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ARTICLE

Daily estimates reveal fine-scale temporal and spatial variation in fish survival across a stream network

Evan S. Childress, Keith H. Nislow, Andrew R. Whiteley, Matthew J. O'Donnell, and Benjamin H. Letcher

Abstract: Environmental drivers of population vital rates, such as temperature and precipitation, often vary at short time scales, and these fluctuations can have important impacts on population dynamics. However, relationships between survival and environmental conditions are typically modeled at coarse temporal scales, ignoring the role of daily environmental variation in survival. Our goal was to determine the importance of fine-scale temporal variation in survival to population dynamics of stream salmonids. We extended the Cormack–Jolly–Seber model to estimate daily survival rates from seasonal samples of individually marked brook trout (*Salvelinus fontinalis*) in a stream network. Daily variation in temperature and flow were strongly associated with survival, but relationships varied between juvenile and adult trout and among streams. In all streams, juveniles had higher mortality in warm, low-flow conditions, but in the two larger streams, cold, high-flow conditions also reduced juvenile survival. Adult survival decreased during low flows, particularly in the fall spawning period. Differing survival responses among stream network components to short-term environmental events created shifts in optimal location for maximum survival across life stages, seasons, and years.

Résumé : Les facteurs environnementaux qui influencent les indices vitaux dans les populations, comme la température et les précipitations, varient souvent à de courtes échelles temporelles, et ces fluctuations peuvent avoir des effets importants sur la dynamique des populations. Cependant, les relations entre la survie et les conditions environnementales sont souvent modélisées à des échelles temporelles grossières, évacuant du coup le rôle des variations environnementales journalières sur la survie. Notre objectif était de déterminer l'importance de variations temporelles de courte durée de la survie pour la dynamique de populations de salmonidés de cours d'eau. Nous avons élargi le modèle de Cormack–Jolly–Seber pour estimer les taux de survie journaliers à partir d'échantillons saisonniers d'ombles de fontaine (*Salvelinus fontinalis*) étiquetés individuellement dans un réseau hydrographique. Les variations journalières de température et de débit étaient fortement associées à la survie, mais les relations étaient différentes entre les juvéniles et les adultes et d'un cours d'eau à l'autre. Dans tous les cours d'eau, les juvéniles présentaient un taux de mortalité plus élevé dans des conditions chaudes et de faible débit, mais dans les deux cours d'eau plus grands, des conditions froides et de débit fort réduisaient également la survie des juvéniles. La survie des adultes diminuait durant de faibles débits, particulièrement durant la saison de frai automnale. Des réactions différentes de la survie dans différentes composantes d'un réseau hydrographique à des épisodes environnementaux de courte durée modifiaient l'emplacement optimal pour une survie maximum pour les différentes étapes de cycle de vie et les différentes saisons et années. [Traduit par la Rédaction]

Introduction

Drivers of population vital rates, such as temperature and streamflow, often vary at short time scales, and these fluctuations can have important impacts on population dynamics. However, studies of population vital rates typically estimate rates at relatively coarse time scales to match the scale of sampling because daily sampling can quickly become prohibitively resource intensive. Important variation in population vital rates between samples can be masked by aggregating environmental variation (Clark et al. 2011), particularly in cases where relatively short periods dominate the overall environmental effects (e.g., floods). Subseasonal variation in vital rates and short-lived events that contribute substantially to determining annual vital rates are important and understudied aspects of population dynamics (Lynch et al. 2014; Shriver 2016).

Daily survival rates have been estimated for species that can be easily observed at high frequency without substantial stress to the study organism, such as pre-fledge birds and plants (Anholt et al. 2001; Dinsmore et al. 2002; Shriver 2016), but fine-scale survival probabilities are more commonly assumed constant between more widely spaced observations (e.g., monthly or annually; Ling et al. 2009; Letcher et al. 2015). Although samples of many animals are taken at coarser time scales, fine-scale data on environmental conditions, which are often major determinants of survival, are typically available. These data can be leveraged to estimate relationships between fine-scale environmental data and fine-scale vital rates, such as survival and growth, which are then aggregated to the scale of vital rate observation (Childress and Letcher 2017). This is in contrast to the more standard approach of aggregating the covariates prior to analysis, for example, by taking the average between sampling occasions (Vindenes et al. 2014; Letcher

et al. 2015). Aggregating the environmental effects after estimation rather than before aligns the model more closely with the process of interest, which is likely to provide a richer picture of the dynamics of interest (Clark et al. 2011). This approach uses the entire distribution of covariates without assuming any particular shape, which is particularly useful when extreme values influence the outcome in ways that are not well characterized by the central tendency of the distribution.

Estimating fine-scale temporal fluctuations in vital rates can yield insights into important population processes that may otherwise be overlooked or place a finer point on the conditions that influence survival the most. For example, extreme weather events often have disproportionate effects on survival (Kingsolver et al. 2013). Similarly, there may be short periods or seasons in which animals are particularly sensitive to environmental variation. While models at more coarse resolution may identify some of these patterns, the details provided by the finer-scale estimates are likely to reveal the key components of variability in vital rates.

Fine-scale temporal variation in environmental conditions can interact with spatial variation in habitat characteristics to create spatial variation in population vital rate responses to environmental conditions (Elliott 2000; Bret et al. 2017). Such variation has important implications for metapopulation dynamics, population persistence, and individual behavior. Spatial variation in vital rates has often been evaluated at the annual scale, but seasonal and short-term variation among locations is also likely to influence the capacity for that variation to buffer against stressful conditions by providing refugia. Understanding how vital rates vary jointly over space and short time scales would provide important information about the sources and implications of vital rate variability; such data are also useful for informing individual-based models.

In this study, we extend the Cormack–Jolly–Seber model (Cormack 1964; Lebreton et al. 1992; Royle 2008) to estimate daily survival probability and its relationship with environmental conditions from seasonal mark–recapture data of brook trout (*Salvelinus fontinalis*) populations in a stream network. Our goals were to understand (*i*) the types of environmental events that influence survival most and (*ii*) the variation in the most influential events across the stream network and brook trout life stages. The model we introduce offers new perspectives on the dynamics of fish survival across a range of time scales, making it possible to compare survival within and among seasons as well as across years, life stages, habitats, and individuals.

Materials and methods

Model

We used a novel extension of the Cormack–Jolly–Seber (CJS) model to leverage seasonal observations to make inferences about the relationship between daily environmental conditions and apparent survival. Because mortality and emigration cannot be separated, CJS models typically estimate apparent survival. We censored data from individuals that were known to emigrate, so our estimates more closely approximate true survival. However, some individuals that emigrated were likely not observed, so although we use the term "survival" hereafter, the estimates are more specifically "apparent survival" and represent a combination of survival and emigration. Recaptures of individually marked animals are used in CJS models to simultaneously estimate capture and survival probability as functions of covariates (Lebreton et al. 1992). For this study, individual alive state ($z_{i,s}$, alive = 1, dead = 0) for individual i at the time of sample s was modeled as a Bernoulli trial, with probability equal to the product of expected survival probability ($\varphi_{s,r,g}$) and latent alive state in the last sample:

$$(1) \qquad z_{i,s} \sim \text{Bernoulli } (\varphi_{s,r,g} \times z_{i,s-1})$$

where r is the known or inferred river that the fish was in during the sample and g is life stage (juvenile or adult). When a fish was not observed it was assumed to have remained in the river where it was last observed, and any movement was assumed to happen immediately prior to capture in another river. Only 4.3% of encounters occurred in a river different from the last river in which a fish was observed, and fitting the model assuming that fish moved immediately after release did not result in statistically significant or qualitative differences in the results. We defined the transition between juvenile and adult as occurring in June of the year following hatching. Each individual's cohort was identified at first capture using size distributions that displayed distinct breaks between young of year and older fish (Letcher et al. 2015).

Expected survival between two sampling events (φ) can be expressed as the cumulative daily survival probability between samples, assuming that each day's survival is independent:

$$(2) \qquad \varphi_s = \prod_{d=s-1}^{s} \phi_d$$

where ϕ_d is the probability of survival on day d, s is the sample day, and $s - 1$ is the day of the previous sample. River-specific daily survival was modeled as a function of daily environmental covariates using a logit link function. In this case we used temperature, flow, and their interaction as the predictors because of their well-documented influence on brook trout populations (Kanno et al. 2015; Letcher et al. 2015; Kovach et al. 2016).

$$(3) \qquad \text{logit}(\phi_{d,r}) = \beta_{0,r,g} + \beta_{1,r,g}T_{d,r} + \beta_{2,r,g}F_{d,r} + \beta_{3,r,g}T_{d,r}F_{d,r}$$

where $T_{d,r}$ is the maximum daily temperature on day d in river r, $F_{d,r}$ is the average daily flow, and β values are river and life stage specific intercept and slope parameters. Maximum temperature was used because we hypothesized that exceedance of the preferred temperature range was the most likely mechanism for temperature to influence survival. Individual fork length at the start of the growth interval (L_i) was also included in the model. Including length directly in the above equation created computational challenges because it requires an estimate for daily survival for each individual (i.e., number of fish × number of days). To avoid overly long run times (on the order of years), environmental effects on daily survival were modeled at the river and life stage level using eq. 3, then the product of daily survival during the interval was taken, and the length effect was added to this product on the logit scale:

$$(4) \qquad \text{logit}(\varphi_{i,s}) = \text{logit}\left(\prod_{d=s-1}^{s} \phi_{d,r} \right) + \beta_{4,r,g}L_{i,s}$$

When fish were not observed, fork length was estimated using a previously developed growth model based on temperature, flow, and trout density (Childress and Letcher 2017).

Individual encounters ($e_{i,s}$) in sample s were modeled as Bernoulli trials, with probability equal to the product of detection probability and latent alive state:

$$(5) \qquad e_{i,s} \sim \text{Bernoulli } (p_{i,s} \times z_{i,s})$$

Individual detection probability was modeled on the logit scale as a function of mean discharge on the day of sampling, individual length, and number of passes based on river as well as stochastic variation across river and sample:

$$(6) \qquad \begin{aligned} \text{logit}(p_{i,s}) &= \beta_{0,r} + \beta_{1,r}F_{s,r} + \beta_{2,r}L_{i,s} + \beta_{3,r}(n\text{Passes}_{s,r} - 1) + \varepsilon_{s,r} \\ \varepsilon_{s,r} &\sim \text{Normal}(0, \sigma) \end{aligned}$$

where $\varepsilon_{s,r}$ is stochastic variation for each sample (*s*) and river (*r*), which was included to account for other sources of variation, such as personnel turnover and weather. Three of the rivers (Jimmy Nolan Brook, Mitchell Brook, and Ground Brook) were always sampled with a single sampling pass, so β_3 did not contribute to detection estimates for those rivers; β_3 represents the increase in detection probability due to the second pass in West Brook.

The model was fit using a Bayesian approach in R 3.2.3 (R Core Team 2015) and JAGS (Plummer 2003). Convergence was determined by visually examining Markov chain Monte Carlo (MCMC) chains and ensuring that $\hat{R}$ values for all parameters were less than 1.1 (Gelman et al. 2004). Model fit was evaluated using a posterior predictive check for the number of individuals recaptured in each sample; data for the posterior predictive check were simulated by conditioning on first capture, selecting 100 random iterations from the MCMC chain, and simulating survival and detection using each of the selected estimates for parameter values.

## Model performance on simulated data

The basic modeling approach was tested on simulated data across a randomized set of conditions to evaluate whether parameters were recovered accurately and without bias. Temperature and flow data from West Brook were used as the basis for the simulations. Parameter values for simulating data were chosen at random using uniform distributions across example parameter values (−2 to 2 for slopes, 5 to 9 for the intercept, and 0 to 2 for standard deviation of random variation on detection probability); parameter values were restricted to these ranges to obtain realistic life-spans for individuals (i.e., on the order of months to years rather than days or decades). For evaluating model performance, detection probability was simulated and modeled as an overall mean, which was randomly selected between 0.5 and 0.9, with stochastic temporal variation with a standard deviation between 0.1 and 1.0 on the logit scale. Sampling events were simulated on the same days that actual samples were collected in the real data set, so a total of 63 samples were simulated. On each sampling occasion, 34 newly marked individuals were added to the population, which is equivalent to the overall average number of marked individuals per river and sample. Survival was simulated using eq. 2. The model was fit to 1000 simulated data sets, and model performance was evaluated by comparing true parameter values used for simulation with the estimated parameter values.

Field data

The study was conducted in the West Brook and three tributaries located in western Massachusetts, USA (see Letcher et al. 2007 for site map). The watershed contains primarily mixed hardwood forest with a dense canopy with a few residences and some small-scale agriculture. The sampling area included a 1 km long reach of the main stem West Brook (WB) and 300 m reaches in each of three tributaries: Jimmy Nolan Brook (hereafter open large, OL), Mitchell Brook (open small, OS), and Ground Brook (isolated small, IS). Trout are able to move among two of the tributaries (OL and OS) and the main stem, while upstream movement into the third tributary (IS) is prevented by a natural waterfall (~3 m), and the system behaves like a metapopulation (Letcher et al. 2007). In two tributaries, the upstream edges of the study area are delimited by impassable waterfalls, and the third tributary (IS) has a waterfall at the study area boundary that is likely passable in some flow conditions.

Naturally reproducing populations of brook trout and brown trout (*Salmo trutta*) inhabit the main stem and connected tributaries, with very few brown trout in OS, while only brook trout are found in IS. Blacknose dace (*Rhinichthys atratulus*) are also found in the study system and Atlantic salmon (*Salmo salar*) fry were stocked in WB until 2004. There is no stocking of trout in the study area and fishing pressure is minimal.

Fig. 1. Median estimated daily survival probabilities for juvenile brook trout with 60 mm fork length (*a*), and for adult brook trout with 100 mm (*b*), 150 mm (*c*), and 200 mm (*d*) fork lengths. Solid lines represent the posterior mean estimate and dotted lines bound the 95% credible interval. Note the different *y* axis scale for panel *d*.
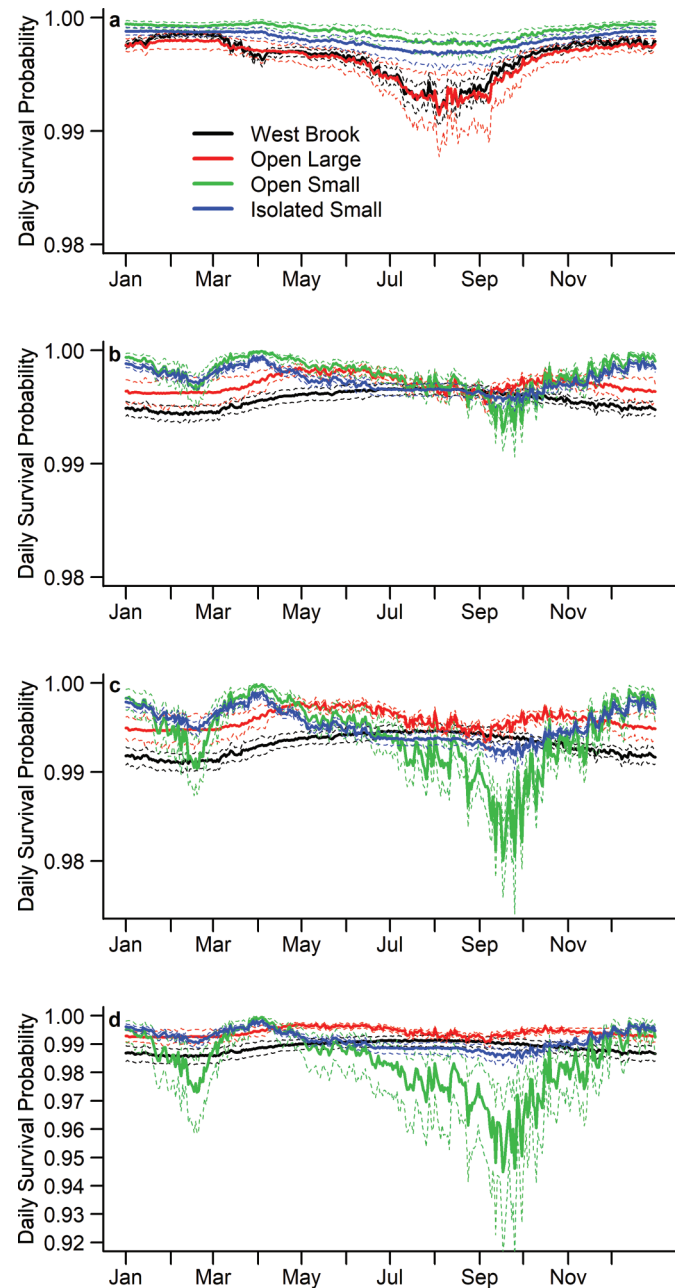
Four samples per year were conducted (late March, June, September, and early December), and we report data from June 2002 to September 2015. During each sample, fish were collected sequentially from downstream to upstream from 20 m sections that were delineated at the beginning of the study and remained consistent throughout. In WB, block nets were used to isolate sections temporarily, and two electrofishing passes (200–300 V unpulsed DC) were conducted in most instances; only a single pass was conducted in WB in 17% of samples. In tributaries, fish mobility was lower and capture rates were higher, so a single pass was conducted without block nets (Letcher et al. 2015). Location (river and section) was recorded and fork length was measured for each fish. Tag number was recorded for all tagged fish, and all

Fig. 2. Estimated effects of stream discharge and water temperature on juvenile brook trout daily survival probability across streams in a network: (*a*) WB, (*b*) OL, (*c*) OS, and (*d*) IS. The coloured area represents the range of observed conditions in each river. Colour and contour lines both show the variation in daily survival probability across stream discharge and temperature. Note the varying scales for contour lines. WB, West Brook, main stem; OL, open large tributary; OS, open small tributary; and IS, isolated small tributary.
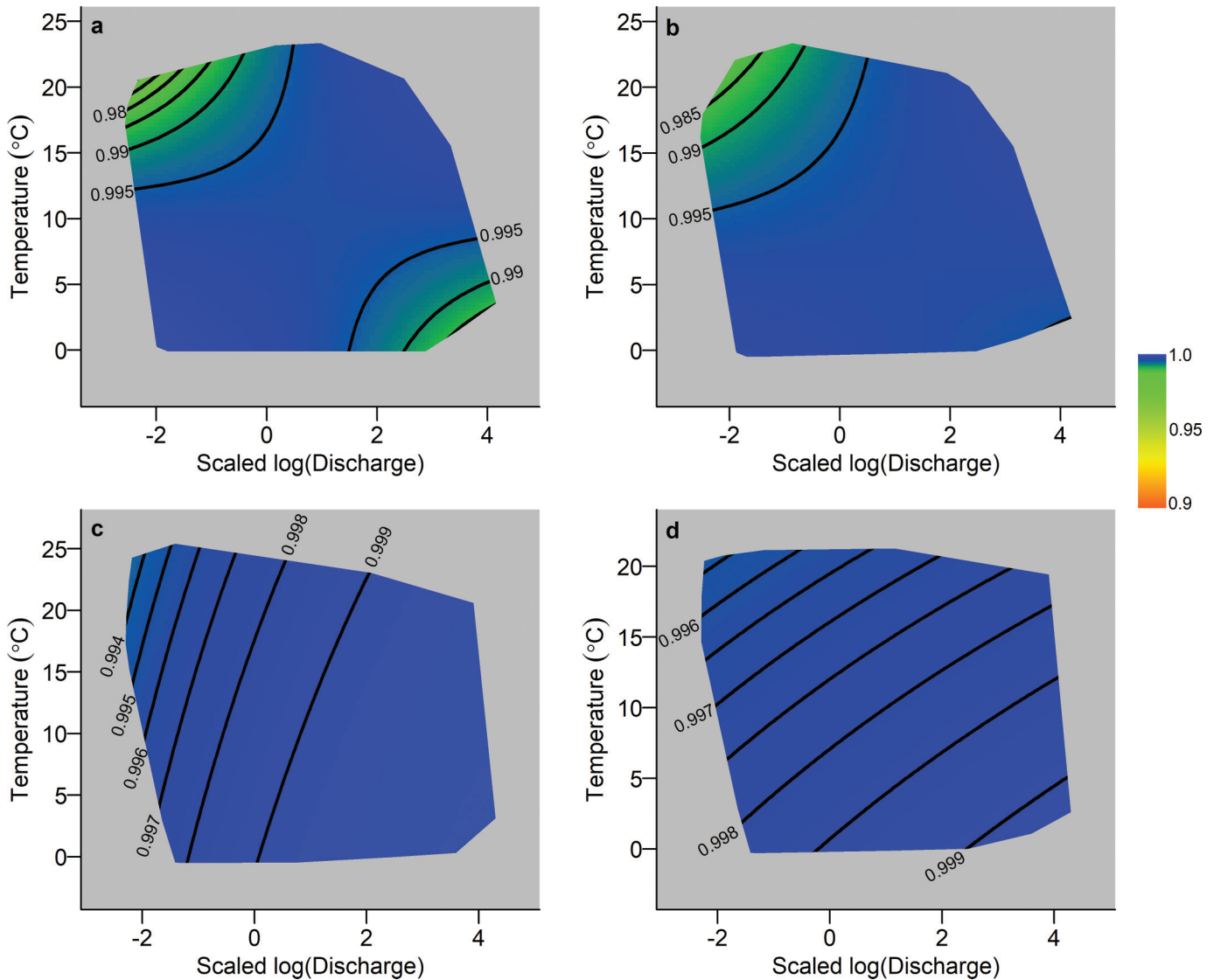
untagged fish with a ≥60 mm fork length were tagged with full-duplex, 12 mm passive integrated transponder (PIT) (Biomark Inc., Boise, Idaho, USA) tags, which provide unique identifiers for each fish. Fish were returned to their capture location after workup. A total of 14 154 brook trout were tagged during this study. PIT tag antennas at the top and bottom of the boundaries of the study area recorded fish leaving the study area in the main stem, and data were censored if an individual was observed for the last time leaving the study area. Tag loss rate for smaller brook trout (<50 mm) was 3.3% (O'Donnell and Letcher 2017), which represents a maximum, and loss rates were probably closer to those for Atlantic salmon in the system at 0.2% (Gries and Letcher 2002).

Stream depth was measured every 2 h using depth loggers (Solinst Canada, Ltd., Ontario, Canada) at the downstream end of the study area and represents an index of flow conditions in the study area. Depth was converted to stream flow (m³·s⁻¹) using a stage–discharge relationship. Temperature was recorded in each river typically at 1 h resolution but sometimes at 2 h resolution (15% of observations early in the study). Data gaps were filled using predictions from linear regression with water temperatures re-

corded at a nearby site within the study area that did have data during the gap (all $R^2 > 0.97$); 13% of the temperature data were predicted using this method.

Results

Model performance on simulated data

Fitting the model to simulated data yielded accurate and precise parameter estimates (Appendix Table A1; Fig. A1). Relative bias was <1% for all parameters except the standard deviation of capture probability, which had a relative bias of 2.5%. The 95% credible intervals contained the true value in approximately 95% of cases for all parameters (93.4%–95.5%).

The model fit to the field data converged based on well-mixed MCMC chains with $\hat{R}$ values of <1.1. A Bayesian *P* value of 0.54 indicated that the estimated model was able to recreate the observed data without bias.

Field data

Individual capture probability averaged 59% overall but varied among rivers and samples and was related to discharge during

Fig. 3. Estimated effects of stream discharge and water temperature on adult brook trout daily survival probability across streams in a network: (*a*) WB, (*b*) OL, (*c*) OS, and (*d*) IS. The coloured area represents the range of observed conditions in each river. Colour and contour lines both show the variation in daily survival probability across stream discharge and temperature. Note the varying scales for contour lines. WB, West Brook, main stem; OL, open large tributary; OS, open small tributary; and IS, isolated small tributary.
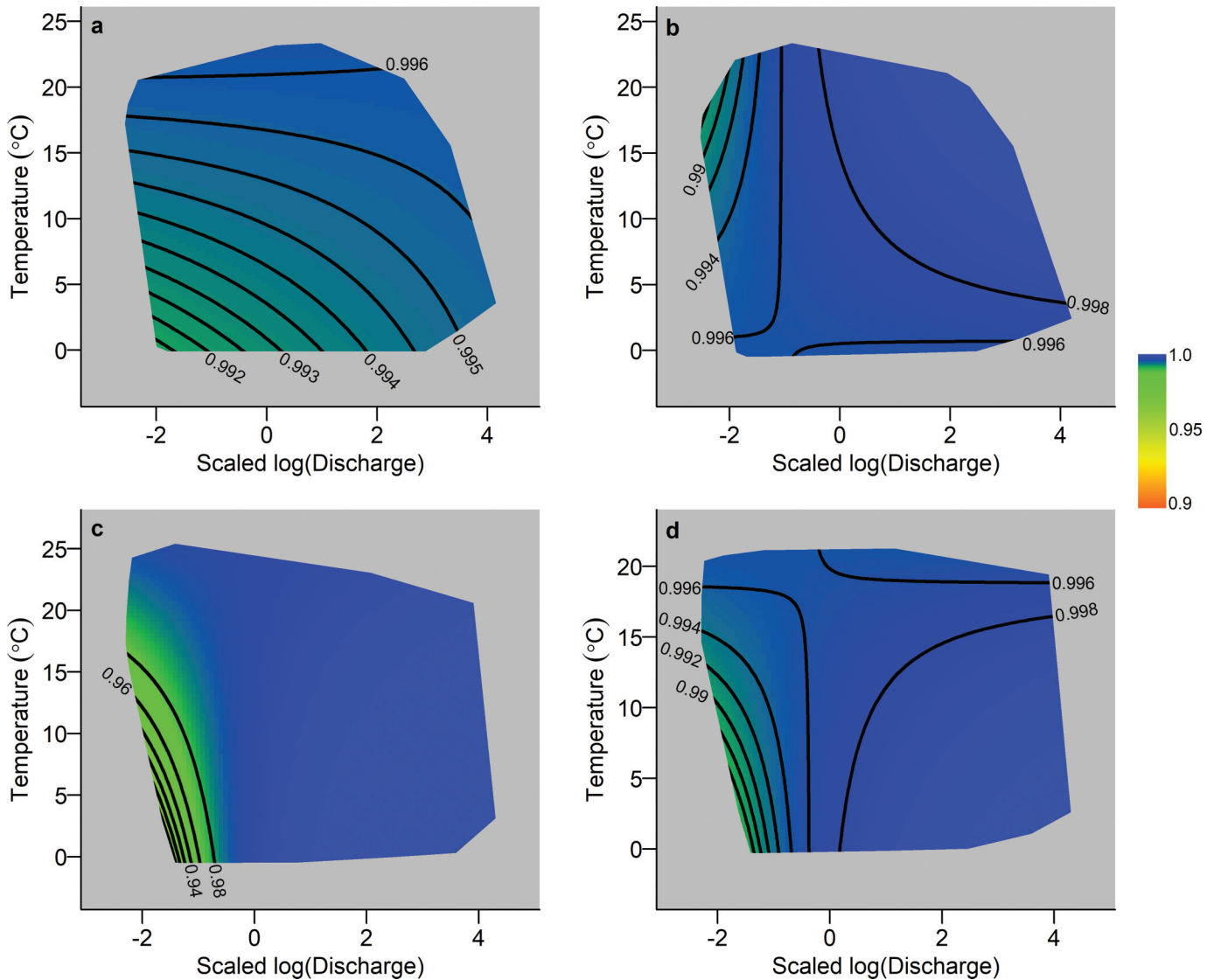
sampling and body length (Fig. A2). When only one sampling pass was conducted in WB (17% of samples), detection was reduced by an estimated 14%. Capture probability declined slightly, but statistically significantly, with stream flow during sampling in all streams (Fig. A2, 95% credible intervals <0). Capture probability increased with body size in WB and IS but did not exhibit a statistically significant relationship with body size in OL and OS (Fig. A2). Additional variation across rivers and samples was captured by the stochastic term in the detection model ($\sigma = 0.63$, logit scale).

Differences in survival across space were driven by different responses to covariates rather than differences in survival rates under average conditions. Credible intervals (95%) for mean daily survival probability overlapped for all rivers and life stages, such that daily survival was not significantly different among rivers for an average-sized individual under average environmental conditions. However, differences in the effects of body size, discharge, and temperature led to variation over time and among rivers and life stages (Figs. 1, A3). Survival decreased for larger fish with significantly stronger effects in the two smaller tributaries than in WB and OL (Fig. A4).

In all rivers, juvenile daily survival declined when temperatures were high and discharge was low (Fig. 2), conditions that typically occur in late summer and early fall (Fig. 1*a*). Additionally, high flows and low temperatures (i.e., winter floods) were associated with lower daily survival in WB and to a lesser extent in OL. Intra-annual variation in juvenile daily survival exhibited similar patterns across rivers, with lower survival in late summer and early fall, but the pattern was more pronounced in WB and OL (Fig. 1*a*).

For adult daily survival, low discharge was associated with lower daily survival particularly in combination with colder temperatures. In OL, survival was also reduced with combined high temperature and low discharge, which was associated with the lowest survival rates in that stream (Fig. 3). In contrast to the pattern of variation in juvenile daily survival, adult daily survival was most stable in WB across the year and most variable in OS (Figs. 1*b*–1*d*).

The ideal location for an individual to maximize survival changed as fish grew and across the year (Fig. 1). The small tributaries had higher juvenile survival rates throughout the year and maintained higher survival for adults during the high-flow periods in

Fig. 4. (*a*, *b*) Examples of estimates of juvenile daily survival from spring 2008 and fall 2010. (*c*, *d*) Average temperature (solid line, left *y* axis) and scaled, log-transformed discharge (dashed line, right *y* axis) across the study rivers. Environmental conditions covaried strongly across the stream network and averages are shown for clarity.
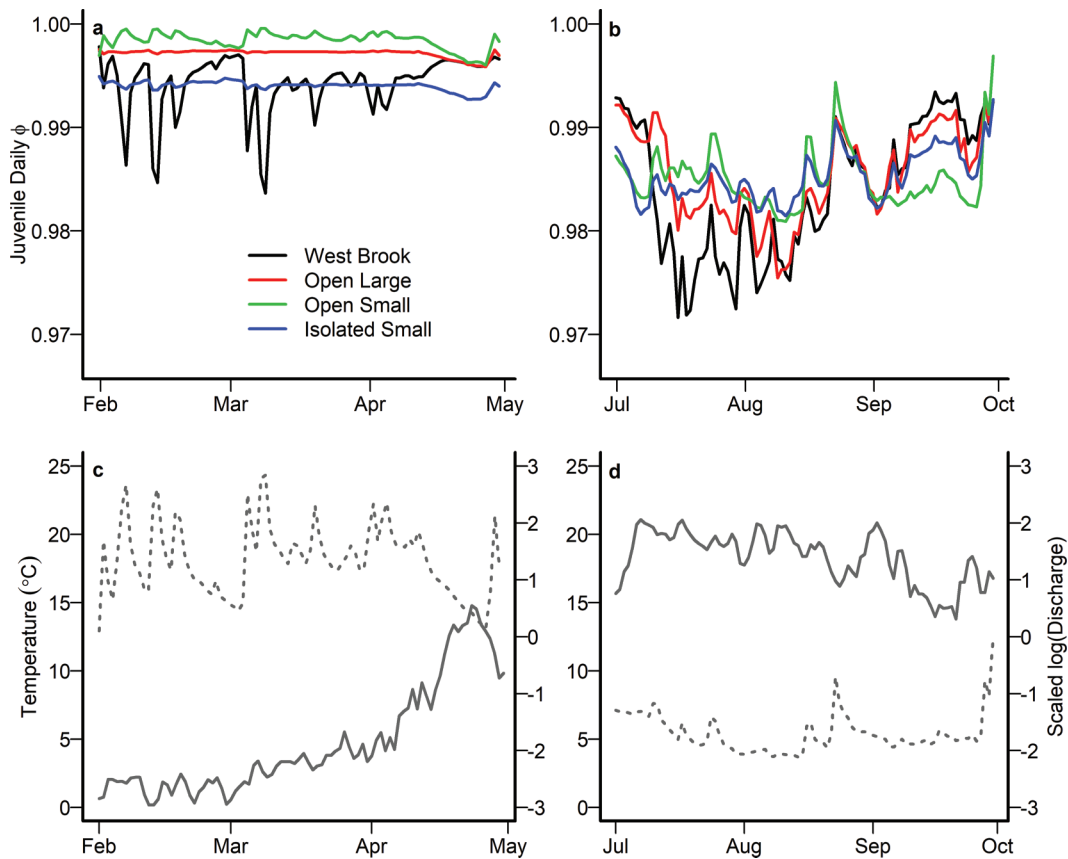
spring. However, survival declined dramatically for larger fish in the smaller tributaries during low-flow periods of the late summer and fall, which led to higher survival for large fish in WB and OL during these periods. Variation among rivers in response to environmental conditions drove different responses to particular events and reordering of which rivers hosted higher survival probabilities (Fig. 4).

At the annual scale, estimated survival probability for an average length juvenile brook trout was higher in OS (average of yearly posterior mean annual estimates = 0.21) and IS (0.14) than in WB (0.08) and OL (0.07) (Fig. 5). For average-length adults, estimated annual survival probability in WB (mean = 0.09) was stable and tended to be lower than in the tributaries (OL = 0.20, OS = 0.14, IS = 0.16). The smallest tributary, OS, had particularly variable adult annual survival, with posterior mean estimates ranging from 0 to 0.34 (Fig. 5).

Discussion

We used a novel extension to the CJS model to estimate daily survival probabilities from seasonal observations and to establish a detailed perspective on the variation in survival across ontogeny, time, and space in response to environmental variation. The basic results on the effects of environmental conditions on survival corroborate previous studies (Kovach et al. 2016; Sweka et al. 2017); however, by estimating survival at the daily scale, this study reveals a complex mosaic of survival probabilities across life stages, rivers, and time with frequent shifts in the locations within the stream network that maximize survival. Interestingly, survival in different streams within the network responded differently to the same events; in particular, winter floods were associated with lower juvenile survival in the larger streams, whereas they did not

affect juvenile survival in the smaller streams. In contrast, adult survival decreased strongly in hot, dry conditions in the smallest stream but was largely unaffected by these conditions in the main stem.

Life stage and body size combined with environmental effects to create strong, fine-scale variation in survival probability with changes in which river had the highest survival probability. For juveniles, the smaller tributaries showed consistently higher survival than the main stem and larger tributary. For adults, the rank of survival probability shifted over the course of the year, with stronger differences among rivers and seasons as fish became larger. The smaller tributaries shifted from having the highest survival probability for juveniles to having the lowest summer–fall survival for larger adults. By modeling survival at the daily scale, we were able to resolve the timing and duration of low-survival periods. Seasonal models may lump critical transition periods in ways that mask variation. For example, there were large changes in survival from June to September for many river–size combinations, but a seasonal model would group that period masking the details of when survival was actually reduced.

The temporal variation in survival probability was driven by relationships between environmental conditions and survival and was largely consistent with previous studies. Low-flow conditions combined with high temperatures — conditions that typically occur in summer — can be challenging for trout (Kovach et al. 2016; Al-Chokhachy et al. 2017). Spawning season has also been identified as a period with high mortality for adults, particularly when discharge is low (Petty et al. 2005; Sweka et al. 2017). Previous findings on the effect of body size on stream salmonid survival have been variable, but similar to our findings, a number of studies have documented higher survival in small fish (Carlson

Fig. 5. Estimated annual survival for brook trout juveniles with 60 mm fork length (*a*) and for adults with 100 mm (*b*), 150 mm (*c*), and 200 mm (*d*) fork lengths. To align with when juveniles enter the sample and transition to the adult stage, annual survival was estimated from 1 June of the nominal year to 31 May of the following year. Solid lines represent the posterior mean estimate, and dotted lines represent 95% credible intervals.
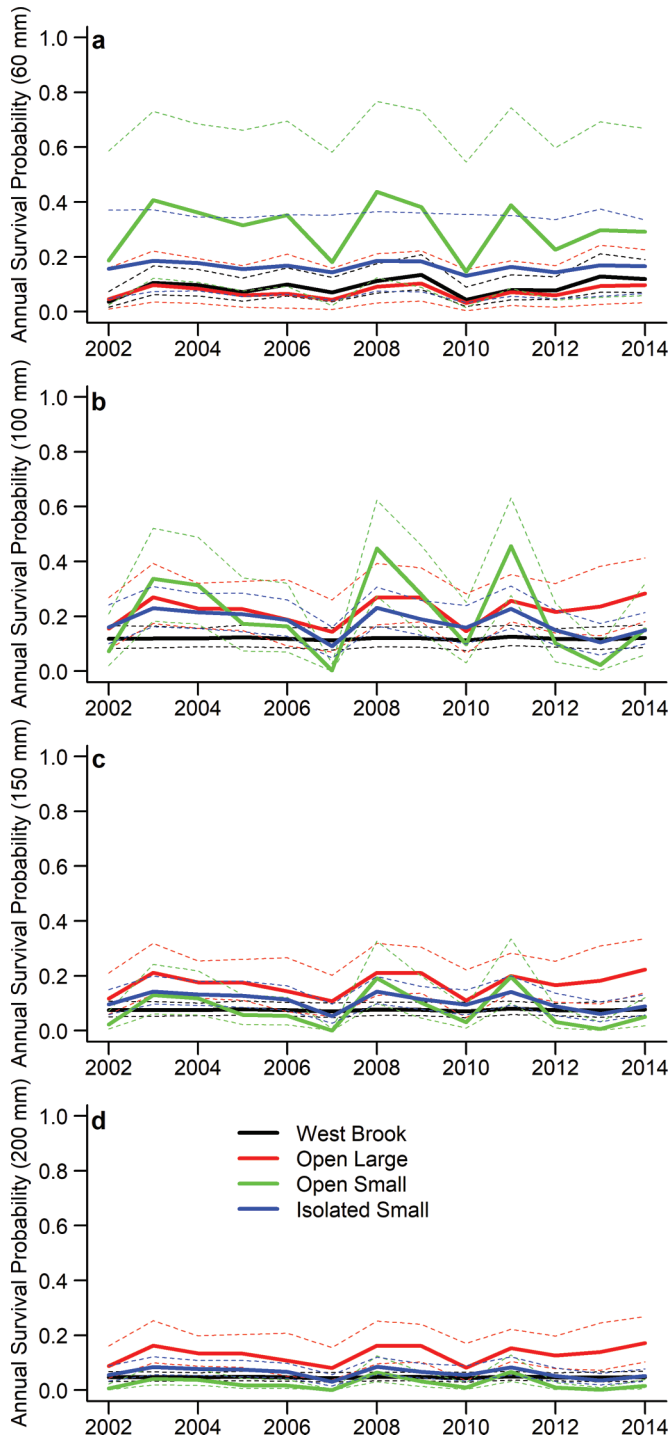
and larger tributary showing much weaker responses of adult survival to low flows. The context-dependence of survival responses to events is likely driven by habitat characteristics, such as depth and slope, and may explain some of the variation in observations from previous studies on size effects in salmonids (Carlson et al. 2008).

Similarly, interactions between intrinsic (body size and life stage) and extrinsic (flow and temperature) factors explained survival variation among rivers. For example, higher juvenile survival in the smaller tributaries reflected a muted response to both hot, dry conditions and wet, cold conditions, which were both associated with strong decreases in survival probability in the larger tributary and the main stem. Additionally, under average conditions, small fish had higher survival probabilities in the tributaries than in the main stem, suggesting that biotic interactions mays also play a role. For example, higher juvenile survival in the smaller tributaries under average conditions may reflect a release from competition with larger fish, which tend to be more common in larger habitats (Petty et al. 2005). Alternatively, predation risk or competition may be lower in the small tributaries because brown trout were concentrated in the main stem and larger tributary (B.H. Letcher, unpublished data).

Diversity in the responses of survival in different rivers to environmental conditions creates opportunities for individuals to maximize fitness through movement. Higher juvenile survival in smaller tributaries creates an impetus for upstream spawning movement and preferential spawning in smaller streams, which have been previously observed in brook trout and other stream-dwelling salmonids (Curry et al. 2002; Petty et al. 2005). Though other factors may also confer benefits to fish that spawn further upstream, such as appropriate spawning substrate and groundwater inputs (Curry and Noakes 1995), higher survival of juveniles in more upstream habitats is likely to be a contributing factor. The locations that maximize survival for larger fish appear to be more nuanced because the locations with highest survival probability changed across the year, which agrees with previous findings that optimal foraging locations and adult densities shift across seasons and years (Gowan and Fausch 2002; Petty et al. 2005).

In addition to offering opportunities for individuals to maximize their survival, the ontogenetic, seasonal, and interannual variation in survival probability is also likely to increase stability in the metapopulation through the portfolio effect (Moore et al. 2010; Schindler et al. 2015). For example, in some years the OS tributary had the highest estimated adult annual survival probability, but in the dry conditions of 2007, survival probability was essentially zero. Thus, this habitat is likely to switch from being a source of recruits in wet years to being a sink in particularly dry years. If this stream were not connected to the main stem, the local population would likely be extirpated fairly quickly (Letcher et al. 2007), which is evidenced by genetic data that suggest the two streams represent a single population, whereas there is genetic differentiation between WB and OL (Whiteley et al. 2017). However, this small stream may create opportunities for strong reproductive years and high survival when conditions are right (Kanno et al. 2014), and it may buffer the effects of winter floods on the juvenile population, which was more susceptible to cold temperatures and high flows in the larger tributary and main stem.

One benefit of estimating daily survival is identifying periods or events that drive mortality. Because most studies evaluate survival at longer time scales, often annually, though sometimes seasonally (e.g., Letcher et al. 2015), the effects of particular events and within-season variation can be masked. Sometimes particularly important periods are identified a priori and used to derive covariates (e.g., 7-day minimum flow during August; Olden and Poff 2003). However, developing and choosing metrics requires substantial prior knowledge of the important processes, with the risk of misspecifying the model due to incomplete information.

et al. 2008). The effect of body size on survival was larger in the smaller tributaries, likely because these smaller habitats offer less suitable habitat for larger fish, which is exacerbated by low flows (Petty et al. 2005). Thus, the response of adult survival to low-flow conditions was context-dependent, with the main stem

Here, we identify the late summer to early fall period as particularly challenging for brook trout juveniles. Additionally, spawning season, which occurs in early fall in the study area was associated with higher mortality in the tributaries. While a previous study using seasonal analysis identified summer as a period of lower survival, lower survival in small tributaries during early fall appears to have been masked by the increasing survival rates later in the season (Letcher et al. 2015). Estimating survival at the daily scale identified the specific timing of this low-survival period and its association with particular environmental conditions. The benefits of estimating daily survival are likely to be particularly pronounced when environmental conditions change substantially between samples, as is typical during spring and fall.

The relationships between covariates and survival in CJS models share the assumptions and potential pitfalls of all correlation models. Of particular note in this case is the potential for spurious relationships. Associations of survival with temperature and discharge may be related to other, unmeasured variables. For example, adult survival was particularly low in the tributaries during low flows and cold temperatures. Spawning movements often occur during these conditions, which may increase predation risk or other sources of mortality (Sweka et al. 2017). Food availability also tends to be low during the fall, which could contribute to the association between these conditions and survival (Cunjak et al. 1987). Teasing apart causality would require experimentation; however, the shifts in survival across combinations of location, life stage, and environmental conditions remain a valuable outcome of these models.

The assumption that daily survival rates are independent may not strictly hold. Cumulative effects of chronic exposure to low-level stress can drive mortality (Menendez 1976; Dickerson and Vinyard 1999), such that multiple consecutive days of stressful conditions may reduce survival probability more than an isolated instance of the same conditions. Cumulative effects could influence the results by inflating the acute sensitivity to certain conditions when they were chronically experienced. However, on average the effects of environmental conditions should reflect realized survival for the combinations of conditions in the data set. This issue could potentially be addressed by including autoregressive processes or antecedent metrics in the model.

By estimating the associations between fine-scale environmental drivers and survival probability, we were able to elucidate important nuances of variation in survival across time, space, and ontogeny. In particular, we identified the timing and duration of late summer, early fall decreases in survival. The daily estimates of survival provided insights into the differences in responses among rivers to particular environmental events, which led to frequent shifts in which locations had the highest survival. Data were not available to examine the particular habitat characteristics (e.g., slope, stream power, pool depth) that could explain the mechanism by the observed differences among streams, which would be an interesting topic for future study. Regardless of the mechanism, the identified fine-scale variation in survival across locations and time is likely to drive individual behavior, metapopulation dynamics, and life history variation.

Data accessibility

Data from this manuscript will be available through the US Geological Survey's ScienceBase data repository: https://www.sciencebase.gov/catalog/.

Acknowledgements

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Appendix A

Detailed results of simulations to evaluate the performance of a process summation CJS model

Table A1. Model performance for simulated data including percent relative bias, root mean squared error (RMSE), and the percent of true parameter values that fell within the estimated 95% credible interval (CI).

| Parameter	Relative bias (%)	RMSE	Percentage falling within 95% CI
β_0	<0.1	0.113	94.3
β_1	0.3	0.104	93.4
β_2	<0.1	0.111	94.2
β_3	−0.8	0.105	94.1
μ_P	0.3	0.112	94.9
σ_P	2.5	0.099	95.5

Note: β values are intercept and slope parameters for survival, μ_P is the mean detection probability, and σ_P is the standard deviation of stochastic variation on detection probability.

Fig. A1. Estimated versus true parameter values from model fit to simulated data. 1:1 lines are shown. All parameters are on the logit scale.
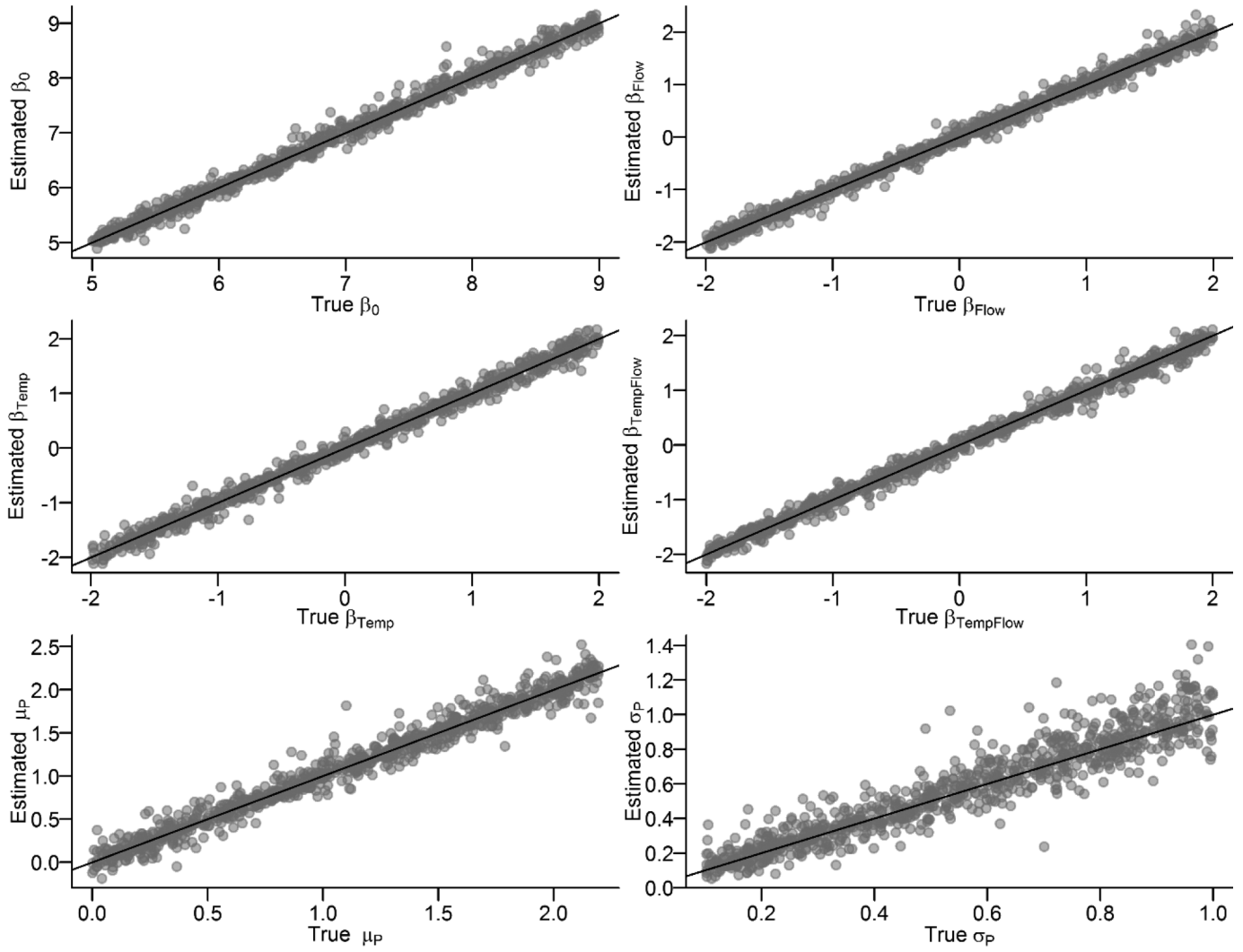
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Fig. A2. Estimated relationships between detection probability and fish length (left column) and flow during sampling (right column) for WB (*a*, *b*), OL (*c*, *d*), OS (*e*, *f*), and IS (*g*, *h*). Blue lines in panels *a* and *e* indicate detection probabilities when two passes were made during sampling. Each line represents a draw from the posterior parameter distributions, so they represent uncertainty when taken together. The black lines show the medians of the posterior distributions (dashed = two passes, solid = one pass). [Colour online.]
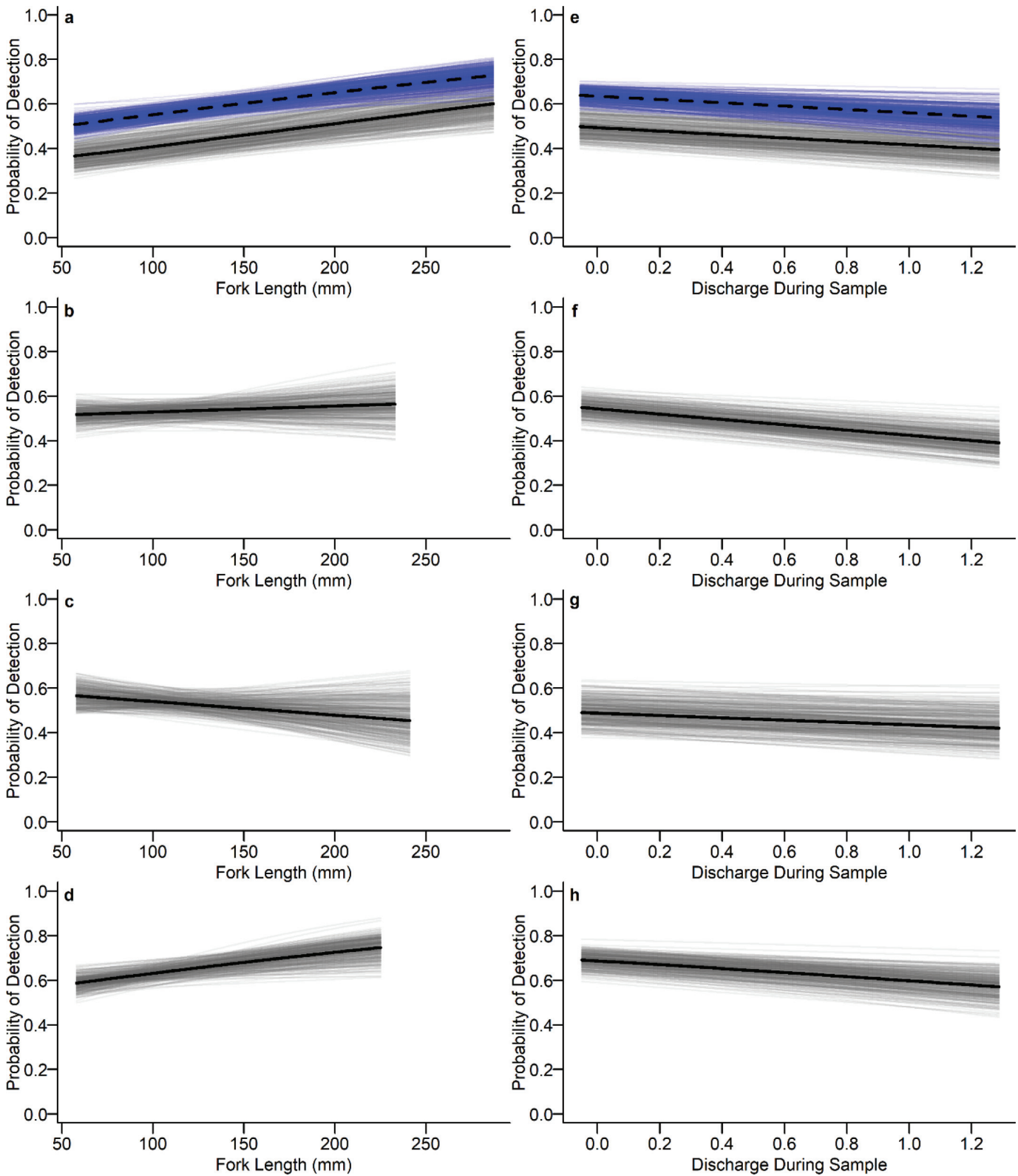
Fig. A3. Seasonal patterns in predicted daily survival (2002–2015) for average-sized juvenile (left column) and adult (right column) brook trout in WB (*a*, *b*), OL (*c*, *d*), OS (*e*, *f*), and IS (*g*, *h*). Gray points represent estimates from each year, and lines represent the median predicted survival for that day of the year across the study period. Note, in panel *f* the *y* axis range does not encompass the full distribution of points; this was done to better display variation among panels.
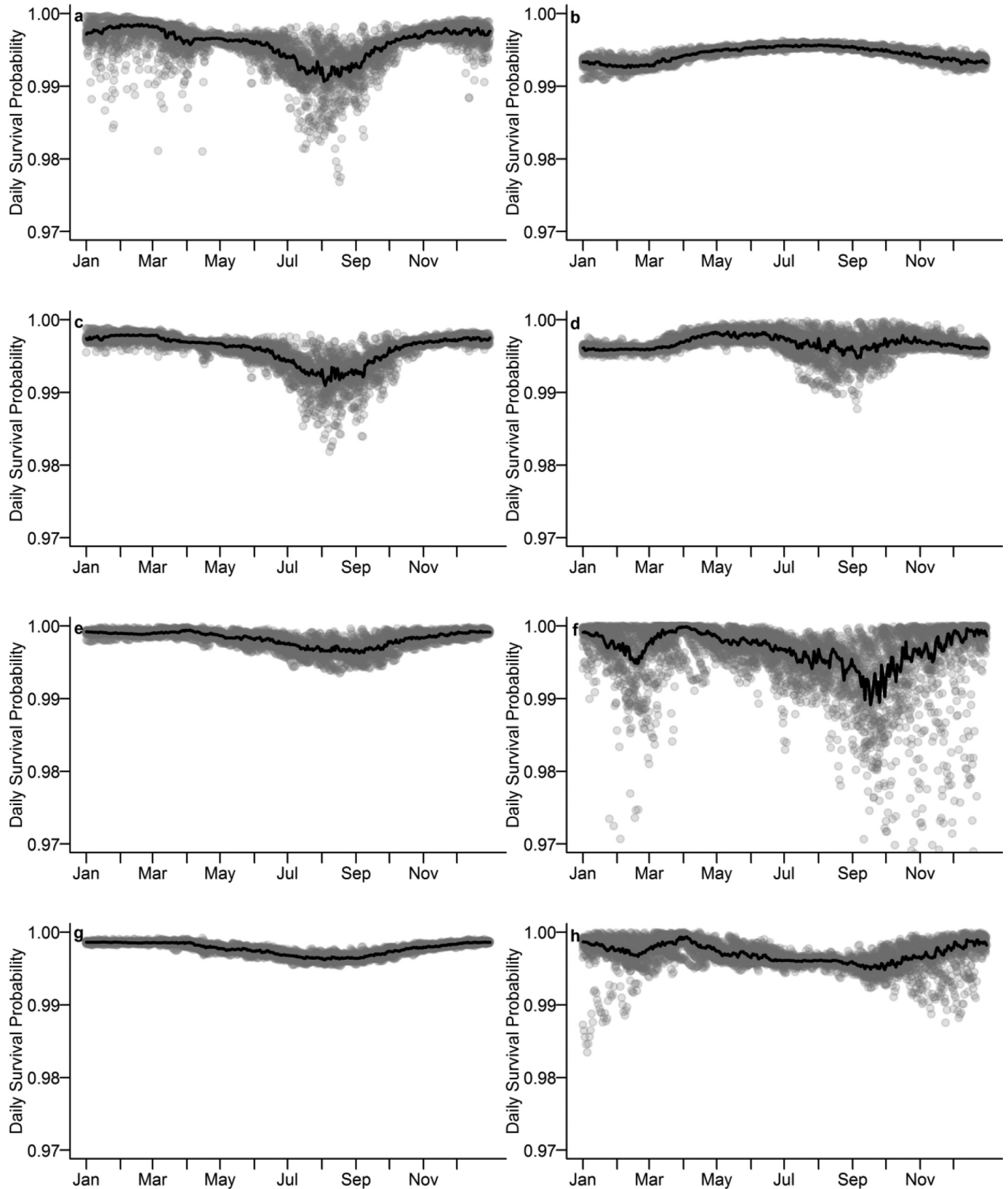
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Fig. A4. Estimated effect of brook trout length on 90-day survival probability under average environmental conditions. Each line represents a draw from the posterior parameter distributions, so they represent uncertainty when taken together. The black lines show the median values from the posterior distributions. [Colour online.]