






Original Article

Incorporating spatial heterogeneity and environmental impacts into stock-recruitment relationships for Gulf of Maine lobster

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Functional stock-recruitment relationships (SRRs) are often difficult to quantify and can differ over space. Additionally, climate change adds to the complexity of recruitment dynamics. This paper's aim was to incorporate spatial heterogeneity and environmental effects on productivity in SRRs with American lobster in the Gulf of Maine (GOM) as a case study. GOM lobster recruitment has substantially increased since the mid-2000s, due to improved survival rates of pre-recruits and increased spawning stock biomass (SSB). GOM bottom water temperatures have increased at a rate of 0.2°C per decade, which caused lobster settlement area to expand and improved survival rates. We first estimated local SSB using bottom trawl survey data and a geostatistical model. Using estimated SSB, recruitment data from a ventless trap survey, and an interpolated bottom water temperature field, we developed modified Ricker stock-recruitment models accounting for spatial heterogeneity and temperature impacts with varying coefficient generalized additive models. Results showed that temperature significantly impacted recruitment. Changes in temperature mediated productivity differed between the eastern and western GOM. Our study demonstrated that the incorporation of spatial heterogeneity and environmental effects impacts our understanding of SRRs. These methods can be applied to other species to understand recruitment dynamics influenced by climate change.

Keywords: non-stationary stock-recruitment relationship, recruitment, fisheries productivity, *Homarus americanus*, varying coefficient generalized additive model.

Introduction

Stock-recruitment relationships (SRRs) are critical for understanding fisheries population dynamics (Cobb and Caddy, 1989). Recruitment dynamics are greatly influenced by many biotic and abiotic factors that affect survival from the eggs to the juveniles in the population (Ulltang, 1996). Because these factors are characterized by large inter-annual variability usually driven by early life history processes, SRRs are often quite variable and are difficult to quantify (Subbey *et al.*, 2014). However, quantifying SRRs, or

estimating parameters for SRRs, is important for determining biological reference points (BRPs), projecting population dynamics under alternative fishery management scenarios, and identifying sustainable harvest rates in fisheries management (Van Poorten *et al.*, 2018). Large uncertainty in quantifying SRRs is often considered a major obstacle for developing and identifying effective fisheries management. Large-scale environmental drivers and physical forcing often impact recruitment patterns in marine species (Koslow, 1984; Myers *et al.*, 1997). Changes in environmental conditions, including temperature, can affect the productivity of the

stock-recruitment (SR) process (Tang, 1985; Jacobson and MacCall, 1995; Rätz and Lloret, 2003). This makes biological sense, as temperature influences energy used for metabolism, respiration (Whiteley *et al.*, 2001), and diet composition (D'Abramo, 1979). Temperature also affects recruitment indirectly by affecting prey and predators of the focus species (Régner *et al.*, 2019).

Previous studies have incorporated environmental effects into SRRs to reduce the unexplained SR variation (Subbey *et al.*, 2014). Usually, Ricker and Beverton-Holt SRRs are modified to incorporate environmental variables (Hilborn and Walters, 1992; Chen and Irvine, 2001). Including temperature in SR models (i.e. blue crab in the Chesapeake Bay, Tang, 1985; Norwegian herring, Fiksen and Slotte, 2002; Japanese sardine and chub mackerel, Mikkelsen and Pedersen, 2004; and brown tiger prawn in Moreton Bay in Australia, Kienzle and Sterling, 2017) has improved recruitment prediction power. These SR models provided a basis for fisheries management under different SR productivities caused by changing environmental conditions and regime shifts. However, few studies have considered the nonstationary influence of the environment on SRRs across space. Varying coefficient models present a tool that can be used to evaluate this nonstationarity. In varying coefficient models, coefficients can vary systematically as smooth functions of other variables (Hastie and Tibshirani, 1993; Kourtellos and Stengos, 2010). Essentially, a smooth function and variable interaction results in a varying coefficient model, which is a subset of generalized additive models (Sterrantino, 2013). In these models, the influence of nearby locations can be incorporated. Although these models have existed for quite some time, they have rarely been used to evaluate SRRs.

American lobster, *Homarus americanus* (H. Milne Edwards, 1837), in the Gulf of Maine (GOM) poses a great case study for evaluating the impact of spatial heterogeneity and environmental effects on productivity in SRRs. Lobster SRRs in the GOM have been a challenge to estimate. In the GOM, lobster recruitment, as well as landings and biomass, increased dramatically in the past few decades, as estimated by the most recent lobster stock assessment model (ASMFC, 2020). A SRR has not been quantified in the most recent benchmark stock assessment (ASMFC, 2020) because of uncertainty in the lag between spawning stock biomass (SSB) and recruitment (NEFSC, pers. comm.) and the small spatial scale at which recruitment processes occur (Chang *et al.*, 2015; ASMFC, 2020).

American lobster recruitment is also influenced by environmental factors, including temperature (Ennis, 1986). Temperature affects lobster settlement, which occurs in the first year of a lobster's life during late summer or early fall, because warming waters increase settlement success in deeper waters (Annis, 2005). Bottom water temperatures in the GOM are increasing at a rate of 0.2°C per decade (Kavanaugh *et al.*, 2017). With increasing bottom water temperature, lobster settlement area expands (Annis, 2005; Goode *et al.*, 2019). Other lobster recruitment processes are also affected by temperature. As sea surface temperatures rise, larval duration decreases and vulnerability to predators decreases as a result (Incze and Naimie, 2000). Increasing water temperatures also decrease the brooding duration of eggs (Templeman, 1940; Goldstein and Watson, 2015), which results in an earlier hatch and thus a longer summer for first-year growth. Warming waters also increase molt frequency (McMahan *et al.*, 2016). These findings suggest that temperature may affect productivity or density-independent processes in a SRR.

Additionally, GOM lobster SRRs may vary over space (Chang *et al.*, 2015). Different oceanographic conditions between the western

GOM and eastern GOM (WGOM and EGOM) may result in different SRRs that occur at different spatial scales. The Western Maine Coastal Current (WMCC) is characterized by strong stratification and slower current speed than the Eastern Maine Coastal Current (EMCC). The EMCC is a strong coastal current that creates a well-mixed water column. During the summer, the bottom water in the west can be colder than the bottom water in the east, while the west has warmer sea surface temperatures than eastern regions (Pettigrew *et al.*, 2005). Using process-based models and connectivity matrices, Incze *et al.* (2006, 2010) and Xue *et al.* (2008) found that American lobster larvae follow the GOM Coastal Current. Also, recruitment in the GOM is often quite localized, as a large proportion of postlarvae in a given management zone originate from within the zone itself. Self-recruitment ranged from a few % to over 90%. Chang *et al.* (2015) tested if the SRR for American lobster was evident only at specific spatial scales using young of the year and SSB lobster data. Chang *et al.* (2015) fit Ricker and Beverton-Holt models at eleven different spatial scales and demonstrated that the model fits are convexly related to the size of the spatial scale. The best type and spatial scale for SR models for GOM lobster was a Ricker SRR at 2 km² in the WGOM and 8 km² in the EGOM (Chang *et al.*, 2015). High levels of self-recruitment, high mortality rates of larvae, and constrained scales of larval transport highlight the importance of small-scale spatial processes in recruitment dynamics (Pineda *et al.*, 2007; Pineda *et al.*, 2009).

The GOM represents an excellent test site for studying spatially varying SRRs because of the differences in oceanography between the WGOM and EGOM. The GOM is also an ideal system to examine the effect of temperature on a SRR because of the wide range of bottom water temperatures experienced in the region. A previous study also found that temperature had varying effects on juvenile GOM lobster over space (Li *et al.*, 2018).

The nature of the demonstrated biology of lobster and the relatively well-developed understanding of the ecosystem comprising the GOM lobster stock's area makes this species/stock an ideal candidate to evaluate the impact of including spatial heterogeneity and environmental effects on productivity in SRRs. Our goal was to incorporate spatial heterogeneity and environmental impacts into a SRR for GOM lobster to further understand GOM lobster recruitment dynamics. The principles and methodologies underlying our analysis suggest ways to identify the impact of environmental variables on spatially varying SRRs.

Materials and Methods

Most recruitment occurs in inshore waters, and therefore this study focused on inshore lobster habitat off the Maine coast. Many processes can impact SRRs, but our study focused on benthic post-settlement processes. Though other definitions have been applied, we defined recruits as lobsters smaller than 50 mm CL, because lobsters under 50 mm CL are not migrating seasonally with reproductive lobsters and stay in or near their shelters, and thus can be assumed to be near the location where they initially settled (Lawton and Lavalli, 1995).

Lobster recruitment data were obtained from the State of Maine's Ventless Trap Survey (VTS; Maine DMR, 2019a; Figures 1, S1, and S2) because this survey covers the sheltered habitat in which young lobsters are found (Maine DMR, pers. comm.; Fogarty and Idoine, 1986). This random stratified survey has been conducted since 2006 over the months of June to August each year. This collaborative,

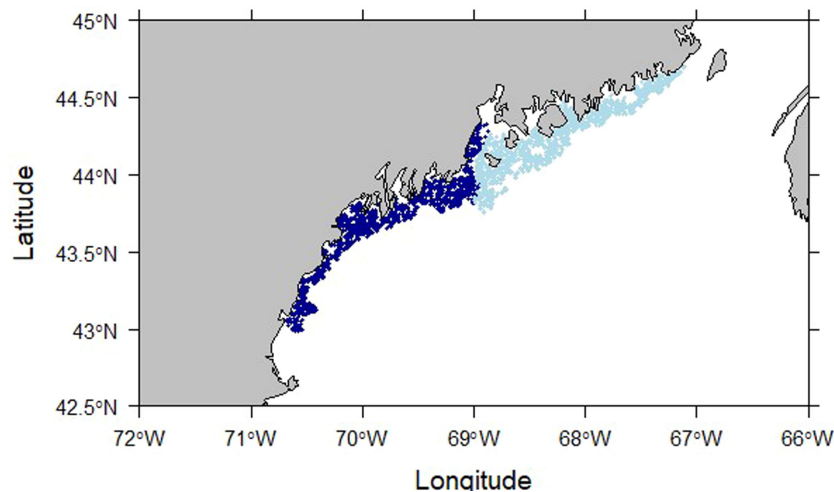


Figure 1. Recruitment data collecting sites ($n = 1508$) from the Maine Department of Marine Resources Ventless Trap Survey from 2006 to 2018 in the western Gulf of Maine (dark blue) and eastern Gulf of Maine (light blue).

fishery-independent survey is conducted by the Maine Department of Marine Resources (DMR); coast of Maine lobster fishers are contracted to conduct the survey. Three ventless traps were deployed at each site. The sites were stratified by depth (1–20, 21–40, 41–60 m). Biological parameters collected with a trap haul included: carapace length (CL) in mm, sex, egg status, cull status (whether the lobster has both claws), and disease status. Along with biological parameters, effort parameters were also collected including depth and soak time (number of nights that the trap was in the water). The standard soak time is three nights; however, soak time may be shorter or longer due to extreme weather or boat break downs.

For a small number of trap hauls, not all the lobsters were measured, but in all cases, number caught was reported. Where length data were missing, we assumed that the size frequency of unmeasured lobsters in the haul was the same as that of the measured lobsters in the haul; from coast-wide surveys, it has been observed that length frequencies are consistent within an area (Maine DMR, pers. comm.). For the hauls with missing length data, recruitment was estimated by multiplying the total number caught by the proportion of recruits derived from the lobsters that were measured in the haul.

The main task was to incorporate spatial heterogeneity and environmental impacts into the SRR. However, other analyses were necessary to gather the data for the spatially varying SRR. Quantifying the desired temperature mediated SRR required co-located estimates of lagged or offset local SSB and temperature for each location and time where recruitment was observed.

Local SSB was estimated with a modeling approach using trawl survey data. The purpose of the modeling approach was to estimate SSB at the same locations as the recruitment data, as the best available SSB data were from a trawl survey conducted at different locations and times than the VTS. The trawl survey produces the best available SSB data due to the selectivity of the survey, because the trawl survey catches more large lobsters than the VTS. Lobster SSB were estimated using data directly from the Maine-New Hampshire fall inshore trawl survey (2000–2018; ME DMR, 2018). This survey is a fishery-independent scientific bottom trawl survey that employs stratified random sampling partitioned by four depth strata and five regions. This annual five-week survey is completed primarily in October from west to east. Prior to modeling, SSB data were calculated as the weight of mature female lobsters from the trawl survey, which

was determined with size and sex information from the survey. The proportion of mature female lobsters at each size was determined by the logistic equation (ASMFC, 2020):

$$P_{matcl} = \frac{e^{-17.14056+0.19664*CL}}{1 + e^{-17.14056+0.19664*CL}}$$

Coefficients were from the most recent lobster stock assessment and represent a landings-weighted 50% size at maturity at 87 mm CL (ASMFC, 2020). Increasing temperatures are expected to decrease the size at maturity (Waller *et al.*, 2019, 2021), but due to lack of available data at a small enough spatial scale, the maturity equation was fixed in this study. To estimate SSB across space and time, we quantified a geostatistical model with the SSB data using the VAST (version 3.2.2) package in R (Thorson, 2019; Figures S3, S4, and S5). Spatio-temporal models, such as the geostatistical model, outperform other models such as generalized linear models and generalized additive models in catch-per-unit-effort standardization (Grüss *et al.*, 2019).

SSB density was inferred throughout the study area with the two-stage geostatistical model. The first stage estimated the probability of encountering SSB, and the second stage estimated catches of SSB when SSB was present. The geostatistical model allowed us to estimate a continuous field of SSB at a spatial scale of two km² in the WGOM and eight km² in the EGOM based on the findings of Chang *et al.* (2015). Variables in the geostatistical model included annual intercepts, spatial random effects, and spatio-temporal random effects. The first and second linear predictors were defined similarly with variables being the same. A stochastic partial differential equation approximation to a Matérn correlation function was used as a spatial smoother for random effect values (Thorson, 2019).

SSB was averaged from three to five years earlier, since it takes lobsters three to five years to grow to 50 mm CL (McCay *et al.*, 2003; Kilada *et al.*, 2012). This way, the SSB from each of these years contributed to the prediction of local recruits. Although the lag between SSB and recruitment may be changing due to warming waters, we used a fixed lag assumption in this study due to lack of available growth data on sub-adult lobsters. Fall SSB was used as a proxy for SSB in the summer, during which egg release occurs. Spring SSB was not used, because lobsters have not migrated to inshore areas during the timing of the spring survey.

Temperature data were from an interpolation procedure described in Friedland *et al.* (2019; 2020b; Figure S6) and have been used in other analyses (Friedland *et al.*, 2020a; 2021; Mazur *et al.*, 2020; Hodgdon *et al.*, 2021). Bottom water temperatures are not monitored at a fine scale throughout the GOM. Therefore, we used interpolated spring and fall bottom water temperature data at a spatial resolution of 0.1°. This procedure combines a kriged interpolation of annual data with climatological data to estimate a complete temperature field, preserving the observational nature of the data, whereas a modeled temperature field might not. The procedure utilizes temperature data collected by Northeast Fisheries Science Center surveys and is augmented with data from the World Ocean Database, which draws in observations from other agencies and academic researchers. Most sample coverage was in the spring (February–April) and fall (September–November), associated with the trawl survey that is the source of the SSB data. Differences in the date of collection between years were corrected by standardizing to the spring and fall mean dates for collection. The standardizations were based on linear regressions of temperature versus day of the year (Friedland *et al.*, 2019).

To account for the effect of temperature on lobster settlement and variation in lobster growth rates, we averaged the three, four, and five-year offset spring and fall bottom water temperature as well as SSB. The moving average accounts for the different rates of lobster growth. As a result of offsetting and averaging SSB and temperature, it was assumed that the recruits during a given year derive from the SSB of three to five years earlier and are affected by temperature at settlement, which occurred three to five years earlier (McCay *et al.*, 2003; Kilada *et al.*, 2012). Throughout this paper, we will refer to these temperatures as offset temperature.

Temperature at the time of capture also affects the catchability of lobsters, because lobsters become more active as temperature increases (McLeese and Wilder, 1958). To account for this, we used the average of the spring and fall bottom water temperature that were simultaneous to the catch year. The ideal temperature to use would be summer temperature at the VTS locations, but these are not available, so the best approximation was an average of spring and fall temperature.

Based on the precedent of successfully quantifying Ricker SR models at small spatial scales with GOM lobster (Chang *et al.*, 2015), we chose to modify the Ricker SR model at a small spatial scale in this study. A Ricker SRR has the general format of:

$$R = \alpha S e^{-\beta S},$$

where R is recruitment, S is the SSB, α is a parameter related to productivity or rate of reproduction, and β is a parameter related to density-dependent effects (Ricker, 1954). The explanatory variables used in this study include offset average SSB, offset temperature, and bottom water temperature simultaneous to the catch year. We assumed the inclusion of these variables achieved specific effects: SSB forms the basis of the SRR; offset temperature captures the effect of temperature on productivity (α); and bottom water temperature simultaneous to the catch year accounts for the effects on the catchability of recruits. Before quantifying SR models, we conducted a Variance Inflation Factor (VIF) test (Table S1), which quantifies the degree of multicollinearity among explanatory variables.

SRRs are likely to differ throughout the GOM due to differences in predation, prey, and settlement habitat. Differences in currents and therefore larval transport also can cause SRRs to differ over space. Due to these differences, temperature might have differing effects on juvenile lobsters across space as well (Li *et al.*, 2018). To

account for this spatial nonstationarity, we modified Ricker SR models using variable coefficient GAMs to allow coefficients to vary across latitude and longitude, which accounts for spatial heterogeneity. A variable coefficient GAM evaluates a local model of the process: in this case, the SRR. In a variable coefficient GAM, the relationship between the response and designated model covariates is spatially variable and locally linear. A variable coefficient GAM allows the relationships to vary over space and accounts for the influence of nearby locations. This accounts for adjacent regional and local larval supply and differences in settlement habitat.

To linearize the Ricker model, we included the log of recruits per SSB as the response variable (Figures S7 and S14). We explored three different modified Ricker models:

$$\log(R_{it}/S_{it-4}) = \gamma_0 + \gamma_1(X_i, Y_i) + \gamma_2(A_i)(S_{it-4}) + \gamma_3(X_i, Y_i)(T_{it-4}) + \gamma_4(X_i, Y_i)(T_{it}) \quad (1)$$

$$\log(R_{it}/S_{it-4}) = \gamma_0 + \gamma_1(X_i, Y_i) + \gamma_2(A_i)(S_{it-4}) + f(T_{it-4}) + f(T_{it}) \quad (2)$$

$$\log(R_{it}/S_{it-4}) = \gamma_0 + \gamma_1(X_i, Y_i) + \gamma_2(A_i)(S_{it-4}) \quad (3)$$

where R_{it} is the number of recruits at location i and year t and S_{it-4} is the averaged SSB at location i and year $t-5$, $t-4$, and $t-3$. γ_0 is the fixed intercept, or the log of the density independent SRR parameter (α). $\gamma_1(X_i, Y_i)$ is the intercept at location i ; or the log of the spatial variation in α , which allows for continuously spatially varying SR productivity. $\gamma_2(A_i)$ is the coefficient for the effect of SSB for the area (WGOM or EGOM) at location i , or the density-dependent effect. $\gamma_3(X_i, Y_i)$ is the coefficient for the effect of offset temperature at location i , which identifies the effect of temperature on productivity. T_{it-4} is offset temperature at location i (average temperature of years $t-5$, $t-4$, and $t-3$). $\gamma_4(X_i, Y_i)$ is the coefficient for the effect of bottom water temperature simultaneous to the catch year at location i (T_{it}), which identifies the effect of temperature on catchability. The shape of the spatial splines for the intercept and the effect of offset temperature and temperature simultaneous to the catch year were determined by thin plate regression splines with automatic smoothness selection using the R package *mgcv* (Wood, 2017). $f(T_{it-4})$ is a smooth function of the offset temperature at location i estimated by a thin plate spline. $f(T_{it})$ is a smooth function of the bottom water temperature simultaneous to the catch year at location i estimated by a thin plate spline, which is representative of a catchability effect. The maximum number of knots for these smooth functions were set to five to ensure that the nonlinear trend was captured but to maintain computational efficiency and biological realism. Previous studies of species in this study area and region have also used five knots in GAMs (Sagarese *et al.*, 2014; Tanaka *et al.*, 2018). Sensitivity to the maximum number of knots was examined by removing the maximum limit of the number of knots. Each location is a VTS site. Equation 1 is the modified Ricker model with non-stationary temperature effects, equation 2 is the modified Ricker model with stationary temperature effects, and equation 3 is the modified Ricker model without temperature effects. We used the Gaussian distribution for each of the models. All GAMs were quantified for the time series 2006–2018 using the R package *mgcv* (Wood, 2017). This time series was not supposed to be representative of a temperature regime, rather it was determined based on the available data. Variables that were not significant were removed from the models.

Table 1. Generalized additive model structures and selection criteria. See methods for description of model terms. Δ AIC, difference in Akaike Information Criterion between the best model and the model being compared; MSE, mean squared error; Dev expl, % deviance explained.

Model	Δ AIC	MSE	Dev expl
$\log(R_{it}/S_{it-4}) = \gamma_0 + \gamma_1(X_i, Y_i) + \gamma_2(A_i)(S_{it-4}) + \gamma_3(X_i, Y_i)(T_{it-4}) + \gamma_4(X_i, Y_i)(T_{it})$	0	0.376	57.50
$\log(R_{it}/S_{it-4}) = \gamma_0 + \gamma_1(X_i, Y_i) + \gamma_2(A_i)(S_{it-4}) + f(T_{it-4}) + f(T_{it})$	280.12	0.385	56.20
$\log(R_{it}/S_{it-4}) = \gamma_0 + \gamma_1(X_i, Y_i) + \gamma_2(A_i)(S_{it-4})$	321.89	0.386	56.00

To find the best model, we used a variety of criteria, including Akaike Information Criterion (AIC), mean squared error (MSE), and deviance explained. Parsimonious GAMs were identified using AIC and MSE. We calculated MSE using 10-fold cross-validation. To do so, the dataset was randomly split into 10 different groups and cross-validation was performed.

Local SSB was used in this study, as many recruits originate from local SSB (Incze *et al.*, 2010). However, some recruits do originate from distant SSB (Incze *et al.*, 2010), so this analysis was also conducted with estimated annual SSB from the most recent GOM and Georges Bank (GB) lobster stock assessment (ASMFC, 2020). With distant SSB, recruits were assumed to have originated equally from all SSB within the GOM and GB. The response variable (the log of recruits divided by SSB) was recalculated with distant SSB. Model structure was the same as in the original analysis but with distant instead of local SSB (Table S3). The purpose of the additional analysis was to evaluate the sensitivity of the impacts of incorporating spatial heterogeneity and environmental effects in SRRs to differences in distant versus local SSB contribution.

From these models, spatially and temporally varying productivity (α) was estimated. Equation 1, with a spatially varying effect of temperature on α , created a linear effect of offset temperature at each location. Equation 2, with a stationary effect of temperature on α , created a nonlinear effect of offset temperature. Equation 3 only resulted in spatially varying productivity since there was no temperature effect. By taking the exponent of the estimated fixed and spatially varying intercepts in equation 3, intercepts can be transformed into the α parameter of the Ricker model:

$$\alpha(X_i, Y_i) = e^{\gamma_0 + \gamma_1(X_i, Y_i)} \quad (4)$$

The alpha is only yielded from the intercepts in equation 3. In equations 1 and 2, we calculated temperature mediated productivity over time, using intercepts, the effect of offset temperature, and offset temperature (Mantzouni *et al.*, 2010):

$$\begin{aligned} \text{For equation 1 : Temperature mediated productivity} \\ = e^{(\gamma_0 + \gamma_1(X_i, Y_i) + (\gamma_3(X_i, Y_i) * T_{it-4}))} \end{aligned} \quad (5)$$

$$\begin{aligned} \text{For equation 2 : Temperature mediated productivity} \\ = e^{(\gamma_0 + \gamma_1(X_i, Y_i) + f(T_{it-4}))} \end{aligned} \quad (6)$$

Thus, changes in temperature mediated productivity over time were based solely on offset temperature and the estimated offset temperature effects. Based on the historical temperature data (Friedland *et al.*, 2020) from 1982 to 2018, we hindcasted temperature mediated productivity from 1982, which is the start of the most recent lobster stock assessment model time series (ASMFC, 2020). Coefficients for density-dependence only vary between the WGOM and EGOM but not continuously over space. The SSB coefficient, or γ_2 , is the $-\beta$ parameter of the Ricker model, which is a linear effect. The Ricker model β is returned by taking the negative

of the SSB coefficient. The catchability effect varies over space in equation 1 but not in equation 2. All statistical analyses were conducted in the R programming environment (v 3.5.3.; R Core Team, 2021).

Results

All VIFs were under 3 (Tables S1 and S2), indicating that multicollinearity was negligible. The GOM lobster SRR with local SSB was best explained with spatially varying productivity, a spatially varying effect of offset temperature, and a spatially varying catchability effect (i.e. the lowest AIC, the lowest MSE, and highest deviance explained; Table 1; Equation 1). However, there were some slight patterns in the residuals as the model tended to underestimate the logged ratio of recruits to SSB (Figures S8–S13). Additionally, there was some “banding” in residuals (Figure S8 and Figure S9) due to the response variable being calculated with recruitment: a count variable with many values equal to one. In the lower band, much of the recruitment values were equal to one. Also, the residuals were skewed slightly to the left due to the tendency of the model to underestimate (Figure S10). The Ricker model without any effect of offset temperature or catchability had the worst fit (i.e. highest MSE, highest AIC and the lowest deviance explained; Table 1; Equation 2). The model with stationary temperature impacts did not explain the variation as well as the model with non-stationary temperature impacts. Removing the maximum limit of knots, which was only applied to the model with stationary temperature impacts, resulted in similar model diagnostics. With the maximum limit removed, the number of knots for the offset temperature effect was seven, and the number of knots for the catchability effect was eight. The best model had a fixed intercept of -4.156 ($p < 2 \cdot 10^{-16}$), a SSB coefficient of -0.0131 in the WGOM and -0.00278 in the EGOM ($p < 2 \cdot 10^{-16}$), significant spatially varying intercepts ($p < 2 \cdot 10^{-16}$), significant spatially varying effects of offset temperature ($p < 2 \cdot 10^{-16}$), and significant spatially varying effects of temperature on catchability ($p < 2 \cdot 10^{-16}$). For the analysis with distant SSB, the residual patterns and model fit were worse, indicating that the model with local SSB was more appropriate (Table S3 and Figures S15–S20). The following results focus on the model with spatially varying productivity, a spatially varying effect of offset temperature, a spatially varying effect of temperature on catchability, and local SSB.

Productivity (α) and the effect of offset temperature had different patterns over space. Productivity varied over space with the highest productivity in the WGOM (Figure 2a). Productivity varied from $8.15 \cdot 10^{-5}$ to 2.78. The effect of offset temperature was highest in the EGOM. Offset temperature had the most negative impact in the WGOM (Figure 2b), which differed from the productivity patterns. The effect of offset temperature varied from -0.524 to 0.289.

Temperature mediated productivity varied throughout space, but with highest temperature mediated productivity in the WGOM

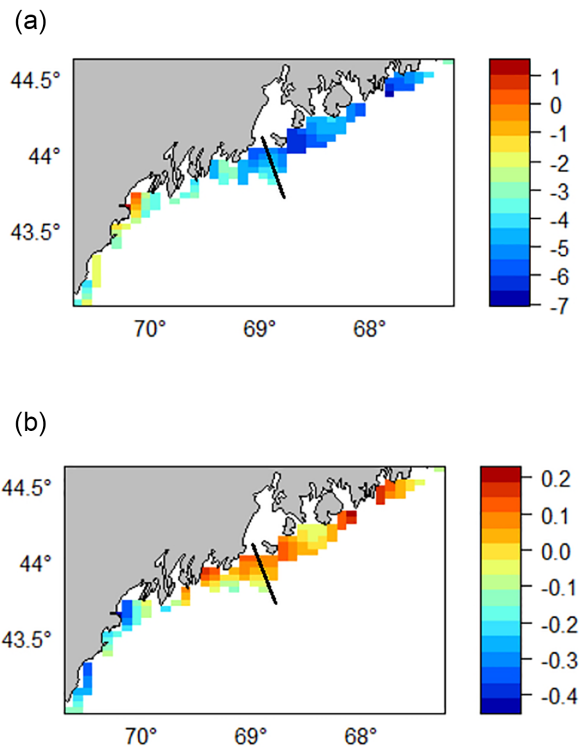


Figure 2. (a) Log productivity (α) in the stock recruitment relationships over space in the inshore Gulf of Maine. (b) Coefficients of offset temperature in the stock recruitment relationships over space in the inshore Gulf of Maine. The black lines represent the division between the western and eastern Gulf of Maine. Results are plotted at a 2 km² spatial scale for visualization purposes.

and far EGOM (Figure 3a). Changes in temperature mediated productivity varied throughout the inshore GOM (Figure 3b). The largest increases in temperature mediated productivity were far east within the EGOM. In the WGOM, most changes in temperature mediated productivity were negative.

Because of the spatial variation of the effect of temperature on productivity, change in temperature-mediated productivity differed between the WGOM and EGOM. Overall, the hind-casted temperature-mediated productivity slightly decreased in the WGOM and slightly increased in the EGOM with increasing bottom water temperatures from 1982 to 2019 (Figure 4). All the above results for the analysis with distant SSB were similar to the results with local SSB and can be found in the supplement (Figures S21–S23).

Discussion

In this study, we demonstrated that including spatial heterogeneity and environmental impacts in SRRs can influence our understanding of SRRs. The varying-coefficient GAM approach used in this study can improve Ricker models with non-stationary assumptions, the most frequent being a change in the productivity parameter over time. Ricker models with this change performed better for many species in the North Atlantic (Ottersen *et al.*, 2013). In this study, the SRR developed allowed for not only change over space, which agrees with the findings of Chang *et al.* (2015), but also change over time related to temperature. Climate change can create directional

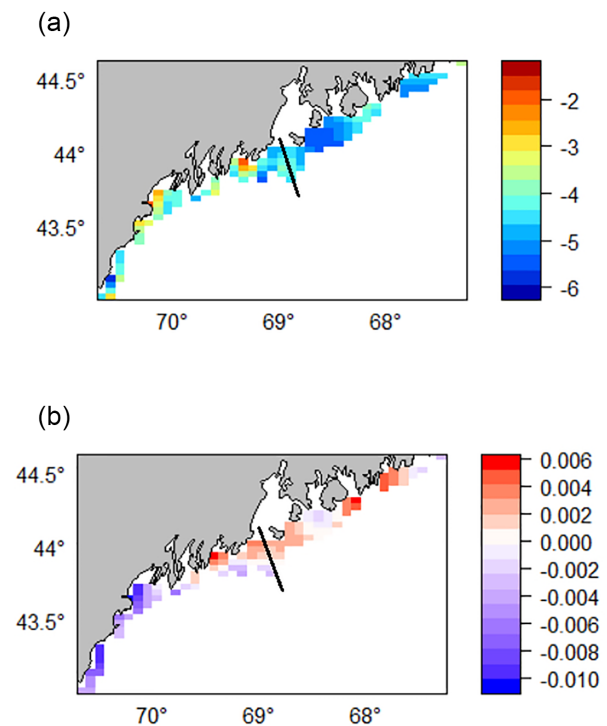


Figure 3. (a) Mean log temperature mediated productivity (calculated using α , the effect of offset temperature, and offset temperature) and (b) slope of the change in log temperature mediated productivity in the stock-recruitment relationship from 1982 to 2018 in the Gulf of Maine. The black lines represent the division between the western and eastern Gulf of Maine. Results are plotted at a 2 km² spatial scale for visualization purposes.

impacts on population biology, but these impacts may be obscured if not evaluated at the correct spatial scale.

Our case study was based on the GOM lobster stock; however, we believe this approach should be applicable to a wide range of taxa, such as shrimp and cod. Shrimp in the GOM and Australia are good candidates for these methods: when water temperatures are warmer, shrimp population productivity declines (Richards *et al.*, 2012; Roberts *et al.*, 2012). Another potential candidate for these methods could be cod in the eastern Atlantic Ocean, as cod recruitment shows different relationships with temperature among different stocks. Cod recruitment in the eastern Atlantic Ocean is positively related to temperature in northern regions and negatively related to temperature in southern regions (Ottersen, 1996). If recruitment, SSB, and temperature data are available across space, this framework can be used. In the face of climate change, other fish populations are likely to have experienced a shift in temperature mediated productivity in their SRRs as well, and these methods can quantify such shifts.

In this case, American lobster exhibited a shift in recruitment dynamics resulting in higher temperature mediated productivity in the EGOM. Likewise, warming water temperatures are predicted to have a positive impact on American lobster abundance (Tanaka *et al.*, 2018). However, if waters become too warm, there are likely to be negative impacts on lobster reproduction, as was observed in Southern New England (Wahle *et al.*, 2015). Above 20°C, lobsters experience increased physiological stress and decreased immune response, which can lead to increased rates of natural

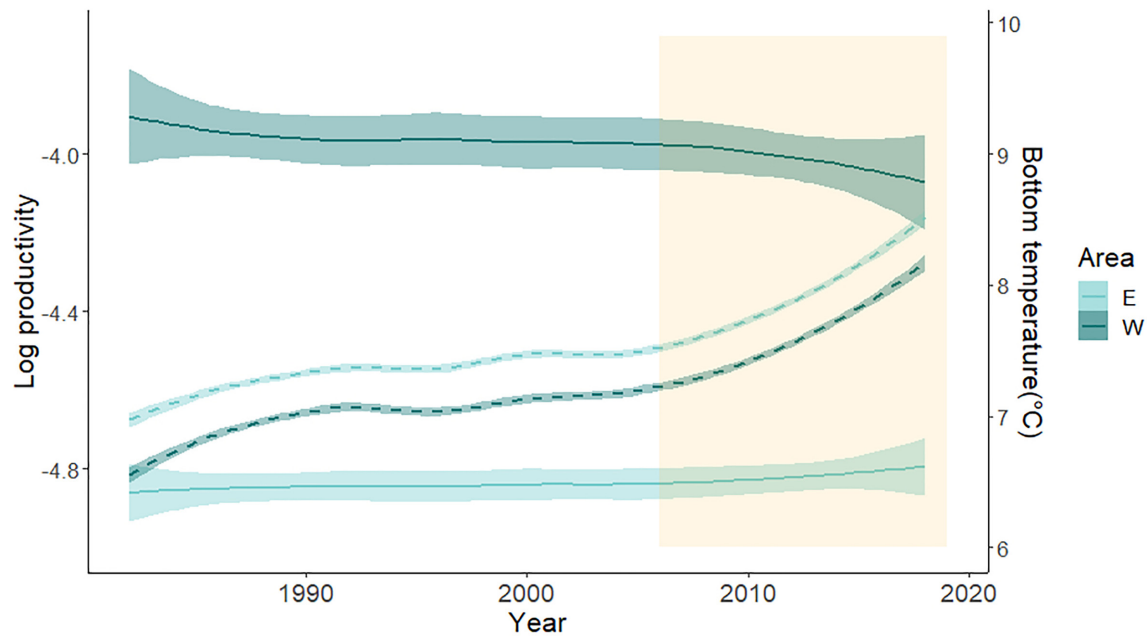


Figure 4. Temperature mediated log productivity in the stock-recruitment relationship (solid lines) and average offset temperature (dashed lines) over time (1982–2019) in the western and eastern Gulf of Maine. The orange transparent box represents the years of data used to fit the stock-recruitment model.

mortality (Dove *et al.*, 2005). While the EGOM has seen an increase in productivity due to temperature changes, the results show the WGOM exhibiting a decrease over time. Given the observed shift in temperature mediated productivity, using data from the whole time series and the whole spatial area for American lobster SRR in the GOM may lead to biased estimates. The most recent lobster stock assessment (ASMFC, 2020) identified productivity regimes due to shifts in lobster dynamics, such as those analyzed in this study.

Such a regional difference in population dynamics can arise from both oceanographic and biological processes. Changes in productivity impacted by temperature differ between the WGOM and EGOM partially due to differences in oceanography causing differences in the rate of temperature increase. Temperature has been increasing faster in some areas of the EGOM, possibly due to shifts in the ratio of water masses that flow into the GOM (Friedland *et al.*, 2020). This would result in higher rates of increase of temperature mediated productivity. Predation and prey may also affect recruitment dynamics by interacting with the effect of temperature in the WGOM. Li *et al.* (2018) found that temperature had a smaller impact on juvenile lobster distribution in the WGOM than in the EGOM and hypothesized that predators may have an impact on juvenile lobster distribution in the WGOM. Survival of lobsters after settlement is affected by predators, as well as habitat quality and body size (Wahle, 2003). Warmer temperatures also increase the growth rate for GOM lobster (Templeman, 1936), but this has not yet been quantified for a wide range of sizes. In addition, size at maturity for American lobster varies spatially and temporally due to temperature (Watson *et al.*, 2013; Waller *et al.*, 2019, 2021), which would affect the proportion of mature lobsters over space and time. Variation in size at maturity over space and time was not considered in this study due to lack of available data at a small enough spatial scale. Overall, productivity can be influenced by many factors not directly represented in these data. As this analysis used a regression

model, it cannot disentangle the actual mechanism by which temperature is changing recruitment rates.

These regional changes in population dynamics and SRRs have important implications for BRPs. Traditional BRPs are often based on maximum sustainable yield (MSY), which are calculated with SRRs and assume equilibrium. MSY-based reference points based on the entire time series and stock area are likely unsuitable because they assume relative equilibrium and temporal and spatial shifts in temperature mediated productivity are probable. Comparing the stock status to reference points identified in a region and period with lower temperature mediated productivity would not be biologically accurate. BRPs estimated from SRRs formed at large spatial and temporal scales without consideration of environmental variables may be biased due to spatial differences in SRRs and the impact of environmental variables on SRRs. This can lead to inappropriate stock status determination and resulting unsuitable fisheries management. In this study, MSY-based reference points were difficult to calculate, because we could not assume equilibrium and lobsters in this study were smaller than the smallest lobsters considered in the stock assessment (53 mm CL; ASMFC, 2020). A better understanding of the migration of lobster is needed to estimate MSY-based reference points over the relevant spatial scales. Lobsters larger than 50 mm CL begin to migrate with adult lobsters (Lawton and Lavalli, 1995) and thus spatially varying MSY-based BRPs would only be estimated correctly with information on the migration patterns of lobsters between 50 mm CL and the size of recruits in the stock assessment (53 mm CL).

Regime specific BRPs should be considered when productivity changes. To do this, environmental regimes should be identified by either splitting time series into different periods or by incorporating environmental factors into SRRs (ICES, 2002, 2003; Köster *et al.*, 2009). Estimating environmentally adaptive BRPs likely requires non-equilibrium assumptions to account for changes in the

system. Environmentally adaptive BRPs are important, because they account for the effects of environmental change on the productivity of populations. For example, changing environmental conditions can delay the rebuilding of depleted fish stocks, which would need to be accounted for in BRPs (Britten *et al.*, 2017).

The results from this study can help inform BRPs by identifying temporal regimes and spatial areas that differ in productivity. Any reference points based on the temperature mediated productivity need to address recruitment overfishing because the shifts in temperature mediated productivity were based on a SRR. In regions and time periods with higher temperature mediated productivity, the spawning stock would provide more recruits. Fishing pressure on lobsters could increase and still result in relatively high abundance. Managing with reference points from a higher temperature mediated productivity region and regime would produce higher abundance reference points and would allow the fishery to act sooner if abundance were to decline. To evaluate the management outcomes of a SRR with a climate variable, scientists can first quantify a simple SRR and a SRR with a climate variable and compare their outcomes using a management strategy evaluation approach. Furthermore, the results of this study suggest that fishery managers should consider environmental drivers impacting stock status, such as incorporating temperature into the stock assessment, which was done in the most recent lobster stock assessment (ASMFC, 2020). To address the temporal shifts in lobster population dynamics, the most recent lobster stock assessment (ASMFC, 2020) also identified productivity regimes, and reference points were based on those regimes.

Lobster population dynamics processes are not completely understood, so in this study, we used statistical models to help develop our understanding and not to predict lobster recruitment. "All models are wrong but some are useful" (Box, 1976) is a common phrase in statistical modelling, and it applies to this study as well. Understanding all the processes related to recruitment dynamics in marine benthic systems is challenging. Recruitment is complex and determined by processes operating at multiple spatial and temporal scales. The results in this study illustrate the impact of incorporating spatial heterogeneity and environmental effects in a SRR, but future research is needed to evaluate the predictive power of the SRRs for GOM lobster.

An important assumption in this study was that changes in temperature mediated productivity in the SRR were based solely on offset temperature. As a result, hindcasted temperature mediated productivity from 1982 onwards was based only on offset temperature. Although temperature has influenced lobster productivity, the GOM ecosystem has changed substantially since 1982, and other factors probably influenced lobster productivity as well, such as predators, prey, and fishing pressure, which should be considered in future studies. Between the 1980s and 1990s, the GOM experienced a regime shift from a system dominated by high trophic groundfish to a system dominated by low trophic crustaceans, including lobsters (Zhang and Chen, 2007). A previous study hypothesized that predators may be affecting juvenile lobster distribution in the WGOM (Li *et al.*, 2018). We additionally hypothesize that there may be other top-down and bottom-up factors besides temperature and SSB affecting recruitment in the WGOM (i.e. predators and prey), which should be considered in future studies. However, predators and prey dynamics are likely also influenced by temperature.

In this study, we considered a direct effect of temperature, but temperature can also indirectly affect the SRR. For example, the

size at maturity for American lobster is decreasing due to increasing water temperatures (Waller *et al.*, 2019, 2021), which will affect the SSB estimates. However, the relationship between size at maturity and temperature has not been quantified at a small enough spatial scale and therefore was not included in this study. Additionally, lobsters molt more frequently with warming waters (McMahan *et al.*, 2016), and this can impact the lag between SSB and recruitment. Future studies should focus on the lag between SSB and recruitment and how the lag is impacted by temperature. Variation in life histories due to adaptation to maximize recruitment success under high fishing pressure can also cause nonstationary SRRs (Hidalgo *et al.*, 2014). Stocks that are heavily fished and as a result have fewer large fish are also more susceptible to temperature variability (Ottersen *et al.*, 2006). This study also assumed that temperature would only affect productivity or density-independent effects in the SRR (α in the Ricker model), but it is possible that temperature might also affect density-dependent effects (β in the Ricker model). Future studies should consider other factors that can affect productivity and nonstationary assumptions over both space and time.

Additionally, there were uncertainties in observed recruitment data, interpolated temperature data, and SSB estimates from the geostatistical model that were not considered in the SRR. Future studies should also consider temperature estimates at a finer temporal resolution. In this study, we assumed the average of fall and spring bottom water temperatures affect the SRR, because we did not have access to bottom water temperatures in the summer months, and trends in temperature overtime are more important for the model than absolute values. However, some years had abnormally cold springs and abnormally warm falls, or vice versa, and the average of those temperatures did not account for those extremes. Another limitation of this study was that the trawl and VTS surveys do not completely overlap spatially. The trawl survey covers different habitat than the VTS, which may result in some bias when estimating SSB in habitat covered by the VTS but not the trawl survey with the geostatistical model due to differences in catchability. Furthermore, the time series of the VTS data is short in comparison to the time scale of changes observed in the lobster population and water temperature. As a result, these findings may not reflect the complete effect of nonstationarity or temperature. Future studies can also explore different models. A mixed effects model or a geographically weighted regression can be other ways to analyze nonstationary SRRs.

Future studies should also focus on further understanding the spatial scale of lobster SRRs. For SRRs, relative values of recruitment and SSB can be used; all the recruits do not need to be considered if the transportation of recruits is the same among years. Oceanographic dynamics and environmental conditions are likely to add complexities to the assumption of SRR spatial scale, and future research should focus on how currents and environmental conditions affect the spatial scales of SRRs for GOM lobster. Small changes in the timing of the release and the duration of the pelagic phase of lobster larvae can affect the SRR spatial scale. Flow between areas and lobster larvae from Canadian waters can also affect the SRRs, and this should be researched in future studies as well. This can be researched with simulations to determine connectivity matrices, which identify the percentage of larvae released from one spatial area that arrived at another spatial area (Xue *et al.*, 2008). However, connectivity matrices were outside the scope of this study for the following reasons. First, ecological processes involved in larval transport are not well understood (Pineda *et al.*, 2007), and our *in situ* data do not provide sufficient information about

spatiotemporal shifts in this species's habitat requirements outside of the observed size ranges. Second, connectivity matrices would require a biophysical model that incorporates the effects of oceanographic processes such as tides, winds, and large-scale interannual forcing (Pineda *et al.*, 2009). However, the accuracy of modeled in-shore current flows is typically limited, because complex flows that are found inshore are typically not captured in biophysical models due to grid sizes larger than the spatial scales of the species' ecological processes (Pineda *et al.*, 2009). The most recent lobster connectivity matrices were developed for the years 2002–2004 (Xue *et al.*, 2008; Ince *et al.*, 2010). However, current flow has changed with changes in climate (Hu *et al.*, 2020). Future studies should focus on connectivity matrices developed with improved modeled flow fields.

Despite the potential impact of connectivity, the results from the analysis with distant SSB were similar to the results with local SSB. Magnitudes of SSB may differ over spatial scales, but the temporal trends in SSB were similar at a larger spatial scale, so we can expect similar estimated impacts of temperature on recruitment. Additionally, Annis *et al.* (2013) found that postlarval abundance did not vary across the coastal GOM, but settlement abundance was related to water temperature, indicating a disconnect between postlarval abundance and settlement. These findings as well as the analysis with distant SSB indicate that our study is robust to the connectivity assumption.

In conclusion, accounting for spatial heterogeneity and environmental impacts can influence our understanding of SRRs. Allowing for spatially varying productivity and the effect of temperature in the SRR explained more variation and revealed trends in recruitment dynamics. We found that lobster recruitment dynamics in the GOM differ over space and were influenced by temperature: a key environmental variable. Considering differences in SRRs across space and temperature in fisheries modeling has important implications for fisheries management. Management implications resulting from this framework are especially important for recruitment fisheries. These methods can quantify spatial differences in recruitment dynamics, which can be useful in spatial management. In closing, accounting for spatial nonstationary and environmental drivers can reveal changes in recruitment dynamics, which is important for informing marine resource management in a rapidly changing world.

Data availability statement

The data underlying this article were accessed from the Maine Department of Marine Resources, the Atlantic States Marine Fisheries Commission, and the National Marine Fisheries Service. The derived data generated in this research and R code will be shared upon reasonable request to the corresponding author.

Supplementary data

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

Author contribution statement

M.D.M. drafted and revised the manuscript and analyzed modeling results along with K.R.T., J.H.C., B.S., K.M.R., C.H., K.D.F., and Y.C. M.D.M. conceived the presented idea and performed the varying

coefficient generalized additive modeling. M.D.M., K.R.T., and C.H. performed the geostatistical modeling. K.M.R. and K.D.F. provided data.

Conflict of interest

The authors have no conflict of interests to declare.

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