

Spatial variability in adult brook trout (*Salvelinus fontinalis*) survival within two intensively surveyed headwater stream networks

Yoichiro Kanno, Benjamin H. Letcher, Jason C. Vokoun, and Elise F. Zipkin

Abstract: Headwater stream networks are considered heterogeneous riverscapes, but it is challenging to characterize spatial variability in demographic rates. We estimated site-scale (50 m) survival of adult (>age 1+) brook trout (*Salvelinus fontinalis*) within two intensively surveyed headwater stream networks by applying an open-population N -mixture approach to count data collected over two consecutive summers. The estimated annual apparent survival rate was 0.37 (95% CI: 0.28–0.46) in one network and 0.31 (95% CI: 0.15–0.45) in the other network. In both networks, trout survival was higher in stream sites characterized by more abundant pool habitats. Trout survival was negatively associated with mean depth in one network and positively associated with stream gradient in the other. Stream temperature was not related to trout survival in either network, possibly because the majority of sites were thermally suitable. A similar analytical approach can be useful for inferring survival rates when count data are available over space and time but individual tagging is not feasible.

Résumé : Si les réseaux hydrographiques de tête de bassin sont considérés comme étant des paysages fluviaux hétérogènes, la caractérisation de la variabilité spatiale des taux démographiques constitue un défi. Nous avons estimé le taux de survie à l'échelle du site (50 m) des ombles de fontaine (*Salvelinus fontinalis*) adultes (âge > 1+ an) dans deux réseaux hydrographiques de tête de bassin intensément étudiés en appliquant une approche de mélange de N de populations ouvertes à des données de comptage recueillies sur deux étés consécutifs. Des taux de survie annuelle apparents de 0,37 (IC à 95 % : 0,28–0,46) et 0,31 (IC à 95 % : 0,15–0,45) ont respectivement été estimés pour les deux réseaux. Dans ces deux réseaux, la survie des ombles était plus élevée dans les sites caractérisés par des habitats de fosses plus abondants. La survie des ombles était négativement associée à la profondeur moyenne dans un réseau et positivement associée au gradient des cours d'eau dans l'autre. La température du cours d'eau n'était par reliée à la survie des ombles dans l'un ou l'autre des réseaux, possiblement en raison du fait que la majorité des sites étaient convenables sur le plan thermique. Une telle approche analytique peut être utile pour estimer les taux de survie quand des données de comptage dans le temps et l'espace sont disponibles, mais que le marquage individuel n'est pas envisageable. [Traduit par la Rédaction]

Introduction

Quantifying species–habitat relationships is critical in effective fisheries management and conservation. Many previous studies have examined associations of stream fishes with fluvial habitat characteristics. Lotic habitat heterogeneity has been linked to occurrence (Labbe and Fausch 2000; Rich et al. 2003), abundance (Deschênes and Rodríguez 2007; Reeves et al. 2011; McMillan et al. 2013), and spatial population structure (Skalski et al. 2008; Kanno et al. 2011a) of stream fishes. However, very little is known about environmental drivers of spatial variability in population vital rates that might exist within complex stream networks. In particular, accurate inferences on survival are necessary to understand population dynamics and the effects of environmental change and to inform management actions such as local stream habitat restoration (Letcher et al. 2007; Armstrong and Nislow 2012; Bowerman and Budy 2012). Headwater stream networks are typically considered heterogeneous riverscapes in which demographic rates differ over space and individuals move to exploit spatial heterogeneity in habitats (Schlosser 1995; Fausch et al.

2002; Kanno et al. 2014). Extinction–colonization dynamics of stream fish populations and assemblages have gained much attention in recent years (Koizumi and Maekawa 2004; Falke et al. 2012), but conducting empirical studies demonstrating riverscape heterogeneity in vital rates has remained challenging.

Two major factors are responsible for difficulties in inferring spatial variability in demographic rates within local stream networks. First, intensive inventories of fish populations and habitats encompassing a majority of a local watershed area are rarely conducted. Accordingly, a spatially continuous data set of local stream networks remains an exception in stream fish research (Fausch et al. 2002; McMillan et al. 2013). Second, inference on demographic rates is often labor-intensive and expensive, requiring identification of unique individuals. Mark–recapture data are most commonly used to infer survival (e.g., Cormack–Jolly–Seber model) and recruitment (e.g., Jolly–Seber model). In stream fish applications, study areas are typically confined to stream sections that are <1–2 km long (e.g., Letcher et al. 2007; Vøllestad et al. 2012), making it challenging to infer vital rates at broader stream network scales.

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Y. Kanno. School of Agricultural, Forest, and Environmental Sciences, Clemson University, 132 Lehotsky Hall, Clemson, SC 29631, USA.

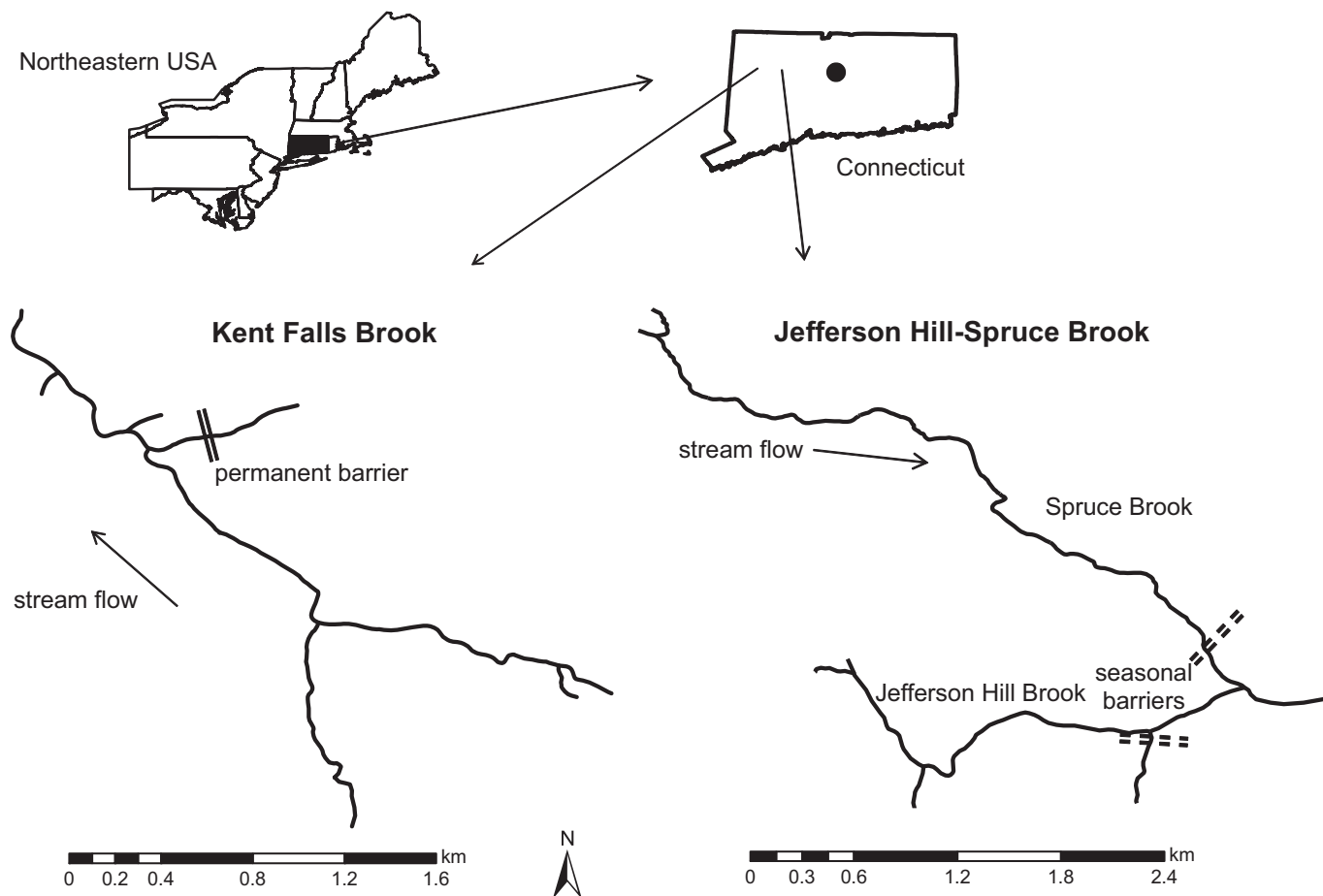
B.H. Letcher. Silvio O. Conte Anadromous Fish Research Center, US Geological Survey, P.O. Box 796, One Migratory Way, Turners Falls, MA 01376, USA.

J.C. Vokoun. Department of Natural Resources and the Environment, University of Connecticut, 1376 Storrs Road, Storrs, CT 06269-4087, USA.

E.F. Zipkin. Department of Zoology, Michigan State University, East Lansing, MI 48824, USA.

Corresponding author: Yoichiro Kanno (e-mail: ykanno@clemson.edu).

Fig. 1. Locations of Jefferson Hill–Spruce Brook (JHSB) and Kent Falls Brook (KFB) in the state of Connecticut, northeastern USA. KFB is located in the Housatonic River basin and JHSB is in the Naugatuck River Basin. Brook trout were sampled in a spatially continuous manner throughout the entire stream networks. The filled circle indicates the location of the city of Hartford in Connecticut.



Recently, Dail and Madsen (2011) proposed a statistical approach that infers demographic rates based on count data replicated over space and time. This approach is based on an N -mixture model (Royle 2004) to estimate animal abundance in a closed population when the detection probability of individuals is not known. Dail and Madsen (2011) extended this model to open populations to estimate demographic rates as well as animal abundance when a number of sites are surveyed repeatedly over time. In brief, the approach explicitly models apparent survival and recruitment rates as the mechanisms by which population size changes. The Dail and Madsen approach has been applied in wildlife studies (e.g., Delany et al. 2013; Hocking et al. 2013) but, to our knowledge, has yet to be applied in a fisheries context. Count data can be collected over a much broader spatial extent than mark–recapture designs allow (e.g., Deschênes and Rodríguez 2007; Ebersole et al. 2009), which renders the Dail–Madsen model particularly useful for an examination of vital rates over stream networks.

In this paper, we estimated spatial variability in survival rates of adult (>age 1+) brook trout (*Salvelinus fontinalis*) within two headwater stream networks and examined associations with site-scale stream habitat characteristics. Our analysis was based on spatially continuous electrofishing count data collected over two consecutive summers throughout the two stream networks (7.7 and 4.4 km). We had previously studied brook trout habitat use and distribution in the same study areas by examining associations between count data (i.e., abundance) and habitat characteristics (Kanno et al. 2012). By inferring annual survival rates, this study

provides additional insights into population ecology and habitat influence in brook trout.

Materials and methods

Study area

This study was conducted in Jefferson Hill–Spruce Brook (JHSB) and Kent Falls Brook (KFB), located in northwestern Connecticut, USA (Fig. 1). Both watersheds contained self-reproducing brook trout populations in stream networks predominantly characterized by cobble (64–256 mm) and pebble (16–63 mm). Notably, the stream networks extended from the downstream end of brook trout distributions to the upstream end, and the entire networks were surveyed in a spatially continuous manner for brook trout and habitat (see below). Brook trout populations are mostly confined to small headwater streams (<15 km²) in Connecticut (Kanno et al. 2010), making it possible to survey and inventory the entire stream networks.

The JHSB watershed (drainage area: 14.56 km²), located in the Naugatuck River basin, spanned approximately 7.7 km of stream channel (Fig. 1). Blacknose dace (*Rhinichthys atratulus*), longnose dace (*Rhinichthys cataractae*), and white sucker (*Catostomus commersonii*) were common in JHSB. Brook trout had been routinely stocked by the state fisheries agency just outside the lowermost boundary of the JHSB study area. Few stocked brook trout were found in this study area (24 individuals in 2008 and five individuals in 2009), and they were reliably identified from a combination of external

and genetic characteristics (Kanno et al. 2011b). Our count data included only wild brook trout.

The KFB watershed had a drainage area of 14.06 km² in the Housatonic River basin and included approximately 4.4 km of stream network (Fig. 1). Naturalized non-native brown trout (*Salmo trutta*) were observed only in the most downstream portion of the study area, and blacknose dace were common throughout KFB. A permanent barrier (a series of natural waterfalls >5 m high) existed in a tributary to KFB (Fig. 1). No brook trout were found above this barrier.

Data collection

Summer brook trout count data were collected by electrofishing over two consecutive years. Electrofishing was conducted in the two stream networks in 2008 (28 July – 22 August) and 2009 (14 July – 12 August). Brook trout were surveyed in a spatially continuous manner throughout each network by a crew consisting of three to four people (Fig. 1). Prior to data collection, streams were travelled by foot and riparian trees were permanently marked at an interval of roughly 50 m (each 50 m section is called a “site” hereafter). JHSB contained 152 fish-bearing sites and KFB had 81 fish-bearing sites. A few sections were slightly shorter or longer than 50 m so that the section boundaries corresponded with mesohabitat units (e.g., pools). Single-pass backpack electrofishing surveys (a pulsed DC waveform, 250–350 V; Smith-Root model LR-24, Vancouver, Washington, USA) were conducted at each site without block nets. Trout counts were recorded at each site and each fish was measured for total length (± 1 mm) and mass (± 0.25 –1.00 g depending on fish size). Additionally, three-pass depletion electrofishing was conducted in 22 sites (14 in JHSB and 8 in KFB) in 2009 to estimate detection probabilities (Zippin 1958). Three-pass depletion electrofishing was limited to a subset of sites owing to logistical constraints.

Stream habitat data were also collected in a spatially continuous manner. Habitat covariates included maximum depth, mean depth, pool ratio, stream gradient, and stream temperature for each 50 m site. These habitat characteristics have been known to affect behavior, abundance, and survival of stream salmonids in lotic systems (Isaak and Hubert 2000; Sotiropoulos et al. 2006; Xu et al. 2010; Reeves et al. 2011).

Maximum depth (cm), mean depth (cm), pool ratio, and stream gradient (%) were measured in the field for each 50 m site during baseflow conditions in fall of 2009 (24 August – 10 November). Data collection was avoided immediately after precipitation events, and US Geological Survey streamgages in nearby watersheds were monitored so that data could be collected at comparable stream discharge levels to the extent possible. Our objective was to characterize spatial variation among sites rather than temporal variation at different discharge levels. Maximum depth was the single deepest measurement identified by wading through each site with a meter stick. Mean depth was calculated based on measurements made at three transects per site (12.5, 25.0, and 37.5 m longitudinally); depth was measured at three points on each transect at approximately 1/4, 1/2, and 3/4 of the distance across the wetted channel width. Pool habitat was identified visually and included various types such as straight scour, lateral scour, plunge, and step pool. Non-pool habitat primarily consisted of riffles but also included rapids and cascades. The total longitudinal length of pool habitat was measured in each site and was divided by the length of non-pool habitat to calculate a pool ratio. Stream gradient was calculated at each site as elevation differences divided by waterway distances. Upstream and downstream boundaries of each site were identified with a Juno ST Handheld GPS receiver (2–5 m accuracy; Trimble Inc., Sunnyvale, California, USA) in early spring of 2009. Elevation values were assigned to the site boundaries from the 3 m (10 ft) Digital Elevation Model GIS layer based on Light Detection and Ranging (LiDaR) remote-sensed data (available from the Center for Land Use Education and Re-

search, University of Connecticut). This approach likely does not lead to high precision in quantifying stream gradient, but the estimated values matched well with visual classifications of high-, medium-, and low-gradient sites in the field (Y.K., unpublished data). We consider that the loss of high precision does not necessarily preclude the use of measured values when conducting a watershed-scale survey of fish–habitat relationships (Fausch et al. 2002).

Stream temperature was the only habitat variable that was measured at a coarser scale than 50 m. Data were recorded between July 2008 and December 2009 at every third site (i.e., 150 m) in most cases, except at tributary confluences where more loggers were deployed. We used stream temperature data from the last 2 weeks of July 2008 (summer temperature hereafter) for statistical analysis because this period represented the warmest 2 weeks during the study period and because spatial variation in stream temperature among stream sites becomes most pronounced during summer in our study region (Kanno et al. 2013; Beauchene et al. 2014). Stream temperature was recorded every hour by HOBO temperature data loggers (Model U22-001, Onset Computer Inc., Bourne, Massachusetts, USA).

Statistical analysis

Variability in survival rates of adult (>age 1+) brook trout among stream sites was inferred using the open *N*-mixture model approach of Dail and Madsen (2011). Adult trout were distinguished from young-of-the-year (YOY) individuals (age 0+) by inspecting length–frequency histograms visually at each stream in each year (Fig. 2). Adult fish were defined as those measuring >90 mm (total length, TL) in 2008 and >100 mm (TL) in 2009 in JHSB. Adult fish were those over >100 mm (TL) in both years in KFB.

Classic, closed-population *N*-mixture models use spatially replicated count data to estimate population abundance through the detection probability of individuals using repeated sampling in a time frame during which the population is assumed to be closed (e.g., no births, deaths, or dispersal; Royle 2004). The Dail and Madsen (2011) extension relaxes the closure assumption by assuming that populations change over time according to a survival process and a “gains” process (e.g., recruitment and immigration) and thus provides inferences on population dynamics parameters as well as annual abundance estimates. The Dail–Madsen approach (Dail and Madsen 2011) also provides a flexible platform to which additional complexities, such as age or size structure, can be readily incorporated (Zipkin et al. 2014).

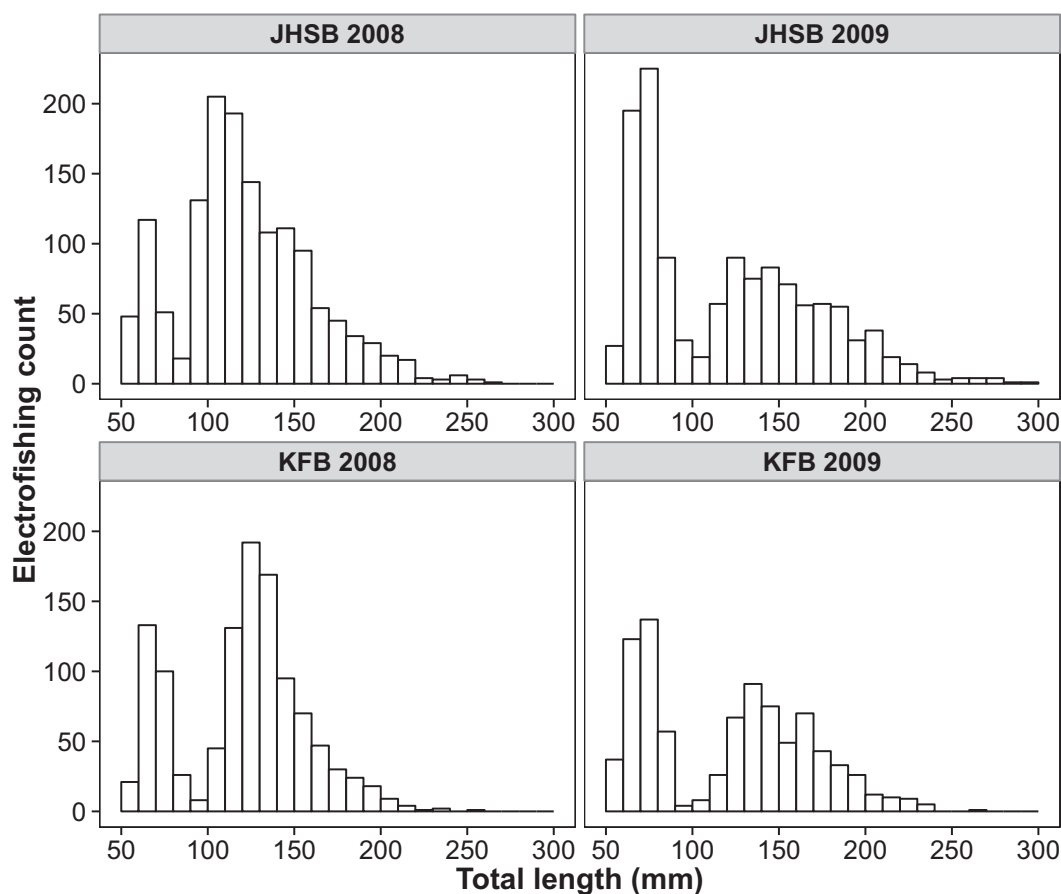
The Dail–Madsen model requires count data at spatially distinct sites $\{i = 1, \dots, R\}$ during sampling occasions $\{t = 1, \dots, T\}$. We applied the Dail–Madsen model separately to JHSB ($R = 152$ sites) and KFB ($R = 81$ sites), where both streams have $T = 2$ years of count data. Adult fish abundance at site i in the first year, denoted $N_{i,1}$, was assumed to follow a discrete count distribution. We used negative binomial distributions to describe the spatial variation in fish counts among sites because sites were contiguous and fish counts were characterized by spatial clustering (Kanno et al. 2012), suggesting that our data were over-dispersed. In the subsequent year of sampling ($t = 2$), we assumed that abundance of adults followed a Markovian process in which fish counts in site i , denoted $N_{i,2}$, were the sum of two random variables:

$$(1) \quad N_{i,2} = S_i + G_i$$

where S_i denotes the number of individuals that survived and remained at site i from the first year to the second, and G_i denotes the number of individuals gained (either through recruitment or immigration, which cannot be distinguished).

The number of individuals that survived between years 1 and 2 at site i (S_i) was assumed to follow a binomial process, conditional on the number of adults present in the first year of sampling:

Fig. 2. Length–frequency histograms of brook trout collected in summers of 2008 and 2009 in Jefferson Hill–Spruce Brook (JHSB) and Kent Falls Brook (KFB).



$$(2) \quad S_i \sim \text{Binomial}(N_{i,1}, w_i)$$

where w_i is the apparent survival probability for all individuals at site i . Hereafter, we use the term “survival”, but note that the Dail–Madsen model cannot distinguish between mortality and permanent emigration. Survival was modeled as a function of stream habitat characteristics using the logit link:

$$(3) \quad \text{logit}(w_i) = \alpha + \beta X_i$$

where α denotes an intercept, X_i is a vector of the site-scale habitat covariates (i.e., maximum depth, mean depth, pool ratio, stream gradient, and stream temperature), and β denotes the effects of each covariate on survival (i.e., the slopes). Habitat covariates were standardized to have a mean of zero and standard deviation of one by subtracting the mean and dividing by the standard deviation prior to statistical analysis (Gelman and Hill 2007). Pool ratio and mean depth were log-transformed prior to standardization to improve normality. Correlation among standardized habitat covariates was checked; when two covariates were highly correlated with one another (Pearson’s correlation coefficient: $|r| > 0.5$), one of the two covariates was dropped from the analysis. Thus, the set of habitat covariates used in the Dail–Madsen model differed between JHSB and KFB (see the Results section).

Recruitment, or the number of new adults gained to sites in the second year of sampling (G_i), was similarly modeled according to a Markovian process. However, in this case we assumed that the “recruitment rate” (γ), or the per capita number of new adult individuals in the population, was dependent not only on abun-

dance in the previous time step but also on abundance of brook trout in the adjacent two sites upstream and downstream in the first year, such that:

$$(4) \quad G_i \sim \text{Poisson}\{\gamma(N_{i-2,1} + N_{i-1,1} + N_{i,1} + N_{i+1,1} + N_{i+2,1})\}$$

Stream sites at or near tributary confluences included two sites upstream and downstream of both branches to reflect the higher connectivity of these sites. Although brook trout in headwater streams are typically sedentary, movement cannot be completely ignored (Hudy et al. 2010; Kanno et al. 2011b). Individual tagging showed that nearly half of individuals (>150 mm in TL) were recaptured in the same 50 m sites within a field season (summer to fall) in our stream networks, while fewer individuals moved longer distances. A maximum movement distance of 1950 m was recorded (Kanno et al. 2011a). In the same study, genetic data provided evidence of limited movement overall and fine-scale population structure. An intensive mark–recapture study in a different stream found that over 60% of tagged individuals were recaptured within ± 20 m, even when sampling occurred four times a year over multiple years; the maximum movement distance recorded was 820 m (Kanno et al. 2014). These results agree with other stream fish movement studies in that many individuals are sedentary but few individuals engage in long-range dispersal (Gowan et al. 1994; Skalski and Gilliam 2000). Thus, extending two sites both upstream and downstream (five sites or 250 m) allowed us to account for the majority of local-scale movement.

Typically, individual detection probabilities are estimated with the Dail–Madsen model using replicate surveys within each year

Table 1. Habitat characteristics within two headwater stream networks (152 sites in Jefferson Hill–Spruce Brook and 81 sites in Kent Falls Brook).

Variable	Jefferson Hill–Spruce Brook		Kent Falls Brook	
	Median	5th to 95th percentiles	Median	5th to 95th percentiles
Maximum depth (cm)	52.0	28.9–111.1	56.0	28.0–126.0
Mean depth (cm)	16.8	7.7–38.2	19.3	9.9–33.7
Pool ratio	0.22	0.00–1.59	0.21	0.01–1.14
Gradient (%)	3.0	0.6–9.1	3.3	1.1–8.9
Mean temperature (°C)				
2008 summer (late July)	18.7	17.8–19.2	19.0	18.0–21.0
2009 summer (late July)	17.2	16.4–17.5	18.3	17.2–20.2

Note: Maximum depth, mean depth, and pool ratio were measured under baseflow conditions in fall of 2009.

during a time frame when the population is closed. Then the number of observed individuals (i.e., data, denoted $n_{i,t,k}$) at each site i during the k th replicate survey event in year t can be modeled with a binomial distribution conditional on the number of individuals present:

$$(5) \quad n_{i,t,k} \sim \text{Binomial}(N_{i,t}, Q)$$

where Q is the detection probability of individuals. It is theoretically possible to use the Dail–Madsen model in cases when only one replicate survey is available ($k = 1$) during a closed season, such as our study. However, data simulations suggest that inferences of detection probability are less precise when $k = 1$ and tend to be biased with only 2 years of data (Zipkin et al. 2014). Therefore, we used an independently estimated detection probability for single-pass electrofishing based on a three-pass depletion method (Zippin 1958) from 22 sites (14 in JHSB and 8 in KFB) that were sampled in 2009. The detection probability in our Dail–Madsen models was then fixed using this estimated detection probability. A drawback of this approach is that the fixed detection probability could affect inferences of other parameters in the models if it were not completely accurate. Thus, we used the estimated mean and its $\pm 20\%$ values to assess the sensitivity of parameter estimates to different fixed values of detection probability.

We analyzed our model with a Bayesian approach using Markov chain Monte Carlo (MCMC) methods in JAGS (Plummer 2011) called from R (R Development Core Team 2012) with the rjags package (see the online Supplementary material for R and JAGS code and an example data set¹). Jeffery's priors (mean = 0 and SD = 1.643) were used for the intercept and slope terms for the survival parameter covariates and uninformative priors were similarly used for all other parameters, except for detection probability as previously noted. Posterior distributions of model parameters were estimated by taking the 50th sample from 50 000 iterations of three chains after discarding 30 000 burn-in iterations. Model convergence was checked by visually examining plots of the MCMC chains for good mixture and using the Brooks and Gelman diagnostic (Brooks and Gelman 1998). This statistic compares variance within and between chains, and models are considered to have converged when the value is less than 1.1 for all model parameters (Gelman and Hill 2007). Model fit was assessed visually by plotting predicted versus observed adult counts among stream sites in the second year; the predicted count at a site was calculated as the mean value of latent local abundance ($N_{i,2}$) multiplied by fixed detection probability. We evaluated the importance of covariates by their estimated coefficient size; in particular, covariates whose 95% credible interval (95% CI) did not overlap with a value of 0 were considered to significantly influence survival rates. Model selection of complex Bayesian models is an area of active research (Plummer 2008), especially for a model in

which abundance is a sum of random variables. Therefore, model selection based on information-theoretic approaches (e.g., deviance information criteria) was not performed in this study. Instead, a set of all uncorrelated covariates was included in the survival model (Gelman and Hill 2007).

Results

Field sampling

Both stream networks were typical of small headwater streams characterized by high to medium stream gradient (Table 1). Mean stream wetted width was 4.8 m in KFB and 4.3 m in JHSB. The two networks were similar in measured stream habitat characteristics (Table 1). Summer stream temperature was lower in 2009 than in 2008, particularly in JHSB (median value of 18.7 °C in 2008 versus 17.2 °C in 2009) (Table 1).

A total of 1196 adult individuals were collected in JHSB and 836 in KFB in the 2008 electrofishing survey. In 2009, we collected 686 adults in JHSB and 524 adults in KFB. Size distributions of brook trout differed slightly between the two summers (Fig. 2). Adult abundance was lower in 2009 and YOY abundance was higher in 2009 in both streams. The mean adult count per 50 m site was 8 (range: 0–39) in 2008 and 5 (range: 0–24) in 2009 in JHSB, and 10 (range: 0–28) in 2008 and 6 (range: 0–23) in 2009 in KFB. The three-pass depletion method estimated the detection probability of individuals at 0.64 (SD = 0.22) in single-pass electrofishing.

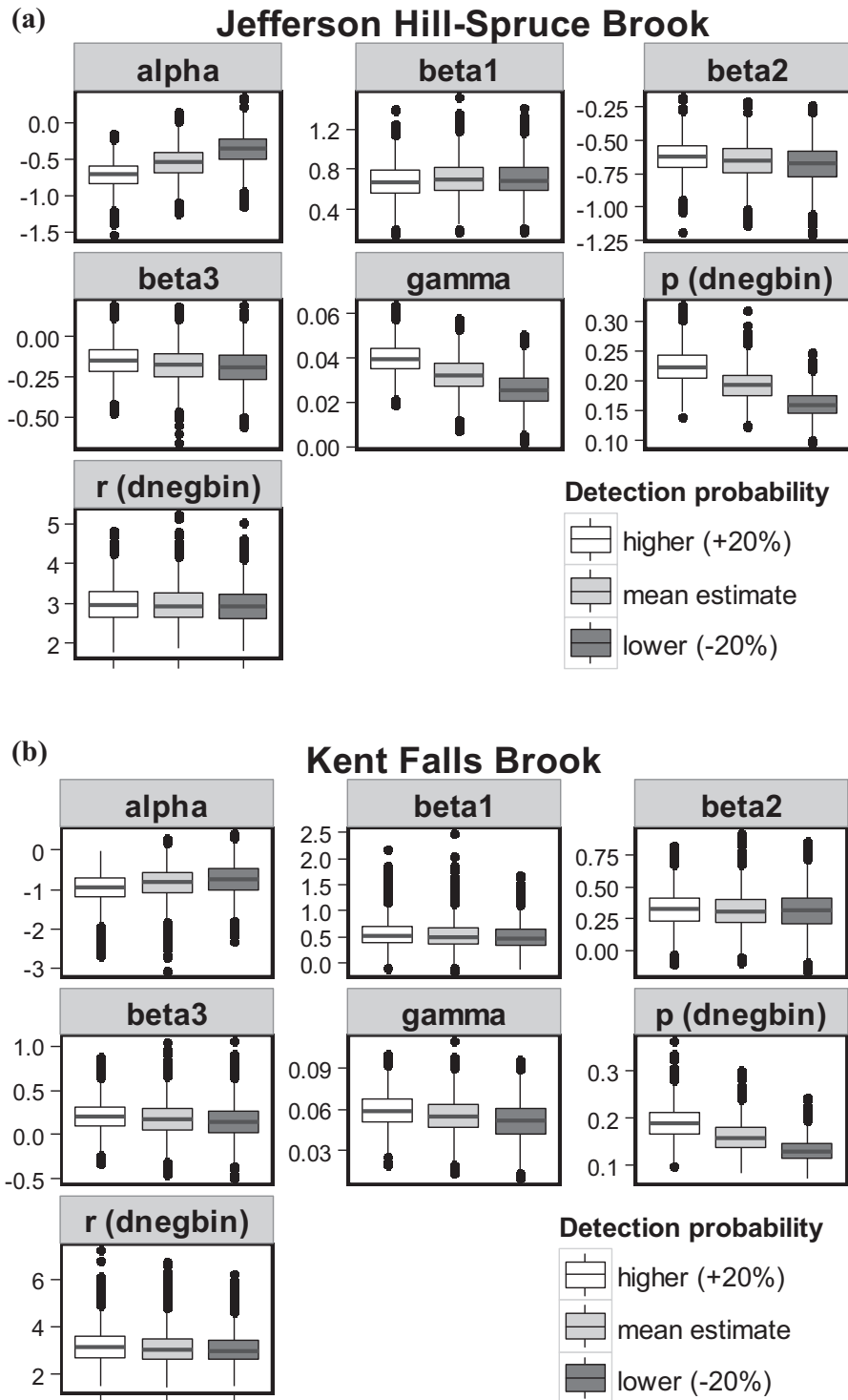
Demographic rates

The convergence of the Dail–Madsen model was confirmed with well-mixed MCMC chains and values of the Gelman statistic ≤ 1.01 for all parameters. Parameter estimates, particularly those related to survival and gains, were nearly identical when detection probability was fixed at different values in the Dail–Madsen model (Fig. 3). In both streams, 95% CIs of survival coefficients and per capita recruitment were similar across different values of detection probability. In JHSB, the intercept (α) of survival probability estimates tended to increase as detection probability (Q) decreased (Fig. 3a). Still, 95% CIs of the survival intercept overlapped considerably between different values of Q ; 95% CIs of annual survival probability at typical sites (i.e., when covariates were at their mean values) were 0.25–0.41 at $Q = 0.77$, 0.28–0.46 at $Q = 0.64$, and 0.31–0.52 at $Q = 0.51$. These results indicate that our inferences were generally insensitive to our assumptions about detection and hereafter we report results based on the mean estimate of detection probability ($Q = 0.64$).

The Dail–Madsen model predicted site-scale brook trout counts in the second year of study (2009) accurately in both streams (Fig. S1¹). Mean annual survival probability (w_i) of adult brook trout among sites was 0.37 (95% CI: 0.28–0.46) in JHSB and 0.31 (95% CI: 0.15–0.45) in KFB. Parameter estimates were less precise (i.e., wider 95% CI) in KFB than in JHSB, likely because of the

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0358>.

Fig. 3. Box plots showing sensitivity of parameter estimates in the Dail–Madsen model to three different values of detection probability in Jefferson Hill–Spruce Brook (a) and Kent Falls Brook (b). Detection probability was 0.77 (20% higher), 0.64 (mean estimate), and 0.51 (20% lower).



smaller sample size in KFB ($R = 81$ sites) compared with JHSB ($R = 152$ sites) (Table 2; Fig. 4).

Pool ratio, stream temperature, and mean depth were used as a set of covariates for survival rate in JHSB. Maximum depth was not included because of its correlation with mean depth ($r = 0.56$), and stream gradient was removed because it was correlated with stream temperature ($r = -0.61$). In JHSB, pool ratio had a significant

positive effect on survival rate (mean = 0.70 (95% CI: 0.40, 1.06)) (Table 2; Fig. 4), indicating that brook trout survival probabilities were higher in sites with more abundant pools. Mean depth had a significant negative effect on survival probabilities (mean = -0.65 (95% CI: $-0.93, -0.40$)) (Table 2; Fig. 4). Brook trout survival was generally higher in Jefferson Hill Brook than in Spruce Brook, particularly in upstream sites and tributaries of Jefferson Hill

Table 2. Estimated values of parameters of the Dail–Madsen model (Dail and Madsen 2011) for each stream network when detection probability was fixed at 0.64.

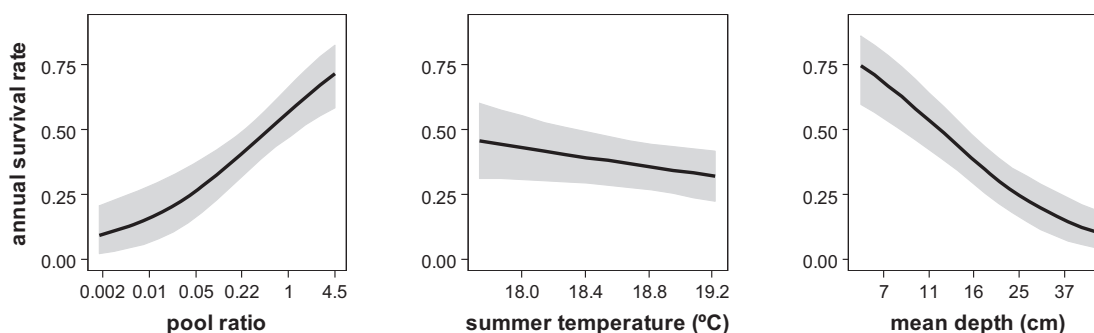
	Jefferson Hill–Spruce Brook	Kent Falls Brook
Survival		
Intercept (alpha)	−0.53 (−0.95, −0.14)	−0.83 (−1.70, −0.20)
Pool ratio (beta1)	0.70 (0.40, 1.06)	0.50 (0.13, 1.12)
Summer temperature (beta2)	−0.18 (−0.39, 0.04)	0.18 (−0.16, 0.55)
Mean depth (beta3*)	−0.65 (−0.93, −0.40)	NA
Gradient (beta3*)	NA	0.31 (0.05, 0.61)
Recruitment		
Recruitment rate (gamma)	0.03 (0.02, 0.05)	0.06 (0.03, 0.09)
Initial abundance		
Negative binomial parameter (<i>p</i>)	0.19 (0.15, 0.25)	0.16 (0.11, 0.23)
Negative binomial parameter (<i>r</i>)	2.93 (2.18, 3.93)	3.02 (2.05, 4.63)

Note: Median values (and 95% credible intervals) are shown, and habitat coefficients whose 95% credible interval does not overlap with zero are shown in bold, excluding the intercept. All covariates for survival were standardized prior to analysis. Descriptions within parentheses (e.g., alpha, gamma) refer to those used in the JAGS code (see the online Supplementary material¹).

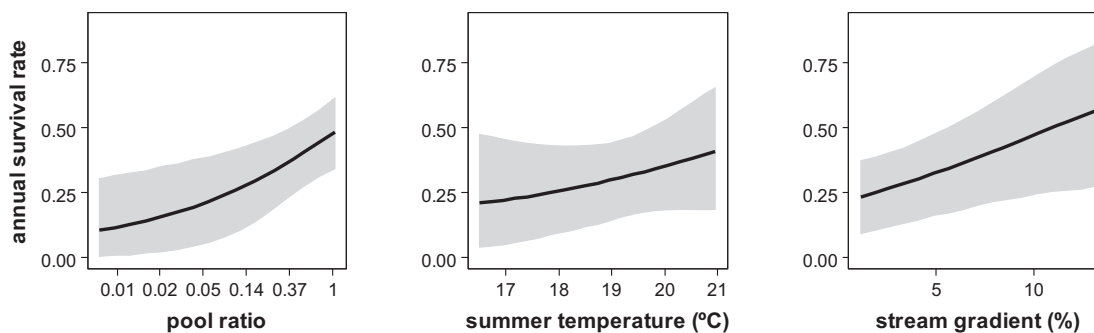
*Different sets of habitat covariates were used for the survival models parameterized for JHSB and KFB. All covariates included in individual models were not correlated (Pearson's correlation coefficient: $|r| \leq 0.5$).

Fig. 4. Effect of habitat covariates on annual survival rate of adult brook trout in Jefferson Hill–Spruce Brook (a) and Kent Falls Brook (b). The mean effect is shown by the black line and the gray shading represents the 95% credible intervals of the coefficients. All other covariates were fixed at their mean values.

(a) Jefferson Hill–Spruce Brook



(b) Kent Falls Brook



Brook (Fig. 5a). Stream temperature did not significantly influence brook trout survival in JHSB (mean = −0.18 (95% CI: −0.39, 0.04)) (Table 2; Fig. 4). The per capita recruitment rate of new adult individuals to sites (γ) was 0.03 (95% CI: 0.02–0.05) in JHSB (Table 2).

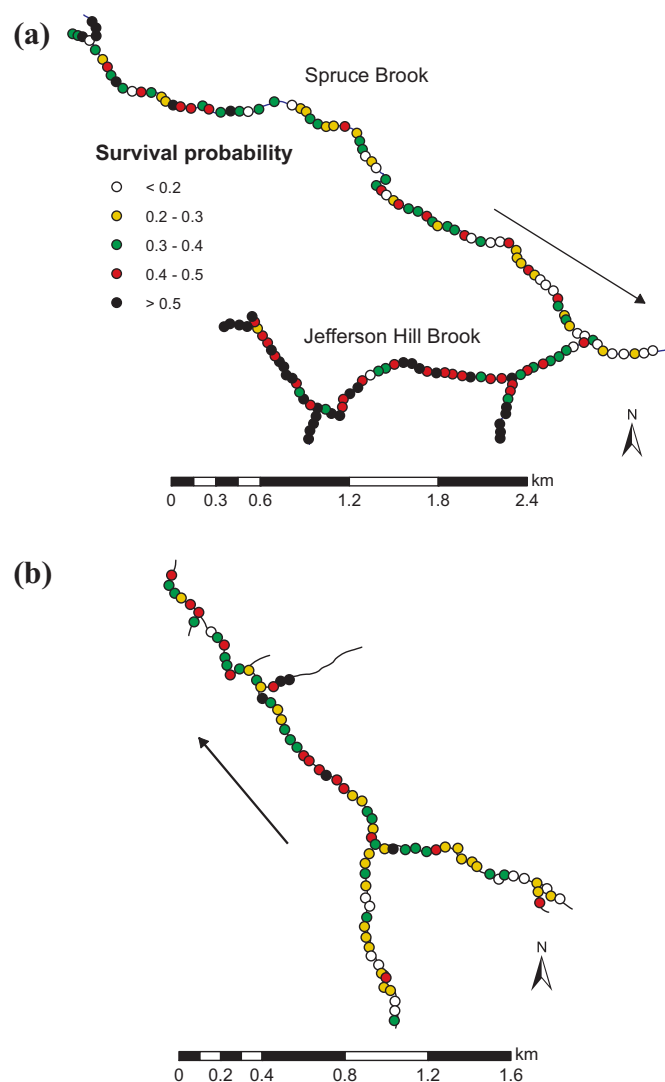
In KFB, maximum depth, mean depth, and pool ratio were positively correlated with each other ($r > 0.58$). Thus, pool ratio, stream gradient, and temperature were used as covariates for estimating survival rate. Pool ratio again had a significant positive effect on brook trout survival in this study site (mean = 0.50 (95% CI: 0.13–1.12)) (Table 2; Fig. 4). Trout survival probability was also positively affected by stream gradient (mean = 0.31 (95% CI:

0.05, 0.61)). As in JHSB, stream temperature did not affect survival rates among sites in KFB (Table 2; Fig. 4). In contrast to JHSB, however, upper sites and tributaries in KFB were not always associated with higher brook trout survival probabilities (Fig. 5b). Mean per capita recruitment rate of new adult individuals (γ) was slightly higher in KFB (0.06) but the 95% CI (0.03–0.09) overlapped with that in JHSB (0.02–0.05) (Table 2).

Discussion

Apparent survival probabilities of adult brook trout were related to site-level habitat characteristics within study stream net-

Fig. 5. Apparent annual survival rate of adult brook trout in each site of Jefferson Hill–Spruce Brook (a) and Kent Falls Brook (b), inferred by the Dail–Madsen model (Dail and Madsen 2011). Arrows indicate stream flow directions.



works. Inferences on demographic rates have traditionally relied on intensive fieldwork involving unique identification of individuals in stream fish studies (e.g., Petty et al. 2005; Letcher et al. 2007). It is challenging to conduct mark–recapture studies at a broad spatial scale such as entire headwater stream networks owing to logistical constraints. In this paper, we inferred spatial variability in survival of adult brook trout within heterogeneous stream networks using repeated count data, eliminating the need to tag individuals. Inference on population dynamics parameters based on “unmarked” data has been largely restricted to persistence and colonization rates of habitat patches in stream fish metapopulations (Koizumi and Maekawa 2004; Falke et al. 2012; Poos and Jackson 2012). Our application of the Dail–Madsen model represents an improvement in quantifying spatial population dynamics of stream fishes.

The annual apparent survival rate was estimated at 0.37 (95% CI: 0.28–0.46) in JHSB and 0.31 (95% CI: 0.15–0.45) in KFB. Apparent survival rate (survival + emigration) depends on the spatial extent of the study area; thus direct comparison of apparent survival estimates is not always easy across different studies. Still, our values fell within the range of survival estimates reported in other

lotic populations of brook trout (Petty et al. 2005; Letcher et al. 2007; Risley and Zydlewski 2010). For example, Petty et al. (2005) reported that apparent survival rate for small adults (mostly age 1+) was approximately 0.50 in 100 m stream sites over seasonal intervals (3–6 months) in West Virginia. Risley and Zydlewski (2010) assumed an annual true survival rate (not apparent survival rate) of 0.50 for age 1+ individuals in an adfluvial brook trout population.

Pool ratio was an important habitat characteristic and sites with a larger proportion of pools had comparatively higher survival rates in both networks. The preference of adult brook trout for pool habitat has been consistently shown based on distributional patterns (Deschênes and Rodríguez 2007; Kanno et al. 2012) and behavioral observations (Nakano et al. 1998; Sotiropoulos et al. 2006). We also found that mean depth was negatively correlated with survival in JHSB, indicating that apparent survival was higher in upstream sites than in downstream sites. Our field sampling was spatially extensive and continuous, including the lowermost boundary of brook trout distribution (characterized by low abundance) within the sub-watersheds and extending to the nearly intermittent stream sites upstream (higher abundance). Petty et al. (2005) similarly reported that apparent survival of adult brook trout decreased with watershed area in some seasons using mark–recapture techniques. Finally, stream gradient was positively related to survival in KFB. Higher survival in steeper sites may have to do with geomorphic features typical of these sites. Small pockets of plunge and step pools were common where stream gradient was high within this watershed. Overall, the inferred influence of reach-scale habitat characteristics such as pool ratio, mean depth, and stream gradient agrees well with known habitat preferences of headwater brook trout (Nakano et al. 1998; Sotiropoulos et al. 2006; Deschênes and Rodríguez 2007; Kanno et al. 2012).

Stream temperature was not related to adult survival in either study stream. Stream temperature has been frequently related to the site occupancy of lotic brook trout populations (Stranko et al. 2008; McKenna and Johnson 2011), and survival rate has been shown to be negatively impacted by higher summer temperature (Xu et al. 2010). The weak influence of stream temperature may be due to the fact that study sites were mostly thermally suitable for brook trout. Hartman and Cox (2008) reported that metabolic rates of brook trout declined sharply above 20 °C in a laboratory setting, and wild brook trout populations suffer when stream temperature exceeds 20 °C for an extended period (Stranko et al. 2008; Robinson et al. 2010). In comparison, summer mean temperature in 2008 was 18.7 °C (5th to 95th percentiles: 17.8–19.2 °C) in JHSB and 19.0 °C (18.0–21.0 °C) in KFB, and stream temperature was lower in 2009 (Table 1). Perhaps it is most appropriate to consider habitat influences in a spatial hierarchy. At a broad spatial scale, brook trout occupancy may be strongly influenced by stream temperature and other landscape features (Hudy et al. 2008; McKenna and Johnson 2011). Given that brook trout are present in a stream, reach-scale variation such as pool availability and mean depth could exert stronger influences on local-scale abundance (Deschênes and Rodríguez 2007; Kanno et al. 2012) and demographic rates (this study).

Inference of population dynamics rates was restricted to >age 1+ individuals in this study. Count data from a single age or size group are used in the Dail–Madsen model (Dail and Madsen 2011). Zipkin et al. (2014) showed that multiple age or size groups could also be considered in the Dail–Madsen framework. Such an approach that accounts for size structure has proved challenging with our brook trout data set (Y.K., unpublished data). However, this remains an active avenue of research. Size-dependent patterns of vital rates have been reported in previous studies in other brook trout populations (Petty et al. 2005; Letcher et al. 2007). In the study streams, ontogenetic habitat shift has been noted based on size-specific abundance patterns among study sites (Kanno

et al. 2012). For example, volume of pool habitat was not as important for YOY fish abundance, and abundance of large adult trout was strongly related to maximum depth as well as pool habitat availability. If these distributional patterns reflect the underlying importance of different mesohabitats to different life stages, population vital rates would be both size- and space-dependent. However, the strong relationship between adult survival and pool habitat in this study suggests that stream habitat management actions that create pool habitat (e.g., addition of large woody debris) could be an effective approach to habitat management if the goal is to increase survival rates of adult brook trout.

The use of unmarked data to estimate demographic rates allows for potential applications in a variety of situations in which spatially and temporally replicated data are available. This approach would be applicable to small-bodied species (e.g., non-game fish species) for which unique identification of individuals is not practically feasible. Other examples would include investigations of spatial variability in demographic rates over a broad area (as opposed to fine-scale spatial variation within stream networks in this study) and temporal variability in population dynamics when a long-term data set is available. The specification of demographic rates in the Dail–Madsen model may also be suitable for integrated population models in which abundance data are combined with mark–recapture data (Brooks et al. 2004; Schaub and Abadi 2011). In general, the Dail–Madsen model is flexible enough to accommodate study-specific situations. In our analysis, adult recruitment to a stream site was modeled as a per capita rate dependent on adult trout abundance in local sites as well as neighboring sites in the previous year. Finally, we used an independently derived detection probability estimate from the depletion method, but estimation of detection probabilities can be effectively incorporated within the Dail–Madsen model if sampling is conducted multiple times within a “closed” period (Royle 2004; Zipkin et al. 2014).

We note some potential limitations of our approach. Our analysis is a model-based inference approach that relies on assumptions about species' life history. We considered brook trout abundance in neighboring sites to be an appropriate index for potential recruitment based on several studies that support restricted movement of brook trout (Hudy et al. 2010; Kanno et al. 2011a, 2011b, 2014), but other researchers should be cautious about making ecological assumptions for lesser-studied species. A sensitivity analysis can shed light on uncertainties in parameter estimates, as we demonstrated with different values of detection probability. Another potential limitation was assuming that detection probability was constant among stream sites. However, we considered our assumption of constant detection probability appropriate for several reasons. First, our use of the Dail–Madsen model is restricted to the inference of demographic parameters, and trout abundance across the stream network is not a parameter of interest. The assumption of constant detection probability would be more problematic if the latter were the interest of this study and if covariates affected both survival and detection probabilities. Second, we considered both spatial and temporal variation in detection probability to be adequately small. All sites were wadeable and were sampled effectively by the same gear. Stream flow affects detection probability of fish (Falke et al. 2010; Anderson et al. 2012), but our electrofishing survey took place during baseflow conditions in August in both study years. We believe that this sampling design allowed an unbiased inference of population dynamics parameters such as survival rates. Third, the senior author (Y.K.) participated in all sampling events and the effect of sampling crews on detection probability was minimized. Finally, the spatial extent of our stream network (7.7 and 4.4 km) precluded replicate surveys within each year, but spatially continuous fish and habitat data sets like ours remain rare in stream fish research (Fausch et al. 2002).

In conclusion, this study used repeated count data to infer fine-scale spatial variability in survival of adult brook trout within heterogeneous stream networks. The use of repeated counts over just two consecutive summers for inference was a promising sign that stream fish ecologists may now be able to quantify spatial variability in vital rates over broad spatial scales. This type of study would have been logistically prohibitive using intensive mark–recapture designs. Understanding population processes across space and the factors affecting spatial heterogeneity will help fisheries ecologists and managers make more robust inferences on the effects of broad-scale anthropogenic disturbances (e.g., climate change, land use change).

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