Estimating spatial non-stationary environmental effects on the distribution of species: a case study from American lobster in the Gulf of Maine

Bai Li*, Jie Cao, Lisha Guan, Mackenzie Mazur, Yong Chen, and Richard A. Wahle

School of Marine Sciences, University of Maine, Orono, ME 04469, USA

Corresponding author: tel: +1 207 581 4325; fax: +1 207 581 4388; e-mail: bai.li@maine.edu

Estimating spatial distribution of a species is traditionally achieved using global regression models with the assumption of spatial stationarity of relationships between species and environmental variables. However, species abundance and environmental variables are often spatially correlated and the strength of environmental effects may exhibit spatial non-stationarity on the species distribution. We applied local models, such as season-, sex-, and size-specific geographically weighted regression (GWR) models, on American lobster to explore non-stationary environmental effects on the presence and density of lobsters in the inshore Gulf of Maine (GOM). This species and its fishery have undergone a dramatic increase in abundance over the past two decades. Model results showed that the strength of the estimated relationships in the western GOM were different with the relationships in the eastern GOM during 2000–2014. Bottom water temperature had a more significant positive impact on the increase of lobsters in the eastern GOM, while the influence of temperature was less significant in the west and the more distinguishable drivers of distribution needed to be identified. The estimation of locally varied relationships can further improve regionally informed management plans. The modeling approach can be widely applied to many other species or study areas.

Keywords: American lobster, bottom water temperature, geographically weighted regression model, non-stationarity

Introduction

Understanding the effects of environmental changes on species distribution is required for many aspects of resource management and environmental research (Franklin and Miller, 2009). There is a growing body of literature suggesting that changes in the spatial structure of a population may be caused by shifts in distribution in response to variations in environmental conditions (Ciannelli et al., 2012; Kotwicki and Lauth, 2013; Szuwalski and Hollowed, 2016). The distribution of a species is influenced by many abiotic (e.g. temperature and salinity) and biotic (e.g. predator, prey, and disease) drivers that operate simultaneously with different strengths at different spatial scales or locations, and may change over time. The dominant drivers of the distribution pattern may depend on the spatial scale and vary by subarea when the spatial scale changes. Therefore, it is difficult to disentangle the effects of multiple environmental variables on the presence or density of a species spatially (Ciannelli et al., 2012). This would require a study being conducted at multiple finer spatial scales. Identification of the spatial non-stationary environmental effects on the distribution of a species can improve our understanding of the species spatial dynamics at finer scales (Windle et al., 2010).

The strength of an environmental effect on a species changes with its life stage or along the species' range if there are sharp hydrographic or biogeographical gradients such as differences in local food availability (Frank et al., 2006). For example, the distribution of American lobster is regulated by both abiotic and biotic drivers but primarily driven by water temperature in the Gulf of Maine (GOM, Boudreau et al., 2015; Tanaka and Chen, 2016). The effect of predation on the lobster population increases

and dominates at the cold and warm extremes of the thermal range (Boudreau *et al.*, 2015; Le Bris *et al.*, 2018). Post-settlement natural mortality rates have increased dramatically with the onset of disease at the southern end of the species' range (Wahle *et al.*, 2009). Previous studies have also indicated that lobster recruitment is derived from local sources in the GOM and the stock–recruitment relationships differ between eastern and western GOM (Incze *et al.*, 2010). This is a result of the variation in primary production that is affected by different temperatures and circulation patterns across these two areas (Chang *et al.*, 2015). Given the differences in the eastern and western GOM, it is important to evaluate the spatial non-stationary environmental effects on the lobster distribution in this area.

There is a regional decrease in the degree of vertical mixing from the eastern to the western GOM lobsters can be exposed to a wide range of bottom temperatures. In the western GOM, the bottom water temperature is below the lower bound of ideal temperature range (i.e. 12–18°C) for lobsters whereas the temperature is within the ideal range in the eastern GOM at same depth stratum besides very shallow nearshore areas in spring and fall (Crossin *et al.*, 1998; Kleisner *et al.*, 2016). Therefore, the depth-wise distribution of lobsters may be expected to vary from east to west during the year because of seasonal differences in the degree of vertical mixing. Other environmental variables, such as salinity and sediment type, may further influence the coastal distribution and density of lobster, and may interact with temperature effects on lobster density (Jury *et al.*, 1994).

Previous studies suggest that recent increases of lobsters in the GOM are related to warming bottom temperature (Chang *et al.*, 2010; Tanaka and Chen, 2016; Le Bris *et al.*, 2018), but these increases have not been uniform in space (ASMFC, 2015). The annual mean density of lobsters from the Maine-New Hampshire Bottom Trawl Survey showed that lobsters have increased considerably more in the eastern GOM than in the west (Sherman *et al.*, 2015). The magnitude of environmental effects from two different temperature conditions may result in this density difference. It is important to understand how densities of lobsters change over space under different environmental conditions. Descriptions of the varied temperature-presence and temperature-density relationships over space would provide managers and fishermen greater insight into the role of temperature on the expansion of lobsters into the eastern GOM.

Regression models are the most common technique used to evaluate statistical relationships between species abundance and environmental variables (Windle *et al.*, 2010; Tseng *et al.*, 2013; Ward *et al.*, 2015). However, global regression models (e.g. generalized linear regression model) estimate only a single relationship between environmental variables and species with the assumption of spatial stationarity over large spatial scales. This creates a challenge in understanding complex local patterns (Cadenasso *et al.*, 2007; Hoeting, 2009; Windle *et al.*, 2010). Given the reality that the impact of environmental variables on the distribution and abundance of a species may differ in intensity in different areas of the species range, local models may better characterize spatially varying relationships between abundance and environmental variables (Brunsdon *et al.*, 1998; Fotheringham and Brunsdon, 1999; Franklin and Miller, 2009; Windle *et al.*, 2010; Tseng *et al.*, 2013; Runge *et al.*, 2014).

There are several approaches which can improve our understanding of non-stationary effects of environmental variables on distribution of a species, such as linear mixed models and geographically weighted regression (GWR) models. Both linear mixed models and GWR models are able to provide geographical varied intercepts and species-environment relationships (Franklin and Miller, 2009). Linear mixed models incorporate random parameters and model the variability detected for a given phenomenon among different locations (Thorson *et al.*, 2015). The GWR model estimates intercepts and coefficients of each predictor variable at each observation point (Fotheringham and Brunsdon, 1999). It shows promise in verifying spatial variability of environmental effects on species distribution and identifying dominant environmental driver at potential subarea. Previous studies also suggested that the GWR could make relatively good predictions (Zhang and Gove, 2005). For example, Windle *et al.* (2010) compared several models in predicting presence of cod in the North Atlantic Ocean. The results showed that the GWR produced more accurate predictions and less spatial pattern in the residuals compared with global logistic regression and generalized additive model (GAM).

In this study, we conduct a comprehensive GWR model framework to analyse the local relationships between environmental variables and presence and density of American lobster in the GOM. To detect locally varied relationships between lobsters and environmental variables in the study area, we developed a two-stage season-, sex-, and size-specific model implementing the GWR approach to explore presence and density distribution of lobsters. We also conducted a simulation approach to examine whether the GWR model under- or overestimates lobster density with spatial patterns. The developed analytical framework is suitable for testing the non-stationary environmental effects on the distribution of other species.

Methods
Study area and data sources
The lobster density data were collected from the Maine-New Hampshire Inshore Bottom Trawl Survey. This biannual survey has been conducted in the coastal waters of Maine and New Hampshire since fall 2000. The survey area includes 16 001 km^2 of coastal shelf from Downeast Maine to southern Maine and New Hampshire (Figure 1; Sherman *et al.*, 2005). This stratified random survey has a target number of 115 stations for each survey resulting in a sampling density of one station for every 137 km^2 (Sherman *et al.*, 2005). However, the actual number of surveyed stations is smaller than 115 for various reasons (Chen *et al.*, 2006). The target tow duration is 20 minutes covering a length of approximately 1.48 km. Data from 261 928 individual lobsters were included in this study.

Lobster biological data were collected from 2000 to 2014. At each survey station, the carapace length (CL), sex, and weight of each individual lobster were measured. Lobster catch per tow was standardized according to tow distance by dividing catch quantity with tow distance then multiplying target tow distance. The standardized lobster densities, measured as the number of lobster per 0.016 km^2 (ASMFC, 2015), were grouped by seasons (i.e. fall and spring), sexes (i.e. female and male), and two size classes (i.e. juvenile and adult). Juveniles were lobsters <50 mm CL; this classification is based on the differences in activity patterns (Lawton and Lavalli, 1995). Lobsters <50 mm CL show limited movement, whereas adult lobsters show more active seasonal movement (Lawton and Lavalli, 1995). A total of eight groups (two
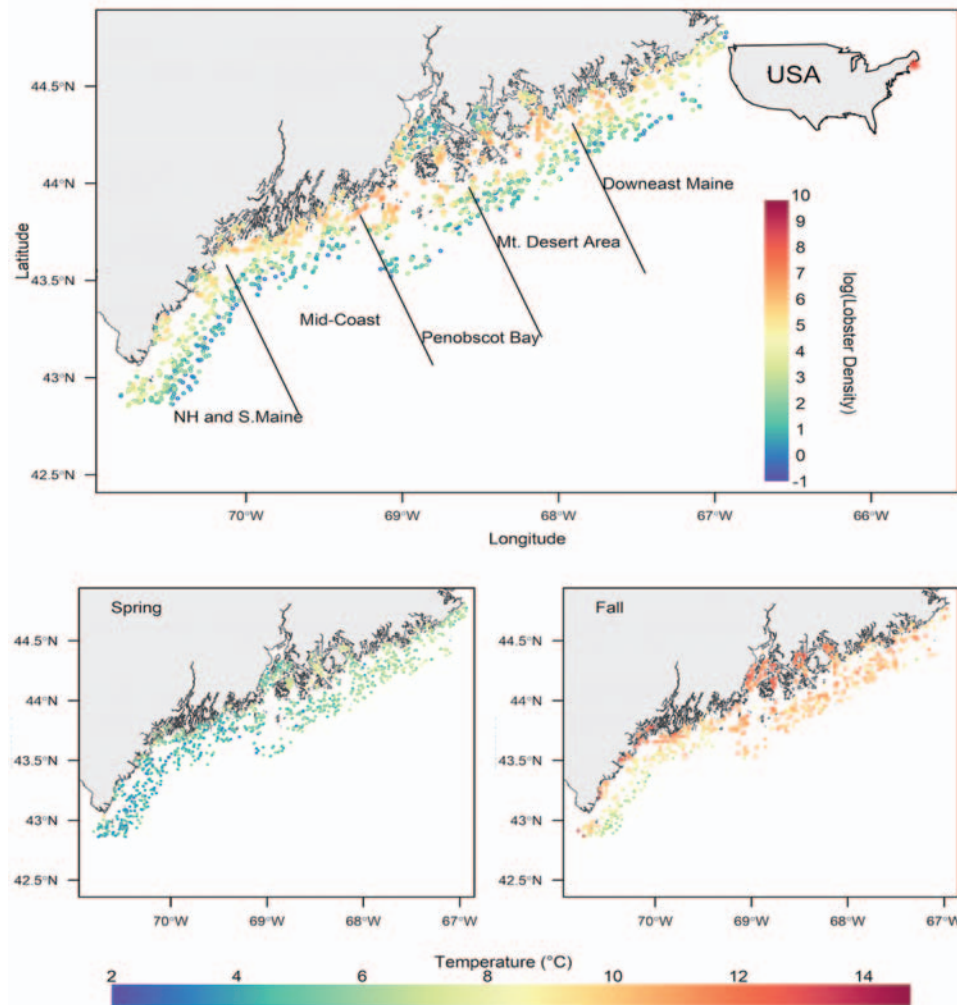
Figure 1. Catch density (log number of lobsters/0.016 km²; top panel) of the Maine-New Hampshire Inshore Bottom Trawl Survey and observed bottom water temperatures (bottom panel) from 2000 to 2014. The star symbol in the US map shows the location of the GOM.

seasons × two sexes × two sizes) of data were modelled independently.

Environmental data and spatial information, such as bottom water temperature (°C, Figure 1), bottom water salinity, depth (m), latitude (decimal degree), and longitude (decimal degree), were collected during the survey. Distance offshore (km), which is defined as shortest distance from the sampling station to the shore, was calculated by using the gdistance package in R (Etten, 2015). Sediment mean grain size (phi; -log of grain size) was obtained from the US Geographical Survey East-Coast Sediment Texture Database (McMullen *et al.*, 2014). The average value of grain size in units of phi was estimated for each survey station using ArcGIS interpolation with kriging. Grain size decreases with increasing phi values, and the range of grain size was from 5.93 to 10.62 phi with a resolution of 0.01 phi.

Model development

Two-stage GWR models were used to evaluate the relationships between lobster density and environmental variables. The first stage GWR was used to estimate the probability of lobster presence (p) as a function of environmental variables with a binomial error distribution:

$$
\begin{aligned}
\text{GWRI}: \; \text{logit}(p_i) &= \beta_0(X_i, \; Y_i) + \beta_1(X_i, \; Y_i)T_i + \beta_2(X_i, \; Y_i)S_i \\
&+ \beta_3(X_i, \; Y_i)De_i + \beta_4(X_i, \; Y_i)DO_i + \beta_5(X_i, \; Y_i)Se_i.
\end{aligned}
$$

The second stage GWR estimated the log-transformed lobster density (d) with a Gaussian error distribution:

$$
\begin{aligned}
\text{GWRII}: \; \ln(d_i) &= \beta_0(X_i, \; Y_i) + \beta_1(X_i, \; Y_i)T_i + \beta_2(X_i, \; Y_i)S_i \\
&+ \beta_3(X_i, \; Y_i)De_i + \beta_4(X_i, \; Y_i)DO_i + \beta_5(X_i, \; Y_i)Se_i,
\end{aligned}
$$

where p is the probability of presence of lobster at location i, d is the density of lobster at location i, β_0 is the intercept specific to location i, and (X_i, Y_i) is the coordinate of the ith location. $\beta_1(X_i, \; Y_i)$ to $\beta_5(X_i, \; Y_i)$ are coefficients of independent variables varying conditional on location i. T_i, S_i, De_i, DO_i, and Se_i, are bottom water temperature (°C), salinity, depth (m), distance

offshore (km), and mean grain size of sediment (phi) at location *i*, respectively.

A preliminary variance inflation factor (VIF) analysis was conducted to remove variables with multicollinearity. We excluded environmental variables with VIFs that exceeded 3 for each model (Sagarese *et al.*, 2014). Based on VIF results and *p*-value (<0.05) from the generalized linear regression model using all the data, temperature, distance offshore, and sediment size were included for all the GWR models. Salinity was included in the first stage male adult and spring male juvenile GWR models. Depth was only included for second stage fall female juvenile GWR model. The input variables were centred on zero because the interpretation of regression coefficients is often sensitive to the scale of the input variables (Franklin and Miller, 2009). The GWR models were conducted applying a generalized linear regression model at each survey station using data from nearest stations with a defined weight. With the moving generalized linear regression model going through each station, location specific intercepts, coefficients, and significances of each explanatory variable ($p <$ 0.05) were determined.

The weighting matrix was calculated based on type of distance, kernel function, and bandwidth (Gollini *et al.*, 2014; Nakaya, 2014). The final weighting matrix was determined based on model optimization criteria such as the smallest corrected Akaike's Information Criterion (AICc) value. The great circle distance between spatial coordinates was used in this study to calculate shortest distance between two points with consideration of the curvature of the Earth (Gollini *et al.*, 2014). A bi-square kernel function was applied by giving a unit weight to each sample point, but null weights to observations with a distance greater than the bandwidth (Gollini *et al.*, 2014). Adaptive bandwidth with a fixed number of points was selected to establish the weight matrix after model optimization (Nakaya, 2014). Golden section search, which is an efficient optimization tool for locating the maximum or minimum of a function by searching between potential bandwidth intervals, was used in order to find optimal bandwidth:

$$w_{ij} = \begin{cases} (1 - d_{ij}^2/b_{i(k)}^2)^2 & if \ |d_{ij}| < b_{i(k)} \\ 0 & otherwise \end{cases},$$

where w_{ij} is the weight value of the observation at station *j* for estimating the coefficient at station *i*, d_{ij} is the great circle distance between stations *i* and *j*, and $b_{i(k)}$ is the adaptive bandwidth size defined as the *k*th nearest neighbour point. The bandwidth of the model that produced the smallest corrected AICc value was determined as the optimal bandwidth. The GWR analysis was conducted using GWR 4.0 software.

Model fitting and validation

Area under the receiver operating characteristic curve (AUC) was used to verify the abilities of the first stage GWR models to fit presence of lobsters. The AUC values range from 0 to 1, and a high AUC value implies that model has a high probability in fitting the presence of lobsters correctly (Zou *et al.*, 2007). Root mean square error (RMSE) and Moran's *I* were used to assess the mode fitting performance of the second stage GWR models. RMSE was calculated to quantify the discrepancy between observed and fitted densities and a value close to 0 indicates better model fit (Stow *et al.*, 2009). Moran's *I* statistic evaluates whether

the pattern of model residuals expressed is clustered, dispersed, or random (Lu *et al.*, 2014). A Moran's *I* value near 1 indicates strong positive autocorrelation of the residuals, and a value near −1 indicates strong negative autocorrelation (Windle *et al.*, 2010).

The eight groups' data for each model were divided into training and testing data to calibrate the model and validate the predictions. Partitioning of training and testing data varies between different models. The proportion of testing data for each model was $1/(1 + \sqrt{p-1})$, where *p* is the number of predictor variables (Franklin and Miller, 2009). Presence and density of lobsters at locations of testing data were predicted based on the model developed using training data. The AUC values were used to evaluate the discrepancy between observed and predicted presence. The adjusted R^2s from linear regression model were used to measure the similarity between observed and predicted density. We repeated the cross validation 100 times for each GWR model and averaged the estimated performance measures.

Results
Model performance and validation

The bi-square kernel bandwidth adapted itself in size depending on the original data density (Table 1). For example, the presence of adults showed a larger spatial coverage in the GOM than juveniles. With few absence values, adults required a larger bandwidth size than juveniles to develop the GWRI model; therefore, the GWRI models for juveniles showed better performances than models for adults with higher deviance explained and AUC values (Table 1). The performance results from GWRII models indicated that the models for adults fitted better in explaining the variation of the density because of the lower RMSE values (Table 1). The mean of 100 cross validation results from the simple linear regression analysis showed that the models had reasonable prediction skill because the fitting lines were close to the 1:1 line (Supplementary Figure S1). The global Moran's *I* ranged from −0.04 to 0.09 and indicated weak autocorrelation of model residuals for all models (Supplementary Figure S2). The estimated coefficients were not highly correlated with observed environmental variables (Supplementary Table S3).

Environmental and spatial variables

Non-stationary environmental effects on distribution of lobsters were visually explored by mapping the local coefficient estimates of each predictor variable. Overall, there was a positive relationship between bottom water temperature and presence of lobsters. The coefficients between presence of lobsters and bottom water temperature varied from −0.44 to 2.97. Positive relationships between presence and bottom water temperature were significant in the eastern GOM, while the western GOM showed non-significant relationships for most of the modelling groups (Figure 2). Near the Mid-Coast region of the GOM, presence of spring female adults showed significant positive relationships with bottom water temperature. However, this relationship was not significant in fall. The significant positive relationships between lobster density and bottom water temperature were more spread throughout the study area (Figure 2). The coefficients for the relationship between lobster density and bottom water temperature ranged from −0.42 to 1.30. When considering different seasons, sex and size of lobsters, there was no large difference in coefficients in GWRII relationship patterns.

Table 1. Summary of optimal bandwidth and model perfomance for the GWR models.

Model	Sample Size	Bandwidth	Deviance (%)	AUC	CV_AUC ±SD
FLFJ I	1059	161	42.77	0.92	0.90 ± 0.05
FLFA I	1059	377	34.10	0.90	0.87 ± 0.10
FLMJ I	1059	131	40.67	0.91	0.89 ± 0.05
FLMA I	1059	495	37.42	0.92	0.67 ± 0.13
SPFJ I	1406	156	34.19	0.90	0.88 ± 0.05
SPFA I	1406	445	20.71	0.83	0.80 ± 0.14
SPMJ I	1406	162	38.26	0.92	0.75 ± 0.07
SPMA I	1406	412	34.84	0.91	0.66 ± 0.12
Model	**Sample Size**	**Bandwidth**	**RMSE**	**R2**	**CV_R2 ± SD**
FLFJ II	561	64	0.37	0.43	0.39 ± 0.12
FLFA II	976	48	0.85	0.54	0.58 ± 0.12
FLMJ II	572	53	0.47	0.41	0.42 ± 0.11
FLMA II	957	48	1.04	0.51	0.60 ± 0.11
SPFJ II	676	58	0.63	0.34	0.37 ± 0.11
SPFA II	1316	62	0.70	0.43	0.57 ± 0.10
SPMJ II	670	65	0.58	0.30	0.30 ± 0.12
SPMA II	1259	65	0.76	0.43	0.55 ± 0.10

The unit of bandwidth is number of points.

The estimated coefficients of the distance offshore varied from −0.81 to 0.34 and −0.64 to 0.88 for GWRI and GWRII, respectively. The negative relationships between the presence of lobster and distance offshore were stronger for juveniles than for adults (Figure 3). The mean sediment size (phi) displayed significant negative relationships with presence of lobsters at most stations. However, there was a cluster of significantly positive relationships between spring adult lobster and sediment size in the Downeast Maine region. The positive relationships indicated that the probability of presence of lobster increases with finer sediment since large phi values indicate finer sediment. In the relationships between presence of lobster and sediment size, the magnitude of the coefficients ranged from −2.80 to 1.99. Lobster density showed patterns of non-significant relationships with sediment size and the range of relationship coefficients was from −5.03 to 2.24 (Supplementary Figure S4). There was no large difference in sediment coefficients among seasons and sexes. The estimated intercepts were the mean of the response when all predictors were zeros and they were also varied over space with ranges of −2.8 to 8.81 and −0.28 to 13.36 for GWRI and GWRII respectively (Supplementary Figure S5). The presence of lobsters showed a lower probability of occurrence outside of the Penobscot Bay compared with the eastern and western GOM and the density of lobsters slightly decreased with increased distance offshore.

Salinity and depth were only included in a few models. The relationships between presence of lobster and salinity were significant in the western GOM in fall and in the eastern GOM in spring. Most of the salinity coefficients were negative and as large as −5.06 (Figure 4). In spring, juvenile lobster presence showed a similar pattern with adult lobster presence. Depth showed a weak relationship (−0.07 to 0.08) with the density of female juveniles in fall (Figure 5). The most significant positive relationship between lobster density and depth was in Mid-Coast Maine, and a negative relationship appeared in Mt Desert outer inshore areas.

Discussion

We developed a modelling approach for understanding the local relationships between environmental variables that influence season-, size-, and sex-specific distribution of American lobster in the GOM. Bottom water temperature, distance offshore, and sediment size were the key variables that affect the spatial distribution of American lobster. The relationships between lobster distribution and these environmental variables varied locally over the GOM. One implication of rapidly changing coefficients in space is that the strength of environmental effects on lobster distribution was non-stationary because of the spatial variations of the environmental variables, showing the importance of spatial scale in studying interactions between lobster distribution and environmental variables.

In a previous study, the temperature has long been recognized to be a key determinant of the distribution and abundance of American lobster using global models (Chang *et al.*, 2010; Tanaka and Chen, 2016). In this study, the GWR models with finer spatial scale showed that the temperature had a significantly positive effect on lobster distribution but the strength of temperature effects varied spatially in the GOM. The relationships were significantly positive in the eastern GOM while most of the area in the western GOM showed non-significant relationships. In addition to the non-significant relationships found in this study, the influence of temperature on lobster presence and density may be obscured by other factors in the western GOM.

It is possible the estimated relationships differed between the western and eastern GOM because there is limited water in the favourable temperature range in the western GOM. A thermal front separates the cold, vertically stratified water in the western GOM from the warm, tidally mixed, bottom water in the eastern GOM (Townsend *et al.*, 2006). Thus, except for the shallowest, nearshore trawl sites, most of the bottom water temperatures in the western GOM were below the ideal temperature range for lobsters, whereas the temperatures at sites in the eastern GOM were above the range. Although the warm stratified layer is not well established in the west at time of the spring trawl survey, it is more conspicuous in the fall survey, when it included depth strata shallower than 37 m (Supplementary Figures S6 and S7). With limited favourable temperature in the western GOM at the seasons of sampling, there was no statistically significant positive relationship between lobster and temperature. The fluctuations of water temperature showed a negligible effect on the presence and density of lobsters. The non-significant relationship between temperature and presence and density of lobsters indicates that other factors (e.g. predators) or a combination of temperature and other factors may influence the lobster population in this region. The relative influence of the predators in regulating the lobster population may intensify at thermal range boundaries (Boudreau *et al.*, 2015).

Distance offshore might be one of the useful variables to predict the lobster distribution in the western GOM. In the western GOM, some relationships between distance offshore and lobster were significantly negative. The rate of decrease in juvenile presence was faster than that of adults given the same value of distance offshore. Juveniles exhibit less mobility than adults (Lawton and Lavalli, 1995; Wahle *et al.*, 2013a); thus, the distance offshore is a better predictor for juveniles than adults, because the limited movement ability of juveniles restricts them inshore where they have been found to settle at highest density (Wahle *et al.*, 2013a). In addition to distance offshore, sediment size was also an important variable showing spatial varying relationships with presence and density of lobsters. The presence of adult lobster in spring showed both positive and negative relationships with sediment
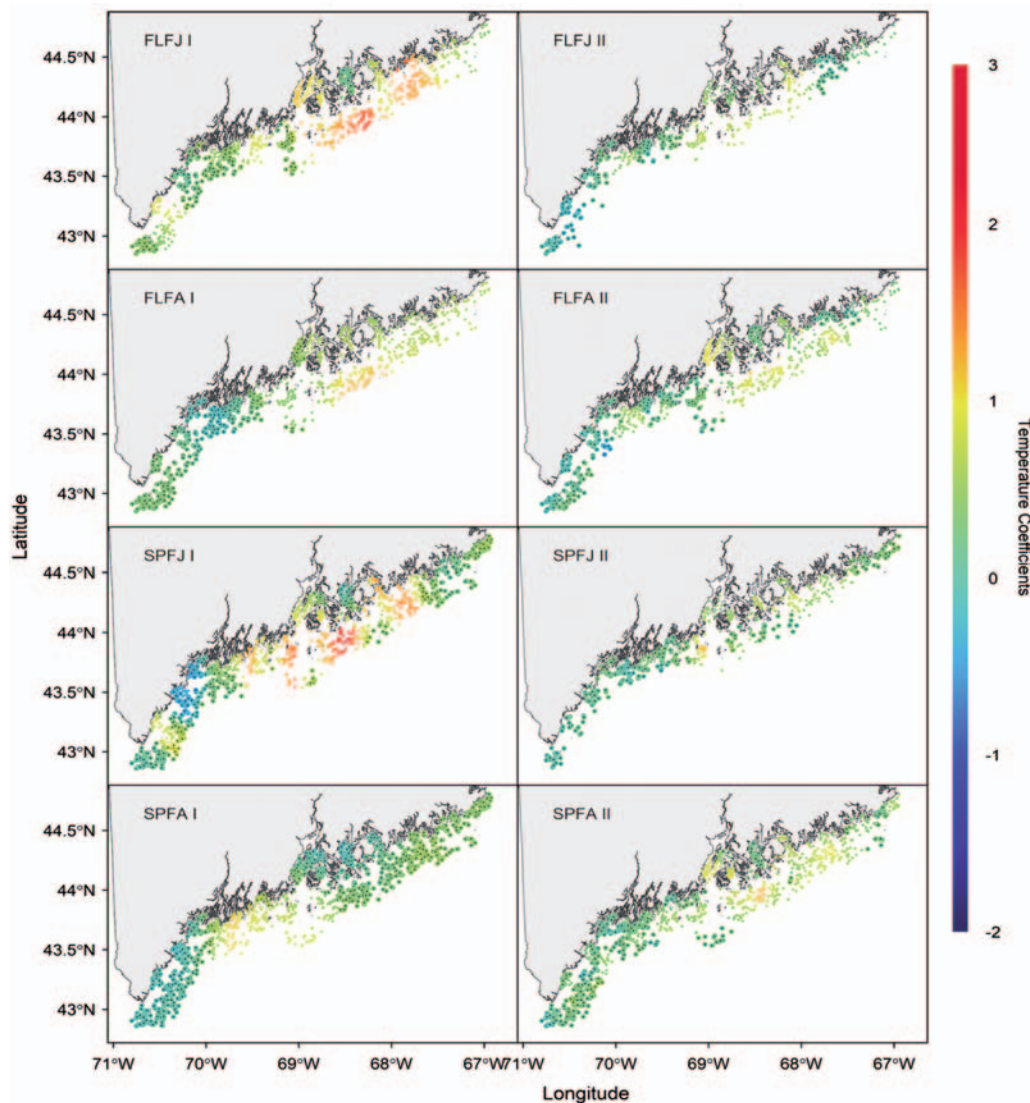
Figure 2. Local coefficient estimates derived from the GWR models for bottom water temperature. The circles with dots denoted that the bottom water temperature were not significant to the models at these locations. FLFJ I: FL denotes fall, F denotes female, J denotes juvenile, and I denotes first stage model. SPFA II: SP denotes spring, F denotes female, A denotes adult, and II denotes second stage model.

size in different regions. The sediment size has no large distance offshore-wise gradient in the Downeast Maine region according to the data from the US Geographical Survey East-Coast Sediment Texture Database (McMullen *et al.*, 2014). The sediment size in other areas gradually changes from coarse to fine with increasing distance offshore. With more options in terms of sediment types, the presence and density of lobsters decreased with increasing sediment size in regions other than the Downeast Maine region. This pattern was not detected in previous studies (Chang *et al.*, 2010) and suggests that the adult lobster is less restricted to the coarse, rocky, cobble sediment found in the Downeast Maine region.

Alternatively, coarse substrate such as boulders and cobble may limit trawl sampling efficiency. The complex relationships between lobster and sediment size require further exploration as catchability of lobsters by the trawl survey may explain some of the spatial variability in apparent lobster density (Somerton *et al.*, 2013). Lobsters often prefer boulder and rocky substrates

(Steneck and Wilson, 2001), but the trawl survey generally showed higher lobster catches in clay and silt areas. The trawl survey in general has poor catch efficiency at those rocky substrates (Chang *et al.*, 2010); therefore, the model might underestimate the importance of sediment related variables. In addition to sediment, the variation in estimated temperature coefficients might be induced by varied catchability at different temperatures. The contrast of temperatures in the western and eastern GOM might cause differences in catchability and therefore, likely affects the explanatory power of temperature in the models from these regions.

All the environmental variables examined in this study are abiotic, and we have not investigated any biotic variables that can impact the distribution of American lobster. Boudreau *et al.* (2015) suggested that both biotic and abiotic effects could affect the abundance of American lobster in the northwest Atlantic Ocean by altering lobster interactions with predators and abiotic environmental variables. Given the non-significant relationship
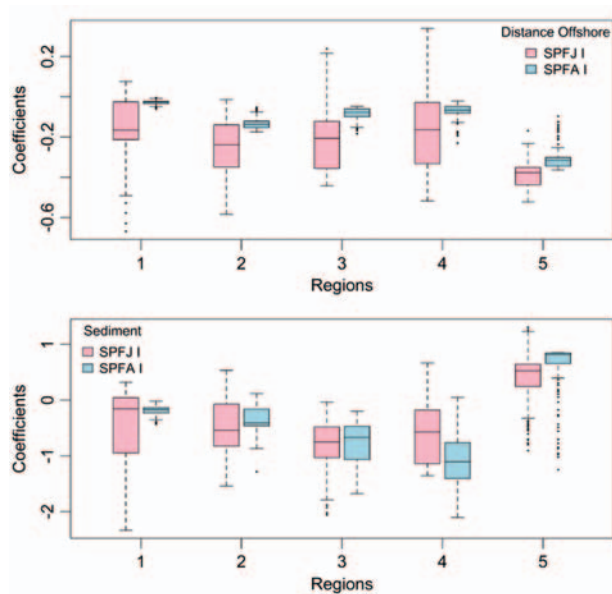
Figure 3. Boxplot of coefficients from distance offshore (top panel) and sediment (bottom panel) at different regions. The regions from 1 to 5 represent New Hampshire and Southern Maine, Mid-coast, Penobscot Bay, Mt Desert Area, and Downeast Maine region respectively. SPFJ I denots presence model with spring female juveniles and SPFA denotes presence model with spring female adults.

between lobster and temperature in the western GOM, incorporating biotic variables such as the abundance of cod, a predator of the American lobster, into the GWR model may further explain the spatial dynamics in the western GOM. The abundance of cod is higher in the western GOM than in the eastern GOM, which is the opposite pattern of the density of American lobster (NEFSC, 2013; Wahle *et al.*, 2013b).

The model validation results suggest low spatial autocorrelation of model residuals, which is consistent with the results of previous GWR model studies (Zhang and Gove, 2005; Windle *et al.*, 2010; Lu *et al.*, 2014). Although global models often assume independence between observations and model residuals, the GWR model assumes and quantifies spatial dependence between observed variables. The lack of spatial patterns in model residuals suggests relative good performance of the GWR models. The GWR model is particularly useful when the target species tends to have a patchy distribution which requires consideration of spatial dependence.

Although using a GWR model to predict the spatial distribution of a marine species has many advantages, GWR models have limitations. Coordinates were the only information required by the GWR model for coefficients prediction at unobserved locations. Thus, the estimated parameters are not suitable to predict future distribution of a species if there are substantial changes in ocean conditions. Like Chang *et al.* (2010), we assumed that the lobster behavioural response to environmental gradients did not vary much between years. Year-to-year variations in lobster density could be used to set up time blocks to explore the distribution under different density conditions. However, data could not be divided into several time blocks since the lobster density from the trawl survey did not have an obvious shift within the study period (2000–2014). Shifts in estimated relationships can

be assumed if low- and high-density periods exist and if there is a density dependent behaviour of lobsters. In addition to the difficulty in adding year as a factor into the models, the GWR model may need to be carefully examined if it is used to conduct annual analyses. The AUC values from the model validation results were lower than the fitting results with an average decrease of 10.83%. This decline is a result of the model being developed with training data, which has fewer data points than the full dataset; therefore, a model developed with a single year's data may not be sufficient to produce ecologically interpretable results. GWR model, compared with global models (e.g. GAM), may have less flexibility in forecasting presence or density of species if there is a sudden change in the environment. The large data quantity required to estimate locally varied relationships constrain the application of the GWR model.

Windle *et al.* (2010) and Lu *et al.* (2014) suggested using the GWR model and global regression model together to better understand how the distribution of a species varies with different factors in a large ecosystem. The GWR model has the ability of producing results that are as accurate as the more frequently used global regression models (Zhang *et al.*, 2008). In addition to the similar performance in prediction, the GWR model can explore spatial non-stationarity of environmental influences at various scales. The GWR can be used as an identifier to determine the spatial scale relationships between species and environmental variables become stationary (Segovia *et al.*, 2016). Thus, the GWR model can first be used to detect the non-stationarity scale, and this defined scale could be used to divide the study area into subareas. Using both GWR and global models can further improve the hindcast or forecast of the species distribution outside of the temporal range of existing data. Furthermore, the estimated coefficients maps can clearly reveal heterogeneity of the relationships throughout the study area and facilitate interpretation of model results (Segovia *et al.*, 2016). The GWR model is also able to predict coefficients/relationships at unsampled locations without additional measurements.

Non-stationary relationships between species and environmental variables have several important implications for management. First, a dominant driver in different subareas can be identified by comparing the magnitudes of the estimated relationships. With a careful examination of the biological mechanism underlying the estimated relationship, a more specific monitoring program can be developed by focussing on sampling data for the identified dominant drivers (e.g. predators). In addition to identify dominant drivers at subareas, this analysis will facilitate derivation of spatially explicit species abundance indices if the species is managed under multiple management areas. Furthermore, the abundance indices can be simulated under various climate scenarios to inform temperature-explicit conservation plans.

Improved conservation of the American lobster requires locally informed management plans to better serve the region's economically and culturally important coastal fishing communities. Fishing communities along the coast may be at a risk if the local lobster density starts to decline with a change in environment. In addition, variation in timing and location of fishing may lead to an increase of variation in the temporal trends of lobster density in different areas. Regarding the different trends of lobster density, each of the seven Maine lobster management zones needs to develop a local management plan to respond to the different challenges it may face. For example, the management zones in the eastern GOM may have laxer management rules because the
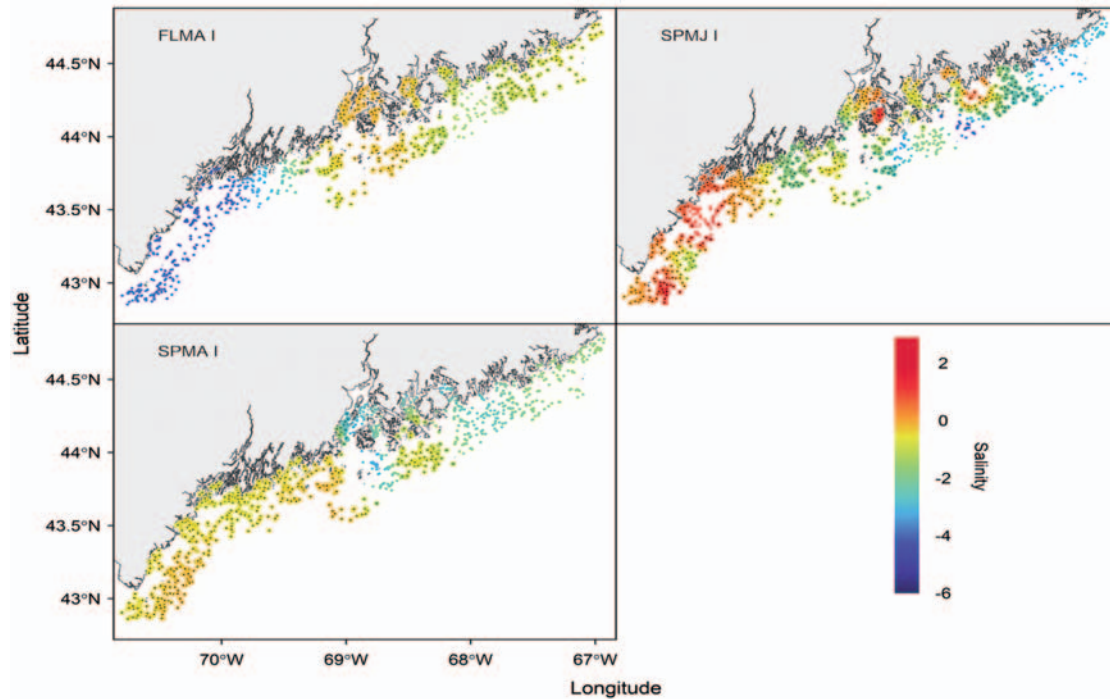
Figure 4. Local coefficient estimates derived from the GWR models for salinity. The circles with dots denoted that the salinity were not significant to the models at these locations. FLMA denotes fall male adult, SPMJ denotes spring male juvenile, SPMA denotes spring male adult, and I denotes first stage of model.
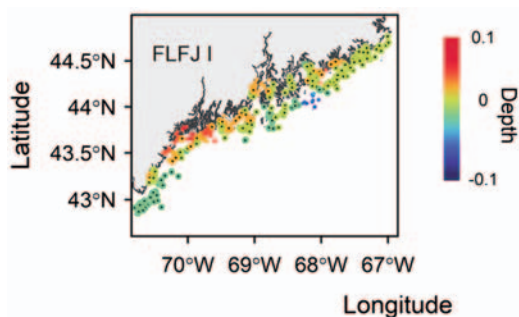
Figure 5. Local coefficient estimates derived from the GWR models for depth. The circles with dots denoted that the salinity were not significant to the models at these locations. FLFJ I denotes first stage of model for fall female juveniles.

fishery is likely to be more abundant if temperature continues to rise within the favourable temperature range of lobsters. On the other hand, zones in the western GOM may need more information on the impact of predation on the fishery before relaxing their management rules.

In conclusion, this modelling approach can be applied to a wide suite of species and has important management implications. The developed GWR models in this study provided details of the relationships between presence or density of a species and other environmental variables. Coefficient maps enable the importance and significance of each environmental variable at a specific location to be easily assessed. The improved performance of using local models compared with global models highlights the limitations of using only a global model to study the distribution of a species in a large marine ecosystem and provides insights in

managing a species by subareas. Future studies need to explore the influences of interactions among abiotic and biotic variables (e.g. the density of predators) on the non-stationary environmental effects on the distribution of a species to achieve better estimation of the lobster population.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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