

Estimating size-specific brook trout abundance in continuously sampled headwater streams using Bayesian mixed models with zero inflation and overdispersion

Yoichiro Kanno^{1*}, Jason C. Vokoun¹, Kent E. Holsinger², Benjamin H. Letcher³

¹Department of Natural Resources and the Environment, University of Connecticut, 1376 Storrs Road, Storrs, CT 06269-4087, USA

²Department of Ecology and Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, Storrs, CT 06269-3043, USA

³Silvio O. Conte Anadromous Fish Research Center, United States Geological Survey, PO Box 796, One Migratory Way, Turners Falls, MA 01376, USA

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Abstract – We examined habitat factors related to reach-scale brook trout *Salvelinus fontinalis* counts of four size classes in two headwater stream networks within two contrasting summers in Connecticut, USA. Two study stream networks (7.7 and 4.4 km) were surveyed in a spatially continuous manner in their entirety, and a set of Bayesian generalised linear mixed models was compared. Trout abundance was best described by a zero-inflated overdispersed Poisson model. The effect of habitat covariates was not always consistent among size classes and years. There were nonlinear relationships between trout counts and stream temperature in both years. Colder reaches harboured higher trout counts in the warmer summer of 2008, but this pattern was not observed in the cooler and very wet summer of 2009. Amount of pool habitat was nearly consistently important across size classes and years, and counts of the largest size class were correlated positively with maximum depth and negatively with stream gradient. Spatial mapping of trout distributions showed that reaches with high trout counts may differ among size classes, particularly between the smallest and largest size classes, suggesting that movement may allow the largest trout to exploit spatially patchy habitats in these small headwaters.

Key words: fish conservation; generalised linear mixed model; global change; Salmonidae; stream habitat

Introduction

Some habitat features affect animals of different life stages uniformly, but others influence them differently. For stream salmonids, stream temperature may have a major impact on distribution and abundance across life stages, but they also exhibit ontogenetic shifts in stream microhabitat characteristics. Adult brook trout *Salvelinus fontinalis* are typically associated with greater depth and more cover, but juveniles may use shallower habitats in tributaries (Johnson & Dropkin 1996; Petty et al. 2005; Deschênes & Rodríguez 2007).

Thus, brook trout may need to move to exploit spatially patchy habitats and resources (Schlosser 1995; Fausch et al. 2002), and the spatial arrangement of habitats may influence population connectivity (Benda et al. 2004; Boughton et al. 2009; Young 2011).

Identifying size-specific patterns of habitat associations and spatial configurations of habitats within a stream channel network is relevant to the conservation of stream fishes. Such understanding is important for assessing the potential impact of anthropogenic disturbances on population dynamics and persistence (Letcher et al. 2007; Xu et al. 2010a). Quantifying the

Correspondence: Yoichiro Kanno, Department of Natural Resources and the Environment, University of Connecticut, 1376 Storrs Road, Storrs, CT 06269-4087, USA. E-mail: ykanno@tntech.edu

*Present address: Center for the Management, Utilization and Protection of Water Resources & Department of Biology, Tennessee Technological University, Box 5063, 1100 North Dixie Avenue, Cookeville, TN 38505, USA.

effect of stream temperature and flow volume is particularly relevant because they affect stream fishes (Poff et al. 1997; Lyons et al. 2010) and will be affected by climate change (Ficke et al. 2007). Brook trout are presently confined to small, cold headwaters in the central and southern parts of the native range in eastern North America (Hudy et al. 2008), where warmer and drier summers predicted by climate change scenarios (Huntington et al. 2009) could have a negative impact on population persistence.

Fish abundance or count data are frequently used to understand species–habitat relationships. In this article, ‘count(s)’ will be used as an index of ‘abundance’, and the former will be consistently used hereafter. Count data, characterised by positive integer values and zero, are typically modelled using the Poisson distribution. However, ecological data rarely conform to the simple Poisson distribution, and analysis may be improved by incorporating processes such as zero inflation and overdispersion (Gelman & Hill 2007; Zuur et al. 2009; Kéry 2010). Zero-inflated models are a two-part model that simultaneously analyses (i) habitat suitability for presence/absence and (ii) count, given that the habitat is suitable. Zero-inflated models are useful for modelling rare species, which inherently have many 0’s in the data set (Wenger & Freeman 2008), and they are one approach to dealing with overdispersion. However, they do not account for overdispersion among positive count values, and the combination of zero inflation and overdispersion may further improve model fit (Gschlößl & Czado 2008; Wenger & Freeman 2008; Zuur et al. 2009).

The primary objective of this study was to explain the size-specific relationships between reach-scale

(50-m) brook trout counts and stream habitat features using electrofishing data collected in two headwater stream networks within two contrasting summers (typical warm and wet vs. cool and very wet summer) in Connecticut, USA. We fitted and compared Bayesian mixed models with different complexities. In addition, our spatially extensive and continuous sampling of the entire headwater watersheds allowed us to examine the size-specific spatial distributions along stream channel networks. Our secondary objective was then to assess such spatial patterns in an exploratory manner, and we discuss the potential role of trout movement based on this study and genetic studies of brook trout in the same study streams (Kanno et al. 2011a,b).

Materials and methods

Study areas

The study was conducted in Jefferson Hill-Spruce Brook (JHSB) and Kent Falls Brook (KFB) located in north-western Connecticut, USA (Fig. 1). Both study streams contained self-reproducing brook trout populations in a stream channel network predominantly characterised by boulder (>256 mm), cobble (64–256 mm) and pebble (16–63 mm) (Bain & Stevenson 1999). The JHSB watershed (drainage area: 14.56 km²) spanned approximately 7.7 km in stream channel length. Common fish species observed in JHSB included blacknose dace *Rhinichthys atratulus*, longnose dace *Rhinichthys cataractae* and white sucker *Catostomus commersoni*. Few stocked brook trout were found in this study area (24 individuals in

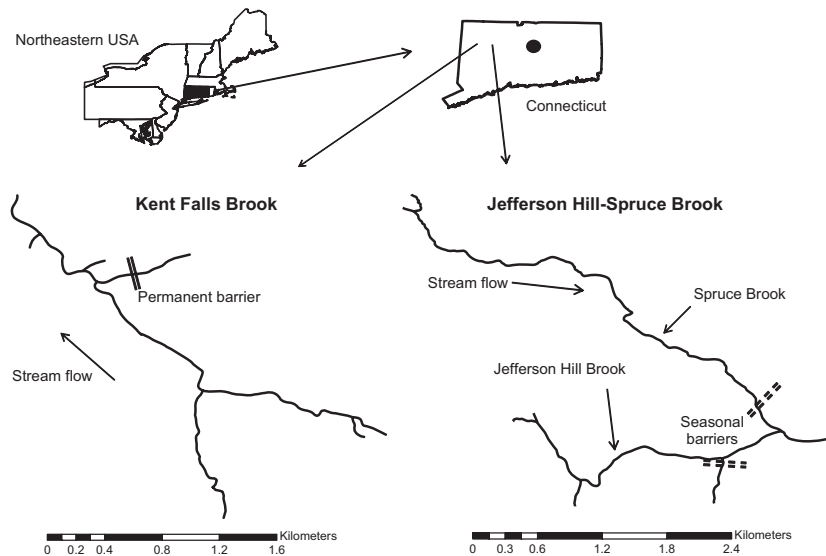


Fig. 1. Locations of Kent Falls Brook and Jefferson Hill-Spruce Brook in the State of Connecticut, north-eastern USA. Brook trout were sampled in a spatially continuous manner throughout the entire stream channel networks shown. A black filled circle indicates the location of Hartford.

2008 and five individuals in 2009), and they were reliably identified in the field from a combination of body size and external characteristics which consistently agreed with genetic assignment methods (Kanno et al. 2011a). Our analysis considered only wild brook trout.

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

Field sampling

Summer brook trout count data were collected over 2 years. The study period covered two contrasting summers in air temperature and precipitation patterns: a typically warm, wet summer (2008) versus a cool and very wet summer (2009). Weather data collected at Hartford, located in mid-central Connecticut (Fig. 1), illustrate summer characteristics experienced across the state. The July mean air temperature in 2008 (24.2 °C) approximated the long-term mean value of 23.3 °C, and precipitation in July (160.24 mm) was higher than the average of 91.44 mm. In 2009, the July mean air temperature was 21.8 °C (1.5 °C cooler than the mean) and precipitation in July (245.33 mm) nearly tripled the monthly mean. Because stream temperature becomes warmest in July in the region (unpublished data) and much of electrofishing data were collected by early August in both years, it was appropriate to use July temperature and precipitation records to characterise summer conditions. In this study, the summer of 2008 was considered typically warm and wet and 2009 was considered a cool and very wet summer.

Identical field protocols were used to collect data on brook trout counts in JHSB and KFB in 2008 (July 28–August 22) and 2009 (July 14–August 12). Brook trout were collected in a spatially continuous manner throughout each stream network (Fig. 1). Prior to collection, the study streams were travelled by foot, and riparian trees were permanently marked at an interval of roughly 50 m (each 50-m zone is called a ‘reach’ hereafter). JHSB contained 152 reaches, and KFB had 86 reaches. Single-pass backpack electrofishing surveys (a pulsed DC waveform, 250–350 V; Smith-Root model LR-24, Vancouver, WA, USA) were conducted without blocknets. Trout counts were recorded by each reach, and each fish was measured for total length (± 1 mm) and weight (± 0.25 –1.00 g depending on fish size).

Habitat data were also collected in a spatially continuous manner. Maximum depth (cm), mean

depth (cm), pool habitat area (m²) and nonpool habitat area (m²) were measured in the field for each 50-m reach during baseflow conditions during the fall of 2009 (August 24–November 10). Our objective was to characterise spatial variation among reaches (i.e., upstream-to-downstream variation), rather than temporal variation at different discharge levels. Thus, data collection was avoided immediately after precipitation events and US Geological Survey stream gauges in nearby watersheds were monitored, so that data could be collected at comparable stream discharge levels to the extent possible. We considered that a single habitat survey would adequately represent trout habitats during the two consecutive years in which electrofishing was conducted, because severe flooding and scouring events were not observed during the study period and habitat characteristics remained similar over time throughout the stream channel networks that were featured by large mean particle sizes (Y. Kanno, personal observation).

Maximum depth was the single deepest measurement identified by wading through each reach with a metre stick. Mean depth was calculated based on measurements taken at three transects per reach (at 12.5, 25.0 and 37.5 m longitudinally); on each transect, depth was measured at three points approximately at 1/4, 1/2 and 3/4 distance across the wetted channel width. Pool habitat was identified visually, and it included various types of pool habitat such as straight scour, lateral scour, plunge and step pools (Bain & Stevenson 1999). Nonpool habitat primarily consisted of riffles, as well as included rapids and cascades. A total longitudinal length of pool habitat was measured in each reach and was multiplied by mean wetted channel width (also measured at three transects per reach) to calculate pool habitat area. The rest was designated as nonpool habitat area (i.e., total habitat area minus pool habitat area).

Stream gradient was calculated for each reach as elevation differences divided by waterway distances. Upstream and downstream boundaries of each reach were identified with a Juno ST Handheld GPS receiver (2- to 5-m accuracy; Trimble Inc., Sunnyvale, CA, USA) in early spring of 2009. Elevation values were assigned to the reach 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 Research, University of Connecticut).

Stream temperature was the only habitat variable that was measured at a coarser scale than the 50-m reach. Data were recorded between July 2008 and December 2009 at an interval of every three reaches (i.e., 150 m); we only used stream temperature data in the last 2 weeks of July (i.e., late July) for analysis and stream temperature for each reach was derived from

the closest temperature logger. There was little longitudinal variation in stream temperature at the scale of 150 m (See Appendix S1 for spatial thermal patterns). Stream temperature was recorded every hour by HOBO temperature data loggers (Model U22-001; Onset Computer Inc., Bourne, MA, USA).

Data assessment and preparation

Our objective was to examine the relationships between reach-scale trout counts and stream habitat features by using mixed models that analysed all size classes in a single analysis in each year. Four size classes were used in this study (Size 1: ≤80 mm, Size 2: 81–140 mm, Size 3: 141–190 mm and Size 4: ≥191 mm) based on length–frequency data. Size 1 was reliably considered to be young-of-the-year (YOY) trout, but age determination is not practically possible for larger size classes for brook trout (Xu et al. 2010b). Each sampling year was analysed separately to identify year-specific patterns that may be attributed to the distinct weather patterns between 2 years, and to decrease the computation time.

Count data from JHSB and KFB were combined for analysis because variation in counts was small between the two streams. Using the lmer function (with the Poisson family) in R (R Development Core Team 2010) specified as count ~ (1|stream/reach) + (1|size class), variance (or random effects) attributed to reaches (0.473) and size classes (0.539) was more than a magnitude larger than that of streams (0.023). Besides, counts were not statistically significant between the two study sites for six of the possible 8 year × size class combinations (2 years × 4 size classes) after the Bonferroni correction (*t*-test: *P*-value > 0.006). Reach-scale counts were higher in KFB for Size 1 in 2008 (*t* = -4.33; *P*-value < 0.001) and Size 3 in 2009 (*t* = -2.96; *P*-value = 0.004). All habitat variables, except stream temperature, were not statistically significant between the two study sites after the Bonferroni correction (*t*-test: *P*-value > 0.008) (Table 1). Stream temperature was colder in JHSB than in KFB in both summers. Still, merging data from the two study sites was appropriate from an ecological perspective because higher count values, when present, were observed in the warmer KFB: this pattern was contrary to the expectation that brook trout counts would be higher in colder reaches and it should not inflate (actually it should deflate) the type-I error rate when testing the direction of correlation (negative) between stream temperature and trout counts. It should also be noted that the vast majority of reaches were thermally suitable for brook trout in both study streams (Table 1) (Hartman & Cox 2008; Robinson et al. 2010).

Our preliminary analysis identified potential outliers in reach-scale habitat variables. Therefore, the range of

Table 1. Habitat characteristics in study sites. The first four habitat variables were collected under baseflow condition in fall of 2009.

Variable	Jefferson Hill-Spruce Brook		Kent Falls Brook	
	Median	5th–95th percentiles	Median	5th–95th percentiles
Maximum depth (cm)	52.0	31.1–96.4	56.0	29.5–113.25
Mean depth (cm)	16.8	8.9–34.7	19.2	10.8–32.6
Pool area (m ²)	35.4	0.0–120.5	39.2	2.6–153.5
Nonpool area (m ²)	170.2	68.8–290.4	176.1	95.7–315.2
Gradient (%)	3.0	0.6–8.2	3.5	1.2–8.6
Mean temperature (°C)				
2008 Late July	18.7	17.8–19.2	19.0	18.0–21.0
2009 Late July	17.2	16.5–17.5	18.4	17.7–20.2

values that included 95% of observations were identified for each habitat variable, and those observations smaller than the 2.5 percentiles were fixed at the 2.5 percentile value and those larger than 97.5 percentiles were fixed at the 97.5 percentile value. Then, each habitat variable was standardised by subtracting its mean and dividing by two times its standard deviation (Gelman & Hill 2007), and standardised values were used throughout subsequent statistical analyses. This procedure helped the model convergence as did the inclusion of linear and quadratic terms for each habitat variable in our models (see below). No single pair of standardised habitat variables was strongly correlated with one another (Pearson’s correlation coefficient: *r* < 0.7).

Model development and comparison

Count data were analysed by fitting and comparing four different distribution models in each year. They were a Poisson distribution, overdispersed Poisson distribution (ODP), zero-inflated Poisson (ZIP) distribution and zero-inflated overdispersed Poisson (ZIODP) distribution. In these models, size class was modelled as a random effect because all size classes were considered to respond similarly to at least some habitat covariates (e.g., stream temperature); such nonindependence is better modelled as a random rather than a fixed effect (See Appendix S2 for the R code). However, treating size class as a fixed effect would also have been justifiable because all potential size classes were included in the analysis. Perhaps, the biggest disadvantage of specifying size class as a random effect in this study was increased computational time.

The Poisson distribution was our ‘null’ model and its distribution was determined by the same mean and variance (λ). Following the notation of Gelman & Hill (2007) for mixed models, the Poisson model was as follows:

$$C_i \sim \text{Poisson}(\lambda_i) \tag{1}$$

$$\log(\lambda_i) = \alpha_{s[i]} + \beta_{s[i]} \mathbf{X}_i \tag{2}$$

where C_i represents the trout count at observation i (note that we define $i = 1, 2, \dots, 952$ observations; i.e., $238 \text{ reaches} \times 4 \text{ size classes}$ for each year), $\alpha_{s[i]}$ denotes an intercept term specific to the size class s ($s = 1, 2, 3, 4$) at observation i , $\beta_{s[i]}$ is a vector of size-class-specific regression coefficients associated with habitat variables, and \mathbf{X}_i is a vector of reach-scale habitat variables (i.e., maximum depth, mean depth, pool habitat area, nonpool habitat area, stream gradient and late July mean stream temperature). Each habitat variable included linear and quadratic terms. The Poisson process model and all subsequent models were ‘varying-intercept, varying-slope’ models (Gelman & Hill 2007): that is, intercept ($\alpha_{s[i]}$) and slopes ($\beta_{s[i]}$) were allowed to vary among size classes.

The ODP model is an extension of the Poisson model that allows for overdispersion. It is similar to the negative binomial distribution that specifies an overdispersion term in addition to the Poisson mean (Zuur et al. 2009; Kéry 2010). Following Kéry (2010), overdispersion was added as a normally distributed random effect (ε_i) in a Poisson model, instead of specifying a negative binomial model directly. We fitted the following ODP model:

$$C_i \sim \text{Poisson}(\lambda_i) \tag{3}$$

$$\log(\lambda_i) = \alpha_{s[i]} + \beta_{s[i]} \mathbf{X}_i + \varepsilon_i \tag{4}$$

The ZIP and ZIODP distributions both account for zero inflation in data (i.e., excessive amount of zeros than what would be expected for the given distribution). Excessive zeros can arise in ecological data because of many reasons including imperfect detection, observer errors and absence of organisms at seemingly suitable areas (Zuur et al. 2009). The two distributions were considered in this study because all size classes in both years were characterised with an excessive number of zero counts, more than expected under the Poisson distribution given the mean trout count per reach (Table 2). The ZIP and ZIODP distributions are ‘two-part models’ (Zuur et al. 2009; Kéry 2010) because two different processes are considered sequentially. The ZIP model we fitted was as follows:

$$w_i \sim \text{Bernoulli}(\psi_{s[i]}) \tag{5}$$

$$C_i \sim \text{Poisson}(w_i \times \lambda_i) \tag{6}$$

$$\log(\lambda_i) = \alpha_{s[i]} + \beta_{s[i]} \mathbf{X}_i \tag{7}$$

where w_i is a binary value (1 if brook trout are present, 0 otherwise) determined by the size-specific probabil-

Table 2. Summary of brook trout count data in 238 reaches in Jefferson Hill-Spruce Brook and Kent Falls Brook combined. Expected number of reaches with zero trout counts is based on the Poisson distribution using the mean count of trout per reach with 100,000 iterations.

Size	2008			2009		
	Mean count per reach	Observed no. of reaches with 0 count	Expected no. of reaches with 0 count	Mean count per reach	Observed no. of reaches with 0 count	Expected no. of reaches with 0 count
Size 1	2.0	91	34	3.2	55	11
Size 2	5.9	13	1	2.6	47	19
Size 3	2.3	62	25	2.4	51	23
Size 4	0.5	173	160	0.7	150	125

ity ($\psi_{s[i]}$) that the stream reach at observation i is suitable for brook trout. For those observations with $w_i = 1$, the Poisson process determines brook trout count (C_i) based on reach-scale habitat features [note that Eq. (7) is equal to Eq. (2) in the Poisson model]. Importantly, in the ZIP distribution, zero counts arise either when $w_i = 0$, or by the Poisson process.

Finally, we extended the ZIP model into the ZIODP model by adding the overdispersion term (ε_i), identical to the approach above to extend the Poisson model into the ODP model. Thus, the ZIODP model was described as

$$w_i \sim \text{Bernoulli}(\psi_{s[i]}) \tag{8}$$

$$C_i \sim \text{Poisson}(w_i \times \lambda_i) \tag{9}$$

$$\log(\lambda_i) = \alpha_{s[i]} + \beta_{s[i]} \mathbf{X}_i + \varepsilon_i \tag{10}$$

The Bayesian models were fitted using Markov chain Monte Carlo (MCMC) methods in WinBUGS 1.4 (Spiegelhalter et al. 2003) called from R with the R2WinBUGS package (Sturtz et al. 2005). ‘Vague’ priors were used throughout the Bayesian models in order to represent the lack of previous knowledge on habitat effects on trout counts in our study streams (See Appendix S2 for the R code for the ZIODP model). Thus, our models should provide outputs similar to a frequentist approach (the maximum-likelihood method), and our use of the Bayesian approach was pragmatic; WinBUGS provides a flexible platform to fit a variety of related models. Marginal posterior distributions of model parameters were estimated by 50,000 iterations of three chains after discarding 20,000 burn-in iterations. To reduce autocorrelation in the sample, only every 90th iteration was retained, resulting in a total sample size of 1000 points from the posterior distribution. Model convergence was checked by visually examining plots of the MCMC chains for good mixture and using the Brooks and Gelman (1998) diagnostic. This statistic compares

variance within and between chains, and a model was considered to have converged when the value was <1.1 for all model parameters (Gelman & Hill 2007).

The predictive ability of Bayesian models was compared in two ways. First, the Poisson mean values of model-predicted counts at 50-m reaches were plotted against observed counts, and the adequacy of the models was assessed visually. Second, the Bayesian P -value was calculated for each model (Kéry 2010). This statistic compares the lack of model fit for the observed data set with that for an 'ideal' data set simulated by the model. The Bayesian P -value ranges from 0 and 1, and a good model has a value around 0.5. The model fit decreases as the Bayesian P -value approaches 0 or 1. The best model was identified using these two criteria, and we report coefficients of habitat covariates in the best Bayesian model for each year (ZIODP model). Effect of covariates was considered statistically significant when the 95% credible interval did not overlap with zero.

Because stream reaches were sampled in a spatially continuous manner, attempting to directly model spatial autocorrelation in *residuals* could have been a potential avenue to explore in our models. However, this approach was not pursued in the current study for several reasons. First, spatial autocorrelation in residuals, based on the best model (i.e., ZIODP model), was assessed by using the Moran's I autocorrelation coefficient (see Appendix S3 for details). Evidence of spatial autocorrelation was not consistently observed among size classes and years, and the result was also scale-dependent. Second, some model structures we explored accounted for overdispersion, and spatial autocorrelation is known to be effectively dealt with in such a manner (Gschlößl & Czado 2008). Thus, autocorrelation was partly and indirectly accounted for when the overdispersion term was included. Third, the inclusion of spatial random effects might have produced a better descriptive model, but such a model cannot be used for predictions for other streams. One cannot extrapolate the model outside the spatial extent of sampling areas when spatial random effects are included. Finally, the potential issue of not modelling spatial random effects is to derive regression coefficient estimates that have a more precise credible interval than when the effects are accounted for. Thus, the exclusion of such effects may result in spuriously precise estimates than they should be due to the violation of the data independence assumption, but it should not bias point estimates strongly.

Size-specific spatial distributions

A correlation matrix was constructed to examine the correlation of reach-scale counts among different size classes. The correlation matrix was designed to

include Pearson's correlation coefficient (r) values in the upper panels and scatterplots in the lower panels. Statistical significance of Pearson's correlation (two-sided) was tested with $\alpha = 0.05$ corrected by the Bonferroni method ($\alpha = 0.05/6 = 0.008$ for each year). Size-specific distributions of trout counts were mapped by each 50-m reach in each summer, similar in style to Ganio et al. (2005) and Gresswell et al. (2006).

Results

Field sampling

Both study areas were typical of small headwater streams characterised with high to medium stream gradient (Table 1). Mean stream wetted width was 4.8 m in KFB and 4.3 m in JHSB. Mean stream temperature in late July was about 1.5 °C colder in 2009 (17.4 °C) compared to 2008 (18.8 °C), which followed air temperature patterns between the two summers. Maps of longitudinal habitat profiles can be found in Appendix S1 (stream temperature) and Appendix S4 (other habitat variables).

A total of 1437 individuals were collected in JHSB and 1259 individuals were collected in KFB in the 2008 electrofishing survey. In 2009, we collected 1128 individuals in JHSB, and 886 individuals were collected in KFB. Size distributions of brook trout differed slightly between the two survey years (Table 2). Trout of Size 2 (81–140 mm) were the most abundant class in 2008, but Size 1 (≤ 80 mm) was the most abundant class in 2009. Few trout reached over 190 mm (Size 4) in the two streams in either year (Table 2).

Model development and comparison

The convergence of the Bayesian mixed models was assured by well-mixed MCMC chains, and the Brooks and Gelman diagnostic <1.1 for all model parameters. The ODP and ZIODP models were nearly comparable in their predictive abilities. The Bayesian P -values for the ODP models were 0.487 in 2008 and 0.499 in 2009, and those for the ZIODP models were 0.508 in 2008 and 0.486 in 2009. Poisson and ZIP models were fitted poorly to our data with their Bayesian P -values < 0.001 in both years. When model-predicted reach-scale trout counts were plotted against observed counts, the ODP and ZIODP models showed excellent model fits and observations were aligned near the 1:1 line (Fig. 2 for 2008 data. 2009 data now shown). In addition, zero-inflated models (ZIP and ZIODP) successfully predicted low trout counts when no individuals were actually observed in a reach (when x -axis = 0 on Fig. 2). Taken together, we considered that the ZIODP models were the best models and we

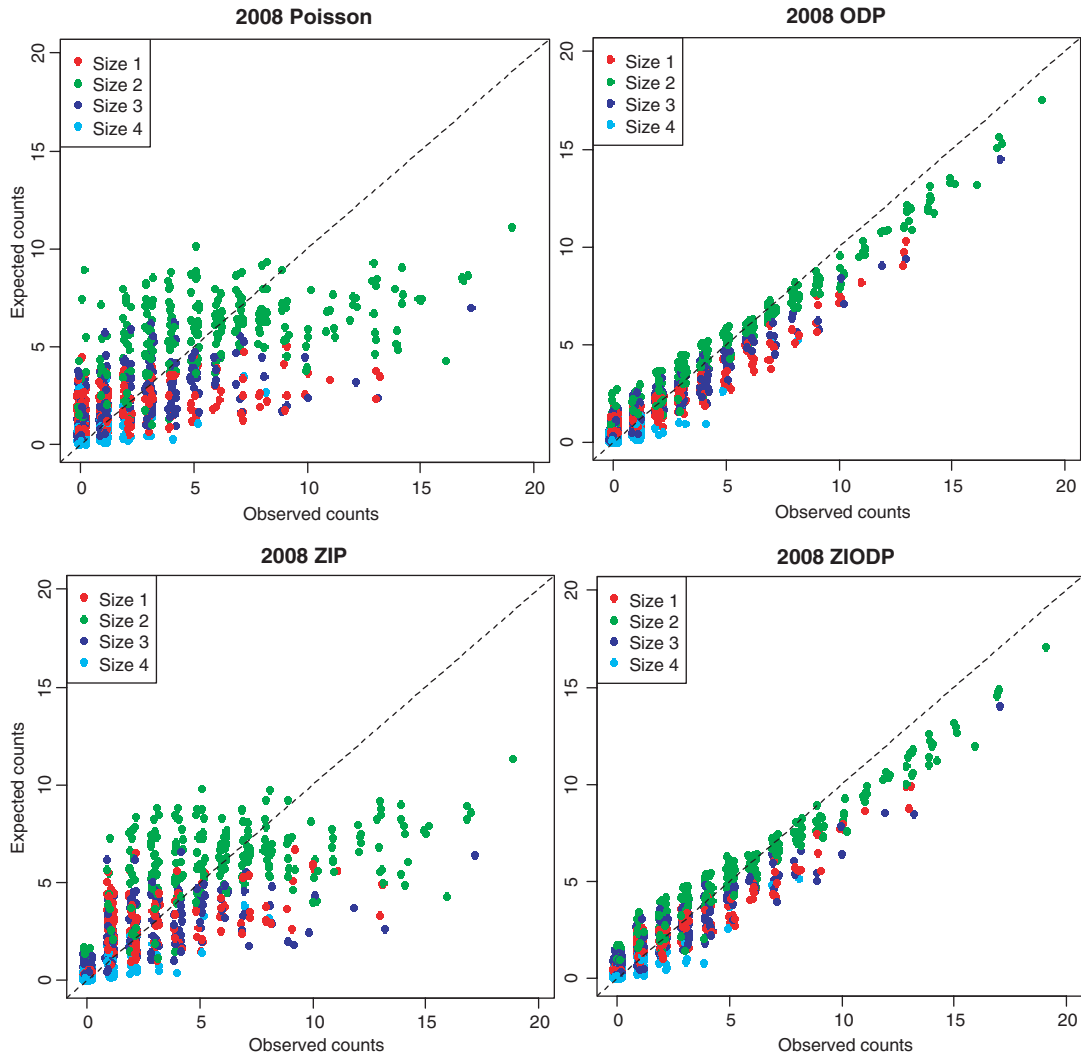


Fig. 2. Observed versus expected brook trout counts using four different models in 2008. Expected counts represent the Poisson means, and points were jittered for graphical clarity. ODP, overdispersed Poisson models; ZIP, zero-inflated Poisson models; ZIODP, zero-inflated overdispersed Poisson models.

report model coefficients of these models in the following subsection.

Covariate effects on trout counts

The effect of habitat covariates was not always consistent among size classes and years, as summarised in Tables 3 and 4 and Figs 3 and 4. There were nonlinear relationships between trout counts and late July stream temperature in all size classes in both years, except that the quadratic term for stream temperature was not statistically significant for Size 1 in 2008 (Table 3). The coefficients for the linear terms for stream temperature were significantly negative for two small size classes in the typically warm and wet year of 2008 (Table 3 and Fig. 3). On the contrary, the coefficients for the linear terms for stream temperature were significantly positive for all size

classes in the cool and very wet summer of 2009 (Table 4 and Fig. 4). These results suggested that increased stream temperature exerted stronger negative influence on trout counts in a warmer summer.

A consistent pattern between 2008 and 2009 was the importance of (deep) pool habitat. Counts increased significantly with area of pool habitat for all size classes in both years, except Size 1 in 2008 (Table 3 and Fig. 3). In both years, maximum depth was consistently important for the two large size classes, particularly Size 4 (Tables 3 and 4; Figs 3 and 4). The linear terms of mean depth were significantly negatively correlated with trout counts of Sizes 1–3 in 2009 (but not in 2008), indicating that brook trout were more abundant in upstream reaches than in downstream reaches in the cool and very wet summer. The linear terms for area of nonpool habitat (e.g., riffles) were significantly negative for Size 4 in

Table 3. Output summary of the zero-inflated overdispersed Poisson model (i.e., ZIODP) in 2008.

	Habitat covariates						
	Probability (reach is suitable)	Maximum depth	Mean depth	Area of pool habitat	Area of nonpool habitat	Stream gradient	Mean late July temp
Size 1	0.76 (0.67, 0.84)	0.03 (-0.56, 0.60)	-0.15 (-0.43, 0.15)	-0.05 (-0.67, 0.55)	0.04 (-0.28, 0.42)	0.76 (0.29, 1.19)	-0.38 (-0.74, -0.09)
Size 2	0.99 (0.96, 1.00)	0.35 (0.00, 0.68)	-0.20 (-0.44, 0.03)	0.41 (0.10, 0.69)	-0.11 (-0.32, 0.09)	0.00 (-0.27, 0.25)	-0.32 (-0.55, -0.10)
Size 3	0.97 (0.92, 1.00)	0.87 (0.39, 1.34)	-0.14 (-0.36, 0.15)	0.75 (0.33, 1.19)	-0.11 (-0.36, 0.14)	-0.17 (-0.49, 0.14)	-0.26 (-0.51, 0.03)
Size 4	0.85 (0.67, 0.99)	1.73 (0.63, 2.75)	-0.14 (-0.42, 0.21)	0.79 (0.17, 1.72)	-0.50 (-1.10, -0.02)	-0.72 (-1.35, -0.08)	-0.14 (-0.50, 0.64)
Intercept		(Maximum depth) ²	(Mean depth) ²	(Area of pool habitat) ²	(Area of nonpool habitat) ²	(Stream gradient) ²	(Mean late July temp) ²
Size 1	0.90 (0.63, 1.17)	-0.23 (-0.82, 0.40)	0.39 (-0.21, 0.98)	0.31 (-0.32, 1.02)	-0.39 (-0.93, 0.10)	-0.51 (-1.06, -0.01)	-0.36 (-0.75, 0.09)
Size 2	1.88 (1.69, 2.04)	-0.23 (-0.55, 0.09)	-0.12 (-0.44, 0.20)	-0.26 (-0.61, 0.10)	-0.13 (-0.45, 0.19)	0.08 (-0.27, 0.42)	-0.46 (-0.75, -0.16)
Size 3	1.00 (0.77, 1.22)	-0.55 (-1.03, -0.13)	-0.16 (-0.60, 0.26)	-0.24 (-0.72, 0.21)	-0.07 (-0.46, 0.36)	-0.22 (-0.69, 0.25)	-0.85 (-1.43, -0.37)
Size 4	-0.81 (-1.27, -0.33)	-0.83 (-1.86, -0.05)	0.16 (-0.38, 0.74)	-0.62 (-1.47, 0.04)	0.49 (-0.26, 1.34)	-0.58 (-1.62, 0.27)	-0.74 (-1.75, -0.03)

Mean values (and 95% credible intervals) are shown, and those coefficients for linear and quadratic terms of habitat covariates whose 95% credible interval does not overlap with zero are shown in boldface. Probability that a reach is suitable is equal to $\Psi_{s,t}$ in Eq. (8). Each habitat covariate was standardised by mean divided by two times standard deviation prior to analysis.

Table 4. Output summary of the zero-inflated overdispersed Poisson model (i.e., ZIODP) in 2009.

	Habitat covariates						
	Probability (reach is suitable)	Maximum depth	Mean depth	Area of pool habitat	Area of nonpool habitat	Stream gradient	Mean late July temp
Size 1	0.91 (0.84, 0.96)	-0.29 (-0.68, 0.11)	-0.38 (-0.67, -0.12)	0.60 (0.25, 0.89)	-0.09 (-0.33, 0.22)	0.05 (-0.21, 0.32)	0.49 (0.16, 0.77)
Size 2	0.96 (0.91, 1.00)	-0.23 (-0.61, 0.15)	-0.42 (-0.70, -0.16)	0.62 (0.28, 0.90)	-0.26 (-0.49, -0.06)	0.46 (0.16, 0.76)	0.57 (0.31, 0.85)
Size 3	0.97 (0.93, 1.00)	0.47 (0.07, 0.85)	-0.39 (-0.67, -0.14)	0.66 (0.36, 0.97)	-0.28 (-0.49, -0.08)	0.45 (0.16, 0.75)	0.61 (0.36, 0.90)
Size 4	0.86 (0.71, 0.98)	1.28 (0.49, 2.06)	-0.18 (-0.54, 0.48)	0.81 (0.42, 1.63)	-0.34 (-0.76, -0.08)	-0.55 (-1.04, -0.06)	0.55 (0.18, 0.92)
Intercept		(Maximum depth) ²	(Mean depth) ²	(Area of pool habitat) ²	(Area of nonpool habitat) ²	(Stream gradient) ²	(Mean late July temp) ²
Size 1	1.54 (1.33, 1.75)	0.22 (-0.18, 0.63)	0.19 (-0.21, 0.65)	-0.42 (-0.85, -0.02)	-0.02 (-0.37, 0.34)	-0.40 (-0.82, 0.02)	-2.03 (-2.61, -1.47)
Size 2	1.23 (1.02, 1.45)	0.03 (-0.37, 0.40)	-0.02 (-0.40, 0.35)	-0.30 (-0.70, 0.11)	0.03 (-0.28, 0.41)	-0.41 (-0.81, -0.01)	-1.29 (-1.72, -0.87)
Size 3	1.30 (1.08, 1.52)	-0.21 (-0.66, 0.22)	-0.16 (-0.57, 0.22)	-0.45 (-0.85, -0.03)	-0.10 (-0.48, 0.24)	-0.47 (-0.87, -0.08)	-1.37 (-1.81, -0.94)
Size 4	-0.04 (-0.42, 0.31)	-0.36 (-1.16, 0.34)	0.12 (-0.40, 0.63)	-0.85 (-1.76, -0.26)	0.03 (-0.50, 0.58)	-0.29 (-0.89, 0.41)	-1.87 (-2.78, -1.12)

Mean values (and 95% credible intervals) are shown, and those coefficients for linear and quadratic terms of habitat covariates whose 95% credible interval does not overlap with zero are shown in boldface. Probability that a reach is suitable is equal to $\Psi_{s,t}$ in Eq. (8). Each habitat covariate was standardised by mean divided by two times standard deviation prior to analysis.

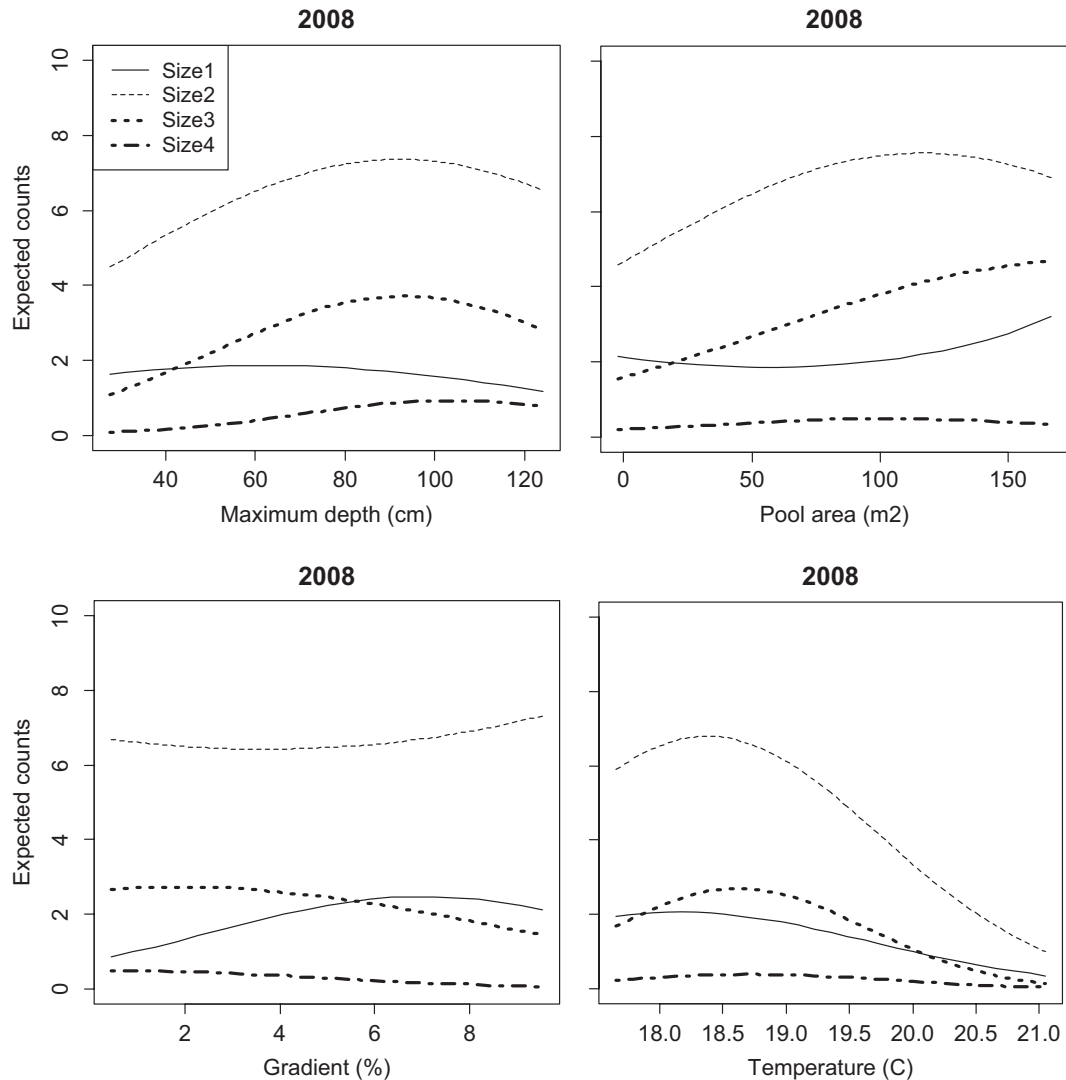


Fig. 3. Effects of select stream habitat features on size-specific brook trout counts using the ZIODP model in 2008. Size-specific curves were derived by using the mean regression coefficient values of linear and quadratic terms for the habitat variable of interest and fixing all other habitat variables to their mean values. The x-axis represents approximately the 5th–95th percentile range for the habitat variable.

2008 (Table 3) and Sizes 1–3 in 2009 (Table 4), although this result was not immediately intuitive.

Stream gradient affected size classes differently in both years (Tables 3 and 4). Brook trout of the largest size class (Size 4) were more abundant in stream reaches with lower gradient in both years. In contrast, significant positive relationships (with negative quadratic terms) existed for Size 1 in 2008 (wet year) (Table 3) and Sizes 2–3 in 2009 (cool and very wet year) (Table 4).

Probabilities of stream reach suitability varied among size classes and followed their count patterns observed in the field (Tables 3 and 4). More abundant size classes had higher probabilities of reach suitability, with Size 2 having the highest probability in 2008 (0.99) (Table 3) and Size 3 having the highest value in 2009 (0.97) (Table 4). The probability of reach

suitability was lowest for Size 1 trout in 2008 (0.76) and Size 4 in 2009 (0.86).

Size-specific spatial distributions

There was no correlation between Size 1 and Size 4 counts in 2008 ($r = -0.06$, P -value = 0.373; Fig. 5) or in 2009 ($r = 0.12$, P -value = 0.057; Fig. 6). In 2008, counts of Size 1 and Size 3 trout were not correlated after the Bonferroni correction ($r = 0.14$, P -value = 0.029; Fig. 5). In 2009, counts of Size 2 and Size 4 were also not correlated ($r = 0.06$, P -value = 0.348; Fig. 6). Counts of all other pairs of size classes were positively correlated with each other (P -value < 0.008; Figs 5 and 6).

When reach-scale counts were mapped and visually assessed for each size class, the spatial distribution of

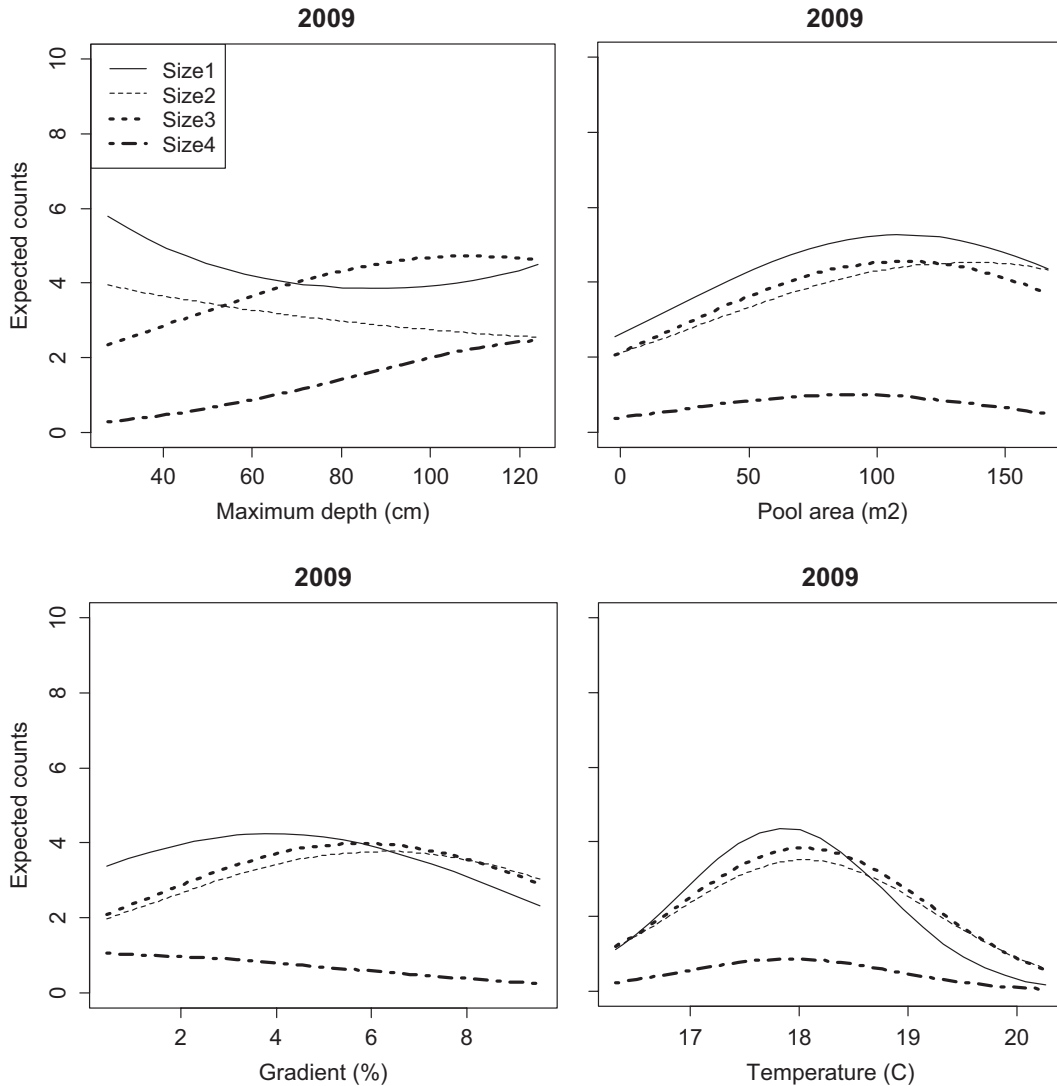


Fig. 4. Effects of select stream habitat features on size-specific brook trout counts using the ZIODP model in 2009. Size-specific curves were derived by using the mean regression coefficient values of linear and quadratic terms for the habitat variable of interest and fixing all other habitat variables to their mean values. The x-axis represents approximately the 5th–95th percentile range for the habitat variable.

Size 4 trout differed from those of other size classes (Fig. 7 and Appendix S5). For example, three small size classes were found ubiquitously within the stream channel network in JHSB in 2009 (Fig. 7). In contrast, Size 4 was rare in tributaries and uppermost headwaters (Segments 1–3 on Fig. 7), where the other three size classes were common. The distribution pattern of Size 1 versus Size 4 trout was the most contrasting: for example, a stream segment with the highest counts of Size 4 (Segment 4 on Fig. 7) was among the least occupied habitat for Size 1.

Discussion

Understanding the effect of stream temperature and flow volume on headwater stream salmonids is important in the face of anticipated climate change.

This study documented species–habitat patterns that are consistent among size classes (e.g., stream temperature) or that vary among size classes (e.g., maximum depth), by taking advantage of (i) a spatially extensive survey of animals and their habitat in select headwater stream networks, (ii) a statistical method that incorporated variation among size classes (i.e., mixed models) and accounted for processes beyond the Poisson distribution (i.e., zero inflation and overdispersion) and (iii) data sets from two distinct summers.

Temperature effect on trout counts

Fewer individuals of the two small size classes were found in warmer reaches in the typically warm and wet summer of 2008, but this pattern was not observed in

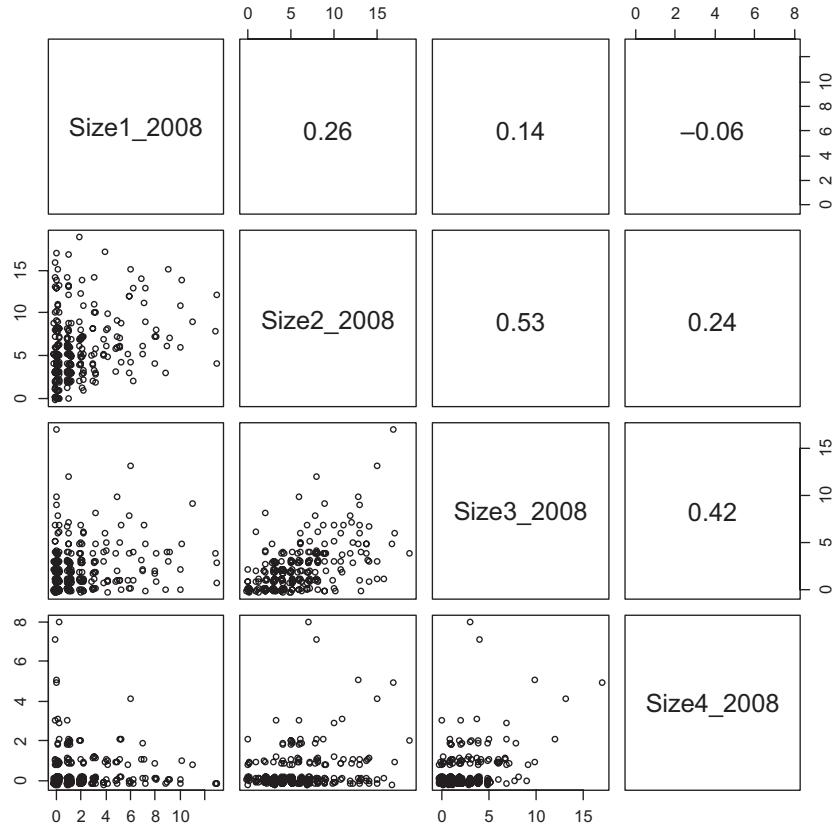


Fig. 5. Correlation matrix of brook trout counts among size classes in 2008. Pearson's correlation coefficient (r) is shown in the upper panels, and pairwise counts are shown in the lower panels. Points were jittered for graphical clarity.

the cool and very wet summer of 2009. Late July mean stream temperature was colder in 2009 (17.4 °C) than in 2008 (18.8 °C), and this narrow stream temperature difference made sizeable differences in thermal effect on among-reach variation in brook trout counts between 2 years. A similar range of stream temperature differences (1–2 °C) have been reported to affect the survival (Xu et al. 2010a) and growth (Xu et al. 2010b) of brook trout during summer in the study region. Thermal effects on counts in this study are also congruent with known temperature ranges for this species; metabolic rates of brook trout declined sharply above 20 °C in a laboratory setting (Hartman & Cox 2008), and wild populations appear to suffer when stream temperatures exceed 20 °C for an extended period in summer (Stranko et al. 2008; Robinson et al. 2010). The observed sensitivity to thermal effects, coupled with the fact that our study streams lie near the upper thermal limit for brook trout, signals evident vulnerability of this species at the southern and central range of distribution under predicted climate change.

Stream temperature was not statistically important for the two larger size classes in 2008. We do not consider that stream temperature was not as important for larger trout. In fact, larger individuals of given fish

species are typically more susceptible to temperature elevation than smaller individuals because of their higher metabolic demands and lower thermal preferences (Hartman & Cox 2008). Field studies provide congruent results and larger brook trout individuals (>age 2+) are reported to suffer higher mortality rates in warmer summers (Drake & Taylor 1996; Robinson et al. 2010). This pattern may be attributed to the ability of smaller trout to exploit physically confined microhabitats with groundwater discharge (Drake & Taylor 1996; Biro 1998) that are inaccessible for larger trout. Our finding probably reflects the overwhelming importance of deep pool habitats for larger brook trout (see below), which might have masked the influence of stream temperature.

Flow volume effect on trout counts

In both study summers, the presence of pool habitat was the primary factor influencing brook trout counts across size classes (except Size 1 in 2008) in our headwater streams. Pool habitat has been identified as preferred habitats for adult and juvenile stream salmonids owing to high efficiency in drift feeding (Nakano et al. 1998; Gowan & Fausch 2002). Ebersole et al. (2009) similarly reported that there was a

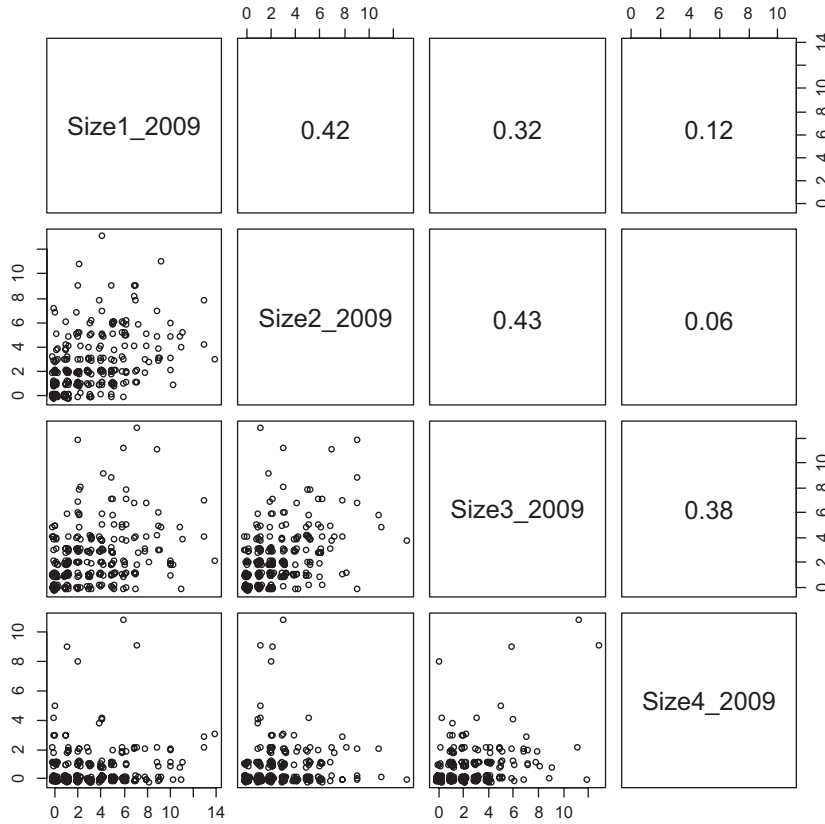


Fig. 6. Correlation matrix of brook trout counts among size classes in 2009. Pearson's correlation coefficient (r) is shown in the upper panels, and pairwise counts are shown in the lower panels. Points were jittered for graphical clarity.

positive relationship between pool area and juvenile coho salmon *Oncorhynchus kisutch* in the upper headwaters in a coastal Oregon basin. Reeves et al. (2011) found that pool habitats were important for three species of salmonids in another coastal Oregon stream, particularly when stream flow decreased.

Although the amount of pool habitats is important for all size classes, stream depth was a critical feature for larger size classes, particularly Size 4. Depth has been identified as cover for large trout to avoid terrestrial/avian predators (Sotiropoulos et al. 2006). Not surprisingly, the largest trout occupied the deepest pools in our small headwater streams. Plus, there was some indication that stream depth affected the counts of Sizes 1–3 as well. Specifically, mean depth and counts of Sizes 1–3 were significantly *negatively* correlated in the exceptionally wet summer of 2009, but the mean depth did not affect any size class in 2008. This observation suggests that stream depth was not a limiting factor for brook trout under the higher flow condition, which likely made tributaries and the uppermost headwaters more hospitable for Sizes 1–3 (but still not for Size 4) in 2009 than an average-flow summer.

Size-specific influence of flow volume on trout counts suggests that summer drought, which is

expected to increase in frequency in the study region under climate change (Huntington et al. 2009), might affect size classes differently. Xu et al. (2010a) reported that summer drought reduced the survival of large brook trout (>135 mm) but not of smaller brook trout in small tributaries in Massachusetts, while elevated stream temperatures uniformly affected all size classes. In high-gradient small headwater streams, riffle habitats typically dry up first under low flow condition, resulting in a chain of isolated pool habitats (Hakala & Hartman 2004). Under such a condition, large trout may suffer higher mortality because shallow depth does not provide cover (Sotiropoulos et al. 2006) or because the quantity of drifting macro-invertebrates is not sufficient to meet their metabolic demands (Hakala & Hartman 2004; Hartman & Cox 2008). Evidently, physical space is the limiting factor for large brook trout individuals during low flow condition in headwaters. Large brook trout individuals have high fecundity, and thus, the greater negative impact on large individuals under drought condition could have important implications in population dynamics and persistence (Letcher et al. 2007).

Stream gradient affected size classes differently, and this result appears to be due partly to its influence on stream geomorphology. Specifically, some of the

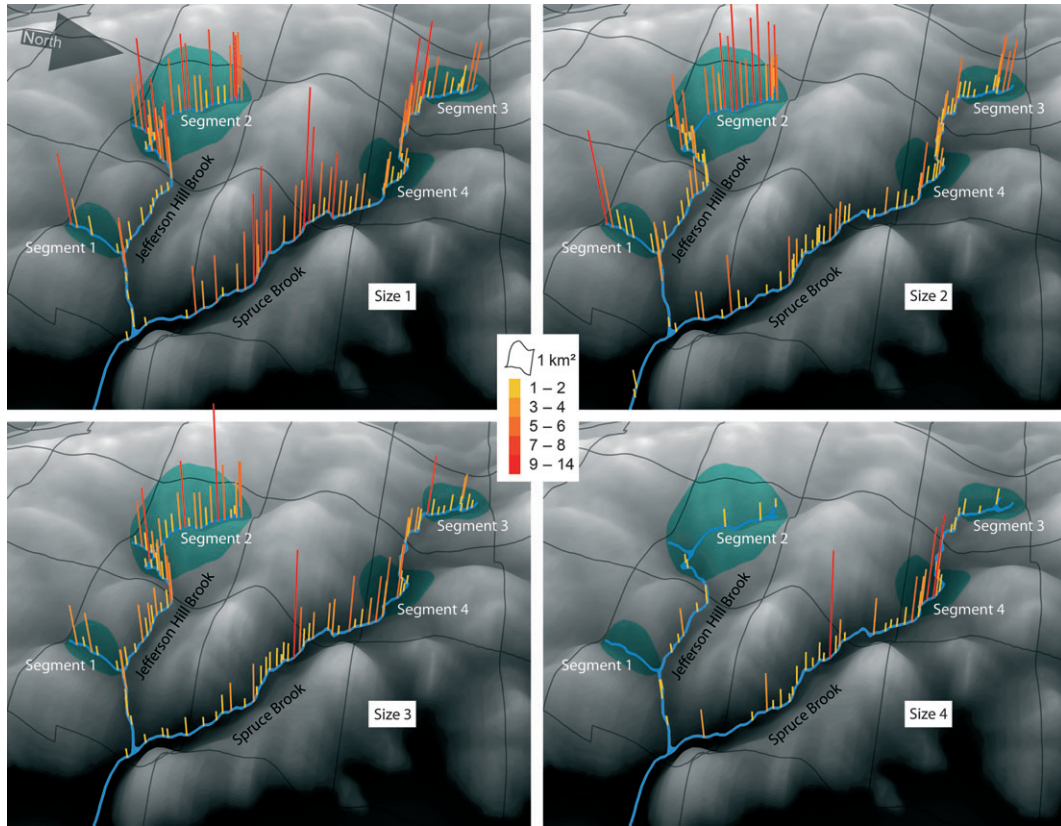


Fig. 7. Size-specific electrofishing counts of brook trout per 50-m reach in 2009 summer in Jefferson Hill-Spruce Brook. Each vertical bar represents the number of brook trout individuals captured in a reach, and its values are categorised by different colours and bar heights. Four example segments are highlighted to indicate the variation in counts among size classes, particularly between Size 1 and Size 4.

deepest and largest pools were located in low-gradient reaches in the study areas, which may explain the negative correlation between stream gradient and trout counts of Size 4 in both summers. The effect of stream gradient was not consistent between years for other size classes, with stream gradient positively correlated with counts of Size 1 (only in 2008) and Sizes 2 and 3 (only in 2009). The inconsistency might be due to the interactions between stream gradient and stream discharge, which might have created heterogeneous microhabitat conditions between the 2 years of different precipitation patterns. It is reasonable to assume that habitat suitability of stream reaches differed between the two summers because of different discharge patterns. Gowan & Fausch (2002) observed that brook trout shifted their microhabitat locations in response to changes in stream discharge levels during summer in a non-native Rocky Mountain stream.

The role of trout movement

Our exploratory analysis via correlation matrices and spatial habitat mapping identified that ‘hotspots’ (i.e., reaches with high trout counts) may differ among size classes, particularly between Size 1 versus Size 4. Similar to our finding, previous studies documented

size-specific patterns of spatial distributions, in which larger or older individuals are more common in the mainstem habitats and smaller or younger individuals become dominant in tributaries (Petty et al. 2005; Young 2011). Gresswell et al. (2006) reported that spatial patterns of cutthroat trout *Oncorhynchus clarkii* distributions also shifted among years in an Oregon headwater stream network. The spatial pattern observed in this study suggested that trout movement is a potentially important mechanism in exploiting spatially patchy habitat resources in the ‘riverscape’ (Fausch et al. 2002) by the time an individual reaches the largest size class.

However, genetic data based on Size 2 brook trout were indicative of limited trout movement at the population level in the study areas (Kanno et al. 2011a,b). That is, full-sibs that share both parents were mostly distributed close to each other in a spatially clustered manner (Kanno et al. 2011a), and a perceptible isolation-by-distance pattern was observed in Jefferson Hill, Spruce and KFB individually (Kanno et al. 2011b). How do we reconcile these observations?

A plausible explanation may be that some individuals, particularly large ones, do move among stream reaches through their life stages, but others are rather sedentary (Gowan et al. 1994; Skalski & Gilliam

2000; Rodríguez 2002). Positive correlation of reach-scale counts was observed among the three small size classes in both summers, and their spatial distributions were qualitatively similar (but counts differed). In our study sites, both males and females of approximately 100 mm in total length (i.e., Size 2) were reproductively mature (i.e., expressing milt or eggs) during fall (Y. Kanno, personal observation), and these individuals may be able to complete their life cycle and reproduce successfully in a spatially limited area (e.g., even within a tributary). Hudy et al. (2010) reported that genetically inferred parents and their offspring were often collected in a restricted area in a Virginia headwater brook trout population. Thus, the coexistence of movers and nonmovers may have resulted in the perceptible spatial population structure.

Alternatively, spatial configurations of heterogeneous habitat types may be such that brook trout can find habitat patches required for ontogenetic shift within a short movement distance. Brook trout of Size 4 were the least common size class in the study areas, but they were still found throughout the stream channel network, except in small tributaries (see Fig. 7). Typical of low-order streams in the region, our study streams were characterised with series of alternating macrohabitat types (i.e., pool–riffle sequences with cascades and steps) in predominantly forested watersheds. Trout movement may be possibly limited when the quality and diversity of stream habitats is high (Bélanger & Rodríguez 2002; Olsson et al. 2006). We had studied the movement of large brook trout (>150 mm: Size 3 and 4) within a single field season (early summer to fall) using a mark–recapture technique; trout were sedentary during the summer, and some moved upstream (maximum distance = 2 km) in fall for spawning but many were still recaptured in the same reaches throughout the study period (Kanno et al. 2011b). Clearly, measuring and quantifying stream habitat ‘beyond reaches’ (Fausch et al. 2002) should be important for understanding if, why and how much distance stream fishes move as they grow.

Statistical model development

Model comparison indicated that our count data, like other ecological data, were characterised by overdispersion. Overdispersion in count data can arise through either excessive number of zeros, excessive dispersion in positive values or both (Zuur et al. 2009). In this study, the ODP distribution was a better fit than the ZIP distribution, and it was nearly comparable to the ZIODP model. Thus, although our data set clearly had many zeros, the ODP model was capable of accounting for much of overdispersion. This observation is likely because the mean trout

counts per reach were small (0.5–5.9: Table 2) and close to zero. If a data set contains many zeros and positive values were much larger than zero and overdispersed, the ZIODP models should noticeably improve model fit relative to the ODP models.

The spatially continuous sampling of brook trout and habitat was helpful in statistical analysis because it avoided the need to stratify sampling among stream reaches. A traditional sampling design might have been to identify obvious habitat groups in the study watersheds (e.g., mainstem versus tributaries) and randomly sample a subset of stream reaches within habitat groups (i.e., stratified random sampling). However, delineating such groups in a continuous habitat is not straightforward and introduces subjective judgment, potentially leading to less robust statistical models. We recognise resource and time constraints on conducting spatially continuous sampling. But, as Fausch et al. (2002) argued, collecting data at a ‘coarse’ spatial grain (e.g., stream habitat features at each 50-m reach) in a spatially extensive fashion (e.g., spanning entire headwater channel networks) can lead to better ecological understanding of riverine organisms.

This study focused on a single season (i.e., late summer) in 2 years, and our inferences are likely to be season-specific. Temperate streams change seasonally in important features including stream temperature and flow volume, and lotic organisms have adapted to predictable seasonality. Stream salmonids are known to select different habitats seasonally (Bardonnnet & Baglinière 2000; Gowan & Fausch 2002; Reeves et al. 2011). Brook trout use tributaries and uppermost headwaters for spawning during fall (Johnson & Dropkin 1996; Petty et al. 2005), and we also observed upstream movement by some large brook trout (>150 mm) into tributaries and uppermost headwaters during fall in the study sites (Kanno et al. 2011b). Our sampling design was spatially extensive but temporally limited, and analysis across seasons will be required to understand the species–habitat relationships fully (e.g., Xu et al. 2010b).

Conclusion

This study quantified size-specific relationships between reach-scale brook trout counts and stream habitat features in two headwater stream networks within two contrasting summers. The primary objective was to understand the influence of local-scale (i.e., reach-scale) habitat features on brook trout counts; however, it should be stressed that spatially extensive sampling of trout and habitat led to some insights into dispersal that might be occurring beyond the local scale. This study represents a successful effort to study stream fishes by collecting spatially continuous data across life stages. Our field sampling literally covered

the potential habitat of the entire local populations that occupied the headwater channel networks and provided unique insights into species–habitat relationships of a stream fish. As more and more stream habitats become fragmented because of anthropogenic activities, including global climate change, understanding small coldwater fish populations will guide conservation actions better.

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Supporting Information

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

Appendix S1. Longitudinal stream temperature profiles in Jefferson Hill-Spruce Brook (JHSB) and Kent Falls Brook (KFB) in 2008 and 2009. Values indicate the mean stream temperature (°C) in late July.

Appendix S2. R code to initiate WinBUGS analysis of the best Bayesian mixed model (i.e., ZIOPD model).

Appendix S3. Summary of Moran's I calculation to assess the spatial autocorrelation in residuals of the best Bayesian mixed model (i.e., ZIOPD model).

Appendix S4. Longitudinal profiles of stream habitat covariates in (a) Jefferson Hill-Spruce Brook and (b) Kent Falls Brook. Each dot represents values for a 50-m stream reach.

Appendix S5. Size-specific electrofishing counts of brook trout per 50-m reach in (a) 2008 summer in Jefferson Hill-Spruce Brook, (b) 2008 summer in Kent Falls Brook and (c) 2009 summer in Kent Falls Brook.

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