AN ABSTRACT OF THE DISSERTATION OF

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Title: On the Estimation and Application of Spatial and Temporal Autocorrelation in Headwater Streams

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This collection of three manuscripts serves to improve methods for collecting, interpreting, and utilizing autocorrelated data from headwater stream networks. Each stream network is comprised of linear segments. These segments lie within a unique branching structure that connects the segments via flowing water, and the connectivity provided by water varies seasonally. These aspects separate stream networks from other landscapes, and provide unique challenges to the statistical analysis of stream-based phenomenon.

Two chapters of this work relied on a unique and comprehensive set of data. These data constitute a complete census of habitat unit fish counts from 40 randomly selected headwater basins in western Oregon. The first objective of this work was to evaluate how different sampling designs captured spatial autocorrelation, given the samples were drawn from a population of spatially autocorrelated observations. Spatially distributed clusters of sampling locations were more apt to capture spatial autocorrelation than samples

without clusters or small clusters located at tributary junctions. A similar investigation was made concerning sampling design performance in relation to estimating autocorrelation function values. All sampling designs lead generally to negatively biased estimates, and practical differences among the sampling designs were not observed. The second objective was to investigate spatial autocorrelation model range parameters as measures of patch sizes. It is common practice to use range parameters to infer the size of patches within spatially autocorrelated data, but this methodology lacks sufficient justification. The census data were used to compute range parameter values, and another proposed autocorrelative measure of patch size: the integral scale. The same data were used to compute patch sizes under several patch definitions, and the relationship of range parameters and integral scale values with patch sizes was explored. Range parameter values did not equal and were not strongly correlated with average patch sizes, though range parameter values were more correlated with maximum patch and gap sizes. Integral scale values matched the magnitude of, but were not strongly correlated with, average patch sizes.

The third objective was to refine the analysis of temporally autocorrelated hydrology data from paired watershed studies. Paired watershed studies are used to evaluate forest harvesting effects on stream biota and hydrology (*i.e.* fish, amphibians, insects, stream flow, and sediment yield). Traditionally, treatment effects are discerned using prediction intervals. This work provided an improved method for constructing prediction intervals for use in change detection in paired watershed studies. The improved prediction intervals included variation associated with estimating linear and autocorrelation model parameters.

On the Estimation and Application of Spatial and Temporal Autocorrelation in Headwater Streams

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Nicholas A. Som, Author

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CONTRIBUTION OF AUTHORS

Robert E. Gresswell provided data for Chapters 2 and 3.

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Nicolas P. Zégre contributed to the contextual development in Chapter 4.

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1. INTRODUCTION

1.1 INTRODUCTION

Data collected across spatial landscapes or over time commonly exhibit autocorrelation (*Legendre*, 1993). This phenomenon is appropriately summed by Tobler's first law of geography, that "everything is related to everything else, but near things are more related than distant things" (*Tobler*, 1970). The presence of autocorrelation lessens the amount of statistical information contained within a sample, and therefore needs to be accounted for in hypothesis tests and parameter estimation uncertainty. The study of autocorrelation in ecological has evolved from simply statistical accounting, and ecologists have begun to focus attention on the spatial process itself (*Pickett and Cadenasso*, 1995).

Stream networks provide a unique landscape for the study of spatial autocorrelation. Each stream network is comprised of linear segments. These segments lie within a unique branching structure that connects the segments via flowing water, and the connectivity provided by water varies seasonally. The connectivity and proximity of locations within streams can be expressed along the path of water moving through the network structure. These traits have led to further developments in the study of autocorrelation methods for stream networks (*Ver Hoef et al.*, 2006), and present interesting arenas for investigating statistical measures for analysis of data collected within them.

Paired watershed studies are used to evaluate forest harvesting effects on biota and hydrology (*i.e.* fish, amphibians, insects, stream flow, and sediment yield) in stream segments adjacent to and downstream of timber harvest. For instance, hydrologic response variables are collected over time

before and after harvest, and the response values within a treated watershed are compared to those within untreated watersheds. Detection of changes in a treated watershed, relative to a control watershed, are indicative of effects due to forest harvesting. These response variables are often temporally autocorrelated, and change detection is assessed using prediction intervals (*Gomi et al.*, 2006; *Moore et al.*, 2005; *Watson et al.*, 2001).

This work seeks to update and fill gaps in relation to the estimation and application of spatial autocorrelation, and improve the prediction interval methodology, for data collected within headwater stream networks.

1.2 CHAPTER DESCRIPTIONS

Chapter 2 investigates how sampling designs impact the ability to detect spatial autocorrelation and estimate autocorrelation parameters in spatially autocorrelated data. This chapter utilizes censuses of fish counts from western Oregon headwater basins. Two cluster-based and two non cluster based sampling protocols are implemented in a resampling exercise to evaluate autocorrelation detection and estimation among protocols.

Chapter 3 uses census fish count data from 40 western Oregon headwater basins to investigate the appropriateness of range parameter and integral scale values for the estimation of patch sizes. Patches are measured for each basin using four patch definitions, each based on increasing within-patch fish count thresholds. The census fish count data are used to compute range parameter and integral scale values for each basin. The relationship between range parameter and integral scale values with patch sizes is assessed graphically and with correlation estimates.

Chapter 4 derives prediction intervals for change detection in temporally

autocorrelated hydrologic data from paired watershed studies. The proposed prediction intervals incorporate variation due to the estimation of linear and autocorrelation model parameters, which is in contrast to current methods of prediction interval calculation for paired watershed studies. An example of their application is given using data from the Hinkle Creek Paired Watershed study from Oregon.

BIBLIOGRAPHY

Gomi, T., R. D. Moore, and A. S. Dhakal (2006), Headwater stream temperature response to clear-cut harvesting with different riparian treatments, coastal British Columbia, Canada, *Water Resources Research*, *42*,

Legendre, P. (1993), Spatial autocorrelation: Trouble or new paradigm?, *Ecology*, *74*(6), 1659–1673.

Moore, R. D., P. Sutherland, T. Gomi, and A. Dhakal (2005), Thermal regime of a headwater stream within a clear-cut, coastal British Columbia, Canada, *Hydrological Processes*, *19*(13), 2591–2608, doi:10.1002/hyp.5733.

Pickett, S. T. A., and M. L. Cadenasso (1995), Landscape ecology: Spatial heterogeneity in ecological systems, *Science*, *269*, 331–334.

Tobler, W. R. (1970), A computer movie simulating urban growth in the Detroit region, *Economic Geography*, *46*, 234–240.

Ver Hoef, J. M., E. Peterson, and D. Theobald (2006), Spatial statistical models that use flow and stream distance, *Environmental and Ecological Statistics*, *13*, 449–464, doi:10.1007/s10651-006-0022-8.

Watson, F., R. Vertessy, T. McMahon, B. Rhodes, and I. Watson (2001), Improved methods to assess water yield changes from paired-catchment studies: Application to the Maroondah catchments, *Forest Ecology and Management*, *143*(1–3), 189–204.

2. SAMPLING HEADWATER STREAM NETWORKS FOR SPATIAL AUTOCORRELATION DETECTION AND AUTOCOVARIANCE PARAMETER ESTIMATION

2.1 ABSTRACT

Spatial autocorrelation is common in data collected for ecological studies, and the use of statistical models for spatial autocorrelation has evolved. Initially, these models where used to improve linear model parameter estimation uncertainty, but more recently ecologists have considered spatial autocorrelation as a valuable tool for describing ecological patterns. The structure and water-driven continuity of stream-networks makes these landscapes unique, and has prompted the development of new models for describing spatial autocorrelation within these networks. We evaluate the spatial autocorrelation detection and parameter estimation of four sampling protocols applied to complete censuses of coastal cutthroat trout (*Oncorhynchuys clarki clarki*) habitat unit fish counts. We consider two cluster- and two non cluster-based sampling protocols. Spatially distributed clusters were the most apt to contain spatial autocorrelation, and spatial autocorrelation detection was also associated with headwater basin attributes. Differences among the sampling protocols in regards to autocorrelation parameter estimation was less distinct.

2.2 INTRODUCTION

Attention to patterns of spatial autocorrelation in ecology has shifted dramatically. Geostatistical methods were first used to account for spatial

autocorrelation in order to estimate the mean, assess relationships between explanatory and response variables, or make predictions at unobserved locations. More recently, ecologists have focused attention on the spatial process itself, recognizing the implications of variance patterns across their systems of study as valuable explanatory and predictive tools, rather than simply sources of background variation (*Pickett and Cadenasso*, 1995). The realization that spatial patterns are important components of ecosystems has rendered the study of spatial heterogeneity important in its own right (*Legendre*, 1993).

Realizations of this shift include *Ettema and Wardle* (2002) recognizing spatial variability as a key, rather than nuisance, to understanding the structure and function of soil biodiversity. Other studies relating spatial variability to soil variables include *Russo and Bresler* (1981), *Schlesinger et al.* (1996), *Solie et al.* (1999), *Grundmann and Debouzie* (2000), *Muneto et al.* (2001), and *Blair* (2005). Examples from forest plants include *Mast and Veblen* (1999) and *Bouza et al.* (2002). *Rossi* (2003) used spatial autocorrelation to study earthworms. There has also been much work utilizing spatial heterogeneity in aquatic ecosystems that include river or stream nutrients and water quality (*Cressie and Majure*, 1997; *Little et al.*, 1997; *Rathbun*, 1998; *Peterson and Urquhart*, 2006; *Dent and Grimm*, 1999; *Cressie et al.*, 2006), tropical sea plankton (*Bulit et al.*, 2003, 2004), seabirds (*Huettmann and Diamond*, 2006), aquatic invertebrates (*Downes et al.*, 1993; *Lloyd et al.*, 2005), stream substrate composition (*Rice and Church*, 1998; *Venditti and Church*, 2005), stream temperature (*Gardner et al.*, 2003), and riverine fish (*Torgersen and Close*, 2004; *Isaak and Thurow*, 2006; *Ganio et al.*, 2005; *Neville et al.*, 2006).

The autocovariance function can be used to model the decaying autoco-

variance (C(h)) between observations as the distance between them (h) increases. The geostatistical model for C(h) often contains the range, nugget, and partial sill parameters (*Schabenberger and Gotway*, 2005). The range and partial sill parameters describe the rate of covariance decay with h, and the partial sill and nugget parameters describe the covariance when h is zero. The autocorrelation function (R(h)) standardizes the autocovariance function between 0 and 1, and can also be used to describe this relationship. $R(h) = C(h)/C(0)$, and utilizes the three autocovariance parameters simultaneously.

Spatially explicit data are needed to describe and compare the spatial autocovariance patterns of ecological phenomenon. Data are obtained through sampling, and sampling is the focus of this work. Even though spatial statistical methods are traditionally used to analyze data that have already been collected, they can also be used to design sampling programs (*Cooper et al.*, 1997). Regardless of the analysis goal, estimation of spatial autocorrelation is among the essential steps in any geostatistical analysis (*Gascuel-Odoux and Boivin*, 1994). Because inferences for spatial data are affected substantially by the configuration of the network of sites where measurements are taken (*Zimmerman*, 2006), a less than optimum selection of sampling locations can result in greater covariance function uncertainty (*Russo and Jury*, 1987), and efficient spatial autocorrelation parameter estimation is significantly affected by the sampling design (*Muller and Zimmerman*, 1999) it is imperative that efficient sampling designs be investigated.

There exists a solid and consistent body of work on the estimation of spatial autocorrelation parameters for geostatistical data. *Zimmerman* (2006) found that for efficient estimation of covariance parameters a design should have a large number of short and long distances between sample points (lags).

This design can be achieved by a distribution of regularly spaced clusters, many of which lie along the periphery of the sampling space. Similarly, *Zhu and Zhang* (2006) conclude that designs including closely spaced points lead to more efficient estimation of covariance parameters, and work from *Zhu and Stein* (2005) found designs with clusters of sampling locations more efficient than non-clustered completely regular or simple random sampling designs. In addition, the most efficient designs for spatial autocorrelation parameter estimation evaluated by *Muller and Zimmerman* (1999) included many tightly clumped groups of sampling locations. In an assessment of maximum likelihood (ML) and restricted maximum likelihood (REML) for estimating autocovariance parameters *Irvine et al.* (2007) also found a cluster-based design provided the smallest inter-quartile range for estimates of the autocorrelation function than regular lattice or random designs for estimating autocovariance parameters.

The above results are satisfactory for covariance parameter estimation in landscape studies. They may not, however, be sufficient for stream ecology studies. Each stream network is comprised of linear segments within a unique branching structure. Water flow connects segments, but connectivity between segments varies because of inputs from upstream segments at each tributary junction. This notion is most succinctly concluded by *Hynes* (1975) that every stream is likely to be an individual. These traits have led to further developments in the study of autocovariance methods for stream networks. *Ver Hoef et al.* (2006) use moving average constructions to develop valid spatial autocovariance models for stream networks based on stream distance that also incorporate relative flow contribution between stream segments. Additionally, new methods for sampling spatially distributed resources, such as generalized random-tessellation stratified (GRTS) designs, that lead to

spatially well distributed probability samples (*Stevens Jr. and Olsen*, 2004) have been created. These developments allow the investigation of covariance parameter estimation performance for stream networks in light of new sampling and analysis methods for stream network spatial data.

Tributary confluences are a common element among stream networks, and there is growing evidence that confluences influence spatial processes in streams. *Poole* (2002) suggests a stream segment's physical context is among important considerations for understanding primary drivers of biotic community composition at stream locations. Confluences are areas of increased morphological (*Benda et al.*, 2004b), chemical, and biological stream heterogeneity (*Kiffney et al.*, 2006). *Benda et al.* (2004a) conclude that the probability of a tributary impact on mainstem morphology increases with the relative size of the tributary to the mainstem. They link this relationship to the spatial distribution of fluvial geomorphic processes and forms. The physical attributes relating to tributary inputs effect fish habitat (*Ferguson et al.*, 2006), and biological responses to increased levels of environmental variability near confluences can be expected (*Rice et al.*, 2006).

Given the benefit for covariance parameter estimation that clusters of sampling locations have, and the role that confluences play in the spatial heterogeneity of stream networks, we hypothesize that sampling designs assigning clusters of sampling locations centered at tributary junctions might lead to improved covariance parameter estimation. The previously cited studies evaluating the performances of sampling designs for autocovariance parameter estimation relied on simulated data, but to our knowledge sampling design performance has not been investigated using real-world data. *Pooler and Smith* (2005) utilized the census of a 40 x 33 m section of the Cacapon River in West Virginia to evaluate sampling designs for estimating

the distribution and abundance of freshwater mussels. In a similar manner, we will compare the spatial autocovariance parameter estimates obtained from a re-sampling exercise of census data. Samples obtained from tributary focused clusters, spatially distributed clusters, and two non-clustered sampling protocols will be compared in a design-based analysis of autocovariance detection and parameter estimation.

2.3 METHODS

2.3.1 40 Basins Dataset

Coastal cutthroat trout (*Oncorhynchuys clarki clarki*) were continuously sampled in 40 watersheds located west of the Cascade Mountains in Oregon (*Gresswell et al.*, 2004). The basins are located above barriers to anadromous fish migration and are part of a larger study examining the effects of landscape pattern on isolated coastal cutthroat trout populations. Each of the 40 basins was randomly selected from a population of 268 second- and third-order catchments and surveyed through the entire fish-bearing extent (*Ganio et al.*, 2005). Adult coastal cutthroat trout abundance was assessed with single-pass electrofishing without blocknets (*Bateman et al.*, 2005) in all pools and cascade habitat units in each watershed. These data constitute a census of the habitat units within each headwater basin. Twelve headwater basins whose fish-bearing extent encompassed between three and ten tributary junctions were selected for this analysis. It should be noted that these data represent a one time snap-shot of habitat unit fish-counts, and it has been shown that habitat unit fish counts can change quickly and dramatically over time (*Bateman et al.*, 2005).

2.3.2 Autocovariance Models for the Census Data

We begin by establishing census data autocovariance parameters for each of i basins. These parameter values are used to construct census values of $R_i(h)$. Values of $\hat{R}_i(h)$ from each of the sampling protocols described in the next section are compared to these $R_i(h)$ values.

We consider four candidate autocovariance models for the census data from each basin. All habitat unit fish counts were transformed via a $logarithm_e(datum + 1)$ transformation. The four autocovariance models for isotropic and stationary spatial processes come from two different classes. The first class represents geostatistical models that utilize the pairwise Euclidean distance between all habitat units. We first consider the exponential with nugget autocovariance model

$$C(h) = \begin{cases} \theta_0 + \theta_1 & \text{if } h = 0 \\ \theta_1 exp(-3h\theta_2^{-1}) & \text{if } h > 0 \end{cases} \tag{2.1}$$

where h is the Euclidean distance between observations, θ_0 is the nugget parameter, θ_1 is the partial sill parameter, and θ_2 is the practical range parameter. The practical range is defined as the distance at which correlation between observations $\approx 5\%$ (*Schabenberger and Gotway*, 2005).

We also considered the spherical with nugget autocovariance model

$$C(h) = \begin{cases} \theta_0 + \theta_1 & \text{if } h = 0 \\ \theta_1\left[1 + .5(h\theta_2^{-1})^3 - 1.5h\theta_2^{-1}\right] & \text{if } 0 < h < \theta_2 \\ 0 & \text{if } \theta_2 \leq h \end{cases} \tag{2.2}$$

where h is the Euclidean distance between observations, θ_0 is the nugget parameter, θ_1 is the partial sill parameter, and θ_2 is the range parameter.

The second class of spatial autocovariance models are tail-up spatial moving average models for stream networks (*Ver Hoef et al.*, 2006) which utilize in-stream distances. For moving average in-stream models, the exponential

model describing the covariance between an observation s_i downstream of observation s_j is

$$C(s_i, s_j) = \begin{cases} \theta_0 + \theta_1 & \text{if } h = 0 \\ \theta_1 exp(-3h\theta_2^{-1})\sqrt{w_{i,j}} & \text{if } h > 0 \text{ and } s_i,\ s_j \text{ are flow connected} \\ 0 & \text{if } s_i,\ s_j \text{ not flow connected} \end{cases} \tag{2.3}$$

where h is the distance along the stream network between locations s_i and s_j, $w_{i,j}$ is the proportion of water flow the stream segment containing s_i receives from the segment containing s_j, and with θ_0, θ_1, and θ_2 as in (2.1). The moving average analog to (2.2) is

$$C(s_i, s_j) = \begin{cases} \theta_0 + \theta_1 & \text{if } h = 0 \\ \theta_1\left[1 + .5(h\theta_2^{-1})^3 - 1.5h\theta_2^{-1}\right]\sqrt{w_{i,j}} & \text{if } 0 < h < \theta_2 \text{ and } s_i,\ s_j \text{ are flow connected} \\ 0 & \text{if } \theta_2 \leq h \text{ or } s_i,\ s_j \text{ not flow connected} \end{cases} \tag{2.4}$$

with h and $w_{i,j}$ as in (2.3) and θ_0, θ_1, and θ_2 as in (2.2). These models differ from the geostatistical models in the distance measure used, and in two other ways. First, the autocovariance between locations is weighted proportionally to the amount of stream flow the downstream location receives from the upstream location. Second, two habitat units are only considered autocorrelated if they are connected via water flow through the stream network. See *Ver Hoef et al.* (2006) and *Peterson et al.* (2007) for more details. Relative flow contribution was not directly measured for each location in the watershed. The proportion of the upstream watershed area drained by each stream segment was used to weight the moving average autocovariance functions at each tributary confluence (*Peterson et al.*, 2007). We computed all confluence weights and in-stream distances via the FLoWS ArcGIS toolbox (http://www.nrel.colostate.edu/projects/starmap/flows_index.htm).

Maximum likelihood equations were optimized to obtain parameter values, given the census data, for each basin using R code from *Ver Hoef and*

Peterson (2007). Akaike's information criterion (AIC) values were used to determine which candidate model was best supported by the data (*Zuur et al.*, 2009). If necessary, we also considered the relative structured variability (RSV) (*Schabenberger and Gotway*, 2005) of each candidate model. RSV is $\frac{\theta_0}{\theta_0+\theta_1}$. The autocovariance model with the highest RSV was chosen if any AIC values from the four autocovariance models were within 2 AIC units of the best fitting model.

For reference, we also fit a model that assumed each observation within each basin was independent and not spatially autocorrelated. AIC values from these models and empirical semivariograms were used to ascertain the presence of autocorrelation in the census data for each basin.

We used the selected spatial autocovariance model from each of the i basins to calculate $R_i(h)$ at distances (h) of 25, 100, and 200m. We chose these lag values for h to represent relatively short, medium, and longer distances between sampling locations within the basins.

2.3.3 Sampling Protocols

We now describe the four sampling protocols and resampling process used to compare each protocol's spatial autocorrelation detection and parameter estimation performance. The evidence of spatial autocorrelation, and $\hat{R}_i(h)$ computed from the autocovariance parameter estimates of each sample will be assessed.

Two cluster-based, and two non cluster-based, sampling protocols were employed in this study (Figure 2.1). For notation, m will represent the number of clusters, l will represent the number of habitat units within each sample cluster, and $n = l * m$ will represent the entire sample size.

The first sampling protocol is simple random sampling (SRS) without replacement. n habitat units were randomly chosen among all the habitat units for each basin using the *sample* function in R statistical computing software (*R Development Core Team*, 2005).

The second sampling protocol is the generalized random tessellation stratified (GRTS) methodology aimed to create spatially balanced probability samples (*Stevens Jr. and Olsen*, 2004). n habitat units were chosen among all habitat units for each basin using the *spsurvey* contributed R package (*Kincaid et al.*, 2008) for the implementation of GRTS sampling.

The third sampling protocol implemented, referred to Mod.GRTS, is a modified GRTS procedure that we applied to select spatially balanced clusters of sampled habitat units throughout the headwater basins. We used *spsurvey* to select a spatially distributed set of m cluster centroids. At each centroid, a continuous cluster sample of size l was obtained by selecting $\frac{l}{2}$ habitat units upstream and including the centroid, and $\frac{l}{2}$ habitats units directly downstream of the centroid. Should $\frac{l}{2}$ habitat units in either direction result in the encountering of a tributary junction, the remaining units yet unassigned were split among the two other segments leading from the junction. The total number of centroids chosen corresponds to the number of tributary junctions within each headwater basin for comparison with the TOCCSIC sampling protocol described below.

The fourth sampling protocol is tributary junction only, continuous cluster sampling in catchments (TOCCSIC). Moving away from m tributary junctions along each stream segment $\frac{l}{3}$ consecutive habitat units were selected for sampling. Should $\frac{l}{3}$ be sufficiently large in a direction as to encounter another tributary junction, the remaining units were split between the other two joining stream segments' habitat units.

2.3.4 Resampling

As each headwater basin's habitat unit survey constitutes a complete census, a sample of the habitat units from each basin was drawn according to each of the four sampling protocols. For each combination of basin and sampling protocol, a sample of size n was drawn D times where

$$D = max(50, tCm); \text{ where } tCm = \frac{t!}{m!(t-m)!} \tag{2.5}$$

for the GRTS, Mod. GRTS, and SRS protocols, and t represents the total number of tributary junctions within each headwater basin. There are only tCm unique samples possible for the TOCCSIC design, and all $D = tCm$ possible samples were generated.

To investigate the performance of the Mod.GRTS and TOCCSIC sampling protocols under different cluster sizes, we used sample sizes of 48 habitat units (2 clusters of 24 units or 4 clusters of 12 units), 72 habitat units (2 of 36, 3 of 24, 4 of 18, and 6 of 12), and 144 habitat units (4 of 36 and 6 of 24) (Table 2.1).

Two autocovariance models were fit to each sample. The first is the autocovariance model chosen for that basin's habitat unit census, and will be hereafter referred to as a spatial autocovariance (SAC) model. The second model, hereafter referred to as SLR, assumes no spatial autocorrelation in the sample and includes a single variance parameter. Model parameters were estimated using maximum likelihood.

2.3.5 Sample Autocovariance Parameter Performance

To evaluate the sampling protocols we first compared their ability to detect the presence of spatial autocorrelation, given that each sample was drawn from spatially autocorrelated census data. Next, we computed $\hat{R}(h)$ for each sample for lag distances of 25, 100, and 200m, and compared the bias and variance of these estimates relative to the $R(h)$ values obtained from the census data of each basin.

We dichotomized each sample into one of two categories based on the SAC and SLR AIC values. We considered the SAC and SLR fits as competing models if the difference between their AIC values was within 2 units (*Burnham and Anderson*, 2002). All samples with competing models or lower SRS AIC values were classified as lacking strong evidence of spatial autocorrelation. All other samples where classified as having evidence of spatial autocorrelation. We used this dichotomization to create a response variable for each sample. Samples lacking evidence of spatial autocorrelation were assigned a value of 0, and all others were assigned a value of 1. We fit a binomial generalized linear model (GLM) to this response variable, with logit link function, to estimate the probability that each sampling protocol would lead to samples with evidence of spatial autocorrelation.

Explanatory covariates in the GLM included indicator variables for sampling protocol types, and continuous basin-specific covariates to account for variation due to basins. We chose covariates that may be obtained from standard geographic information system (GIS) software. These covariates were the relative maximum distance of each sample, basin shape, the basin's drainage density, and the proportion of the basin's stream length comprised of first-order streams. Relative maximum distance is calculated by taking

the maximum distance of any two locations within a sample, and dividing by the maximum distance between sampling locations from the census data for that basin. Basin shape is calculated in two steps. First, the longest straight-line distance between a basin boundary and the basin outlet is determined. Next, this value is squared and divided by the basin area (Figure 2.2). We also included the total number of habitat units from the census of each headwater basin. All non-sampling protocol covariates where centered at their means to allow the interpretation of the sampling protocol coefficients relative to the model intercept (GRTS sampling protocol) at the average level of all basin covariates and to minimize multicollinearity. Interactions among basin covariates and between basin covariates and sampling protocols were investigated using likelihood ratio drop in deviance tests.

The relative bias, mean-squared error (MSE), and variance of each protocol was compared for $\hat{R}(h)$ values at distances (h) of 25, 100, and 200m. For the $j = 1 \ldots D$ samples from the ith basin for each protocol and sample size we compute relative bias as

$$Relative\ Bias = \frac{\sum_{j=1}^{D} \left(\hat{R}(h)_{j,i} - R(h)_i\right)}{R(h)_i D} \tag{2.6}$$

and MSE as

$$MSE = \frac{\sum_{j=1}^{D} \left(\hat{R}(h)_{j,i} - R(h)_i\right)^2}{D} \tag{2.7}$$

MSE is the sum of variance and the squared bias, so we also computed the variance as

$$Variance = MSE - \left(\frac{\sum_{j=1}^{D} \left(\hat{R}(h)_{j,i} - R(h)_i\right)}{D}\right)^2 \tag{2.8}$$

To summarize the performance of the sampling protocols we will present the relative bias and variance values in the results section. We will also compute the relative bias for the nugget parameter for sample sizes of 48.

2.3.6 Distribution of Interpoint Lag Distances

A benefit of including distributed sets of clusters is to ensure both small and large lag distances among the sampling locations. To evaluate this we first divided all interpoint sample distances by the largest distance within each basin. Next, we partitioned these distances into 20 bins. Finally, we computed the average proportion, across all samples and basins for each of the sampling protocols, of all inter-point distances that fell within each bin for sample sizes of 48 and 144.

2.4 RESULTS

2.4.1 Census Data

All twelve headwater basins exhibited evidence of spatial autocorrelation via inspection of AIC values and empirical semivariograms. The census data from each headwater basin also indicated strong nugget contributions with RSV values ranging from 0.20 to 0.55. Ten of the twelve headwater basins considered for the 48 and 72 sample sizes were best fit via traditional Euclidean distance autocovariance models, and two were best fit via in-stream distance moving average autocovariance models. Only six of the twelve basins had fish-bearing stream segments within a network of sufficient tributary junctions for consideration at sample sizes of 144. All six of the basins used for the 144 sample size analysis were best fit via Euclidean distance autocovariance models.

2.4.2 Sampling Protocol Performance

We present the results obtained from samples with relative maximum distances greater than 0.5, and TOCCSIC protocols from the largest cluster sizes for sample sizes of 48 and 72 ($m = 2$ and $m = 2$ and 3, respectively). The TOCCSIC protocol performance for the smallest-sized clusters at sample sizes of 48 and 72 were removed from the analysis due to very small numbers of possible samples (D).

2.4.2.1 Probability of Obtaining Samples with Evidence of Spatial Autocorrelation

As sample sizes increase, regardless of basin shape or drainage density, the overall estimates of the probability of obtaining samples with evidence of spatial autocorrelation increases (Figure 2.3).

For sample sizes of 48, the estimated odds that a sample has evidence of spatial autocorrelation differs among sampling protocols, and there is evidence that sampling protocol behavior depends on basin covariates (Table 2.2). Compared to the GRTS sampling protocol, all other protocols have higher estimated probabilities of obtaining a sample with evidence of spatial autocorrelation (Figure 2.3), and the two cluster protocols have higher estimated probabilities than the non-cluster protocols. For all sampling protocols, the odds of obtaining a sample with evidence of spatial autocorrelation is negatively associated with the number of census habitat units, headwater basin area, and the percentage of stream length comprised of first-order streams, and positively associated with the relative maximum distance of each sample (Table 2.2). The effect of drainage density depends on basin

shape (Figure 2.3). Increasing drainage densities are estimated to decrease the probability of obtaining a sample with evidence of spatial autocorrelation more sharply in spherical shaped basins than linear shaped basins. At lower drainage densities, the estimated probability of obtaining a sample with spatial autocorrelation is higher in spherical basins than linear basins. The TOCCSIC sampling protocol shows lower estimated probabilities of obtaining samples with spatial autocorrelation than the Mod. GRTS protocols at higher drainage densities, regardless of basin shape (Figure 2.3).

For sample sizes of 72, the differences among sampling protocols and associations with basin covariates (Table 2.3) are very similar to those observed for samples sizes of 48, though the estimated probabilities of obtaining samples with evidence of spatial autocorrelation are generally higher across all sampling protocols (Figure 2.3). The estimated probabilities for the larger TOCCSIC ($m = 2$) samples are very similar to those from the Mod. GRTS protocols, but the probability of obtaining samples with spatial autocorrelation for smaller TOCCSIC ($m = 3$) samples is estimated to decrease more sharply with increasing drainage densities than the Mod. GRTS protocols.

At sample sizes of 144, the interacting effect of drainage density by headwater basin shape was more pronounced than that from sample sizes of 48 and 72 (Figure 2.3), but all sampling protocols responded similarly to changes in drainage density by basin shape (Table 2.4). In more linearly shaped basins, there is no estimated effect of drainage density on the probability of obtaining samples with evidence of spatial autocorrelation (Figure 2.3). Increasing samples sizes to 144 lead to higher estimated probabilities of obtaining samples with evidence of spatial autocorrelation across all sampling protocols compared to smaller sample sizes. The pattern among sampling protocols is similar to that observed with the smaller samples sizes, but over the major-

ity of the drainage density range in both basin shapes the smaller TOCCSIC (m=6) cluster samples have the lowest probability of obtaining samples with evidence of spatial autocorrelation.

For all three sample sizes the Mod. GRTS protocols were among the highest probabilities of obtaining samples with evidence of spatial autocorrelation, and were less affected by increasing drainage densities in more linearly shaped basins. Except for the largest sample size, the GRTS and SRS protocols had the lowest probabilities of obtaining samples with evidence of spatial autocorrelation.

2.4.2.2 Bias and Variance of $\hat{R}(h)$

Overall, the bias of the GRTS and SRS protocols approached that of the cluster methods as samples sizes increased. Changes in relative bias with increasing sample size were not observed for the cluster-based sampling protocols. The variance of all protocols generally decreased as lags increased, but at 200m few changes were observed. Across all lags and sampling protocols variance did generally decrease with increasing sample size.

Sample Size = 48

At 25m, the GRTS sampling protocol was unbiased, the SRS protocol was slightly negatively biased, and all cluster-based sampling methods were negatively biased (Figure 2.4). The GRTS and SRS protocols had higher variance than the cluster-based sampling methods. At 100m, the bias was

more similar among sampling protocols, but the GRTS protocol was still less biased and the TOCCSIC protocol exhibited more negative bias than the other sampling methods. The difference in variance among sampling protocols was less pronounced than at 25m, though TOCCSIC exhibited lower variance. At 200m, all protocols were negatively biased, with only the TOCCISC protocol separating as lower than the other methods. Consistent with the other distances for sample sizes of 48, the TOCCSIC also had smaller variance.

The unbiased yet highly variant nature of the GRTS and SRS protocols prompted a closer look at the relative bias of the nugget parameter. At this sample size, both the GRTS and SRS protocols demonstrated stronger negative relative bias for the nugget parameter than the cluster-based protocols (Figure 2.5).

Sample Size = 72

At 25m, all Mod. GRTS and TOCCSIC protocols were negatively biased, and the GRTS and SRS protocols were less biased (Figure 2.6). Though the TOCCCSIC protocols showed slightly less variance, there is generally little difference among the variances of the other protocols. The pattern was similar for a lag of 100m, though the difference in bias between the cluster-based and non-cluster based methods was smaller than at a lag of 25m. At 200m, the TOCCSIC protocols showed more negative bias than the other protocols, and there was generally little difference in the variances among the protocols.

Sample Size = 144

At 25m, the GRTS and SRS were generally less biased than the cluster-based protocols, and contrary to the smaller sample sizes, the GRTS and SRS variances at 25m were comparable to the other protocols (Figure 2.7). For a lag of 100m, the TOCCSIC protocols showed more negative bias, but the box-plot quantiles of all protocols overlap, and the variance of the GRTS and 6-cluster TOCCSIC protocols were generally lower than the SRS and Mod. GRTS protocols. At 200m, the TOCCSIC protocols showed the most negative bias and generally smaller variances. The other protocols were comparably negatively biased, but the GRTS protocols had generally smaller variance.

2.4.2.3 Distribution of Interpoint Lag Distances

The continuous sampling of the two cluster-based protocols lead to higher proportions of small interpoint distances compared to the GRTS and SRS protocols, but no other substantial differences were observed in other distance bins (Figure 2.8).

2.5 DISCUSSION

The basin-specific covariate values of the 12 basins utilized in this study are generally representative of those from the 40 basins dataset of which the 12 were selected. With the exception of total census size, the mean of all covariate values we considered were very close to the mean values of those

covariates from the 40-basins dataset. The mean census size for the subset of basins within this analysis was 470 and roughly 200 units higher than the overall mean of 277. The values of the basin shape covariate included the minimum and maximum values of the 40 basins, and the area covariate included the minimum and 2nd largest values. The drainage density values for the 12 basins we used included the maximum value from the 40 basins, but 7 density values from the 40 basins were smaller. Our subset included the smallest percentage of first-order stream length, but there were 5 higher values within the 40 basins than the subset's maximum. The subset considered here was specifically selected to have sufficient fish-bearing tributaries to investigate sampling clusters located at tributary confluences.

The investigation into the probability that each sampling protocol leads to a sample with evidence of spatial autocorrelation suggests interesting notions about the role of basin structure in sampling. A stronger decrease in the probability of obtaining samples with evidence of spatial autocorrelation was observed for spherically shaped basins than linearly shaped basins. The increased number of flow-connected habitat units per distance might account for the dampened effect of increasing drainage density in more linearly shaped basins. Given a fixed area and fixed sample size, an increase in drainage density within a spherically shape basin implies more un-flow connected habitat units, as opposed to an increasing drainage density within a more linear shaped headwater basin.

In this analysis the extent of the sampling domain was important. Increasing values of relative maximum distance were associated with increased probabilities of a sample capturing spatial autocorrelation.

Estimation of autocorrelation functions was less affected by differences among sampling protocols than was the detection of the presence of spatial

autocorrelation. In general, for all sample sizes and lag distances, the autocorrelation function estimates were negatively biased. This is consistent with the work of *Irvine et al.* (2007) that found maximum likelihood estimates lead to underestimated autocorrelation function values when range parameters are large.

The GRTS and SRS protocols showed the least relative bias for lags of 25m and 100m at sample sizes of 48 and 72, but also showed larger variance, especially at sample sizes of 48. This is likely due to the severe negative relative bias of the nugget parameter for the GRTS and SRS protocols. A similar, though less extreme, difference was observed for the nugget parameter for samples sizes of 72. As noted in Section 2.2, the divisor of the autocorrelation function contains the nugget parameter, and severe underestimation of the nugget will inflate autocorrelation estimates. The GRTS and SRS protocols were less likely to result in samples with evidence of spatial autocorrelation. When their samples were spatially autocorrelated they were estimated to have very small nugget values. The lack of sample points occurring at the smallest lag distances might explain the inability for proper nugget parameter estimation at smaller sample sizes, but the cluster based protocols had more small interpoint distances at sample sizes of 144 when relative bias values were generally consistent among protocols.

The tributary junctions were indeed sources of heterogeneity, and seemingly too heterogeneous for effective estimation of spatial autocovariance parameters. The smallest TOCCSIC clusters at sample sizes of 48 and 72 were the most affected by changes in drainage density and had the lowest estimated probability of obtaining samples with evidence of spatial autocorrelation at sample sizes of 144. Only the larger-clustered TOCCSIC protocol performance was comparable to the Mod. GRTS generated samples,

when the three "arms" of the TOCCSIC clusters extended further into the three stream segments joining at each tributary junction. Smaller-clustered TOCCSIC samples were also generally the most negatively biased among the sampling protocols.

The size of the clusters we considered could be a reason that we did not see superior performance from our cluster-based sampling protocols in regards to estimation of autocorrelation function parameters. At the onset, we were interested in comparing Mod. GRTS and TOCCSIC clusters containing the same number of habitat units. We therefore restricted our cluster-based sampling designs to contain small numbers of large clusters. The designs deemed optimal by *Zimmerman* (2006) and *Zhu and Stein* (2005) contained many more, and hence, smaller, clusters distributed across the sampling domain, and those of *Zhu and Zhang* (2006) contained several clusters of varying sizes and non-clustered sampling locations. An investigation comparing GRTS, larger numbers of smaller- sized Mod. GRTS, and a combination of GRTS and Mod. GRTS might prove a useful exercise. This would more closely mimic the cluster sizes and distributions of these studies. It would also allow an increased number of the 40 headwater basins to be used by eschewing the need to consider the number of tributary confluences.

Variation among basins could be another reason for not observing more distinctive bias and variance differences among the sampling protocols. In particular, the sample sizes represented different proportions of the census size from each basin. The average number of census habitat units was 470 for the 12 basins used for sample sizes of 48 and 72 (range: 195 - 713). The analysis for a sample size of 144 was carried out with 6 basins, whose number of habitat units ranged from 340 to 713 (5 of those six had more than 600 habitat units). As the sample size became a smaller proportion of the census

size the probability of obtaining a sample with autocorrelation decreased. To generalize the relative merits of sampling designs for autocovariance parameter estimation across streams we considered a broad set of census sizes, but this may have clouded our ability to detect differences.

Our investigation is based on the assumption that the goal of the analysis is to estimate the spatial autocovariance function to describe the spatial pattern within headwater basins. If the analysis goal is estimating autocovariance parameters for prediction of fish counts in habitat units, both *Zhu and Stein* (2005) and *Zimmerman* (2006) suggest that regularly spaced sample points, that also contain several small clusters, may be optimal. This differs from their recommendations for the estimation of autocovariance function parameters in which all sample points are within clusters. The GRTS and Mod. GRTS combination described above may also prove fruitful for an investigation regarding sampling designs for optimal prediction performance.

Only two of the basins considered here were best fit by up-stream moving average models. Further developments have led to valid moving average autocovariance models that incorporate both flow-connected and unconnected locations (*Garreta et al.*, 2009). These may be more appropriate for lotic organisms, like fish, that are capable of moving up and downstream. If only up-stream moving average models are considered, utilizing some larger TOCCSIC samples within a broader sampling plan may help improve autocovariance parameter estimation. TOCCSIC samples do ensure a sample would contain flow-connected locations, and also provide better nugget parameter estimation via clustering.

Our work demonstrates that implementing a GRTS sampling protocol may be sensible if obtaining spatially distributed samples without spatial autocorrelation is of interest, especially when the sample size is small in

comparison to the census size. The GRTS protocol did have lower estimated probabilities of obtaining samples with evidence of spatial autocorrelation than even the SRS protocol. Additionally, the GRTS protocol would provide a spatially distributed sample.

In terms of estimating autocovariance function parameters in headwater stream networks, implementing a sampling protocol that includes a spatially distributed set of large clusters, akin to the Mod. GRTS framework we proposed, may be preferred in that better nugget estimation performance can be expected. There remains substantial room for refinement in regards to general results for optimal sampling designs across heterogeneous systems such as headwater stream networks.

Table. 2.1: Sample sizes by number of clusters and cluster size.

Sample Size n	Number of Clusters m	Cluster Size l
48	2	24
	4	12
72	2	36
	3	24
	4	18
	6	12
144	4	36
	6	24

Table. 2.2: Estimated effects of basin covariates and sampling protocols on the odds a sample has spatial autocorrelation for sample sizes equal to 48. Odds effects represent 50-unit increases in basin census size and $.25km^2$ increases in basin area.

Variable	Estimate	Std. Error	Effect	Lower 95% CI	Upper 95% CI
Intercept	-1.9257	0.1251	0.1458	0.1141	0.1863
Census Size	-0.0018	0.0003	0.9142	0.8887	0.9403
Drainage Density	-3.0485	0.3375	0.0474	0.0245	0.0919
Basin Shape	0.1473	0.0636	1.1587	1.0230	1.3124
Area (km^2)	-0.3912	0.0548	0.9068	0.8828	0.9315
First-order Percentage	-7.7055	0.9419	0.0005	0.0001	0.0029
Sample Rel. Max. Dist	3.1750	0.5635	1.0323	1.0209	1.0437
Mod. GRTS-2	1.7468	0.2189	5.7362	3.7350	8.8097
Mod. GRTS-4	2.1011	0.2028	8.1753	5.4940	12.1653
SRS	0.5338	0.1346	1.7054	1.3100	2.2201
TOCCSIC-2	1.6933	0.4323	5.4373	2.3303	12.6869
DrainDens*Basin Shape	1.7294	0.2098	5.6375	3.7365	8.5057
DrainDens*Mod.GRTS-2	0.9904	0.4129	2.6922	1.1984	6.0479
DrainDens*Mod.GRTS-4	0.4815	0.3566	1.6185	0.8046	3.2559
DrainDens*SRS	0.0236	0.3373	1.0238	0.5286	1.9831
DrainDens*TOCCSIC-2	-0.6286	0.8776	0.5333	0.0955	2.9787

Table. 2.3: Estimated effects of basin covariates and sampling protocols on the odds a sample has spatial autocorrelation for sample sizes equal to 72. Odds effects represent 50-unit increases in basin census size and $.25km^2$ increases in basin area.

Variable	Estimate	Std. Error	Effect	Lower 95% CI	Upper 95% CI
Intercept	-1.1660	0.1171	0.3116	0.2477	0.3920
Census Size	-0.0025	0.0003	0.8825	0.8597	0.9059
Drainage Density	-3.6388	0.2814	0.0263	0.0151	0.0456
Basin Shape	0.4976	0.0628	1.6449	1.4545	1.8601
Area (km^2)	-0.4145	0.0484	0.9016	0.8804	0.9232
First-order Percentage	-9.2341	0.8137	0.0001	0.0000	0.0005
Sample Rel. Max. Dist	4.8425	0.4507	1.0496	1.0404	1.0589
Mod. GRTS-2	1.8886	0.1973	6.6101	4.4900	9.7311
Mod. GRTS-3	1.8408	0.1770	6.3014	4.4541	8.9150
Mod. GRTS-4	2.0083	0.1791	7.4506	5.2449	10.5839
Mod. GRTS-6	2.0342	0.2062	7.6460	5.1045	11.4528
SRS	0.5223	0.1242	1.6858	1.3216	2.1505
TOCCSIC-2	2.1648	0.3660	8.7128	4.2524	17.8520
TOCCSIC-3	1.5957	0.2548	4.9317	2.9930	8.1260
DrainDens*Basin Shape	1.0995	0.1908	3.0026	2.0656	4.3646
DrainDens*Mod.GRTS-2	1.5453	0.3721	4.6894	2.2616	9.7235
DrainDens*Mod.GRTS-3	1.7947	0.3095	6.0178	3.2807	11.0388
DrainDens*Mod.GRTS-4	1.0335	0.2939	2.8110	1.5801	5.0008
DrainDens*Mod.GRTS-6	0.6612	0.3804	1.9372	0.9191	4.0831
DrainDens*SRS	0.0968	0.3055	1.1017	0.6054	2.0048
DrainDens*TOCCSIC-2	0.6907	0.6432	1.9952	0.5656	7.0385
DrainDens*TOCCSIC-3	-0.8164	0.4784	0.4420	0.1731	1.1290

Table. 2.4: Estimated effects of basin covariates and sampling protocols on the odds a sample has spatial autocorrelation for sample sizes equal to 144.

Variable	Estimate	Std. Error	Effect	Lower 95% CI	Upper 95% CI
Intercept	0.4853	0.1766	1.6247	1.1494	2.2964
Drainage Density	-1.8114	0.1402	0.1634	0.1242	0.2151
Basin Shape	-1.2609	0.2793	0.2834	0.1639	0.4899
Sample Rel. Max. Dist	7.4422	0.7476	1.0773	1.0616	1.0932
Mod. GRTS-4	1.7568	0.2926	5.7937	3.2649	10.2811
Mod. GRTS-6	1.5483	0.3107	4.7034	2.5584	8.6468
SRS	0.2420	0.2101	1.2738	0.8439	1.9226
TOCCSIC-4	2.0339	0.3213	7.6438	4.0723	14.3476
TOCCSIC-6	-0.0141	0.2688	0.9860	0.5822	1.6699
DrainDens*Basin Shape	3.7200	0.5166	41.2640	14.9919	113.5754

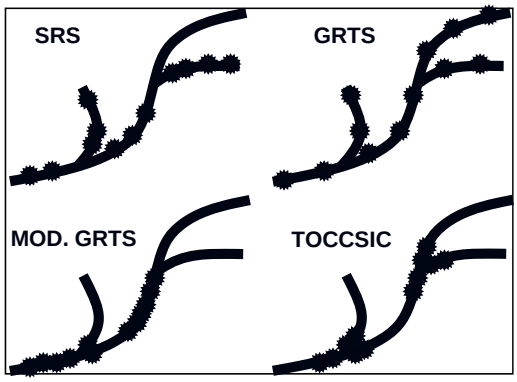

Figure. 2.1: Basic representations of each sampling protocol.

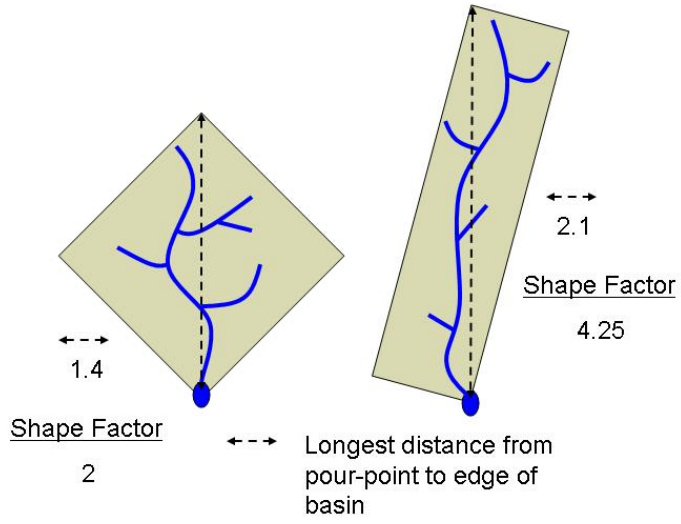

Figure. 2.2: Examples of shape factor calculation. Each basin has area equal to 1 unit^2.

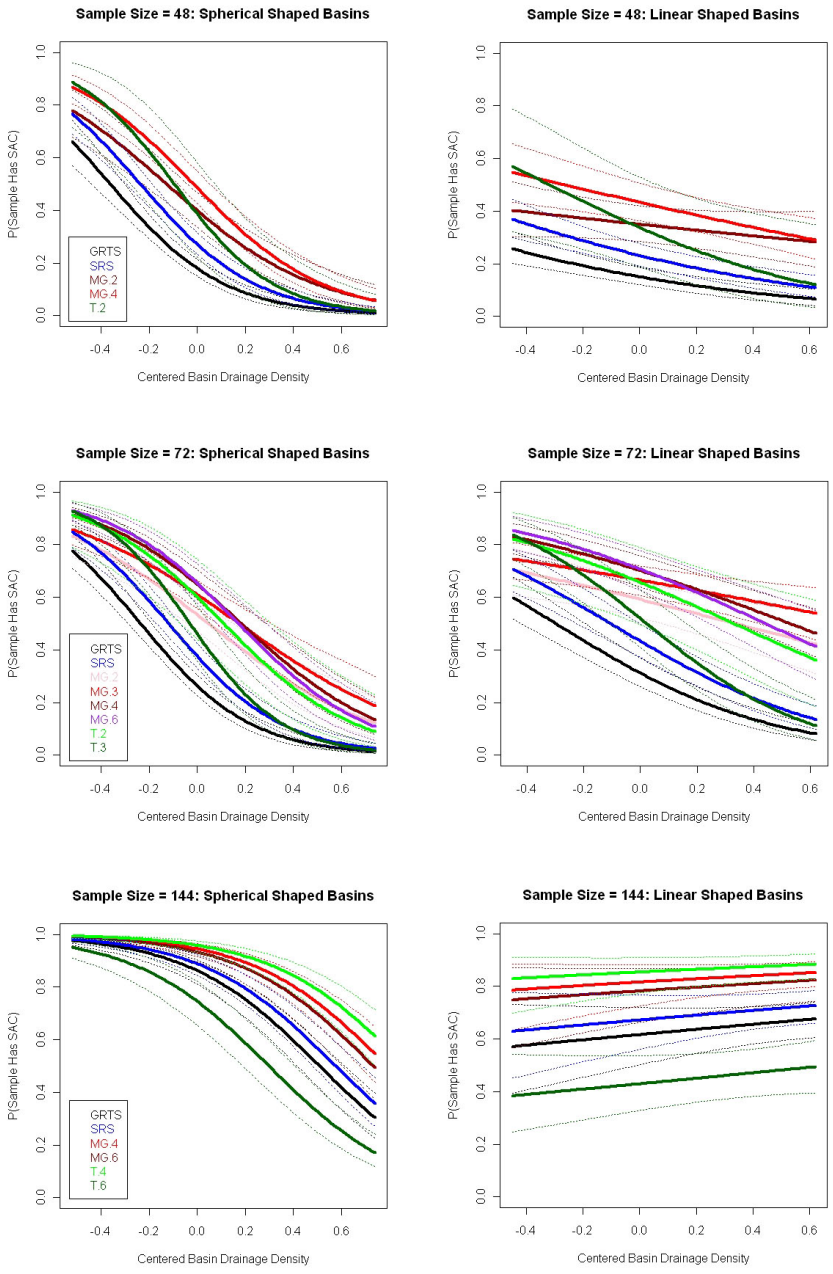

Figure. 2.3: Effects of sampling design and headwater basin drainage density on the probability that samples contain spatial autocorrelation, by basin shape. In each graph the relative maximum distance is set to the average of each sampling protocol. The first-order percentage, maximum census size, and headwater basin areas are set to the average within each basin shape. The x-axis in each plot represents the range of centered drainage densities within each shape, and the spherical-shaped basins span a slightly larger range of values. Dotted lines represent 95% confidence intervals.

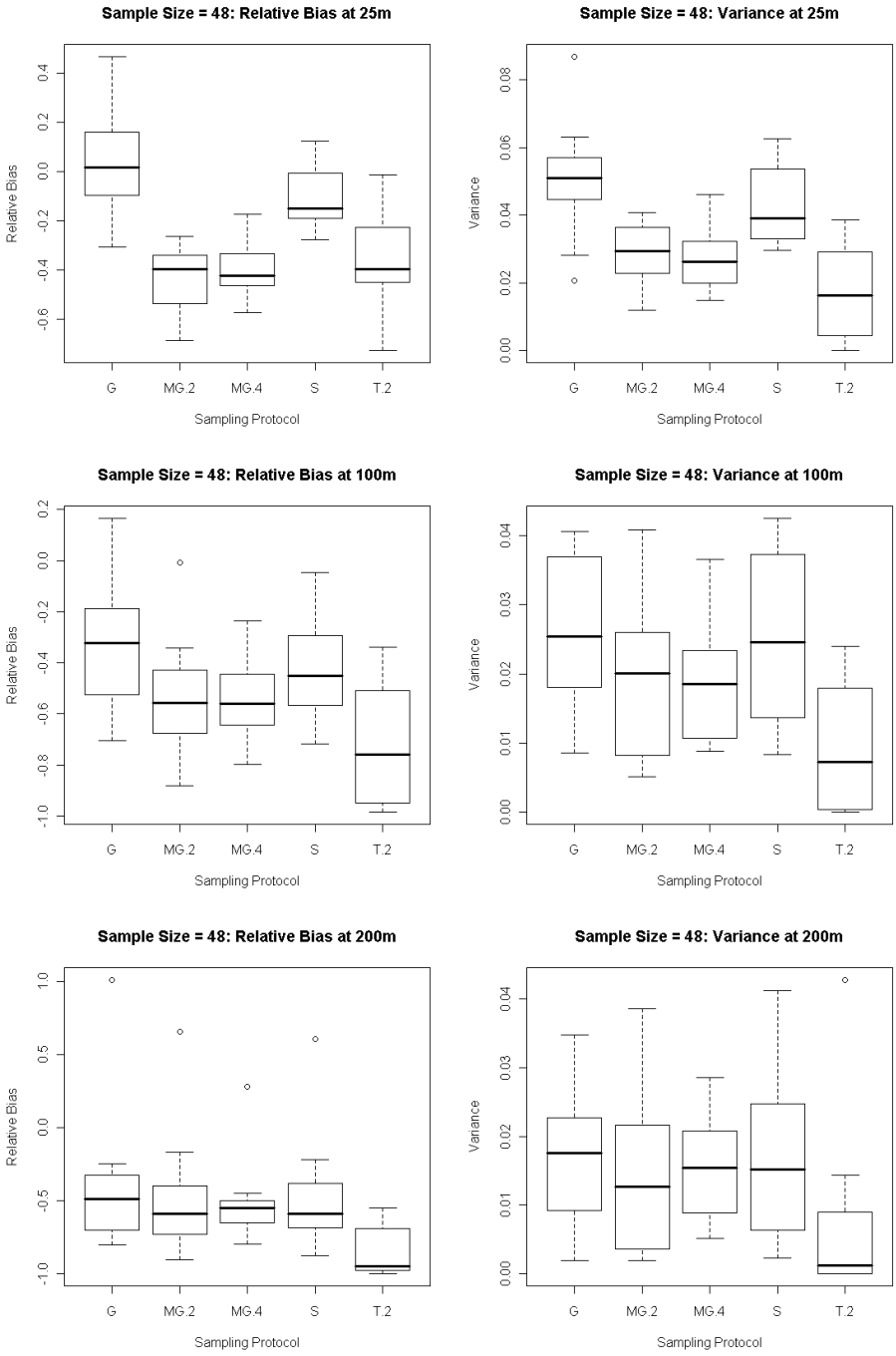

Figure. 2.4: Relative bias and variance of estimating the autocorrelation function at 25m, 100m, and 200m for sample sizes of 48 and GRTS (G), SRS (S), Mod. GRTS (MG.x) and TOCCSIC (T.x) sampling protocols. .x refers to the number of clusters. Each protocol includes values calculated at each basin.

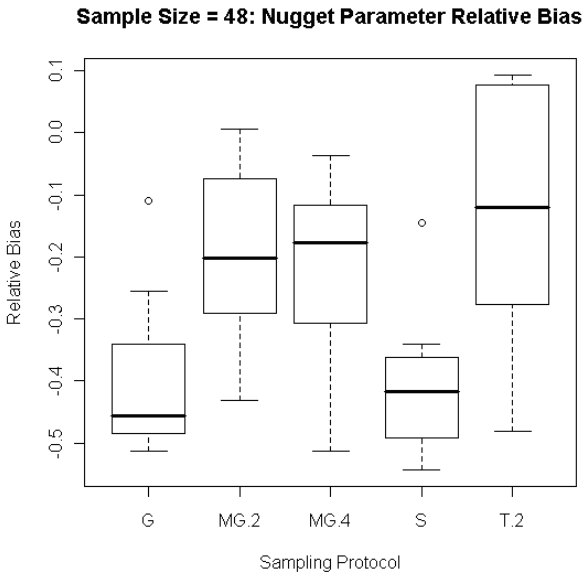

Figure. 2.5: Relative bias of the nugget parameter for sample sizes of 48 and GRTS (G), SRS (S), Mod. GRTS (MG.x) and TOCCSIC (T.x) sampling protocols. .x refers to the number of clusters. Each protocol includes values calculated at each basin.

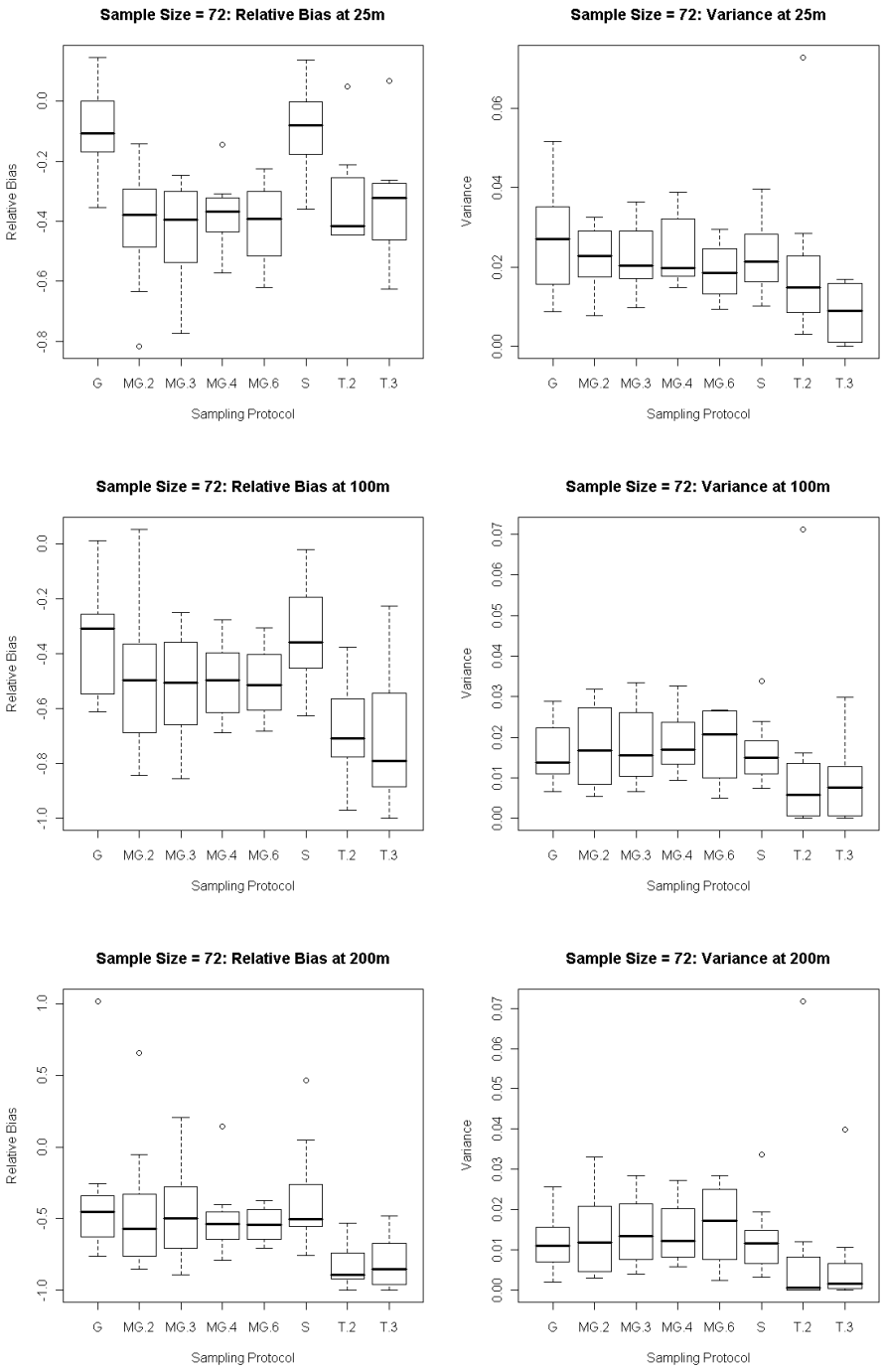

Figure. 2.6: Relative bias and variance of estimating the autocorrelation function at 25m, 100m, and 200m for sample sizes of 72 and GRTS (G), SRS (S), Mod. GRTS (MG.x) and TOCCSIC (T.x) sampling protocols. .x refers to the number of clusters. Each protocol includes values calculated at each basin.

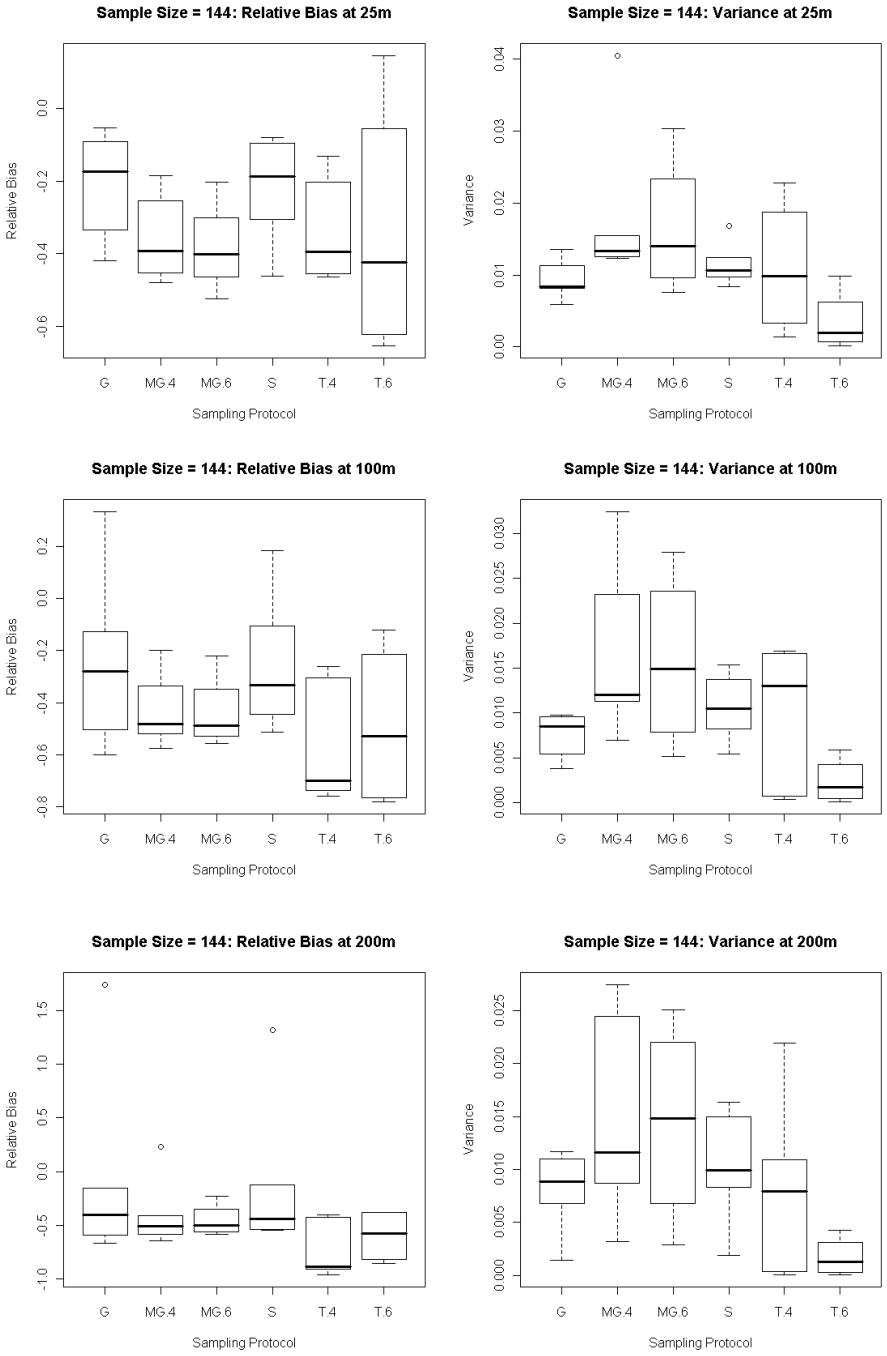

Figure. 2.7: Relative bias and variance of estimating the autocorrelation function at 25m, 100m, and 200m for sample sizes of 144 and GRTS (G), SRS (S), Mod. GRTS (MG.x) and TOCCSIC (T.x) sampling protocols. .x refers to the number of clusters. Each protocol includes values calculated at each basin.

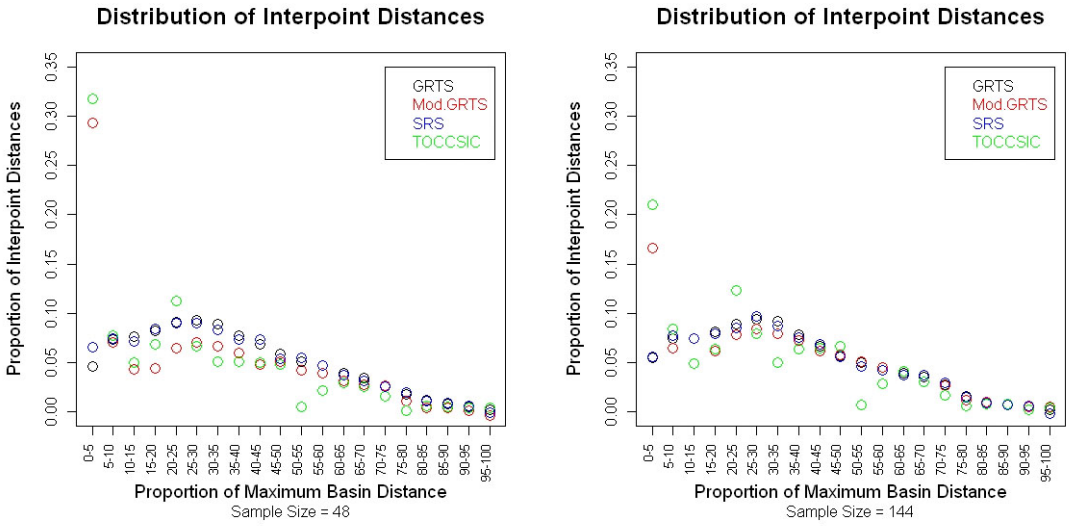

Figure. 2.8: Distribution of interpoint relative distances averaged by sampling protocol and across all headwater basins, for sample sizes of 48 and 144.

BIBLIOGRAPHY

Bateman, D. S., R. E. Gresswell, and C. E. Torgersen (2005), Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution, *Journal of Freshwater Ecology*, *20*, 335–345.

Benda, L., K. Andras, D. Miller, and P. Bigelow (2004a), Confluence effects in rivers: Interactions of basin scale, network geometry, and disturbance regimes, *Water Resources Research*, *40*,

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock (2004b), The network dynamics hypothesis: How channel networks structure riverine habitats, *BioScience*, *54*(4), 413–427.

Blair, B. C. (2005), Fire effects on the spatial patterns of soil resources in a Nicaraguan wet tropical forest, *Journal of Tropical Ecology*, *21*, 435–444, doi:10.1017/S0266467405002452.

Bouza, N., J. Caujape-Castells, M. A. Gonzalez-Perez, F. Batista, and P. A. Sosa (2002), Population structure and genetic diversity of two endangered endemic species of the Canarian laurel forest: *Dorycnim spectabile (fabaceae)* and *Isoplexis chalcantha (scrophulariaceae)*, *International Journal of Plant Sciences*, *163*(4), 619–630.

Bulit, C., C. Diaz-Avalos, M. Signoret, and D. J. S. Montagnes (2003), Spatial structure of planktonic ciliate patches in a tropical coastal lagoon: an application of geostatistical methods, *Aquatic Microbial Ecology*, *30*, 185–196.

Bulit, C., C. Diaz-Avalos, and D. J. S. Montagnes (2004), Assessing spatial and temporal patchiness of the autotrophic ciliate *Myrionecta rubra*: a case study in a coastal lagoon, *Marine Ecology Progress Series*, *268*, 55–67.

Burnham, K. P., and D. R. Anderson (2002), *Model Selection and Multimodel Inference: A Practical InformationTheoretic Approach*, 2 ed., Springer-Verlag, New York, NY.

Cooper, S. D., L. Barmuta, O. Sarnelle, K. Kratz, and S. Diehl (1997), Quantifying spatial heterogeneity in streams, *Journal of the North American Benthological Society*, *16*(1), 174–188.

Cressie, N., and J. J. Majure (1997), Spatio-temporal statistical modeling of livestock waste in streams, *Journal of Agricultural, Biological, and Environmental Statistics*, *2*(1), 24–47.

Cressie, N., J. Frey, B. Harch, and M. Smith (2006), Spatial prediction on a river network, *Journal of Agricultural, Biological, and Environmental Statistics*, *11*(2), 127–150.

Dent, C. L., and N. B. Grimm (1999), Spatial heterogeneity of stream water nutrient concentrations over successional time, *Ecology*, *80*(7), 2283–2298.

Downes, B. J., P. S. Lake, and E. S. G. Schreiber (1993), Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organization, *Freshwater Biology*, *30*, 119–132.

Ettema, C. H., and D. A. Wardle (2002), Spatial soil ecology, *TRENDS in Ecology & Evolution*, *17*(4), 177–183.

Ferguson, R. I., J. T. Cudden, T. B. Hoey, and S. P. Rice (2006), River system discontinuities due to lateral inputs: generic styles and controls, *Earth Surface Processes and Landforms*, *31*, 1149–1116, doi:10.1002/esp.1309.

Ganio, L. M., C. E. Torgersen, and R. E. Gresswell (2005), A geostatistical approach for describing spatial pattern in stream networks, *Frontiers in Ecology and the Environment*, *3*(3), 138–144.

Gardner, B., P. J. Sullivan, and J. L. Arthur Jr. (2003), Predicting stream temperatures: Geostatistical model comparison using alternative distance metrics, *Canadian Journal of Fisheries and Aquatic Sciences*, *60*, 344–351, doi:10.1139/F03-025.

Garreta, V., P. Monestiez, and J. M. Ver Hoef (2009), Spatial modelling and prediction on river networks: up model, down model or hybrid?, *Environmetrics*, doi:10.1002/env.995.

Gascuel-Odoux, C., and P. Boivin (1994), Variability of variograms and spatial estimates due to soil sampling: a case study, *Geoderma*, *62*, 165–182.

Gresswell, R. E., D. S. Bateman, G. W. Lienkaemper, and T. J. Guy (2004), Geospatial techniques for developing a sampling frame of watersheds across a region, in *GIS/Spatial Analyses in Fishery and Aquatic Sciences*, vol. 2, edited by T. Nishida, P. J. Kailola, and C. E. Hollingworth, pp. 515–528, Fishery-Aquatic GIS Research Group, Saitama, Japan.

Grundmann, G. L., and D. Debouzie (2000), Geostatistical analysis of the distribution of NH4+ and NO3- -oxidizing bacteria and serotypes at the millimeter scale along a soil transect, *FEMS Microbiology Ecology*, *34*, 57–62.

Huettmann, F., and A. W. Diamond (2006), Large-scale effects on the spatial distribution of seabirds in the northwest Atlantic, *Landscape Ecology*, *21*, 1089–1108, doi:10.1007/s10980-006-7246-8.

Hynes, H. B. N. (1975), The stream and its valley, *Internationale Vereinigung fr Theoretische und Angewandte Limnologie*, *19*, 1–15.

Irvine, K. M., A. I. Gitelman, and J. A. Hoeting (2007), Spatial designs and properties of spatial correlation: Effects on covariance estimation, *Journal of Agricultural, Biological, and Environmental Statistics*, *12*(4), 450–469, doi:10.1198/108571107X249799.

Isaak, D. J., and R. F. Thurow (2006), Network-scale spatial and temporal variation in chinook salmon (*Oncorhynchus tshawutscha*) redd distributions: Patterns inferred from spatially continuous replicate surveys, *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 285–296, doi: 10.1139/F05-214.

Kiffney, P. M., C. M. Greene, J. E. Hall, and J. R. Davies (2006), Tributary streams create spatial discontinuities in habitat, biological productivity, and diversity in mainstem rivers, *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 2518–2530, doi:10.1139/F06-138.

Kincaid, T., T. w. c. f. D. S. Olsen, C. Platt, D. White, and R. Remington (2008), *spsurvey: Spatial Survey Design and Analysis*, r package version 2.0.

Legendre, P. (1993), Spatial autocorrelation: Trouble or new paradigm?, *Ecology*, *74*(6), 1659–1673.

Little, L. S., D. Edwards, and D. E. Porter (1997), Kriging in estuaries: as the crow flies, or as the fish swims?, *Journal of Experimental Marine Biology and Ecology*, *213*, 1–11.

Lloyd, N. J., R. Mac Nally, and P. S. Lake (2005), Spatial autocorrelation of assemblages of benthic invertebrates and its relationship to environmental factors in two upland river in southeastern Australia, *Diversity and Distributions*, *11*, 375–386, doi:10.1111/j.1366-9516.2005.00166.x.

Mast, J. N., and T. T. Veblen (1999), Tree spatial patterns and stand development along the pinegrassland ecotone in the Colorado Front Range, *Canadian Journal of Forest Research*, *29*, 575–584.

Muller, W. G., and D. L. Zimmerman (1999), Optimal designs for variogram estimation, *Environmetrics*, *10*, 23–37.

Muneto, H., N. Ohte, N. Karasawa, G.-s. Zhang, L.-h. Wang, and K. Yoshikawa (2001), Plant species effect on the spatial patterns of soil properties in the Mu-us desert ecosystem, inner Mongolia, China, *Plant and Soil*, *234*, 195–205.

Neville, H. M., D. J. Isaak, J. B. Dunham, R. F. Thurow, and B. E. Rieman (2006), Fine-scale natal homing and localized movement as shaped by sex and spawning babitat in chinook salmon: insights from spatial autocorrelation analysis of individual genotypes, *Molecular Ecology*, *15*, 4589–4602, doi:10.1111/j.1365-294X.2006.03082.x.

Peterson, E. E., and N. S. Urquhart (2006), Predicting water quality impaired stream segments using landscape-scale data and a regional geostatistical model: A case study in Maryland, *Environmental Monitoring and Assessment*, *121*, 615–638, doi:10.1007/s10661-005-9163-8.

Peterson, E. E., D. M. Theobald, and J. M. Ver Hoef (2007), Geostatistical modelling on stream networks: Developing valid covariance matrices based on hydrologic distance and stream flow, *Freshwater Biology*, *52*, 267–279, doi:10.1111/j.1365-2427.2006.01686.x.

Pickett, S. T. A., and M. L. Cadenasso (1995), Landscape ecology: Spatial heterogeneity in ecological systems, *Science*, *269*, 331–334.

Poole, G. C. (2002), Fluvial landscape ecology: Addressing uniqueness within the river discontinuum, *Freshwater Biology*, *47*, 641–660.

Pooler, P. S., and D. R. Smith (2005), Optimal sampling design for estimating spatial distribution and abundance of a freshwater mussel population, *Journal of the North American Benthological Society*, *24*(3), 525–537, doi: 10.1139/F06-145.

R Development Core Team (2005), *R: A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0.

Rathbun, S. L. (1998), Spatial modelling in irregularly shaped regions: Kriging estuaries, *Environmetrics*, *9*, 109–129.

Rice, S., and M. Church (1998), Grain size along two gravel-bed rivers: statistical variation, spatial pattern and sedimentary links, *Earth surface processes and landforms*, *23*, 345–363.

Rice, S. P., R. I. Ferguson, and T. B. Hoey (2006), Tributary control of physical heterogeneity and biological diversity at river confluences, *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 2553–2566, doi: 10.1139/F06-145.

Rossi, J.-P. (2003), Clusters in earthworm spatial distribution, *Pedobiologia*, *47*, 490–496.

Russo, D., and E. Bresler (1981), Soil hydraulic properties as stochastic processes: I. an analysis of field spatial varability, *Soil Science Society of America Journal*, *45*, 682–687.

Russo, D., and W. A. Jury (1987), A theoretical study of the estimation of the correlation scale in spatially variable fields 1: Stationary fields, *Water Resources Research*, *23*(7), 1257–1268.

Schabenberger, O., and C. A. Gotway (2005), *Statistical Methods for Spatial Data Analysis*, Texts in Statistical Science Series, Chapman and Hall/CRC, Boca Raton, FL.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross (1996), On the spatial pattern of soil nutrients in desert ecosystems, *Ecology*, *77*(2), 364–374.

Solie, J. B., W. R. Raun, and M. L. Stone (1999), Submeter spatial variability of selected soil and bermudagrass production variables, *Soil Science Society of America Journal*, *63*, 1724–1733.

Stevens Jr., D., and A. R. Olsen (2004), Spatially balanced sampling of natural resources, *Journal of the American Statistical Association*, *99*(465), 262–278.

Torgersen, C. E., and D. A. Close (2004), Influence of habitat heterogeneity on the distribution of larval pacific lamprey (*Lampetra tridentata*) at two spatial scales, *Freshwater Biology*, *49*(5), 614–630.

Venditti, J. G., and M. A. Church (2005), Bed form initiation from a flat sand bed, *Journal of Geophysical Research*, *110*, doi:10.1029/2004JF000149.

Ver Hoef, J. M., and E. E. Peterson (2007), Spatial modeling of stream network data, in *Proceedings of the 92nd Annual Meeting of the Ecological Society of America*, San Jose, CA.

Ver Hoef, J. M., E. Peterson, and D. Theobald (2006), Spatial statistical models that use flow and stream distance, *Environmental and Ecological Statistics*, *13*, 449–464, doi:10.1007/s10651-006-0022-8.

Zhu, Z., and M. L. Stein (2005), Spatial sampling design for parameter estimation of the covariance function, *Journal of Statisitcal Planning and Inference*, *134*, 583–603, doi:10.1016/j.jspi.2004.04.017.

Zhu, Z., and H. Zhang (2006), Spatial sampling design under the infill asymptotic framework, *Environmetrics*, *17*(4), 323–337, doi:10.1002/env.772.

Zimmerman, D. L. (2006), Optimal network design for spatial prediction, covariance parameter estimation, and empirical prediction, *Environmetrics*, *17*, 635–652, doi:10.1002/env.769.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith (2009), *Mixed Effects Models and Extensions in Ecology with R*, Statistics for Biology and Health, 3 ed., Springer, New York, NY.

3. INVESTIGATING THE APPROPRIATENESS OF SPATIAL AUTOCOVARIANCE FUNCTION RANGE PARAMETERS TO DESCRIBE THE SIZE OF PATCHES

3.1 ABSTRACT

The geostatistical range parameter is often used to describe the size of patches in ecological landscapes. Theoretical or empirical justification for this technique is lacking. The integral scale is computed using the sill, range, and nugget autocovariance parameters simultaneously, and has been proposed as an alternate to the range parameter alone to describe the size of patches. We use complete censuses of coastal cutthroat trout (*Oncorhynchuys clarki clarki*) habitat unit fish counts obtained from 40 western Oregon headwater streams to compute range parameter and integral scale values. We compare these values to the lengths of patches computed from four patch definitions. Range parameter values were generally larger than, and only weakly correlated with, average patch lengths. Range parameter values were more strongly correlated with maximum patch and maximum gap lengths. Integral scale values were not strongly correlated with average patch lengths, but integral scale values more closely matched the magnitude of average patch sizes than range parameters. We discuss potential reasons for our findings, and highlight the role that gaps play in the computation of autocovariance parameters. We contend that range parameters should not be used to describe patch sizes in data where heterogeneous within- patch response values or large patch size variation can be expected.

3.2 INTRODUCTION

Many ecological landscapes and associated phenomenon are spatially organized into patches (*Bange et al.*, 2006; *Blair*, 2005; *Bouza et al.*, 2002; *Bulit et al.*, 2003; *Dent and Grimm*, 1999; *Ettema and Wardle*, 2002; *Huettmann and Diamond*, 2006; *Kotliar and Wiens*, 1990; *Legendre*, 1993; *Lindenmayer*, 2000; *Mast and Veblen*, 1999; *Paola and Seal*, 1995; *Perry*, 1998; *Pickett and Cadenasso*, 1995; *Rossi*, 2003; *Schmuki et al.*, 2006), and lotic ecosystems are no exception (*Poole*, 2002; *Benda et al.*, 2004; *Cooper et al.*, 1997; *Fisher et al.*, 1998; *Isaak and Thurow*, 2006; *Neville et al.*, 2006; *Torgersen et al.*, 1999; *Torgersen and Close*, 2004; *Venditti and Church*, 2005; *Ward*, 1989; *Ward et al.*, 1998; *Wiens*, 2002; *Wright and Li*, 2002). Further, patchiness is an inherent property of aquatic ecosystems (*Bulit et al.*, 2004) and particularly apparent in stream habitats (*Downes et al.*, 1993). Despite the theoretical and empirical work demonstrating the importance and implications of spatial heterogeneity for lotic systems, patchiness and spatial heterogeneity have received little rigorous quantification (*Cooper et al.*, 1997).

The field of geostatistics focuses on the detection, estimation, and prediction of spatial patterns (*Rossi et al.*, 1992). Geostatistical models can be used for investigations regarding the observed structure and hypothesized generating processes (*Legendre*, 1993). These geostatistical models include semivariograms or autocovariance functions that use sill, range, and nugget parameters to describe changes in variance associated with distances between observations. More specifically, the range is the shortest distance between observations at which they are uncorrelated and at which the maximum variance of the process is reached (*Schabenberger and Gotway*, 2005, pg. 138). It is common in the literature to find range parameters used as estimates of

patch size (*Cooper et al.*, 1997; *Fletcher and Sumner*, 1999; *Dalthorp et al.*, 2000; *Franklin et al.*, 2002), average patch size (*Pastor et al.*, 1998; *Dent and Grimm*, 1999; *Augustine and Frank*, 2001; *Blair*, 2005; *Bouza et al.*, 2002), or the average patch and gap size (*Perry et al.*, 2002; *Cubillos et al.*, 2008). *Bulit et al.* (2003) note the range parameter as an upper bound for the size of patches, indicating that patch size could be a value up to the range, but probably not larger. None of these papers cite a source which describes the appropriateness of range parameters for describing patch size.

There is some indication that range parameter values and patch sizes may be associated. *Meisel and Turner* (1998) simulated patches consisting of binary blocks of internally homogenous values. They defined the range by visual location of empirical semivariogram inflection points. They found the inflection points did reflect the patch size when all patches where the same size. They also found the range reflected the size of the larger patch size in a simulated landscape containing only two patch sizes. They were not able to detect similar results for simulated landscapes containing multiple patch sizes.

Schabenberger and Gotway (2005, pg. 140) question why the distance at which observations are no longer spatially correlated should be equal to the size of patches. They suggest using measures of the distance over which observations are highly correlated, and propose the integral scale which incorporates the shape and range, sill, and nugget parameters of the autocorrelation function. An integral scale describes the largest average distance over which observations are correlated (*Russo and Bresler*, 1981; *Russo and Jury*, 1987). Integral scale values are computed by integrating the autocorrelation function with respect to distance up to the range parameter.

Integral scales have received significantly less attention than range pa-

rameters in the ecological literature. Applications of integral scales from the environmental sciences include *Venditti and Church* (2005) correlating integral scale values for initiated and existing stream beds to the average eddy size that existed before bed form development, *Solie et al.* (1999) studying the spatial variability of soil and bermudagrass using semivariance statistics that include both range parameters and integral scales, and *Bange et al.* (2006) using integral scales to describe relationships between the vertical transport of sensible and latent heat and soil moisture conditions. The total covariance statistic defined by *Dalthorp et al.* (2000) to investigate patch characteristics in simulated Japanese beetle grub data is equivalent to the integral scale.

Quantitative measures of patch characteristics are essential for studying ecological questions regarding how these characteristics vary in time and space (*Dalthorp et al.*, 2000), but despite interest in patchiness, many ecologists view patches simplistically (*Kotliar and Wiens*, 1990). Current notions of patchiness and heterogeneity are vague (*Cooper et al.*, 1997), and patches are rarely quantifiably defined (*Bulit et al.*, 2003). This work investigates the appropriateness of range parameter and integral scale values for describing the size of patches in headwater stream basins. Utilizing censuses of coastal cutthroat trout (*Oncorhynchuys clarki clarki*) from continuously sampled habitat units in 40 randomly selected headwater streams from Western Oregon we define and measure patch sizes. We also fit autocovariance models to these count data to obtain range parameter and integral scales values and quantify the relationships between these values and patch sizes.

3.3 METHODS

3.3.1 Patch Definitions

Kotliar and Wiens (1990) propose that patches should be determined using objective criteria to define their boundaries. We present four objective patch definitions each determined by increasing boundary thresholds. The first definition represents patches as consecutive habitat units defined by the presence or absence of adult fish. The second, third, and fourth patch definitions represent patches as consecutive habitat units of fish counts above the 25th, 50th, and 75th percentiles of the fish count distribution in each basin. Defining patches also directly defines gaps as consecutive habitat units which are not included in patches. For each basin and all four patch definitions, the size of every patch and gap was computed as the distance along the stream channel from the beginning of the downstream habitat unit to the end of the upstream unit. Within each basin the mean, maximum, and standard deviation of patch and gap lengths for each patch definition was computed.

3.3.2 40 Basins Dataset

The 40 censused watersheds, located above barriers to anadromous fish migration, are part of a larger study examining the effects of landscape pattern on isolated coastal cutthroat trout populations (*Gresswell et al.*, 2004). Each watershed was randomly selected from a population of 268 second- and third-order catchments west of the Cascade Mountains in Oregon and surveyed through the entire fish-bearing extent (*Ganio et al.*, 2005). Adult

coastal cutthroat trout abundance was assessed with single-pass electrofishing without blocknets (*Bateman et al.*, 2005) in all pools and cascades in each watershed. These census datasets represent the spatial distribution of fish at one point in time, and previous work has shown that the spatial arrangement and patch configuration of fish changes over time (*Bateman et al.*, 2005).

3.3.3 Statistical Methods: Candidate Models

3.3.3.1 Autocovariance Models

Three classes of spatial autocovariance models were fit to the habitat unit fish counts from each watershed. The first two classes of models assume isotropic and stationary spatial processes, and their mathematic expressions can be found in the appendix. The first class represents traditional geostatistical models that use the pairwise Euclidean distance between all habitat units. Exponential, spherical, and Gaussian models, each with nugget, were fit as candidate autocovariance models to the data.

The second class are spatial moving average constructions for stream networks (*Ver Hoef et al.*, 2006). These models differ from the first class of autocovariance models in three ways. First, they use in-stream distance, rather than Euclidean distance, between locations. Second, the autocovariance between locations is weighted proportionally to the amount of stream flow the downstream location receives from the upstream location. Third, observations are only considered autocorrelated if they are connected by water flow. See *Ver Hoef et al.* (2006) and *Peterson et al.* (2007) for more details. Exponential with nugget and spherical with nugget spatial moving average models were fit to the data as candidate models. Because relative flow contribution

was not directly measured for each location in the watersheds, the proportional upstream watershed area drained by each stream segment was used as a proxy variable to weight the moving average autocovariance functions at each tributary confluence (*Peterson et al.*, 2007). All confluence weight and in-stream distance matrices were created utilizing the FLoWS ArcGIS toolbox (http://www.nrel.colostate.edu/projects/starmap/flows_index.htm).

The third class is a simple linear regression (SLR) model fit without a spatial autocovariance function. This model was used to determine if spatial autocorrelation was present in the habitat unit fish count data. Combining the three traditional geostatistical models, the two spatial moving average models, and the one SLR model leads to a total of six candidate autocovariance models fit to the fish count data from each watershed.

3.3.3.2 Linear Models for the Mean

In addition to the six spatial autocovariance models, two types of models for the mean of fish counts were used. The first model type contained only a single overall mean. The second model type contained the overall mean, the maximum depth of the habitat unit, a measure of the surface area of the habitat unit (the square root of a unit's length times its average whetted width), and the interaction of these explanatory variables. We use LC-SAC to refer to models that included the three spatial autocovariance parameters (*i.e.* sill, range, nugget) and the explanatory variables for the mean. We use OM-SAC to refer to models that include the three autocovariance parameters and only an overall mean. We use OM-SLR and LC-SLR to refer to models that do not include any autocovariance parameters but include the

overall mean parameter only, or the overall mean and explanatory variables, respectively. Table (3.1) provides a summary of the candidate classes and types of models described above.

3.3.4 Statistical Methods: Analysis

3.3.4.1 Model Selection

The parameter values for each candidate autocovariance function and mean model-type were obtained by maximum likelihood using R code from *Ver Hoef and Peterson* (2007). All habitat unit fish counts were $logarithm_e(datum + 1)$ transformed. For each watershed and each type of model for the mean, the best fitting spatial autocovariance model was determined by the lowest Akaike's information criterion (AIC) value (*Zuur et al.*, 2009). In the event that several candidate autocovariance models had AIC values within 2 AIC units, the model with the highest ratio of the partial sill to the nugget plus partial sill was chosen because it described a higher proportion of structured spatial pattern.

We also fit exploratory empirical semivariograms to each basin. These semivariograms were used to provide visual evidence of non-stationarity via excessive trend, and to help discern the presence of spatial autocorrelation in each basin's habitat unit fish counts. Lower AIC values for OM-SLR or LC-SLR fits compared to corresponding OM-SAC or LC-SAC fits, and empirical semivariograms lacking semivariance pattern indicated a lack of spatial autocorrelation.

3.3.4.2 Relating Patch Characteristics to Range Parameters

The best fitting autocovariance model was used to compute the range parameter value, and the integral scale value for each basin was computed using the best fitting traditional geostatistical autocovariance function. Associations of the patch and gap characteristics with range parameter and integral scale values were investigated using Spearman's rho nonparametric rank-based measure of correlation (*Conover*, 1999). P-values provided with Spearman's rho statistics were computed using Algorithm AS 89 (*Best and Roberts*, 1975). For graphical presentation we $logarithm_e$- transformed all range, integral scale, patch, and gap characteristic values. If range parameter or integral scale values are a direct measure of average patch lengths we would expect a graph of patch lengths versus range or integral scale values to track a 1-to-1 line and the correlation estimates to be positive and high. Should a direct relationship not be evident, but an associative relationship exist we would expect likewise graphical and correlational evidence. The same analysis approach was also applied to the average gap lengths, maximum patch and gap lengths, and the larger of patch or gap average and maximum lengths from each basin.

3.4 RESULTS

For the OM-type models, four headwater basins showed excessive trend via empirical semivariograms without sills and the corresponding estimates of their range parameters were unreasonable. We did not consider these four basins in the correlation analysis of range parameters or integral scales with patch length characteristics. Four of the watersheds with OM-type

models and one watershed from the LC-type models lacked evidence of spatial autocorrelation. The range and integral scale values for these basins were recorded as 1 to appear as zeros on all graphs with log-transformed axes. The moving average autocovariance models were the best fitting in 17 headwater basins for the OM- and in 23 basins for the LC- type models. Traditional geostatistical autocovariance models fit best in 15 headwater basins for the OM- and in 14 basins for the LC-type models.

3.4.1 Range Parameter Values and Patch Lengths

Regardless of patch definition or the inclusion of linear model coefficients, graphical analysis indicated there was not strong evidence that range parameter values were equal to the average lengths of patches (Figures 3.1 and 3.2). Range values were typically greater than average patch lengths. Although the very smallest range values may be associated with some of the watersheds with smaller average patch lengths, the observed relationship for the majority of the watersheds provided no evidence of a strong relationship. There was also very little evidence to suggest a strong associative relationship between range values and average patch lengths (Table 3.2).

Maximum patch lengths showed much more promise for correlating with range values (Figures 3.3 and 3.4). The maximum patch lengths translated into more coverage around 1-to-1 lines, and in all cases showed stronger evidence of association with range values via higher estimates of rank-based correlation and stronger p-value evidence testing against a null hypothesis that the correlation equals zero (Table 3.2). The range values from OM-SAC models were modestly more related to maximum patch lengths than those computed from the LC-SAC models (Table 3.2).

The pattern of association between range parameter values and gap characteristics was similar to that of range parameter values and patch characteristics. Range parameter values were generally larger than average gap lengths (Figures 3.5 - 3.8). Maximum gap lengths show stronger correlation with range parameters than average gap lengths (Table 3.2), and the range values for OM-SAC models were generally more related to maximum gap lengths than those from LC-SAC models.

For both patches and gaps, the patch definitions based on counts above the 25th and 50th percentiles generally provided stronger correlations with range values than definitions based on the 75th percentile or fish presence (Table 3.2).

There is no marked improvement in the correlation with range values when considering the larger of the patch or gap means and maximums (Figures 3.9 - 3.12 and Table 3.3) as compared to each patch characteristic individually.

3.4.2 Integral Scale Values and Patch Lengths

Integral scale values more closely matched the magnitude of average patch and gap lengths than range parameters (Figures 3.13 - 3.16). Overall, integral scale values were not strongly correlated with average patch or gap lengths (Table 3.4). The integral scale values from the OM- and LC-type models were strongly correlated with the range parameter values from each basin (Figure 3.17). The estimated rank-basked correlation estimates were 0.878 and 0.809, respectively, and each had p-values against the null hypothesis that correlation = 0 of less than 0.0001.

3.5 DISCUSSION

Given the relatively weak association between average patch lengths described by our four patch definitions and range parameter or integral scales, we consider three reasons for our results. One reason may be that none of our patch definitions are appropriate. *Kotliar and Wiens* (1990) suggest that patches exist in a hierarchical structure. Relatively internally homogenous patches with rather discrete edges make up first-order patches, second order patches consist of clusters of first-order patches, and third-order patches are formed by variation within and among first- and second-order patches. The fact that range values were predominantly much larger than our patches might suggest that range values are more associated with second-order patches.

In studying planktonic ciliate patches in a tropical coastal lagoon, *Bulit et al.* (2003) posited that patches should be rare, covering less than 50% of the sampled area, and investigated two working definitions of patch. They used the common spatial prediction method know as ordinary kriging (*Isaaks and Srivastava*, 1989) to predict values over their entire sampling extent, and found that patches defined by clusters of values containing predicted abundances greater than the 75th percentile were better predicted than clusters defined by values exceeding the 50th percentile. The continuous sampling of the 40 watersheds dataset eschewed the need for kriging. It is not clear why patches should be rare, as posited by *Bulit et al.* (2003). However, rarer patches implies larger gaps and our analysis could not indicate that patch lengths were more associated with range parameters than gap lengths were.

In an analysis of littoral zone fish habitat within a Canadian Shield lake *Brind Ámour and Boisclair* (2006) defined patches of habitat as contigu-

ous sites with similar environmental characteristics. Similarly, we defined patches as contiguous habitat units with similar fish counts. *Swartzman et al.* (1999b,a) identified fish shoal and plankton patches in data obtained via acoustic sampling in the Bering Sea. Shoals and patches were defined as contiguous pixels with clearly defined boundaries set apart from backscatter thresholds. In essence, our changing percentile patch cut-offs were an exploration changing patch boundaries via increasing backscatter thresholds. It appears that our definitions of patches are consistent with others found in the literature, and it seems unlikely that our findings are simply a product of poor patch definitions.

Another reason for our results could be that none of the suite of models we considered adequately described the spatial pattern of our data. A key reason that the LC- type of model for the mean was included in our analyses is that including the habitat unit coefficients stabilized potential trends observed from the aforementioned empirical semivariograms, but their inclusion could have accounted for spatial information previously manifested solely in the spatial pattern of the variance.

It could be true that the moving average spatial autocovariance models that incorporate in-stream distance and flow contribution did not adequately described the spatial pattern of the patches. Autocorrelation is the result of small-scale, stochastically dependent random innovations. Whereas random innovations at different locations are independent, the attribute being ultimately observed is the result of a mixing process that combines these innovations. *Ver Hoef et al.* (2006) extended this notion to construct moving average covariance functions that use in-stream distance and incorporate stream flow information.

Despite the fact that using moving average constructions to generate valid

covariance matrices for geostatistical modeling based on stream distance and water flow more accurately represents the connectivity and flow relationships in stream networks (*Peterson et al.*, 2007), the relative benefit of their application over traditional geostatistical models that utilize Euclidean distances has yet to be demonstrated. To our knowledge, due to the relatively recent derivation of these techniques, there have been very few applications in the literature. *Peterson and Urquhart* (2006) compared the moving average and traditional geostatistical approaches in an analysis of dissolved organic carbon (DOC) for the Maryland Biological Stream Survey. They found that using Euclidean distances consistently produced geostatistical models that described a greater amount of variability in DOC than moving average models that used in-stream distance and weighted flow contributions. *Cressie et al.* (2006) also considered the spatial moving average approach in an analysis aimed to predict daily change in dissolved oxygen within a river network in South East Queensland, Australia. They fit a covariance mixture model that incorporated a spherical geostatistical spatial model and a spherical spatial moving average model. The estimated proportion of covariance accounted for by the spherical model incorporating in-stream distances was zero, and the authors concluded that their response variable exhibited spatial dependence according to Euclidean distance rather than in-stream distance.

The spatial extents of each of these two examples (the entire state of Maryland and over $15{,}000 km^2$ in Australia) are much larger than those considered in this work, though flow-connectedness can only be defined for points occurring within the same stream network. As such, spatial autocorrelation exhibited in the Maryland Biological Stream Survey and Australian river network datasets may be driven predominantly via meteorological inputs, so it is of no surprise that Euclidean distance covariance matrices were found to

more accurately reflect the spatial dependence among observations. Though there is variation in the total areas of the randomly selected 40 watersheds, ranging from roughly 497 to 1093 hectares, these smaller spatial extents as compared to the two aforementioned examples may allow for better insights into the merits of moving average autocovariance approaches for stream-network data. In addition to the work described here, we carried out a similar analysis correlating range parameters and patch characteristics using only traditional geostatistical models and another analysis using only in-stream distance models and found no considerable changes to the results for the best fitting overall models presented herein. Given the suite of candidate autocovariance models considered, we feel confident that our results were not simply a consequence of poorly chosen models.

The final reason could simply be that range parameters are not practical measures of average patch lengths for data types similar to ours. *Meisel and Turner* (1998) did find that their range parameters described patch sizes in artificial binary data with patches of uniform size. They did not find similar patterns in their analysis of large ungulate winter foraging and associated environmental variables, and noted that variation in patch sizes could contribute noise that might make detection of fine-scale spatial patterns, like patch sizes, in real-world data difficult. Given its definition, the range parameter seems an intuitive measure of patch size in a landscape with uniformly sized patches and gaps each containing internally homogeneous response values. This data structure seems unlikely for many ecological phenomenon, and especially for those in streams where patch characteristics and arrangements are generally quite heterogeneous (*Cooper et al.*, 1997).

It might not be sufficient to rely on simulated patchy landscapes to further investigate the use of range parameters to infer patch size. This could

demonstrate that patch size infers range values, but concluding that range parameters equate the size of patches would be a logical fallacy termed affirming the consequent (*Matthews*, 2009). This argument could suggest range parameters as serviceable approximations for patch sizes (*Floridi*, 2009) in landscapes similar to those simulated, but would not sufficiently justify that range parameters equal the size of patches.

Our work highlights the need to consider both patches and gaps. Computationally, data within gaps are utilized just as data within patches are, and our work indicates gaps are no less associated with range parameters than patches. The strongest associations we found related the range parameters to either the largest patch or gap length, or the largest among the patch or gap lengths. This suggests that comparing range values of like data across landscapes may allow for an ordering of largest patches or gaps.

In general, we contend that range parameter values should not be used to estimate the size of patches in data where variation in patch or gap sizes, nor varying response values within patches and gaps, is expected. We look forward to future real-world data analyses that might lead to an increased breadth of data types where range parameters, or integral scale values, may be useful for describing patch sizes.

APPENDIX: MATHEMATICAL EXPRESSIONS OF AUTOCOVARIANCE FUNCTIONS

Geostatistical Autocovariance Functions

Each geostatistical autocovariance function models the autocovariance between any two observations with changes in the Euclidean distance (h) between them.

Exponential with nugget autocovariance model

$$C(h) = \begin{cases} \theta_0 + \theta_1 & \text{if } h = 0 \\ \theta_1 exp(-3h\theta_2^{-1}) & \text{if } h > 0 \end{cases}$$

where θ_0 is the nugget parameter, θ_1 is the partial sill parameter, and θ_2 is the practical range parameter. The practical range is defined as the distance at which correlation between observations $\approx 5\%$ (*Schabenberger and Gotway*, 2005).

Spherical with nugget autocovariance model

$$C(h) = \begin{cases} \theta_0 + \theta_1 & \text{if } h = 0 \\ \theta_1\left[1 + .5(h\theta_2^{-1})^3 - 1.5h\theta_2^{-1}\right] & \text{if } 0 < h < \theta_2 \\ 0 & \text{if } \theta_2 \leq h \end{cases}$$

where θ_0 is the nugget parameter, θ_1 is the partial sill parameter, and θ_2 is the range parameter.

Gaussian with nugget autocovariance model

$$C(h) = \begin{cases} \theta_0 + \theta_1 & \text{if } h = 0 \\ \theta_1 exp(-3h^2\theta_2^{-2}) & \text{if } h > 0 \end{cases}$$

where θ_0 is the nugget parameter, θ_1 is the partial sill parameter, and θ_2 is the practical range parameter. The practical range is defined as the distance at which correlation between observations $\approx 5\%$ (*Schabenberger and Gotway*, 2005).

Up-Stream Moving Average Autocovariance Functions

Each up-stream moving average autocovariance function models the covariance between an observation s_i downstream of observation s_j with changes in the in-stream distance (h) between s_i and s_j, and the proportion of water flow ($w_{i,j}$) the stream segment containing s_i receives from the segment containing s_j.

Exponential with nugget autocovariance model

$$C(s_i, s_j) = \begin{cases} \theta_0 + \theta_1 & \text{if } h = 0 \\ \theta_1 exp(-3h\theta_2^{-1})\sqrt{w_{i,j}} & \text{if } h > 0 \text{ and } s_i,\ s_j \text{ are flow connected} \\ 0 & \text{if } s_i,\ s_j \text{ not flow connected} \end{cases}$$

where θ_0 is the nugget parameter, θ_1 is the partial sill parameter, and θ_2 is the practical range parameter. The practical range is defined as the distance at which correlation between observations $\approx 5\%$ (*Schabenberger and Gotway*, 2005).

Spherical with nugget autocovariance model

$$C(s_i, s_j) = \begin{cases} \theta_0 + \theta_1 & \text{if } h = 0 \\ \theta_1\left[1 + .5(h\theta_2^{-1})^3 - 1.5h\theta_2^{-1}\right]\sqrt{w_{i,j}} & \text{if } 0 < h < \theta_2 \text{ and } s_i,\ s_j \text{ are flow connected} \\ 0 & \text{if } \theta_2 \leq h \text{ or } s_i,\ s_j \text{ not flow connected} \end{cases}$$

where θ_0 is the nugget parameter, θ_1 is the partial sill parameter, and θ_2 is the range parameter.

Table. 3.1: Summary of all models fit to each watershed.

Spatial Autocovariance Models		
Class	**Distance Metric**	**Autocovariance Functions***
SAC: Traditional Geostatistical	Euclidian	Exponential, Spherical, Gaussian
SAC: Spatial Moving Average	In-Stream	Exponential, Spherical
SLR	None	None
* all autocovariance functions include the sill, range, and nugget parameters		
Models for Mean of Fish Counts		
Type	**Parameters**	
OM	Overall Mean	
LC	Overall Mean, Habitat Unit Size, Depth, Interaction	
Type-Class Combinations		
	Spatial Autocovariance Model	
Model for Mean	SAC	SLR
LC	LC-SAC	LC-SLR
OM	OM-SAC	OM-SLR

Table. 3.2: Rank-based correlation estimates (p-value against null hypothesis that correlation = 0) between range parameter values and average or maximum patch lengths.

Patch Characteristic	Model	Patch Threshold			
		0	25th Percentile	50th Percentile	75th Percentile
Patch: Average Length	OM-SAC	-0.026 (0.88)	0.079 (0.65)	0.349 (0.04)	0.317 (0.06)
	LC-SAC	0.126 (0.44)	0.285 (0.07)	0.333 (0.04)	0.272 (0.09)
Patch: Maximum Length	OM-SAC	0.230 (0.18)	0.576 (<0.01)	0.701 (<0.01)	0.646 (<0.01)
	LC-SAC	0.293 (0.07)	0.391 (0.01)	0.401 (0.01)	0.431 (0.01)
Gap: Average Length	OM-SAC	0.360 (0.03)	0.327 (0.05)	0.366 (0.03)	0.104 (0.55)
	LC-SAC	0.306 (0.06)	0.277 (0.06)	0.218 (0.18)	0.078 (0.63)
Gap: Maximum Length	OM-SAC	0.618 (<0.01)	0.658 (<0.01)	0.678 (<0.01)	0.646 (<0.01)
	LC-SAC	0.427 (0.01)	0.419 (0.01)	0.534 (<0.01)	0.506 (<0.01)

Table. 3.3: Rank-based correlation estimates (p-value against null hypothesis that correlation = 0) between the larger of patch or gap average, and larger of patch or gap maximum, compared to range values.

Patch Characteristic	Model	Patch Threshold			
		0	25th Percentile	50th Percentile	75th Percentile
Larger of Patch or Gap Average Length	OM-SAC	-0.076 (0.66)	0.025 (0.87)	0.276 (0.12)	0.104 (0.55)
	LC-SAC	0.202 (0.21)	0.379 (0.02)	0.357 (0.02)	0.078 (0.63)
Larger of Patch or Gap Maximum Length	OM-SAC	0.287 (0.09)	0.643 (<0.01)	0.773 (<0.01)	0.657 (<0.01)
	LC-SAC	0.490 (<0.01)	0.578 (<0.01)	0.638 (<0.01)	0.503 (<0.01)

Table. 3.4: Rank-based correlation estimates (p-value against null hypothesis that correlation = 0) between integral scale values and average patch or gap lengths.

Patch Characteristic	Model	Patch Threshold			
		0	25th Percentile	50th Percentile	75th Percentile
Patch: Average Length	OM-SAC	0.005 (0.98)	0.137 (0.43)	0.416 (0.02)	0.296 (0.08)
	LC-SAC	0.022 (0.89)	0.227 (0.16)	0.342 (0.03)	0.258 (0.11)
Gap: Average Length	OM-SAC	0.435 (0.01)	0.419 (0.01)	0.321 (0.06)	0.126 (0.46)
	LC-SAC	0.400 (0.01)	0.340 (0.03)	0.296 (0.06)	0.223 (0.17)

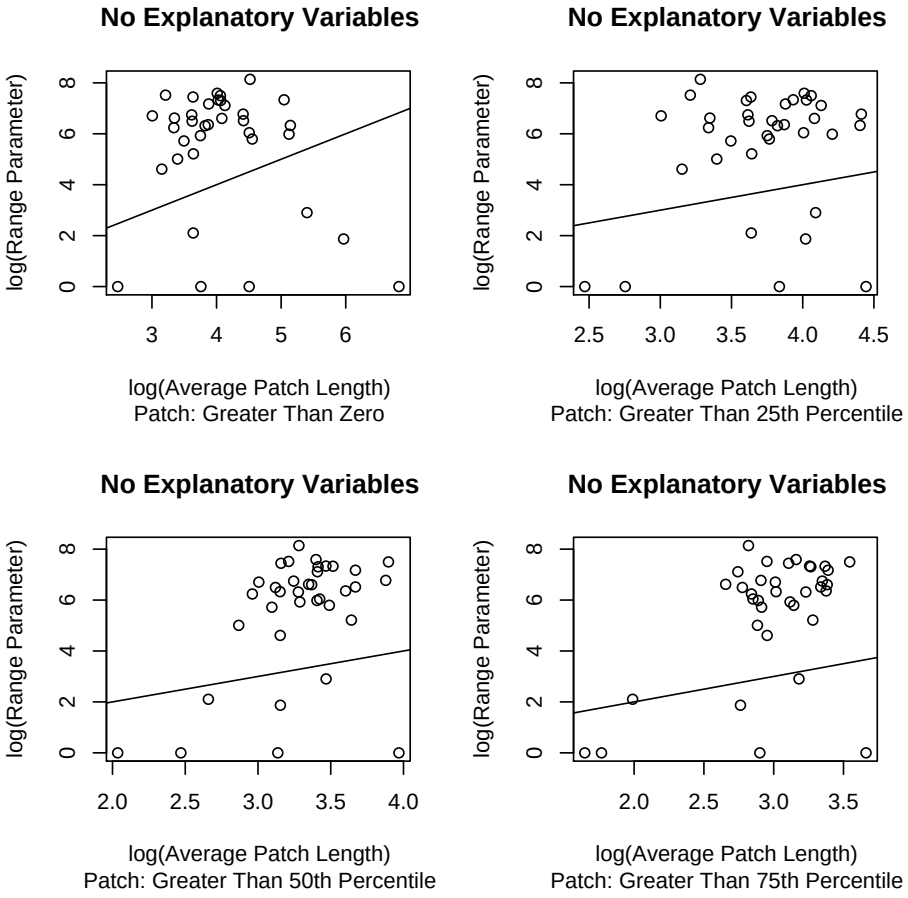

Figure. 3.1: Plots of OM-type model range parameter values vs. average patch lengths for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

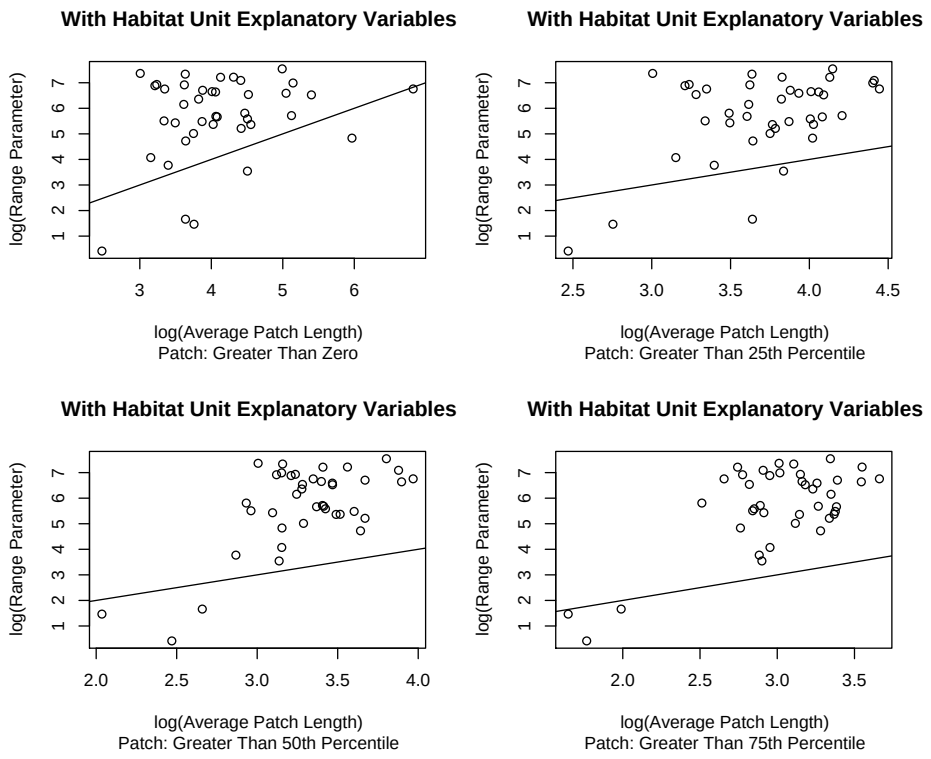

Figure. 3.2: Plots of LC-type model range parameter values vs. average patch lengths for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

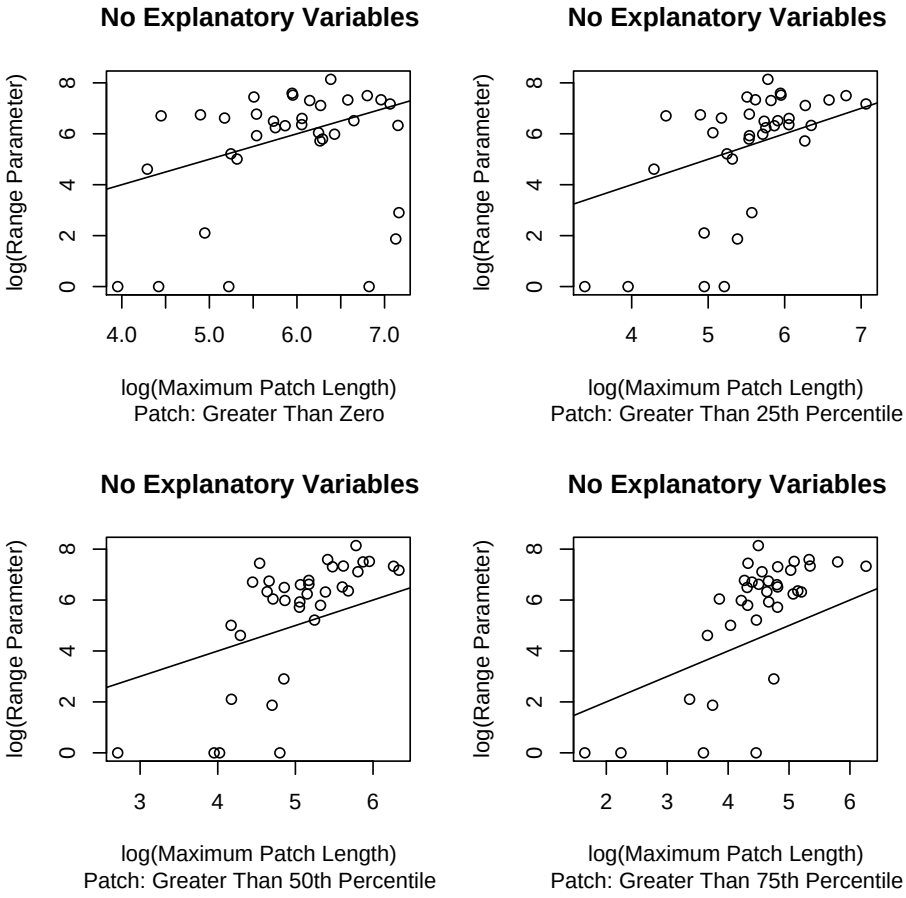

Figure. 3.3: Plots of OM-type model range parameter values vs. maximum patch lengths for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

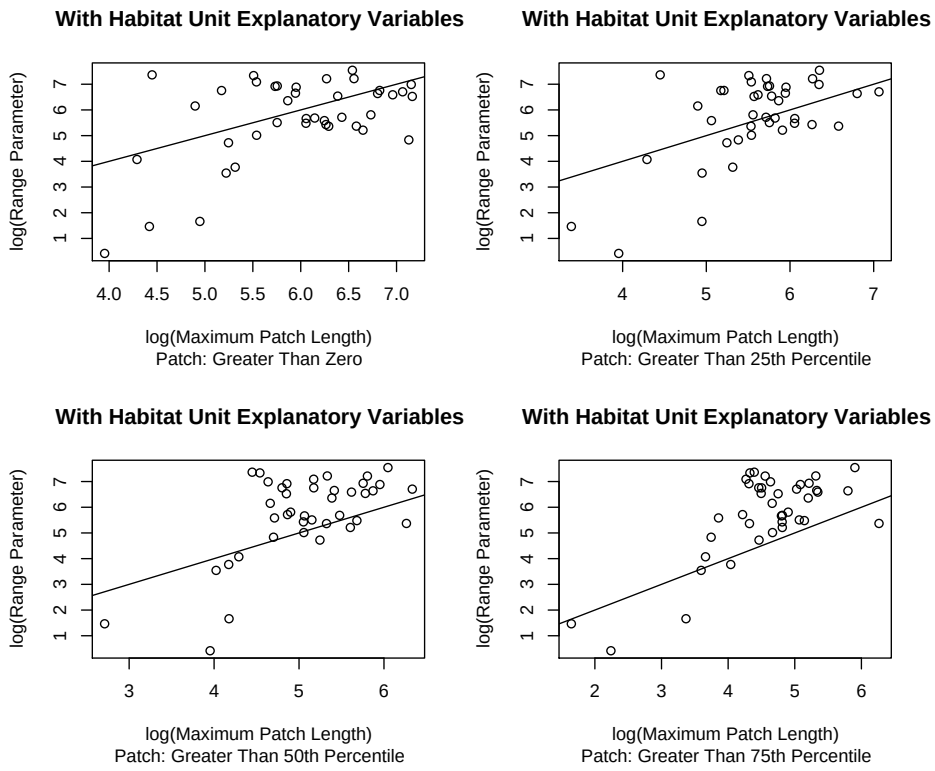

Figure. 3.4: Plots of LC-type model range parameter values vs. maximum patch lengths for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

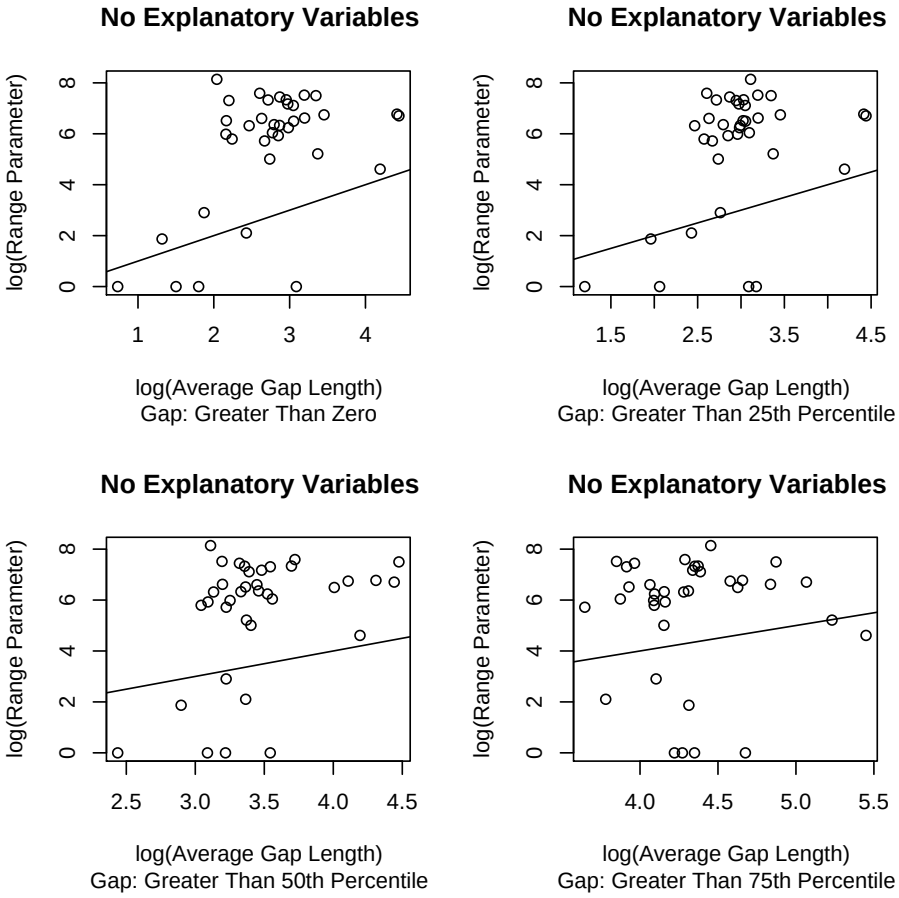

Figure. 3.5: Plots of OM-type model range parameter values vs. average gap lengths for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

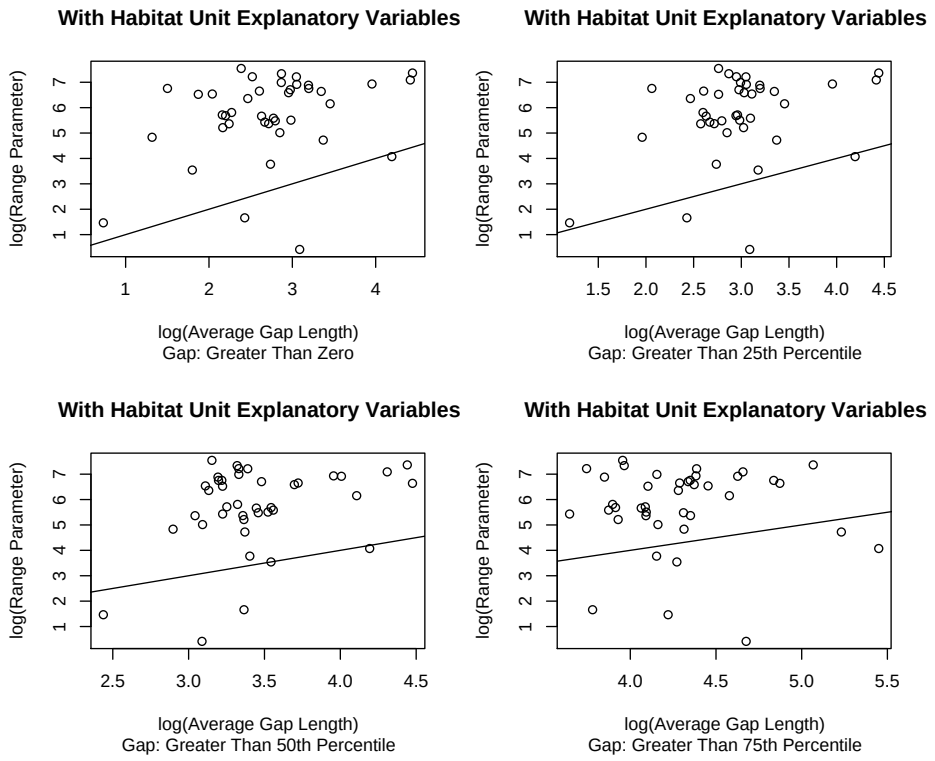

Figure. 3.6: Plots of LC-type model range parameter values vs. average gap lengths for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

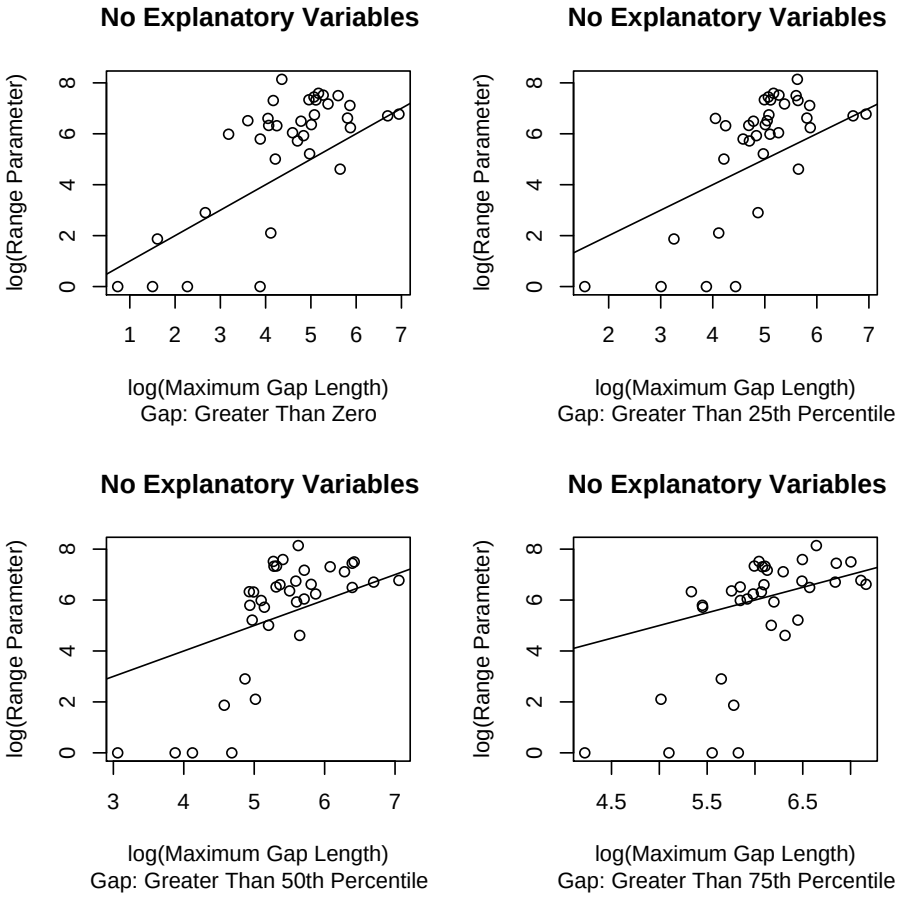

Figure. 3.7: Plots of OM-type model range parameter values vs. maximum gap lengths for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

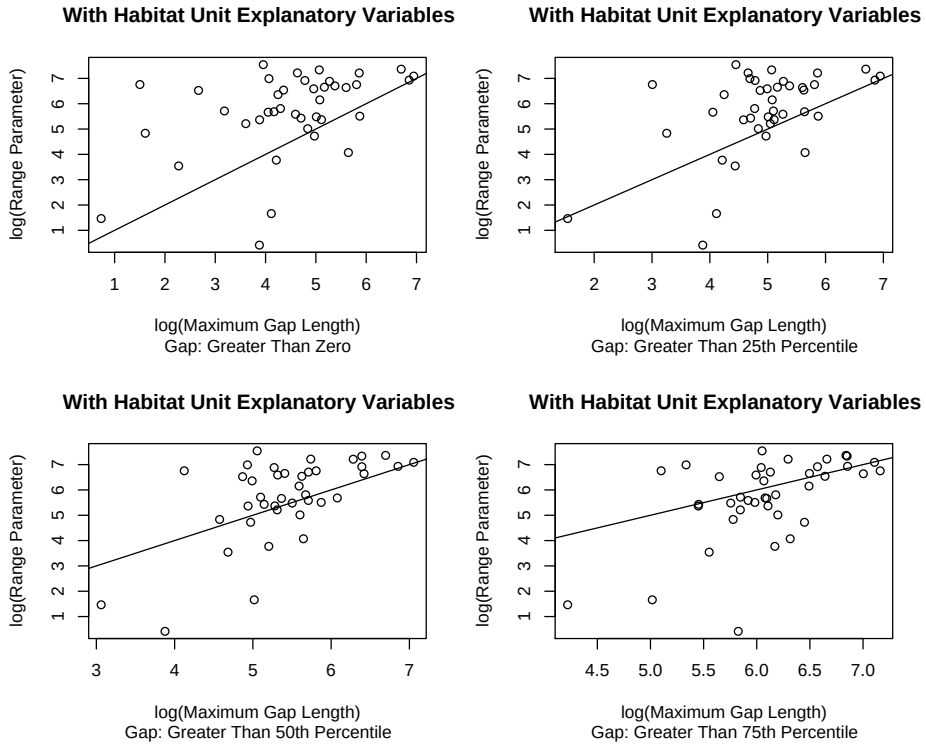

Figure. 3.8: Plots of LC-type model range parameter values vs. maximum gap lengths for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

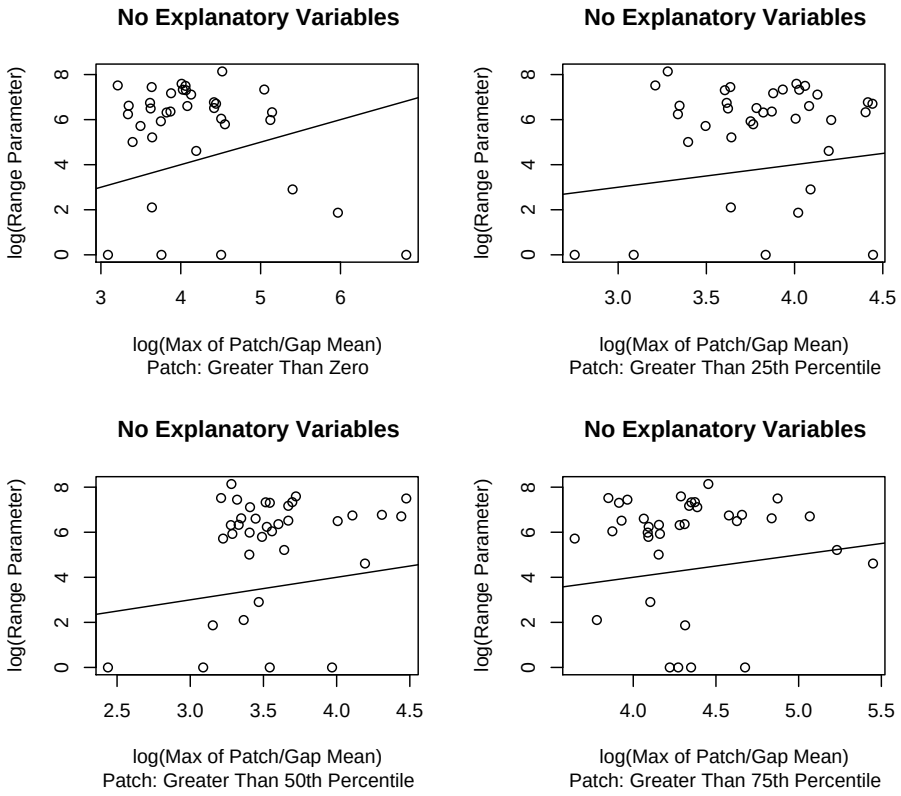

Figure. 3.9: Plots of OM-type model range parameter values vs. the largest of each basin's average patch or gap length for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

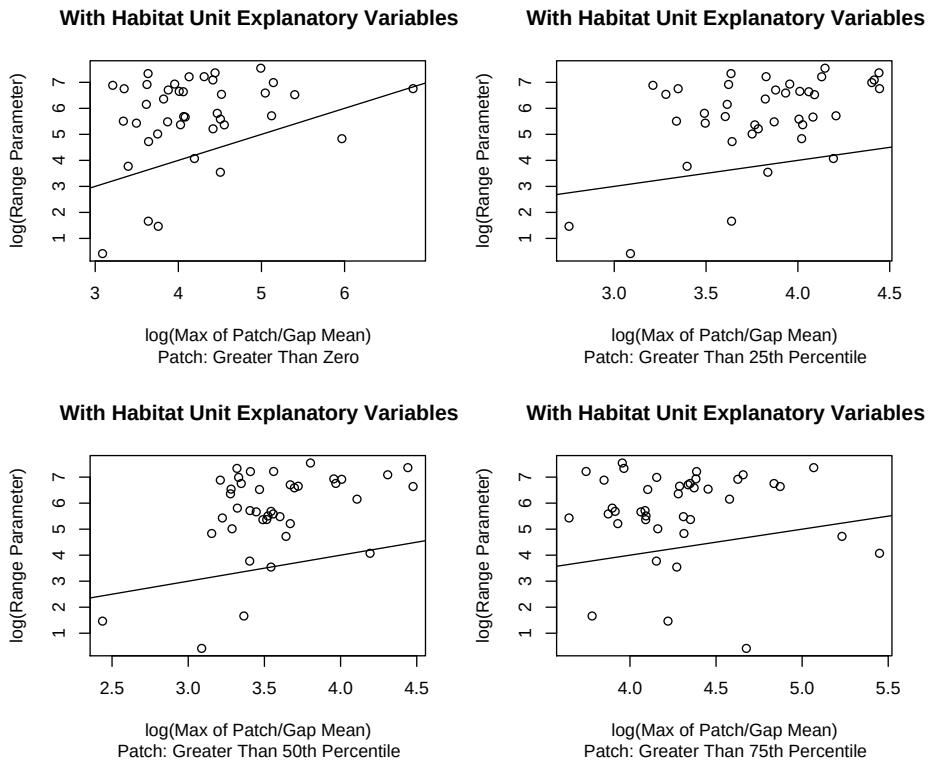

Figure. 3.10: Plots of LC-type model range parameter values vs. the largest of each basin's average patch or gap length for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

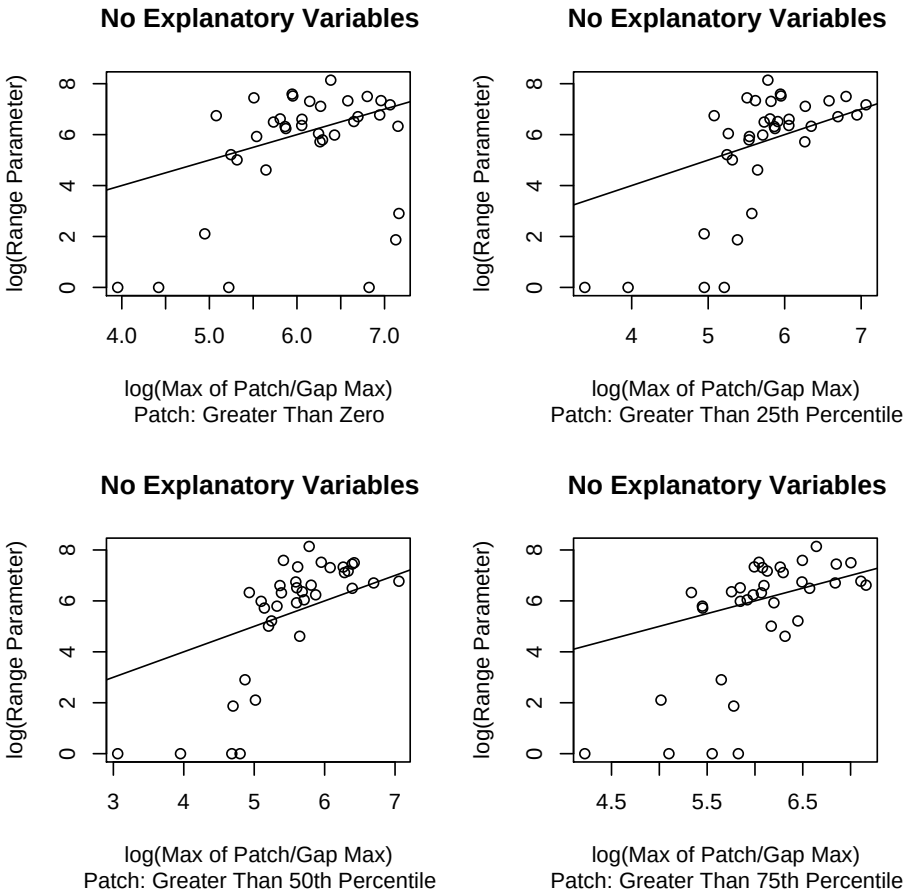

Figure. 3.11: Plots of OM-type model range parameter values vs. the largest of each basin's maximum patch or gap length for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

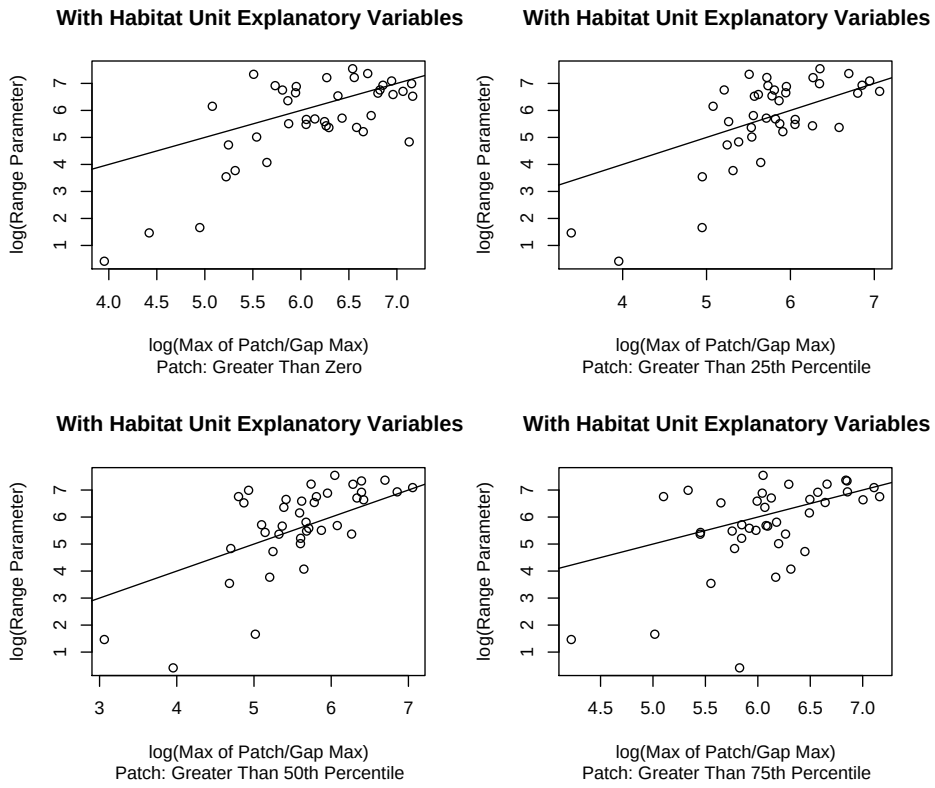

Figure. 3.12: Plots of LC-type model range parameter values vs. the largest of each basin's maximum patch or gap length for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

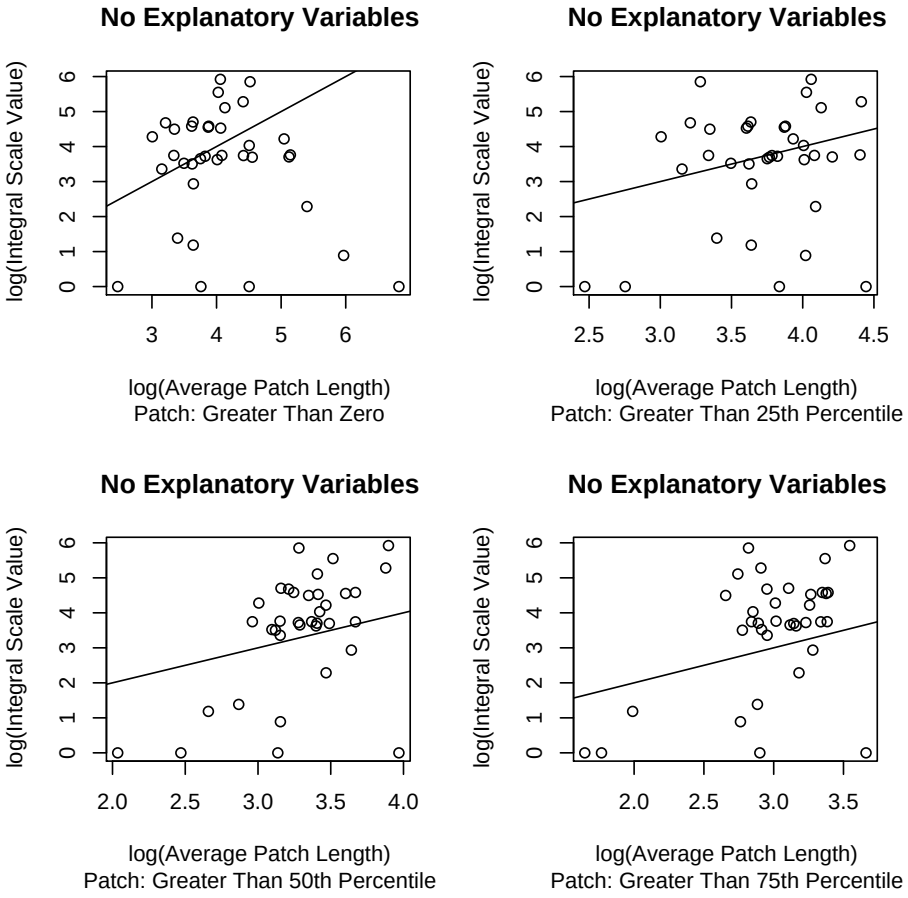

Figure. 3.13: Plots of OM-type model integral scale values vs. average patch length for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

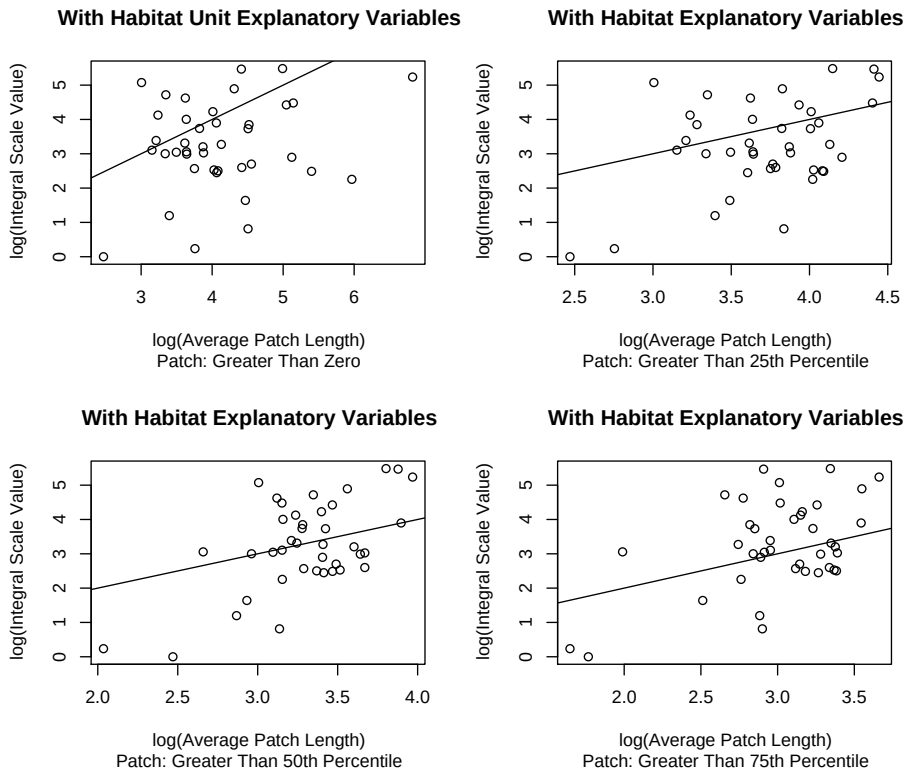

Figure. 3.14: Plots of LC-type model integral scale values vs. average patch length for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

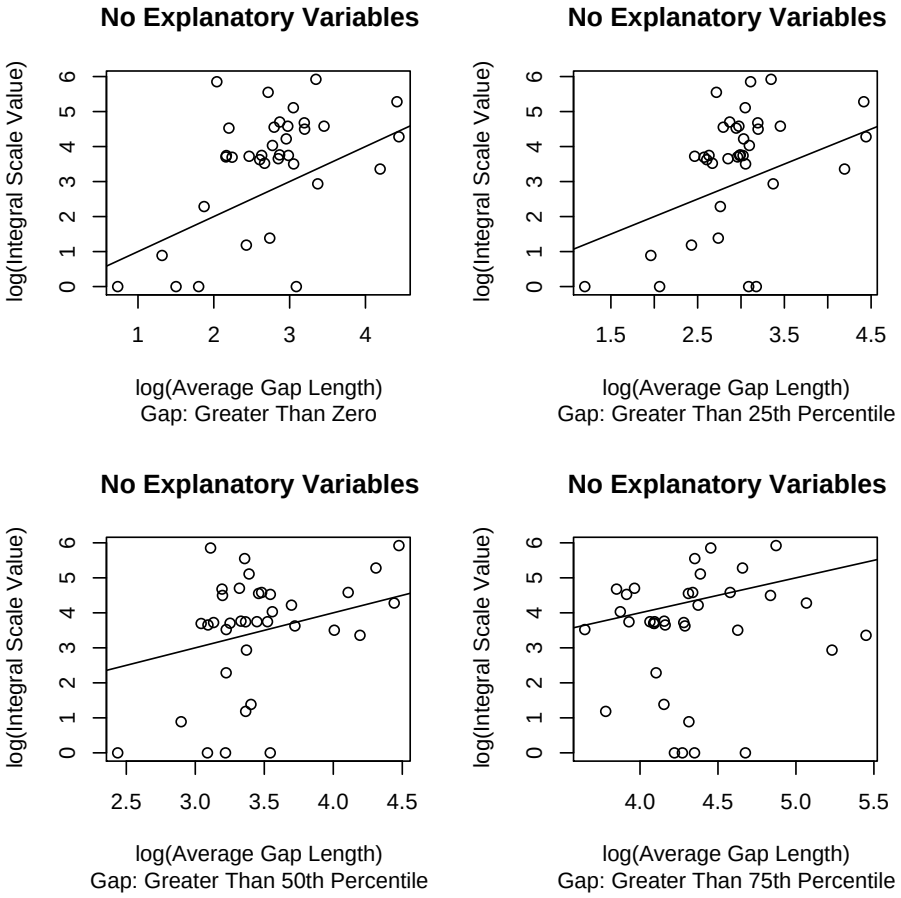

Figure. 3.15: Plots of OM-type model integral scale values vs. average gap length for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

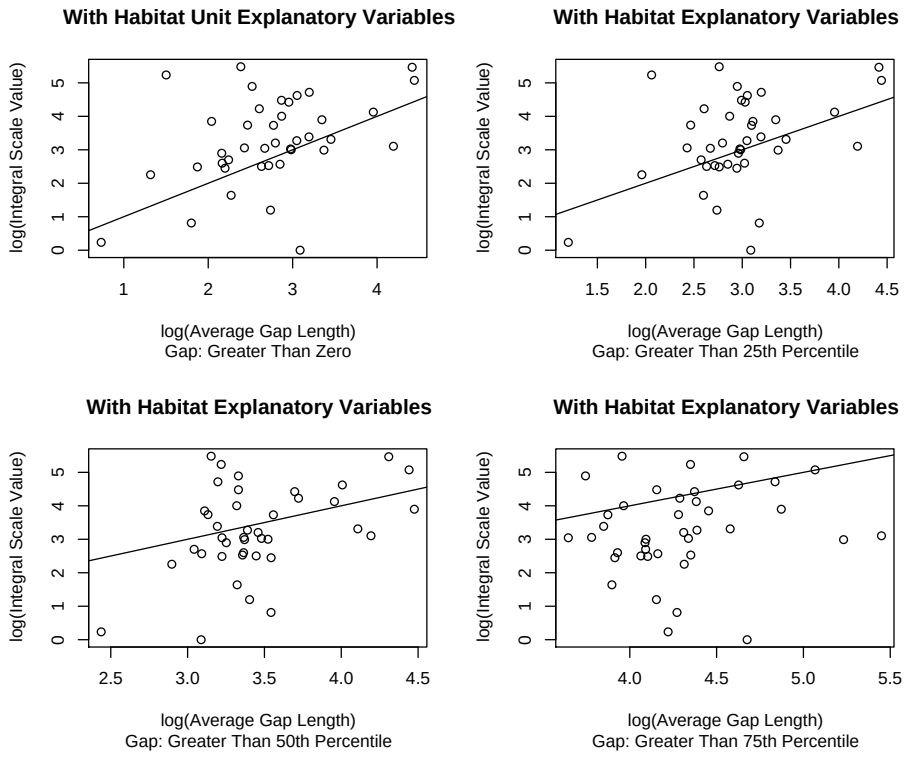

Figure. 3.16: Plots of LC-type model integral scale values vs. average gap length for each patch definition, on the log scale. The solid line represents a 1-to-1 correlation reference.

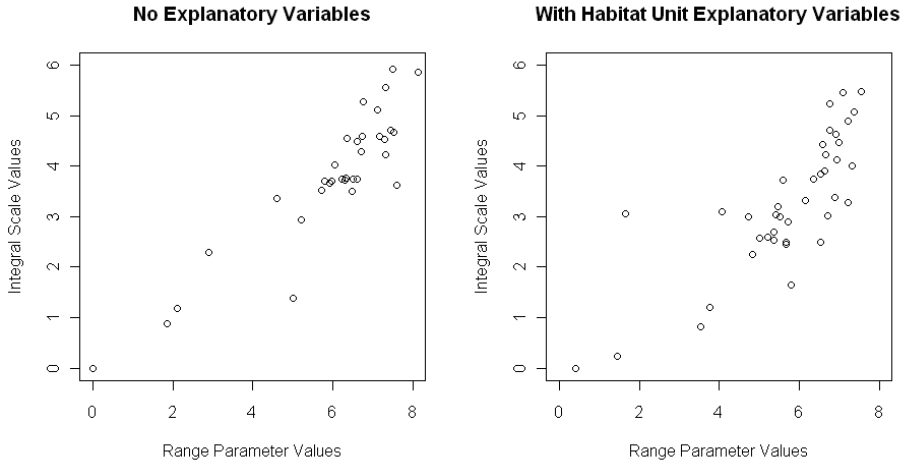

Figure. 3.17: Plots of integral scale values vs. range parameter values for OM- and LC-type models.

BIBLIOGRAPHY

Augustine, D. J., and D. A. Frank (2001), Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem, *Ecology*, *82*(11), 3149–3162.

Bange, J., T. Spiess, M. Herold, F. Beyrich, and B. Hennemuth (2006), Turbulent fluxes from helipod flights above quasi-homogeneous patches within the LITFASS area, *Boundary-layer Meteorology*, *121*, 127–151, doi: 10.1007/s10546-006-9106-0.

Bateman, D. S., R. E. Gresswell, and C. E. Torgersen (2005), Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution, *Journal of Freshwater Ecology*, *20*, 335–345.

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock (2004), The network dynamics hypothesis: How channel networks structure riverine habitats, *BioScience*, *54*(4), 413–427.

Best, D. J., and D. E. Roberts (1975), Algorithm AS 89: The upper tail probabilities of Spearman's rho, *Journal of the Royal Statistical Society*, *24*(3), 377–379.

Blair, B. C. (2005), Fire effects on the spatial patterns of soil resources in a Nicaraguan wet tropical forest, *Journal of Tropical Ecology*, *21*, 435–444, doi:10.1017/S0266467405002452.

Bouza, N., J. Caujape-Castells, M. A. Gonzalez-Perez, F. Batista, and P. A. Sosa (2002), Population structure and genetic diversity of two endangered endemic species of the Canarian laurel forest: *Dorycnim spectabile (fabaceae)* and *Isoplexis chalcantha (scrophulariaceae)*, *International Journal of Plant Sciences*, *163*(4), 619–630.

Brind Ámour, A., and D. Boisclair (2006), Effect of the spatial arrangement of habitat patches on the development of fish habitat models in the littoral zone of a Canadian shield lake, *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 737–753.

Bulit, C., C. Diaz-Avalos, M. Signoret, and D. J. S. Montagnes (2003), Spatial structure of planktonic ciliate patches in a tropical coastal lagoon: an application of geostatistical methods, *Aquatic Microbial Ecology*, *30*, 185–196.

Bulit, C., C. Diaz-Avalos, and D. J. S. Montagnes (2004), Assessing spatial and temporal patchiness of the autotrophic ciliate *Myrionecta rubra*: a case study in a coastal lagoon, *Marine Ecology Progress Series*, *268*, 55–67.

Conover, W. J. (1999), *Practical Nonparametric Statistics*, Wiley Series in Probability and Statistics, 3 ed., John Wiley and Sons, New York, NY.

Cooper, S. D., L. Barmuta, O. Sarnelle, K. Kratz, and S. Diehl (1997), Quantifying spatial heterogeneity in streams, *Journal of the North American Benthological Society*, *16*(1), 174–188.

Cressie, N., J. Frey, B. Harch, and M. Smith (2006), Spatial prediction on a river network, *Journal of Agricultural, Biological, and Environmental Statistics*, *11*(2), 127–150.

Cubillos, L. A., J. Paramo, P. Ruiz, S. Nunez, and A. Sepulveda (2008), The spatial structure of the oceanic spawning of jack mackerel (*Trachurus murphyi*) off central Chile (1998-2001), *Fisheries Research*, *90*, 261–270.

Dalthorp, D., J. Nyrop, and M. G. Villani (2000), Foundations of spatial ecology: the reification of patches through quantitative description of patterns and pattern repetition, *Entomologia Experimentalis et Applicata*, *96*, 119–127.

Dent, C. L., and N. B. Grimm (1999), Spatial heterogeneity of stream water nutrient concentrations over successional time, *Ecology*, *80*(7), 2283–2298.

Downes, B. J., P. S. Lake, and E. S. G. Schreiber (1993), Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organization, *Freshwater Biology*, *30*, 119–132.

Ettema, C. H., and D. A. Wardle (2002), Spatial soil ecology, *TRENDS in Ecology & Evolution*, *17*(4), 177–183.

Fisher, S. G., N. B. Grimm, E. Marti, and R. Gomez (1998), Hierarchy, spatial configuration, and nutrient cycling in a desert stream, *Australian Journal of Ecology*, *23*, 41–52.

Fletcher, W. J., and N. R. Sumner (1999), Spatial distribution of sardine (*Sardinops sagax*) eggs and larvae: an application of geostatistics and resampling to survey data, *Canadian Journal of Fisheries and Aquatic Sciences*, *56*, 907–914.

Floridi, L. (2009), Logical fallacies as informational shortcuts, *Synthese*, *167*, 317–325, doi:10.1007/s11229-008-9410-y.

Franklin, R. B., L. K. Blum, A. C. McComb, and A. L. Mills (2002), A geostatistical analysis of small-scale spatial variability in bacterial abundance and community structure in salt marsh creek bank sediments, *FEMS Microbiology Ecology*, *42*, 71–80.

Ganio, L. M., C. E. Torgersen, and R. E. Gresswell (2005), A geostatistical approach for describing spatial pattern in stream networks, *Frontiers in Ecology and the Environment*, *3*(3), 138–144.

Gresswell, R. E., D. S. Bateman, G. W. Lienkaemper, and T. J. Guy (2004), Geospatial techniques for developing a sampling frame of watersheds across a region, in *GIS/Spatial Analyses in Fishery and Aquatic Sciences*, vol. 2, edited by T. Nishida, P. J. Kailola, and C. E. Hollingworth, pp. 515–528, Fishery-Aquatic GIS Research Group, Saitama, Japan.

Huettmann, F., and A. W. Diamond (2006), Large-scale effects on the spatial distribution of seabirds in the northwest Atlantic, *Landscape Ecology*, *21*, 1089–1108, doi:10.1007/s10980-006-7246-8.

Isaak, D. J., and R. F. Thurow (2006), Network-scale spatial and temporal variation in chinook salmon (*Oncorhynchus tshawutscha*) redd distributions: Patterns inferred from spatially continuous replicate surveys, *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 285–296, doi: 10.1139/F05-214.

Isaaks, E. H., and R. M. Srivastava (1989), *Applied Geostatistics*, 3 ed., Oxford University Press, New York, NY.

Kotliar, N. B., and J. A. Wiens (1990), Multiple scales of patchiess and patch structure: a hierarchical framework for the study of heterogeneity, *OIKOS*, *59*, 253–260.

Legendre, P. (1993), Spatial autocorrelation: Trouble or new paradigm?, *Ecology*, *74*(6), 1659–1673.

Lindenmayer, D. B. (2000), Factors at multiple scales affecting distribution patterns and their implications for animal conservation leadbeaters possum as a case study, *Biodiversity and Conservation*, *9*, 15–35.

Mast, J. N., and T. T. Veblen (1999), Tree spatial patterns and stand development along the pinegrassland ecotone in the Colorado Front Range, *Canadian Journal of Forest Research*, *29*, 575–584.

Matthews, M. R. (2009), Teaching the philosophical and worldview components of science, *Science & Education*, *18*, 697–728, doi:10.1007/s11191-007-9132-4.

Meisel, J. E., and M. G. Turner (1998), Scale detection in real and artificial landscapes using semivariance analysis, *Landscape Ecology*, *13*, 347–362.

Neville, H. M., D. J. Isaak, J. B. Dunham, R. F. Thurow, and B. E. Rieman (2006), Fine-scale natal homing and localized movement as shaped by sex and spawning babitat in chinook salmon: insights from spatial autocorrelation analysis of individual genotypes, *Molecular Ecology*, *15*, 4589–4602, doi:10.1111/j.1365-294X.2006.03082.x.

Paola, C., and R. Seal (1995), Grain size patchiness as a cause of selective deposition and downstream fining, *Water Resources Research*, *31*(5), 1395–1407.

Pastor, J., B. Dewey, R. Moen, D. J. Mladenoff, M. White, and Y. Cohen (1998), Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA, *Ecological Applications*, *8*(2), 411–424.

Perry, J. N. (1998), Measures of spatial pattern for counts, *Ecology*, *79*(3), 1008–1017.

Perry, J. N., A. M. Liebhold, M. S. Rosenberg, J. Dungan, M. Miriti, A. Jakomulska, and S. Citron-Pousty (2002), Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data, *Ecography*, *25*, 578–600.

Peterson, E. E., and N. S. Urquhart (2006), Predicting water quality impaired stream segments using landscape-scale data and a regional geostatistical model: A case study in Maryland, *Environmental Monitoring and Assessment*, *121*, 615–638, doi:10.1007/s10661-005-9163-8.

Peterson, E. E., D. M. Theobald, and J. M. Ver Hoef (2007), Geostatistical modelling on stream networks: Developing valid covariance matrices based on hydrologic distance and stream flow, *Freshwater Biology*, *52*, 267–279, doi:10.1111/j.1365-2427.2006.01686.x.

Pickett, S. T. A., and M. L. Cadenasso (1995), Landscape ecology: Spatial heterogeneity in ecological systems, *Science*, *269*, 331–334.

Poole, G. C. (2002), Fluvial landscape ecology: Addressing uniqueness within the river discontinuum, *Freshwater Biology*, *47*, 641–660.

Rossi, J.-P. (2003), Clusters in earthworm spatial distribution, *Pedobiologia*, *47*, 490–496.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz (1992), Geostatistical tools for modeling and interpreting ecological spatial dependence, *Ecological Monographs*, *62*(2), 277–314.

Russo, D., and E. Bresler (1981), Soil hydraulic properties as stochastic processes: I. an analysis of field spatial varability, *Soil Science Society of America Journal*, *45*, 682–687.

Russo, D., and W. A. Jury (1987), A theoretical study of the estimation of the correlation scale in spatially variable fields 1: Stationary fields, *Water Resources Research*, *23*(7), 1257–1268.

Schabenberger, O., and C. A. Gotway (2005), *Statistical Methods for Spatial Data Analysis*, Texts in Statistical Science Series, Chapman and Hall/CRC, Boca Raton, FL.

Schmuki, C., C. Vorburger, C. Runciman, and S. Maceachern (2006), When log-dwellers meet loggers: impacts of forest fragmentation on two endemic log-dwelling beetles in southeastern Australia, *Molecular Ecology*, *15*, 1481–1492, doi:10.1111/j.1365-294X.2006.02849.x.

Solie, J. B., W. R. Raun, and M. L. Stone (1999), Submeter spatial variability of selected soil and bermudagrass production variables, *Soil Science Society of America Journal*, *63*, 1724–1733.

Swartzman, G., R. Brodeur, J. Napp, G. Hunt, D. Demer, and R. Hewitt (1999a), Spatial proximity of age-0 walleye pollock (*Theragra chalcogramma*) to zooplankton near the Pribilof Islands, Bering Sea, Alaska, *ICES Journal of Marine Science*, *56*, 545–560.

Swartzman, G., R. Brodeur, J. Napp, D. Walsh, R. Hewitt, D. Demer, G. Hunt, and E. Logerwell (1999b), Relating spatial distributions of acoustically determined patches of fish and plankton: data viewing, image analysis, and spatial proximity, *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(Suppl. 1), 188–198.

Torgersen, C. E., and D. A. Close (2004), Influence of habitat heterogeneity on the distribution of larval pacific lamprey (*Lampetra tridentata*) at two spatial scales, *Freshwater Biology*, *49*(5), 614–630.

Torgersen, C. E., D. M. Price, L. H. W, and B. A. McIntosh (1999), Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon, *Ecological Applications*, *9*(1), 301–319.

Venditti, J. G., and M. A. Church (2005), Bed form initiation from a flat sand bed, *Journal of Geophysical Research*, *110*, doi:10.1029/2004JF000149.

Ver Hoef, J. M., and E. E. Peterson (2007), Spatial modeling of stream network data, in *Proceedings of the 92nd Annual Meeting of the Ecological Society of America*, San Jose, CA.

Ver Hoef, J. M., E. Peterson, and D. Theobald (2006), Spatial statistical models that use flow and stream distance, *Environmental and Ecological Statistics*, *13*, 449–464, doi:10.1007/s10651-006-0022-8.

Ward, J. V. (1989), The four-dimensional nature of lotic ecosystems, *Journal of the North American Benthological Society*, *8*(1), 2–8.

Ward, J. V., G. Bretschko, M. Brunke, D. Danielopol, J. Gibert, T. Gonser, and A. G. Hildrew (1998), The boundaries of river systems: the metazoan perspective, *Freshwater Biology*, *40*, 531–569.

Wiens, J. A. (2002), Riverine landscapes: Taking landscape ecology into the water, *Freshwater Biology*, *47*, 501–515.

Wright, K. K., and J. L. Li (2002), From continua to patches: examining stream community structure over large environmental gradients, *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 1404–1417.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith (2009), *Mixed Effects Models and Extensions in Ecology with R*, Statistics for Biology and Health, 3 ed., Springer, New York, NY.

4. PREDICTION INTERVALS FOR CHANGE DETECTION IN PAIRED WATERSHED STUDIES

4.1 ABSTRACT

Hydrologic data may be temporally autocorrelated requiring autoregressive process parameters to be estimated. Current statistical methods for hydrologic change detection in paired watershed studies rely on prediction intervals, but the current form of prediction intervals does not include all appropriate sources of variation. Corrected prediction intervals for the analysis of paired watershed study data that include variation associated with covariance and linear model parameter estimation are presented. We provide an example of their application to data from the Hinkle Creek Paired Watershed Study located in the western Cascade foothills of Southern Oregon. Research implications of using the correct prediction limits and incorporating the estimation uncertainty of autoregressive process parameters are discussed.

4.2 INTRODUCTION

The analysis of a paired watershed study (PWS) design establishes a statistical relationship between hydrologic responses in a control and a treated catchment area over a given time period to determine if forest management treatments affect hydrologic processes within the treated catchment area. During a calibration phase the statistical relationship is estimated. Following this phase, forest management practices are applied to the treatment catchment only. Post-treatment predictions based on the calibration phase relationship are used to predict the hydrologic response in the treated catch-

ment absent of forest harvesting. Treatment effects are discerned as the difference between the observed and predicted response of the treated catchment area.

The prediction interval method of change detection for paired watershed studies followed from the work of *Harr et al.* (1979) using ordinary least squares (OLS) regression based on annual and storm-based mean and maximum water yield, peak flow, sediment load, and temperature to evaluate the effects of forest management on water quality and quantity; for review see *Andrassian* (2004); *Bosch and Hewlett* (1982); *Brown et al.* (2005). After regressing the observed values of the treatment watershed on the observed control watershed values via OLS during the calibration period, predicted values and prediction intervals are computed for the post-treatment time period. Prediction intervals should not be confused with confidence intervals, though each provides a plausible range for an estimated value and conveys the precision of the estimate.

The use of data collected on daily or monthly time scales prompted adjustments to the prediction interval method of change detection. To continue the prediction interval change detection methodology in the presence of autocorrelated data, researchers began to filter the model residuals via auto-regressive (AR) analysis and use the estimated variance of the AR disturbances to construct prediction intervals and assess treatment effects (*Gomi et al.*, 2006; *Moore et al.*, 2005; *Watson et al.*, 2001). This method ignores variation attributed to the estimation of autocorrelation model parameters, and changes in prediction precision due to where the control watershed response values lie in relation to their range during the calibration period. Both of these sources of variation should be considered in the construction of prediction intervals for change detection. Excluding these known sources

of variation will result in underestimates of prediction variance leading to prediction intervals that are too narrow, and increased Type I error rates.

PWS have been used to directly inform policy makers of the effects of forest management on catchment hydrology. The ability to correctly identify management effects requires statistically powerful analysis methods that incorporate well-defined and measured sources of prediction variation. The objective of this paper is to provide an updated form of prediction limits for use in detecting treatment effects in paired watershed studies that incorporate appropriate sources of variation.

4.3 PREVIOUS METHODS OF CHANGE DETECTION

The standard approach for change detection in PWS begins by establishing a linear model with the control watershed response (e.g. sediment load) used as a covariate to predict the treated watershed response during a calibration time period. During this period, observations are made before any experimental treatments are applied. If the observations are temporally scaled such that autocorrelation is not an issue, as may be expected for hydrological data summarized during storm events, the model is:

$$y_i = \beta_0 + x_i\beta_1 + \epsilon_i \tag{4.1}$$

with y_i representing the observed value from the treated watershed, x_i the observed value from the control watershed, $i = 1, 2, \ldots n$ representing the number of storms during the calibration time period, β_0 and β_1 are the intercept and slope parameters, and $\epsilon_i \sim N(0, \sigma^2)$. After treatment begins, observations continue to be collected at both the treated and control watersheds. At the completion of the treatment period, the calibration model is

used to make predictions and prediction intervals for the treated watershed response based on values of the control watershed during the post-treatment time period. Each prediction interval value is calculated via

$$\hat{y_j} \mid x_j \pm t_{(\frac{\alpha}{2},n-2)}\hat{\sigma}\sqrt{1+\frac{1}{n}+\frac{(x_j-\overline{x})^2}{\sum(x_i-\overline{x})^2}}. \tag{4.2}$$

where j runs from $n+1$ to the final storm of data collection m, x_j represents the observed control catchment response for storm j during the treatment period, $\hat{\sigma}^2$ estimates σ^2, and $t_{(\frac{\alpha}{2},n-2)}$ is the α-level quantile of a t-distribution with $n-2$ degrees of freedom. For each observation within the post-treatment period, a residual value R_j is computed as $y_j - (\hat{y_j} \mid x_j)$ where $(\hat{y_j} \mid x_j)$ is the predicted value using (4.1). Subtracting $(\hat{y_j} \mid x_j)$ from the upper and lower bounds of the prediction interval computed using (4.2) provides a prediction interval for the set of R_j. A disproportionate number of post-treatment residuals that exceed the prediction intervals is an indication of a treatment effect (*Harr, Fredriksen, and Rothacher*, 1979).

Of concern with most traditional paired-catchment studies, however; is the relatively small number of pre-treatment observations used to construct the statistics-based change detection models. In the absence of large sample sizes, diminished statistical power undermines the ability to detect changes in physical behavior. Notable PWS such as the Alsea and Caspar Creek studies used annual values of water yield and sediment load with sample sizes of $n = 7$ and $n = 4$, respectively (*Lewis*, 1998; *Harris*, 1977).

To address the limitations that annual or storm-based data pose for change detection in watershed studies, researchers began data collection on monthly and daily time scales (*Gomi et al.*, 2006; *Moore et al.*, 2005; *Scott and Lesch*, 1997; *Watson et al.*, 2001). Seasonal periodicity and serial auto-correlation have been present in measurements observed close in time which

violates the assumptions of independence and homoscedastic variance of OLS regression (*Salas*, 1993). If unaccounted for, autocorrelation can result in incorrect estimates of regression coefficients and invalid tests of significance (*Carroll and Pearson*, 1998). Logarithmic transformations of explanatory and response variables are used to address non-constant variance and sinusoidal trigonometric terms can be used to describe seasonality (*Helsel and Hirsch*, 1992). *Salas* (1993) addressed autocorrelation by fitting a stochastic time-series model to model residuals.

Watson et al. (2001) recognized the need to consider temporal autocorrelation when moving to finer time scales. To evaluate changes in monthly water yield at the Maroondah paired-catchment study in Australia, they fit a model similar to (4.1), but with additional sinusoidal terms to account for seasonal monthly variation and a log_{10} transformation of the measured response variable to account for non-constant variance. In this model, i now represents each month of the calibration time period. Following *Salas* (1993), they fit a stochastic time series model to their residuals. They selected a first-order autoregressive model (AR(1)). An AR(1) models autocorrelation among the ϵ_i values as

$$\epsilon_i = \phi_1 \epsilon_{i-1} + \gamma_i \tag{4.3}$$

where ϕ_1 accounts for the autocorrelation between previous ϵ_i's and γ_i is an independent innovation. After estimating ϕ_1 *Watson et al.* (2001) solved (4.3) for $\hat{\gamma}_i$ to compute the estimated random innovation at each observed value. They computed the sample standard deviation of the set of $\hat{\gamma}_i$ values, multiplied this value by 1.96, and then added and subtracted this value from 0 to obtain upper and lower 95% "prediction limits" to assess change due to forest harvesting (Watson, personal communication).

Following *Harr et al.* (1979), *Watson et al.* (2001) computed predicted

values for the treated watershed using the observed values of the control watershed during the post-treatment period. Next, they computed the residual (R_j) values as described above. They substituted R_j for ϵ_i in (4.3) and used $\hat{\phi}_1$ to solve for each $\hat{\gamma}_j$. The percentage of these post-treatment $\hat{\gamma}_j$ values that exceeded the prediction limits was computed, and a treatment effect was declared if more than 5% of these values exceed the 95% prediction limits since 5% of all $\hat{\gamma}_i$ values are expected to exceed the 95% prediction intervals by construction (*Watson et al.*, 2001).

Moore et al. (2005) and *Gomi et al.* (2006) modified the estimation and analysis method proposed by *Watson et al.* (2001) using daily stream temperature data to evaluate the headwater catchment responses to clear-cut harvesting in coastal British Columbia, Canada. These researchers correctly recognized that autocorrelated data not only require attention in the analysis of residuals, but additionally in the estimation of linear model parameters from (4.3). Accordingly, they used generalized least squares (GLS), and not OLS, for linear model parameter estimation (*Myers*, 1990, p. 278). Moving from the simple linear regression scenario of (4.1), (4.2), and (4.3) to the multiple linear regression and GLS frameworks it is much more efficient to represent models and formula components using matrix notation.

Using common matrix notation, the multiple linear regression analog to (4.1) is expressed as

$$\underset{\sim}{\mathbf{y}} = \underset{\sim}{\mathbf{X}}\underset{\sim}{\beta} + \underset{\sim}{\epsilon} \tag{4.4}$$

where $\underset{\sim}{\mathbf{y}}$ is an n x 1 vector of responses, $\underset{\sim}{\mathbf{X}}$ is an n x k design matrix, k is the number of model parameters, $\underset{\sim}{\beta}$ is a k x 1 vector of model parameters, $\underset{\sim}{\epsilon} \sim N(\underset{\sim}{0}, \sigma^2\underset{\sim}{\mathbf{I_n}})$, and $\underset{\sim}{\mathbf{I_n}}$ is an n x n identity matrix. It should be noted that this model assumes the elements of $\underset{\sim}{\mathbf{y}}$ are independent. For autocorrelated data, GLS regression allows the independent errors assumption to be

relaxed and assumes $\underset{\sim}{\epsilon} \sim N(\underset{\sim}{0}, \sigma^2\underset{\sim}{\Psi})$. $\sigma^2\underset{\sim}{\Psi}$ is an n x n symmetric variance-covariance matrix with variance values along the diagonal and covariance values in the non-diagonal matrix elements. The appropriate estimator for $\underset{\sim}{\beta}$ when $Var(\underset{\sim}{\epsilon}) \neq \sigma^2\underset{\sim}{\mathbf{I}}$ is not the OLS estimator, but rather the GLS estimator given by (*Myers*, 1990, p. 278)

$$\underset{\sim}{\hat{\beta}} = (\underset{\sim}{\mathbf{X}}'\underset{\sim}{\Psi}^{-1}\underset{\sim}{\mathbf{X}})^{-1}\underset{\sim}{\mathbf{X}}'\underset{\sim}{\Psi}^{-1}\underset{\sim}{\mathbf{y}}. \tag{4.5}$$

In addition to recognizing that the covariance structure should be incorporated into the linear model parameters estimator, *Moore et al.* (2005) and *Gomi et al.* (2006) also recognized that using the partial autocorrelation function (PACF) can aid in determining the appropriate order of the autoregressive process. After determining the autoregressive structure and estimating the linear model and autoregressive parameters for the calibration period data, the residuals, innovations, prediction intervals, and assessment of treatment effects were computed following the methods of *Watson et al.* (2001) described above.

Though *Harr et al.* (1979) correctly produced prediction intervals in the OLS setting and the above studies are significant developments for the use of temporally autocorrelated hydrologic data, the intervals created by *Watson et al.* (2001), *Moore et al.* (2005), and *Gomi et al.* (2006) are not prediction intervals. Their intervals are based on an estimate of the innovations variance, and do not account for prediction variance that includes variation due to the estimation of linear model and autoregressive function parameters, and covariance between observations (autocorrelation). Incorporating these sources of variation will lead to improved prediction limits for evaluating treated catchment behavior after management relative to pre-management conditions.

4.4 IMPROVED METHODS FOR CHANGE DETECTION

This section begins by establishing the correct form of the GLS prediction variance that incorporates variation due to the estimation of linear model and autocorrelation parameters, and then derives the prediction variance of the innovations that are used to determine if treatment effects have likely occurred.

To begin, consider a vector of the combined data containing the observed stream discharge over the pre-treatment time interval and the predicted stream discharge in the post-treatment interval that is predicted using the calibration equation. Note that the terms "prediction" and "predicted values" refer to predictions for the treated watershed during the post-treatment period but in the absence of treatment. The variance-covariance matrix of the observed and predicted values can be partitioned as follows (*Judge et al.*, 1980, p. 209)

$$\sigma^2 \begin{pmatrix} \underset{\sim}{\mathbf{\Psi}} & \underset{\sim}{\mathbf{V}} \\ \underset{\sim}{\mathbf{V}}' & \underset{\sim}{\mathbf{\Psi}_\mathbf{j}} \end{pmatrix} \tag{4.6}$$

where $\sigma^2 \underset{\sim}{\mathbf{\Psi}_\mathbf{j}}$ is the variance-covariance matrix of the predicted values and $\sigma^2 \underset{\sim}{\mathbf{V}}$ is the covariance matrix between observed and predicted observations. For ease of notation, we will proceed by referring to the elements of (4.6) as having been multiplied by σ^2. If the variance and covariance parameters are known, the prediction equation has the form

$$\underset{\sim}{\widehat{\mathbf{y}}} \,|\, \underset{\sim}{\mathbf{x}_\mathbf{j}} = \underset{\sim}{\mathbf{x}_\mathbf{j}} \underset{\sim}{\hat{\beta}} + \underset{\sim}{\mathbf{V}}' \underset{\sim}{\mathbf{\Psi}}^{-1} (\underset{\sim}{\mathbf{y}} - \underset{\sim}{\mathbf{X}} \underset{\sim}{\hat{\beta}}) \tag{4.7}$$

where $\underset{\sim}{\hat{\beta}}$ is estimated from (4.5), and (4.7) is the best linear unbiased predictor (BLUP) for $\underset{\sim}{\mathbf{y}} \,|\, \underset{\sim}{\mathbf{x}_\mathbf{j}}$ (*Kariya and Kurata*, 2004, p. 70). Given this unbiased estimator for $\underset{\sim}{\mathbf{y}} \,|\, \underset{\sim}{\mathbf{x}_\mathbf{j}}$ and again that the variance and covariance parameters

are known, the prediction mean-squared error (MSE) can be computed as (*Harville and Jeske*, 1992; *Zimmerman and Cressie*, 1992)

$$MSE\big[\widehat{\underset{\sim}{\mathbf{y}}}\,|\,\underset{\sim}{\mathbf{x_j}},\underset{\sim}{\mathbf{y_j}}\big] = \underset{\sim}{\mathbf{\Psi_j}} - \underset{\sim}{\mathbf{V}}'\underset{\sim}{\mathbf{\Psi}}^{-1}\underset{\sim}{\mathbf{V}} + (\underset{\sim}{\mathbf{x_j}}' - \underset{\sim}{\mathbf{V}}'\underset{\sim}{\mathbf{\Psi}}^{-1}\underset{\sim}{\mathbf{X}})(\underset{\sim}{\mathbf{X}}'\underset{\sim}{\mathbf{\Psi}}^{-1}\underset{\sim}{\mathbf{X}})^{-1}(\underset{\sim}{\mathbf{x_j}} - \underset{\sim}{\mathbf{X}}'\underset{\sim}{\mathbf{\Psi}}^{-1}\underset{\sim}{\mathbf{V}}). \tag{4.8}$$

Note that since our estimator is unbiased, the terms "prediction MSE" and "prediction variance" are equivalent.

In practical settings the parameters of variance-covariance matrices are generally not known, and need to be estimated from the observed data. A common method to obtain prediction variances has been to estimate the variance-covariance parameters, and simply plug-in these values to (4.8) as fixed and known; however, this estimator is biased (*Harville and Jeske*, 1992; *Kackar and Harville*, 1984; *Schabenberger and Gotway*, 2005; *Zimmerman and Cressie*, 1992).

To demonstrate the origin of this bias, start by defining $\underset{\sim}{\mathbf{y_j}}$ as the true values of observations at values of $\underset{\sim}{\mathbf{x_j}}$, $\widehat{\underset{\sim}{\mathbf{y_j}}}(\underset{\sim}{\mathbf{\Psi}})$ to be predicted values of $\underset{\sim}{\mathbf{y_j}}$ at values of $\underset{\sim}{\mathbf{x_j}}$ with known covariance parameters, and $\widehat{\underset{\sim}{\mathbf{y_j}}}(\hat{\underset{\sim}{\mathbf{\Psi}}})$ to be the predicted values when the covariance parameters are also estimated. Additionally, restrict the class of estimators of $\underset{\sim}{\mathbf{\Psi}}$ to those that are even (symmetric around zero) and translation invariant. These properties are shared by both maximum likelihood (ML) and restricted maximum likelihood (REML) estimators (*Schabenberger and Gotway*, 2005, p. 265). *Kackar and Harville* (1984) decompose the prediction error into

$$\widehat{\underset{\sim}{\mathbf{y_j}}}(\hat{\underset{\sim}{\mathbf{\Psi}}}) - \underset{\sim}{\mathbf{y_j}} = \big(\widehat{\underset{\sim}{\mathbf{y_j}}}(\underset{\sim}{\mathbf{\Psi}}) - \underset{\sim}{\mathbf{y_j}}\big) + \big(\widehat{\underset{\sim}{\mathbf{y_j}}}(\hat{\underset{\sim}{\mathbf{\Psi}}}) - \widehat{\underset{\sim}{\mathbf{y_j}}}(\underset{\sim}{\mathbf{\Psi}})\big) \tag{4.9}$$

and show that given the translation invariant restriction, the two partitions of $\widehat{\underset{\sim}{\mathbf{y_j}}}(\hat{\underset{\sim}{\mathbf{\Psi}}}) - \underset{\sim}{\mathbf{y_j}}$ in (4.9) are distributed independently. This leads to a prediction

MSE of

$$MSE\big[\widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\hat{\underset{\sim}{\boldsymbol{\Psi}}}), \underset{\sim}{\mathbf{y}}_{\mathbf{j}}\big] = MSE\big[\widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\underset{\sim}{\boldsymbol{\Psi}}), \underset{\sim}{\mathbf{y}}_{\mathbf{j}}\big] + Var\big[\widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\hat{\underset{\sim}{\boldsymbol{\Psi}}}) - \widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\underset{\sim}{\boldsymbol{\Psi}})\big]. \tag{4.10}$$

Thus, by substituting $\hat{\underset{\sim}{\boldsymbol{\Psi}}}$ for $\underset{\sim}{\boldsymbol{\Psi}}$ one simply estimates $MSE\big[\widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\underset{\sim}{\boldsymbol{\Psi}}), \underset{\sim}{\mathbf{y}}_{\mathbf{j}}\big]$ and therefore underestimates the $MSE\big[\widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\hat{\underset{\sim}{\boldsymbol{\Psi}}}), \underset{\sim}{\mathbf{y}}_{\mathbf{j}}\big]$ by $Var\big[\widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\hat{\underset{\sim}{\boldsymbol{\Psi}}}) - \widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\underset{\sim}{\boldsymbol{\Psi}})\big]$.

Again given the class of even and translation invariant estimators, and additionally that the combined vector of stream discharge follows a Gaussian distribution, a first-order approximately unbiased estimator of $MSE\big[\widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\hat{\underset{\sim}{\boldsymbol{\Psi}}}), \underset{\sim}{\mathbf{y}}_{\mathbf{j}}\big]$ is

$$MSE\big[\widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\underset{\sim}{\boldsymbol{\Psi}}), \underset{\sim}{\mathbf{y}}_{\mathbf{j}}\big] + 2tr\big(A(\hat{\underset{\sim}{\boldsymbol{\Psi}}})B(\hat{\underset{\sim}{\boldsymbol{\Psi}}})\big) \tag{4.11}$$

which is referred to as the Prasad-Rao MSE estimator (*Harville and Jeske*, 1992; *Schabenberger and Gotway*, 2005). $2tr\big(A(\hat{\underset{\sim}{\boldsymbol{\Psi}}})B(\hat{\underset{\sim}{\boldsymbol{\Psi}}})\big)$ unbiasedly approximates $Var\big[\widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\hat{\underset{\sim}{\boldsymbol{\Psi}}}) - \widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\underset{\sim}{\boldsymbol{\Psi}})\big]$ with $A(\hat{\underset{\sim}{\boldsymbol{\Psi}}})$ approximating $Var\Big[\frac{\partial \widehat{\underset{\sim}{\mathbf{y}}}_{\mathbf{j}}(\underset{\sim}{\boldsymbol{\Psi}})}{\partial \underset{\sim}{\boldsymbol{\Psi}}}\Big]$ and $B(\hat{\underset{\sim}{\boldsymbol{\Psi}}})$ approximating $MSE\big[\hat{\underset{\sim}{\boldsymbol{\Psi}}}, \underset{\sim}{\boldsymbol{\Psi}}\big]$. The theoretical justification for (4.11) can be found in *Prasad and Rao* (1990) and *Harville and Jeske* (1992), and examples of the computation of $A(\hat{\underset{\sim}{\boldsymbol{\Psi}}})$ and $B(\hat{\underset{\sim}{\boldsymbol{\Psi}}})$ can be found in *Harville and Jeske* (1992), *Kackar and Harville* (1984), *Prasad and Rao* (1990), and *Zimmerman and Cressie* (1989). Note that (4.11) is the variance-covariance matrix of prediction, and as such, the diagonal elements of (4.11) represent the prediction variance.

This approximation of the prediction variance can be used to obtain prediction intervals for the post-treatment time period to assess whether change has likely occurred, as discussed in Section 2. Prediction residuals are obtained by subtracting predicted values from observed values for the treated watershed during the post-treatment time period, and this sequence of potentially temporally autocorrelated residuals $(R_1, R_2, \ldots R_m)$, the autocorrelation function, and estimates of the autocorrelation parameters $(\hat{\phi}_1, \hat{\phi}_2, \ldots \hat{\phi}_p)$

can be used to create prediction intervals. In essence, we consider each post-treatment innovation ($\hat{\gamma}_j$) as a linear combination of autocorrelated residuals, and compute the variance of this linear combination. To match the example in Section 4, the prediction variance associated with each innovation is now derived for an AR(p) autocorrelation structure. A similar approach can be used to derive the prediction variance of more general classes of autocorrelated processes. If we assume:

1. $\hat{\phi}_q$ independent $\hat{\phi}_{q'}$ for all q, q'
2. $\hat{\phi}_q$ independent R_j for all q, j

then for each $R_j, j = 0, \ldots, m$ forming a stationary time series,

$$R_j = \sum_{q=1}^{p} \hat{\phi}_q R_{j-q} + \hat{\gamma}_j \tag{4.12}$$

and basic algebra leads to

$$\hat{\gamma}_t = R_t - \sum_{j=1}^{p} \hat{\phi}_j R_{t-j}. \tag{4.13}$$

Using more algebra and basic properties of linear combinations of variances and covariances (*Goodman*, 1960), the prediction variance of each $\hat{\gamma}_j$ can be found as

$$\begin{aligned} Var(\hat{\gamma}_j) &= Var(R_j - \sum_{q=1}^{p} \hat{\phi}_q R_{j-q}) \qquad (4.14) \\ &= Var(R_j) \\ &\quad + \sum_{q=1}^{p} \Big[\hat{\phi}_q^2 Var(R_{j-q}) + (R_{j-q})^2 Var(\hat{\phi}_q) - Var(R_{j-q}) Var(\hat{\phi}_q) \\ &\qquad -2\sigma^2 \Big(\rho_q \big(\hat{\phi}_q + \sum \hat{\phi}_k \hat{\phi}_w \big) \Big) \Big]; \text{ for all } w - k = \qquad (4.15) \end{aligned}$$

where $Var(R_j)$ is estimated using (4.11). Innovations are normally distributed with an expected mean of 0, hence upper and lower prediction intervals at each time j are then simply computed by

$$0 \pm 1.96\sqrt{Var(\hat{\gamma}_j)} \tag{4.16}$$

4.5 EXAMPLE: DAILY DISCHARGE DATA AT HINKLE CREEK

To demonstrate the differences between the prediction limits proposed by *Watson et al.* (2001) and the improved limits described in Section 3, we present an example from the Hinkle Creek Paired Watershed Study. The Hinkle Creek Paired Watershed Study, located in the foothills of the Cascade Mountains in southern Oregon, was designed to evaluate the influence of contemporary forest practices on hydrology and stream biota at the headwater scale. Detailed descriptions of the Hinkle Creek Paired Watershed Study, including watershed description, data collection methodology, and additional analysis can be found at the Watersheds Research Cooperative homepage (http://watershedsresearch.org/). Average daily discharge for this example was extracted for both DeMersseman (control) and Fenton (treated) catchments. Two years of pre-treatment discharge data were used to develop calibration equations and the relationship between control and treated catchments. Due to equipment constraints, data were not collected during extremely low flow periods each summer. After the calibration time period, 65% of the Fenton Creek watershed was clear-felled in accordance with the Oregon Forest Practices Act. We used R software *R Development Core Team* (2005) for all analysis and computations.

We used a log_{10} transformation of daily discharge for treatment and con-

trol watersheds and subtracted the mean monthly discharge from each observation to achieve stationarity. Stationarity is a required assumption for fitting AR, moving average (MA), or autoregressive-moving average (ARMA) time series models (*Chatfield*, 2004, p. 48).

We used partial autocorrelation functions and Akaike's Information Criterion (AIC) to choose the most parsimonious model. We considered all sets of ARMA(p,q) autoregressive-moving average time series models with both p and q parameters ranging from 0 to 4, and found a second-order autoregressive model provided the best fit. Next, we fit a GLS model, and then obtained predicted values, residuals, innovations, and prediction intervals as described in Section 3. Figure 1 shows the post-treatment innovations and prediction intervals based on the *Watson et al.* (2001) method and our improved method. The horizontal axis is ordered chronologically, which is the common display for these analyses within the field of hydrology. The improved prediction intervals are indeed wider than the *Watson et al.* (2001) intervals, and are not constant across time. Prediction intervals are narrowest at the mean of the control watershed daily discharge values, and widen progressively as the values move further from the mean. The non-systematic variation in the width of the improved prediction intervals is due to the fact that the innovations and prediction intervals are ordered by time, not by covariate values.

If the proportion of post-treatment innovations that exceed the prediction intervals is greater than a specified limit, typically 5%, it is determined that a change due to forest management has occurred. The *Watson et al.* (2001) intervals would lead one to conclude that a treatment effect has occurred, as 11.0% of the innovations exceed those limits. In contrast, the conclusion would be different using the improved prediction limits. Only 5.7% of the

innovations exceeding the prediction limits indicate suggestive, but inconclusive, evidence of a treatment effect.

4.6 DISCUSSION

First, a cautionary note about the regression-based approach for change detection in paired watershed studies. Prediction of future observations is only valid for post treatment values of the control watershed that lie within the range of values during the calibration phase. Daily discharge, for example, is strongly connected to climatic events. Should a post-treatment storm produce larger control watershed daily discharge values than any observed during the calibration phase, it would be technically inappropriate to define a prediction limit over the days of this event.

Our example demonstrates that the improved prediction limits are wider than those computed using the *Watson et al.* (2001) method, and that the difference between the two methods is great enough to effect final conclusions. From Figure 1 it appears that many of the points exceeding the *Watson et al.* (2001) method, but not our prediction limits, occur when covariate values are furthest from their means and our prediction limits are the widest. Statistical tools attempt to differentiate the variation within treatments from the variation among treatments. This partition of variance is clouded by imprecision induced by estimating the parameters associated with the statistical model. Not accounting for this imprecision can lead to incorrect conclusions.

In a review of decades of studies on the effects of forest management on annual-scale stream hydrology, *Bosch and Hewlett* (1982) conclude that treatment effects are expected when at least 20% of the watershed is harvested. With 65% of the Fenton Creek watershed harvested, the fact that

these data may not show evidence of treatment effects highlights the potential for daily hydrology data from paired watershed studies to be too noisy for efficient change detection. Since paired watershed studies can inform political, social, and economic policies, it is imperative that researchers judiciously choose appropriate analysis methods for their data analysis.

It is clear that incorporating prediction variance is necessary for constructing prediction intervals. The effort involved in obtaining the correction term of the Prasad-Rao MSE estimator warrants investigating the improvement this correction term gives over simply using the biased plug-in estimator presented in Section 3. *Schabenberger and Gotway* (2005, p. 266) note that the bias of the plug-in estimator can be substantive for small sample sizes. A small sample size is not an issue in our example, where n= 414 for the calibration time period. For spatially autocorrelated data, in addition to the assumptions necessary for (4.11), *Zimmerman and Cressie* (1992) suggest using the Prasad-Rao MSE estimator when the spatial correlation is known or estimated to be weak, and when the estimated variance-covariance matrix of the observed data is known to be negatively biased. The estimated value of the first autoregressive parameter for our example is 0.996 (95% CI: 0.90, 1.09), which is consistent with values of strong autocorrelation as seen in *Vijapurkar and Gotway* (2001). There is another piece of evidence that may indicate that the use of the correction term may not be necessary for daily discharge data. We ran the analysis again without the Prasad-Rao correction term, this time using the plug-in version of (4.8) for the prediction variance. Relative to the variance estimates computed using the correction term, the plug-in estimates average nearly 100% of the corrected values. This suggests the bias of the plug-in estimator for these data is essentially zero. To balance this result, we applied the same approach to a similar dataset from the

Hinkle Creek PWS summarized to monthly intervals, and with a calibration period sample size of 20. This data was fit with a first-order autoregressive model and the estimated autoregressive parameter was 0.28 (95% CI: -0.17, .74). The plug-in estimator showed much more bias, only averaging 83% of the corrected Prasad-Rao MSE estimator values. It may not be necessary to use the Prasad-Rao MSE estimator for daily summarized paired watershed data, though this warrants thorough investigation.

The prediction intervals we present are a further development for change detection analysis of hydrologic data from paired watershed studies. These refinements build upon improvements presented by *Watson et al.* (2001) and *Gomi et al.* (2006). We recommend that prediction intervals incorporating prediction variance be used for change detection analysis.

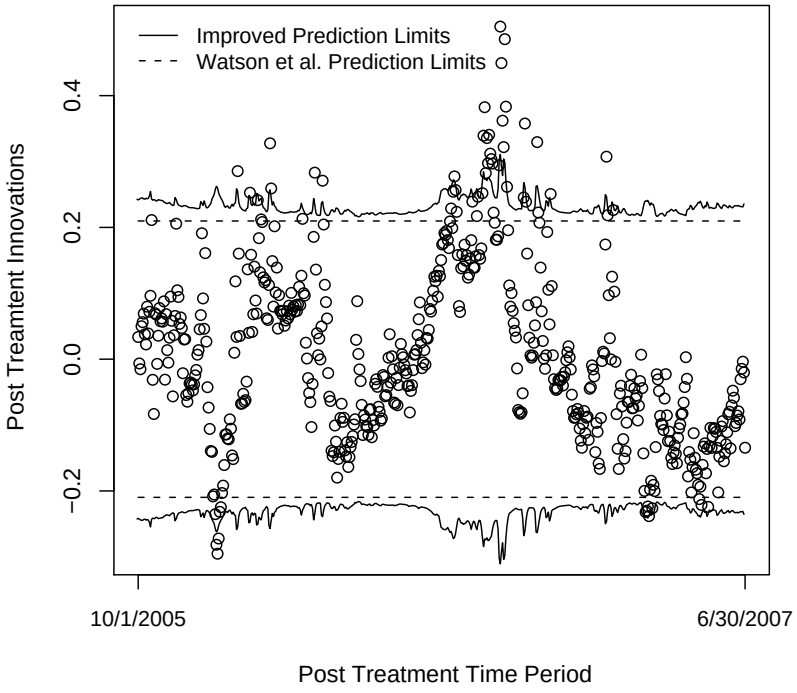

Figure. 4.1: Post-treatment daily discharge innovations from paired De-Mersseman and Fenton Creeks, from the Hinkle Creek Paired Watershed Study, Oregon.

BIBLIOGRAPHY

Andrassian, V. (2004), Waters and forests: From historical controversy to scientific debate, *Journal of Hydrology*, *291*(1–2), 1–27.

Bosch, J. M., and J. D. Hewlett (1982), A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration, *Journal of Hydrology*, *55*(1–4), 3–23.

Brown, J. D., L. Zhang, T. A. McMahon, A. W. Western, and R. A. Vertessy (2005), A review of paired catchment studies for determining changes in water yield resulting from alterations in vegetation, *Journal of Hydrology*, *310*(1–4), 28–61.

Carroll, S. S., and D. L. Pearson (1998), Spatial modeling of butterfly species richness using tiger beetles (*Cicindelidae*) as a bioindicator taxon, *Ecological Applications*, *8*(2), 531–543.

Chatfield, C. (2004), *The Analysis of Time Series: An Introduction*, Texts in Statistical Science Series, 6 ed., Chapman and Hall/CRC, Boca Raton, FL.

Gomi, T., R. D. Moore, and A. S. Dhakal (2006), Headwater stream temperature response to clear-cut harvesting with different riparian treatments, coastal British Columbia, Canada, *Water Resources Research*, *42*,

Goodman, L. A. (1960), On the exact variance of products, *Journal of the American Statistical Association*, *55*(292), 708–713.

Harr, R. D., R. L. Fredriksen, and J. Rothacher (1979), Changes in streamflow following timber harvest in southwestern Oregon, *Research Paper PNW 249*, USDA Forest Service: Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Harris, D. D. (1977), Hydrologic changes after logging in two small Oregon coastal watersheds, *Water-Supply Paper 2037*, United States Geological Survey, Arlington, VA.

Harville, D. A., and D. R. Jeske (1992), Mean squared error of estimation or prediction under a general linear model, *Journal of the American Statistical Association*, *87*(419), 724–731.

Helsel, D. R., and R. M. Hirsch (1992), *Statistical Methods in Water Resources*, Elsevier, Amsterdam.

Judge, G. G., W. E. Griffiths, R. C. Hill, and T.-C. Lee (1980), *The Theory and Practice of Econometrics*, John Wiley and Sons, New York, NY.

Kackar, R. N., and D. A. Harville (1984), Approximations for standard errors of estimators of fixed and random effects in mixed linear models, *Journal of the American Statistical Association*, *79*(388), 853–862.

Kariya, T., and H. Kurata (2004), *Generalized Least Squares*, John Wiley and Sons, West Sussex, England.

Lewis, J. (1998), Evaluating the impacts of logging activites on erosion and suspended sediment transport in the Caspar Creek watersheds, *General Technical Report 168*, USDA Forest Service: Pacific Southwest Research Station, Ukiah, CA.

Moore, R. D., P. Sutherland, T. Gomi, and A. Dhakal (2005), Thermal regime of a headwater stream within a clear-cut, coastal British Columbia, Canada, *Hydrological Processes*, *19*(13), 2591–2608, doi:10.1002/hyp.5733.

Myers, R. H. (1990), *Classical and Modern Regression with Applications*, Duxbury Classic Series, Duxbury, Pacific Grove, CA.

Prasad, N. G. N., and J. N. K. Rao (1990), The estimation of the mean squared error of small-area estimators, *Journal of the American Statistical Association*, *85*(409), 163–171.

R Development Core Team (2005), *R: A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0.

Salas, J. D. (1993), *Handbook of Hydrology*, chap. Analysis and Modeling of Hydrologic Time Series, pp. 19.1–19.72, McGraw-Hill, New York, NY.

Schabenberger, O., and C. A. Gotway (2005), *Statistical Methods for Spatial Data Analysis*, Texts in Statistical Science Series, Chapman and Hall/CRC, Boca Raton, FL.

Scott, D. F., and W. Lesch (1997), Streamflow responses to afforestation with *Eucalyptus grandis* and *Pinus patula* and to felling in the Mokobulaan experimental catchments, South Africa, *Journal Of Hydrology*, *199*(3–4), 360–377.

Vijapurkar, U. P., and C. A. Gotway (2001), Assessment of forecasts and forecast uncertainty using generalized linear regression models for time series count data, *Journal of Statistical Computation and Simulation*, *68*(4), 321–349.

Watson, F., R. Vertessy, T. McMahon, B. Rhodes, and I. Watson (2001), Improved methods to assess water yield changes from paired-catchment studies: Application to the Maroondah catchments, *Forest Ecology and Management*, *143*(1–3), 189–204.

Zimmerman, D. L., and N. A. C. Cressie (1989), Improved estimation of the kriging variance, *Technical Report 161*, The University of Iowa, Iowa City, Iowa.

Zimmerman, D. L., and N. A. C. Cressie (1992), Mean squared prediction error in the spatial linear model with estimated covariance parameters, *Annals of the Institute of Statistical Mathematics*, *44*(1), 27–43.

5. CONCLUSIONS

5.1 CONCLUDING REMARKS

This collection of manuscripts serves to refine the the collection, interpretation, and application of autocorrelated data in headwater stream networks.

Chapter 2 demonstrated that sampling design affects the detection of spatial autocorrelation in samples drawn from spatially autocorrelated stream-network data. Incorporating clusters of samples lead to increased chances of obtaining samples with evidence of spatial autocorrelation than non-clustered sampling protocols, and spatially distributed clusters were more apt to contain spatial autocorrelation than small tributary focused clusters. Chapter 2 also revealed that basin and stream-network characteristics are associated with the ability to detect spatial autocorrelation in stream networks. Detection of spatial autocorrelation was the most difficult in more spherically shaped basins with higher drainage densities. Strong differences among sampling designs for the estimation of autocorrelation function values at several lag distances were not observed, and all sampling protocols generally exhibited negatively biased estimates.

Chapter 3 demonstrated that using the range parameter to estimate the size of patches can be problematic for data containing patches of varying sizes and heterogenous response values. Range parameters were generally much larger than, and did not show evidence of strong correlation with, average patch or gap lengths. Integral scale values more closely matched the magnitude of average patch and gap lengths, but were no more correlated with patch lengths than were range parameters. Range parameters were most strongly correlated with the largest patch and gap lengths within each basin.

Chapter 4 demonstrated a refinement in the construction of prediction intervals for hydrologic change detection in paired watershed studies. Prediction interval improvement resulted from explicitly incorporating the variation associated with estimating linear and autocorrelation model parameters. In a comparison between the former and improved methods of prediction interval construction, it was shown that the difference between the two methods is large enough to effect conclusions drawn from an analysis.

5.2 RELATED FUTURE WORK

The results of the work within this dissertation suggest some interesting ideas for future research.

As discussed in Chapter 2, it seems that considering a broader range of cluster sizes, and samples containing both clustered and unclustered locations may be beneficial. Additionally, a more realistic scenario that involves estimation of both linear and autocorrelation model parameters seems a very logical progression.

In light of the results from Chapter 3, there several future directions to take in regards to autocorrelative measures of patch size. First, only first-order patches, as defined by *Kotliar and Wiens* (1990), were considered. Given that our range parameter values were predominantly larger than our average patch lengths, it seems considering second-order patches would be useful. Second-order patches are defined as groups of first-order patches (*Kotliar and Wiens*, 1990). Using the 40 basins dataset, second-order patches could be computed by joining nearby patches separated by only one or two gaps, for example.

Another direction for future work comes from the conclusion that varia-

tion in patch sizes within a landscape and variation in response values within patches may have led to poor correlation of average patch sizes with range parameters and integral scales; and other recent work regarding empirical semivariograms and patch sizes (*Satterthwaite*, 2009). Response values could be dichotomized based on occurring within a patch (response value = 1) or a gap (response value = 0). Semivariograms computed from these transformed data may indicate sizes of patches via inflection points.

Paired watershed studies are used to inform public policy. The importance of the conclusions reached has led to a continuous evolution of their design and methods for their analysis. When hydrologic data was considered on an annual scale (*Harr et al.*, 1979), it was argued that this temporal scale was too coarse for effective change detection. Paired watershed studies have been designed to collect data at finer scales, but even these face challenges, as recent work has shown data summarized at daily time scales contribute too much statistical noise to effectively detect treatment effects (*Zégre et al.*, 2008). Future work should help elucidate the most effective temporal scales for change detection. Additionally, an investigation into the most effective analysis methods should be conducted. Comparing current methods, like the prediction interval approach, with other current and newly proposed methodologies will further refine the paired watershed study.

BIBLIOGRAPHY

Harr, R. D., R. L. Fredriksen, and J. Rothacher (1979), Changes in streamflow following timber harvest in southwestern Oregon, *Research Paper PNW 249*, USDA Forest Service: Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Kotliar, N. B., and J. A. Wiens (1990), Multiple scales of patchiess and patch structure: a hierarchical framework for the study of heterogeneity, *OIKOS*, *59*, 253–260.

Satterthwaite, P. M. (2009), Field and simulation studies of spatial patterns in forest understories: responses to overstory structure and influences on understory plant diversity, Master's thesis, Oregon State Univeristy.

Zégre, N., A. E. Skaugset, N. A. Som, J. J. McDonnell, and L. M. Ganio (2008), In lieu of the paired catchment approach: Hydrologic model change detection at the catchment scale, submitted to *Water Resources Research*, In Revision.

BIBLIOGRAPHY

Andrassian, V. (2004), Waters and forests: From historical controversy to scientific debate, *Journal of Hydrology*, *291*(1–2), 1–27.

Augustine, D. J., and D. A. Frank (2001), Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem, *Ecology*, *82*(11), 3149–3162.

Bange, J., T. Spiess, M. Herold, F. Beyrich, and B. Hennemuth (2006), Turbulent fluxes from helipod flights above quasi-homogeneous patches within the LITFASS area, *Boundary-layer Meteorology*, *121*, 127–151, doi: 10.1007/s10546-006-9106-0.

Bateman, D. S., R. E. Gresswell, and C. E. Torgersen (2005), Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution, *Journal of Freshwater Ecology*, *20*, 335–345.

Benda, L., K. Andras, D. Miller, and P. Bigelow (2004a), Confluence effects in rivers: Interactions of basin scale, network geometry, and disturbance regimes, *Water Resources Research*, *40*,

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock (2004b), The network dynamics hypothesis: How channel networks structure riverine habitats, *BioScience*, *54*(4), 413–427.

Best, D. J., and D. E. Roberts (1975), Algorithm AS 89: The upper tail probabilities of Spearman's rho, *Journal of the Royal Statistical Society*, *24*(3), 377–379.

Blair, B. C. (2005), Fire effects on the spatial patterns of soil resources in a Nicaraguan wet tropical forest, *Journal of Tropical Ecology*, *21*, 435–444, doi:10.1017/S0266467405002452.

Bosch, J. M., and J. D. Hewlett (1982), A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration, *Journal of Hydrology*, *55*(1–4), 3–23.

Bouza, N., J. Caujape-Castells, M. A. Gonzalez-Perez, F. Batista, and P. A. Sosa (2002), Population structure and genetic diversity of two endangered endemic species of the Canarian laurel forest: *Dorycnim spectabile*

(fabaceae) and *Isoplexis chalcantha (scrophulariaceae)*, *International Journal of Plant Sciences*, *163*(4), 619–630.

Brind Ámour, A., and D. Boisclair (2006), Effect of the spatial arrangement of habitat patches on the development of fish habitat models in the littoral zone of a Canadian shield lake, *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 737–753.

Brown, J. D., L. Zhang, T. A. McMahon, A. W. Western, and R. A. Vertessy (2005), A review of paired catchment studies for determining changes in water yield resulting from alterations in vegetation, *Journal of Hydrology*, *310*(1–4), 28–61.

Bulit, C., C. Diaz-Avalos, M. Signoret, and D. J. S. Montagnes (2003), Spatial structure of planktonic ciliate patches in a tropical coastal lagoon: an application of geostatistical methods, *Aquatic Microbial Ecology*, *30*, 185–196.

Bulit, C., C. Diaz-Avalos, and D. J. S. Montagnes (2004), Assessing spatial and temporal patchiness of the autotrophic ciliate *Myrionecta rubra*: a case study in a coastal lagoon, *Marine Ecology Progress Series*, *268*, 55–67.

Burnham, K. P., and D. R. Anderson (2002), *Model Selection and Multimodel Inference: A Practical InformationTheoretic Approach*, 2 ed., Springer-Verlag, New York, NY.

Carroll, S. S., and D. L. Pearson (1998), Spatial modeling of butterfly species richness using tiger beetles (*Cicindelidae*) as a bioindicator taxon, *Ecological Applications*, *8*(2), 531–543.

Chatfield, C. (2004), *The Analysis of Time Series: An Introduction*, Texts in Statistical Science Series, 6 ed., Chapman and Hall/CRC, Boca Raton, FL.

Conover, W. J. (1999), *Practical Nonparametric Statistics*, Wiley Series in Probability and Statistics, 3 ed., John Wiley and Sons, New York, NY.

Cooper, S. D., L. Barmuta, O. Sarnelle, K. Kratz, and S. Diehl (1997), Quantifying spatial heterogeneity in streams, *Journal of the North American Benthological Society*, *16*(1), 174–188.

Cressie, N., and J. J. Majure (1997), Spatio-temporal statistical modeling of livestock waste in streams, *Journal of Agricultural, Biological, and Environmental Statistics*, *2*(1), 24–47.

Cressie, N., J. Frey, B. Harch, and M. Smith (2006), Spatial prediction on a river network, *Journal of Agricultural, Biological, and Environmental Statistics*, *11*(2), 127–150.

Cubillos, L. A., J. Paramo, P. Ruiz, S. Nunez, and A. Sepulveda (2008), The spatial structure of the oceanic spawning of jack mackerel (*Trachurus murphyi*) off central Chile (1998-2001), *Fisheries Research*, *90*, 261–270.

Dalthorp, D., J. Nyrop, and M. G. Villani (2000), Foundations of spatial ecology: the reification of patches through quantitative description of patterns and pattern repetition, *Entomologia Experimentalis et Applicata*, *96*, 119–127.

Dent, C. L., and N. B. Grimm (1999), Spatial heterogeneity of stream water nutrient concentrations over successional time, *Ecology*, *80*(7), 2283–2298.

Downes, B. J., P. S. Lake, and E. S. G. Schreiber (1993), Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organization, *Freshwater Biology*, *30*, 119–132.

Ettema, C. H., and D. A. Wardle (2002), Spatial soil ecology, *TRENDS in Ecology & Evolution*, *17*(4), 177–183.

Ferguson, R. I., J. T. Cudden, T. B. Hoey, and S. P. Rice (2006), River system discontinuities due to lateral inputs: generic styles and controls, *Earth Surface Processes and Landforms*, *31*, 1149–1116, doi:10.1002/esp.1309.

Fisher, S. G., N. B. Grimm, E. Marti, and R. Gomez (1998), Hierarchy, spatial configuration, and nutrient cycling in a desert stream, *Australian Journal of Ecology*, *23*, 41–52.

Fletcher, W. J., and N. R. Sumner (1999), Spatial distribution of sardine (*Sardinops sagax*) eggs and larvae: an application of geostatistics and resampling to survey data, *Canadian Journal of Fisheries and Aquatic Sciences*, *56*, 907–914.

Floridi, L. (2009), Logical fallacies as informational shortcuts, *Synthese*, *167*, 317–325, doi:10.1007/s11229-008-9410-y.

Franklin, R. B., L. K. Blum, A. C. McComb, and A. L. Mills (2002), A geostatistical analysis of small-scale spatial variability in bacterial abundance and community structure in salt marsh creek bank sediments, *FEMS Microbiology Ecology*, *42*, 71–80.

Ganio, L. M., C. E. Torgersen, and R. E. Gresswell (2005), A geostatistical approach for describing spatial pattern in stream networks, *Frontiers in Ecology and the Environment*, *3*(3), 138–144.

Gardner, B., P. J. Sullivan, and J. L. Arthur Jr. (2003), Predicting stream temperatures: Geostatistical model comparison using alternative distance metrics, *Canadian Journal of Fisheries and Aquatic Sciences*, *60*, 344–351, doi:10.1139/F03-025.

Garreta, V., P. Monestiez, and J. M. Ver Hoef (2009), Spatial modelling and prediction on river networks: up model, down model or hybrid?, *Environmetrics*, doi:10.1002/env.995.

Gascuel-Odoux, C., and P. Boivin (1994), Variability of variograms and spatial estimates due to soil sampling: a case study, *Geoderma*, *62*, 165–182.

Gomi, T., R. D. Moore, and A. S. Dhakal (2006), Headwater stream temperature response to clear-cut harvesting with different riparian treatments, coastal British Columbia, Canada, *Water Resources Research*, *42*,

Goodman, L. A. (1960), On the exact variance of products, *Journal of the American Statistical Association*, *55*(292), 708–713.

Gresswell, R. E., D. S. Bateman, G. W. Lienkaemper, and T. J. Guy (2004), Geospatial techniques for developing a sampling frame of watersheds across a region, in *GIS/Spatial Analyses in Fishery and Aquatic Sciences*, vol. 2, edited by T. Nishida, P. J. Kailola, and C. E. Hollingworth, pp. 515–528, Fishery-Aquatic GIS Research Group, Saitama, Japan.

Grundmann, G. L., and D. Debouzie (2000), Geostatistical analysis of the distribution of NH4+ and NO3- -oxidizing bacteria and serotypes at the millimeter scale along a soil transect, *FEMS Microbiology Ecology*, *34*, 57–62.

Harr, R. D., R. L. Fredriksen, and J. Rothacher (1979), Changes in streamflow following timber harvest in southwestern Oregon, *Research Paper PNW 249*, USDA Forest Service: Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Harris, D. D. (1977), Hydrologic changes after logging in two small Oregon coastal watersheds, *Water-Supply Paper 2037*, United States Geological Survey, Arlington, VA.

Harville, D. A., and D. R. Jeske (1992), Mean squared error of estimation or prediction under a general linear model, *Journal of the American Statistical Association*, *87*(419), 724–731.

Helsel, D. R., and R. M. Hirsch (1992), *Statistical Methods in Water Resources*, Elsevier, Amsterdam.

Huettmann, F., and A. W. Diamond (2006), Large-scale effects on the spatial distribution of seabirds in the northwest Atlantic, *Landscape Ecology*, *21*, 1089–1108, doi:10.1007/s10980-006-7246-8.

Hynes, H. B. N. (1975), The stream and its valley, *Internationale Vereinigung fr Theoretische und Angewandte Limnologie*, *19*, 1–15.

Irvine, K. M., A. I. Gitelman, and J. A. Hoeting (2007), Spatial designs and properties of spatial correlation: Effects on covariance estimation, *Journal of Agricultural, Biological, and Environmental Statistics*, *12*(4), 450–469, doi:10.1198/108571107X249799.

Isaak, D. J., and R. F. Thurow (2006), Network-scale spatial and temporal variation in chinook salmon (*Oncorhynchus tshawutscha*) redd distributions: Patterns inferred from spatially continuous replicate surveys, *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 285–296, doi: 10.1139/F05-214.

Isaaks, E. H., and R. M. Srivastava (1989), *Applied Geostatistics*, 3 ed., Oxford University Press, New York, NY.

Judge, G. G., W. E. Griffiths, R. C. Hill, and T.-C. Lee (1980), *The Theory and Practice of Econometrics*, John Wiley and Sons, New York, NY.

Kackar, R. N., and D. A. Harville (1984), Approximations for standard errors of estimators of fixed and random effects in mixed linear models, *Journal of the American Statistical Association*, *79*(388), 853–862.

Kariya, T., and H. Kurata (2004), *Generalized Least Squares*, John Wiley and Sons, West Sussex, England.

Kiffney, P. M., C. M. Greene, J. E. Hall, and J. R. Davies (2006), Tributary streams create spatial discontinuities in habitat, biological productivity, and diversity in mainstem rivers, *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 2518–2530, doi:10.1139/F06-138.

Kincaid, T., T. w. c. f. D. S. Olsen, C. Platt, D. White, and R. Remington (2008), *spsurvey: Spatial Survey Design and Analysis*, r package version 2.0.

Kotliar, N. B., and J. A. Wiens (1990), Multiple scales of patchiess and patch structure: a hierarchical framework for the study of heterogeneity, *OIKOS*, *59*, 253–260.

Legendre, P. (1993), Spatial autocorrelation: Trouble or new paradigm?, *Ecology*, *74*(6), 1659–1673.

Lewis, J. (1998), Evaluating the impacts of logging activites on erosion and suspended sediment transport in the Caspar Creek watersheds, *General Technical Report 168*, USDA Forest Service: Pacific Southwest Research Station, Ukiah, CA.

Lindenmayer, D. B. (2000), Factors at multiple scales affecting distribution patterns and their implications for animal conservation leadbeaters possum as a case study, *Biodiversity and Conservation*, *9*, 15–35.

Little, L. S., D. Edwards, and D. E. Porter (1997), Kriging in estuaries: as the crow flies, or as the fish swims?, *Journal of Experimental Marine Biology and Ecology*, *213*, 1–11.

Lloyd, N. J., R. Mac Nally, and P. S. Lake (2005), Spatial autocorrelation of assemblages of benthic invertebrates and its relationship to environmental factors in two upland river in southeastern Australia, *Diversity and Distributions*, *11*, 375–386, doi:10.1111/j.1366-9516.2005.00166.x.

Mast, J. N., and T. T. Veblen (1999), Tree spatial patterns and stand development along the pinegrassland ecotone in the Colorado Front Range, *Canadian Journal of Forest Research*, *29*, 575–584.

Matthews, M. R. (2009), Teaching the philosophical and worldview components of science, *Science & Education*, *18*, 697–728, doi:10.1007/s11191-007-9132-4.

Meisel, J. E., and M. G. Turner (1998), Scale detection in real and artificial landscapes using semivariance analysis, *Landscape Ecology*, *13*, 347–362.

Moore, R. D., P. Sutherland, T. Gomi, and A. Dhakal (2005), Thermal regime of a headwater stream within a clear-cut, coastal British Columbia, Canada, *Hydrological Processes*, *19*(13), 2591–2608, doi:10.1002/hyp.5733.

Muller, W. G., and D. L. Zimmerman (1999), Optimal designs for variogram estimation, *Environmetrics*, *10*, 23–37.

Muneto, H., N. Ohte, N. Karasawa, G.-s. Zhang, L.-h. Wang, and K. Yoshikawa (2001), Plant species effect on the spatial patterns of soil properties in the Mu-us desert ecosystem, inner Mongolia, China, *Plant and Soil*, *234*, 195–205.

Myers, R. H. (1990), *Classical and Modern Regression with Applications*, Duxbury Classic Series, Duxbury, Pacific Grove, CA.

Neville, H. M., D. J. Isaak, J. B. Dunham, R. F. Thurow, and B. E. Rieman (2006), Fine-scale natal homing and localized movement as shaped by sex

and spawning babitat in chinook salmon: insights from spatial autocorrelation analysis of individual genotypes, *Molecular Ecology*, *15*, 4589–4602, doi:10.1111/j.1365-294X.2006.03082.x.

Paola, C., and R. Seal (1995), Grain size patchiness as a cause of selective deposition and downstream fining, *Water Resources Research*, *31*(5), 1395–1407.

Pastor, J., B. Dewey, R. Moen, D. J. Mladenoff, M. White, and Y. Cohen (1998), Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA, *Ecological Applications*, *8*(2), 411–424.

Perry, J. N. (1998), Measures of spatial pattern for counts, *Ecology*, *79*(3), 1008–1017.

Perry, J. N., A. M. Liebhold, M. S. Rosenberg, J. Dungan, M. Miriti, A. Jakomulska, and S. Citron-Pousty (2002), Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data, *Ecography*, *25*, 578–600.

Peterson, E. E., and N. S. Urquhart (2006), Predicting water quality impaired stream segments using landscape-scale data and a regional geostatistical model: A case study in Maryland, *Environmental Monitoring and Assessment*, *121*, 615–638, doi:10.1007/s10661-005-9163-8.

Peterson, E. E., D. M. Theobald, and J. M. Ver Hoef (2007), Geostatistical modelling on stream networks: Developing valid covariance matrices based on hydrologic distance and stream flow, *Freshwater Biology*, *52*, 267–279, doi:10.1111/j.1365-2427.2006.01686.x.

Pickett, S. T. A., and M. L. Cadenasso (1995), Landscape ecology: Spatial heterogeneity in ecological systems, *Science*, *269*, 331–334.

Poole, G. C. (2002), Fluvial landscape ecology: Addressing uniqueness within the river discontinuum, *Freshwater Biology*, *47*, 641–660.

Pooler, P. S., and D. R. Smith (2005), Optimal sampling design for estimating spatial distribution and abundance of a freshwater mussel population, *Journal of the North American Benthological Society*, *24*(3), 525–537, doi: 10.1139/F06-145.

Prasad, N. G. N., and J. N. K. Rao (1990), The estimation of the mean squared error of small-area estimators, *Journal of the American Statistical Association*, *85*(409), 163–171.

R Development Core Team (2005), *R: A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0.

Rathbun, S. L. (1998), Spatial modelling in irregularly shaped regions: Kriging estuaries, *Environmetrics*, *9*, 109–129.

Rice, S., and M. Church (1998), Grain size along two gravel-bed rivers: statistical variation, spatial pattern and sedimentary links, *Earth surface processes and landforms*, *23*, 345–363.

Rice, S. P., R. I. Ferguson, and T. B. Hoey (2006), Tributary control of physical heterogeneity and biological diversity at river confluences, *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 2553–2566, doi: 10.1139/F06-145.

Rossi, J.-P. (2003), Clusters in earthworm spatial distribution, *Pedobiologia*, *47*, 490–496.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz (1992), Geostatistical tools for modeling and interpreting ecological spatial dependence, *Ecological Monographs*, *62*(2), 277–314.

Russo, D., and E. Bresler (1981), Soil hydraulic properties as stochastic processes: I. an analysis of field spatial varability, *Soil Science Society of America Journal*, *45*, 682–687.

Russo, D., and W. A. Jury (1987), A theoretical study of the estimation of the correlation scale in spatially variable fields 1: Stationary fields, *Water Resources Research*, *23*(7), 1257–1268.

Salas, J. D. (1993), *Handbook of Hydrology*, chap. Analysis and Modeling of Hydrologic Time Series, pp. 19.1–19.72, McGraw-Hill, New York, NY.

Satterthwaite, P. M. (2009), Field and simulation studies of spatial patterns in forest understories: responses to overstory structure and influences on understory plant diversity, Master's thesis, Oregon State Univeristy.

Schabenberger, O., and C. A. Gotway (2005), *Statistical Methods for Spatial Data Analysis*, Texts in Statistical Science Series, Chapman and Hall/CRC, Boca Raton, FL.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross (1996), On the spatial pattern of soil nutrients in desert ecosystems, *Ecology*, *77*(2), 364–374.

Schmuki, C., C. Vorburger, C. Runciman, and S. Maceachern (2006), When log-dwellers meet loggers: impacts of forest fragmentation on two endemic log-dwelling beetles in southeastern Australia, *Molecular Ecology*, *15*, 1481–1492, doi:10.1111/j.1365-294X.2006.02849.x.

Scott, D. F., and W. Lesch (1997), Streamflow responses to afforestation with *Eucalyptus grandis* and *Pinus patula* and to felling in the Mokobulaan experimental catchments, South Africa, *Journal Of Hydrology*, *199*(3–4), 360–377.

Solie, J. B., W. R. Raun, and M. L. Stone (1999), Submeter spatial variability of selected soil and bermudagrass production variables, *Soil Science Society of America Journal*, *63*, 1724–1733.

Stevens Jr., D., and A. R. Olsen (2004), Spatially balanced sampling of natural resources, *Journal of the American Statistical Association*, *99*(465), 262–278.

Swartzman, G., R. Brodeur, J. Napp, G. Hunt, D. Demer, and R. Hewitt (1999a), Spatial proximity of age-0 walleye pollock (*Theragra chalcogramma*) to zooplankton near the Pribilof Islands, Bering Sea, Alaska, *ICES Journal of Marine Science*, *56*, 545–560.

Swartzman, G., R. Brodeur, J. Napp, D. Walsh, R. Hewitt, D. Demer, G. Hunt, and E. Logerwell (1999b), Relating spatial distributions of acoustically determined patches of fish and plankton: data viewing, image analysis, and spatial proximity, *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(Suppl. 1), 188–198.

Tobler, W. R. (1970), A computer movie simulating urban growth in the Detroit region, *Economic Geography*, *46*, 234–240.

Torgersen, C. E., and D. A. Close (2004), Influence of habitat heterogeneity on the distribution of larval pacific lamprey (*Lampetra tridentata*) at two spatial scales, *Freshwater Biology*, *49*(5), 614–630.

Torgersen, C. E., D. M. Price, L. H. W, and B. A. McIntosh (1999), Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon, *Ecological Applications*, *9*(1), 301–319.

Venditti, J. G., and M. A. Church (2005), Bed form initiation from a flat sand bed, *Journal of Geophysical Research*, *110*, doi:10.1029/2004JF000149.

Ver Hoef, J. M., and E. E. Peterson (2007), Spatial modeling of stream network data, in *Proceedings of the 92nd Annual Meeting of the Ecological Society of America*, San Jose, CA.

Ver Hoef, J. M., E. Peterson, and D. Theobald (2006), Spatial statistical models that use flow and stream distance, *Environmental and Ecological Statistics*, *13*, 449–464, doi:10.1007/s10651-006-0022-8.

Vijapurkar, U. P., and C. A. Gotway (2001), Assessment of forecasts and forecast uncertainty using generalized linear regression models for time series count data, *Journal of Statistical Computation and Simulation*, *68*(4), 321–349.

Ward, J. V. (1989), The four-dimensional nature of lotic ecosystems, *Journal of the North American Benthological Society*, *8*(1), 2–8.

Ward, J. V., G. Bretschko, M. Brunke, D. Danielopol, J. Gibert, T. Gonser, and A. G. Hildrew (1998), The boundaries of river systems: the metazoan perspective, *Freshwater Biology*, *40*, 531–569.

Watson, F., R. Vertessy, T. McMahon, B. Rhodes, and I. Watson (2001), Improved methods to assess water yield changes from paired-catchment studies: Application to the Maroondah catchments, *Forest Ecology and Management*, *143*(1–3), 189–204.

Wiens, J. A. (2002), Riverine landscapes: Taking landscape ecology into the water, *Freshwater Biology*, *47*, 501–515.

Wright, K. K., and J. L. Li (2002), From continua to patches: examining stream community structure over large environmental gradients, *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 1404–1417.

Zégre, N., A. E. Skaugset, N. A. Som, J. J. McDonnell, and L. M. Ganio (2008), In lieu of the paired catchment approach: Hydrologic model change detection at the catchment scale, submitted to *Water Resources Research*, In Revision.

Zhu, Z., and M. L. Stein (2005), Spatial sampling design for parameter estimation of the covariance function, *Journal of Statisitcal Planning and Inference*, *134*, 583–603, doi:10.1016/j.jspi.2004.04.017.

Zhu, Z., and H. Zhang (2006), Spatial sampling design under the infill asymptotic framework, *Environmetrics*, *17*(4), 323–337, doi:10.1002/env.772.

Zimmerman, D. L. (2006), Optimal network design for spatial prediction, covariance parameter estimation, and empirical prediction, *Environmetrics*, *17*, 635–652, doi:10.1002/env.769.

Zimmerman, D. L., and N. A. C. Cressie (1989), Improved estimation of the kriging variance, *Technical Report 161*, The University of Iowa, Iowa City, Iowa.

Zimmerman, D. L., and N. A. C. Cressie (1992), Mean squared prediction error in the spatial linear model with estimated covariance parameters, *Annals of the Institute of Statistical Mathematics*, *44*(1), 27–43.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith (2009), *Mixed Effects Models and Extensions in Ecology with R*, Statistics for Biology and Health, 3 ed., Springer, New York, NY.