Modeling spatially-varying ecological relationships using geographically weighted generalized linear model: a simulation study based on longline seabird bycatch

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ABSTRACT

Geographically weighted regression (GWR) is a relatively new technique to explore spatially-varying relationships between biological and environmental processes. It allows parameters to vary over space and assumes data to follow a normal distribution. We extend GWR to a geographically weighted generalized linear model (GW-GLM) by incorporating statistical distributions other than the normal distribution (i.e., the binomial distribution). We demonstrate the application of GW-GLM with an empirical example, U.S. Atlantic pelagic longline seabird bycatch. Due to the high percentage of zero observations in the seabird bycatch data, we analyzed the positive catch rates (number of seabirds caught per 1000 hooks) and the probability of catching a seabird separately. Parameter estimates exhibited considerable spatial variation, especially for target catch rate when analyzing the positive catch data, and for intercept, water depth and water temperature when estimating the probability of catching seabirds. We compared model performance of GW-GLM with a global generalized linear model, a mixed effect model with a random areal effect, and a spatial expansion model that is an early technique to model spatially-varying ecological relationships by modeling each of the parameters as a function of location. The GW-GLM performed best. Simulations with hypothetical datasets having different percentages of zeros showed that, regardless of the zero percentage in the data, GW-GLM performed best on average. Applying a range of bandwidth indicated that the GW-GLM was more robust to an overestimated bandwidth than an underestimated bandwidth.

Keywords: spatially varying relationships; seabird bycatch; binomial distribution; spatial expansion model; geographically weighted regression

1. Introduction

Understanding key relationships between biological processes and environmental factors is important in natural resource management and conservation. For example, catch rate standardization based on relationships between catch rate and environmental factors can be used to estimate annual patterns of catch rate for fish stock assessment (e.g., Stefansson, 1996; Maunder and Punt, 2004; Damalas et al., 2007). Bycatch assessment using these relationships can enable prediction of bycatch hotspots (e.g., Murray, 2004; Li et al., 2011; Winter et al., 2011). A “global” model is commonly applied to examine the relationships between biological processes and environmental factors. The global model assumes these relationships to be stationary over the entire study area, i.e., constant and independent of location and direction. This assumption may not be well suited to spatial ecological data given the dynamic spatial interactions between biological and environmental factors in natural ecosystems. Instead, assuming spatially-varying relationships between biological and environmental factors (Brunsdon et al., 1996) is more appropriate.

One of the early techniques to model spatially-varying ecological relationships is the spatial expansion model (SEM) (Casetti, 1972; Casetti and Jones III, 1992). In the SEM model, each of the parameters is itself a function of location. The nature of the function must be predetermined (e.g., linear or polynomial) based on prior knowledge. However, model results may be sensitive to the specification of the expansion function (Charlton et al., 2009). In addition, computation and interpretation may become difficult when higher order polynomials are used for the expansion function, especially in the case of limited data.

A relatively new technique to address spatial variation in ecological data is geographically weighted regression (GWR, Brunsdon et al., 1996; Fotheringham et al., 1998). In GWR, neighboring observations are weighted based on the strength of spatial dependence and thus drive parameters to vary across the study area. GWR has several advantages in exploration of spatial variation in ecological relationships. First, it yields a set of estimates for each of the parameters that vary over space. The set of estimates can be mapped over the entire study area, which provides a visualization of the spatially-varying relationships between biological and environmental variables. Second, GWR extends the traditional regression approach with spatially-varying parameters and can easily be fitted using the weighted least square (WLS) method. Third, spatial relationships among observations in GWR can be investigated by testing different spatial weighting matrices that combine information on neighbor structure and spatial dependence. The original formulation of GWR (Brunsdon et al., 1996; Fotheringham et al., 1998), is limited to the normal assumption. We extend GWR to the geographically weighted generalized linear model (GW-GLM) by applying distributions other than the normal from the exponential family (i.e., the binomial and Poisson distributions). GW-GLM can be fitted using iteratively reweighted least squares (IRLS, McCullagh and Nelder, 1989). GW-GLM is also an extension of the global generalized linear model (GLM) in which spatial weights are applied in the fitting procedure (i.e., the IRLS) to consider spatial locations in parameter estimation. GWR is a special case of GW-GLM in which a normal distribution and an identity link function are applied, and spatial weights are directly applied to observations.

We demonstrate the application of GW-GLM using the example of seabird bycatch from the U.S. pelagic longline fishery in the Western North Atlantic. The incidental mortality of seabirds in longline fisheries has raised a global concern among marine conservationists because it has threatened several albatross (Diomedidae) species and other species in the order of

Procellariiformes (Brothers et al., 1999a; Tasker et al., 2000; Belda and Sanchez, 2001; Furness, 2003). Occurrence of seabird bycatch has been related to environmental variables such as wind speed (Klaer and Polacheck, 1998; Brothers et al., 1999b). Seabird bycatch is likely to be spatially-varying given the highly mobile nature of seabirds and the large heterogeneous habitat covered by longline fishing. Therefore, conservation and management of seabird bycatch will benefit from a more complete understanding of the relationships (e.g., the spatially-varying relationships) between behavioral processes and environmental factors.

We address two major questions. First, is GW-GLM better than the global GLM, the mixed effect model (MEM) where observations were assumed dependent within the same fishing zone and independent between zones, and the SEM, an alternative model for spatially-varying relationships? Second, are relationships between biological processes and environmental factors in GW-GLM significantly varying over space?

2. Methods

2.1 Geographically weighted generalized linear model (GW-GLM)

The GW-GLM is an extension of the global generalized linear model by considering locations in parameter estimation and thus allowing parameters to vary locally rather than being constant over space. A global GLM takes the form:

$$(1) \quad g(E[y_i]) = b_0 + \sum_{k=1}^p b_k x_{ik},$$

where $i = 1, 2, \dots, n$ denotes the i th location, y is the observation, $E[y]$ is the expectation of y , b_0 is the intercept, b_k is parameter for the k th explanatory variable x_k and $k = 1, 2, \dots, p$, and $g(\cdot)$ is the link function that describes the relationship between $E[y]$ and explanatory variables. The parameters in the global GLM can be estimated using an iterative algorithm in which weighted least squares (WLS) is applied to the adjusted response variable $Z = [z_1, z_2, \dots, z_n]^T$ at each iteration step (McCullagh and Nelder, 1989):

$$(2) \quad \hat{b}^{new} = (X^T W^{old} X)^{-1} X^T W^{old} Z,$$

where T denotes the transpose of a matrix, $\hat{b}^{new} = [\hat{b}_0^{new}, \hat{b}_1^{new}, \dots, \hat{b}_p^{new}]^T$ is a vector of estimated parameters that are updated at each iteration step, and X is the design matrix defined as:

$$(3) \quad X = \begin{pmatrix} 1 & x_{11} & x_{12} & \cdots & x_{1p} \\ 1 & x_{21} & x_{22} & \cdots & x_{2p} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 1 & x_{n1} & x_{n2} & \cdots & x_{np} \end{pmatrix}$$

The adjusted response variable z_i is defined as:

$$(4) \quad z_i = x_i^T \hat{b}^{old} + (y_i - E[y_i]) \left(G'(x_i^T \hat{b}^{old}) \right)^{-1},$$

where $G(\cdot)$ is the inverse function of $g(\cdot)$ and $G'(\cdot)$ denotes the first derivative of function $G(\cdot)$ with respect to parameters β . The $n \times n$ weighting matrix $W = [w_i]$ can be written as:

$$\begin{aligned}
 & \begin{matrix} \hat{e} \\ \hat{e} \\ \hat{e} \\ \hat{e} \\ \hat{e} \\ \hat{e} \end{matrix} \begin{matrix} w_1 & 0 & 0 & \cdots & 0 \\ 0 & w_2 & 0 & \cdots & 0 \\ 0 & 0 & w_3 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & w_n \end{matrix} \begin{matrix} \hat{u} \\ \hat{u} \\ \hat{u} \\ \hat{u} \\ \hat{u} \\ \hat{u} \end{matrix} \\
 (5) \quad W &= \begin{matrix} \hat{e} \\ \hat{e} \\ \hat{e} \\ \hat{e} \\ \hat{e} \\ \hat{e} \end{matrix} \begin{matrix} w_1 & 0 & 0 & \cdots & 0 \\ 0 & w_2 & 0 & \cdots & 0 \\ 0 & 0 & w_3 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & w_n \end{matrix} \begin{matrix} \hat{u} \\ \hat{u} \\ \hat{u} \\ \hat{u} \\ \hat{u} \\ \hat{u} \end{matrix},
 \end{aligned}$$

and w_i is updated accordingly at each iteration step:

$$(6) \quad w_i^{new} = \frac{G'(x_i^T \hat{b}^{new})^2}{V(E[y_i])},$$

where $V(\cdot)$ is the score function that is defined as the first derivative of the log-likelihood with respect to parameters β . The whole algorithm progresses until parameter estimates converge. In the global GLM, a unity weight is assigned to each observation as the prior weights. parameter estimation can be adjusted by controlling prior weights. Linear regression is a special case of GLM in which $G'(\cdot) \sim 1$ and $E[y_i] = x_i^T \beta$, and thus prior weights can be applied directly to the observations and no iteration is necessary.

As an extension of the global GLM with locally varying parameters, the geographically weighted generalized linear model (GW-GLM) can be written as:

$$(7) \quad g(E[y_i]) = \beta_0(u_i, v_i) + \sum_{k=1}^p \beta_k(u_i, v_i) x_{ik},$$

where (u_i, v_i) denotes the coordinates of the i th location (longitude, latitude), and $\beta_0(u_i, v_i)$ and $\beta_k(u_i, v_i)$ are parameters for the i th location. In common with most spatial analyses methods, GW-GLM implicitly assumes that observations nearer to location i have more influence on the parameter estimation for this location than observations farther away from location i (Cressie, 1993; Fotheringham et al., 1998). Thus, in a GW-GLM, parameters for the i th location are estimated using its neighboring observations through the IRLS method as described above, except that prior weights are assigned to its neighboring observations according to their influence on the i th location. We denote the prior weight for the j th neighboring observation according to its influence on location i by w_{ij} and $j = 1, 2, \dots, n$.

In common with GWR, the prior weight w_{ij} in GW-GLM is assumed to be a function of distance between locations i and j (d_{ij}), with the weight decreasing as the distance increases. This weighting function can take various forms (e.g., Brunsdon et al., 1996; Fotheringham et al., 1998). We applied the Gaussian weighting function that has been widely used in spatial analysis due to its continuity (i.e., this function is smooth everywhere, making calculations such as differential easier in practice):

$$(8) \quad w_{ij} = \exp\left\{-\frac{d_{ij}^2}{2h^2}\right\},$$

where the bandwidth h has a great impact on model outcomes, i.e., smaller h leads to highly localized parameter estimates while larger h drives parameter estimates towards those from the global model (Brunsdon et al., 1996; Fotheringham et al., 1998). The optimal value of h can be determined by optimizing the selection criterion, e.g., minimizing the leave-one-out sum of squares (also termed the cross-validation score, Brunsdon et al., 1996; Fotheringham et al.,

1998), or minimizing the Akaike Informaiton Criterion (AIC, Akaike, 1974; Fotheringham et al., 2002). The cross-validation score may not be the best choice for certain types of data such as the binary data that take values of either zero or one. The AIC works well for GW-GLM with an assumption of normal distribution and an identity link (i.e., GWR), but determination of the effective number of parameters in the calcuation of AIC may be problematic for GW-GLM with other distributions (e.g., the binomial distribution). The effective number of parameters in GWR-GLM depends on the number of independent parameters and the bandwidth h . For GW-GLM with an assumption of normal distribution and an identity link (i.e., GWR), the effective number of parameters can be approximated by a function of the trace of the hat matrix (Charlton et al., 2009). However, for GW-GLM with binomial distributions, there is no closed form of the hat matrix. In the seabird bycatch example, to determine the optimal value of h , we minimized the AIC for the normal data (positive catch rates of seabird) and maximized the area under the receiver operating characteristic (ROC) curve (AUC) for the binary data (capture or no capture of a seabird). The ROC curve plots the true positive rate $\Pr(\hat{y} = 1 | y = 1)$ against the false positive rate $\Pr(\hat{y} = 1 | y = 0)$, and has long been used to evaluate the accuracy of a classification algorithm (Bradley, 1997). Modeling the binary data can be treated as a classification algorithm, and a larger AUC value suggests higher discrimination accuracy of the model. In the determination of h , a very small value of h will drive the weights of observations at all locations to be negligible except for the i th location itself, which suggests that the fitted value for the i th location will tend to be the observed value (Brunsdon et al., 1996; Fotheringham et al., 1998), and an AUC value close to one will be yielded. Thus, in the calculation of AUC, we estimated the probability for the i th location using data excluding the observation at the i th location (i.e., leave one out) to avoid this problem.

A permutation test was conducted to test for the significance of spatial variation in ecological relationships (Brunsdon et al., 1996; Fotheringham et al., 1998). Under the null hypothesis of constant parameters over space, any permutaion of (u_i, v_i) pairs amongst the geographical sampling points i is equally likely to occur. As in GWR, there are n estimates for each of the parameters in GW-GLM. The test statistic is an estimate of variability in these n parameter estimates, i.e, standard deviation.

2.2 Mixed effect model (MEM)

We also tested a MEM that included a random areal effect r_t , which was assumed to follow a normal distribution with a zero mean and a constant variance, which represented the variability in observed data across areas (McCulloch and Searle, 2001):

$$(9) \quad g(E[y_{st}]) = b_0 + \sum_{k=1}^p b_k x_{stk} + r_t,$$

where s and t index the s th observation in area t . In the MEM, observations from the same area were assumed dependent, and those from different areas were assumed independent.

2.3 Spatial expansion model (SEM)

The original SEM is also an extension of the traditional regression model (Casetti, 1972; Casetti and Jones III, 1992). The SEM expands parameters to be a function of locations (u_i, v_i) so that parameter estimates vary over space. Because of the limited data, we employed a first order linear polynomial function as the expansion function in the seabird bycatch example:

$$(10) \quad \begin{aligned} b_0(u_i, v_i) &= a_0 + a_1 u_i + a_2 v_i, \\ b_k(u_i, v_i) &= b_{0k} + b_{1k} u_i + b_{2k} v_i, \end{aligned}$$

where (a_0, a_1, a_2) and (b_{k0}, b_{k1}, b_{k2}) are parameters in the expansion function to determine β_0 and β_k for the i th location, respectively. Applying the spatial expansion technique to the global GLM and modifying the global model with such a linear expansion function, the SEM can be written as:

$$(11) \quad g(E(y_i)) = a_0 + a_1 u_i + a_2 v_i + \sum_{k=1}^p (b_{0k} + b_{1k} u_i + b_{2k} v_i) x_{ik},$$

The SEM can be fitted using IRLS with unity prior weights.

2.4 Model evaluation and a simulation study

We compared the performance of GW-GLM with the global GLM, MEM and SEM. We used the AIC and AUC as criteria for normal and binary data respectively. The model providing a lower AIC value or a higher AUC value would be judged to have better performance.

To explore the impact of zeros in the dataset to the model performance, other than the original dataset that contained $> 98\%$ zeros, we constructed three datasets that contained 30%, 60% and 90% zeros, and compared the performance of candidate models on these datasets. We ran this analysis for the binary data. To construct these three datasets in the seabird bycatch example, we combined the original positive longline sets with zero sets that were randomly selected from the original dataset to achieve the targeted percentage of zeros. We ran 500 iterations.

To explore the impact of estimation of bandwidth h on the performance of GW-GLM, we conducted a simulation study in which we evaluated the performance of GW-GLM when h was underestimated or overestimated by 30% and 50%. We ran this simulation for four binary datasets in the seabird bycatch example, i.e., the original dataset and the three datasets with 30%, 60% and 90% zeros. For each dataset except the original dataset, we randomly selected one iteration from the above 500 iterations, and used that dataset and the results of GW-GLM from this iteration as the true h value and the true probability of catching seabirds. Figure 1 shows the flowchart of simulation. For each scenario, we generated a dataset given the true probability of catching seabirds; we fit the generated data using the candidate model including GW-GLM with a biased h value; we evaluated performance of each model by calculating its mean absolute error (MAE) and mean bias:

$$(12) \quad MAE = \frac{1}{N} \sum_{i=1}^N |fitted - true|,$$

$$(13) \quad Mean \text{ bias} = \frac{1}{N} \sum_{i=1}^N (fitted - true),$$

where N is the total number of observations and i indexes the i th observation; *fitted* refers to the estimated probability of catching seabirds, and *true* refers to the true probability of catching seabirds. Lower MAE values and the mean bias closer to zero suggest better performance of the model. We ran 500 iterations for each scenario.

2.5 Longline seabird bycatch examples

GW-GLM was used to investigate spatially-varying ecological relationships for seabird bycatch provided by the National Marine Fisheries Service Southeast Fisheries Science Center Pelagic Observer Program (POP). The POP program was initiated for monitoring the United States Atlantic pelagic longline fishery. The fishery primarily targets tunas, swordfish, sharks and dolphin fish. There were over 10,000 longline sets deployed in this fishery in 2012, and fishing effort focused on waters along the south to middle-east coast of the USA. In the POP, randomly selected fishing trips are attended by an observer, and detailed information on gear specification, fishing effort, fishing tactics, target catch, bycatch, and environmental conditions is recorded. The environmental variables (mean $\pm$ standard deviation) that we analyzed included water depth (fathom, 744 ± 551.2), water temperature (Fahrenheit, 74.2 ± 7.5), target species catch rate (number per 1000 hooks, 25.7 ± 34.1), wind speed (knot, 13.7 ± 7.1), wind direction (degree, 175.7 ± 102.7) and wave height (feet, 3.7 ± 2.6). The POP data covered 11 fishing areas (Lee and Brown, 1998), and we constrained our analysis to the three areas with highest seabird bycatch, i.e., northeast coast, middle Atlantic bight and south Atlantic bight (Fig. 2). We analyzed 3,751 longline sets during 1992 to 2012, of which only 58 sets caught 120 seabirds; i.e. 98.5% of the observations were zero. We projected the geographic coordinates in the data (i.e., degree north and degree west) to the Universal Transverse Mercator (UTM) system zone 17 based on the NAD83 geodetic datum.

We analyzed the positive catch rates (number per 1000 hooks) and the probability of capturing a seabird (p) separately, i.e. the same idea as the delta or hurdle model that handles data with excess zeros (Aitchison, 1955; Lo et al., 1992; Fletcher et al., 2005). To model the probability of catching a seabird, we converted the original data into binary data, i.e., zero or one in which a zero represented the event of no seabird captured and a one represented the event of at least one seabird captured. The global GLM for positive catch rate assumed the logarithm of the catch rate to follow a normal distribution with an identity link, which is equivalent to a GWR model:

$$\ln(\text{seabird catch rate}) = \text{intercept} + \text{water depth} + \text{water temperature} + \text{target species catch rate} + \text{wind speed} + \text{wind direction} + \text{wave height},$$

The global GLM for the probability of catching a seabird assumed the catch event to follow a binomial distribution with a logit link:

$$\ln\left(\frac{p}{1-p}\right) = \text{intercept} + \text{water depth} + \text{water temperature} + \text{target species catch rate} + \text{wind speed} + \text{wind direction} + \text{wave height}.$$

To determine the value of h and to compare candidate models, we applied the AIC for the positive catch rate models and the leave-one-out AUC for the probability models. With the AIC criterion, we determined $h = 7.24$ (100 km) for the positive catch rate GW-GLM (AIC = 120.71), and with the AUC criterion, we determined $h = 1.01$ (100 km) for the probability GW-GLM (leave-one-out AUC = 0.693). This study was programmed using R package 'spgwr' (Version 0.6-22 by Bivand et al., 2008).

We selected predictors from the set of continuous environmental variables that had sufficient information recorded in the dataset, and that were biologically important in explaining seabird bycatch. We confined our analysis to environmental variables because we would like to focus on the spatially-varying relationships between biological processes and environmental factors. We did not include categorical variables as predictors because categorical variables could be

p]redundant locally when categories are spatially clustered or some categories are missing in some places. Zhang et al. (2011) suggested avoiding use of categorical variables that are spatially clustered or to combine and reduce the number of categories, or to combine with other variables. In additional, interpretation and mapping of the localized estimates of a categorical variable are problematic. The highest correlation between the environmental variables (0.6) was between wind speed and wave height. The rest of correlations had a magnitude less than 0.2. Thus, we considered these variables to be not highly correlated.

3. Results

3.1 Spatially-varying relationships

Spatial patterns of parameters appeared to characterize the three fishing zones defined in the U.S. Atlantic pelagic longline fishery (Fig. 2). Estimates of parameters in the positive catch rate model showed great spatial variation (Fig. 3). Derived from both GW-GLM and the SEM, parameter estimates for intercept and wave height were positive and appeared to become higher from north to south in the study region. Parameter estimates for target catch rate were mostly negative and became more negative towards the north. In GW-GLM, parameter estimates for water depth, water temperature and wind direction were all negative and exhibited a trend of higher values running from north to south, except for water depth, which had a saddle in the middle (Fig. 3). In the SEM model, parameter estimates for water depth, water temperature and wind direction were mostly negative, with values being more negative from the middle of the study region spreading north and south (Fig. 3). Maps of the parameter estimates for wind speed derived from GW-GLM and SEM both exhibited a trend of becoming more positive towards the north but differed in estimated values (Fig. 3). Parameter estimates for wind speed from GW-GLM tended to be negative, while those from the SEM model were mostly positive. Overall, estimates from the SEM model were larger than those from GW-GLM when analyzing positive catch rates.

Parameter estimates in the probability model also varied across the study area (Fig. 4). Parameter estimates for intercept from both GW-GLM and the SEM model were more positive in the middle and at the southern tip of the study area, and became more negative towards north and south. Parameter estimates for target catch rate and wind direction from both models tended to become more positive towards the north. Parameter estimates for water depth and wind speed from the SEM showed the reverse trend of being more positive towards the south (Fig. 4). Compared to the SEM, GW-GLM produced quite different maps for water depth and wind speed (Fig. 4). Parameter estimates for water depth from GW-GLM were positive in the middle of the study area and became more negative towards the north and south. Parameter estimates for wind speed from GW-GLM had a complicated trend in which more negative values were found in the middle, northern and southern tips, and more positive values lay in between. Parameter estimates for water temperature and wave height from both GW-GLM and the SEM were dominated by positive values, and became larger in the north and south and smaller in the middle, suggesting that the probability of catching a seabird was less sensitive to water temperature and wave height in the middle of the study region. Overall, maps of parameter estimates derived from GW-GLM showed spatial patterns at finer spatial scales than those from the SEM. In contrast to the estimates from the positive catch rate model, estimates of the probability of catching a seabird were lower from the SEM than the GW-GLM.

When analyzing positive catch rates, only the relationship with target catch rate exhibited significant spatial variation (p -value = 0.01) (Table 1). Relationships between the probability of

catching a seabird and environmental factors, including intercept (p -value = 0.01), water depth (p -value $\ll$ 0.0001) and water temperature (p -value = 0.01), varied significantly across the study region (Table 2).

3.2 Model comparison

Among the four candidate models (Tables 1 and 2), GW-GLM performed the best when analyzing positive catch rates and when estimating the probability of catching a seabird, producing the smallest AIC value (120.71) and the highest AUC value (0.84). For analyzing positive catch rates, the global model outperformed the SEM and MEM, having an AIC value 5.5% and 31.4% lower, respectively. However, for the probability of catching a seabird, the other three models performed equivalently, with the SEM having a slightly higher AUC value than the MEM and global model.

According to the simulation with different zero percentages in the data, among the four candidate models that estimated the probability of catching seabirds, regardless of the zero percentage in the data, the models that assumed spatial variation in ecological relationships (i.e., GW-GLM and SEM) performed better than those not allowing spatial variation (i.e., global GLM and MEM, Table 3), and the GW-GLM had the best performance with the highest AUC values on average. Performance of all models decreased as the percentage of zeros in the data increased.

3.3 Influence of bandwidth (h) estimation to the performance of GW-GLM

In terms of estimation precision (indicated by the MAE value), the GW-GLM produced estimates that were equivalent to (in the scenarios with 30% and 98% zeros in the data) or more precise than (in the scenarios with 60% and 90% zero in the data) the other three candidate models (i.e., the global GLM, MEM and SEM), even when the bandwidth (h) was biased by up to 50% (Table 4). In terms of estimation accuracy (indicated by the mean bias), the other three candidate models (medium of the mean bias -0.001 – 0.0015) outperformed the GW-GLM (medium of the mean bias -0.0034 – -0.0001), regardless of the zero percentage in the data and the bias in the estimated h . However, the mean bias for all candidate models was so small that it is difficult to differentiate their performances solely by the mean bias. Regardless of the zero percentage in the data, the GW-GLM seemed more robust to an overestimated h than an underestimated h , with the MAE values and mean biases in the overestimated- h scenarios being close to those in the unbiased- h scenarios, and being lower than those in the underestimated- h scenarios. Although the data with more zeros led to a lower MAE or a smaller mean bias, this result alone cannot indicate that more zeros in the data would lead to better model performance because the MAE or mean bias itself tended to become smaller as the zero percentage in the data increased.

4. Discussion

4.1 Modeling spatially-varying ecological relationships

The geographically-weighted approach (i.e. GWR and GW-GLM) is a flexible way to explore spatially-varying ecological relationships. The spatial weighting matrix contains all information about the spatial distribution of observations, and the weighting matrix can take various forms by assuming different neighbor structure and distance-decay functions. Whatever specific weighting matrix is employed, the essential idea of the geographically-weighted

approach is that, for a location i , observations closer to i have more influence on the estimation of parameters at location i than those farther away (Fotheringham et al., 1998). By controlling the weighting matrix, several other techniques can be generalized into the geographically-weighted approach. For example, a weighting matrix with a weight of unity for all locations results in a global model, and a weighting matrix that assigns a weight of unity if locations i and j lie within a square and zero otherwise leads to the moving window method (Brunsdon et al., 1996; Fotheringham et al., 1997).

The ability to capture the spatially-varying relationships is the biggest advantage of using a geographically-weighted approach over a global model. Although the averaged parameter values over space from a GW-GLM may seem similar to the constant value from a global GLM, the estimated values from a GW-GLM may have a large variance, which would suggest that the parameter values are different across locations. By simply assuming a constant parameter value over space in the global model, these spatially-varying dynamics are being ignored. Taking the analysis of positive catch rate as an example (Table 1), the averaged parameter value for wave height from the GW-GLM (0.0689) was similar to the value from the global GLM (0.0617). However, the GW-GLM estimated values ranged from 0.0454 to 0.0873, which indicated that some locations could have a value twice the value in other locations. For water depth, the GW-GLM gave both negative and positive values, which suggested an opposite direction of influence of water depth on seabird bycatch at different locations. There are cases where the averaged parameter values over space from a GW-GLM are substantially different from the constant value from a global GLM, e.g., the parameter values for wind speed when estimating the probability of catching a seabird (-0.0083 from the GW-GLM and 0.0004 from the global GLM, Table 2). In such cases, ignoring spatial variation in ecological relationships and using a global model may lead to biased estimation and conclusions. Compared to the global GLM, the GW-GLM gave better performance (9% lower AIC when analyzing positive catch rate [Table 1], and 22% higher AUC when estimating probability of catching seabird [Table 2]), which provided more support for using a geographically weighted approach when the ecological relationships vary over space.

Besides the SEM, there have been other techniques to explore spatially-varying ecological relationships in the early development of the methodology. For example, spatially-adaptive filtering (Foster and Gorr, 1986) iteratively adjusts parameters based on neighboring observations. The random coefficient model (Rao, 1965; Swamy, 1971) and multilevel modeling approach (Goldstein, 1987) allow parameters to vary randomly across the study area. The random coefficient model assumes parameters follow a certain statistical distribution. The multilevel modeling approach uses hierarchies to represent variation between spatial regions and combines models for individual regions within an overall model. In this study, we used SEM as one of the candidate models for comparison because tit can be easily fitted with the same fitting method as GW-GLM and global GLM, i.e., IRLS. Using the same fitting method with all three models being compared reduces any bias that using different fitting methods might cause.

Although various discrete weighting functions are also available, they should be used with great caution. First, discrete functions may cause a sudden change in parameter estimates, which may rarely occur in the real world, given the interactions among neighboring locations. Second, with discrete weighting functions, localized parameter estimates may become sensitive to the observations at the cutting edge, i.e., parameter estimates may change dramatically depending upon whether any one observation is determined to be a neighbor (Brunsdon et al., 1996). Third, use of discrete weighting functions may introduce an edge effect in which localized parameter

estimates near edges suffer large variances when too few observations are determined to be neighbors (Brunsdon et al., 1996).

Our results showed that GW-GLM and the SEM produced parameter estimates that were quite different in magnitude. For example, when analyzing positive catch rates, parameter estimates of intercept from GW-GLM were double those from the SEM. Fotheringham et al. (1998) noted that GWR produced parameter estimates of different magnitude from SEM; and, even using SEM, the parameter estimates were different between linear expansion and quadratic expansion. Presumably, these differences in parameter estimates between candidate models are caused by the different ways of modeling spatially-varying ecological relationships. These findings highlight the importance of determining appropriate models to explore spatially-varying ecological relationships, and the determination of such models may depend on dataset, selection criterion, and the number of candidate models for comparison.

As a critical parameter in GW-GLM, we found that determination of bandwidth (h) is highly sensitive to the selection criteria. For example, when analyzing the positive catch rates, we determined $h = 7.24$, according to AIC, whereas, a value of 5.17 would be determined if the cross-validation sum of squares (Brunsdon et al., 1996) were used as the selection criterion. We determined $h = 1.01$ for the probability model, based on the leave-one-out AUC value, while the cross-validation sum of squares gave a value of 7.06. Thus, determination of the parameter h needs to be done with caution, and the ecology of the studied species should be considered. For example, in the seabird bycatch example, the connections between seabird home range and feeding ground, and the connections among multiple feeding grounds may provide information to aid in the determination of h .

4.2 Application of GW-GLM in seabird bycatch assessment and management

Spatial patterns in the biological-environmental relationships shown in Figs. 3-4 appear to characterize the three fishing zones defined by the NMFS for analysis of data from the U.S Atlantic longline fishery and the pelagic observer program (Fig. 2), i.e., northeast coast, middle Atlantic bight and south Atlantic bight. These three fishing zones could appropriately serve as management zones for seabird bycatch reduction. Our results for seabird bycatch support the notion that longline catches have a distinct biological-environmental relationship roughly within each NMFS fishing zone, and these spatially varying relationships need to be taken into account when developing management plans.

The continental shelf break and adjacent northward flowing Gulf Stream are common to all three areas, and longline effort is distributed along the shelf break, with seabird bycatch nested within the effort matrix (Fig. 2). Distinctive oceanographic characteristics of each of the three fishing zones interact with the shelf break, the Gulf Stream, and other factors to produce a pelagic environment that promotes high marine productivity, co-locates seabirds with large pelagic fish such as swordfish and tunas, and shapes the unique spatial patterns in biological-environmental relationships within each zone.

4.3 Extending the application of GW-GLM

We analyzed the positive catch rates and the probability of catching a seabird in two models to compensate for the high percentage of zero observations. This approach is the same as the delta model/hurdle model except that, in the delta model, final estimates of the response variable are the product of the estimates from these two sub-models (Aitchison, 1955; Lo et al., 1992;

Fletcher et al., 2005). To extend the application of GW-GLM to the two-step delta model, at least two questions need to be addressed. The first is how to extrapolate the localized parameter estimates derived from the positive data to the entire study region. This extrapolation can be achieved using the SEM because each parameter is a function of location. The second question is how to determine the bandwidth (h) for the entire delta model. In this study, we determined values of h for the positive catch rate model and the probability model separately. However, in the delta model, a value of h to balance the selection criteria in both sub-models simultaneously is needed. One possible way might be to maximize the sum of log-likelihoods of both sub-models. The zero-inflated model is another approach that is commonly used to handle data with excess zeros (e.g., Hall, 2000). Similar to the delta model, the zero-inflated model also has two sub-models, one sub-model for the binary data (probability sub-model) and one sub-model for the entire dataset including zero observations (e.g., a Poisson model for count data). Their major difference lies in the way of dealing with zeros. The probability sub-model in the delta model handles all the zeros whereas the one in the zero-inflated model handles part of the zeros. When applying the geographically weighted approach to the zero-inflated model, it would not suffer the first problem as the delta model regarding extrapolation of localized parameter estimates from partial data to the entire dataset because both sub-models in the zero-inflated model use the entire dataset. However, determination of the bandwidth (h) would still be a concern for the zero-inflated model due to its two-step modeling feature.

The current study can be extended in several ways. First, we did not test the sensitivity of parameter estimation to the choice of the weighting matrix, which is necessary to fully understand the geographically-weighted approach. Second, the weighting function can also vary over space (Brunsdon et al., 1996), which suggests a direction for future exploration of the methodology. Third, for a given weighting function, e.g., the Gaussian weighting function that we used in this study, we applied a global estimate of the bandwidth (h), which assumes the value of h is constant over space. However, it is very likely that h also has spatial variation. Thus, determination and use of localized h estimates are worthwhile to explore (Brunsdon et al., 1996; Fotheringham et al., 1998). Fourth, we fixed the set of environmental variables over space, but the set itself may vary over space, i.e., one environmental variable may be important at one location but not at another (Brunsdon et al., 1996). Localized sets of environmental variables may provide another direction for future exploration of the geographically weighted approach.

5. Conclusion

The geographically-weighted approach is a flexible tool to explore spatially varying relationships in ecological data. As an extension of the traditional GLM, the GW-GLM allows parameter estimates to vary over space by assigning prior weights to observations during the model fitting procedure. In the meanwhile, as an extension of the GWR, the GW-GLM analyzes data with statistical distributions in the exponential family other than the normal, e.g., the binomial distribution in our seabird bycatch example. With the empirical example of the U.S. Atlantic pelagic longline seabird bycatch, we demonstrated the application of GW-GLM and revealed great spatial variation in relationships between the seabird bycatch process and environmental factors. Compared with the global GLM and the SEM method, GW-GLM performed best in terms of goodness-of-fit and prediction.

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581 **Tables**

582 **Table 1**

583 Results of the models for analyzing positive catch rate data. Four candidate models include the global generalized linear model
 584 (GLM), the mixed effect model with random areal effect (MEM, variance of the random areal effect = $5.73 \cdot 10^{-7}$), the spatial
 585 expansion model (SEM) and the geographically weighted generalized linear model (GW-GLM). In the SEM model, u and v index the
 586 parameters expanding along longitude and latitude, respectively. Parentheses in the GW-GLM column represent the variation of mean
 587 parameter estimates (95% confidence interval) across space.

Parameter	Global GLM	MEM	SEM	GW-GLM	p -value for permutation test
Intercept	1.9624	1.9624	31.55	1.938 (1.7179, 2.4962)	0.34
Intercept (u)			0.8099		
Intercept (v)			-0.9169		
Water depth	$-2.10 \cdot 10^{-4}$	$-2.10 \cdot 10^{-4}$	-0.0038	$-2.17 \cdot 10^{-4}$ ($-2.23 \cdot 10^{-4}$, $2.16 \cdot 10^{-4}$)	0.99
Water depth (u)			-0.0001		
Water depth (v)			0.0001		
Water temperature	-0.0102	-0.0102	-0.4245	-0.0092 (-0.0162, -0.0061)	0.32
Water temperature (u)			-0.0101		
Water temperature (v)			0.0126		
Target catch rate	-0.0029	-0.0029	0.0963	-0.0042 (-0.0075, -0.0019)	0.01
Target catch rate (u)			$3.67 \cdot 10^{-4}$		
Target catch rate (v)			-0.0028		
Wind speed	-0.0055	-0.0055	0.1143	-0.0081 (-0.0142, -0.0013)	0.52
Wind speed (u)			0.0095		
Wind speed (v)			-0.0057		
Wind direction	-0.0020	-0.0020	-0.0298	-0.0019 (-0.0027, -0.0015)	0.12
Wind direction (u)			$-4.36 \cdot 10^{-4}$		
Wind direction (v)			$7.88 \cdot 10^{-4}$		
Wave height	0.0617	0.0617	1.6720	0.0689 (0.0454, 0.0873)	0.38
Wave height (u)			0.0278		
Wave height (v)			-0.0470		

588	AIC	133.2	194.2	141	120.7	-
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589 **Table 2**

590 Results of the models for estimating the probability of catching a seabird. Four candidate models include the global generalized linear
 591 model (GLM), the mixed effect model with random areal effect (MEM, variance of the random areal effect = 0.13), the spatial
 592 expansion model (SEM) and the geographically weighted generalized linear model (GW-GLM). In the SEM model, u and v index the
 593 parameters expanding along longitude and latitude, respectively. Parentheses in the GW-GLM column represent the variation of mean
 594 parameter estimates (95% confidence interval) across space.

Parameter	Global GLM	MEM	SEM	GW-GLM	p -value permutaion test for
Intercept	0.8285	0.0853	-24.89	0.4946 (-15.5767, 3.5406)	0.01
Intercept (u)			-2.1		
Intercept (v)			1.2030		
Water depth	$-6.08 \cdot 10^{-5}$	-0.0001	$9.23 \cdot 10^{-4}$	$-6.78 \cdot 10^{-4}$ (-0.0107, $8.07 \cdot 10^{-4}$)	$<< 0.0001$
Water depth (u)			$-1.90 \cdot 10^{-5}$		
Water depth (v)			$-2.16 \cdot 10^{-5}$		
Water temperature	-0.0770	-0.0675	0.2765	-0.0523 (-0.1155, 0.1452)	0.01
Water temperature (u)			0.0310		
Water temperature (v)			-0.0172		
Target catch rate	0.0061	0.0072	-0.0923	0.0126 (-0.0036, 0.0247)	0.49
Target catch rate (u)			-0.0036		
Target catch rate (v)			0.0035		
Wind speed	0.0003	-0.0002	0.1270	-0.0083 (-0.2535, 0.0429)	0.23
Wind speed (u)			-0.0053		
Wind speed (v)			-0.0014		
Wind direction	0.0020	0.0019	-0.0315	0.0012 (-0.0187, 0.0078)	0.11
Wind direction (u)			$-2.79 \cdot 10^{-4}$		
Wind direction (v)			$8.72 \cdot 10^{-4}$		
Wave height	0.0161	0.0205	0.7646	0.0161 (-0.1990, 0.3745)	0.5
Wave height (u)			0.0278		
Wave height (v)			-0.0264		
AUC	0.69	0.71	0.73	0.84	-

595 **Table 3**

596 The AUC (area under the receiver operating characteristic curve) values for the candidate models that estimate the probability of
 597 catching a seabird using datasets with different zero percentages. The table shows the mean (95% confidence interval) from 500
 598 simulaiton runs. The four candidate models are the global generalized linear model (GLM), the mixed effect model with random areal
 599 effect (MEM), the spatial expansion model (SEM) and the geographically weighted generalized linear model (GW-GLM). The
 600 estimated h (spatial parameter in GW-GLM) is also shown.

Dataset	Global GLM	MEM	SEM	GW-GLM	h	Number of observations
30% zero	0.7344 (0.6363, 0.8207)	0.7541 (0.647, 0.8421)	0.8674 (0.7761, 0.9519)	0.9145 (0.7286, 0.99)	4.14 (0.1, 16)	83
60% zero	0.7028 (0.6441, 0.7522)	0.7235 (0.6641, 0.7809)	0.7853 (0.7255, 0.8354)	0.8648 (0.7051, 0.9889)	3.27 (0.3, 15.95)	145
90% zero	0.6937 (0.6717, 0.7145)	0.6999 (0.6781, 0.7222)	0.7451 (0.7221, 0.7672)	0.8528 (0.7833, 0.9655)	1.24 (0.2, 2.4)	580

601

602

Table 4
Mean absolute error (MAE) and mean bias for candidate models that estimates the probability of catching a seabird in the simulation study. The candidate models include the global generalized linear model (GLM), the mixed effect model with random areal effect (MEM), the spatial expansion model (SEM), and the geographically weighted generalized linear model (GW-GLM) with a bandwidth (h) that underestimated or overestimated by 30% and 50%. Table shows the median from 500 simulation runs.

Dataset	Global GLM	MEM	SEM	GW-GLM				
				Unbiased	Under 50%	Under 30%	Over 30%	Over 50%
MAE								
30%	0.0949	0.0961	0.1786	0.0941	0.1086	0.0989	0.0939	0.0936
60%	0.2037	0.1880	0.1855	0.1333	0.1896	0.1595	0.1285	0.1308
90%	0.0745	0.0708	0.0691	0.0486	0.0678	0.0576	0.0478	0.0490
> 98%	0.0043	0.0043	0.0067	0.0043	0.0050	0.0045	0.0043	0.0043
Mean bias								
30%	-0.0003	-0.0003	-0.0003	-0.0009	-0.0010	-0.0009	-0.0008	-0.0008
60%	0.0015	0.0010	0.0015	-0.0022	-0.0115	-0.0034	-0.0024	-0.0020
90%	-0.0008	-0.0010	-0.0008	-0.0009	-0.0028	-0.0014	-0.0007	-0.0009
> 98%	<0.0001	<0.0001	<0.0001	-0.0001	-0.0001	-0.0001	-0.0001	-0.0001

Figure captions

Fig. 1. A flowchart for the simulation study to evaluate performance of the geographically weighted generalized linear model (GW-GLM) given a skewed bandwidth (h).

Fig. 2. Spatial distribution of longline set and seabird bycatch in the study area. NEC-northeast coast, MAB-middle Atlantic bight, SAB-south Atlantic bight.

Fig. 3. Spatial distribution of the parameters from the geographically weighted generalized linear model (GW-GLM) and the spatial expansion model (SEM) for analyzing positive catch rate data. The last column of the figure shows the spatial distribution of each predictor variable.

Fig. 4. Spatial distribution of the parameters from the geographically weighted generalized linear model (GW-GLM) and the spatial expansion model (SEM) for estimating the probability of catching a seabird. The last column of the figure shows the spatial distribution of each predictor variable.

Figure 1

Figure 2

Figure 3 GW-GLM SEM Predictor

Figure 4 GW-GLM SEM Predictor