number of fish ever observed in a cohort. For each time step in the simulation, we estimated body growth, survival and movement based on parameter estimates from the model and environmental data (flow and temperature) aligned with the sampling occasion. For each cohort, we ran 10 replicate simulations for each of 40 evenly spaced iterations (sets of parameter estimates) and calculated mean state values for each iteration. To evaluate bias in the predictions, we plotted mean values against observed values (40 predicted values for each observation). We also calculated Bayesian *P*-values (Gelman 2003) for each state as the overall proportion of predicted values that were above observed values.

PREDICTED VALUES

To assist in interpreting the parameter estimates, we generated predicted values of body growth and survival across stream flows and temperatures for each river and growth year. We also generated predictions for body growth and survival across body sizes for each river and growth year. We present predicted curves for each iteration. In addition to patterns in the strength and direction of predictions, the overlap in predicted curves provides a visual representation of prediction (combined parameter) uncertainty among iterations.

SENSITIVITY OF ANNUAL SURVIVAL

Based on our parameter estimates, we developed stage transition matrices of a periodic integral projection model (IPM; Easterling, Ellner & Dixon 2000). We used the projection model to estimate sensitivities of annual survival to seasonal variation in stream flow and temperature. We also identified sensitivity pathways, the magnitude and direction of environmental effects via either survival or growth. Details of the annual survival calculations are in the Supporting information and see (Caswell 2007, 2008).

Results

MODEL SELECTION

Model selection results for the modules guided development of the integrated model structure. The most highly supported growth model (Table S2, Supporting information) included an intercept structured by river, season, growth year and year, an interaction between stream temperature and flow structured by growth year, season and river and an effect of body size also structured by growth year, season and river. We used this model structure for the growth model in the integrated model. The most highly supported survival model (Table S2, Supporting information) had the same structure as the growth model. We also used this model structure for the survival model in the integrated model. The most highly supported model for probability of capture based on AIC-estimated separate probabilities for young and old fish and a size trend within growth years (delta AIC = 3·7 compared to a model with separate capture estimates for each state).

INTEGRATED MODULAR MODEL

Convergence diagnostics

The 'potential scale reduction factor' (values $\leq 1{\cdot}1$ indicate acceptable model convergence) was $<1{\cdot}1$ for all of the parameters related to survival, probability of capture and movement. The reduction factor for model deviance equalled 1·01 with an upper CI of 1·03 (Fig. S3, Supporting information). Some of the growth rate parameters had reduction factors $>1{\cdot}1$, but these parameters were associated with sampling occasions with limited data, either at the beginning of the study. Convergence diagnostics of growth rate parameters were more sensitive to missing sampling occasions compared to the other parameters because they were also indexed by year.

Goodness-of-fit

Bayesian *P*-values (body size = 0·75, abundance = 0·32, river proportions = 0·47) indicated no bias in state estimates from the simulations. Graphical representation of the posterior predictive checks also demonstrated that the model parameter estimates generated unbiased state estimates (Fig. S4, Supporting information).

PARAMETER ESTIMATES

Probability of capture

Capture (p) was highly variable among seasons, rivers, growth years and years, with an overall average of p intercepts (p at average body size) of 0·57 (individual estimates in Fig. S5, Supporting information). Capture estimates for individual combinations of season, river, growth year and year ranged from lows of around 0·25 to highs of 0·8 (Fig. S5, Supporting information). Capture across years was most consistent in WB and IS in the summer and most variable among years in the winter for growth year 0/1 fish.

Size-dependent capture ($\beta_{1,s,r,y,g}$) was generally positive (larger fish within an age class had a higher probability of capture), with an overall average value of 0·14 (Fig. S6, Supporting information). Younger fish generally had higher average size-dependent p than growth year 1+ fish

(Fig. S6, Supporting information). Across seasons, size-dependent *p* in spring and winter was almost twice as strong as in the summer and fall. Size-dependent *p* did not vary substantially across rivers.

Seasonal movement

Proportion of fish moving among tributaries and the mainstem WB was generally low (<0·15), with most of the movement occurring from the tributaries to WB (darkest bars in Fig. 3). Across all seasons, between 0·02 and 0·15 of the fish moved from OS and OL to the WB, with the greatest movement (0·15) from OS to WB in the spring. In the summer, small, non-zero movement (<0·05) was estimated from the WB to OS and from the WB to OL.

Growth

The overall average of the growth rate intercepts (growth at average body size, flow and temperature) was 14·0 mm per season (Fig. S7, Supporting information), but the average masked considerable growth rate variation among seasons (Fig. S7, Supporting information). Average growth in the spring was more than double average growth in the summer and at least fourfold faster than average growth in the autumn or winter (Fig. S7, Supporting information).

Growth rate intercept priors (eqn 11) did not appear to constrain posterior estimates (Fig. S7, Supporting information). Effects of body size and stream flow on growth were generally positive, while temperature effects were usually negative (Fig. S8, Supporting information). Yearly variation in the SD of growth (sigma $\in \delta_{s,r,y,g}$) was greatest in the summer and was fairly consistent among years in the other seasons (Fig. S9, Supporting information).

Survival

The overall average of seasonal survival was 0·76. Among seasons, average survival was greatest in the spring and lowest in the summer (‘Int’ in Fig. S10, Supporting information). Average survival for fish in OS and IS was slightly greater than average survival in the WB and OL (Fig. S10, Supporting information). Size-dependent survival was consistently negative, while the effects of flow and temperature varied across seasons and rivers (Fig. S10, Supporting information).

PREDICTED VALUES

Body growth

Effects of flow and temperature on growth rate were remarkably consistent across seasons and rivers. For younger fish, we observed strong interactive effects of flow

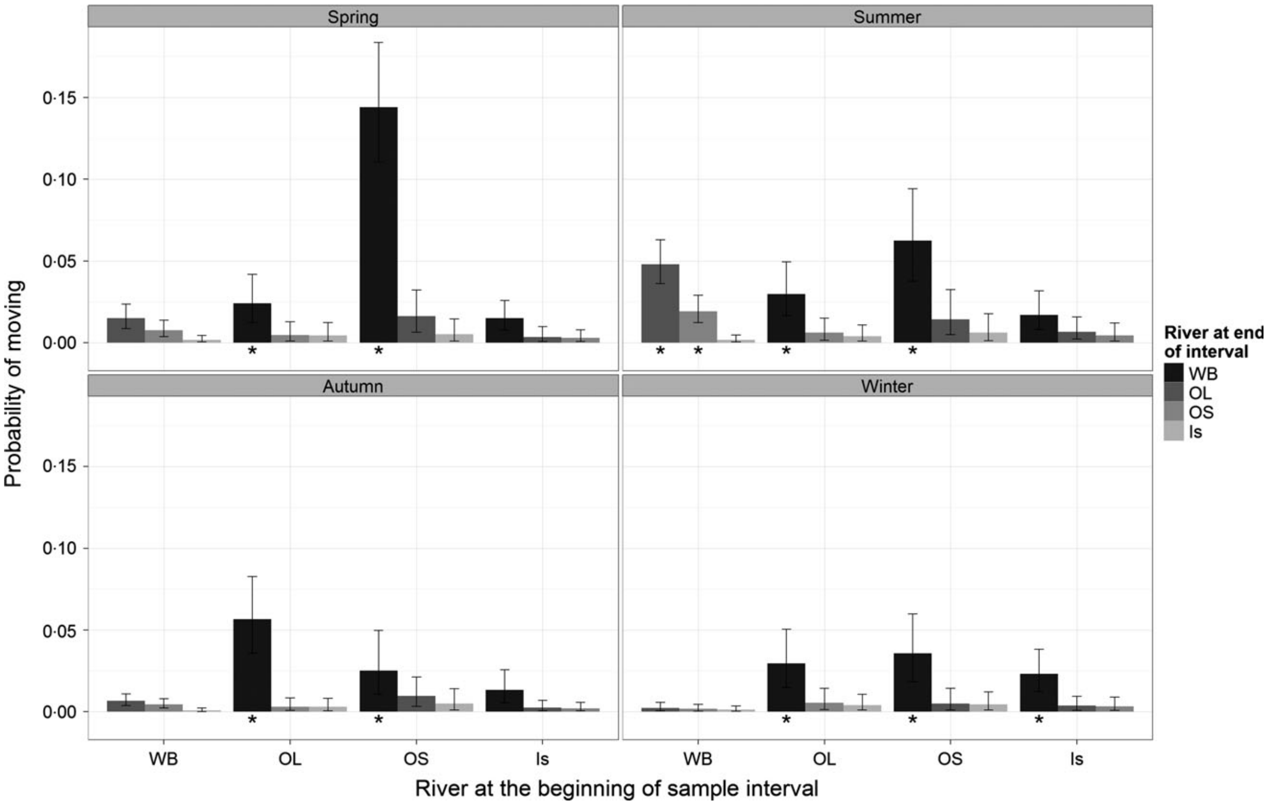

Fig. 3. Averages and 95% credible intervals for posteriors of movement probabilities (Ψ) from one river (*x*-axis) to another (bar colours) for each season. ‘*’ indicates that the lower 95% credible interval did not overlap a movement probability of 0·01.

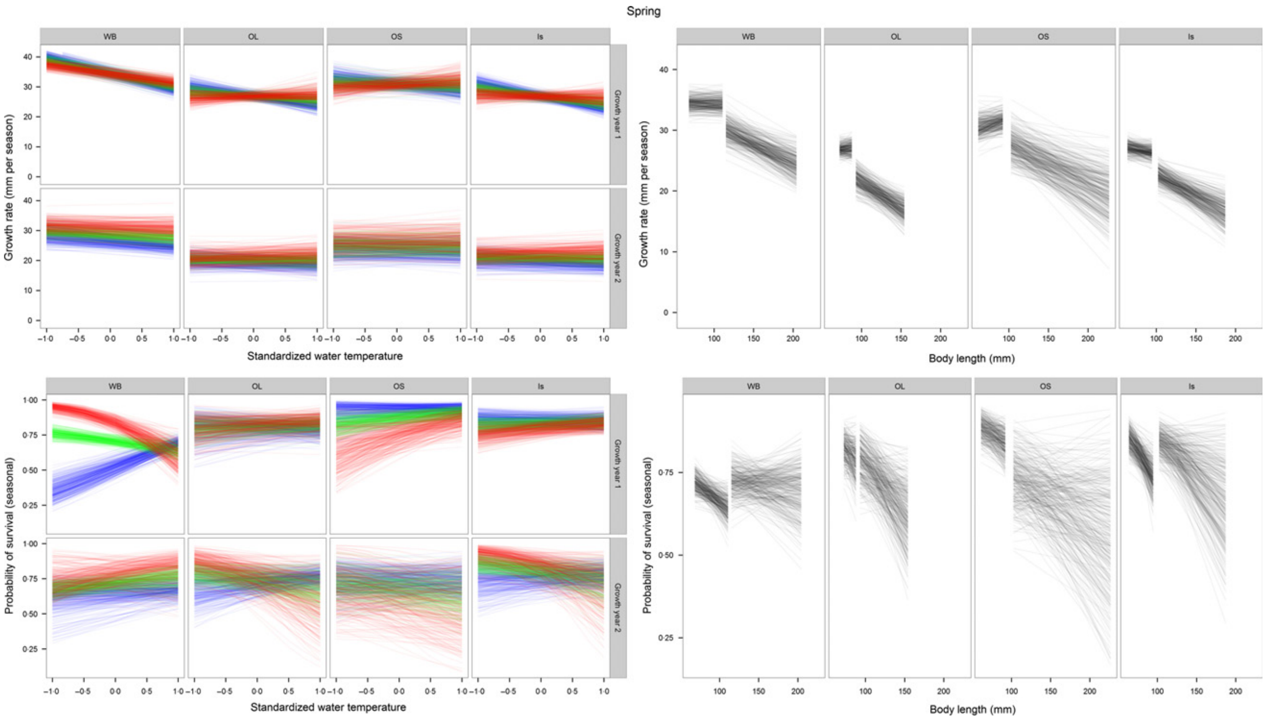

Fig. 4. Predicted growth rates and survivals in the spring as a function of stream temperature, stream flow and body size. Stream discharge is represented by the different colours [red = high flow (+1 SD units), green = average flow (0 SD units), blue = low flow (−1 SD units)]. Graphs in the first column represent growth rates (above) and survivals (below) for each combination of river and growth year as a function of stream temperature and flow (line colours). The second column contains estimates of size-dependent growth (above) and survival (below) for each river for average flow and temperature conditions. Lines on the left (smaller fish) in each panel are for growth year 0/1 fish and on the right (larger fish) are for growth year 1+ fish. Each line in the graphs is the predicted relationship for one MCMC iteration.

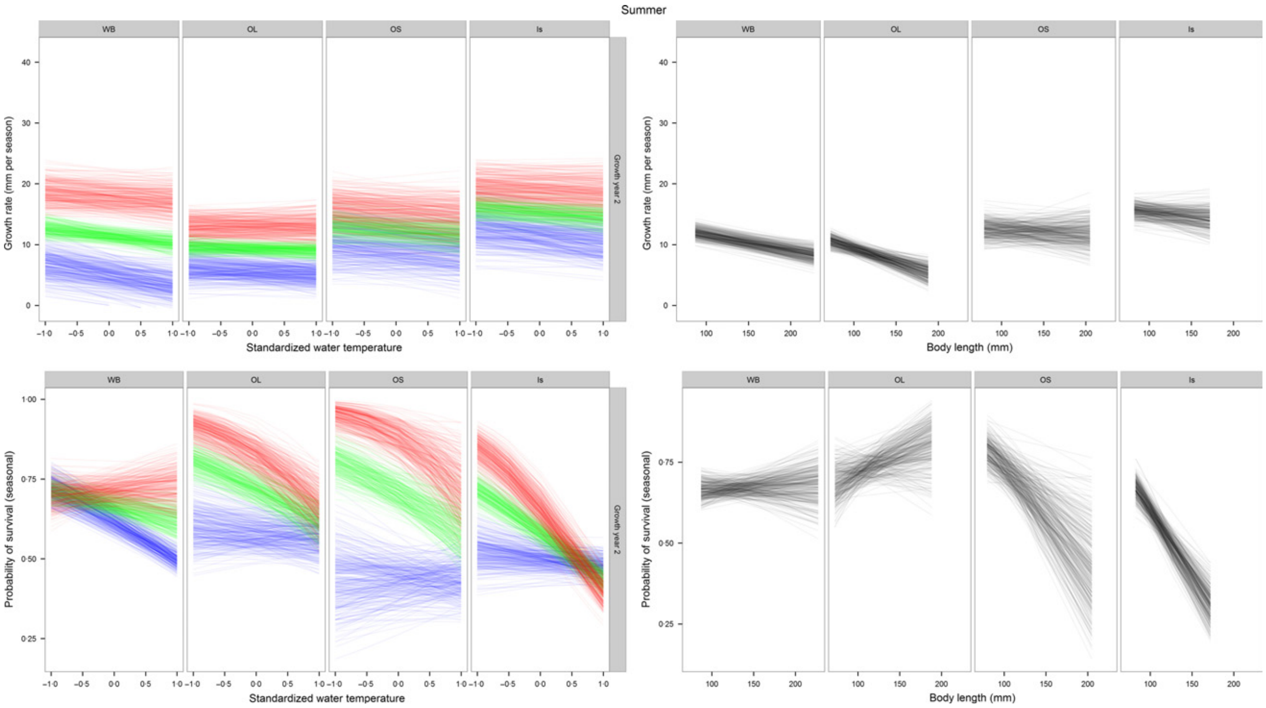

Fig. 5. Predicted growth rates and survivals in the summer (see description of Fig. 4 for details).

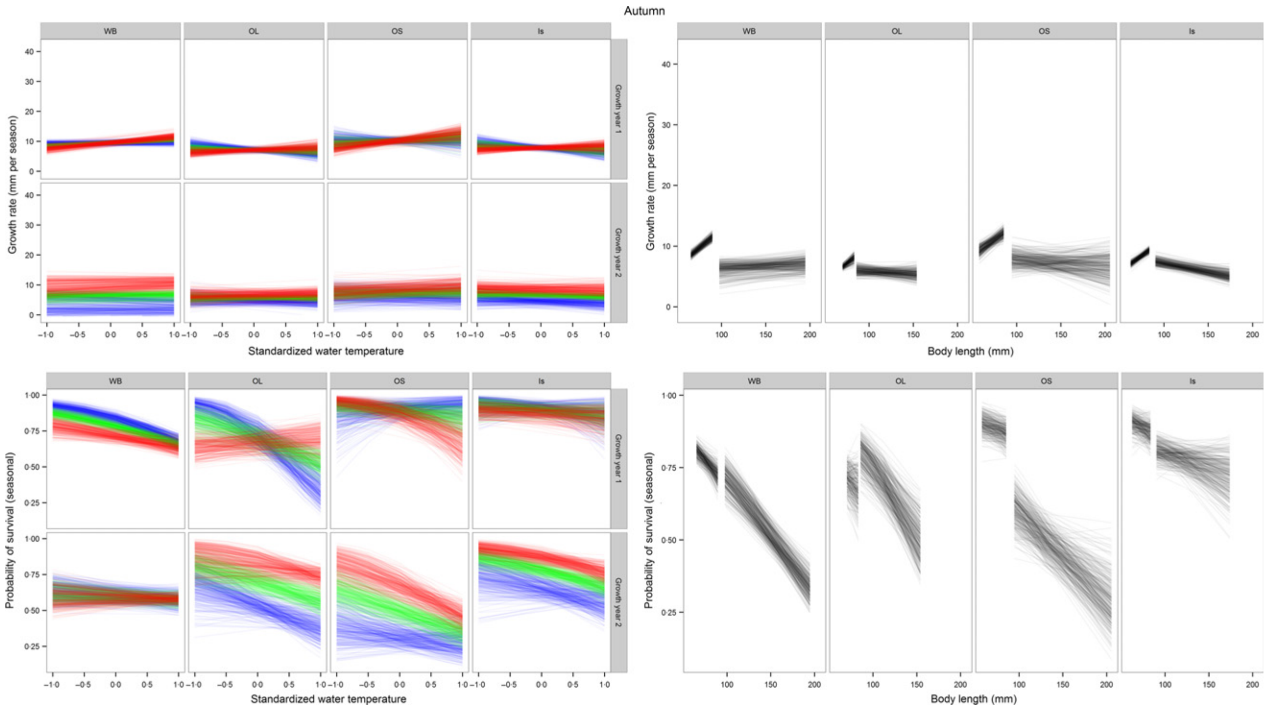

Fig. 6. Predicted growth rates and survivals in the autumn (see description of Fig. 4 for details).

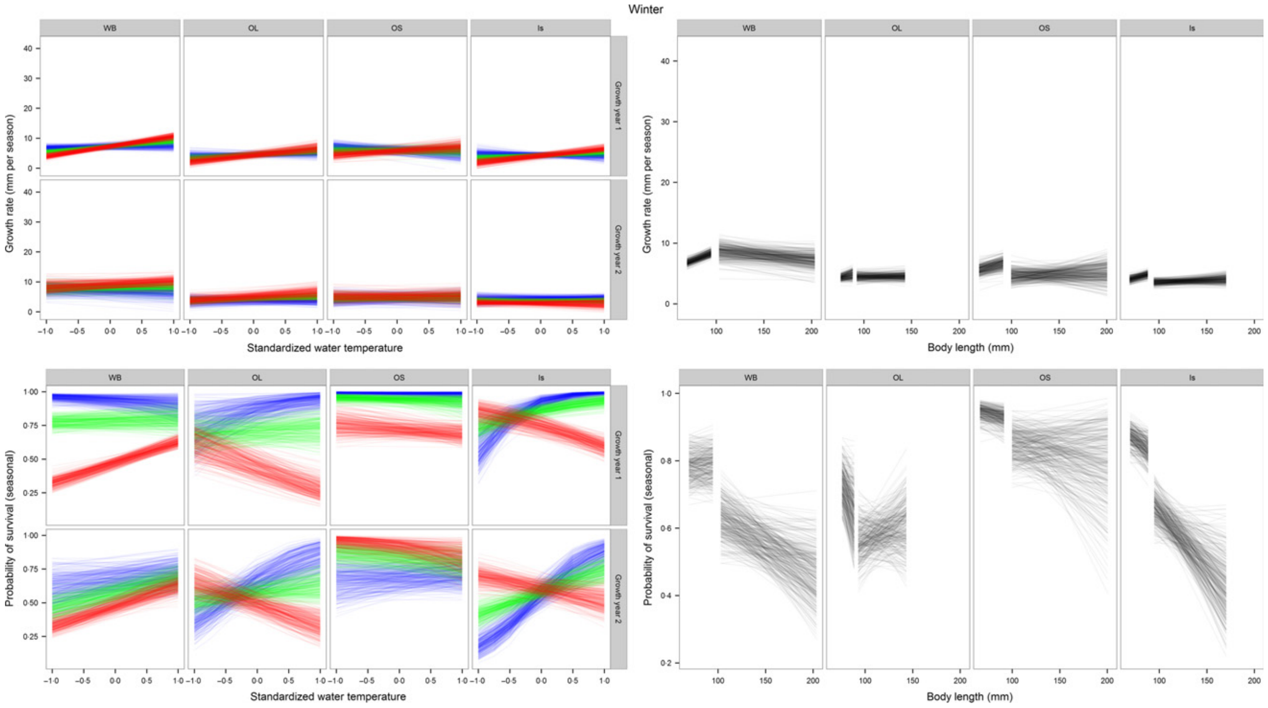

Fig. 7. Predicted growth rates and survivals in the winter (see description of Fig. 4 for details).

and temperature, with high growth at high temperatures but only when flow was also high (Figs 4–7). For older fish, the effect of flow dominated growth rates, especially in the summer. Growth was consistently greatest across the observed range of temperatures for older fish when flows were high (Figs 4–7).

The strength and direction of size-dependent growth varied dramatically between younger and older fish, but was quite consistent among rivers and seasons. For young fish, size-dependent growth was almost always positive (larger fish grow faster) and was particularly strong in the autumn (Fig. 6). For older fish, size-dependent growth was neutral or negative, with the most negative size-dependent growth in the spring (Fig. 4).

Survival

Patterns of flow and temperature-dependent survival were complex and site-specific, but some general patterns emerge (Figs 4–7). Seasonal effects of flow and temperature on survival tended to be similar among the tributaries, but quite different between the tributaries and the WB. For cold springs, survival of young fish in the WB was substantially higher (approximately threefold) with higher flows but effects of flow were negligible at warmer temperature (Fig. 4). For both young and old fish in the spring, the direction of flow and temperature effects were opposite in the WB compared with the tributaries, and flow and temperature effects were more uncertain for older fish (Fig. 4). In the summer, flow and temperature effects on survival were very similar among the tributaries, with highest survival at high flow and lower survival when it was warm (Fig. 5). In the WB, summer survival was also greatest when flow was high, but only when it was warm. Summer WB survival decreased dramatically at low flow when it was warmer (Fig. 5). In autumn, survival generally decreased when it was warmer, but the effect of flow was opposite in the WB vs. the tributaries: survival was greatest at lower flow in the WB but greatest at high flow in the tributaries (Fig. 6). In winter, survival patterns were generally quite similar between younger and older fish in each river, but patterns were quite different among rivers (Fig. 7).

Across all seasons, seasonal size-dependent survival was generally negative for both young and old fish (Figs 4–7). However, in the summer, we observed a strong difference in direction and magnitude as a function of river with size-dependent survival strongly negative in small rivers (OS and IS) and positive in larger rivers (WB and OL, Fig. 5).

SENSITIVITY OF ANNUAL SURVIVAL

Annual survival was sensitive to both stream flow and temperature but the magnitude and direction of effects varied seasonally across rivers (Fig. 8). Despite the variability, some general patterns emerge. Body growth effects (black portion of the bars in the figures) on annual survival were miniscule compared to the direct effects of seasonal survival. The magnitudes of flow and temperature effects were similar (directly comparable owing to standardization in the model), although directions were often opposite. In summer and autumn, flow sensitivities were generally positive or neutral (annual survival increasing or relatively unaffected by increased stream flows) and

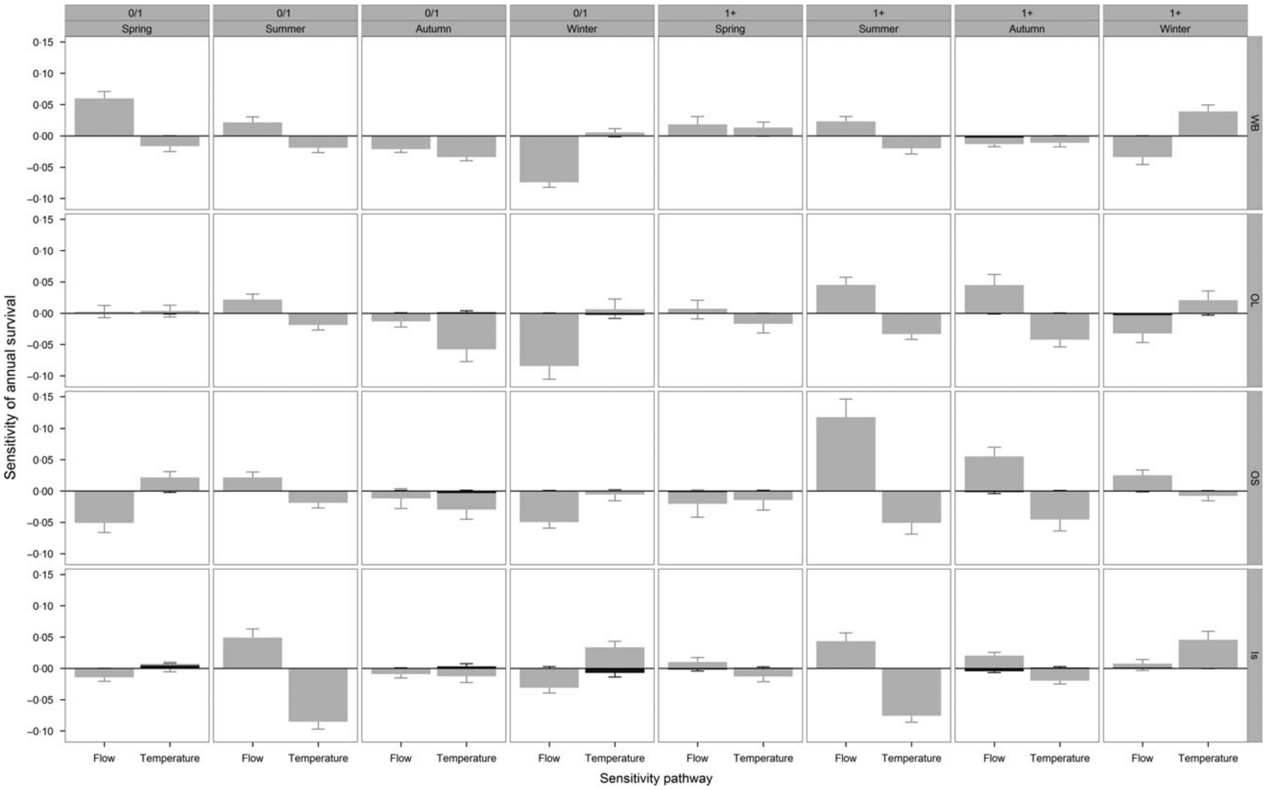

Fig. 8. Sensitivity (±95% credible interval) of annual survival for growth year 0/1 and growth year 1+ fish to seasonal survival (grey bars) and body growth (black bars) acting through stream flow or temperature. Sensitivities are shown for average flow, temperature and body size for each season.

temperature sensitivities were generally negative for both 0/1 and 1+ age-class fish. By contrast in winter, flow sensitivities were consistently negative and moderate-strong for growth year 0/1 fish, but weaker and less consistent across sites for growth year 1+ fish.

Discussion

Forecasting population fates in the context of environmental change requires robust estimates of the effects of the environment on vital rates (Coulson *et al*. 2011; Crone *et al*. 2013). In this study, we used long-term, high-resolution data and a novel integrated model to establish relationships between stream flow, temperature and population processes in a wild brook trout population. Developing these relationships is a key step towards forecasting environmental effects on population persistence. Flow and temperature had effects on brook trout growth and survival rates and also on annual survival, suggesting that future climate-driven changes in stream flow and temperature are likely to affect population dynamics and risk of local extirpation. We were able to uncover these effects because we combined data collected at appropriate resolution with a model that could surmount many of the difficulties in estimating environmental effects on population dynamics (Crone *et al*. 2013). Because many long-term population studies face similar challenges, we expect our modelling approach could be useful in a variety of systems.

The general utility of the integrated model approach has several limitations, however. There is no 'manual' for building these kinds of models, although there are now a number of good starting examples (King, Brooks & Coulson 2008; Royle 2008, 2009; Bonner, Morgan & King 2010; Kery & Schaub 2011). As one consequence, extending existing models by integrating new components (i.e. body growth, movement) requires substantial effort to incorporate the components and to select appropriate hierarchical structure for the priors. These models are also computationally intensive and require considerable computer resources; the model described here requires *c*. 62 GB of RAM to run five chains in parallel. Run times can be long (*c*. 4 weeks for our model). However, in many situations, these challenges are worth taking on for a number of reasons.

Perhaps the most desirable feature of the modelling approach we adopt is the ability to reveal emergent effects while accounting for processes responding to multiple and interacting sources of variation in a complex system. Simultaneous estimation in a single integrated model allows direct comparison of strength, direction and consistency of effects. We observed several cases of strong, consistent effects of variation in flow and temperature on key demographic rates. For example, in the summer, we found that low stream flows and high temperatures decreased annual survival across age classes and sites. Similar effects have been observed in previous studies (Xu, Letcher & Nislow 2010), but these effects have not been put in context (e.g. the relative strength across seasons and sites). Potential increases in summer temperatures are currently a major focus of vulnerability assessments for cold-water trout species (Beauchene *et al*. 2014). Our results support this emphasis, but further suggest that incorporating changes in summer stream flows may help strengthen the utility of these assessments. We also found effects of flow and temperature in winter on annual survival rates that were opposite in direction to summer effects, with lower stream temperatures and higher stream flows generally associated with decreased survival. Both summer and winter effects are largely consistent with the general physiological ecology of stream-dwelling salmonid fishes. Physiological performance in brook trout is maximized at temperatures between 12 and 16 °C (McCormick 1972), and warm summers in our study site readily exceed physiological optima. Low summer flows reduce encounter rates with drifting invertebrate prey and increase intraspecific competition for food and space by increasing local densities via reductions in habitat area (McNicol & Noakes 1984; Grant & Noakes 1988). In contrast, high flows in winter present swimming performance challenges (to maintain position in flowing water and to avoid winter-active predators) to fish that are operating at temperatures well below their physiological optima, but relatively warmer winters are closer to performance optima and could therefore result in higher survival. This concordance between our results, previous field and laboratory research, and the fundamental biology of this and similar species suggests that these findings are likely to be general and applicable across a broad range of conditions. For the spring season, however, the influence of stream flow and temperature on annual survival was variable in direction and magnitude across both age classes and sites, suggesting that our current understanding of spring flow and temperature effects is insufficient to apply to broader-scale dynamics.

Simultaneous estimation in a single integrated model also allows the comprehensive propagation of uncertainty among linked model components. A key benefit of our approach is the ability to incorporate uncertainty in states (alive, body size and location) and link these with uncertainty in parameter estimates (survival, growth and movement). Because we modelled both the parameters and the states in a single integrated model using MCMC, there is complete 'feedback' between all model components (see Fig. 2). This means that uncertainty in the parameters will influence the states and vice versa. For example, for individuals that were present but not captured for a given sampling occasion, we can estimate not only whether the individual was alive, but also its size and location. Further, the uncertainty in these predictions is incorporated into parameter estimates that are size- and location-dependent (growth, survival). The net result is an increase in the number of observations that are available to model the relationship between environmental drivers and parameters. This increase in useful data can be substantial. For example, using raw data, we need captures on consecutive sampling occasions to estimate individual seasonal growth or movement but only 34% of our individual captures were from consecutive occasions. Modelling values for the missing observations in the integrated model provide state estimates (and uncertainty) for 100% of the sampling occasions. Robust estimates of parameter uncertainty are a critical component of forecasting and using models to guide natural resources management decisions (Nichols *et al.* 2011; Williams & Johnson 2013).

While our model provides full integration over uncertainty, the long run times present serious challenges. Alternatives to the fully integrated model include (i) describing the states as discrete variables and estimating effects with a multistate model (Brownie *et al.* 1993; Schwarz, Schweigert & Arnason 1993; Lebreton & Pradel 2002) and (ii) estimating time-varying covariates with an external model and linking the estimates to the CJS model (Worthington, King & Buckland 2014). Based on successes with multistate models for estimating size-dependent survival in Atlantic salmon (Letcher & Horton 2008) and brook trout (Letcher *et al.* 2007), we initially attempted to use a multistate model to estimate individual covariate effects. Unfortunately, a seasonal model with both the individual covariates (five size states, four location states and four seasons) combined with the environmental variables resulted in a model that would not converge in program MARK. An additional drawback of using a multistate model to describe continuous variables such as body size is the inevitable lumping across the variable, resulting in a loss of information (Bonner & Schwarz 2006; Bonner, Morgan & King 2010). The second alternative, a 'two-step' approach generating state imputations with an external model (Worthington, King & Buckland 2014), can decrease run times substantially, traditional model selection and parameter uncertainty estimation via bootstrap are possible and the models are simpler, but an analysis of the trade-offs between reduced run times and loss of full integration has not yet been performed. With the two-step approach, however, there is no longer 'feedback' among model components, resulting in incomplete covariance structure among parameters and incomplete error propagation across model components. Further research is needed to evaluate fully these trade-offs.

In size structured populations with indeterminate growth and size-dependent fecundity, it is important to consider the effects of environmental drivers on growth and size in addition to direct effects on survival. We developed an integral projection matrix (stage transitions only) based directly on modelled parameter estimates to evaluate sensitivity of annual survival to direct and indirect effects of flow and temperature acting through either body growth or survival. This analysis allowed us to identify strength, direction and uncertainty of flow and temperature effects on annual survival. We found that body growth, like survival, was sensitive to flow and temperature, but the strength, direction and level of interaction differed substantially between young and old fish. For older fish, higher flows almost always resulted in faster growth. In contrast, the effect of flow on growth in young fish was temperature dependent, with faster growth for high flows only at higher temperatures. Similar to the seasonal effects on annual survival discussed earlier, these differences are largely consistent with size- and age-dependent ecological considerations. In general, for stream salmonids, larger individuals are capable of higher sustained swimming speeds, and higher flows therefore yield the benefits of high prey encounter rates with relatively minor metabolic costs (Fausch 1993), resulting in higher growth rates. In contrast, for younger, smaller fish, the benefits and costs of higher flows are more likely to trade off, with net benefits only accruing at optimal temperatures. Young and old fish also exhibited strikingly different patterns of size-dependent growth, with strong positive size-dependent growth for young fish and the opposite for older fish. All these patterns were consistent across sites, suggesting a fundamental difference in the growth strategies and response of growth to environmental drivers between fish of different age classes. While previous studies have addressed age-specific differences in environmental tolerances (Breau, Cunjak & Bremset 2007) and behavioural strategies (Clarke 1994), our modelling framework allowed us to detect potential consequences of these effects for population vital rates in the context of environmental change. At the same time, environmental effects on growth had minimal effect on annual survival in our model. However, annual survival estimates did not include potential effects of growth and body size on reproduction, which could be strong in species with size-dependent maturation and fecundity, like brook trout. A full accounting of body size and growth effects on population growth is possible with population projection models (Caswell 2001; Caswell & Shyu 2012). The parameter estimates generated with our model combined with reproduction and early growth/survival (pre-tagging) can provide the information needed to build a full IPM (Ellner & Rees 2006).

In addition to their general importance, robust estimates of environmental effects (including uncertainty) help evaluate fundamental concepts of species response to environmental change. For example, among-site and among-life history stage variation in the response to environmental drivers can help stabilize populations and increase resilience to environmental change via a 'portfolio effect' (Schindler *et al.* 2010) as conditions which negatively affect populations in one location or at one stage are counterbalanced by neutral or positive effects in others. In our study, we were able to demonstrate several components of a potential portfolio effect for brook trout populations. Perhaps most importantly, we found that tributary and mainstem sites responded differently to variation in flow and temperature. In general, brook trout were more negatively affected by low flows in the tributaries than in larger mainstem habitats, responses to flow were more temperature dependent in the mainstem, and negative size-dependent survival was much stronger in tributaries (Figs 4–7). As a specific example, summer-fall droughts may be bad years for fish in tributary habitats, but may be counterbalanced by better condition in mainstem habitats (Figs 4–7). These habitat-, age- and season-specific vital rates, combined with our ability to estimate the occurrence, magnitude and direction of movement between these habitat types, lay the groundwork for a quantitative assessment of the value of a diversified conservation portfolio.

Our model estimates and their uncertainty can also be incorporated directly into population projection matrices (Caswell 2001), which can be used to evaluate likely population response to environmental change. For example, IPMs (Easterling, Ellner & Dixon 2000; Ellner & Rees 2006) provide a framework for incorporation of continuous state variables, such as body size, into projection models. As demonstrated with our annual survival sensitivity analysis (a partial version of an IPM), the parameter estimates from our integrated model provide the necessary growth, survival and movement estimates to form the core of an IPM. A full IPM would require the addition of two components: (i) early (pre-tagging) growth, survival and movement, and (ii) reproduction. The full IPM could be used to evaluate population response to a changing environment by examining sensitivities (Rees & Ellner 2009) of demographic rates in the model to changes in stream flow and temperature and by running scenarios of alternate future environmental conditions. Thus, estimates from our integrated model, while interesting and informative alone, also provide the key estimates needed for a broader analysis of population response to environmental change.

Acknowledgements

Many thanks to all the students and interns who have helped sample the West Brook. Partial funding was provided by the US Fish and Wildlife Service North Atlantic Conservation Cooperative and the National Institute of Food and Agriculture, U.S. Department of Agriculture, the Massachusetts Agricultural Experiment Station and the Environmental Conservation Department of the University of Massachusetts Amherst, under project number MAS # 14. Thanks also to Jeff Falgout of the USGS Core Science Analytics and Synthesis Center in Denver CO, USA, for facilitating computer runs on the USGS computer cluster in Denver. We thank two anonymous reviewers, Dan Hocking and Will Fields, for helpful comments on a manuscript draft.

Data accessibility

Data are archived at github in a public repository, https://github.com/bletcher/data.

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Received 16 April 2014; accepted 7 October 2014
Handling Editor: Dylan Childs

Supporting Information

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

Data S1. Description of annual survival sensitivity calculations and JAGS code for the integrated model.

Fig. S1. Map of the study area in western MA, USA, including the study area range (stippled line), the mainstem (WB) and the three tributaries (OL, OS, IS).

Fig. S2. Size frequency distributions for the West Brook for each sampling occasion.

Fig. S3. Deviance of the five chains (white to black) across iterations.

Fig. S4. Observed vs. predicted state values for mean body size, abundance, and proportion of fish in each river.

Fig. S5. Mean and 95% CI for probability of detection ($\beta_{0,s,y,r,g}$ in eqn 5) across years for each combination of season (rows), river (columns) and growth year (columns; 1 = 0/1, 2 = 1+).

Fig. S6. Mean and 95% CI for the probability of detection slope ($\beta_{1,s,y,r,g}$ in eqn 5) across years for each combination of season (rows), river (columns) and growth year (columns; 1 = 0/1, 2 = 1+).

Fig. S7. Mean and 95% CI for intercepts of the growth model ($\beta_{0,s,r,y,g}$ in eqn 9) across years for each combination of season (rows), river (columns) and growth year (columns; 1 = 0/1, 2 = 1+).

Fig. S8. Mean and 95% CI for the four betas of the growth model ($\beta_{1:4,s,r,g}$ in eqn 9) for each combination of season (rows), river (columns) and growth year (columns; 1 = 0/1, 2 = 1+).

Fig. S9. Mean and 95% CI for standard deviation in growth model (sigma $\in \delta_{s,r,y,g}$ in eqn 12) across years for each combination of season (rows), river (columns) and growth year (columns; 1 = 0/1, 2 = 1+).

Fig. S10. Mean and 95% CI for the intercept and four beta parameters of the survival model ($\beta_{1:4,s,r,g}$ in eqn 2) for each combination of season (rows), river (columns) and growth year (columns; 1 = 0/1, 2 = 1+).

Table S1. Counts of brook trout captured in each river, season and year.

Table S2. Model selection for the growth model and the survival model.