Improving estimation of length–weight relationships using spatiotemporal models

Yihao Yin[a], **Jessica A. Sameoto**[a], **David M. Keith**[a], and **Joanna Mills Flemming**[b]

[a]Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, NS B2Y 4A2, Canada; [b]Department of Mathematics & Statistics, Dalhousie University, Halifax, NS B3H 4R2, Canada

Corresponding author: **Yihao Yin** (email: yihao.yin@dfo-mpo.gc.ca)

Abstract

Length–weight relationships (LWRs) are an essential component of fishery stock assessments. They are used to develop indices of condition and to convert length data into estimates of biomass. Attempts to capture variability in underlying ecological processes within statistical modeling frameworks for LWRs have typically relied on the inclusion of environmental variables. Here, using a case study of sea scallop (*Placopecten magellanicus*), we demonstrate that introducing spatiotemporal random effects into generalized linear mixed models can improve LWRs. We compare models with and without potentially informative environmental variables. We find that the explicit incorporation of spatiotemporal dependence structures reduces bias and increases precision in the estimation of weight. The combination of both spatiotemporal effects and environmental variables provided the best predictions in most years. Spatiotemporal random effects can provide a comprehensive means of improving LWRs for various species, even when influential environmental variables are unavailable.

Key words: spatiotemporal model, environmental variables, generalized linear mixed model, allometric relationship, stock assessment, sea scallop

Résumé

Les relations entre la longueur et la masse (RLM) constituent un élément essentiel des évaluations des stocks de pêche. Elles sont utilisées pour établir des indices de condition et pour convertir des données de longueur en estimations de la biomasse. Les tentatives visant à saisir la variabilité de processus écologiques sous-jacents dans des cadres de modélisation statistique pour les RLM reposent typiquement sur l'inclusion de variables environnementales. En utilisant une étude de cas du pétoncle géant *Placopecten magellanicus*, nous démontrons que l'introduction d'effets spatiotemporels aléatoires dans des modèles linéaires mixtes généralisés peut améliorer les RLM. Nous comparons des modèles qui intègrent ou non des variables environnementales potentiellement informatives. Nous constatons que l'incorporation explicite de structures de dépendance spatiotemporelle réduit le biais et rehausse la précision de l'estimation de la masse. La combinaison d'effets spatiotemporels et de variables environnementales produit les meilleures prédictions pour la plupart des années. Les effets spatiotemporels aléatoires peuvent fournir une approche exhaustive pour améliorer les relations entre la longueur et la masse pour différentes espèces, même si des variables environnementales influentes ne sont pas disponibles. [Traduit par la Rédaction]

Mots-clés : modèle spatiotemporel, variables environnementales, modèle linéaire mixte généralisé, relation allométrique, évaluation des stocks, pétoncle géant

1. Introduction

In marine ecosystems, ecological processes are known to vary in space and time; however, describing their complex spatiotemporal patterns has historically proven challenging. Attempts to account for spatiotemporal variability within standard statistical modeling frameworks have largely been undertaken using environmental variables and categorical variables for time and space that are relatively coarse (Bolker et al. 2009; Potts and Rose 2018). However, recent statistical developments have focused instead on capturing spatiotemporal patterns through the introduction of random effects,

into modeling frameworks, most often resulting in mixed effect models (Thorson and Minto 2014). Generalized linear mixed models (GLMMs) are a popular statistical framework for such purposes commonly used in ecological modeling (Venables and Dichmont 2004; Bolker et al. 2009). GLMMs are extensions of ordinary linear regression models; they include both fixed and random effects (i.e., mixed effects models) and allow for non-Gaussian distributions of the response variable (i.e., generalized linear models). Traditional GLMMs typically employ spatially explicit covariates (defining regions, zones, etc.) in an attempt to approximate spatial structures.

Such approaches can be effective at explaining some variability in the response variable in the absence of more complex random-effect structures that explicitly model spatial characteristics, which were historically difficult to construct and incorporate.

The incorporation of spatiotemporal dependence structures within the framework of mixed effect models has been made much easier recently by the development of cutting-edge, highly efficient statistical tools, notably R-INLA (Lindgren 2012) and TMB (Template Model Builder) (Kristensen et al. 2016). Essentially, these tools have made it possible to efficiently fit such models to complex spatiotemporal data in practice. Spatial and spatiotemporal models implemented with these tools are quickly emerging in fishery research as best practice for investigating important ecological processes such as population density (Thorson et al. 2015; Thorson 2019), by-catch (Cosandey-Godin et al. 2014), abundance (Cao et al. 2017; Cavieres and Nicolis 2018), growth (Cahill et al. 2020), and stock dynamics (McDonald et al. 2021). Results have confirmed that accounting for spatiotemporal variability can reduce bias and uncertainty in parameter estimates, while also providing unique insights into fishery behavior, ecosystem functioning, and population dynamics.

Given that the drivers of productivity are inherently spatial, individuals sampled from locations in close proximity are likely to exhibit more similar growth. This has been observed for both mobile and sedentary species (Thouzeau et al. 1991; Smith et al. 2001; Smith and Rago 2004; Gerritsen and McGrath 2007; Hart and Chute 2009; Thorson 2015; Adams et al. 2018), although this geographic assumption may be less pronounced for mobile species due to individual migration and mixing. For sedentary species, local physical, chemical, and biological processes can result in localized and predicable differences in growth throughout the seascape (Thouzeau et al. 1991; Smith et al. 2001; Smith and Rago 2004; Hart and Chute 2009). As a result, covariates that are relatively easy to obtain (e.g., depth) often serve as proxies for the complex interaction of processes that drive spatiotemporal variability. Unfortunately, understanding the influence of complex spatiotemporal processes remains elusive when using simple proxies. This is especially true when other local sources of environmental variation are not included in the modeling methods due to either a lack of knowledge of the process or simply a lack of available data. The spatiotemporal modeling framework can overcome these limitations by utilizing the spatial autocorrelation found in the data itself to provide more accurate parameter estimation and novel insights into the patterns and processes underlying this variability (Thorson 2015; Hodgdon et al. 2020).

In sedentary species, spatiotemporal patterns in somatic growth are often reflected in their condition, defined as the relationship between individual length and weight, where differences in length-to-weight relationships (LWRs) reflect differences in the physiological state of the individuals at given locations (Murphy et al. 1990). Since length data are easier and faster to obtain in the field than data on weight, sampling protocols often include extensive monitoring of individual lengths, whereas only a subsample of individuals caught in the field is actually weighed (Kimmerer et al. 2005; Gerritsen and McGrath 2007; Hennen and Hart 2012). LWRs developed from these subsampled data are then used to convert between numbers, biomass, and catch (Froese 2006; Gerritsen and McGrath 2007), with any uncertainty or bias due to this conversion propagated into subsequent stock assessment indicators, model inputs, and fishery management advice.

Traditionally, spatiotemporal variability in LWRs is accounted for using environmental variables, such as year, season, area, and depth (Lai and Helser 2004; Gerritsen and McGrath 2007; Sarro and Stokesbury 2009; Hennen and Hart 2012; Al Nahdi et al. 2016). Harnessing the latent spatiotemporal information in length–weight data may improve subsequent LWR model performance. Our objective here is to demonstrate how explicitly incorporating a spatiotemporal component into a mixed effect model framework can improve the prediction of LWRs compared to more traditional GLMMs. We demonstrate this spatiotemporal approach with a case study of the Bay of Fundy sea scallop (*Placopecten magellanicus*).
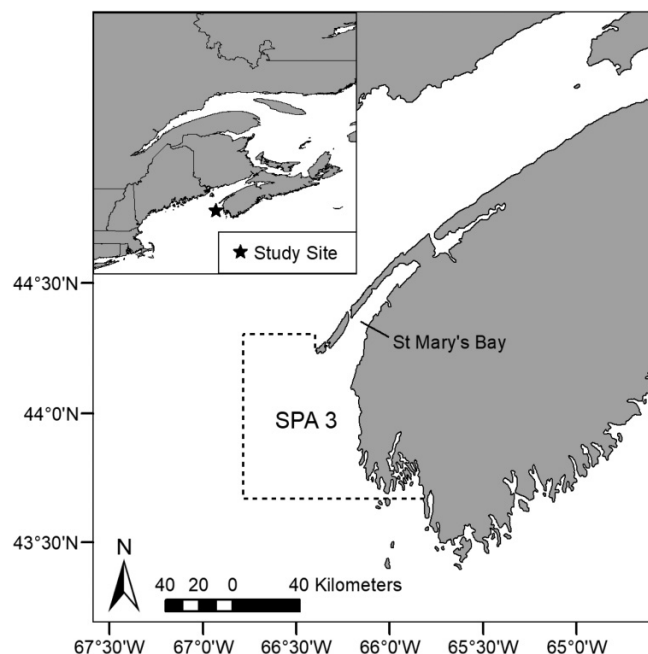
2. Methods

The generic GLMM formulation we propose for further development of LWR models is as follows:

$$
\begin{aligned}
f(\mu) &= X\alpha + Z\beta \\
w|\mu &\sim D \\
\beta &\sim \Sigma
\end{aligned}
\tag{1}
$$

Here, w is the response variable, meat weight, and μ is the predicted value of meat weight. f is a link function relating μ to both fixed and random effects ($X\alpha$ and $Z\beta$). X and Z are design matrices from predictors such as shell height, etc.; α and β are the fixed and random parameters, respectively, where the random parameters are assumed to follow a generic distribution Σ. Finally, D denotes the response distribution for w and must be a member of the exponential family of distributions.

Fixed effects can include informative predictors such as measurements of relevant environmental variables; random effects are often used to model variations in parameters (e.g., β) that potentially arise from shared stochastic processes (Thorson and Minto 2014). Traditionally, simple statistical distributions are often employed for explaining these variations when such stochastic processes are abstruse and difficult to model explicitly, e.g., Gaussian distribution for symmetric dispersion. However, recent developments in spatial statistics can allow for efficient incorporation of more complex structures in random effects for underlying spatial and temporal processes (Lindgren 2012; Kristensen et al. 2016). Mixed effect models with random spatial and spatiotemporal effects based on Gaussian Markov random fields (GMRFs) are characterized by their explicit modeling of spatial autocorrelation within the data and have the potential for improving ecological modeling of interested quantities that historically have relied on simple GLMMs. Herein, we denote models with spatial

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Fig. 1. Location of the scallop production area (SPA) 3 in the Bay of Fundy, Canada. Base map sources from U.S. Geological Survey and National Oceanic and Atmospheric National Ocean Service, map projection WGS84 Web Mercator.

the shell height and meat weight measurements were taken). Scallops greater than 50 mm in shell height are sorted into 5 mm shell height size bins and up to three scallops per 5 mm bin are retained for dissection. Shell heights (umbo to the margin) are measured to the nearest millimeter and corresponding meats have excess water removed and are weighed to the nearest 0.1 g. The total number of individual scallops sampled per year ranged from 1832 to 2151 during the study period. Temperature is recorded for each tow using a Vemco Minilog II temperature recorder attached to the survey gear. Although temperature is an in-situ measurement at the time of the survey, the study area is located at the mouth of the Bay of Fundy, which is a tidally dominated funnel-shaped bay that experiences some of the world's highest tides (O'Reilly et al. 2004). The tidal currents strongly influence the oceanographic conditions in this area and, this results in persistent oceanographic differences across the area (Greenlaw et al. 2010; Li et al. 2015). Temperature was therefore included for evaluation as a potential candidate environmental variable in subsequent analyses. Depth information is recorded at sea for each tow; however, due to significant variation in tides in the Bay of Fundy (O'Reilly et al. 2004; Shaw et al. 2012), standardized depths are obtained by spatial analysis of the tow positions with a 50 m resolution DEM (Digital Elevation Model) standardized to mean water level. Further details on the survey design and sampling protocols can be found in Glass (2017).

2.2. Preliminary analysis

Evaluation of various model settings in a preliminary analysis (https://github.com/Mar-scal/SPA3_Spatial_LWRs) indicated that using a Gaussian distribution for the response variable (meat weight) with a log-link function resulted in the best model predictions and that the best random-effect structure included both a random slope and intercept. The variance inflation factor value was 2.15 for depth and temperature; given this value was <3 (Zuur et al. 2009), both depth and temperature were retained as candidate environmental variables. As a result, four comparable models were presented in this study and tested further: two using a traditional GLMM framework and two using an STM framework. All models incorporated year as an additive fixed effect. The model formulations were designed to evaluate the impact of incorporating environmental variables (depth and temperature) as additive fixed effects, and to evaluate the relative difference between incorporating spatial heterogeneity using tow location as an independent random effect in a GLMM framework, or via an STM framework with spatial and spatiotemporal random effects for the year and tow location. In STMs, it is possible to incorporate various assumptions of autodependence (or independence) into any of the temporal, spatial, and spatiotemporal effects. The STM structures in the method below were formulated to allow for the best relative comparison to the GLMMs. Analyses were conducted in the statistical software R v4.0.3 (R Core Team 2020) using the packages lme4 (Bates et al. 2015), TMB (Kristensen et al. 2016), and INLA (Lindgren et al. 2011). For reproducibility and for those interested in application to other surveys and species, the datasets and

and spatiotemporal effects as spatiotemporal models (STMs) to distinguish them from traditional GLMMs without such effects.

This section provides a data description for the case study, a summary of exploratory and preliminary analyses for LWRs, and the theoretical background for the four selected models presented in this study: a GLMM, a GLMM with environmental variables including depth and temperature (GLMM-DT), an STM, and an STM with environmental variables (STM-DT). Performance of these models was assessed in the case study and compared by a rigorous and objective-oriented cross-validation procedure. Three additional model formulations (a GLMM with depth, temperature, and area effect, a spatial model with a static spatial effect, and a spatial model with a static spatial effect, depth, and temperature) were also evaluated and can be found in the Appendix.

2.1. Data description

Fisheries and Oceans Canada conducts annual scallop surveys in scallop production area (SPA) 3, which is a scallop management area in the Bay of Fundy, Canada (Fig. 1). This random-stratified survey occurs over a period of 7–8 days in June each year and the number of tows per year has ranged from 135 to 155 during the study period (2012–2018). At sea, all scallops caught are measured for shell height to the nearest millimeter and measurement error is negligible (< 1%). However, due to resource limitations the meat weight is only measured for approximately half of the tows (ranged from 60 to 66; see Fig. 2 for the annual survey tow locations where

Fig. 2. Spatial residuals (grams) for the four models in each year. Residuals were spatially aggregated and averaged over tows to highlight remaining spatial patterns. Base map was made with Natural Earth, map projection WGS84 Web Mercator. [Colour online]
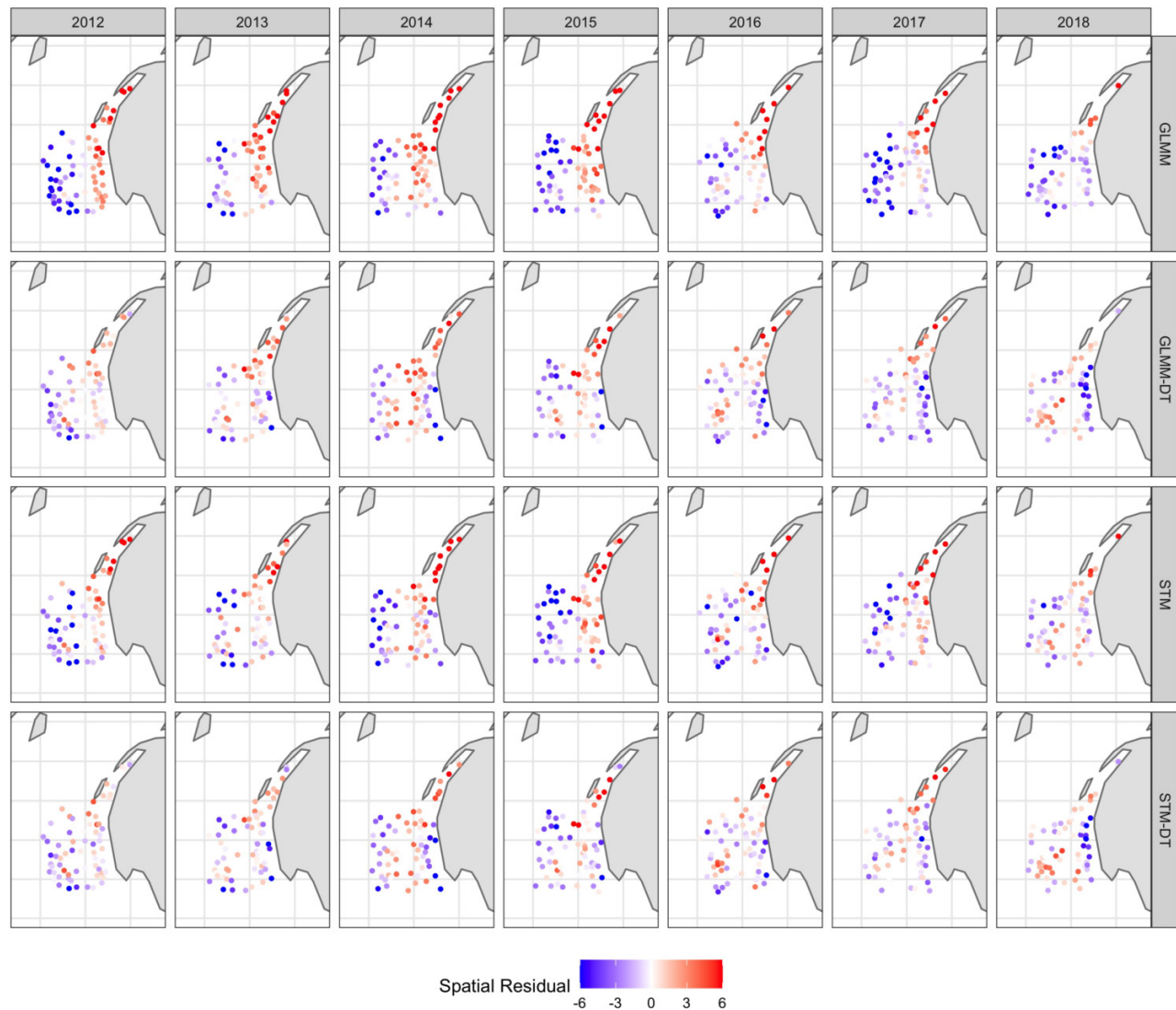
scripts for the analyses performed in this study are publicly accessible on GitHub (https://github.com/Mar-scal/SPA3_Spatial_LWRs). The preliminary analyses that guided selection of the four models presented in this study can be found in the same GitHub repository; however, three models that may be of additional interest are included in the Appendix.

2.3. Analytical models

2.3.1. Generalized linear mixed model (GLMM)

There are two levels of variation in the dataset as described, the groups (i.e., the tows) and the individual observations (i.e., weights and heights) within a tow. The following GLMM is considered, where tow location is included as a random effect to account for potential spatial and spatiotemporal vari-

ability in the parameters among tows:

$$
\begin{aligned}
\log(\mu_i) &= \alpha_0(t_i) + \alpha_1 \log(h_i) + \beta_0(s_i, t_i) + \beta_1(s_i, t_i)\log(h_i) \\
w_i &\sim N(\mu_i, \phi^2) \\
\beta_0(s_i, t_i) &\sim N(0, \varepsilon_0^2) \\
\beta_1(s_i, t_i) &\sim N(0, \varepsilon_1^2)
\end{aligned}
$$

(2)

where w_i and h_i are the meat weight and shell height of the i-th observation, respectively, and μ_i is the expected meat weight. A log transformation of the shell height and a log-link function of the meat weight are used, which amounts to a power relationship between the two variables. $\alpha_0(t_i)$ are fixed parameters and correspond to the year effect. β_0 and β_1 are the random parameters relating to tow locations s_i; however, since tow locations are chosen randomly in each year, these two random parameters represent variation in

both space and time (i.e., location s_i and year t_i). In practice, they are implemented with the categorical variable, tow ID. The random effects and the response variable are assumed to follow Gaussian distributions.

2.3.2. Generalized linear mixed model with environmental variables (GLMM-DT)

Some mechanistic processes are believed to be major contributors to spatial variation in meat weight–shell height relationships and in particular, measured variables such as depth and temperature may contain information about these processes. In order to assess the influence of the two environmental variables, they are incorporated into the above GLMM as auxiliary fixed effects to form a second GLMM, GLMM-DT, as follows:

$$\log(\mu_i) = \alpha_0(t_i) + \alpha_1 \log(h_i) + \alpha_2 d_i + \alpha_3 c_i + \beta_0(s_i, t_i)$$
$$+ \beta_1(s_i, t_i) \log(h_i)$$
$$(3) \quad w_i \sim N(\mu_i, \phi^2)$$
$$\beta_0(s_i, t_i) \sim N(0, \varepsilon_0^2)$$
$$\beta_1(s_i, t_i) \sim N(0, \varepsilon_1^2)$$

where d_i and c_i are depth and temperature corresponding to the i-th observation, respectively, and α_2 and α_3 are their associated coefficients. Both environmental variables are in situ measurements from the survey and are in fact tow-level observations, as scallops from the same tow are considered to share the same environmental conditions. The measurements are log-transformed and normalized for numerical stability in model estimation and their variability is represented in their respective linear coefficients.

2.3.3. Spatiotemporal model (STM)

To assess the effectiveness of a spatially explicit meat weight–shell height model, an STM was designed assuming the same allometric relationship between meat weight and shell height with tow-level linear coefficients to capture spatial, temporal, and spatiotemporal effects. The additive formula facilitates the decomposition of multiple random effects. We consider these effects to reside in both the intercept and slope (corresponding to shell height),

$$\log(\mu_i) = [\alpha_0(t_i) + \beta_0(s_i) + \beta_0(s_i, t_i)]$$
$$(4) \quad + [\alpha_1(t_i) + \beta_1(s_i) + \beta_1(s_i, t_i)] \cdot \log(h_i)$$
$$w_i \sim N(\mu_i, \phi^2)$$

where w_i and h_i are the meat weight and shell height for the i-th observation, respectively. μ_i is the expected meat weight. $\alpha(t_i)$ represent the temporal effect and are fixed parameters; $\beta(s_i)$ and $\beta(s_i, t_i)$ are the spatial and spatiotemporal random effects for the year t_i and location s_i, respectively. Subindices 0 and 1 denote the linear intercept and slope, respectively. Prediction for the meat weight is derived conditioning on these random effects assuming a Gaussian distribution. The following assumptions for these effects apply similarly to both the

intercept and slope, so the equations below apply to both β_0 and β_1 and are presented without subindices to reduce redundancy.

The temporal effect, $\alpha(t)$, is assumed to be fixed so that the annual mean is estimated independently. The annual survey occurs over a period of 7–8 days in June each year. All scallops within a survey are tagged with the same time index; therefore, the sea scallops sampled within the same year share a common year effect.

For the spatial effect, $\beta(s)$, we assume a Matérn GMRF where spatial locations jointly follow a conditional multivariate normal distribution and the covariance between any two locations follows a distance-based de-correlation Matérn function (Rue and Held 2005). The spatial effect $\beta(s)$ is also assumed invariant of time,

$$(5) \quad \begin{aligned} \beta(s_i) &\sim \text{GMRF}(0, \Sigma^S) \\ \Sigma^S_{s_i, s_j} &= \text{Matérn}[d(s_i, s_j), \theta^S] \end{aligned}$$

where Σ^S is the covariance matrix whose elements describe the pairwise covariances among sample locations, and θ^S are the parameters defining the random field, including the smoothness, scale, and variance parameters. In practice, the smoothness is specified so that the GMRF can be defined via a sparse precision matrix; the scale describes the range of spatial dependence and the precision relates to the variance and covariance in the space–time matrix and the two parameters are estimated. $d(s_i, s_j)$ is the Euclidean UTM distance (O'Keefe 1952) between the two tow locations converted from their longitude and latitude recordings.

Similarly, the spatiotemporal effect, $\beta(s, t)$, or the dynamic spatial effect, is also assumed as a Matérn GMRF but fits to each year as an independent realization,

$$(6) \quad \begin{aligned} \beta(s_i, t_i) &\sim \text{GMRF}(0, \Sigma^{ST}(t)), \forall t_i = t \\ \Sigma^{ST}_{s_i, s_j}(t) &= \text{Matérn}[d(s_i, s_j), \theta^{ST}] \end{aligned}$$

where t denotes the survey year and in this study $t \in \{2012–2018\}$. The covariance matrices for each year are composed of pairwise covariances between observation locations and are assumed as different realizations from a shared latent field.

The random effects are structured to resemble measurable environmental conditions, but may be more flexible and encompassing than specific environmental variables. For example, the static spatial effect is likely related, but not limited to depth, and the secondary spatiotemporal effect could be informed by temperature.

2.3.4. Spatiotemporal model with environmental variables (STM-DT)

An STM with environmental variables (STM-DT) is also considered, where depth and temperature are incorporated sim-

ilar to the GLMM-DT,

$$\log(\mu_i) = \alpha_0(t_i) + \alpha_1(t_i)\log(h_i) + \alpha_2 d_i + \alpha_3 c_i$$
$$\text{(7)} \quad + \beta_0(s_i) + \beta_0(s_i, t_i) + [\beta_1(s_i) + \beta_1(s_i, t_i)]\log(h_i)$$
$$w_i \sim N(\mu_i, \phi^2)$$

Variables in the STM-DT are identically defined as in the STM with an addition of the linear coefficients α_2 and α_3 corresponding to depth and temperature, respectively. For the spatial and spatiotemporal effects, the same GMRF structure is used as described in 2.3.3.

While both STM and STM-DT fall into the category of generalized linear mixed effect models, they were characterized by their structured spatial and spatiotemporal random effects and were denoted as STMs to distinguish them from the GLMMs presented in this study.

2.4. Model comparison

10-fold cross-validation is used for model comparison and to evaluate whether there is overfitting, which is likely to occur in models with complex structures (containing a substantial number of parameters that are estimated with a limited amount of data). Cross-validation also assesses the reliability of the four models to predict "new" observations (additional observations that are not included in the model fitting phase) and is most suitable for model validation for this purpose (Ding et al. 2018). Information criteria such as AIC/BIC (Akaike Information Criterion and Bayesian Information Criterion, respectively) are commonly used for model comparison but for models with complicated random-effect structures such as spatial models, the degrees of freedom can be difficult to determine and the performance of information criteria may not be reliable (Anderson and Burnham 2004; Bolker et al. 2009; Hastie et al. 2009; Lee and Ghosh 2009). We also calculated AIC and BIC for the four selected models; AIC and BIC were calculated from fitting the models to the complete dataset and based on their respective log-likelihoods and numbers of fixed parameters. However, these were provided only as supplementary to the cross-validation model comparison technique in the Appendix (Table C1).

Since the meat weight is only collected for approximately half of the tows, it must be predicted for tows where the meat weight sampling did not occur. However, not accounting for the spatial variation across the sampling domain can result in prediction bias in the meat weight and, ultimately, subsequent biomass estimates. For this reason, we stratified the cross-validation on tow locations rather than individual observations so that prediction for each scallop excludes other scallops within the same tow.

In 10-fold cross-validation, all tow locations in all years are randomly partitioned into 10 groups. For each group (test set), the model parameters are estimated using observations within the other nine groups (training set), the trained model is then used to predict on the test set, and residuals are calculated (test residuals). This training–testing process is iterated for all 10 groups so that predictions and residuals are obtained for every observation. Test residuals are compared

across models as well as the residual variance. Partitioning of the dataset is consistent across different models to ensure results are comparable.

In the stratified cross-validation, since observations are aggregated by spatial location (i.e., by tow) prior to partitioning, their prediction residuals are in effect tow-level residuals or "spatial residuals". These residuals are an indication of "leftover" spatial variation and patterns in them are indicative of spatial bias in the model predictions. The tow-level residuals for the meat weight of each observation are obtained for the four models. Average residuals are calculated to assess the scale of the residual spatial variation and to compare prediction accuracy of the four models. The residual standard deviations are also calculated to evaluate the precision of predictions and the extent of each model's ability to explain the spatial variability.

The four models were used to fit the complete dataset and predict the yearly meat weight spatial distribution of a standard commercial size scallop (100 mm shell height). The GLMM can only predict spatial variation of the weight at tow locations where there is sampling of both meat weight and shell height; predictions at unsampled locations are based solely on the fixed effect terms within the model. The GLMM-DT predicts at locations that are sampled for depth and temperature; given supplementary data on ocean bathymetry and bottom temperature, it can predict unsampled locations but the spatial variation relies on the two covariates. The STM has the ability to predict for any spatial location within the region as this model estimates a latent field over the study area and interpolates to unsampled locations via spatial autocorrelation. The STM-DT has the ability to potentially predict any spatial locations as well, but also requires additional depth and temperature data. For the convenience of comparison of the models in this study, we only generate predictions for the meat weight at tow locations where detailed sampling of meat weight and shell height occurs.

3. Results

Spatial patterns in tow-level residuals are observed for each model (Fig. 2). GLMM has the strongest residual patterns with positive residuals throughout St. Mary's Bay (SMB) where this model consistently underestimates meat weight; in contrast, it overestimates meat weight outside of SMB further from shore. For nearshore outside of SMB, GLMM tends to underestimate meat weight in 2012–2015, captures the observations relatively well in 2016–2017, and slightly overestimates in 2018, implying a potential transition over time in the meat weight–shell height relationship in this nearshore area that differs from other areas. Compared to GLMM, GLMM-DT diminishes the residual patterns within SMB and the offshore area but the inclusion of depth and temperatures leads to a consistent overestimation for nearshore locations in 2016–2018.

STM tends to underestimate meat weight in SMB and overestimate in the offshore areas, while capturing the nearshore observations relatively well in most years. Notably, STM performs the best among all models across the study area

for year 2018, where the environmental variables adversely impact the predictions of both GLMM-DT and STM-DT for nearshore locations. The spatial patterns in tow-level residuals are similar between STM-DT and GLMM-DT. However, STM-DT tends to have the smallest residuals of the four models. For example, while STM-DT also underestimates weight in SMB in 2014–2017 the sizes of the residuals are the smallest of any of the models.

Across all years, GLMM has the largest average residuals of the four models, followed by STM, GLMM-DT, and then STM-DT (Table 1). Of these four models, STM-DT has the smallest average residuals and residual standard deviations in most years. However, within-year comparisons demonstrate that the relative performance of the models varies between years. Although GLMM-DT has smaller overall residuals than STM for the full study period, GLMM-DT residuals are higher than STM in 2013, 2015, and 2018. Further, in 2018, STM outperforms the three other models.

The four models are fitted to all available data (see the Appendix for estimated parameters) and the fitted models are used to predict the yearly meat weight of a standard commercial size scallop (100 mm shell height) for each sampled tow (Fig. 3). All models capture the relative spatial differences in productivity across SPA 3 with higher meat weight for the same-size scallop observed in SMB; lower meat weights are observed outside SMB, and weight declines with distance from shore. This variability in meat weight is substantial, with meat weights ranging from approximately 5 to 20 g for 100 mm shell height animals over distances of approximately 40–60 km. The average predicted meat weight for 100 mm-shell height animals was calculated for each year (Fig. 4). The STMs predicted slightly smaller meat weights than GLMM and GLMM-DT when averaged across the spatial domain in most years, except in 2014, when predicted meat weights were similar among all four models. In addition, the STMs tended to predict more homogeneity across space in meat weights than the GLMMs especially in 2017 and 2018 with smaller standard deviations (Fig. 4), possibly related to increasingly homogenized ocean conditions in the region in these years. On average across all years, the difference in meat weight estimates is largest between GLMM and STM-DT, with STM-DT estimates being approximately 4% smaller than the GLMM estimates (median predicted meat weights for GLMM and STM-DT were 11.4 g and 11.0 g, respectively).

4. Discussion

Increasingly, fishery assessment and management advice are focused on including environmental drivers within modeling frameworks to understand the influence of environmental change on fish population dynamics. A great deal of effort is often spent trying to relate measures of productivity to various environmental variables (Walters and Collie 1988; Myers 1998; Brander 2010; Baudron et al. 2014; Swain and Benoît 2015). However, it is often the case that these relationships are assumed correlative and are based on environmental variables that are easily measured in the ecosystem. Such variables are typically proxies for underlying pro-

cesses that may not be well understood. Further, these relationships tend to break down over time and often may not explain a great deal of the variability in the productivity parameter of interest (Myers 1998). Here, we show that STMs can provide accurate predictions even without the inclusion of environmental variables, and potentially further improve predictions when used in conjunction with informative environmental variables.

Mixed effect models include both fixed and random effects and are often employed when data can be reasonably clustered or grouped (Zuur et al. 2009; Stroup 2012). Fisheries data are often structured in such a way, where samples from multiple individuals are taken at specific locations (e.g., tows) throughout a sampling domain and the finest spatial information on environmental variables is at the scale of the sampling unit. Mixed effect models have been demonstrated to provide more accurate out-of-sample predictions for LWRs compared to fixed effects-only models (Lai and Helser 2004). Nevertheless, a wealth of information in the original data is often not utilized to its full extent. Although undoubtedly related to environmental variables, spatial and spatiotemporal random effects can capture variability beyond what can be attributed to (often coarse scale) environmental variables appearing additively in the GLMM. The GLMM-DT and STM both improve the prediction of weight compared to the GLMM, with the improvement in GLMM-DT due to the inclusion of environmental information, while STM relies on the spatial structure inherent in the data itself. Combining the advantages of both influential covariates and spatial autocorrelation, the STM-DT provides the best predictions in most years. This suggests that incorporating such random effects is beneficial both when environmental data are available and when they are not.

Although both the incorporation of environmental variables and spatial modeling of autocorrelation reduced bias and increased precision in the estimation of weight, the spatial and spatiotemporal effects can offer increased flexibility to capture underlying patterns in productivity. For example, depth and the spatial random effects account for spatially variable but temporally unchanging patterns observed in the environment. The depth effect in GLMM-DT is the same irrespective of the actual location, whereas the spatial random effects in the STMs can vary across the region and may contain more information than depth alone. The spatiotemporal random effects in the STMs are dynamic over time and behave similarly to the temperature effect but are again more flexible, as their contribution can change over both space and time. The inclusion of spatiotemporal effects explains a portion of variance in the weight related to historical changes in the spatial characteristics of the LWRs that improve within-year predictions, but may not apply in terms of forecasting into future years because the exact nature of this field is difficult to predict.

This modeling framework effectively decomposes the LWR into a known predictable component that is consistent from year to year, and a second dynamic component, both of which could inform research into the mechanisms underlying the observed patterns in productivity. In sea scallops, larger meats are found at shallow water depths where temperature

Table 1. A summary of cross-validated residuals for the four models: mean and standard deviation for each year and all years (see the Appendix for a visualization of these cross-validated residuals).

Year	GLMM	GLMM-DT	STM	STM-DT
2012	0.7418 (6.8661)	0.0895 (4.7415)	0.5484 (6.167)	− 0.1197 (4.4737)
2013	2.2728 (6.5703)	0.5308 (4.7449)	0.4206 (4.748)	− 0.1756 (4.0785)
2014	2.3850 (7.1551)	1.1008 (5.7618)	1.5247 (7.0436)	0.4069 (5.5615)
2015	1.3338 (7.1474)	0.6544 (5.2991)	0.5740 (6.4192)	0.1870 (5.1388)
2016	0.8354 (6.1352)	0.2605 (4.8229)	0.5858 (6.0367)	0.3267 (4.6395)
2017	− 0.4587 (6.4972)	− 0.2957 (5.1969)	0.6304 (6.5844)	0.3137 (5.2215)
2018	− 1.1535 (4.5767)	− 0.9354 (4.7299)	0.0352 (4.4021)	− 0.5116 (4.765)
2012–2018	0.8828 (6.6001)	0.2175 (5.1013)	0.6266 (6.0063)	0.0607 (4.8776)

Fig. 3. Predicted meat weight in grams for a scallop of standard commercial shell height of 100 mm at sampled tow locations in each year for the four models. Base map was made with Natural Earth, map projection WGS84 Web Mercator. [Colour online]
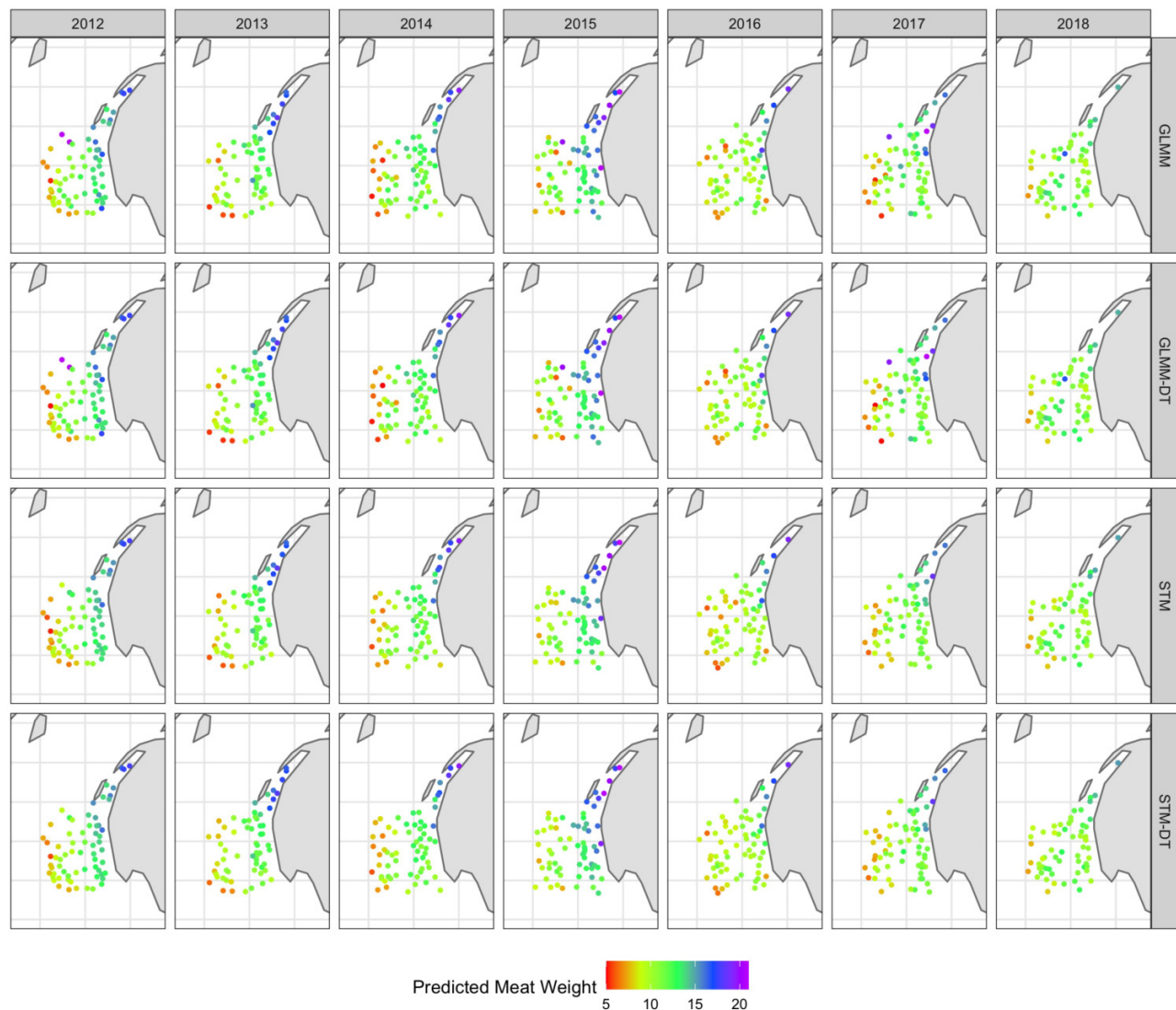
and food availability are often more favorable (MacDonald and Thompson 1985, 1986; MacDonald et al. 1987; Schick et al. 1992) and food ration, consisting of suspended detrital material and phytoplankton, is a major factor in the regulation of growth and production (Shumway 1987; Cranford and Grant 1990; MacDonald et al. 2016). Although depth and temperature were both influential variables, unexplained variability in the model residuals may be related to currently

Fig. 4. Average predicted meat weight in grams (with one standard deviation in vertical bars) for a scallop of standard commercial shell height of 100 mm for each year and across the spatial domain using sampled animals for the four models. [Colour online]

unobserved conditions,[1] such as variability in substrate (e.g., grain size) or habitat type (Kostylev et al. 2003; Brown et al. 2012). However, although the spatial distribution of substrate may be relatively static, its influence on scallop growth is likely modulated by temporally variable oceanographic conditions (Kirby-Smith 1972; Wildish et al. 1987; Cahalan et al. 1989; Pilditch et al. 1997). In this species, the environmental conditions during the winter of the current year and the previous year influence the size of the meat weight during the summer (Liu et al. 2021). However, identifying lagged environmental relationships is challenging as the dimensionality increases quickly as additional lags are explored with multiple covariates, and the risk of identifying transient and spurious correlations increases following the increase of this dimensionality. The addition of spatiotemporal random effects can explicitly identify how a physical quantity (e.g., meat weight) varies both through time and space; these patterns can then be used to identify candidate environmental variables that have the potential to explain the observed patterns. Understanding these patterns will help inform testable hypotheses regarding the mechanisms driving the underlying patterns and can be used to identify candidate environmental variables at appropriate temporal and spatial scales, without having to undertake dubious high-dimensional correlative data-mining analyses.

The inclusion of the spatial and spatiotemporal effects within the GLMM enables a more intrinsic accounting of both spatial and temporal variability; the data inform how the model varies both in time and space without the need of artificial categorizations such as pre-defined spatial areas coded as factor levels (e.g., survey strata), as is often done within a traditional GLMM framework (Thorson and Ward 2013). For sedentary species, such as scallop, the growth of individuals in close proximity to each other is expected to be strongly correlated (Thouzeau et al. 1991; Lai and Helser 2004; Smith and Rago 2004; Hart and Chute 2009; Sarro and Stokesbury 2009; Hennen and Hart 2012; Hodgdon et al. 2020) since their physiological condition will reflect the integrated physiological response to the history of environmental conditions at their location. Here, we demonstrate that substantial spatial variability occurs over relatively small spatial scales (10s km) where meat weights are often four times greater for the same-size scallop in SMB than in offshore areas and that the spatial and temporal variability in the LWR is a natural feature of the STM results. Fine-tuning of traditional GLMMs to improve residual spatial patterns often includes further discretizing of data (e.g., area effect via spatial blocking and using categorical area variables) but this may not be effective when residual patterns are not consistently defined over time (see Appendix D for a supplementary analysis of a GLMM with fixed area effect). Compared to an area effect, the benefit of the STMs is that no a priori knowledge of the spatial patterns is necessary for them to be accurately captured.

As demonstrated in this case study, the patterns that spatial and spatiotemporal random effects capture reflect underlying ecosystem processes. Although the direct mechanistic drivers of these patterns are often unknown, spatial and spatiotemporal random effects can provide a comprehensive means of improving LWRs, even when influential environ-

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[1] Further significance of the environmental variables and of the spatial and spatiotemporal effects are demonstrated by the comparison of GLMMs, STMs, and the additional model formulations in the Appendix.

mental variables are unavailable. The bank-wide meat weight predictions from STM-DT tend to have less uncertainty than the estimates from the GLMMs (cross-validated residual variations), likely due to its ability to better represent the underlying spatial patterns in the data. The lower uncertainty from STM-DT modeled meat weights can reduce uncertainty in biomass estimates from these models, thus improving the science advice provided to fishery managers. More broadly, given the increased interest in incorporating spatiotemporal heterogeneity into next-generation stock assessment (Punt 2019; Cadrin et al. 2020), the STMs developed herein can be utilized to help advance the development of next-generation stock assessment models. As identified in Cadrin et al. (2020), accurate spatial modeling requires the correct specification of major features of population dynamics, including growth; further, these aspects should be resolved and inform spatially structured stock assessment (Cadrin et al. 2020). Integrated and spatiotemporal modeling frameworks for this stock have recently been developed (McDonald et al. 2021, 2022). These STMs can be directly integrated into these stock assessment models with the associated uncertainties fully propagated into the biomass estimates and incorporated into the resulting science advice.

Although the STMs offered improvements in capturing the LWR across the stock, all models struggled to consistently capture the LWR in SMB. In this study, the spatial dependence was modeled based on an assumption of isotropic Matérn GMRF, the theory and practice around which have been well developed (Lindgren et al. 2011; Blangiardo et al. 2013; Auger-Méthé et al. 2017). Further study should explore and identify other spatial, temporal, or spatiotemporal assumptions. This could include the structure of autodependence both in space and time, implementing anisotropy to account for asymmetric de-correlation (Allard et al. 2016), testing alternative assumptions of the interaction between space and time (Thorson 2019), or moving beyond GMRFs to better accommodate extreme observations with heavy-tailed distributions (Anderson and Ward 2019). These refinements may better capture observed patterns and lead to improved model prediction and reduced uncertainty. In addition, the response distribution in these LWR models used a Gaussian distribution for improved predictive performance, even though distributions such as gamma and lognormal are more immediate candidates for response variables that are constrained to be positive. The advantage from a Gaussian distribution may be related to its symmetric shape that allows for balanced bidirectional prediction errors.

Finally, this case study demonstrates a development process for upgrading existing statistical models to incorporate recent statistical methods that could be incorporated into stock assessment frameworks. While statistical advancements are relatively easily incorporated into ecological modeling; fishery stock assessment modeling requires an additional focus on providing accurate and reliable predictions. As such, implementation of novel techniques into existing stock assessment frameworks often requires a more rigorous review of the implications of the new technique and proper model validation is required to justify additional complexities. Complicated models can overfit data; as such, model comparison or selection techniques in the model development process should include their own consideration of suitability in order to avoid false selection of models that in fact, generate worse predictions (see Appendix C for alternative model comparison techniques based on information criteria). With a comprehensive assessment and comparison of the four LWR models where improvements from incorporation of environmental variables and spatial effects were thoroughly validated, this study can also be used as a guidance for model development.

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Article information

History dates

Copyright

Data availability

Data generated or analyzed during this study are available in the GitHub repository, https://github.com/Mar-scal/SPA3_Spatial_LWRs.

Author information

Author contributions

Yihao Yin: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing – original draft, writing – review & editing; Jessica Sameoto: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing – original draft, writing – review & editing; David Keith: conceptualization, data curation, funding acquisition, investigation, project administration, resources, supervision, validation, writing – original draft, writing – review & editing; Joanna Mills Flemming: conceptualization, data curation, funding

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Competing interests

The authors declare there are no competing interests.

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Appendix A: Visualization of cross-validated residuals

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Fig. A1. A visualization of the summary of cross-validated residuals for the four models and all years (Table 1). The residual means were summarized for each survey year with point-wise ranges for residual standard deviations and each color corresponds to a model.
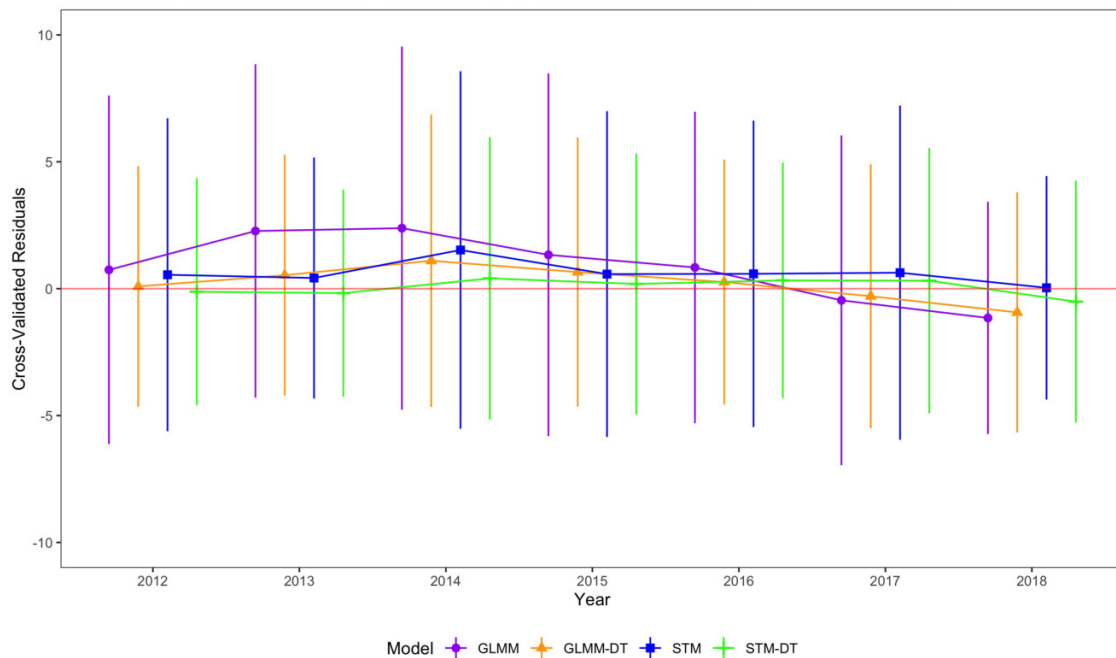
Appendix B: Parameter estimates for the models

Table B1. Estimated year effect for the four models (standard error in parenthesis).

Year	GLMM	GLMM-DT	STM	STM-DT
2012	2.67 (0.03)	2.52 (0.04)	2.70 (0.06)	2.48 (0.05)
2013	2.61 (0.03)	2.65 (0.03)	2.70 (0.06)	2.64 (0.04)
2014	2.60 (0.03)	2.76 (0.03)	2.63 (0.06)	2.80 (0.04)
2015	2.73 (0.03)	2.89 (0.03)	2.78 (0.06)	2.91 (0.04)
2016	2.54 (0.03)	2.50 (0.03)	2.54 (0.06)	2.47 (0.04)
2017	2.61 (0.03)	2.67 (0.03)	2.48 (0.06)	2.63 (0.04)
2018	2.62 (0.03)	2.58 (0.02)	2.54 (0.06)	2.56 (0.04)

Note: The year effect is included as a fixed effect on the intercept.

Table B2. Estimated linear coefficients with corresponding standard errors and p values for the environmental variables in GLMM-DT and STM-DT (eqs. 3 and 7).

Variable	GLMM-DT			STM-DT		
	Estimate	Std. error	p value	Estimate	Std. error	p value
Depth	−0.074	0.0258	0.004	−0.053	0.0236	0.024
Temperature	0.164	0.0336	<0.001	0.190	0.0307	<0.001

Table B3. A comparison of parameter estimates and standard errors (in parenthesis) for the random effects in STM and STM-DT (eqs. 4–7).

Description	Parameter	STM	STM-DT
Spatial effect (intercept)	Scale	−4.45 (6.12)	−3.09 (1.04)
Spatial effect (intercept)	Precision	11.70 (8.89)	5.23 (1.52)
Spatial effect (slope)	Scale	0.63 (0.30)	0.92 (0.24)
Spatial effect (slope)	Precision	−0.49 (0.42)	−0.32 (0.38)
Spatiotemporal effect (intercept)	Scale	−0.09 (0.27)	−0.56 (0.12)
Spatiotemporal effect (intercept)	Precision	0.68 (0.35)	0.96 (0.13)
Spatiotemporal effect (slope)	Scale	−1.51 (0.14)	−1.58 (0.24)
Spatiotemporal effect (slope)	Precision	1.64 (0.16)	2.66 (0.29)

Note: The spatial and spatiotemporal effects are included on both the intercept and slope, each consisting of a scale parameter and a precision parameter (inverse variance). The scale describes the range of spatial autocorrelation and the precision relates to the space–time covariance matrix. Both parameters are log-transformed for the optimization process and hence, estimates reported are on the log scale.

Table B4. A comparison of variances for the random effects in GLMM and GLMM-DT (eqs. 2 and 3).

Description	Parameter	GLMM	GLMM-DT
Tow effect (intercept)	ε_0^2	0.85	0.39
Tow effect (slope)	ε_1^2	0.32	0.32

Table B5. A comparison of variances for the response distributions in the four models (eqs. 2–7).

Description	Parameter	GLMM	GLMM-DT	STM	STM-DT
Variance	ϕ^2	11.98	11.97	12.74	12.83

Appendix C: Alternative model comparison techniques

Table C1. AIC and BIC for the models GLMM, GLMM-DT, STM, and STM-DT.

	GLMM	GLMM-DT	STM	STM-DT
logLik	−39 969.4	−39 820.9	−38 805.18	−38 629.44
nf	12	14	23	25
AIC	79 962.9	79 669.9	77 656.36	77 308.88
BIC	80 053.4	79 775.5	77 829.95	77 497.57

Note: Calculation of AIC/BIC used log-likelihood (logLik) and number of fixed parameters (nf).

The four models in this study, GLMM, GLMM-DT, STM, and STM-DT, were fitted to the complete dataset and their respective AIC and BIC were calculated to provide an alternative model comparison to the cross-validation in Section 3. The calculation of AIC/BIC used log-likelihood and the number of fixed parameters. Cross-validation was most suitable for this study and was used as the main model comparison technique; AIC and BIC are commonly used for comparing model fit to "existing" data and typically do not focus on predicting "new" data.

These model comparison techniques mostly provide similar results and indicated an advantage in STM-DT. However, both AIC and BIC preferred STM over GLMM-DT, and this may be a false advantage related to overfitting, since cross-validation showed better out-of-sample predictions by GLMM-DT. As a result, model comparison techniques should be used cautiously like any statistical methods used in ecological modeling.

Appendix D: GLMM with area effect

Discretized area effects are commonly used to improve GLMMs when there are apparent spatial patterns in the residuals. The STMs in this study were able to explain such patterns with spatially autocorrelated structures, but are arguably a big leap in model complexity; a more natural progression from a traditional GLMM would be to include more explanatory variables for residual improvement. This section presents another GLMM that includes a fixed, categorical area effect to GLMM-DT and is termed as GLMM-DTA hereafter. The variable for this area effect was informed by the cross-validated residual patterns from GLMM and GLMM-DT in Fig. 2; the study area was partitioned into three subareas, Saint Mary's Bay (SMB), Inside, and Outside (see Fig. D1 for sampled tow locations for each subarea).

The addition of an area predictor improved model fit in terms of AIC and BIC: AIC for GLMM-DTA was 78 729.7 and BIC was 78 850.4; AIC and BIC for GLMM-DT were 79 669.9 and

Fig. D1. Partitioning of sampled survey tow locations for an area effect in the generalized linear mixed model. The study area was partitioned into three subareas based on residual patterns from GLMM-DT. Base map was made with Natural Earth, map projection WGS84 Web Mercator.
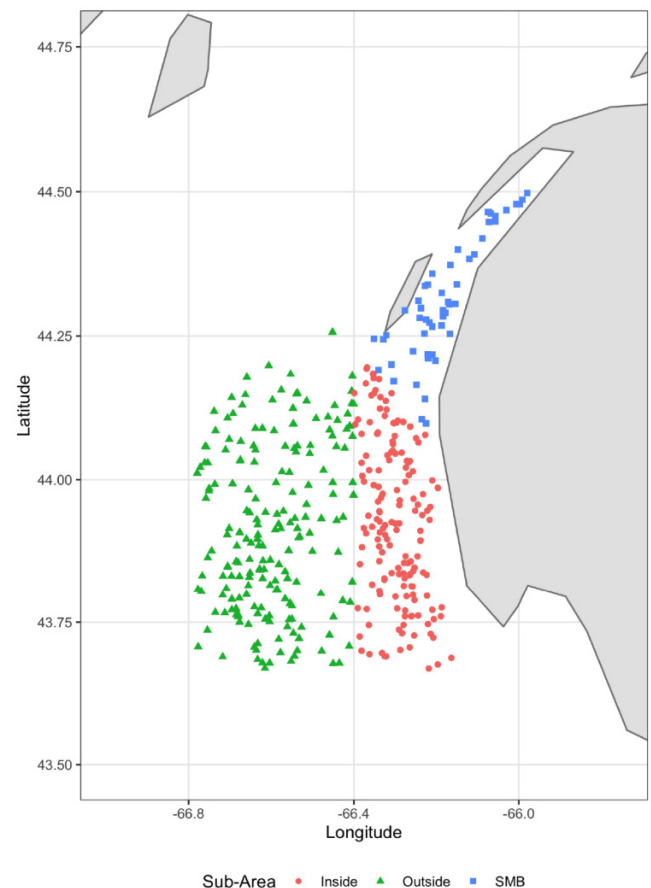

79 775.5, respectively (Table C1). However, this is likely overfitting since cross-validated residuals from GLMM-DTA were higher than both GLMM-DT and GLMM (Table D1; Fig. D2). The random tow effect in both GLMMs was intended for potential spatial variation and was more flexible than the three-level fixed area effect; besides, even though there were spatial patterns in the residuals, such patterns were not consistent over time and hence a fixed area effect was not effective for explanation of variance. Notwithstanding, GLMM-DTA did have small improvements from GLMM-DT in years 2016–2018, indicating a more consistent spatial pattern in the later years. In conclusion, the fixed area effect in GLMM-DTA was not as effective as the spatial effect in STM-DT. This is as expected, since the spatially explicit structure was more adaptive and flexible in capturing fine scale spatial variations than a simple area division.

Table D1. Cross-validated residual means and standard deviations (in parenthesis) for each year and all years for the three supplementary models, GLMM-DTA, SPM, and SPM-DT.

Year	GLMM-DTA	SPM	SPM-DT
2012	0.8624 (5.3436)	−0.8466 (6.6891)	−0.0903 (4.7089)
2013	2.3423 (5.3165)	0.4876 (5.7284)	0.0784 (4.1801)
2014	1.7503 (5.8808)	1.4689 (6.7888)	−0.0002 (5.6183)
2015	1.3014 (5.6935)	1.2796 (7.1216)	0.5395 (5.5028)
2016	1.0664 (4.9726)	0.4918 (6.316)	0.5685 (4.9803)
2017	−0.1641 (5.2418)	2.7364 (6.8121)	0.9501 (5.5547)
2018	−0.7664 (4.2438)	0.6100 (4.7137)	0.1325 (4.7045)
2012–2018	0.9336 (5.3669)	0.8729 (6.441)	0.2991 (5.0751)

Fig. D2. Spatial residuals (grams) for GLMM-DTA in each year. Residuals were spatially aggregated and averaged over tows to highlight remaining spatial patterns. Base map was made with Natural Earth, map projection WGS84 Web Mercator.
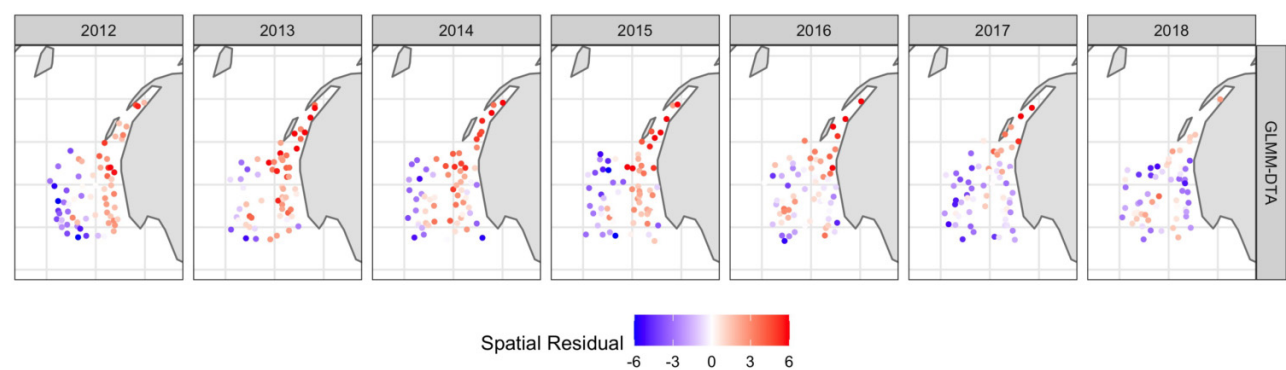
Appendix E: Spatial models

Two supplementary spatial models with only the static spatial effects were tested, i.e., STM without the spatiotemporal component (denoted as SPM) and STM-DT without the spatiotemporal component (denoted as SPM-DT). Cross-validated residuals for SPM and SPM-DT are presented in Table D1 for comparison with the STMs in this study (Table 1) and to illustrate the necessity of the spatiotemporal components in the STMs. Results indicated that such temporally varying spatial effects were important for improving model predictions: STM performed better than SPM and STM-DT performed better than SPM-DT.