Project and evaluate impacts of environmental variations on the spatio-temporal distributions of lobster population and suitable habitat in a changing Gulf of Maine

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By

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Summary

A proactive approach to understanding potential impacts of climatic forcing on American lobster (Homarus americanus) in a ever changing Gulf of Maine is imperative in planning for an uncertain future. Forecasting the species' habitat availability, its utilization, and changes in the species abundance under different climatic scenarios and using the information in the lobster stock assessment are a critical step towards an ecosystem-based fisheries management. This research aims to develop and apply various modeling tools to evaluate spatio-temporal dynamics of lobster stock and better understand potential changes in the Gulf of Maine lobster fishery. We developed and applied an ensemble species distribution model to project lobster distribution and evaluate uncertainty associated with the projection. We quantified the environmental-lobster relationship and incorporated the environmental variables in lobster stock assessment. We evaluated assumptions associated with lobster-environmental models and identified possible consequences of violating these assumptions when projecting habitat suitability.

The Gulf of Maine is a highly complex environment and previous studies have suggested needs to account for spatial nonstationarity in species distribution models for the American lobster. To explore impacts of spatial nonstationarity on species distribution, we developed species distribution and bioclimate envelope (habitat suitability) models with the following three assumptions informed by the GOM coastal currents: (1) stationary relationships between lobster density and environmental variables; (2) nonstationary density-environment relationships between eastern and western GOM, and (3) nonstationary density-environment relationships across eastern, central, and western GOM. We forecasted distributions for the period 2028-2055 using each of these models under the Representative Concentration Pathway (RPC) 8.5 "business as usual" climate warming scenario. We found that the model with the finest scale performed best. This suggests that accounting for spatial nonstationarity in the GOM leads to improved distribution estimates. Forecasted distributions revealed that stationary models tended to comparatively overestimate most season x sex x size group lobster abundances in western GOM, underestimate in the western portion of central GOM, and overestimate in the eastern portion of central GOM, with slightly less consistent and patchy trends amongst groups in eastern GOM. We demonstrate how estimates of season-, sex-, and size- specific American lobster spatial distribution would vary based on the spatial scale assumption of nonstationarity in the GOM. This study supports the existence of spatially non-stationary lobster-environmental relationships, which highlights the importance of spatial scales in modeling lobster habitat suitability and abundance distributions.

This project provides a suite of modeling framework to project lobster spatial distributions and population dynamics and improves our understanding of how lobster population may respond to climate changes.

Acknowledgement

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This project has resulted in the following four peer-reviewed papers and one submitted paper:

- Key components in Section I is published in *Tanaka K., Torre M., Saba V., Stock C., and Chen Y. 2020. An ensemble high-resolution projection of changes in the future habitat of American lobster and sea scallop in the Northeast US continental shelf. Diversity and Distributions, 26(8): 987–1001.*
- Key components in Section II is published in *Hodgdon C., Tanaka K., Runnebaum J., Cao J., Chen Y. 2020. A framework to incorporate environmental effects into stock assessments informed by fishery-independent surveys: a case study with American lobster (Homarus Americanus). Canadian Journal of Fisheries and Aquatic Sciences, 77: 1700–1710.*
- Key components in Section III is published in *Hodgdon, C.T., Mazur, M.D., Friedland, K.D., Willse, N., and Chen, Y. Consequences of model assumptions when projecting habitat suitability: a caution of forecasting under uncertainties. ICES Journal of Marine Science. 78(6): 2092–2108.*
- Key components in Section IV is published in *Behan J, Li B and Y. Chen. 2021. Examining Scale Dependent Environmental Effects on American Lobster (Homarus americanus) Spatial Distribution in a Changing Gulf of Maine. Front. Mar. Sci. 8:680541. doi: 10.3389/fmars.2021.680541*
- Key components in Section V is included in the following manusxruipt currently under review in Ecological Modelling: *Behan, J., C.T. Hodgdon, Y. Chen. 2021. Scale-Dependent Assumptions Influence Habitat Suitability Estimates for the American Lobster (Homarus americanus): Implications for a Changing Gulf of Maine.*

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Project Introduction

American lobster, a benthic crustacean distributed along the coast of northeastern United States, is a major fishery resource throughout the species' range (Atlantic States Marine Fisheries Commission (ASMFC) 2015), worth over $669 million in 2016 (ACCSP, 2017). Lobster landings accounted for 81% of all commercial fish landings in the State of Maine in 2015 (ACCSP, 2017). There are an estimated 5,000 license holders, accounting for approximately 55% of all commercial fishing licenses held in the state (State of Maine Department of Marine Resources (Maine DMR) 2016). Such dependence on the lobster fishery leaves the coupled natural and human system vulnerable to environmental and regulatory changes.

Studies suggest that the population dynamics of American lobster experience strong top-down (e.g., fishing pressure) and bottom-up (e.g., climate and resources) controls (ASMFC 2015; Boudreau et al. 2015; Caputi et al. 2013). For sustainable management of this species, it is critical to (1) evaluate the relative importance and synergistic impacts of these environmental drivers, (2) maximizing the efficiency and accuracy of the existing stock monitoring and assessment program, and (3) develop the capacity for predicting changes in ecology, biogeography and phenology of American lobster which potentially can limit the lobstering grounds in future.

Climate-driven changes in the GoM ecosystem structure have been identified as a likely primary stressor to the specie's commercial fisheries within its whole geographic distribution (Dove et al. 2005; Caputi et al. 2013; Mills et al. 2013). American lobster is an ectothermic species and tracks its climatic niches in space (distribution shifts) or time (phenological shifts). Changes in temperatures are likely to cause shifts in the lobster distribution, behavioral changes such as early and more frequent molting, and increased seasonal migrations (Fogarty et al. 2007; Pinsky et al. 2013). Temperature has also been shown to influence the regulation of hormones, specifically those that control the molting cycle (Qadri et al. 2007). Record warm temperatures in the GoM during 2012 coincided with an unusually early spring molt and high landings of newly recruited lobsters to the fishery as a result, which contributed to a decline in total value of the GoM lobster fishery (Mills et al. 2013). The water temperature in the GoM has increased over the last 40 years (Nye et al. 2009; ASMFC 2015). Sea surface temperature in GoM shows an increase of 0.03 °C per year, resulting in a 1 °C increase in the mean temperature since 1982 (Mills et al. 2013). Under the latest Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathways (RCP) 8.5 emissions scenario, average bottom temperature in Northeast U.S. Continental Shelf system is expected to increase more than 1 °C by 2050 (IPCC 2013; NOAA 2015). As the rate of climate change is predicted to accelerate in the future, there is a growing need to understand the dynamic interactions between climate change and biogeography, phenology and population dynamics of American lobster through the development of predictive and analytical modeling frameworks (Hare et al. 2012; Shackell et al. 2014).

Top-down forces such as predators may also affect the distribution of American lobster in the GoM (Boudreau et al. 2015). The importance of predators had been identified through laboratory experiments (Wahle 1992; Wahle and Steneck 1992) and temporal scale assessments (Boudreau et al. 2015). The widespread decrease of groundfish may contribute to the historically high levels of lobsters in the GoM (Steneck and Wahle 2013). It is necessary to incorporate predator information into spatial distribution models in order to understand the effects of top-down forces on lobster distribution at a fine spatial scale.

Relevant modeling framework for American lobster has been accomplished in the Chen Lab with funding from NSF, Maine Sea Grant, and University of Maine. The modeling framework consists of three components: 1) size, season, and stage specific Habitat Suitability Index (HSI) to quantify the spatiotemporal variability of bioclimate envelope (i.e. lobster habitat quality and boundaries defined by physical and climatic variables), 2) Tweedie generalized additive models (Tweedie GAM) to quantify the spatiotemporal size, season, and stage specific lobster abundance distribution forced by meso-scale climatic variations, and 3) geographically weighted regression model to quantify the spatially varied strength of abiotic environmental effects on the presence and density of lobsters. The HSI is a numerical index that describes the capacity of a given habitat to support a given species, and is based on suitability indices (SI) that can quantify the optimal environmental conditions from 0 (least suitable habitat) to 1 (most suitable habitat). The use of HSI will allow us to evaluate suitability of habitat considering key environmental variables (e.g., bottom temperature) for the GoM lobster stock at different life history stages (Franklin 2010; Tanaka and Chen 2016). A GAM is a non-parametric statistical modeling approach commonly applied in ecological studies. GAMs use cubic or spline smooth function to define nonlinear relationships between the response and explanatory variables, and can serve as either a descriptive or predictive statistical model. GAMs that incorporate the Tweedie error distribution are commonly used in the fisheries ecological studies where data are often highly skewed with a large proportion of zero observations (Shono 2008; Tanaka et al. In Prep). The Tweedie GAM can handle both zero and positive values simultaneously, and provides a clear advantage in reconciling non-linear and non-monotonic relationships between the response and explanatory variables that are common in nature (Guisan et al. 2002). Both modeling components developed by Tanaka and Chen have been integrated into the FVCOM to achieve sufficient spatial (NW Atlantic Continental Shelf) and temporal (1978-2015) coverage. A geographically weighted regression model is a local model that estimates a set of local coefficients for each observation point by specifically giving more weight to the data at closer locations than those farther away (Windle et al. 2010). The use of geographically weighted regression model will allow us to identify and quantify the relative importance of key environmental variables that impact the spatiotemporal distribution of lobsters by area.

Tanaka and Chen (2016) reconstructed spatiotemporal variability of bioclimate envelopes for American lobster in coastal waters of Maine and New Hampshire from 1978 to 2013, and the results showed (1) higher habitat suitability in inshore waters for both adult and juvenile lobsters, and (2) a statistically significant increasing trend in habitat suitability for American lobster during the spring. (Tanaka et al. 2017 & In Review) have also developed a statistical climate-niche model based on the generalized additive modeling approach to quantify the spatio-temporal GoM lobster distribution dynamics. Tanaka et al. (2017) showed that spatial distribution of lobster shell disease prevalence was found to be strongly influenced by the interactive effects of bottom temperature, bottom salinity, and depth. Tanaka et al. (In Review) quantified environmental effects on season, sex- and size-specific lobster distribution in the inshore Gulf of Maine, and predicted significantly higher lobster abundance under a warm climate climatology scenario. The model results have been peer-reviewed and presented to the DMR and ASMFC scientists (Tanaka and Chen 2015; Tanaka and Chen 2016; Tanaka et al.

2017 & In Review). Li et al. (In Review) quantified the spatial variability in lobster-habitat relationships in coastal waters of Maine and New Hampshire from 2000 to 2014. The results showed that the direction and strength of the estimated lobster-habitat relationships in the western GoM were different with the relationships in the eastern GoM. The bottom water temperature played a more significant positive impact on the increase of lobsters in the eastern GoM, while the influence of temperature was less significant in the west and the more distinguishable drivers of distribution in the western GoM needed to be identified.

Climate-driven changes in the GoM ecosystem structure is a growing concern for the GoM lobster fisheries. Incorporating ecosystem variability into assessment and management of the GoM lobster stock has been advocated as a key step towards an ecosystem-based fisheries management in mitigating the negative effects of climate change (ASMFC 2014, 2015). However, there remains a critical knowledge gap in evaluating the synergistic impacts of climate change on functional lobster biogeography and subsequent population dynamics as well as maximizing the efficiency and accuracy of the existing assessment and management program. Tools are required that allow fishery resource managers to predict the biological and ecological consequences of climate change on assessment and management of GoM lobster stock. One of the best ways to adapt to altered marine ecosystems brought on by a changing climate is to develop modeling capability to improve our ability to forecast the dynamics of populations and ecosystems (NMFS 2010). Building on the previous work conducted and current work funded by other programs in the Chen Lab, our proposed "coupled biophysical modeling framework" make it ideal hind-, now-, and forecasting tool to study the impact of climate change on the GoM lobster stock dynamics.

Project Objectives

The overarching goal of this study is to develop predictive and analytical coupled biophysical modeling framework that improve the assessment and management of American lobster (*Homarus americanus*) in a climatically-altered GoM ecosystem. The framework is composed of our peer-reviewed bioclimate envelope model, statistical climate-niche model, and geographically weighted regression model to project potential changes in functional biogeography of American lobster under three different greenhouse gas (GHG) emission scenarios developed by the Intergovernmental Panel on Climate Change - Representative Concentration Pathways (IPCC-RCPs: 2.6, 6.0, 8.5). Downscaled bottom temperature and salinity projections under each GHG emission scenario are used as inputs to the coupled biophysical modeling framework to project changes in available habitat and distributional shifts. Building on the previous work conducted in the Chen Lab, we want to achieve the following objectives:

- ***Project possible climate-driven changes in functional biogeography (i.e. spatio-temporal changes in lobster distribution and suitable habitat availability) of American lobster in the Gulf of Maine.***
- ***Quantify the spatial variability in lobster-environment relationships and identify key biotic and abiotic factors that impact the distribution of American lobster in the Gulf of Maine.***

Section I. Project possible climate-driven changes in functional biogeography of American lobster in the Gulf of Maine

To address the uncertainty associated with climate-driven biogeographical changes in commercial fisheries species through an ensemble species distribution modelling (SDM) approach, Tanaka et al. has combined an ensemble SDM platform (BIOMOD 2) and a high-resolution global climate model (NOAA GFDL CM2.6) to quantify spatiotemporal changes in habitat of two commercially important species in the Northeast US Continental Shelf Large Marine Ecosystem (NEUS-LME); American lobster (*Homarus americanus*); and sea scallop (*Placopecten magellanicus*).

Projected oceanographic conditions were developed using the delta method (Fogarty, Incze, Hayhoe, Mountain, & Manning, 2008; Hare et al., 2012). The delta method is commonly used for future climate projection, which relies on the difference between future climate anomalies and a baseline regional climatology (historical climate condition). The delta method can remove the climate model projection biases (e.g. drift) and provide a simple and robust projection of future climate conditions (Hare et al., 2012). The historical bottom temperature and salinity climatologies within the NEUS-LME were developed using high-resolution, quali- ty-controlled monthly means from the Northwest Atlantic regional bottom temperature and salinity climatology for 1955–2012 (0.1°; Seidov et al., 2016). Bathymetry data were obtained from the U.S. Coastal Relief Model (NGDC, 1999). Projected bottom temperature and salinity conditions used in this modelling framework are from a high-resolution global climate model developed at the NOAA Geophysical Fluid Dynamics Laboratory (GFDL CM2.6; Delworth et al., 2012; Saba et al., 2016; Figures S4 and S5). CM2.6 is a coupled atmosphere-ocean-land-sea ice global climate model, with a 0.1° average horizontal resolution for its ocean component (Saba et al., 2016). CM2.6 resolves mesoscale oceanographic processes and fine-scale bathymetry within the NEUS-LME, leading to a better simulation of the regional ocean and shelf circulation when compared to global climate models with coarser ocean components (Saba et al., 2016). The monthly bottom temperature and salinity anomalies projections that correspond to spring and fall survey efforts were used in this study. The projected temperature and anomalies from CM2.6 are based on (a) the standard model initialization procedure where global atmospheric CO_2 is fixed at a 1,860 pre-industrial concentration to bring the climate system into near-equilibrium, and (b) a transient climate response to simulated 1% year-1 increase in global atmospheric CO_2 run (i.e. $2xCO_2$ simulation) up to 70 years and is then fixed for an additional 10 years. The CM2.6 $2xCO_2$ simulation can be roughly compared to the IPCC highest greenhouse gas emissions scenario (IPCC-RCP8.5). Under the IPCC RCP8.5 scenario, the global mean surface temperature increases by 2°C by 2060–2070 relative to the 1986–2005 climatology (Winton, Anderson, et al., 2014), whereas the CM2.6 $2xCO_2$ simulation projects the global mean temperature increases by 2°C by year 60–80. This results in bottom temperature warming on the scale of 1.8–2.9°C over the simulated 80 years across the NEUS-LMES.

An ensemble SDM was calibrated using multi-decadal fisheries-independent surveys (1984–2016). The environmental variables used for the ensemble lobster and scallop habitat modelling were directly obtained from the scientific bottom trawl survey dataset (1984–2016; Figure S2). We used bottom temperature, salinity and depth that were available at each tow location (Tanaka & Chen, 2016; Torre, Tanaka, & Chen, 2018). The BIOMOD2-based ensemble

SDM algorithm can incorporate species presence–absence data and combine multiple SDM algorithms to provide robust species occurrence–environment relationships. Once SDMs were fitted with optimized parameters, all SDMs were run three times each using a randomly chosen 80% of the presence–absence data, with the remaining 20% of the data being used to cross-validate model results. Statistically weighted species-specific ensemble SDM outputs were combined with 80 years of projected bottom temperature and salinity changes in response to a high greenhouse gas emissions scenario (an annual 1% increase in atmospheric CO_2). Weighted species-specific ensemble SDM was used to project habitat suitability of lobster and scallop across the NEUS-LME under historic bottom temperature and salinity conditions and over the future 80 years based on the transient climate-driven bot- tom temperature and salinity changes in response to the doubling of 1% CO_2 per year increase scenario applied in the NOAA GFDL CM2.6 (Saba et al., 2016).

The final ensemble model for lobster and scallop produced a spatial distribution of habitat that corresponds well to consensus of the general, broad-scale distribution of these species over the NEUS-LME (Figure I-1). In general, a highly suitable habitat (>0.66) for lobster was found along the inshore GOM up into the Bay of Fundy. During the spring, western Long Island Sound and the area south of Rhode Island showed high habitat suitability. For scallop, a highly suitable habitat (>0.66) was found along offshore MAB, SNE and GB areas (Figure I-1). Additionally, a highly suitable scallop habitat was found along the inshore GOM along with select offshore shoal areas.

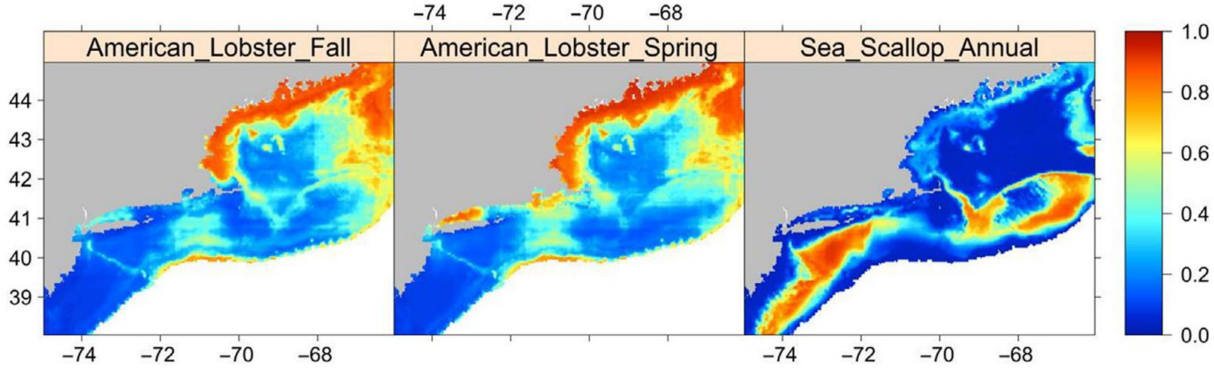


Figure I-1. Maps showing the habitat suitability (probability of presence) for American lobster and sea scallop across the study area as predicted by the final ensemble model under the historical climatology (1955–2012). The colour ramp corresponds to predicted habitat suitability, where dark blue indicates low habitat suitability and red indicates high habitat suitability (scaled 0–1)

Projected warming across the NEUS-LME over the 80 years resulted in large spatial changes in habitat suitability of lobster and scallop (Figure I-2). For lobster, deep areas within the GOM showed a strong increasing trend in habitat suitability. Lobster habitat suitability in inshore areas remained stable during the spring but showed a declining trend during the fall. The general distribution of changes in scallop habitat suitability over the study period showed a clear north-positive, south-negative trend (Figure I-2), with habitat suit- ability declined in the MAB, SNE and GB areas. Within GOM-GB, inshore areas along with select shoal areas showed an increase in scallop habitat suitability while deeper offshore areas remained relatively stable.

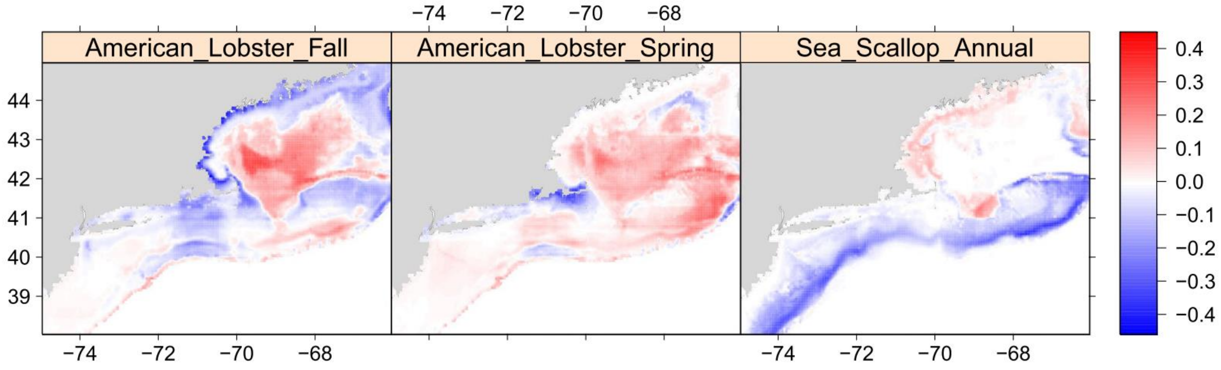


Figure I-2. Temporal change in habitat suitability (probability of presence) over the future 80 years of changes (linear trend per 80 years) in bottom temperature and salinity for American lobster and sea scallop. The colour ramp corresponds to a linear trend in habitat suitability with red areas having a positive change and blue areas having a negative change scallop

Statistically significant changes ($p < 0.05$) in habitat suitability for both species were found over a large portion of the study area (Table I-1). Sea scallop undergoes a northward shift over the study period, while American lobster moves further offshore. The ensemble projections showed that several management zones were identified with increases and decreases in species-specific habitat. Uncertainty due to variations in ensemble member models was also found in the direction of change within each management zone (Table I-2).

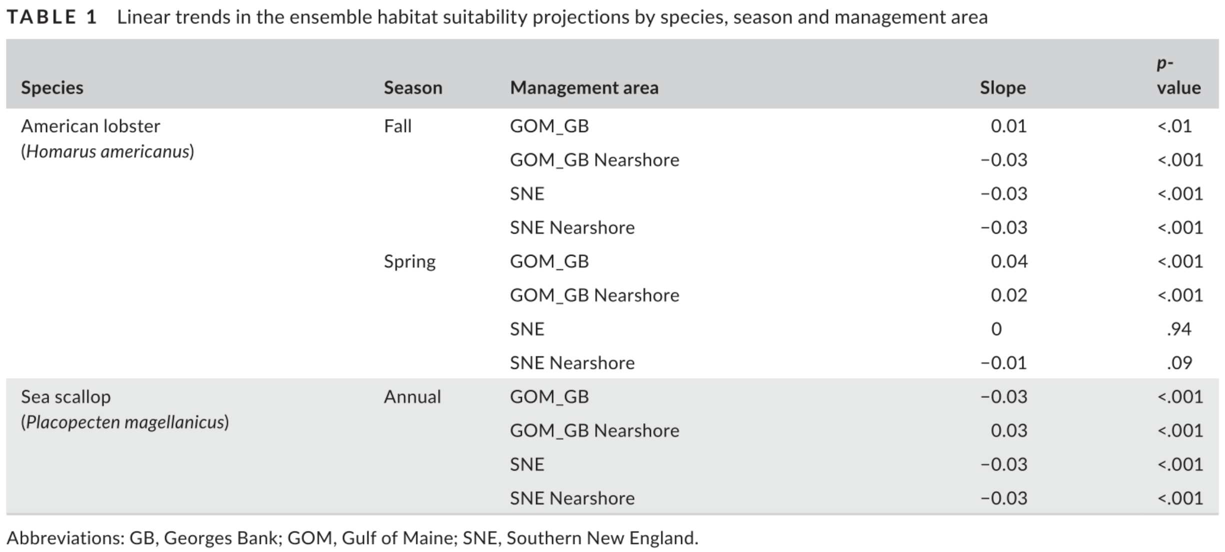


TABLE 1 Linear trends in the ensemble habitat suitability projections by species, season and management area

Species	Season	Management area	Slope	*p*-value
American lobster (*Homarus americanus*)	Fall	GOM_GB	0.01	<.01
		GOM_GB Nearshore	−0.03	<.001
		SNE	−0.03	<.001
		SNE Nearshore	−0.03	<.001
	Spring	GOM_GB	0.04	<.001
		GOM_GB Nearshore	0.02	<.001
		SNE	0	.94
		SNE Nearshore	−0.01	.09
Sea scallop (*Placopecten magellanicus*)	Annual	GOM_GB	−0.03	<.001
		GOM_GB Nearshore	0.03	<.001
		SNE	−0.03	<.001
		SNE Nearshore	−0.03	<.001

Abbreviations: GB, Georges Bank; GOM, Gulf of Maine; SNE, Southern New England.

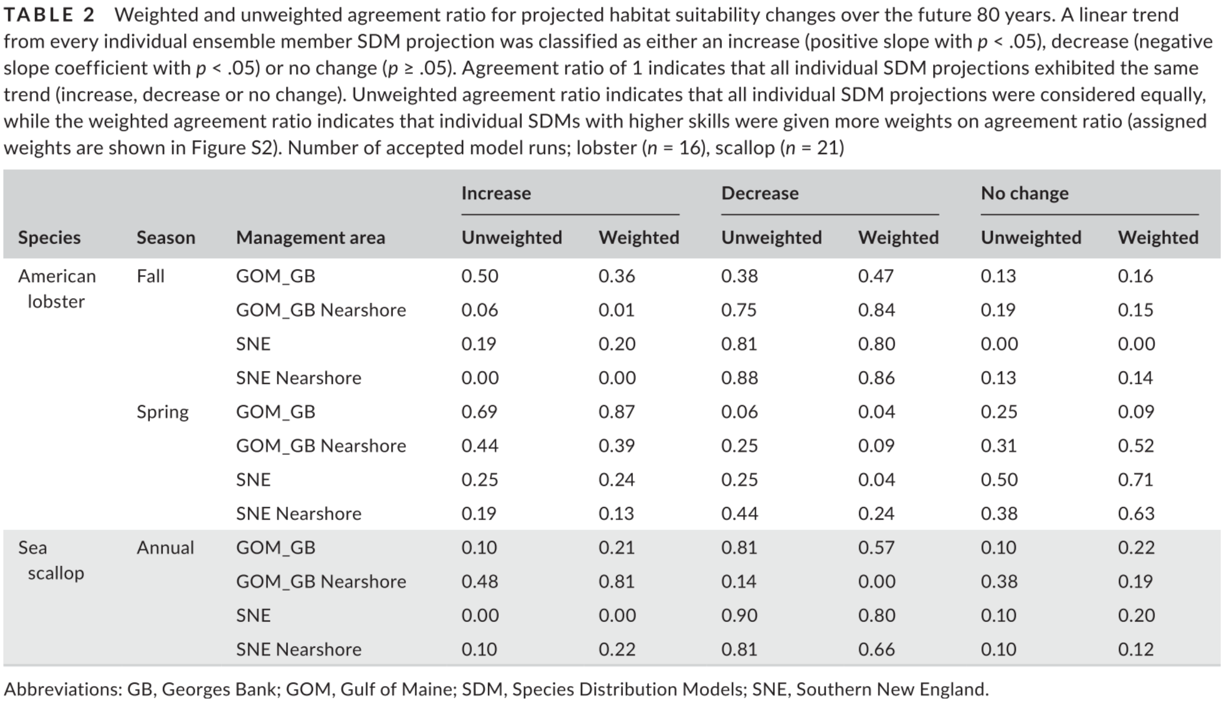


TABLE 2 Weighted and unweighted agreement ratio for projected habitat suitability changes over the future 80 years. A linear trend from every individual ensemble member SDM projection was classified as either an increase (positive slope with $p < .05$), decrease (negative slope coefficient with $p < .05$) or no change ($p \geq .05$). Agreement ratio of 1 indicates that all individual SDM projections exhibited the same trend (increase, decrease or no change). Unweighted agreement ratio indicates that all individual SDM projections were considered equally, while the weighted agreement ratio indicates that individual SDMs with higher skills were given more weights on agreement ratio (assigned weights are shown in Figure S2). Number of accepted model runs; lobster ($n = 16$), scallop ($n = 21$)

			Increase		Decrease		No change	
Species	**Season**	**Management area**	**Unweighted**	**Weighted**	**Unweighted**	**Weighted**	**Unweighted**	**Weighted**
American lobster	Fall	GOM_GB	0.50	0.36	0.38	0.47	0.13	0.16
		GOM_GB Nearshore	0.06	0.01	0.75	0.84	0.19	0.15
		SNE	0.19	0.20	0.81	0.80	0.00	0.00
		SNE Nearshore	0.00	0.00	0.88	0.86	0.13	0.14
	Spring	GOM_GB	0.69	0.87	0.06	0.04	0.25	0.09
		GOM_GB Nearshore	0.44	0.39	0.25	0.09	0.31	0.52
		SNE	0.25	0.24	0.25	0.04	0.50	0.71
		SNE Nearshore	0.19	0.13	0.44	0.24	0.38	0.63
Sea scallop	Annual	GOM_GB	0.10	0.21	0.81	0.57	0.10	0.22
		GOM_GB Nearshore	0.48	0.81	0.14	0.00	0.38	0.19
		SNE	0.00	0.00	0.90	0.80	0.10	0.20
		SNE Nearshore	0.10	0.22	0.81	0.66	0.10	0.12

Abbreviations: GB, Georges Bank; GOM, Gulf of Maine; SDM, Species Distribution Models; SNE, Southern New England.

This study provides ensemble estimates of climate-driven changes and associated uncertainties in the biogeography of two economically important species in the United States. Projected climate change in the NEUS-LME will pose management challenges, and our ensemble projections provide useful information for climate-ready management of commercial fisheries.

Section II. ***Quantify the spatial variability in lobster-environment relationships to improve American lobster stock assessment in the Gulf of Maine.***

To determine whether consideration of dynamic bottom temperatures and water column depth improved estimation of abundance indices for the lobster stock in the Gulf of Maine/Georges' Bank Large Marine Ecosystem (GOM-GB LME), retrospective patterns and model fit were compared between runs of a length-based assessment model for lobster using traditional design-based abundance indices and model-based abundance indices created with environmental covariates bottom temperature and depth.

Modelled abundance indices were generated using a delta-GLMM approach. The delta-GLMM applied in this study (R VAST package version 3.2.2; Thorson and Barnett 2017; Thorson 2019) uses catch data from a single given survey with optional environmental covariates for density and (or) catchability to derive modelled abundance indices. These modelled indices replaced the traditionally used design-based abundances indices in the Lobster Stock Assessment model (LSA).

The LSA is a seasonal, integrated, length-structured assessment model for lobster in the GOM–GB LME. It was initially developed and coded with ADMB (Chen et al. 2005; ASMFC 2015). The program codes were later modified by Cao et al. (2017*a*, 2017*b*) and Tanaka et al.

(2019). Owing to the inability to appropriately and reliably age wild-caught lobster and thus lack of knowledge on age–length relationships (Wahle et al. 1996; Chang et al. 2011; ASMFC 2015), a length-based assessment model was deemed more appropriate than an age-based assessment model (Chen et al. 2005), a practice common with many crustacean species (Chang et al. 2011; Punt et al. 2013). The population dynamics equation this model employs is:

$$\boldsymbol{N}_{t,m} = \boldsymbol{N}_{t,m-1} \times \mathrm{e}^{-\boldsymbol{F}_{t,m}+M} \times \mathbf{G}_{m-1} + \boldsymbol{R}_{t,m}$$

where $\boldsymbol{N}_{t,m}$ is a vector of the number of lobster in each of the pre-specified size bins in year t and season m, $\boldsymbol{F}$ is seasonal fishing mortality, M is seasonal natural mortality, $\mathbf{G}$ is the seasonal growth transition matrix (estimated a priori from an individual-based model; Mazur et al. 2018), and $\boldsymbol{R}$ is the recruitment to each size bin (Chen et al. 2005). In the LSA, $\mathbf{G}$ and M are pre-specified, and $\boldsymbol{R}$ and $\boldsymbol{F}$ are estimated. $\mathbf{G}$ is averaged across both sexes, a practice commonly and historically done with the LSA (Tanaka et al. 2019). M is expected to be the same for both sexes and so no average is taken (ASMFC 2015). Additionally, spawning stock biomass (SSB) can be estimated using proportion female and proportion mature per-size-bin vectors. A detailed explanation of this model can be found in Chen et al. (2005), ASMFC (2015), and Tanaka et al. (2019).

For this study, the delta-GLMM was run on each of six surveys individually before being used in the LSA. The six surveys were the spring and fall MEDMR–NHFGD Inshore Bottom Trawl Surveys, the spring and fall MADMF Inshore Bottom Trawl Surveys, and the spring and fall NEFSC Bottom Trawl Surveys. Model fit, retrospective patterns, and hindcasted biological reference points were all compared between LSA runs to determine any improvements to modelling from modelled indices over design-based.

Retrospective patterns are summarized in Figure II-1. Mohn's Rhos for SSB and R improved across all model runs, whereas Mohn's rho for F was worse across all nine runs. Overall, two of nine model runs showed improved cumulative retrospective patterns over the design-based runs. It also appears that temperature as a density covariate produces smaller retrospective patterns over temperature as a catchability covariate and that the reverse is true for depth. Model fits are summarized in Figure II-2. OFV remained the lowest in the stock assessment when using the traditional design-based indices. All other OFVs were between 9% and 42% larger. However, of the model-based OFVs, the addition of covariates over model-based with no covariates yielded significantly improved results, the smallest OFV being for Run No. 5 (temperature and depth as catchability covariates). Hindcasted fishery statuses did not match, revealing that historical management would have been different if these modelled indices were used in place of the design-based (Figure III-3).

Overall, these indices provided relatively small improvements to retrospective bias and moderate worsening of model fit for the American lobster assessment model. This could be due to survey design and coverage of the population, which may be sufficient enough as to capture the variability caused by environmental covariates that this study was explicitly estimating (Yu et al. 2013; Thorson et al. 2015) It is important to note that even though incorporation of these variables improves retrospective patterns in the stock assessment, this is at the cost of decreased model fit. The disagreement between retrospective patterns and OFVs could point to robust survey designs that accurately capture changes in population density when spatiotemporal changes in catchability are accounted for. The American lobster stock in the GOM–GB LME is unique compared with most other marine stocks. They are privileged with near-full spatial coverage of multiple fishery-independent surveys over a long time series (Chen et al. 2006). These high-intensity sampling efforts seem capable of accurately tracking population changes over space and time independent of explicit consideration of environmental effects. The strength of geostatistical models such as the delta-GLMM comes from their ability to extrapolate into low-sampled areas and times using statistical assumptions of population densities and often using environmental covariates (Thorson et al. 2015). This ability appears fruitless with a well-surveyed species like American lobster, whose fine-scale population densities appear to be well-documented already from surveys that encompass both their inshore and offshore ranges (Chen et al. 2006).

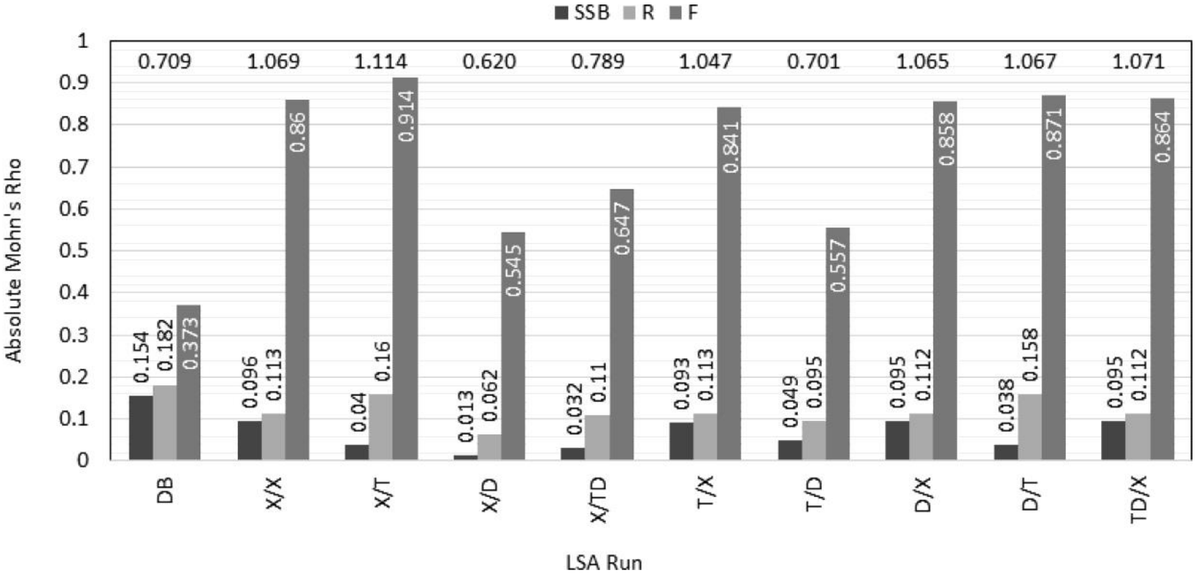


Figure II-1. Absolute Mohn's rho values for each Lobster Stock Assessment model (LSA) run for SSB, *R*, and *F*. Mohn's rho values are displayed on top or inside of their respective boxes. Absolute summed Mohn's rho values for each run are at the top of each column. The *X* axis denotes each LSA run as either "DB" (design-based) or as "*A*/*B*", where *A* represents the density covariates used in index calculation and *B* represents the catchability covariates used. X = none, T = bottom temperature, D = depth, TD = temperature and depth.

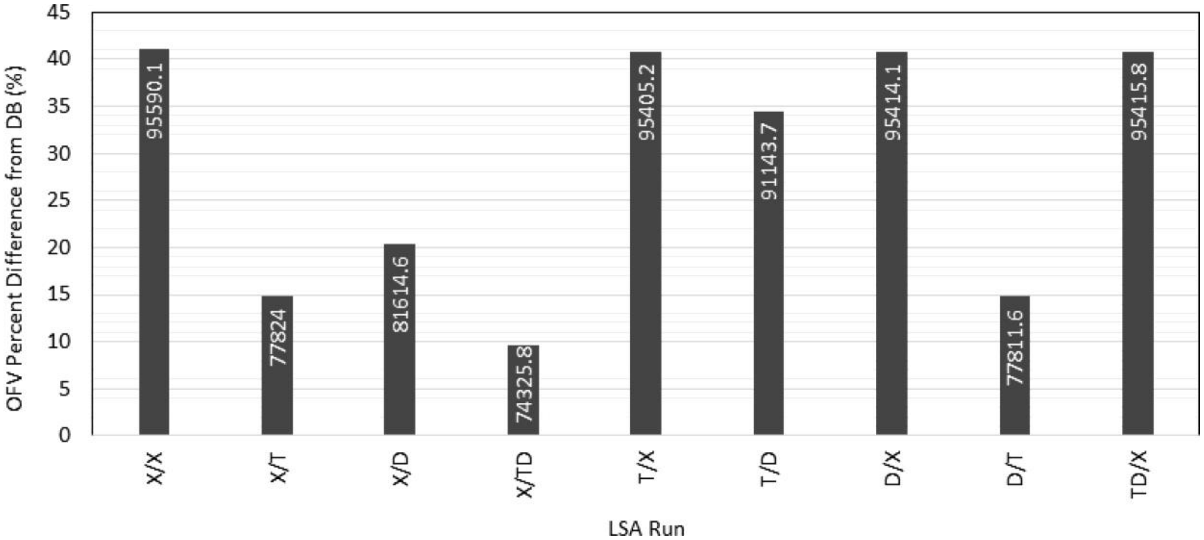
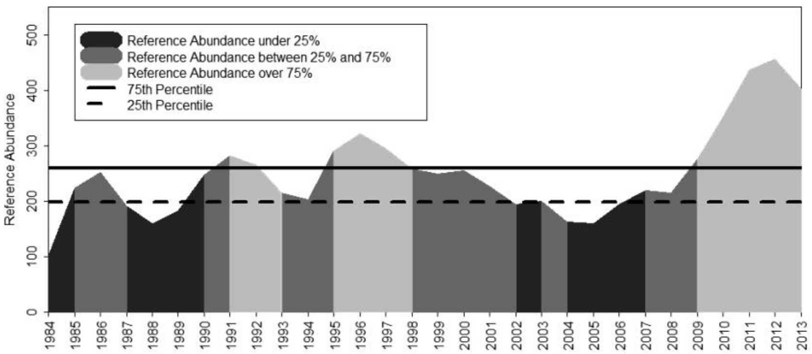


Figure II-2. Differences between objective function values (OFVs) for each LSA run with model-based indices from OFVs of the LSA run with design-based indices. The design-based OFV was 67 777.7. OFVs for each model-based run are displayed inside their respective bars. The *X* axis denotes each LSA run as "*A*/*B*", where *A* represents the density covariates used in index calculation and *B* represents the catchability covariates used. X = none, T = bottom temperature, D = depth, TD = temperature and depth. Order of indices left to right represent highest to lowest differences. All OFVs from LSA runs using model-based indices were higher than those using the design-based indices, making the design-based the optimal model using OFV as the indicator.



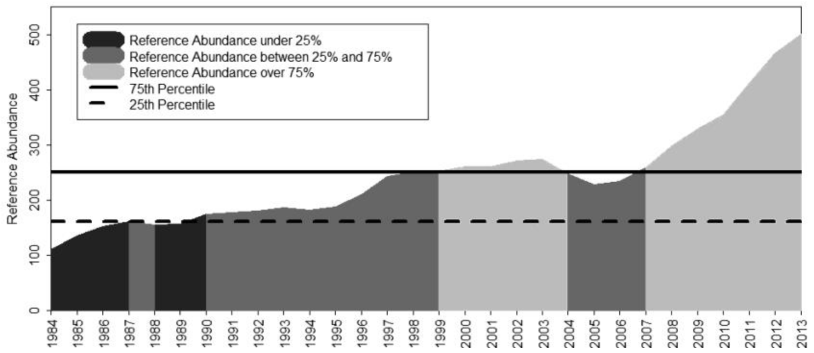


Figure II-3. Reference abundance 1984–2013 for the optimal model (top panel) and design-based model (bottom panel). Biological reference points (BRPs) are calculated separately for each model. Numbers are in millions of individuals.

Section III. Evaluating consequences of lobster-environmental model assumptions when projecting habitat suitability

Relationships between lobster survey catch and environmental conditions were used to estimate and forecast lobster habitat suitability using a bioclimate model under a future warming schema. Furthermore, we employed use of "what-if" scenarios in an attempt to determine how changes in model assumptions changed bioclimate model output.

The bioclimate model used in this study was developed by Tanaka and Chen (2015; 2016). It can determine spatially explicit changes in habitat suitability over time from regional environmental conditions using relationships between lobster survey catch and environmental variables and extrapolating onto grids with environmental data independent of those used in determining the relationships.

Bottom temperature and bottom salinity anomalies from the IPCC were used to estimate future bottom temperature and salinity fields through a downscaling process known as the delta method: a commonly used and robust statistical approach (Hare et al. 2012; Tanaka et al. 2020) shown to reduce bias in these types of estimations (Navarro-Racines et al. 2020). Lobster habitat suitability index (HSI) values for each sex, season, and life stage were then calculated for each field. Each HSI field was mapped using ordinary Kriging.

A what-if scenario in the context of this study was an experimental simulation of the bioclimate model in which one aspect of the input data is altered from the base case. Thus, all changes made were to the calculation of SIs and extrapolation grids, not to our forecasting methodologies. The intent of these scenarios was to determine changes in model output and to infer larger possible effects on fisheries management. There were seven what-if scenarios tested in this study:

- *Scenario 1: Model-Generated vs. Interpolated Environmental Data.*
- *Scenario 2: Full vs. Partial Spatial Coverage of Survey Data.*
- *Scenario 3: Stock-wide vs Species-wide Suitability Indices.*
- *Scenario 4: Inclusion vs. Exclusion of Important Components of Habitat.*
- *Scenario 5: Seasonal vs. Annual Suitability Relationships.*
- *Scenario 6: Separate vs. Combined Sexes.*
- *Scenario 7: Separate vs. Combined Life Stages.*

Considering the base case, inshore habitat (and Georges Bank to some extent) appeared more preferential than offshore habitat, with the highest HSI values found in the inshore eastern GOM (Figures III-1, III-2). Additionally, spring had higher HSIs than the fall for all combinations of sex and life stage for both the historical reference period and the future scenario. Differences between sexes and between life stages appeared negligible. The trends discussed previously remained largely constant from the base case through the remaining scenarios, with each scenario causing small intuitive changes in HSI based on variables considered.

Input data used in this type of HSI modelling shapes the inherent biological and population assumptions that govern model predictions: the input data chosen is a consequence of the researcher's assumptions (Rolaff and Kernohan 1999). This study further asserts that in these types of situations, biological realism must be determined a priori by the researcher as there is a lack of reliable metrics to determine this from bioclimate model results. It is shown here that alterations to this assumed realism as was done in the "what-if" scenarios have potential to severely impact model output and thus negatively impact fisheries management decisions. Direct comparisons to explain this point can only be done with a stock or population that is well described with associated data and a large knowledgebase explaining its function. These features made American lobster in the GOM an ideal testbed for the scenarios evaluated in this research framework, especially those that were known to be biologically unrealistic prior to testing.

The American lobster fishery in the GOM is expected to change due to shifting environmental conditions. Historically, the bulk of fishing effort has been concentrated in the summer and fall months (Boenish and Chen 2018), targeting the lobster when they are in shallower waters. This may be expected to shift later into the fall as spring HSI decreases and fall HSI increases. This is due to lobsters' propensity to behaviorally thermoregulate by following suitable thermal habitats inshore in the spring and offshore in the fall (Aiken and Waddy 1986; Crossin et al. 1998). Initially, the downward trends over time for HSI in the spring seemed to be consistent with upwards trends in the fall in this study. However, the spring forecasts show a loss of the best environments for lobster over time (complete loss of "excellent" habitat and halving of "good" habitat), whereas the fall is simply gaining new areas of "fair" habitat. Thus, overall suitability in the GOM is expected to decline out to 2099. This, coupled with the fact that areas with the most suitable habitat historically seem to be the areas most affected by a changing environment, illustrates a scenario similar to what happened to the lobster population and fishery in SNE where climate change has partially led to low recruitment and subsequent fishery collapse (Howell 2012; ASMFC 2015). Climate change is predicted to negatively alter the suitability of habitat for lobster in the GOM and this poses a threat to the future of the fishery in this region.

The non-lobster specific results have led to four separate discussions, each of which is summarized here. Choice of the type of extrapolation data for environmental covariates used in the HSI process can ultimately affect results, but in often unpredictable ways. Spatial and temporal scales are exceedingly important and data from outside extrapolation areas should never be used to generate suitability indices for inside the area. If seasonality is important in the target population, than it must be considered in the bioclimate process. Exclusion of important habitat variables can lead to severe under or overestimations of future habitat change and careful a priori decisions about these variables must be made. If there exist differences in environmental preference between sexes or life history stages, these may or may not be important depending on the scale of the analysis. However, unlike the other problems discussed thus far, conducting an analysis of separate life history groups can determine whether that action is appropriate for the final model.

GOM lobster is a very well-studied, well surveyed, and data-rich species (Chen et al. 2006; ASMFC 2015; Hodgdon et al. 2020). In this sense, it is different from many other economically important species across the oceans. This inherent knowledge of GOM lobster dynamics and life history provided insight into the appropriate model assumptions and input data. For species with a lack of biological knowledge or data availability, it can be more treacherous to calculate and forecast HSIs. Biological realism would be harder to interpret and understand, potentially leading to inherently less than accurate information about the target species habitat and misleading interpretations of forecasts. Data input and their inherent assumptions when forecasting HSI should be as biologically realistic as possible.

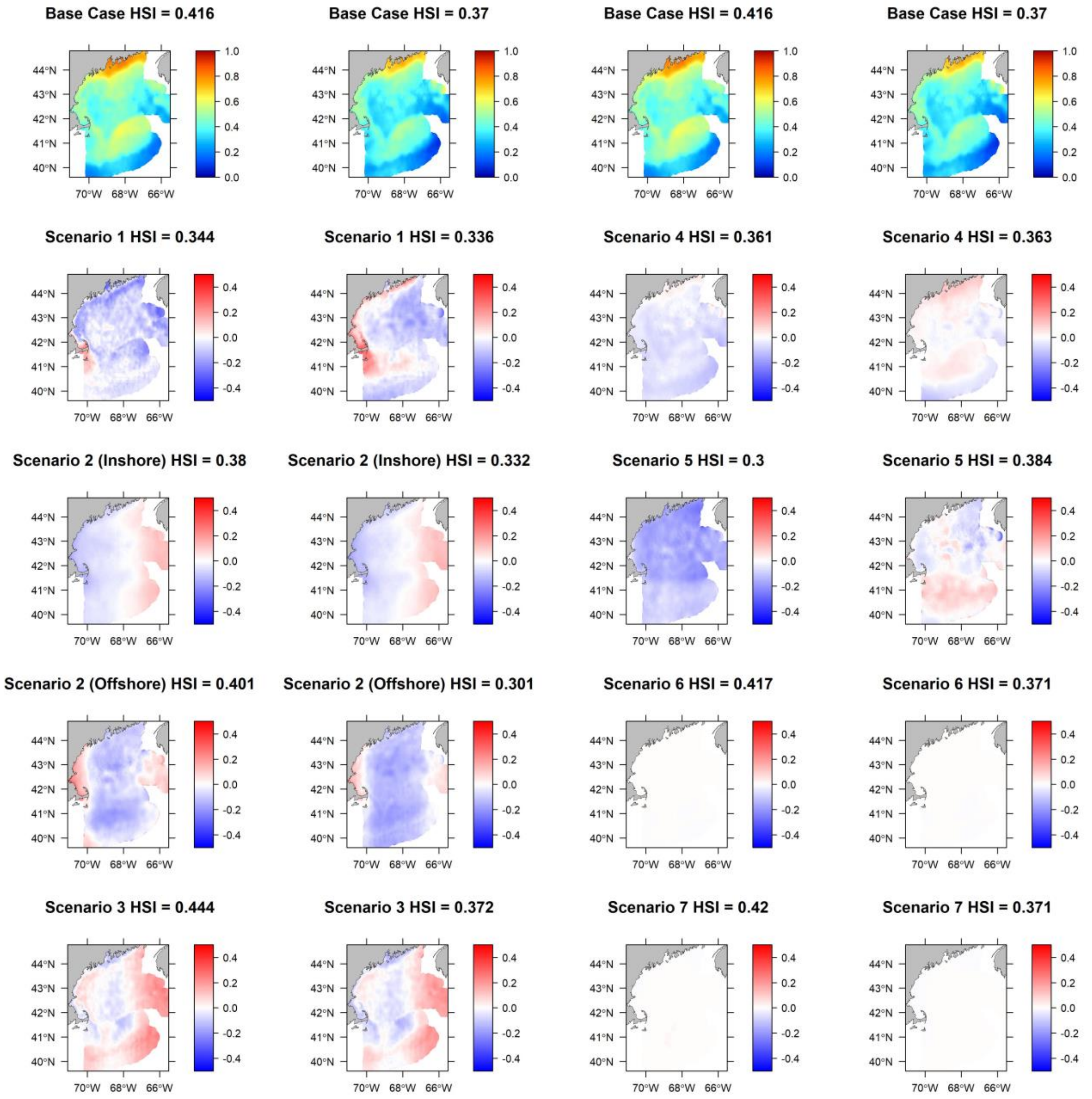


Figure III-1. Spatial HSI from the base case (Row 1) for the historical period (Columns 1 and 3) and the future period (Columns 2 and 4) as well as spatial differences for each of the seven scenarios (Rows 2 through 5) to their respective base case maps in row 1 (Note that the base case maps in columns 1 and 3 are the same and those in columns 2 and 4 are the same). Blue represents areas in a given scenario that were predicted to have a lower HSI than the base case did. Red represents areas in a given scenario that were predicted to have a higher HSI than the base case did. The darker the respective shade, the greater the difference from the base case. Above each map is the scenario name and the average spatial HSI for that period and scenario. Results are for spring female adults. Note scenario 5 is combined seasons, scenario 6 is combined sexes, and scenario 7 is combined life stages.

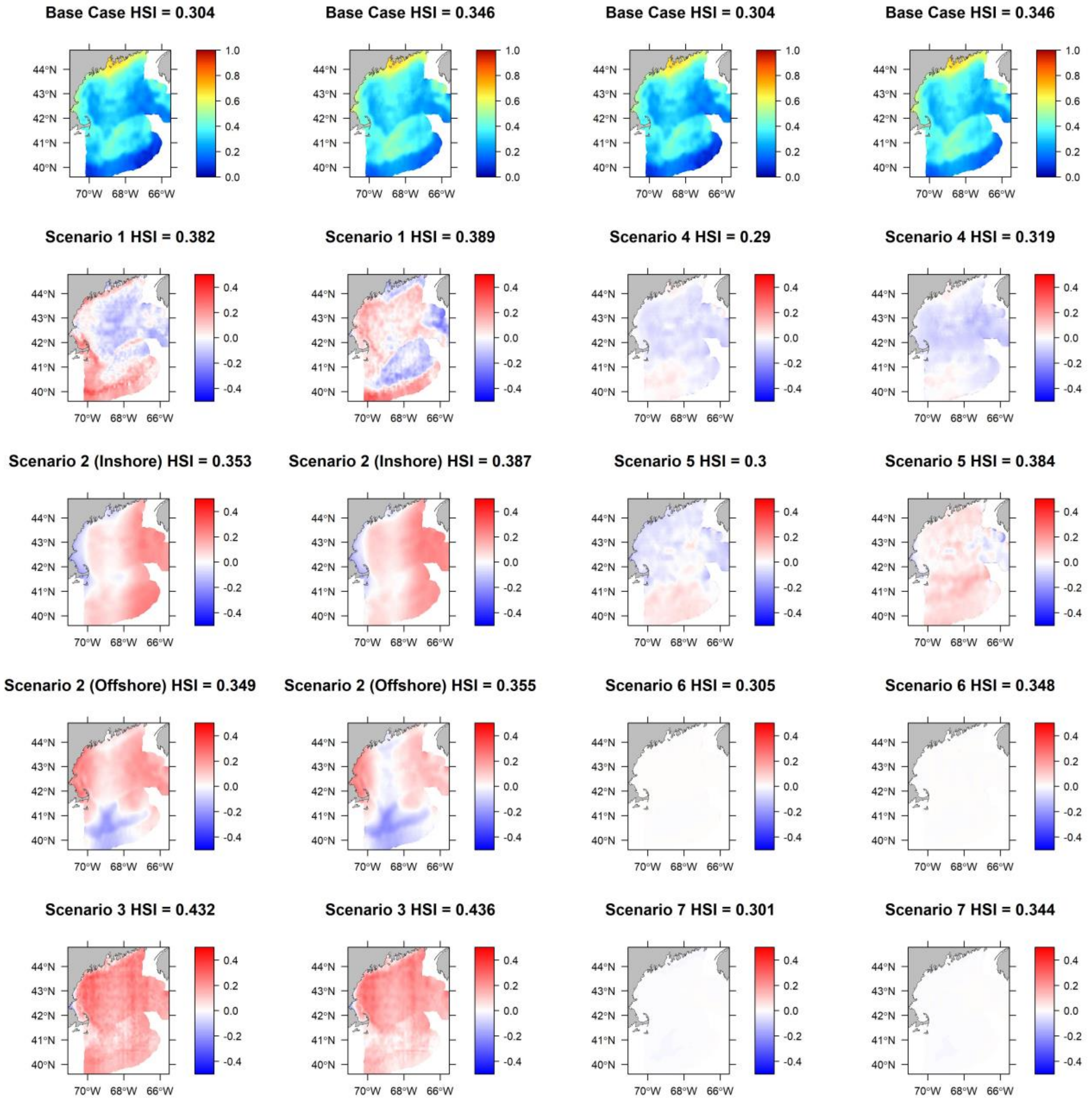


Figure III-2. Spatial HSI from the base case (Row 1) for the historical period (Columns 1 and 3) and the future period (Columns 2 and 4) as well as spatial differences for each of the seven scenarios (Rows 2 through 5) to their respective base case maps in row 1 (Note that the base case maps in columns 1 and 3 are the same and those in columns 2 and 4 are the same). Blue represents areas in a given scenario that were predicted to have a lower HSI than the base case did. Red represents areas in a given scenario that were predicted to have a higher HSI than the base case did. The darker the respective shade, the greater the difference from the base case. Above each map is the scenario name and the average spatial HSI for that period and scenario. Results are for fall female adults. Note scenario 5 is combined seasons, scenario 6 is combined sexes, and scenario 7 is combined life stages.

The work in the Chen Lab continues beyond this research grant. There are ongoing projects focused on lobster life history in the context of changing environments. One such project is determining how stock assessment modelling may be affected by shifting growth and size-at-maturity in relation to lobster and another is focused on establishing relationships between spawning biomass, recruitment, and thermal habitat.

Section IV. Examining scale-dependent nonstationary environmental effects on American lobster spatial distribution and habitat suitability

IV-1. Introduction

Knowing that the American lobster fishery is the most valuable fishery and that species' distributions commonly shift in pursuit of ideal habitat conditions (Pinsky et al., 2013; Greenan et al., 2019), it is important to understand and accurately estimate the spatial distribution of this species, especially in a rapidly changing environment.

Although the GOM/GBK lobster stock is not overfished and overfishing is not occurring (ASMFC, 2020), lobster abundance throughout the GOM is not uniformly or randomly distributed (Steneck & Wilson, 2001). Environmental factors contribute to the spatial distribution of lobster abundance, and evidence of temperature, salinity, and productivity gradients that range from northeast to southwest GOM have been observed (Lynch et al., 1997; Pettigrew et al., 1998; Chang et al., 2016). These gradients may be attributed in part by the Gulf of Maine Coastal Currents (GMCC), which form cyclonic currents across the GOM (Townsend et al., 2015; Chang et al., 2016). The GMCC can be further distinguished as two sub currents; the Eastern Maine Coastal Current (EMCC) and the Western Maine Coastal Current (WMCC), where the EMCC diverges offshore in the Penobscot bay area and the WMCC begins along the coast (Xue et al., 2008; Chang et al., 2016). These currents can affect environmental variables as well as processes and interactions such as primary production levels, stock-recruitment relationships, and vertical mixing (Incze et al, 2010; Chang et al., 2016).

Species distribution models (SDMs) are widely used to estimate and predict organisms' spatial and/or temporal distributions across the world (Bakka, 2016; Diarra et al., 2018; Becker et al., 2020). Spatial and/or temporal nonstationarity is often present in ecological systems when relationships between response and explanatory variables vary across space and/or time, which means that the association between response and explanatory variables decrease with increasing distance (Brunsdon et al., 1996; Fotheringham et al., 2002). Past literature has demonstrated evidence of spatial nonstationarity in the GOM region (Li et al., 2018; Staples et al., 2018). Accounting for nonstationarity in SDMs allows for the incorporation of spatial and/or temporal dependencies that cannot be explained by environmental variables alone (Bakka et al., 2016). However, past literature often have not utilized SDMs in ways that can account for spatial and/or temporal nonstationary processes (Gorman et al., 2013; Chang et al., 2016; Becker et al., 2020) .

Generalized linear models (GLMs, Nelder and Wedderburn, 1972), generalized additive models (GAMs; Hastie and Tibshirani, 1986), and geographically weighted regression (GWR; Brunsdon et al., 1996) are a few commonly used models for estimating species distributions. Inherently, GLMs and GAMs are stationary models because they estimate global relationships between the response and explanatory variables that are applied to all locations. In contrast, GWR models can estimate unique parameters at each location across space, thus allowing for the assumption of spatial nonstationarity to be met (Charlton & Fotheringham, 2009). However, a limitation of GWR models is that they cannot be used to make estimations outside the study area (extrapolation) or for forecasting to novel periods, as doing so would violate the assumption of nonstationarity one is trying to meet (Osbourne et al., 2007; Hothorn et al., 2011; Li et al., 2018). Since extrapolation and forecasted estimations are often desired when modeling species distributions, one recommended approach is to utilize multiple stationary models across a region of interest (Fortheringham et al., 2002; Windle et al., 2009). This approach will not only allow for extrapolation and forecasting procedures, but also better account for assumptions of nonstationarity as using more than one model will result in multiple unique parameters estimated across localized areas.

We explore the effects of nonstationary modeling on lobster spatial distributions and compare the results to those of a stationary model. To test the effects of spatial nonstationarity, we develop season-, sex-, and size- specific models that predict the spatial distribution of American lobsters using GAMs of varying spatial scales and extents. Variation in spatial distribution between the models is evaluated and potential management implications are discussed.

IV-2. Methods and materials

IV-2-1. Data

American lobster abundance data were sourced from the Maine-New Hampshire Inshore Bottom Trawl Survey. The Maine-New Hampshire Inshore Bottom Trawl Survey will be referenced as the bottom trawl survey. The bottom trawl survey has been conducted by the Maine Department of Marine Resources (DMR) since the fall of 2000. This survey is semiannual, where separate surveys are conducted in the fall and spring seasons of each year. The bottom trawl survey spans 4,665 square nautical miles (16000.5 km^2) (Sherman et al., 2005) and is subdivided into five regions (Figure IV-1). The five regions include (1) New Hampshire and Southern Maine, (2) Mid-Coast Maine, (3) Penobscot Bay, (4) Mt. Desert Island, and (5) Downeast Maine (Figure IV-1).

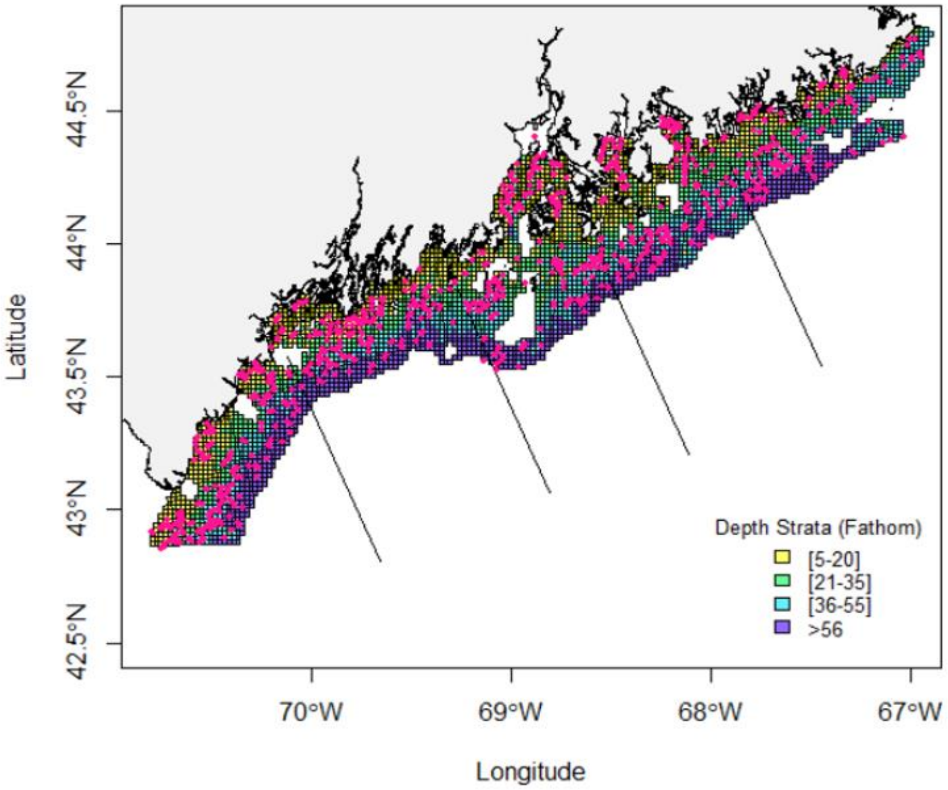


Figure IV-1: Maine-New Hampshire Inshore Bottom Trawl Survey regions and depth strata. This survey is subdivided into five regions which include (1) New Hampshire and Southern Maine, (2) Mid-Coast Maine, (3) Penobscot Bay, (4) Mt. Desert Island, and (5) Downeast Maine. White spots are areas where the survey are not able to sample due to oceanographic or topography limitations. Pink points are previous trawl sample locations from the 2000-2019 surveys.

The survey area extends 12 nautical miles (22.22 km) offshore and is broken up into 4 different strata (Figure IV-1). A target of 115 stations is set for each survey, creating a sampling density of roughly 1 station for every 40 NM^2 (137.20 km^2). Random stations in this survey are chosen by dividing the survey area into a 1NM^2 (3.43 km^2) grid, where cells are chosen at random using an Excel random number generator (Sherman et al., 2005). The data used in this study only included random stations, as fixed stations were removed from the surveys over time because they caused inconsistencies between years (R. J. Peters, personal communication, February 24, 2020). Each survey aims for a target tow of 20 minutes at a speed of 2.2-2.3 knots (4.1-4.3 km/h), which covers approximately 0.8 NM (1.48 km). Data from 486,971 individual lobsters were included in this study.

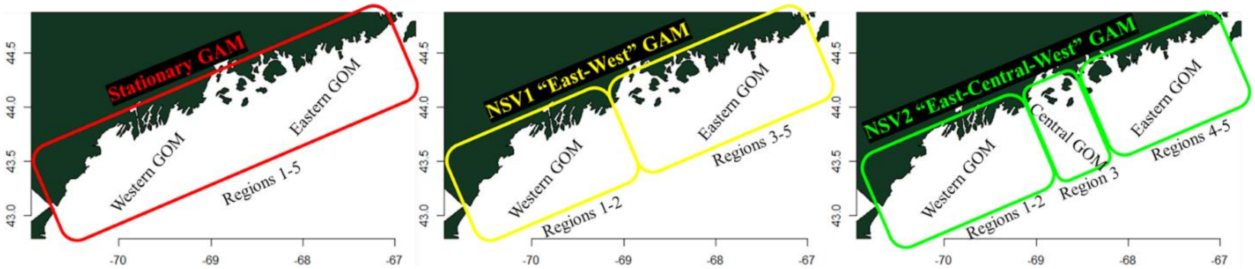


Figure IV-2: Visual representation of each model utilized in this study. Each colored rectangle represents a separate GAM that was run on the observed data points contained within that area/ regions of the ME-NH Bottom Trawl Survey.

This study utilizes data from the 2000-2019 bottom trawl surveys. Biological data taken on each lobster include carapace length (mm), sex, presence of eggs or v-notches, and if any noticeable damage is present. Lobsters are then sorted into baskets by sex and baskets are weighed once filled (Sherman et al., 2005). Data have been standardized to twenty-minute tows to ensure all catch, weight, and length frequency information is comparable. In addition to biological data, bottom water salinity, bottom water temperature, and depth data were collected during each tow by using a Sea-Bird ElectronicsTM 19plus SEACAT profiler, which was attached to the starboard door wire, turned on and lowered overboard (Sherman et al., 2005). The net used for this survey is a type of modified shrimp net that is used for "near-bottom dwelling species", although not intended for any single species in particular (Sherman et al., 2005). More information about the Maine-New Hampshire Inshore Bottom Trawl survey procedures, protocols, or specifics can be found in Sherman et al. (2005). This survey has been found to yield informative data for studying lobster distributions and habitats in the GOM (Tanaka & Chen, 2016; Tanaka et al., 2019; Hodgdon et al., 2020).

Bottom temperature, bottom salinity, average depth, latitude, and longitude information were used from the bottom trawl survey. Distance from shore and median sediment size were also estimated. Distance from shore was estimated using the "distances" function from the package "distances" (Savje, 2019) in R, which finds the shortest distance between points, in this case, the distance between the midpoint latitude and longitude of a tow and the closest point on the coast. Sediment data were sourced from the East-coast Sediment Texture Database which is run by the United States Geological Survey (USGS, 2014). This survey was last updated in 2014 and contains information such as location, description, texture, and size (phi, -log of grain size) taken by different marine sampling programs across various locations around the world. Both mean and median sediment size values are supplied in this dataset, but median sediment size was used over mean sediment size, as the former is more robust to outliers (Tůmová et al., 2019). The median grain size at each survey location was estimated using thin plate splines. These data can be found at https://woodshole.er.usgs.gov/openfile/of2005-1001/htmldocs/datacatalog.htm and More information about the East Coast Sediment Texture Database can be found in U.S Geological Survey (2014).

Although models were built using bottom trawl survey data, additional bottom water temperature and bottom water salinity data were needed to create interpolated distribution plots. Thus, bottom temperature and bottom salinity data throughout the study area were obtained by spatially interpolating Finite-Volume Community Ocean Model (FVCOM) data. The FVCOM is an advanced ocean circulation model that uses an unstructured grid format, making it highly applicable for use in regions with complex coastlines and bathymetry (Chen et al., 2006; Li et al., 2017). The FVCOM was developed by University of Massachusetts Dartmouth and Woods Hole Oceanographic Institution. More information about the FVCOM can be found in Chen et al. (2006).

Forecasted distributions were made for the period 2028-2055. The forecasted bottom temperature and bottom salinity data were sourced from the National Oceanic and Atmospheric Administration (NOAA) and represent an ensemble projection of all models used to create the Intergovernmental Panel on Climate Change's (IPCC) Coupled Model Intercomparison Project Phase 5 (CMIP5) data (available from https://psl.noaa.gov/ipcc/ocn/). Data for the Representative Concentration Pathway (RPC) 8.5 "business as usual" scenario were used. These data are forecasted *anomalies* based on the reference time period 1956-2005 and are estimated for the period 2006-2055. These data are anomalies, and thus hindcasted bottom temperature and bottom salinity data must be used in tandem from the same reference period. The earliest available FVCOM data begins in 1978 rather than 1956, limiting the available reference period in this study to 1978-2005. With the reference period reduced from 50 to 27 years, the CMIP5 forecasting period must also be reduced respectively, from the initial 2006-2055 to 2028-2055 for this study. The forecasting period 2028-2055 is used because it represents the maximum amount of FVCOM data that can be used while also confidently applying IPCC forecasted anomalies. Delta downscaling methods were also applied so that forecasted anomalies could be applied to the same scale as the FVCOM data. Specifically, bivariate spline interpolation was applied using the package "akima" in R (Akima and Gebhardt; 2016). A spatial resolution of 0.01 (1.11 km error) was used for all data to ensure comparability between datasets.

IV-2-2 Model Development

Lobster densities were standardized per tow and divided into eight groups based on season (fall and spring), sex (female and male), and size (adult and juvenile; Li et al., 2018; Chang et al. 2016). Juvenile lobsters were distinguished as lobsters with carapace lengths <50mm due to differences in activity patterns (Lawton & Lavalli, 1995). Each of the eight groups were modeled independently under 3 different techniques: (1) A generalized additive model (GAM) that assumes stationary relationships between a species density and environmental variables; (2) a GAM that assumes nonstationary density-environment relationships between eastern and western GOM (nonstationary version 1, NSV1), and (3) a GAM that assumes density-environment nonstationary relationships across eastern, central, and western GOM (nonstationary version 2, NSV2). Partitioning of data for these models can be visualized in Figure IV-2.

Previous literature in the GOM have estimated species distributions using stationary models at a large spatial scale (Chang et al., 2016; Becker et al., 2020). This technique is represented in this study by the "Stationary GAM" model, which assumes spatial stationarity and is applied at the largest spatial scale. This technique also assumes that nonlinear (but stationary) relationships between lobster density and environmental factors are sufficient to accurately predict a species spatial distribution across an ecologically complex region. Other literature has highlighted differences in environment-abundance relationships between localized regions (Li et al., 2018; Liu et al., 2019). Thus, the bisected (NSV1) and trisected (NSV2) models were

constructed at smaller spatial scales to capture evidence of these differences. The purpose of this study is to explore how spatial distribution predictions change under models with varying assumptions of nonstationarity (or lack thereof) in hindcasting and forecasting scenarios.
The first set of nonstationary models (NSV1) broke up the data into east and west zones. The western zone used data in regions one and two from the ME-NH bottom trawl survey (Figures IV-1 and IV-2). Eastern GOM was represented by data from regions three, four, and five in the trawl survey (Figures IV-1 and IV-2). The decision to split the data up in this way was driven by the GOM coastal currents and the supporting literature that states the southern extent of the EMCC *includes* the Penobscot Bay region (Xue et al., 2008; Chang et al., 2016).

Although some literature supports this decision, it is difficult to pinpoint a fine line of where the EMCC diverges and the WMCC begins. Thus, another argument can be made in which the Penobscot Bay area (≅region 3 in the bottom trawl survey) could act as a potential buffer zone, in which this area of possible mixing between currents could throw off GAM relationship curves if the this area were to be included into a particular side. One previous study has used a similar trisected approach to view relationships between initial intra-annual molts of American lobster and bottom temperatures in the GOM (Staples et al., 2018). Consequently, the NSV2 model is built in such way that regions one and two of the bottom trawl survey represent the western GOM, region three will have its own separate models built to represent central GOM (the buffer zone between the EMCC and WMCC; Figure IV-1), and regions four and five will represent eastern GOM (Figure IV-1).

Prior to model construction, covariance matrices and variance inflation factor (VIF) tests were run to check for variable independence and multicollinearity. Running multiple covariance metrics showed a high dependence between distance from shore and average depth variables. Distance from shore was kept over average depth because distance from shore had a lower covariance value amongst the rest of the variables than average depth. Variance inflation factors quantify the multicollinearity amongst variables. Variables with VIF numbers >3 were excluded from the model (Zuur et al., 2009), supporting the decision to remove average depth as a variable when building the models. VIF numbers larger than 3 were excluded because including highly correlated variables in the same model would be statistically similar to including a variable in the same model twice, which could lead to biased or incorrect model estimates (Gareth et al., 2014). The following variables were shown to be significant in every GAM: latitude and longitude combined as an interaction term, and bottom temperature. Bottom salinity, distance from shore, and sediment size were found to be significant in some models, but not all. Significant variables and deviance explained for each group are summarized in Tables IV-1 & IV-2, respectively.

Table IV-1: Non-Significant Variables for Each Model and Group Type. Group acronyms are denoted as follows: FL= fall, SP= spring, FJ= female juvenile, FA=female adult, MJ=male juvenile, MA= male adult. Such that for example FLFJ represents data taken from female juvenile lobsters in the fall season. "AS"= all significant, meaning all tested variables were significant to that particular model and group. "DFS"= distance from shore variable. "Sediment"= median sediment size variable, and "Salinity" = bottom salinity variable.

Group	**Traditional GAM**	**NSV1 (East)**	**NSV1 (West)**	**NSV2 (East)**	**NSV2 (Middle)**	**NSV2 (West)**
FLFJ	Salinity	Salinity	Sediment	Salinity	Salinity, DFS	Sediment
FLMJ	AS	Salinity	Sediment	Salinity	Salinity	Sediment
FLFA	Salinity	Salinity	Sediment	AS	Salinity, DFS, Sediment	Sediment
FMLA	Salinity	AS	Sediment	AS	Salinity, DFS	Sediment
SPFJ	AS	AS	AS	AS	Salinity, Sediment	AS
SPMJ	AS	AS	Sediment	AS	Salinity, Sediment	Sediment
SPFA	AS	AS	AS	AS	Salinity, Sediment	AS
SPMA	AS	AS	AS	AS	Salinity, DFS	AS

Table IV-2: Deviance Explained for Each Model and Group Type. See Table IV-1 for group acronym explanation.

Group	**Traditional GAM**	**Average NSV1**	**NSV1 (East)**	**NSV1 (West)**	**Average NSV2**	**NSV2 (East)**	**NSV2 (Middle)**	**NSV2 (West)**
FLFJ	40.0%	52.5%	52.8%	52.2%	62.1%	62.3%	71.8%	52.2%
FLMJ	40.7%	52.5%	52.8%	52.2%	63.2%	63.7%	73.6%	52.2%
FLFA	42.6%	51.8%	47.9%	55.6%	56.3%	57.7%	55.7%	55.6%
FLMA	41.7%	51.9%	49.2%	54.6%	55.6%	56.6%	55.5%	54.6%
SPFJ	41.7%	51.9%	47.6%	56.1%	56.8%	48.5%	65.8%	56.1%
SPMJ	44.0%	52.5%	50.5%	54.5%	58.1%	52.6%	67.1%	54.5%
SPFA	34.4%	36.2%	35.0%	37.3%	40.9%	37.3%	48.2%	37.3%
SPMA	38.8%	39.8%	41.8%	37.7%	44.5%	45.7%	50.6%	37.7%

Generalized Additive Models (GAMs) were used to evaluate the relationships between lobster abundance and environmental variables. A GAM is an extension of a generalized linear model, with a smoothing function added. GAMs follow the assumptions that the functions are additive, and the components of the functions are smooth (Guisan et al., 2002). A separate GAM was created for each group of lobsters that differs in season, sex, and size, based on the assumption that males, females, juveniles, and adults will all respond to environmental variables differently, and that seasons will also impact the relationships with the environment differently. We used a tweedie GAM to estimate lobster abundance (y). GAMs were built using a backward fitting technique based on covariate significance ($p<0.05$; Chang et al., 2016). A GAM using all potential environmental variables can be written as:

$$\text{Lobster abundance } (y) = s(La, Lo)+s(Bt)+s(Bs)+s(DFS)+s(Ss)$$

where s is a spline smoother, La, Lo is an interaction term between latitude and longitude, Bt is bottom temperature (°C), BS is bottom salinity (ppt), DFS is distance from shore (decimal degrees), and Ss is median sediment size (phi).

Hindcasted distribution plots were created for each lobster season x sex x size group and for each model for the years 2000, 2006, 2012, and 2017 for a total of 98 plots. Although there are bottom trawl survey data available from 2000-2019, environmental FVCOM data used is only available until 2017, limiting the most recent available hindcasting year that can be spatially interpolated to 2017. Additionally, these years were chosen because they are roughly evenly spaced throughout the hindcast period of interest, albeit these methods could be applied to any year(s) 2000-2017. Forecast distribution plots were also estimated for the 2028-2055 year period, for a total of 24 forecast distribution plots. Differences between stationary and nonstationary approaches were determined by calculating relative differences between density distribution estimates. Relative differences were estimated using the equation

$$\text{Relative difference (i)}=\frac{nonstationary\ estimated\ density\ (i)-stationary\ estimated\ density}{(i)stationary\ estimated\ density\ (i)100}$$

where *i* is a location within the study area and “nonstationary” represents the estimated lobster density from either the NSV1 or the NSV2 model. Relative difference plots were generated for each lobster season x sex x size group and for the same years as the hindcast and forecast distribution plots. These plots demonstrate the magnitude and location of where the stationary models tend to over or under predict abundances in relation to the other approaches. All distribution and relative difference plots were interpolated using bivariate splines using the package “akima” in R in order to achieve high resolution smooth distributions (Akima and Gebhardt, 2016).

After calculating the relative differences between stationary and nonstationary models, the interquartile ranges (IQRs) of the relative differences were calculated for each localized region. The interquartile range represents the middle 50% of the data (e.g. IQR≅ -2 to 13%), where the first number listed represents quartile one and the second number listed represents quartile 3. The IQR can be found by subtracting quartile 1 from quartile 3. Negative quartile numbers quantify how much the stationary model predicted higher density estimates than the nonstationary model (in percent relative difference), while positive quartile numbers quantify how much the stationary model predicted lower density estimates than the nonstationary models (in percent relative differences). For example, an IQR≅ -2 to 13% would indicate that quartile 1 is at -2% and quartile 3 of the data is at 13%. This means that the middle 50% of data for this region ranges from a 2% relative overestimation to a 13% underestimation of lobster densities by the stationary model, when compared to the nonstationary model. This also indicates that the majority of the IQR in this region is positive, suggesting that the stationary model tends to estimate lower densities than the nonstationary model in this region.

IV-2-3 Model fitting and validation

Root Mean Square Error (RMSE), Akaike Information Criterion (AIC), and Moran’s I were used to access model fit for all models. RMSE measures the differences between predicted and observed values where values closer to zero represent better model fit (Stow et al., 2009). AIC is another method to test goodness of fit and model complexity with a model having smaller returned AIC value being the better model (Zuur et al., 2009). Moran’s I tests for spatial autocorrelation in residuals where a significant Moran’s I of -1 signifies perfect clustering of dissimilar values, a significant Moran’s I value of 0 signifies no autocorrelation, and a significant Moran’s I of +1 signifies perfect clustering of similar values. If values are found to be spatially autocorrelated, this is an issue as it violates the assumption of independence of data (Zuur et al., 2009; Stephanie, 2016). Additionally, two-fold cross validation was performed by separating each of the 8 groups’ (2 season x 2 sexes x 2 sizes) data into random training and a testing subset to calibrate the model and validate its predictions (Li et al., 2018). The percentage of data allocated for the testing portion was determined by the equation

$$1/(1+\sqrt{P-1})$$

where *P* is the number of predictor variables (Franklin, 2010; Li et al., 2018). Cross validation allows visualization of model performance to examine if model predictions are on average, over or under predicting abundance compared to observed values. 100 iterations of cross validation were repeated for each model group and average performance was estimated.

IV-3 Results

IV-3-1 Model Performance and Validation

Significant variables differed between model types and between groups. Under the stationary model, only salinity was found to be non-significant in some groups, whereas both salinity and sediment size were found to be non-significant in some NSV1 model groups. Moreover, salinity, sediment, and distance from shore were found to be non-significant in some NSV2 model groups. Table IV-1 summarizes the non-significant variables which were not included in the final model for each group and spatial scale. The deviance explained for lobster abundance varied between 34.4 - 44.0% for each group of the stationary GAM, 36.2 - 52.5% for the average NSV1 group, and 40.9 - 63.2% for the average NSV2 group. Full deviance explained for each specific group can be found in Table 2.2. Likewise, the RMSE, AIC and Moran's I tests showed similar trends in model fit, with the stationary GAM demonstrating the lowest model fit estimates, the NSV1 model demonstrating intermediate model fits, and the NSV2 model demonstrating the greatest model fits (Table IV-3).

Table IV-3: RMSE, Moran's I, and AIC Values for Each Model and Group Type. "SG" = "Stationary GAM". See Table 2.1 for group acronym explanation. RMSE values closer to zero represent better model fit. Moran's I tests for spatial autocorrelation in residuals where significant values closer to 0 signifies no autocorrelation. All reported Moran's I values were significant ($p<0.05$). Smallest AIC values also indicate a better model.

Group	**SG RMSE**	**NSV1 RMSE**	**NSV2 RMSE**	**SG Moran's I**	**NSV1 Moran's I**	**NSV2 Moran's I**	**SG AIC**	**Average NSV1 AIC**	**Average NSV2 AIC**
FLFJ	1.67	1.53	1.44	0.51	0.42	0.16	9,009	4,341	2,757
FLMJ	1.67	1.54	1.43	0.49	0.38	0.14	8,978	4,327	2,736
FLFA	1.29	1.17	1.09	0.45	0.32	0.07	14,398	7,064	4,585
FLMA	1.24	1.12	1.06	0.43	0.30	0.07	14,428	7,069	4,597
SPFJ	1.68	1.57	1.51	0.51	0.41	0.17	10,256	4,950	3,121
SPMJ	1.67	1.58	1.52	0.46	0.37	0.15	10,011	4,884	3,060
SPFA	1.49	1.37	1.32	0.29	0.22	0.09	19,279	9,548	6,087
SPMA	1.41	1.32	1.28	0.28	0.22	0.09	19,124	9,480	6,055

The two-fold cross validation results from 100 iterations revealed that the models had reasonable prediction skill, as the average between the 100 iterations was near the 1:1 prediction line for most groups and models. These tests revealed that most models tended to slightly underpredict abundance, with exception of the average spring female adult (SPFA) NSV1 model which revealed average slight overpredictions. NSV2 model cross validation results demonstrated more precision than NSV1 or stationary model results. Results from the two-fold cross validation can be found in the supplementary material section (Supplementary Figures A.3-A.5 in Behan 2021).

IV-3-2 Environmental and Spatial Variables

Environmental and spatial variables were also explored via GAM response curves for each significant predictor variable. Latitude and longitude variables were combined as an interaction term in each model to help account for spatial autocorrelation (Siegel and Volk, 2019). Response curves varied greatly depending on independent variable, season, sex, size, and spatial scale of the model. For bottom temperature, highest partial effect on abundance was seen between 6-10 ℃ in the spring and around 10-14 ℃ in the fall for stationary models, and between 4-10 ℃ in the spring and 10-14 ℃ in the fall for nonstationary models. For bottom salinity, highest abundance was seen between 31-33 psu for both spring and fall across all models. The relationship spring male adult (SPMA), spring female juvenile (SPFJ), and spring male juvenile (SPMJ) groups had with salinity was unique, compared to other groups. These group's response curves demonstrated a higher partial effect on abundance at salinity levels >32 psu in the west. This may help explain the distinctive relative difference trends generally observed in western GOM for the SPMA group. This difference did not seem to affect the spring juvenile groups, as juvenile lobsters tend to stay in more nearshore waters (Lawton and Lavalli, 1995), where FVCOM data has shown salinity levels are generally lower in western GOM. For distance offshore, highest partial effect on abundance was seen generally between 0.00-0.1 decimal degrees (≅0-6 nautical miles offshore), and then gradually declined with increasing distance from shore across most models. For sediment size, highest partial effect on abundance was seen between 2-6 phi (silt - medium grain sand) across most models. Some season, sex, and size group curves changed more in shape across spatial extents than others, but variation was apparent and supports evidence of spatial nonstationarity in this region.

Figure IV-3 depicts the response curves between lobster abundance and bottom temperature for spring male adults (Figure IV-3A & 3C) and fall female juveniles (Figure IV-3B & 3D). These figures show how the response curves change, depending on the spatial scale and location of the testing data. These figure panels also show where estimated relationship curves overlap, if at all. For example, in Figure IV-3C, one can see high overlap between most model response curves between 5-7 ℃. However, at temperatures greater than 7 ℃, the relationship curve for the stationary GAM more closely resembles that of the response curve for the eastern GOM than for the western or central GOM. This suggests that if a stationary model were used to represent spring male adult lobster data, it would better represent eastern GOM data than central or western GOM data in that temperature range, and in a climate warming scenario, would underestimate western GOM abundances. In a region which is expected to continue experiencing warming temperatures, the implications of subordinate model spatial scale selection may increase. Many lobster groupings (season x sex x size) tended to show similar patterns, where the stationary GAM response curve for a variable, more closely resembled the response curve of one localized region of the GOM more than the other regions.

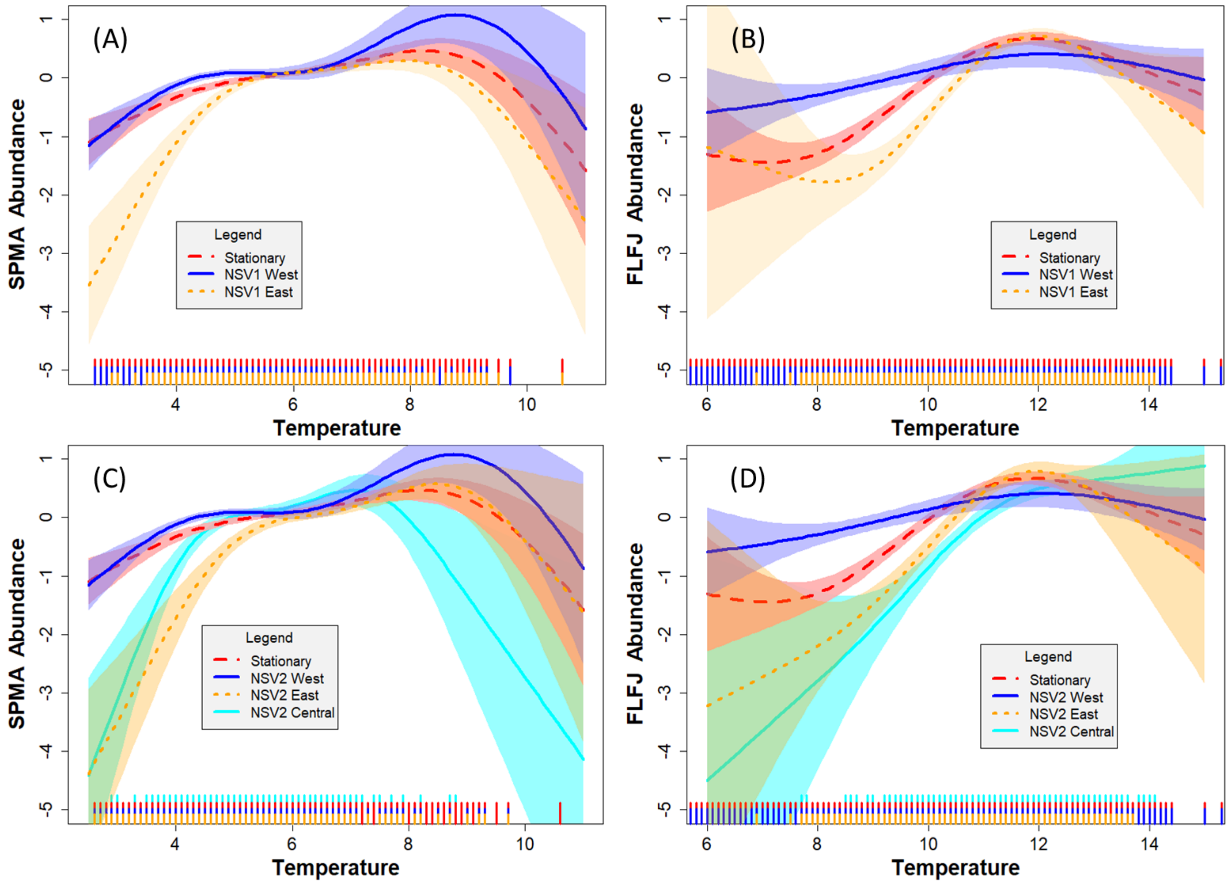


Figure IV-3: A comparison of spring male adult (SPMA) and fall female juvenile (FLFJ) lobster GAM bottom temperature response curves to by spatial location in the GOM. Each plot shows the response curve of bottom temperature (°C) on the x-axis, against the partial effect of lobster density on the y-axis. Figure panels (A) and (C) compare response curves estimated for the stationary model and eastern and western NSV1 models, while figure panels (B) and (D) compare response curves estimated for the stationary model, and eastern, central, and western NSV2 models. Shaded regions on either side of the response curve line indicate the standard error confidence intervals. Rug plot lines along the x-axis of each plot indicate distribution of the bottom temperature data.

IV-3-3 Model Prediction and Distribution Plots

Fall distribution plots showed greater abundance estimates than spring plots, which correlates with observations in raw trawl survey data. Raw fall trawl survey trends show slight declines in catch in regions 3 and 4 since 2015 and in region 5 since 2016 (Supplementary Figure A.1; Behan 2021), with trends of offshore catch increasing overtime. All three model estimates demonstrated offshore abundance estimates increasing from the 2012-2017 hindcasts, but only the NSV2 model showed indications of a slight decrease in eastern GOM abundance. Model estimates in central GOM were most distinctive between models. A trend emerged in all tested years which demonstrated that as model spatial scale became finer, clear “hot” and “cold” spots emerged within the Penobscot Bay area. The NSV2 model showed this pattern well, with a “hotspot” emerging along the southwest mouth of Penobscot Bay, and a “coldspot” in the northeast Penobscot Bay region (Figures IV-4 – IV-7). These patterns correlate well with American lobster settlement patterns found in Steneck and Wilson (2001), as well as estimated spawning stock sizes in Chang et al. (2016).

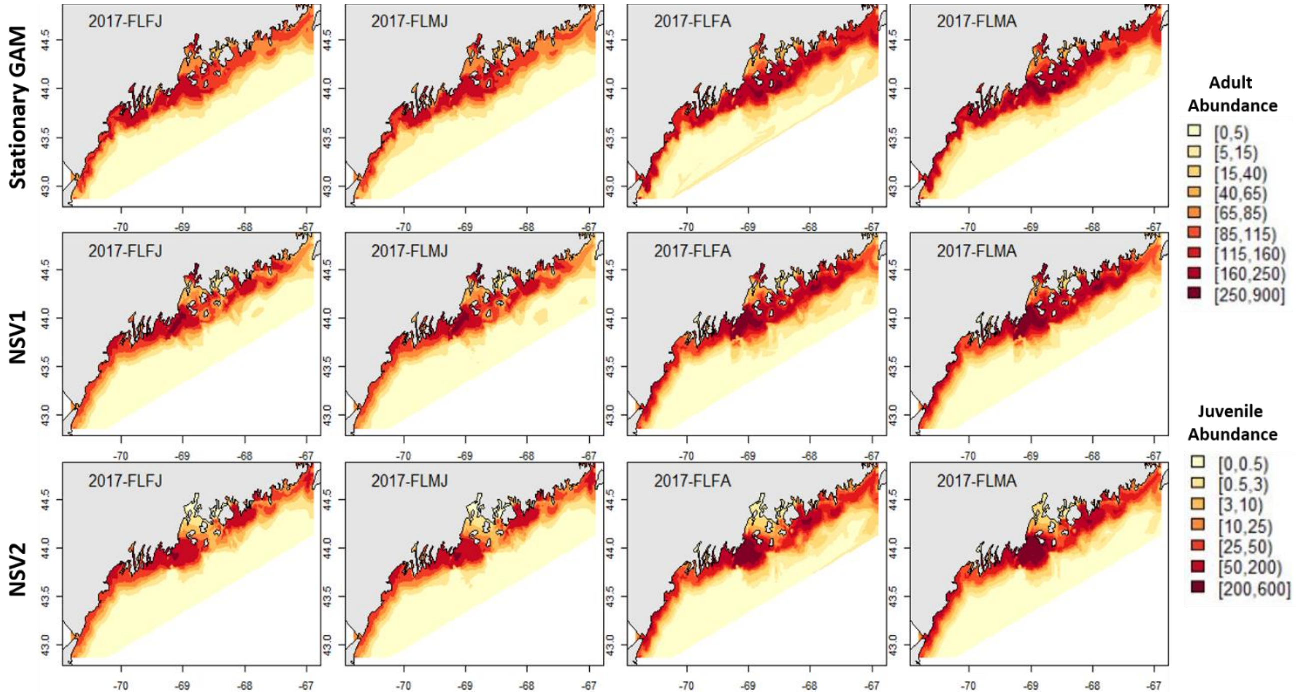


Figure IV-4: 2017 fall American lobster estimated spatial distribution. Legend colors increase in abundance estimates from pale yellow to dark red. Each column represents a season x sex x size group. Each row represents the model type used to generate the abundance estimations. Adult abundance legend corresponds with adult lobster group estimates. Juvenile abundance legend corresponds with juvenile lobster group estimates.

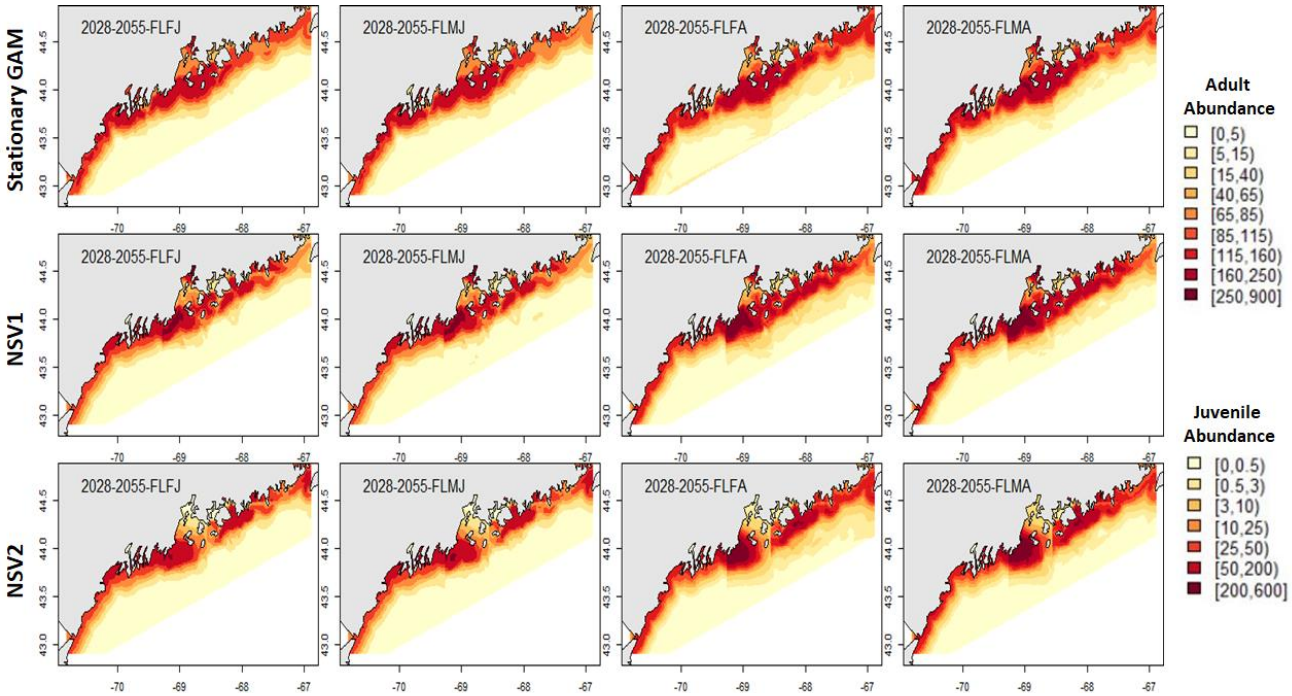


Figure IV-5: Forecasted fall American lobster estimated spatial distribution for the time period 2028-2055. See Figure IV-4 for figure details.

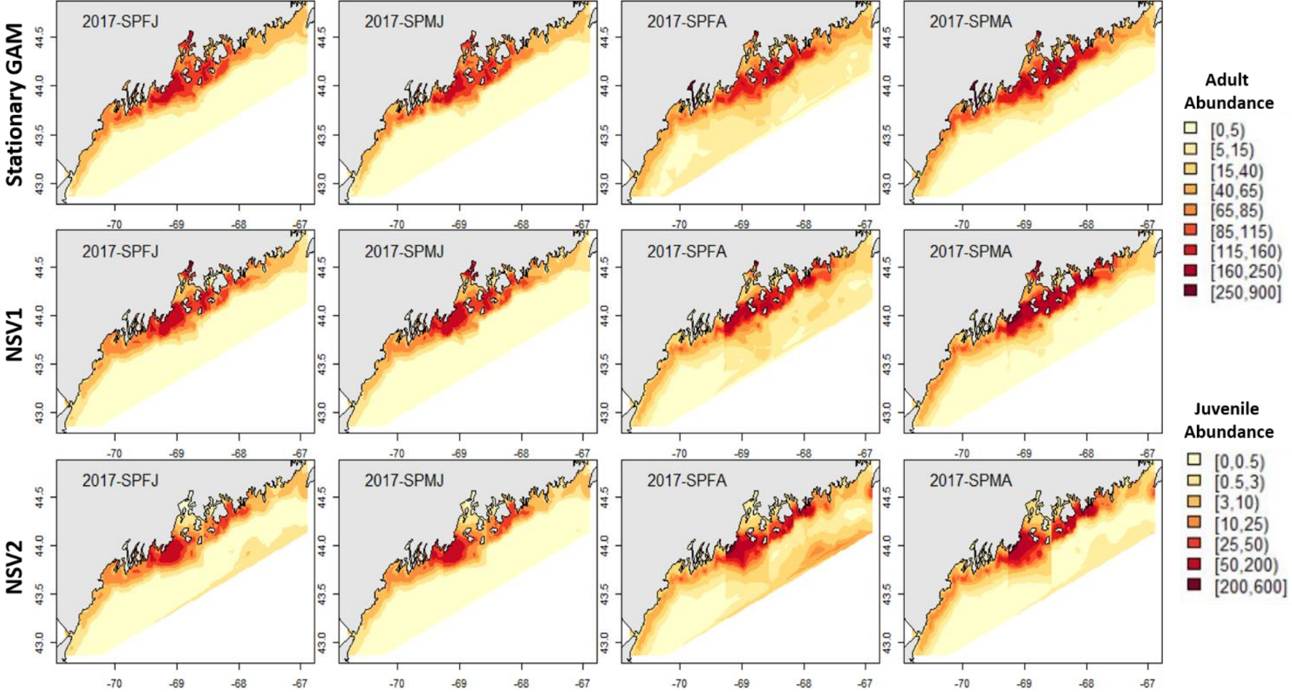


Figure IV-6: 2017 spring American lobster estimated spatial distribution. See Figure 2IV-4 for figure details.

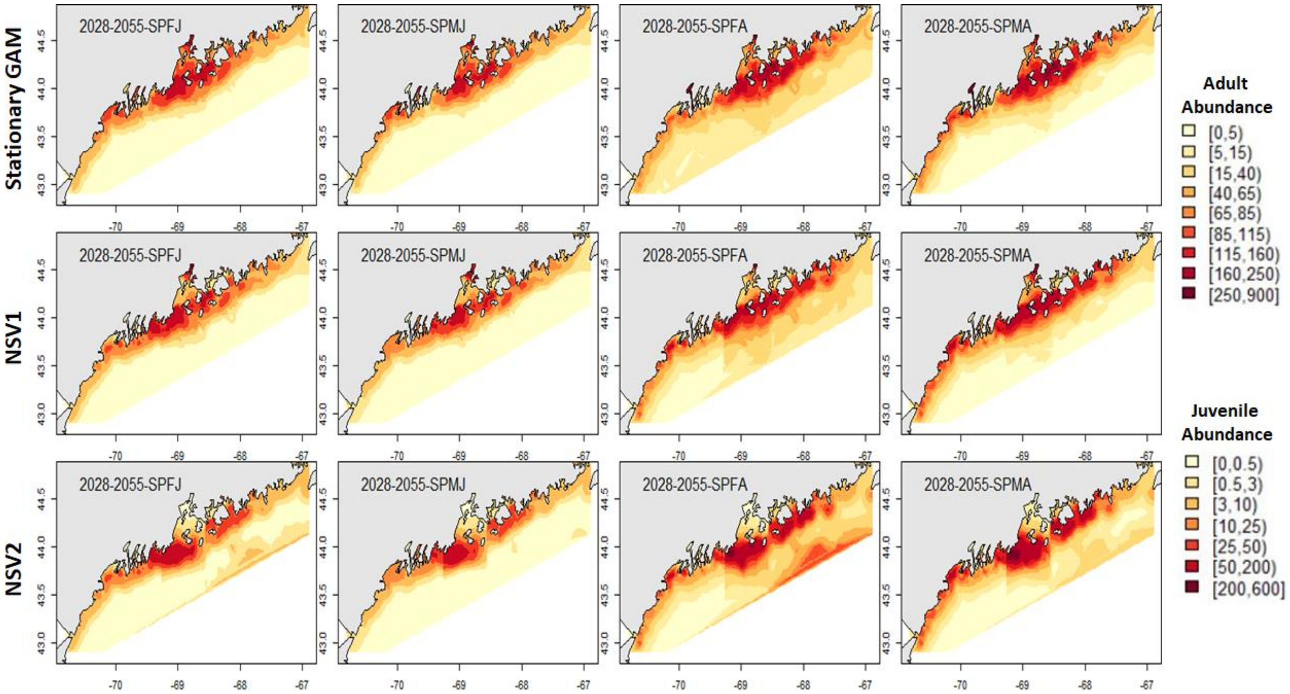


Figure IV-7: Forecasted spring American lobster estimated spatial distribution for the time period 2028-2055. See Figure IV-4 for figure details.

The stationary GAM tended to comparatively overpredict the 2017 hindcast distributions in western GOM, apart from the SPMA group (Figure IV-8). In central GOM, the stationary models tended to comparatively underpredict in the western part of Penobscot Bay and overpredict in the eastern part of Penobscot Bay. This was evident in both NSV1 and NSV2 relative difference model comparisons (Figure IV-8) across all years. In eastern GOM, many stationary models estimated less abundance approximately between -68.5° and -67.5° W, and higher abundance estimates between -67.5° and -67° W when compared to NSV1 models (Figures IV-8 and IV-9). These trends were present across all tested years.
2028-2055. See Figure IV-6 for figure details.

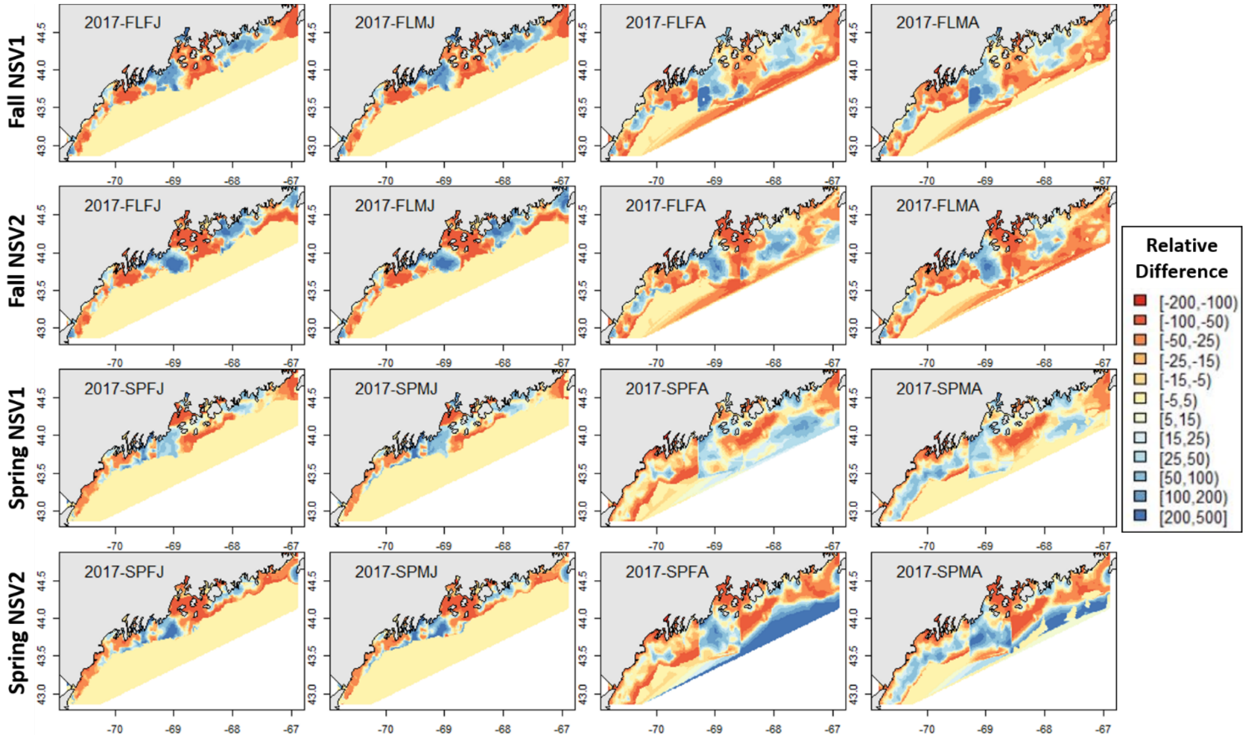


Figure IV-8: 2017 American lobster relative differences in model abundance estimates. Legend numbers represent relative differences (%) between NSV1 or NSV2 models and the stationary GAM. Red legend colors indicate areas where the stationary GAM model is predicting higher lobster abundance than the model in comparison. Blue legend colors indicate areas where the stationary GAM model is predicting lower lobster abundance then the model in comparison. Pale yellow colors indicate similar abundance estimates between the stationary and nonstationary models. Each column represents a lobster season x sex x size group. Each row represents the season and model type compared to the corresponding stationary GAM.

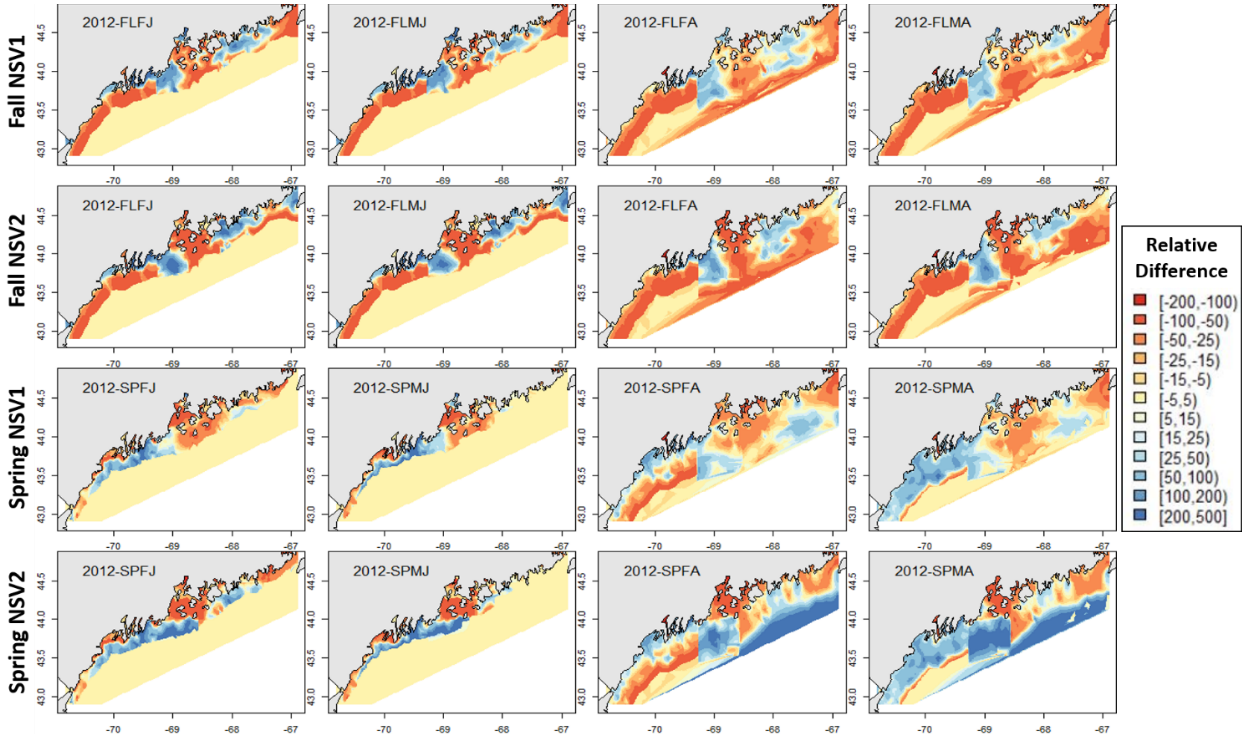


Figure IV-9: 2012 American lobster relative differences in model abundance estimates. See Figure IV-8 for figure details.

Density distribution estimates for the 2028-2055 period from nonstationary and stationary models exemplify similar spatial patterns seen in the corresponding distributions from 2000 to 2017. Some season x sex x size groups estimated abundances that extend further offshore than their hindcast counterparts (see Figures IV-4 – IV-7). Spring abundance estimates demonstrate an increase in central and eastern GOM from 2017 to 2028-2055, and this is more notable in the nonstationary models than the stationary ones (see Figures IV-6 & IV-7). These forecasted estimates correlate with raw spring bottom trawl survey data thus far for regions 3-5, which have all demonstrated general increasing average catch rates (number/tow) from 2000-2019 (Supplementary Figure A.2 in Behan 2021).

In general, relative differences between stationary and NSV2 distributions resulted in larger differences when compared to the relative differences between stationary and NSV1 distributions. This trend was apparent across all tested years. These observations correlate with observations in model fit, as the NSV2 model showed highest model fit, and the NSV1 models showing model fit more similar to that of the stationary models. Fall relative difference plots revealed that the stationary model was likely to estimate higher abundance in western GOM when compared to both the NSV1 and NSV2 models (Figure IV-10, IQR ≅ -36 to 0%). In the spring, the stationary model comparatively estimated lower abundance in western GOM for spring adult males in the 2028-2055 period (Figure IV-10, IQR ≅ -29 to 45%). For adult females in both fall and spring however, stationary models estimated higher abundance than either the NSV1 or NSV2 models in the west for the 2028-2055 period (Figure IV-10, IQR ≅ -62 to 16%). Forecasted stationary abundance plots estimated lower abundance in the western portion of central GOM (≈-69.3 to -68.9° W) and estimated higher abundance in the eastern portion of central GOM (≈-68.9 to -68.1° W), when compared with distribution estimates derived from the NSV1 model (Figure IV-10). This trend was also apparent in NSV2 forecasted relative difference plots, but differences were slightly more polarized (IQR ≅ -66 to 29%). There were slightly patchy trends in relative differences amongst groups in eastern GOM for the 2028-2055 forecasted period, where both higher and lower estimates were evident (Figure IV-10, IQR ≅ -15 to 62% for models 1:2 comparison and IQR ≅ -31 to 28% for models 1:3 comparison). These patchy trends were also observed in the eastern GOM region for hindcast plots as well, and may be due to the higher degree of vertical mixing, due to strong tides and upwelling in the eastern GOM, compared to the more stratified waters of the western GOM (Brooks and Townsend, 1989; Brooks, 1985; Townsend et al., 2015).

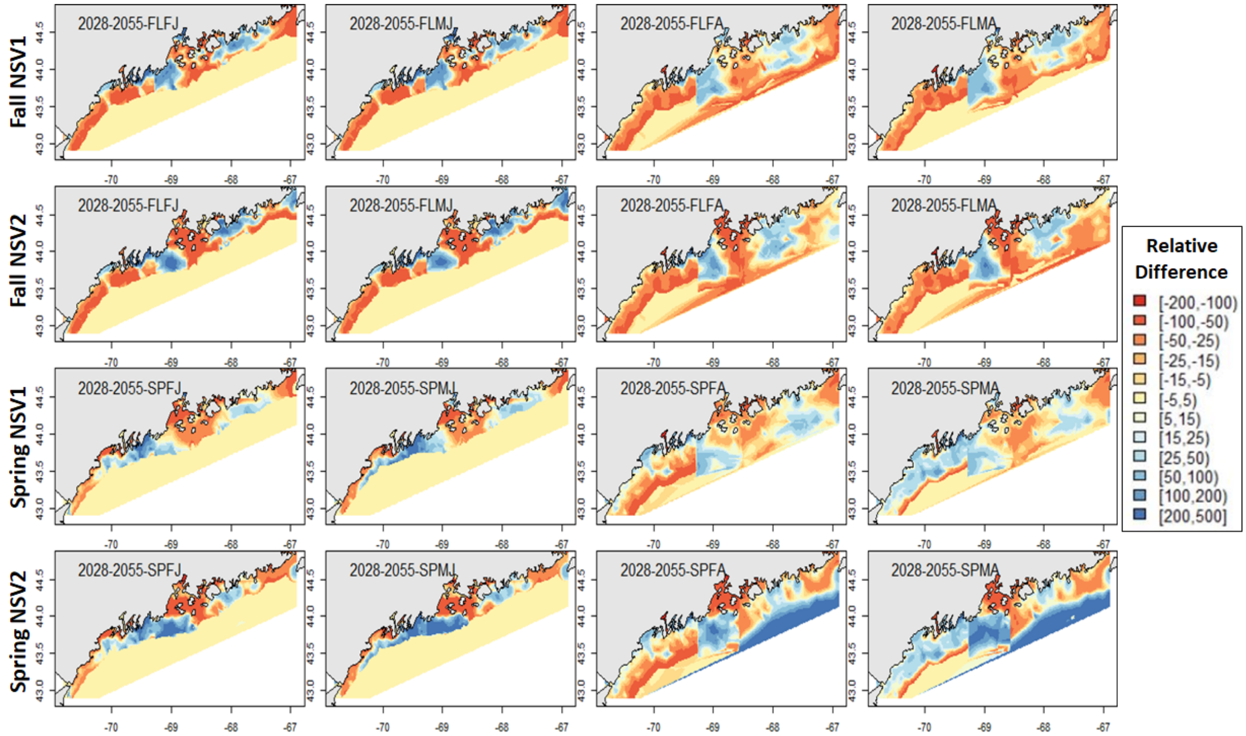


Figure IV-10: Forecasted American lobster relative differences in model abundance estimates for the period 2028-2055. Legend numbers represent relative differences (%) between NSV1 or NSV2 models and the stationary GAM. Red legend colors indicate areas where the stationary GAM model is predicting higher lobster abundance than the model in comparison. Blue legend colors indicate areas where the stationary GAM model is predicting lower lobster abundance then the model in comparison. Pale yellow colors indicate similar abundance estimates between the stationary and nonstationary models. Each column represents a lobster season x sex x size group. Each row represents the season and model type compared to the corresponding stationary GAM.

IV-4. Discussion

We developed a modeling approach to explore and demonstrate how estimates of season-, sex-, and size- specific American lobster spatial distribution and abundance would vary based on the spatial scale and extent of the area being modeled in the GOM. Validation tests run for each model type and season x sex x size group suggested reasonable predictive ability. Nonsignificant variables varied by model and spatial location. These results correspond with the notion that local patterns may get masked by global statistics, if stationary assumptions are made (Brunsdon et al., 1996; Windle et al., 2012). Stationary assumptions are likely to be violated in the GOM, where northeast to southwest gradients of temperature, salinity, and productivity have been observed (Lynch et al., 1997; Pettigrew et al., 1998; Chang et al., 2016), as well as spatial differences in American lobster stock-recruitment relationships (Chang et al., 2016), and spatially varying patterns in initial molt timing and suddenness (Staples et al., 2018).

A trend in model fit was observed in which as the spatial scale of models became more localized, model fit increased. The NSV2 model demonstrated the greatest model fit to the bottom trawl survey data and showed the most correlation in abundance estimates with raw bottom trawl survey data, indicating greater distribution estimation capabilities. The NSV1 model demonstrated the next highest model fit and estimation capabilities, while the stationary model demonstrated the lowest model fit to the data. We speculate that the NSV2 model shows the greatest model fit and potential predictive capabilities because of the modeling technique used on these data. By taking into consideration the oceanographic processes in the GOM to determine which localized areas are likely to be the most and least similar in relationships between American lobster abundance and environmental variables, the amount of data used for model estimation can be maximized, while limitations of stationary models over a large and biologically complex region can be minimized. Out of the nonstationary models, the results of the NSV2 model suggest an improvement upon the NSV1 model. Although these models are similar, the evidence of the NSV2 model being an improvement upon the NSV1 model suggests enough nonstationarity exists between central and eastern GOM to make the tripartite model subdivision worthwhile and that this technique may be more biologically reflective.

Spatial distribution estimates of the NSV2 model also seem to correlate well with raw bottom trawl survey data and past literature, especially in region three which has shown high increases in average catch over the course of the survey, and where localized “hot” and “cold” spots may be reflective of areas of high spawning stock size (Chang et al., 2016), or lobster settlement patterns observed in that region (Steneck and Wilson, 2001). Although lobster larvae were not included in this study, lobster spatial distributions are likely influenced and driven by settlement (Incze et al., 1997; Steneck & Wilson, 2001; Incze et al., 2010), and post-settlement natural mortality is considered low for American lobster (Incze et al., 1997; Palma et al., 1999; Steneck & Wilson, 2001). This may culture a scenario where areas of high lobster settlement lead to high lobster densities of larger carapace lengths (Steneck & Wilson, 2001).

Most lobster groups demonstrated similar spatial patterns or temporal trends in model results and analysis, with the frequent exception of spring male adult groups. We speculate the spring male adult lobster groups often did not respond in the same way due to differences in responses to both bottom temperature and bottom salinity. Although each group had more than one significant environmental variable across model techniques, bottom temperature was a significant variable in all models, and spring adult bottom temperature response curves were most distinct among groups. Most other season x sex x size groups displayed a relationship with bottom temperature similar to that of the FLFJ group (Figure IV-3D), where the partial effect of temperature on abundance generally increased then plateaus with increasing temperature. Spring adult lobster often did not follow this pattern, as exemplified in Figure IV-3C, where spring adult curves were typically domed-shaped. This dome-shaped pattern was present in both female and male spring adult groups however, so it is likely that other influences, such as salinity, may be a potential factor. The relationship spring adult males had with salinity was unique, compared to spring adult females, which demonstrated a similar pattern to the other season, sex, and size groups.

American lobsters are known to avoid areas of low salinity, and salinity preferences between 20-32 ppt have been recorded ((Jury et al. 1994; Tanaka and Chen, 2015). The spring adult male group response curve demonstrated a higher partial effect on abundance at salinity levels >32 psu in the west, which may explain why stationary models were more likely to comparatively underestimate lobster abundance in that region. Additionally, spring adult females are known to have greater sensitivities to temperature and salinity, especially ovigerous females (Lawton and Lavalli, 1995; Cowan et al., 2007), which may explain why the adult male and female abundance estimates differ in the west. These differences may also be more apparent in the spring than in the fall because in the spring months when the ME-NH Inshore Bottom Trawl Survey data were collected, the western GOM water isn't as stratified as it is in the fall (Li et al., 2018), allowing for less consistent environmental conditions, which may affect males and females differently.

The NSV2 model demonstrated the greatest relative differences across all years when comparing its spatial abundance predictions to those of the stationary GAM. This observation is the result of the multiple unique GAMs run on localized data, and thus assumptions of spatial nonstationarity are better satisfied. However, it is important to recognize that the largest difference from the stationary model does not automatically equate to the best model, as it is difficult to determine the starting biological accuracy of the stationary GAM. Estimates from the three modeling techniques at bottom trawl survey locations could be compared to raw bottom trawl data or other surveys, such as the Ventless Trap Survey, which may better capture areas where trawl surveys are unable to sample due to the satire of the gear. Comparing estimates from the modeling techniques utilized in this paper to raw data or other survey data at the same locations could be done to get a better understanding of how biologically accurate each technique is. However, between evidence of model fit and validation, distribution plot results, and correlation with raw survey data, we conclude that applying model techniques that better account for spatial nonstationarity will result in increased model performance.

While the NSV2 model demonstrated the best model fit out of the tested models, it is important to acknowledge some of the limitations of this model and the techniques used. First, all models tested only included environmental variables. No biological variables were included in the models, thus these models are working under the assumption that lobster abundance is dependent solely upon environmental variables and spatial scales used in the NSV1 and NSV2 models. Future studies may benefit from including biological variables, such as predator and/or prey abundance, into the models to see how the results would differ. Secondly, the subdivision of data techniques used for the nonstationary models (NSV1 & NSV2) sometimes resulted in variegated or “patchwork” spatial distribution estimates. Such abrupt changes in abundance estimates along the model extent lines are not likely to be biologically representative of true American lobster spatial distributions in the GOM. Consequently, this nonstationary modeling approach should only be used to observe trends in spatial distribution estimates, and not for precise estimations of “true” abundance, especially near the model extent lines. Thirdly, future studies may also benefit from exploring how different ways of subdividing data can impact model results, and if model fit can be further improved with more data partitions. Lastly, this study only considers spatial nonstationarity in model development, as gradients in environmental conditions throughout the study area have been observed. We did not consider temporal nonstationarity in this study due to the relatively short time period of data available to this study. If longer-term projections were to be made, temporal nonstationarity may need to be considered. However, this is beyond the scope of this study.

This study indicates that SDM estimations are dependent upon spatial scale and assumptions of nonstationarity. Results from a model that implicitly assumes spatial stationarity would differ from results of a model that better accounts for spatial nonstationary processes.

Thus, using results generated by stationary models could lead to different, or potentially even ill-informed management decisions which may result in less effective management results. Moreover, accounting for spatial nonstationary processes may be essential when devising localized regulations, as indications of change or unique dependencies of a species may be masked when using global statistics which are present in stationary models (Fotheringham et al., 2002; Windle et al., 2012). Management decisions informed by stationary models could result in regulations being more effective in one local area and less in others, if the relationship curves that drive the predictions are more representative of a particular area of the study area, rather than well represented throughout. If the NSV2 model distribution estimates are more biologically realistic as the analyses suggest, then comparatively, under an RPC 8.5 "business as usual" climate scenario prediction for the years 2028-2055, stationary models could overestimate lobster abundances in western GOM, with the exception of spring adult males. In such case, it is important local heterogeneity is considered in American lobster management in the GOM because false overestimations of abundance could lead to relaxed regulations or ill-informed biological reference point calculations, which could potentially lead to overfishing in western GOM.

Using stationary modeling techniques to forecast American lobster spatial distribution could result in inferior perceptions of where lobster populations will be spatially, and to what extent. More accurate predictions of American lobster spatial distributions will help stakeholders prepare and employ best practice measures to ensure the sustainability and longevity of the industry.

Section V. Scale-dependent assumptions of nonstationarity influence habitat suitability estimates for the American lobster: implications for a changing Gulf of Maine

V-1. Introduction

American lobsters are found in a variety of habitats, where the preference of these habitats has been thought to be influenced by environmental factors such as water temperature, salinity, substrate, and presence or absence of shelter. Previous literature has shown that American lobsters tend to exhibit a thermal preference between 12-18℃ (Crossin et al., 1998), and salinity preference between 20–32 ppt (Jury et al. 1994; Tanaka and Chen, 2015). Although their substrate preference has been known to vary between life stages, lobsters have been observed across a wide range of substrate types, including cobble, rock, mud, bedrock, sand, peat reefs, and eelgrass beds (Lawton & Lavalli, 1995).

Habitat Suitability Index (HSI) models, also known as Bioclimate, or Bioclimate Envelope models, are widely used to estimate and predict the habitat suitability for a species at a given location (Tanaka & Chen, 2015; Runnebaum et al., 2018; Torre et al., 2018; Tanaka et al., 2019). There are many types of bioclimate model approaches, but the approach used in this study is the statistical bioclimate model (Heikkinen et al., 2006). HSI models are useful for evaluating the quality of habitat for a particular species, based on density observations and environmental conditions across a spatial extent of interest. Information generated by these models can be crucial to assessing how habitat quality is changing over space and/or time (Guan et al., 2017; Torre et al., 2018). HSI models estimate suitability indices (SIs) for each environmental variable included in the model. These SIs represent a relationship between abundance and the selected environmental variable, and assume that observations of high density are indicative of high quality habitat conditions for that species (Runnebaum et al., 2018).

The bioclimate models used in this study were applied to the the Gulf of Maine (GOM) coastal region. The GOM is an inlet of the Atlantic Ocean that spans from Nova Scotia to Massachusetts, and is considered to be one of the most biologically productive marine ecosystems (Townsend, 1991), but a northeast to southwest productivity gradient has been observed in in the GOM (Chang et al., 2016). Gradients in temperature and salinity have also been observed (Pettigrew et al., 1998; Chang et al., 2016), and these variables are known to have significant influences on American lobster life history parameters (Lawton & Lavalli, 1995; Quinn & Rochette, 2015; ASMFC, 2020).

Evidence of environmental and ecological gradients throughout the GOM suggests the culturing of nonstationary species-environment relationships. Spatial nonstationarity can be defined as the presence of variation in relationships between independent and dependent variables across space (Windle et al., 2012). However, it is common for species-environmental models to assume spatial stationarity, which assumes relationships to be constant over space (Chang et al., 2016, Tanaka et al., 2019). Biases and model inaccuracies may arise when assuming spatial stationarity because the association between dependent and independent variables decreases with increasing distance (Brunsdon et al., 1996; Fotheringham et al., 2002). Past literature has found evidence of spatial nonstationarity existing within the GOM (Li et al., 2018. Staples et al., 2018). Although evidence of spatial nonstationarity exists within this region, previous literature has not explored how HSI model estimates could change, based on the spatial scale at which the model is run. This idea is called “the zoning effect” and occurs when statistical analysis results can differ based on how zones of an area of interest are defined and grouped (Fotheringham et al., 2002). We postulate that the zoning effect is likely to occur when analyzing species abundance data in the GOM due to the nonstationarity that has been observed in this region. Extrapolation and forecasting estimates onto unsampled areas and novel time periods are commonly desired when modeling habitat suitability. Previous literature has suggested that one way to achieve these desires while also including considerations of nonstationarity is to run multiple unique models at localized scales by partitioning the data (Fortheringham et al., 2002; Windle et al., 2009).

We explore the effects of spatial scale, and thus, varying assumptions of nonstationary, on lobster habitat suitability estimates and compare those results to those of coarse-scale models which assume spatial stationary. To do this, we developed season-, sex-, and size- specific models to estimate the habitat suitability of American lobsters using Bioclimate Envelope models of varying spatial scales and extents. Variation in estimated habitat suitability between models is evaluated and the implications for what these differences can mean in a region susceptible to climate change are discussed.

V-2 Materials and Methods

V-2-1 Study Area and Data Sources

American lobster abundance data were sourced from the Maine-New Hampshire Inshore Bottom Trawl Survey (Maine Department of Marine Resources (MEDMR) and the New Hampshire Fish and Game Department (NHFGD). 2000-2019. Inshore Bottom Trawl Survey.

Raw data). This survey is semiannual, with separate fall and spring seasonal surveys conducted each year. The bottom trawl survey spans 16000.5 km^2 and is subdivided into five survey regions (Figure V-1; Sherman et al., 2005). These five regions include (1) New Hampshire and Southern Maine, (2) Mid-Coast Maine, (3) Penobscot Bay, (4) Mt. Desert Island, and (5) Downeast Maine (Figure V-1). The potential sampling area for this survey extends up to 22.22 km offshore (Figure V-1). Each survey aims to sample 115 stations, resulting in a sampling density of approximately 1 station for every 137.20 km^2. The data included in this study was composed of random stations, which were chosen by dividing the survey area into a 1NM^2 (3.43 km^2) grid, and randomly chosen (Sherman et al., 2005). A target tow of 20 minutes is set at a speed of 2.2-2.3 knots, which covers roughly 1.48 km. Data from 486,971 individual lobsters were included in this study, and all tow data were standardized to 20 minutes, allowing for consistency and compatibility amongst tows. Tow data were standardized by the following equation

$$Abundance_{i20} = \frac{Abundance_{ib} * 20}{time_{ib}}$$

where “Abundance$_{i20}$” is the estimated lobster abundance for a 20 minute tow at location i, “Abundance$_{ib}$” is the observed abundance at time b, and “time$_{ib}$” is the number of minutes trawl b surveyed for.

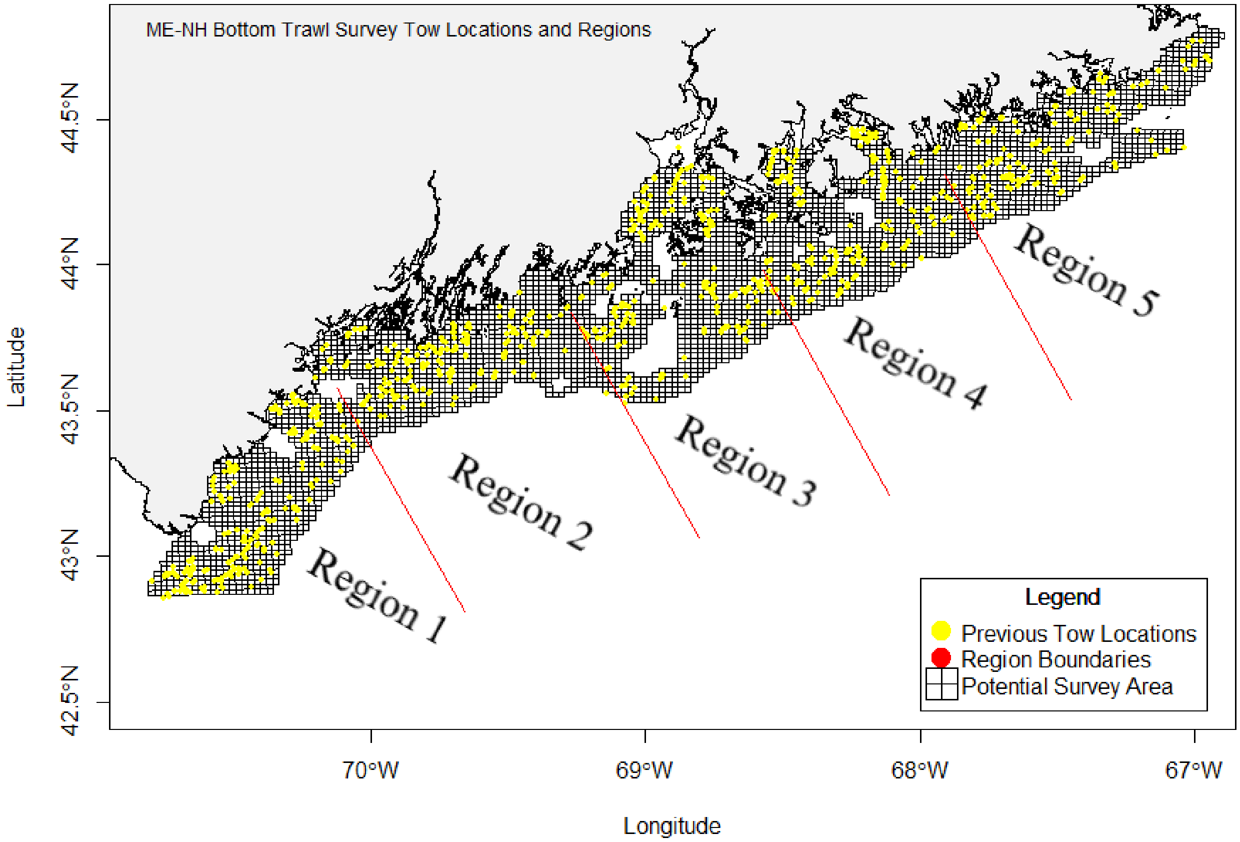


Figure V-1: Maine-New Hampshire Inshore Bottom Trawl Survey Past Tow Locations, Potential Surveyable Area, and Regional Boundaries. Missing white areas not included in the potential survey area grid are non-surveyable locations due to the topography of the ocean floor at those locations.

The bottom trawl survey records biological and environmental data, such as species, sex, size, bottom water temperature, bottom water salinity, latitude, longitude, and depth data at each tow location (Sherman et al., 2005). Additional information about the Maine-New Hampshire Inshore Bottom Trawl survey procedures, protocols, or specifics can be found in Sherman et al. (2005). The ME-NH Inshore Bottom Trawl Survey has been found to render reliable and informative data for studying lobster habitat quality in the GOM (Tanaka et al., 2019; Hodgdon et al., 2020).

Bottom temperature, bottom salinity, latitude, and longitude information from the years 2000-2019 were used from the bottom trawl survey to inform the Bioclimate models. Distance from shore and median sediment size variables were also estimated and utilized. The distance offshore for each tow of the bottom trawl survey was estimated as the distance between the midpoint latitude and longitude of a tow and the closest point on the coast. Sediment data were sourced from the East-coast Sediment Texture Database which is run by the United States Geological Survey (USGS, 2014). This survey was last updated in 2014 and contains information such as location, description, texture, and size (phi, -log of grain size) taken by different marine sampling programs across various locations around the world. Both mean and median sediment size values are supplied in this dataset, but median sediment size was used over mean sediment size, as the former is more robust to outliers (Tůmová et al., 2019). The median grain size at each survey location was estimated using thin plate splines. These data can be found at https://woodshole.er.usgs.gov/openfile/of2005-1001/htmldocs/datacatalog.htm and more information about the East Coast Sediment Texture Database can be found in U.S Geological Survey (2014).

Bioclimate models were built using bottom trawl survey data from years 2000-2019. However, to be able to interpolate onto unsampled areas and novel time periods that are not covered by the bottom trawl survey, additional bottom temperature and bottom salinity data were needed to create interpolated habitat suitability plots. Fine scale bottom temperature and bottom salinity data throughout the study area were obtained by spatially interpolating Finite-Volume Community Ocean Model (FVCOM) data. The FVCOM is an advanced ocean circulation model that uses an unstructured grid format, making it highly applicable for use in regions with complex coastlines and bathymetry (Chen et al., 2006; Li et al., 2017). The FVCOM was developed by University of Massachusetts Dartmouth and Woods Hole Oceanographic Institution. More information about the FVCOM can be found in Chen et al. (2006).
Forecasted distributions were made for the period 2028-2055. The forecasted bottom temperature and bottom salinity data were sourced from the National Oceanic and Atmospheric Administration (NOAA) and represent an ensemble projection of all models used to create the Intergovernmental Panel on Climate Change's (IPCC) Coupled Model Intercomparison Project Phase 5 (CMIP5) data (available from https://psl.noaa.gov/ipcc/ocn/). Data for the Representative Concentration Pathway (RPC) 8.5 "business as usual" scenario were used. These data are forecasted *anomalies* based on the reference time period 1956-2005 and are estimated for the period 2006-2055. These data are anomalies, and thus hindcasted bottom temperature and bottom salinity data must be used in tandem from the same reference period. The earliest

available FVCOM data begins in 1978 rather than 1956, limiting the available reference period in this study to 1978-2005. With the reference period reduced from 50 to 27 years, the CMIP5 forecasting period must also be reduced respectively, from the initial 2006-2055 to 2028-2055 for this study. The forecasting period 2028-2055 is used because it represents the maximum amount of FVCOM data than can be used while also confidently applying IPCC forecasted anomalies and keeping the same projection distance from the reference period. Delta downscaling methods were also applied so that forecasted anomalies could be applied to the same scale as the FVCOM data. Specifically, bivariate spline interpolation was applied using the package "akima" in R (Akima & Gebhardt, 2016).

V-2-2 Model Development

Lobster data was divided into eight groups based on season (fall and spring), sex (female and male), and size (adult and juvenile; Li et al., 2018; Chang et al. 2016). Juvenile lobsters were distinguished as lobsters with carapace lengths <50mm due to differences in activity patterns (Lawton & Lavalli, 1995). Each of the eight groups were modeled independently under 3 different techniques: (1) A coarse-scale Bioclimate Envelope model that assumes spatial stationary relationships between lobster abundance and environmental variables; (2) a meso-scale Bioclimate Envelope model that assumes spatial nonstationary relationships between eastern and western GOM, and (3) a fine-scale Bioclimate Envelope model that assumes spatial nonstationary relationships between eastern, central, and western GOM. Partitioning of data for these models can be visualized in Figure V-2.

Previous literature in the GOM have estimated habitat suitability using the bioclimate envelope model at large spatial scales (Tanaka and Chen, 2015; Runnebaum et al., 2018). This traditionally applied technique is represented in this study by "Model 1", which assumes spatial homogeneity and is applied at the largest spatial scale. This technique also assumes that nonlinear (but stationary) relationships between lobster abundance and environmental factors are sufficient to accurately predict the suitability of a potential or realized habitat location, in a region that is ecologically complex. Other literature has demonstrated the existence of variation in environment-abundance relationships across localized regions (Li et al., 2018; Liu et al., 2019). To test the effects of these differences, the bisected (Model 2) and trisected (Model 3) models were constructed at increasingly finer spatial scales, respectively. The purpose of this study is to explore how habitat suitability predictions change under models with varying assumptions of nonstationarity (or lack thereof) in hindcasting and forecasting scenarios.

The meso-scale model (Model 2) broke up the data into east and west zones. The western zone used data in regions one and two from the ME-NH bottom trawl survey (Figure V-2). Eastern GOM was represented by data from regions three, four, and five in the trawl survey (Figure V-2). The decision to split the data up in this way was driven by the GOM coastal currents, which have been thought to be one of the factors that contributes to the spatial environmental gradients seen across the gulf (Lynch et al., 1997; Pettigrew et al., 1998; Chang et al., 2016) and the nonstationarity that has been observed in this region (Li et al., 2018). Supporting literature that states the southern extent of the Eastern Maine Coastal Current (EMCC) includes the Penobscot Bay region (Xue et al., 2008; Chang et al., 2016), which is why in Model 2, region 3 of the trawl survey (Penobscot Bay) is included into the representation of the eastern GOM.

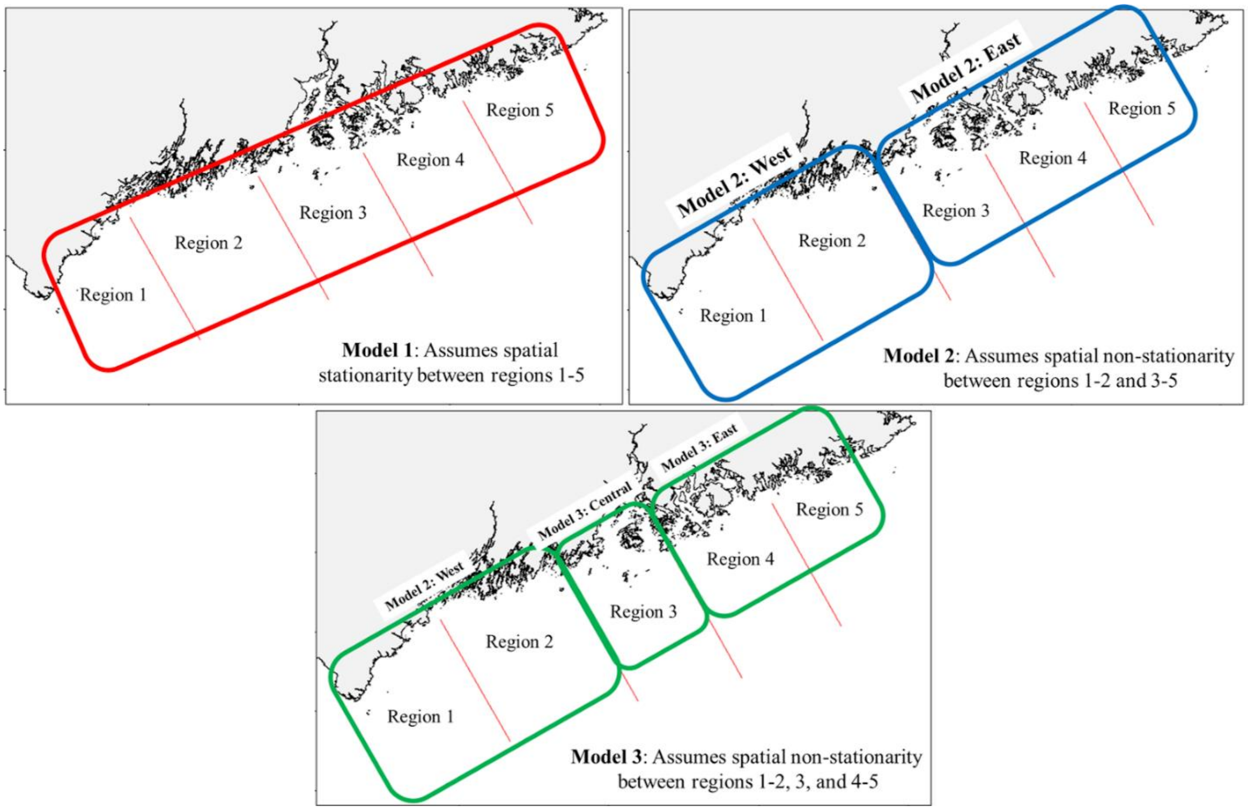


Figure V-2: Visual representation of each model approach utilized in this study. Each colored rectangle represents a separate bioclimate model that was run on the observed data points contained within those region(s) of the ME-NH Bottom Trawl Survey. Extents of the colored rectangles in this figure are not exact, but rather serve as general visualization of how the data were partitioned in this study.

Although some literature supports this decision, it is difficult to exactly pinpoint a fine line of where the EMCC bifurcates and the Western Maine Coastal Current (WMCC) begins. Some literature describes the EMCC diverging within the Penobscot Bay region (Pettigrew et al., 2005) or that the location of the split can be variable, based on the distribution of Slope Water in the Jordan Basin (Brooks and Townsend, 1989; Brooks, 1985). Thus, another argument can be made in which the Penobscot Bay area (≅region 3 in the bottom trawl survey) could act as a potential buffer zone, in which this area of possible mixing between currents could warp clearer relationships that may be established if central GOM was represented by its own localized bioclimate model. One previous study has used a similar trisected approach to view relationships between initial intra-annual molts of American lobster and bottom temperatures in the GOM (Staples et al., 2018). Consequently, the NSV2 model is built in such way that regions one and two of the bottom trawl survey represent the western GOM, region three will have its own separate season-, sex-, and size- specific models built to represent central GOM (the buffer zone between the EMCC and WMCC), and regions four and five will represent eastern GOM. Spatial coverage for each localized model can be visualized in Figure V-1.

Prior to model construction, covariance matrices and variance inflation factor (VIF) tests were run to check for variable independence and multicollinearity. Running multiple covariance metrics showed a high dependence between distance from shore and average depth variables. Distance from shore was kept over average depth because distance from shore had a lower covariance value amongst the rest of the variables than average depth. Variance inflation factors quantify the multicollinearity amongst variables. Variables with VIF numbers >3 were excluded from the model (Zuur et al., 2009), supporting the decision to remove average depth as a variable when building the models. Additionally, latitude and longitude variables were highly correlated and resulted in VIF numbers >3, so latitude was chosen to be kept over longitude because latitude was more significant at predicting lobster abundance in this study region.

Significant variables for each localized model were chosen based on results from Section IV, where Generalized Additive Models (GAMs) were run on the same localized spatial areas and back-fitted to check for spatial variable significance. Only variables that were shown to be statistically significant ($p<0.05$) at each localized area were included in the respective bioclimate models (Chang et al., 2016). Latitude and bottom water temperature variables were included in every bioclimate model. Bottom salinity, distance from shore, and sediment size were included in some models, but not all, based on local significance. Variables included in each model are summarized in Table V-1.

Table V-1: Significant environmental variables included in each respective model in this study. All significant variables were assumed to have equal weights. Abbreviations for environmental variables are as follows: Temp = temperature, Sal = salinity, DFS = distance from shore, Sed = sediment grain size, Lat = latitude, and AS = all potential environmental variables were significant.

Group	**Model 1**	**Model 2 (East)**	**Model 2 (West)**	**Model 3 (East)**	**Model 3 (Middle)**	**Model 3 (West)**
FLFJ	Temp, DFS, Sed, Lat	Temp, DFS, Sed, Lat	Temp, DFS, Sal, Lat	Temp, DFS, Sed, Lat	Salinity, DFS	Temp, DFS, Sal, Lat
FLMJ	AS	Temp, DFS, Sed, Lat	Temp, DFS, Sal, Lat	Temp, DFS, Sed, Lat	Temp, DFS, Sed, Lat	Temp, DFS, Sal, Lat
FLFA	Temp, DFS, Sed, Lat	Temp, DFS, Sed, Lat	Temp, DFS, Sal, Lat	AS	Salinity, DFS, Sediment	Temp, DFS, Sal, Lat
FMLA	Temp, DFS, Sed, Lat	AS	Temp, DFS, Sal, Lat	AS	Temp, Sed, Lat	Temp, DFS, Sal, Lat
SPFJ	AS	AS	AS	AS	Temp, DFS, Lat	AS
SPMJ	AS	AS	Temp, DFS, Sal, Lat	AS	Temp, DFS, Lat	Temp, DFS, Sal, Lat
SPFA	AS	AS	AS	AS	Temp, DFS, Lat	AS
SPMA	AS	AS	AS	AS	Temp, Sed, Lat	AS

Once significant variables were determined, a Bioclimate Envelope model was run on each spatial region outlined in Figure V-2. The Bioclimate Envelope model generates habitat suitability indices (HSIs) on a scale from 0 (least suitable habitat) to 1 (most suitable habitat) based on suitability indices (SIs) of covariates thought to influence habitat quality and preference (Tanaka and Chen, 2015). The relationship between an environmental variable and lobster abundance is quantified by the SI, where then all SIs are combined to form the overall HSI for a specific location (Runnebaum et al., 2018). SIs were determined via a technique known as the histogram method (Vinagre et al., 2006, Tanaka and Chen, 2015). To determine the optimum number of bins for the histograms, the Freedman-Diaconis rule (Freedman & Diaconis, 1981) was applied to the region with the least amount of data (Model 3, central GOM region) and the resulting optimum number of bins, 14, was kept constant for all models. The Freedman-Diaconis rule finds the optimum bin width with the following equation:

$$bin\ width\ =\ 2\ *\ IQR\ *\ n^{-1/3}$$

where "IQR" is the interquartile range and "n" is the number of observations. The optimum number of bins could then be determined by

$$(max - min)/bin\ width$$

where "max" is the maximum value in the dataset and "min" is the minimum value in the dataset (Freedman & Diaconis, 1981). The Freedman-Diaconis rule was only used to find the optimum number of bins to use for the histogram method and Fisher's natural breaks classification method was used to distinguish bin extents (Bivand, 2019; Tanaka and Chen, 2015). Once SIs were estimated for each variable and for each lobster group, SIs of significant variables for each respective lobster group were combined to form and overall HSI, which ranged from 0-1. We used the arithmetic mean model (AMM, Tanaka and Chen, 2015), which can be written as

$$HSI\ =\sum_{v=1}^{V}\ \frac{SI_v}{V}$$

where SI_v is the SI of environmental variable v and V is the total number of environmental variables. Thus, all variables had equal weighting as was done in Tanaka and Chen (2015) and Runnebaum et al. (2018).

V-2-3 Habitat Suitability Index and Relative Difference Plots

Hindcasted distribution plots were created for each of the 8 lobster groups and for each model for the years 2000, 2006, 2012, and 2017 for a total of 98 plots. Although there are bottom trawl survey data available from 2000-2019, the environmental (FVCOM) data used to be able to spatially interpolate plots is only available until 2017, limiting the most recent available hindcasting year that can be spatially interpolated to 2017. Additionally, these specific years were chosen because they are approximately evenly spaced throughout the hindcast period of interest, albeit these methods could be applied to any year(s) between 2000 and 2017. Forecast distribution plots were also estimated for each of the 8 lobster groups and model for the 2028-2055 year period, for a total of 24 forecast distribution plots. Differences between model 1 and models 2 or 3 were determined by calculating relative differences between habitat suitability estimates. Relative differences were estimated using the equation

$$Relative\ difference\ (i)\ =\ \frac{NS\ estimated\ HSI\ (i) - S\ estimated\ HSI\ (i)}{S\ estimated\ HSI\ (i)} * 100$$

where *i* is a location within the study area, "S estimated HSI (i)" is the estimated lobster habitat quality from Model 1, and "NS estimated HSI (i)" is the estimated lobster habitat quality from either the Model 2 or Model 3. Relative difference plots were generated for each lobster group, model and for the same years as the hindcast and forecast distribution plots. These plots demonstrate the magnitude and location of where Model 1, the traditional approach, tends to either over or under predict abundances in relation to the other approaches (Models 2 or 3). All distribution and relative difference plots were interpolated using bivariate splines using the package "akima" in R in order to achieve high resolution smooth distributions (Akima and Gebhardt, 2016).

V-3, Results

V-3-1 Suitability Indices

Estimated suitability indices varied between lobster groups and between spatial scales. The environmental variable bottom temperature was significant in all models and has been known to be an important habitat indicator for lobster in the GOM (Boudreau et al., 2015; Tanaka et al., 2019). The shape of the temperature SI curves for both seasons and for all models generally followed a positive increasing pattern with increasing bottom temperature values, followed by a decrease in suitability at higher temperatures for each season. Estimated SI curves for fall female juvenile and spring male adult groups can be seen in Figure V-3. Latitude was also significant in every model. Model 1 and Models 3 (east and central) latitude SI curves were similar in shape, with a gradual increase with increasing latitude, followed by slight decrease. Western region SI curves for latitude all tended to slowly increase overtime, while Model 2 east curves showed either a quick increase in SI followed by a long and gradual decline (adults), or a consistently decreasing SI with increasing latitude (juveniles). Other environmental variables such as salinity, distance offshore, and sediment were not all significant across all models, but for those that were and included in the model development, estimated SI curves still showed similar pattern where the SI curve estimated for model one tended to more closely resemble the SI curve of a specific region in the GOM, and less of the others.

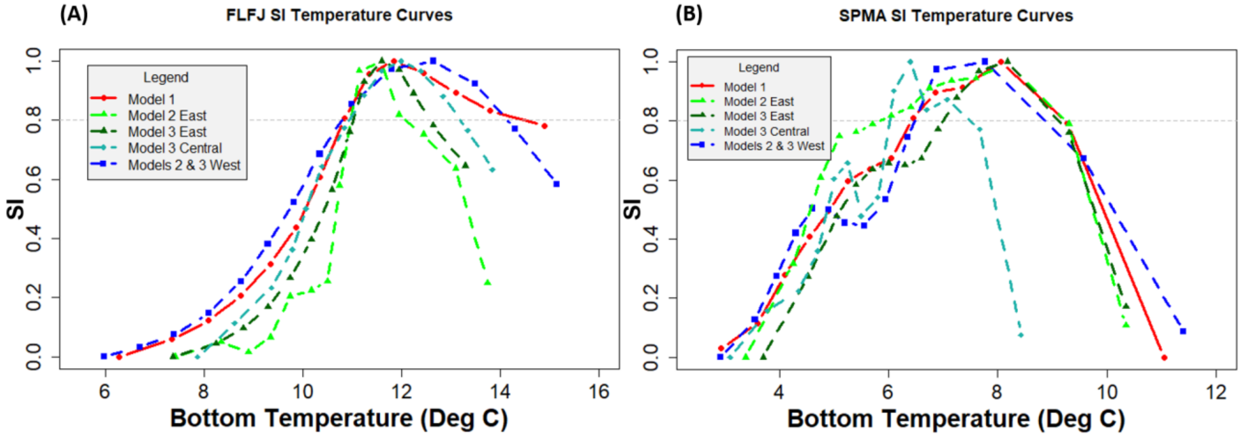


Figure V-3: Fall female juvenile (FLFJ, figure panel A) and spring male adult (SPMA, figure panel B) bottom temperature suitability index (SI) curves for each model and region tested in this study. Y axes are SI estimates, ranging from 0.0 (poor habitat quality) to 1.0 (best habitat quality). X axes are bottom temperatures in degrees Celsius. Each x axis point for each curve is the midpoint of each of the 14 bins using Fisher's Natural Breaks methods. Gray horizontal dashed line at 0.8 SI distinguishes suitable thermal ranges.

V-3-2. Habitat Suitability Index Plots

Results derived from the AMM-HSI models were plotted for the hindcast years of 2000, 2006, 2012, and 2017, and for the forecast period of 2028-2055. All models (1-3) generally estimated high suitability of habitat in coastal eastern GOM, where adult and fall groups showed higher suitability estimates slightly father offshore than their juvenile or spring group counterparts. See 2017 estimates in Figures V-4 and V-5 as examples. A trend was also observed in all hindcast years where higher HSIs were estimated in the east in fall models that were applied at smaller spatial scales (i.e. models 2 and 3) than for the fall model at the largest spatial scale, model 1 (Figure V-4).

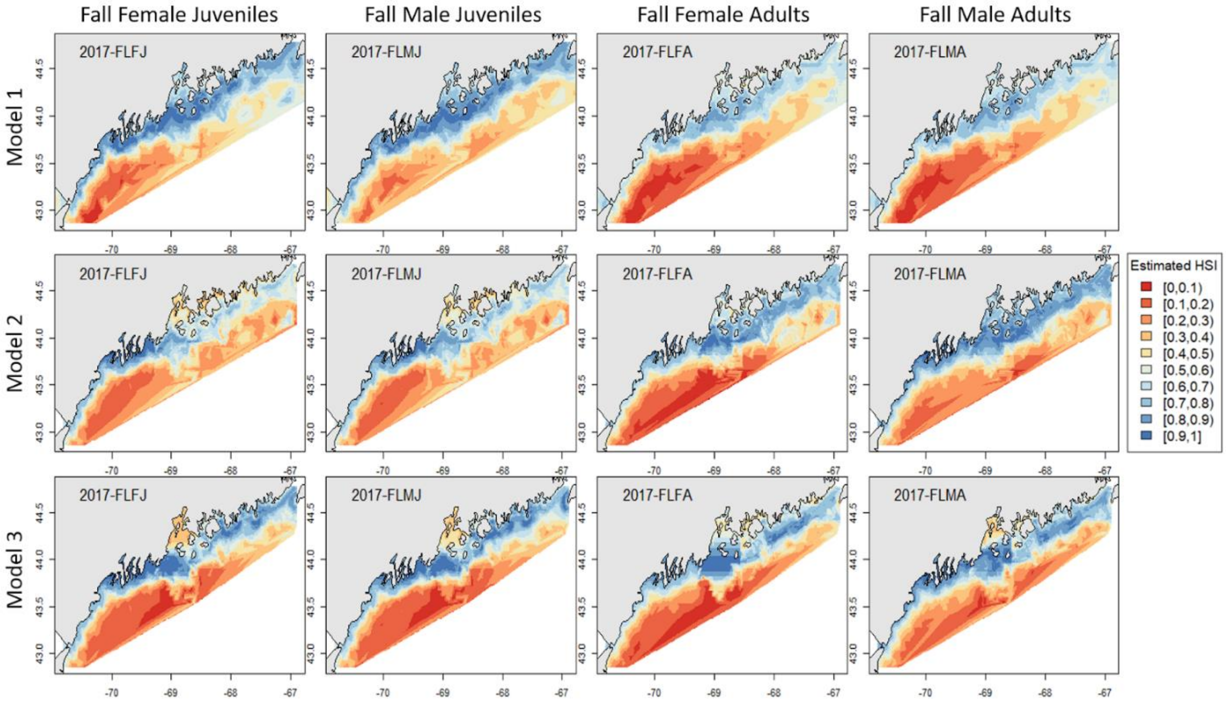


Figure V-4: Comparison of 2017 fall American lobster habitat suitability index (HSI) model estimates. Red indicates estimated areas of poor habitat while blue indicates estimated areas of suitable habitat. Each row represents estimates from a different model: model 1, 2, or 3, respectively. Each column represents specific estimates for different sex- and size lobster groups.

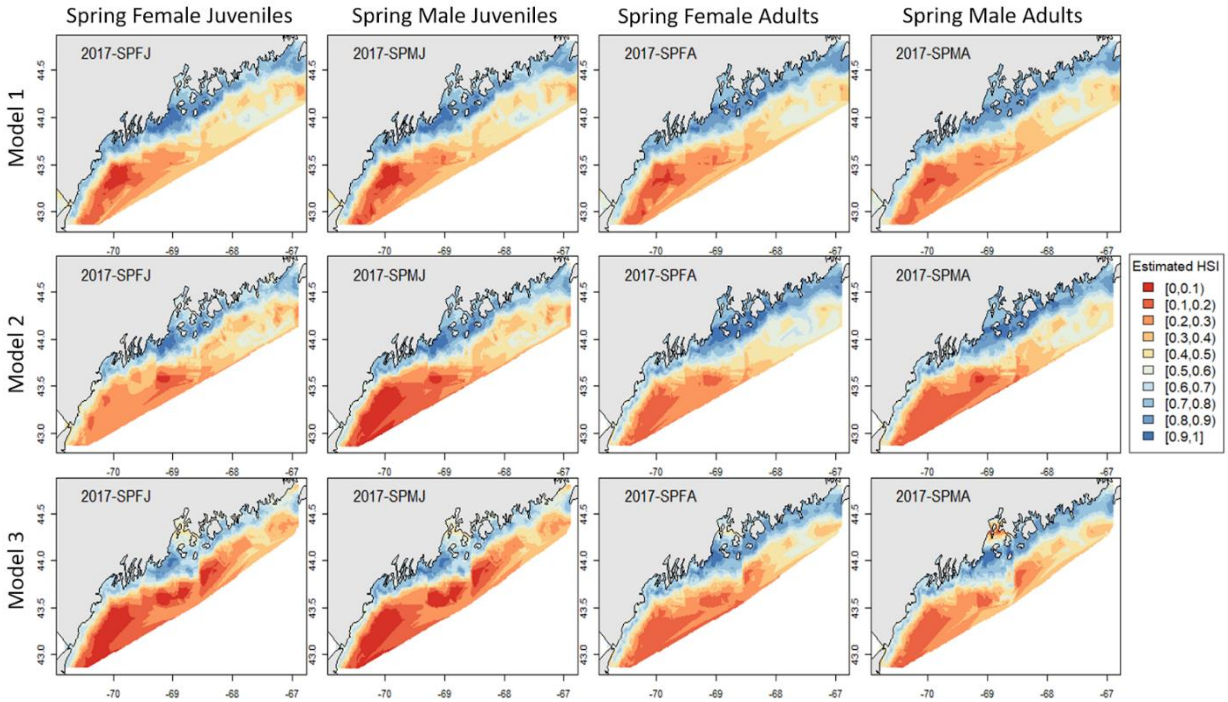


Figure V-5: Comparison of 2017 spring American lobster habitat suitability index (HSI) model estimates. See Figure V-4 for figure details.

In the central GOM region, comparative HSI plots demonstrate that fall plots for model 3 tended to estimate a "hot spot" of suitable habitat (HSI >0.9) around the Owl's Head to Tenants Harbor coastal regions of central GOM. Model 3 estimates higher HSIs in this area than any other model. Model 1 estimated higher values in fall juvenile groups for some years during the hindcast period, while model 2 estimated higher HSI values in fall adult groups for some years of the hindcast period as well; but model 3 estimated higher values for all sex-, and size- fall lobster groups, and for almost all hindcast years. 2017 fall hindcast HSI model comparison estimates exemplify this and can be seen in Figure V-4. There was a similar trend in finer-scale models estimating higher HSI in this region in the spring as well, but to a lesser extent.

Models 2 and 3 in the fall better showcase the known "cold spot" seen in the inshore Penobscot Bay or Sears Island region (Figure V-4), an area where poor lobster settlement has been observed (Steneck and Wilson, 2001) and is also likely associated with poor habitat suitability. Specifically, model 3 estimated HSIs as low as 0.2 in the 2006 and 2012 hindcasts, model 2 estimated this same area at an HSI of around 0.3 or higher, and model 1, estimated HSIs of at least 0.6 or higher for almost all hindcasted years. This supports evidence that model localization may better reflect biological realism. In the spring, results showed that model three also predicted lower HSI values in the inner Penobscot Bay region, and highlighted the "cold spot" more than models 1 or 2 did, although estimated suitability were overall higher than they were for the fall.

Comparison of HSI distribution plots, show that by comparing the most recent hindcast plots (2017) to the forecast estimates, the proportion of suitable habitat in the fall that is ≥0.6 has declined in farther offshore waters from 2017 to the 2028-2055 period (Figures V-4 and V-6).

This observation was more prominent in eastern GOM than for western. Conversely, in the spring, the proportion of suitable habitat that is ≥0.6 had increased in more offshore waters from 2017 to 2028-2055 (Figures V-5 and V-7). Similar to the trends observed in the hindcast plots, fall forecast model 3 plots estimated higher HSIs around the Owl's Head to Tenants Harbor coastal regions of central GOM, with exception to the fall male adults (FLMA) group. Fall forecast model 3 plots also estimate low HSIs in the Sears Island region compared to models 1 or 2, with an exception to the FLFA group. Spring forecast model 3 plots also show these distinctions around Sears Island and Tenants Harbor, but the common settlement "hot spot" that was observed around the Owl's Head to Tenants Harbor coastal regions appears to have moved further offshore and to the east (Figure V-7).

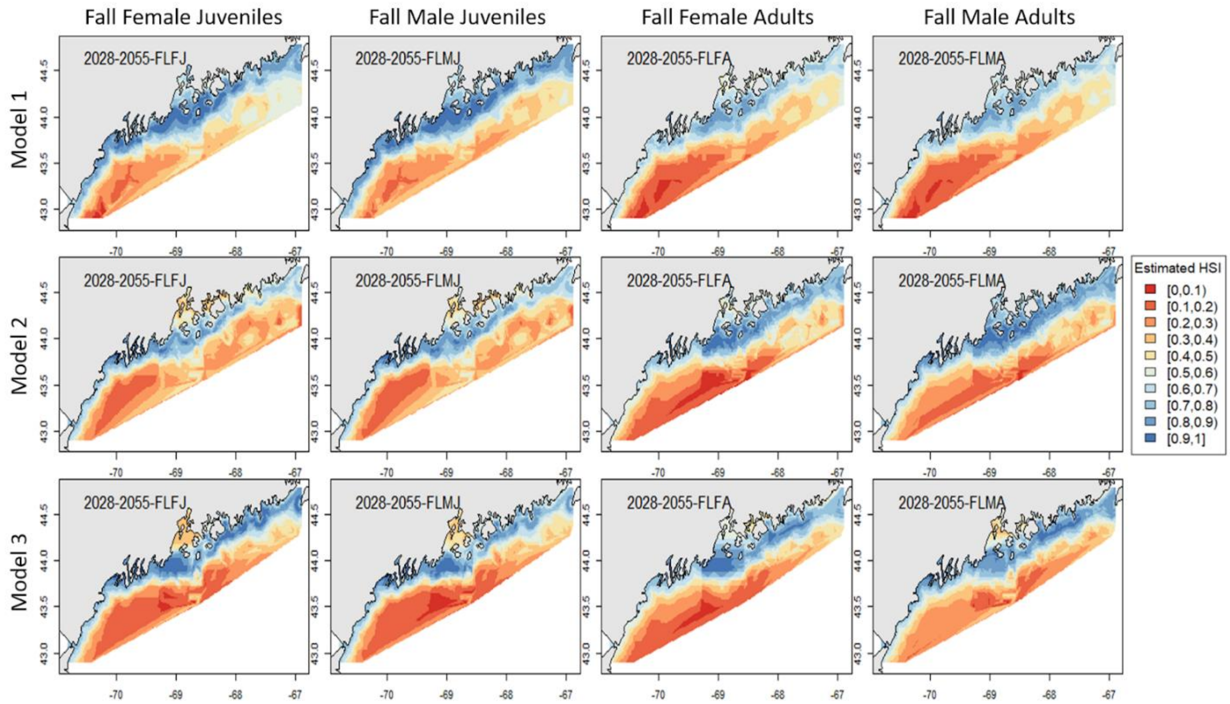


Figure V-6: Comparison of 2028-2055 fall American lobster habitat suitability index (HSI) model estimates. Red indicates estimated areas of poor habitat while blue indicates estimated areas of suitable habitat. Each row represents estimates from a different model: model 1, 2, or 3, respectively. Each column represents specific estimates for different sex- and size lobster groups.

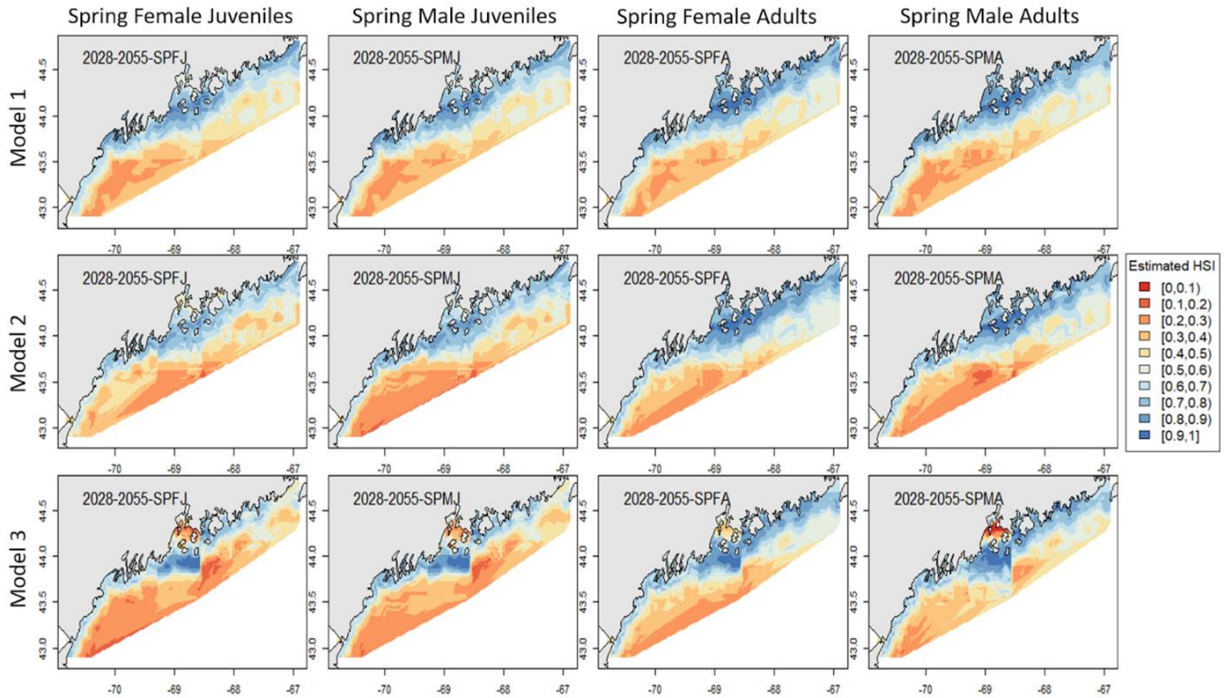


Figure V-7: Comparison of 2028-2055 spring American lobster habitat suitability index (HSI) model estimates. See Figure V-6 for figure details.

3.3.3 Relative Difference HSI Plots

Relative differences were estimated between models 1 and 2, as well as between models 1 and 3. Hindcast relative difference plots in the fall show that model 1 tends to estimate HSI higher than model 2 does, throughout the GOM in fall juveniles, as well as in spring juveniles, but to a lesser extent. In fall and spring juvenile relative difference plots for almost all hindcast years (2000-2017), there is some evidence of model 2 estimating higher habitat suitability in waters farther offshore than model 1 did in western GOM. This could be a sign that the finer scale model (model 2), is suggesting that suitable habitat for juvenile lobster is not limited to the most inshore regions of western GOM. This also supports observations that lobsters have been moving towards farther offshore waters than in previous decades (AMFSC, 2020; Tanaka et al., 2020). For adults, model 2 estimated higher or similar HSIs in western GOM, especially in fall male adult (FLMA) groups in 2017 (Figure V-8). Similar to juveniles, model 2 adult estimations were lower in eastern GOM when compared to model 1 estimations in the same region, but these differences occurred in waters further offshore, while model 2 estimated higher suitability in more nearshore waters when compared to model 1 HSI estimates in eastern GOM. This was especially true for the FLMA group in eastern GOM in 2017 (Figure V-8).

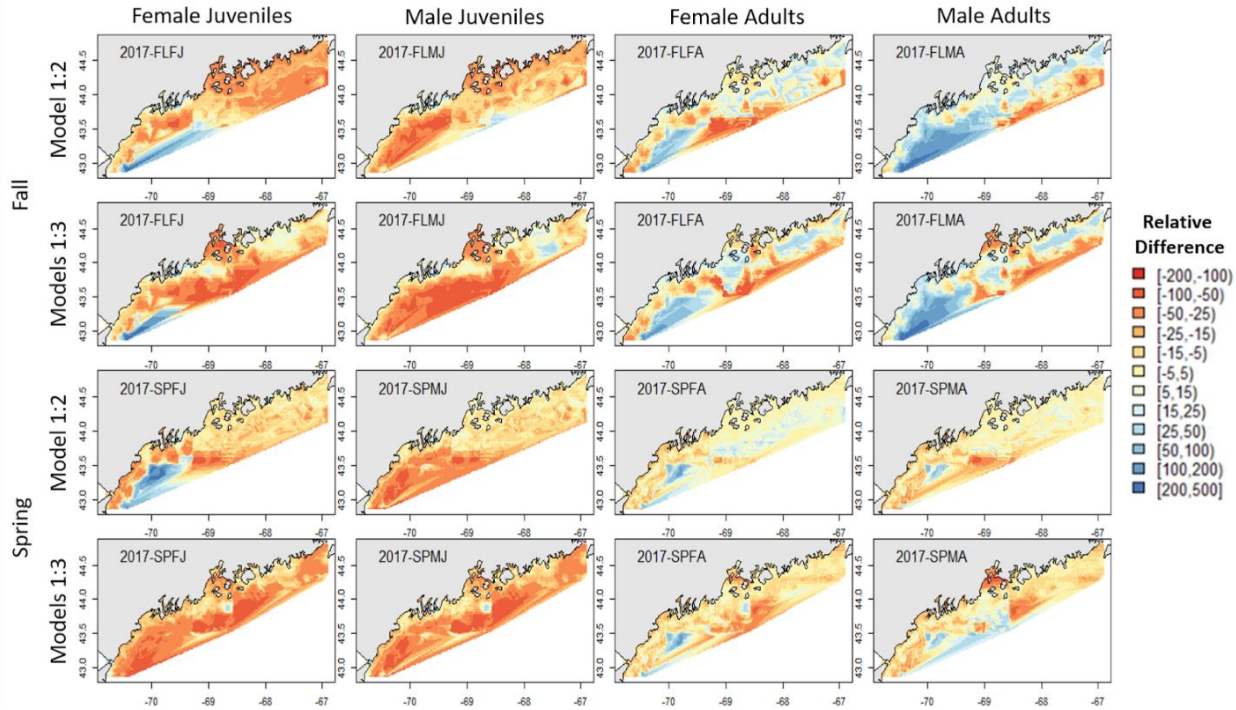


Figure V-8: American lobster relative differences in 2017 model HSI estimates. Legend numbers represent relative differences (%) between models 2 or 3 and model 1. Red legend colors indicate areas where the finer scale model (2 or 3) is estimating a lower HSI than model 1 did for that same area. Blue legend colors indicate areas where the finer scale model (2 or 3) estimated greater HSI values than model 1 did for that same area. Pale yellow colors indicate similar HSI estimates between the stationary and nonstationary models. Each column represents a lobster sex x size group. Each row represents the season and which models are being compared.

In relative difference plots for the forecast period 2028-2055, many of the same trends persisted from the hindcast period to the forecast period. For both seasons, juvenile relative difference plots revealed that both models 2 and 3 (Figure V-9) tended to estimate lower HSIs than their model 1 counterparts throughout the majority of the GOM (IQR ≅ -28 to 1%). This can be seen by the overwhelmingly higher proportion of red, orange, and yellow colors in these plots, which designate that the finer scale models (2 or 3) had a lower estimated HSI at a specific location than model 1 did. In adult groups, there was more of an even spread of relative underestimation and overestimation by model 1, where in fall adult groups, models 2 and 3 both estimated greater HSIs in coastal inshore eastern GOM and farther offshore western GOM waters, and estimated lower HSIs in farther offshore central and eastern waters and coastal western GOM. In the spring, there weren't as large of relative differences between adult groups in models 1 and 2 (Figure V-10), but there were greater relative differences highlighted in the central GOM region, where model 3 estimated lower HSIs in the inner Penobscot Bay region (Sears Island) and where model 3 estimated higher HSIs in more offshore waters in central GOM (Figure V-9, IQR ≅ -28 to 10%).

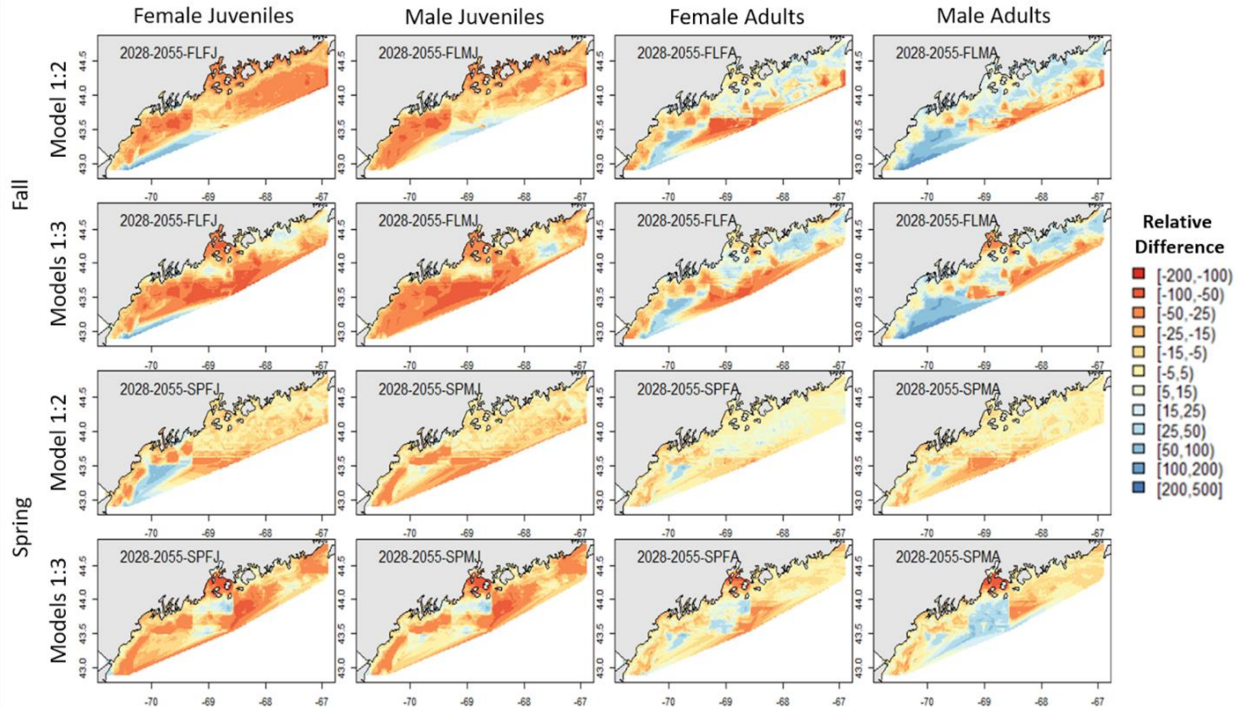


Figure V-9: American lobster relative differences in 2028-2055 model HSI estimates. See Figure V-4 for figure details.

V-4 Discussion

This study developed a modeling approach to explore the possible impacts of ignoring spatial heterogeneity of species-environment relationships in habitat suitability index models across a environmentally and ecologically complex area, the GOM. Final HSI estimates yielded from the Bioclimate model ultimately depend on the combination of estimated shape of the SI curves between lobster abundance and environmental variables. From these SI curves, many factors such as the proportion, range, and magnitude of suitable habitat have the potential to vary based on inclusion, exclusion, or partitioning of data in the model. The shape and suitable range for environmental variable SI curves exhibited variation across different localized scales. This suggests that if a bioclimate model were applied to an environmentally and ecologically complex area at coarse spatial scale, then the results may more accurately represent one localized region of the entire study area, rather than well representing all spatial areas throughout the extent of the area of interest. We speculate that one reason for these observations is that the coarse scale model could have a tendency to favor regions with higher variance in its data when estimating relationships between habitat suitability and environmental conditions. This further highlights the importance of considering spatial scale in model development so that the “masking effect” (Brunsdon et al., 1996; Windle et al., 2012) commonly observed in stationary models and global statistics can be limited, and that localized differences can be better captured.

Spring forecast models demonstrated a easterly shift in the estimated “hot spot” location, when compared to hindcast estimates around the same location. This shift in “hot spot” location is unique to spring model 3 forecasts and could be a result of this model better detecting northeast and offshore temporal shifts that have been thought to be occurring and are thought to continue to occur into the future (Goode et al., 2019; Mazur et al., 2020). Although there are no explicit temporal variables included in the development of any models tested in this study, accounting for assumptions of nonstationarity have been thought to account for spatial and temporal dependencies that cannot be explained by environmental variables alone (Bakka et al., 2016).

Results from the relative difference plots between model 1 and model 2 or 3 highlighted the effects that assumptions of spatial scale have on model results. Some of the clearest patterns in spatial differences occurred in the central GOM region. We speculate the most prominent differences between models could be seen in this region because in model 3, central GOM had its own unique model ran on this area and therefore had the most potential to pick up on localized patterns. The model 3 central GOM region was the smallest scale model in this study and thus, localized patterns are more likely to be emphasized because spatially irrelevant (or less relevant) data are not included in the model, and thus only the most spatially relevant data can influence relationships in that area. The relative differences between models 1 and 3 generally followed many of the same patterns of relative differences observed between models 1 and 2, but were typically more extreme. We speculate this is the result of the differences in spatial scales between models 2 and 3, where assumptions of spatial nonstationarity in model 3 are better satisfied and thus more distinct from model 1's assumptions of stationarity.

It is important to recognize that larger differences from model 1 do not automatically mean that model 3 is the most biologically realistic model, as it is difficult to determine the starting biological accuracy of model 1. Determining the amount of biological realism a bioclimate model captures is particularly challenging as there are no raw data for lobster habitat suitability available, and thus estimates of HSI cannot be compared to any observed estimates. However, model 3 results of this study correlate well with findings from Chapter 2, and Steneck and Wilson (2001), especially in the central GOM region, which suggests strong model fit and biological realism.

In bioclimate models, areas of "good" habitat are assumed to correlate with areas where high abundance have been observed, and vice versa with areas of "poor" habitat. Biases can arise in conjunction of this assumption because lobsters tend to prefer rocky, cobble, or boulder habitat, with plentiful locations to hide or take shelter (Lawton and Lavalli, 1995). These optimal shelter locations may not always be included in trawl surveys because trawls cannot be swept over areas with complex bottom topography, or other obstructions, such as areas densely fished with lobster traps. It has also been thought that as a species density increases, the spatial distribution of that species will also expand (Brown, 1984; Petitgas, 1998; Anderson and Gregory; 2000). This may lead to situations where individuals occupy a less suitable habitat because locations with the most suitable habitat are already occupied. American lobster stocks have increased fivefold since the 1980s (Goode et al., 2019), and densely populated areas could become less suitable as competition or susceptibility of disease increase. Effects of density-dependent habitat selection could ultimately lead to differences between fundamental and realized niches, and thus HSI model estimates. A limitation of this study is that it only considers environmental variables as covariates. Future studies may benefit from the inclusion of biological covariates such as lobster density, or predator and prey densities. Future studies should also explore how HSI estimates change using non-trawl data, such as scuba surveys or traps, which might better survey sheltered habitat locations.

In this study, all covariates are assumed to have equal influence on habitat suitability, which is not likely to be a biologically reflective assumption. Although this study only considered statistically significant environmental covariates unique to each local model (Table 1), the influence of each significant covariate is not likely equal and future studies may benefit from incorporating weighted covariates in tandem with nonstationarity studies. The smallest spatial scale explored in this study was approximately 986 miles^2 (2554 km^2; Sherman et al., 2005). Future studies may also benefit from exploring how different methodologies of data partitioning can impact model results, or if model fit can be further improved at smaller spatial scales. Other limitations of this study include the variegated or "patchwork" results observed in models 2 and 3. Such abrupt changes in HSI estimates along the model edge lines are not likely to be biologically representative of true habitat suitability throughout the GOM. Consequently, these nonstationary modeling approaches should only be used to observe trends in HSI estimates, and not for precise estimations of "true" habitat suitability, especially near the model edge lines. Lastly, temporal nonstationarity was not considered in this study as the focus of this study was to explore the effects of spatial nonstationarity due to the evidence that has been observed in past studies (Li et al., 2018). In regard to exploring temporal nonstationarity, due to the relatively short time period of data available to this study, we made the assumption that temporal stationarity is present, but if longer-term projections were to be made, temporal nonstationarity would likely need to be considered. However, this is beyond the scope of this study.

This study indicates that estimates of lobster habitat suitability are dependent upon spatial scale and assumptions of nonstationarity. Results from a model that implicitly assumes spatial stationarity would differ from results of a model that better accounts for spatial heterogeneity. Thus, using results generated by stationary models could lead to different, or potentially even ill-informed management decisions which may result in less effective management results. Moreover, accounting for spatial nonstationary processes may be essential when devising localized regulations, as indications of change or unique dependencies of a species may be masked when using global statistics. Management decisions informed by coarse-scale models could result in regulations being more effective in one local area and less in others, if the relationship curves that drive the estimates are more representative of a particular area of the study area, rather than well represented throughout. If model 3 HSI estimates are more biologically realistic as the correlation with past literature suggests, then comparatively, under an RPC 8.5 "business as usual" climate scenario prediction for the 2028-2055 forecast time period, traditionally utilized stationary models could overestimate juvenile lobster habitat suitability. This could result in a false security of recruitment expectations in future years, as the suitability of habitat would likely be lower than a coarse-scale model would predict. For adult lobsters, coarse-scale models are likely to comparatively overestimate habitat suitability in western GOM nearshore waters and further offshore waters of eastern GOM, while also underestimating further offshore waters in western GOM and coastal waters of eastern GOM.

In light of these differences, it is important to consider the possibility of local heterogeneity in American lobster habitat modeling and management in the GOM. False overestimations of habitat suitability could lead to false perceptions of the current and future state and location of lobster stock. Such false perceptions could result in relaxed regulations or ill-informed biological reference point calculations, which could potentially lead to overfishing and potential population decline at some localized areas, or underfishing at other localized areas, which could result in economic loss. Quality lobster habitat suitability estimates will help stakeholders prepare and employ best practice measures to ensure the sustainability and longevity of the lobstering industry as we enter a new climate regime, and smaller-scale models may better capture these localized changes.

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Evaluating impacts of conservation measures on lobster population dynamics in a changing Gulf of Maine

Final report

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By

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Summary

This project examines two major conservation measures used in the American lobster (Homarus americanus) fishery in a changing Gulf of Maine (GOM). We used computer simulation approach with simulation scenarios informed by stakeholders. The two conservations evaluated in this project include V-notching and minimum/maximum legal sizes, both of which are intended to ensure the sufficient spawning stock abundance to support sustainable fisheries and have been hypothesized to have contributed to the dramatic increase in lobster landings and stock biomass since the 1990s in the GOM. Based on semi-structured and oral history interviews, v-notching compliance and lobster fishers' perceptions of v-notching were analyzed. All lobster fishers interviewed described v-notching as important for the lobster fishery's sustainability, while also reporting that the v-notching practice has been declining in recent years. An individual-based lobster simulator (IBLS), which can capture complex processes with a flexible probabilistic approach, was modified, conditioned, and applied to the fishery. To evaluate the impact of v-notching, scenarios examining different v-notching compliance rates and v-notch definitions were simulated using the IBLS with different recruitment dynamics scenarios. These simulation results suggest that the lobster fishery would not have experienced the observed large positive increases in biomass and landings without a high v-notching compliance rate (i.e. 90 or 100% compliance) or a strict definition of the notch. Although v-notching has contributed to the increases in the fishery and population, to fully understand the role of conservation, the stock-recruitment relationship (SRR) in a changing GOM needs to be better understood. Projections of the lobster fishery under different v-notching scenarios show that in the near future, although v-notching does not increase landings, v-notching still preserves the spawning stock. Minimum and maximum legal sizes also made a great contribution to the dramatic increase of the GOM lobster fishery. An increase of 2 mm carapace length in minimum legal size with no changes in maximum legal size would result in a 279.92% increase in landings compared with the reference landings in 2013. These results show that the v-notching conservation measure and legal sizes are valuable tool for precautionary management. Overall, these results suggest that input controls, such as protecting the spawning stock and legal sizes, can provide benefits to both the fish population and fishery. The implications of a decline in the v-notching practice and weak enforcement of legal sizes may have negative impacts for the future sustainability of the fishery if the spawning stock and productivity were to decline. The simulation framework proposed in this study can be used to evaluate future dynamics of the lobster stock and fishery under different management regulations in a changing GOM.

Acknowledgement

We would like to thank the Maine Department of Marine Resources for providing funds and relevant information/data for us to conduct this work. In particular, we would like to thank Jesica Waller, Kathleen Reardon, Carl Wilson, Rob Watts and Katherine Thompson for providing advice on the simulation design and results interpretations and all the logistic support. This project is part of the two PhD dissertations by Dr. Bail Li and Dr. Mackenzie Mazur. Key components in Sections III and IV have been published in Canadian Journal of Fisheries and Aquatic Sciences and Marine Ecology Progress Series.

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SECTION PAGE

I. Project Introduction

The American lobster, *Homarus americanus*, supports one of the most valuable commercial fisheries in the northeast United States (ASMFC 2020). Most landings have occurred in the state of Maine. The Maine landings have increased steadily since the early 1970s and fishing effort is intense (Chen et al. 2005, ASMFC 2020). The American lobster fishery is currently managed by NOAA National Marine Fisheries Service (State, Federal and Constituent Programs Office) in federal waters under the Atlantic Coastal Fisheries Cooperative Management Act; but is managed under the Atlantic States Marine Fisheries Commission (ASMFC) Interstate Fishery Management Plan in state waters where most landings occur (ASMFC 2009). The management regulations control lobster fishing effort with trap limits. The American lobster in the northern USA is currently divided into two stocks in the most recent assessment (ASMFC 2020): Gulf of Maine (GOM)/ Georges Bank (GBK) and Southern New England. For the GOM/GBK stock, conservation measures such as minimum legal size, maximum legal size, V-notching egg-bearing lobster, and no taking of egg-bearing and V-notched lobster form the backbone of management systems.

Minimum legal size is commonly used in fisheries management for allowing individuals to spawn at least once in their lifespan; while maximum legal size is often used for protecting large spawners who tend to be more fecund and produce higher quality of eggs compared to small spawners. Legal size regulations were used more than century ago in the Maine lobster fishery. The minimum legal size was set at 266.7 mm (10.5 inch) total length in 1874; 88.9 mm (3.5 inch) carapace length (CL) in 1919; 77.8 mm (3-1/16 inch) CL 1933; and 82.6 mm (3-1/4 inch) CL since 1989. The maximum legal size was set at 120.7 mm (4.75 inch) CL in 1933, and 127 mm (5 inch) CL since 1960 (ASMFC 2000).

Protection of egg-bearing lobster has a long history in the state of Maine. Egg-bearing female lobster were prohibited from being landed since 1872. Since 1947, an industry-initiated V-notching program has been widely used in the state of Maine to protect broodstock. Current Maine Law (Title 12, Section 6436, Rule 25.15) states: “A female lobster marked with a v-notch in the right flipper next to the middle flipper is illegal to possess” and “It is illegal to possess a female lobster mutilated in a manner which could hide or obliterate a v-notch, including that missing flipper”. Because the V-notching mark may become invisible after one or two molts, compared to the discard of egg-bearing lobster alone, this further extends the lobster broodstock protection.

Despite of high fishing pressure and landings, the GOM lobster population has increased dramatically since the early 1990s (ASMFC 2000, 2009, 2015, 2020). Various hypotheses have been developed to explain such an increase in the GOM lobster population and fishery landings, ranging from reduced biomass of major predators (e.g., Atlantic cod; Crooks and Soule 1999; Hanson and Lanteigne 2000), warming ocean temperatures (Spees et al. 2002), increased herring bait discards in the lobster fishery (Grabowski et al.2010), improved habitat (Tanaka and Chen 2016), and fluctuations in lobster larval supply in the GOM (Steneck and Wilson 2001). Conservation measures such as minimum legal size, maximum legal size, V-notching lobster program and protection of egg-bearing lobster are also considered to play an important role in large increases in the GOM lobster population size and landings under high fishing pressure; but no systematic study had been done to evaluate and quantify their contributions to the improved lobster stock and landings and no peer-reviewed publications were found. Thus, our understanding of the effectiveness of these conservation measures was limited, which raised some concerns from stakeholders regarding the necessity of implementing these measures in the lobster fishery managements. Given the perceived climate-induced changes in the ecosystem which may greatly influence the lobster recruitment and growth dynamics (ASMFC 2020, Tanaka and Chen 2016, McMahan et al. 2016), such research becomes even more urgent and necessary for a careful evaluation of effectiveness of the conservation measures in regulating the lobster population dynamics in a changing GOM.

The objective of this study is to evaluate the role of conservation measures used in the management of Maine lobster fishery (GOM/GBK) such as minimum legal size, maximum legal size, and v-notching practice in regulating the lobster population dynamics in a changing GOM. This work addresses component E: Integration, as this work integrates both assessment and fishery components.

This report includes three sections: Section II is to condition an individual-based lobster simulator for the use in evaluating impacts of conservation measures on the lobster stock dynamics; Section III is to evaluate the impacts of V-notching; and Section IV is to evaluate the impacts of maximum and minimum legal sizes. The sections II and III are part of PhD dissertation of Dr. Mackenzie Mazur (Mazur 2020) and section IV is part of PhD dissertation of Dr. Bai Li (Li 2018). Relevant peer-reviewed publications include Mazur et al. (2019a, 2019b).

II. Conditioning an individual-based model to simulate the lobster fishery for the study

II-1. Introduction

Identifying a simulation tool for the complex American lobster fishery, in which fishery and life history processes vary among individuals, is necessary for the evaluation of conservation measures. The complexity of American lobster biological and fisheries processes makes the use of traditional mathematical formulation-based models difficult (ASMFC 2000). Growth of the American lobster is not continuous, as lobsters grow by molting, which mainly occurs in summer and fall (Factor 1995). Molting frequency is dependent on the size and maturation status of the lobster (Factor 1995; Comeau and Fernand 2001).

Additionally, conservation measures used in the GOM fishery, including minimum and maximum legal sizes, prohibition of the taking of egg-bearing lobsters, and protection of ovigerous females through a v-notching program, are difficult to consider as separate processes with traditional fishery models (ASMFC 2000). Consideration of all these fishery processes as separate from one another is important when evaluating changes in one process but not the others. For example, fishery conservation processes need to be considered as separate to evaluate the effect of minimum size but not maximum size and protection of egg-bearing lobsters.

An individual-based model (IBM) may be an alternative modeling approach used to develop a fishery simulator because it can track the detailed life history and fishery processes of individual lobsters. IBMs describe a population consisting of different individuals and changes in the number of individuals (instead of population density) and consider the population dynamics under complex processes (Uchmański and Grimm 1996). With a probabilistic approach, IBMs allow for much more complexity than traditional mathematical-formulation-based models (Uchmański and Grimm 1996). When mathematical methods are used to model complex processes, unrealistic assumptions are often introduced to attain mathematical solutions, whereas IBMs can assume individuals are different from one another (Grimm 1999; Judson 1994). In addition to the incorporation of variability among individuals, IBMs can simulate life cycles of individuals that are not usually included in analytical models.

In this project, we modified, parameterized, and tuned an individual-based lobster simulator (IBLS), which is an IBM for a lobster fishery, to simulate the historical GOM lobster fishery. This study includes (i) the description and parameterization of the IBLS that mimics the dynamics of the life history and fishery processes of individual lobsters; (ii) calibration of the IBLS, using coefficients for specific parameters to predict historical landings and population size composition of lobsters; and (iii) application of the simulator to evaluate the robustness of current management regulations under different levels of recruitment. This study discusses how simulations can highlight uncertainties in input data and model structure and set up the stage for the simulation study to evaluate impacts of conservation measures on the lobster population dynamics.

II-2. Methods

The IBLS was developed by Chen et al. (2005) to test the performance of the stock assessment model and further developed by Chang (2015) for management evaluation. An IBM was used to develop the IBLS for the GOM lobster fishery by expressing numerous components of the model equations as random Bernoulli trials (Chen et al. 2006; Chang 2015; Fig. II-1). Instead of calculating the number of lobsters that survive a given process such as natural mortality or fishing mortality, we simulate natural or fishing mortality acting on *Nt* individual lobsters. Because IBMs are not based on traditional mathematical formula, the IBLS cannot be described in one or a few equations. IBMs are bottom-up models in which population-level outcomes emerge from variation among individuals (DeAngelis and Grimm 2014).

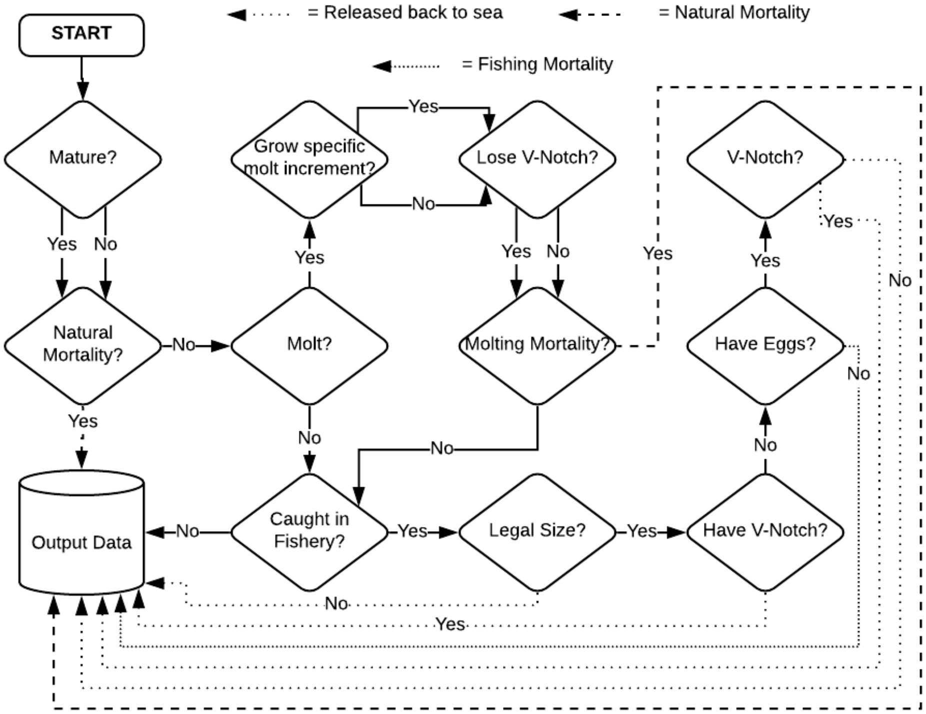


Figure II-1. Flowchart of the individual-based American lobster simulator. Each lobster has a conditional probability of going through each process, as the probability at each process depends on what processes the lobster previously went through. The diagram was modified from Chen et al. (2005) and Chang (2015).

II-2-1. Model Description

II-2-1-1. Inputs

The IBLS requires abundance, recruitment, and other types of data (Table II-1). Most of the probabilities and other input data are from the stock assessment data (ASMFC 2015), but fishing effort data are from the Maine Department of Marine Resources (DMR) harvester data, and v-notching information is from personal communication with managers (Table II-1). These are the best available data representing the GOM lobster fishery dynamics. Most of the probabilities have means that are parameters from stock assessment model. In this case, the stock assessment parameters and output are assumed to be the true state of the lobster fishery. Select input and probabilities are tuned or calibrated as described later.

Table II-1. Input data for the individual-based American lobster simulator. The most recent American lobster stock assessment is the Atlantic States Marine Fisheries Commission (ASMFC, 2015) source. Personal communication was with Maine lobstermen and Maine Department of Marine Resources staff. Harvester data are from the Maine DMR.

Inputs	Values	Source
Initial abundance	93,200,000	ASMFC 2015
Initial size composition	Differs among sizes	ASMFC 2015
Initial sex ratio	0.546	ASMFC 2015
Recruitment	Differs among years in summer and fall; 0 in winter and spring	ASMFC 2015
Recruit size composition	Differs among sizes	ASMFC 2015
Natural mortality probability	0.025 each timestep	ASMFC 2015
Molting probability	Differs among sizes	ASMFC 2015
Probability of growth increments per molt	Differs among sizes	ASMFC 2015
Maximum interval in between molts	7 seasons	Personal communication
Time between first molt and second molt if there is a double molt in a year	1 season	ASMFC 2015
Maximum molt increment (mm)	20	ASMFC 2015
Number of molts a V-Notch lasts	2	Personal communication
Molting mortality probability	0.05	ASMFC 2015
Fishing effort (trap haul set over days)	Average of 1,085,440 in winter, 4,512,963 in spring, 25,485,938 in summer, and 8,606,713 in fall	Harvester data
Landings	Differs among sizes, sexes, seasons, and years	ASMFC 2015

Conservation selectivity	Differs among sizes, sexes, seasons, and years	ASMFC 2015
Legal selectivity	Differs among sizes, sexes, seasons, and years	ASMFC 2015
Abundance	Differs among sizes, sexes, seasons, and years	ASMFC 2015
Maximum legal size (mm CL)	128	ASMFC 2015
Minimum legal size (mm CL)	1982-1987: 81, 1988: 82, 1989-2013: 83	ASMFC 2015

Table 3.1. continued

Number of timesteps until a mature female lobster can have eggs after she molts	4 seasons	Personal communication
Maximum number of timesteps a mature female lobster can keep her eggs	4 seasons	Personal communication
Probability of a lobster caught with eggs being V-Notched by a lobsterman	0.9	Personal communication

Some of the probabilities, such as encounter probability, were calculated from the input data. Encounter probability is the probability that a lobster is caught in a trap and is calculated for each season, year, sex, and size class (Chang 2015). This is conceptually similar to catchability. Encounter probability was calculated as:

$$Enrate_{t,s,k} = \frac{C_{t,s,k}}{C_{t,s,k}+N_{t+1,s,k}} \tag{1}$$

where $C_{t,s,k}$ is the catch on boats before the lobsters that are illegal to be landed are thrown back, or the total number of lobsters that are caught in time t for sex s and size class k and $N_{t+1,s,k}$ is the abundance in time $t+1$ for sex s and size class k. Catch on boats, or the amount of lobsters on the boat before protection from conservation measures occurs, was calculated as:

$$C_{t,s,k} = \frac{L_{t,s,k}}{S_{t,s,k}^{cons} S_{t,s,k}^{legal}} \tag{2}$$

where $L_{t,s,k}$ is the landings (of the fishery) in time t for sex s and size class k, $S_{t,s,k}^{cons}$ is the conservation selectivity in time t for sex s and size class k, and $S_{t,s,k}^{legal}$ is the legal selectivity in time t for sex s and sizeclass k. Conservation selectivity is the proportion of lobster landed from not being protected from having eggs or being v-notched. Legal selectivity is the proportion of lobster landed from being of legal size. $C_{t,s,k}$ plus $N_{t+1,s,k}$ is the abundance of the current timestep before fishing mortality, the last process in the IBLS but after natural mortality and growth, plus the lobsters that are released. The denominator in equation 1 includes lobsters that are released, because in reality, those lobsters could be caught again in a given timestep and need to be included in the total number of lobsters that the catch on boat can be removed from. Encounter probability is then scaled by fishing effort to represent the probability of being caught in the fishery.

II-2-1-2. State variables and scales

Individual lobsters are characterized by the state variables size (carapace length (CL) in millimeters), sex, maturity status, egg status, survival status (if the lobster is alive or dead because of either fishing or natural mortality), and V-notch presence. The temporal range is from the years 1982 to 2013 because the time range of the most recent American lobster stock assessment model output is from 1982 to 2013 (ASMFC 2015). The spatial extent is the GOM lobster stock area (Fig. II-2). The model has four timesteps: winter (January–March), spring (April–June), summer (July– September), and fall (October–December). There are 35 size classes. The largest size class is a plus group that includes all lobsters larger than or equal to 223 mm CL, and the smallest size class is 53 mm CL; this is the smallest size at which a lobster can grow above legal minimum size in one molt. The size class interval of 5 mm CL was chosen because the minimum molting increment is 5 mm CL (ASMFC 2015).

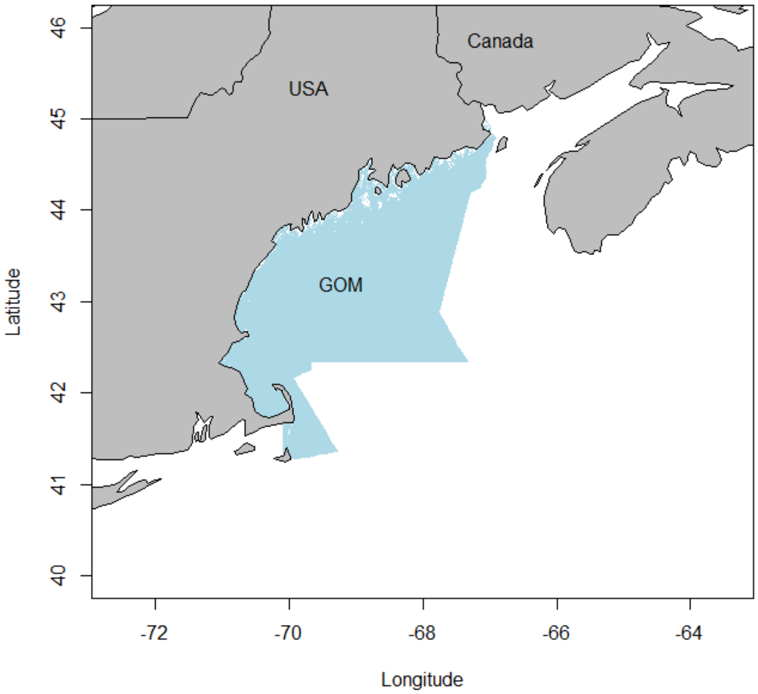


Figure II-2. The Gulf of Maine (GOM) lobster stock area.

II-2.1.3. Process overview and scheduling

Individual lobsters are traced throughout the simulation, which includes biological and fishery processes, until the individuals die of natural or fishing mortality. At first, 93,200,000 lobsters are traced, but this number changes due to mortality and recruitment. The first part of the IBLS includes the biological processes such as natural mortality and growth. In each time step in the IBLS, each individual lobster is first assessed to see if it is mature; this determines if the lobster is a part of the spawning stock biomass (SSB) and can produce eggs. It then has a probability of dying from natural mortality such as predation. If the lobster does not die, it has a probability of molting and growing a specific molt increment. Larger lobsters molt less frequently and have smaller molt increments. If it has been two molts since its last v-notch, it will lose its v-notch, as the v-notch will grow out with each molt. After molting, the lobster then has a probability of dying from molting mortality.

If it survives or did not molt, it has a probability of being caught in the fishery (encounter probability). Once caught, if it is of illegal size or has a v-notch from a previous timestep, it is released back to the population. There is no mortality when lobsters are released back to the population. If it has eggs, it has a probability of being v-notched by a lobster fisher and then released back to the population. Once v-notched, it is released back to the population and protected from harvest for two molts. The released lobster can be harvested in the next time step if it is legal to be caught. If an egg-bearing lobster is not v-notched, the lobster fisher still releases the lobster back to the population because it is illegal to land lobsters with eggs. If the lobster did not die from fishing mortality, it survives to the next time step.

The lobsters that survive to the next time step plus the recruits into the fishery equals the number of lobsters that go through the life history and fishery processes in the next time step. Each individual lobster entering the IBLS goes through all the processes repeatedly until it dies due to natural mortality or is caught in the fishery. Two recruitment events occur in the summer and fall, when molting occurs. At the end of each discrete time step, the state variables are updated and recorded. The internal process of the IBLS is programmed in C++ (Chang 2015), and the input and output data are handled and analyzed in the R programming environment (R Core Team 2017).

II-2-1-4. Initialization

The initial size composition ($p_{k,1982}^{s}$) and abundance (N_{1982}^{s}) for each sex is specified, so that the number of lobsters for each sex *s* in size class *k* in the first assessment timestep (i.e., winter in 1982 (the first timestep of the stock assessment output)) is:

$$N_{k,1982}^{s} = p_{k,1982}^{s} N_{1982}^{s} \qquad (3)$$

The fishery was initially occupied with 93.2 million lobsters with an initial sex ratio of 0.546. There was a burn in period of five years to get the amount of lobsters with a v-notch to the levels of that in 1982.

II-2-1-5. Submodels

II-2-1-5-1. Recruitment

For the historical simulation and calibration parts of the study, historical recruitment was used. For evaluating the current management regulations under different levels of recruitment, we used three different recruitment levels: low, intermediate, and high. Under the assumption that estimated historical recruitment from the stock assessment has some errors, recruitment was drawn from a normal distribution with a given mean and a coefficient of variation (CV) of 10%. The means of the low and high recruitment levels were the means of the five lowest and five highest historical recruitment values, respectively. The intermediate recruitment level mean was the mean of all the historical recruitment values.

II-2-1-5-2. Maturity

The proportion of females that are mature, which make up the SSB, at a certain CL is defined with a logistic equation (ASMFC 2015):

$$P_{matcl} = \frac{1}{1+e^{27.243-0.3CL}} \tag{4}$$

The size of 50% maturity is estimated to be around 91 mm CL (ASMFC 2015). This equation determines the probability that an individual lobster is mature.

II-2-1-5-3. Weight-length relationship

The weight-length relationship used in the IBLS to calculate stock biomass for males is described as (ASMFC 2015):

$$W_L = 5.21\ X\ 10^{-7} CL^{3.07814} \tag{5}$$

For females it is described as (ASMFC 2015):

$$W_L = 8.67\ X\ 10^{-7} CL^{2.97157} \tag{6}$$

where *CL* is carapace length in mm for each lobster (ASMFC 2015).

II-2-1-6. Output

The output from each simulation is carefully documented. The output data can be aggregated into fishery indicators such as year-, season-, and size-specific abundance, biomass, and catch. Biomass can be estimated by summing the weights of individual lobsters after weight is determined from the weight-length models (ASMFC, 2015). Total biomass, $\mathrm{B_y^{total,s}}$, and legal biomass, $\mathrm{B_y^{legal,s}}$, in year *y* for sex *s* are estimated as:

$$B_y^{total,s} = \sum_k N_{k,y}^s w_k^s \tag{7}$$

$$B_y^{legal,s} = \sum_{si} N_{k,y}^s p_{k,y}^s w_k^s \tag{8}$$

where w_k^s is the weight of the lobster in size k, and $p_{k,y}^s$ is a switch (0 for size classes not of legal size, and 1 for legal size classes).

II-2-1-7. Model calibration

With these probabilities and input data, the base case, or historical fishery, was simulated. Additionally, catch and size composition data were aggregated from the American lobster stock assessment, and these data were used to tune the IBLS. The historical fishery simulation is systematically calibrated, or tuned, to minimize the objective function to match the observed data (from the stock assessment) using all possible combinations of coefficients or scalers for specific parameters with equal weight on both catch and size composition. A range of values of coefficients was chosen for initial abundance, recruitment, and season-specific encounter probabilities. The historical fishery was simulated from 1982 to 2013 with every possible combination of coefficients. The coefficients that minimized the objective function, which was the coefficient of variation of the root mean square error (CVRMSE) between the observed (from the stock assessment) and simulated catch and size composition, were chosen (Table II-2). In this case, parameters are not estimated in a statistical estimation, but coefficients or scalers for predetermined parameters are identified. These variables are tuned with the scalers rather than estimated. Tuning the IBLS with coefficients is necessary to find the optimal coefficient values given the data so that the observed historical fishery can be simulated. With the calibrated IBLS, we then observed trends in the outputs such as catch and abundance. The calibrated IBLS could then be used to evaluate management regulations.

Table II-2. The optimal coefficients for the parameters that were tuned in the IBM. These coefficients produced the smallest objective function.

Parameter	**Coefficient value**
Initial abundance	0.7
Recruitment	1.2
Encounter probability	
Winter	1.9
Spring	2.9
Summer	0.7
Fall	0.7

II-2-1-8. Application

To illustrate some of capabilities of the simulator, we evaluated the current management regulations under different levels of recruitment: low, intermediate, and high. The different recruitment levels were projected for the years 2014–2023. Mean encounter rates of the most recent 5 years were used for each of the projection years. The status of the fishery was assessed using ad hoc biological reference points that were used in the most recent lobster stock assessment (ASMFC 2015). The target reference points were the 25th percentile of historical exploitation rate and the 75th percentile of historical reference abundance, and the limit reference points were the 75th percentile of historical exploitation rate and the 25th percentile of historical reference abundance. Reference abundance and exploitation rate are calculated using lobsters greater than 78 mm CL (ASMFC 2015).

By comparing the reference abundance, exploitation rate, and landings of the different scenarios, we can ask (i) how would the fishery and lobster population be different if recruitment were to change, and (ii) are current management regulations robust to variability in recruitment? The simulations were run 50 times for each of the three scenarios: (i) low recruitment, (ii) intermediate recruitment, and (iii) high recruitment.

II-3. Results

II-3-1. Calibration

The parameter coefficients that produced the smallest objective function (Table II-2) increased recruitment and decreased initial abundance. These coefficients also increased the winter and spring encounter probabilities and decreased the summer and fall encounter probabilities, as encounter probabilities can vary by season. The objective function seeks to minimize the sum of the CVRMSE of observed and predicted catch and size composition by time step. The error indicator (e.g., CVRMSE) was 0.92 with the coefficients and 1.11 without the coefficients.

With these values of coefficients or scalers, the tuned IBLS accurately captured the historical annual and seasonal landings (Figs. II-3 and 4). Before tuning, the simulated annual landings were lower than the observed landings (Fig. II-3). Without the coefficients, the simulated seasonal landings were lower than the observed landings in the spring and summer but higher in the winter and fall (Fig. II-4).

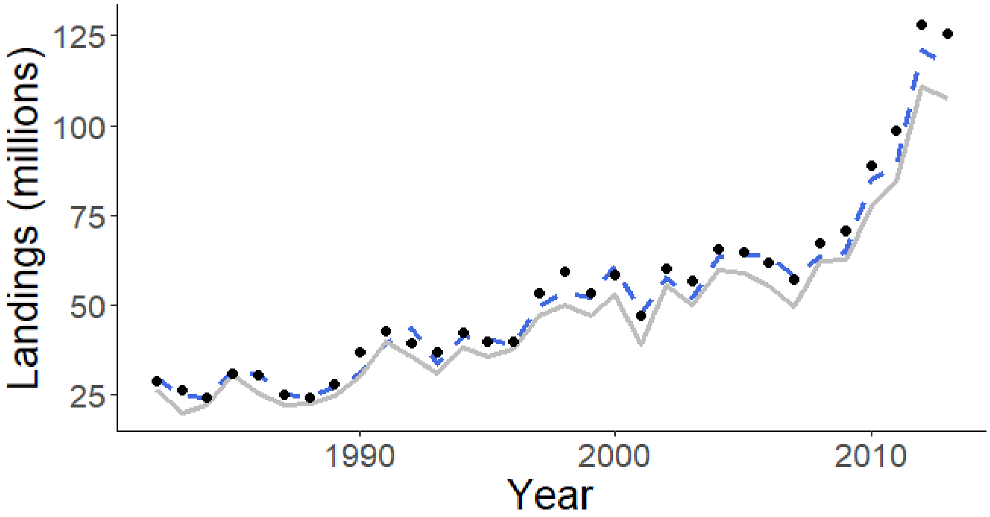


Figure II-3. Simulated annual landings overtime. Observed = black dots, simulated with coefficients (tuned) = dashed blue line, and simulated without coefficients (not tuned) = grey line.

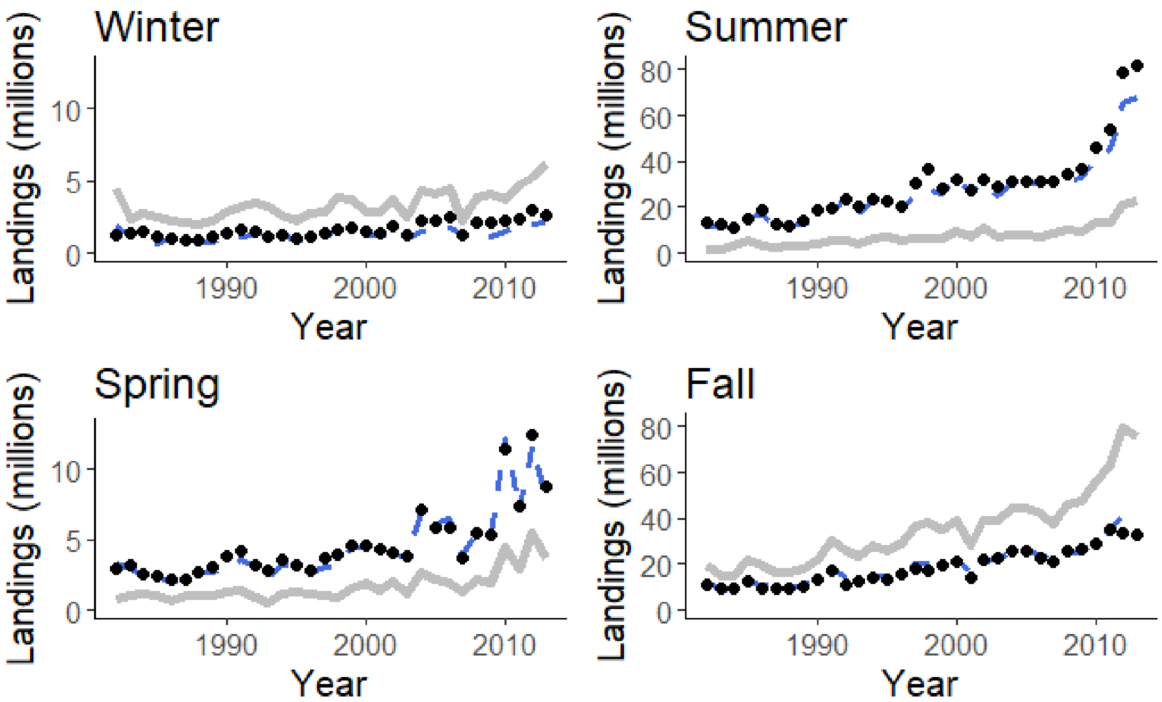


Figure II-4. Simulated seasonal landings over time. Observed = black dots, simulated with coefficients = dashed blue lines, and simulated without coefficients = grey lines.

The IBLS simulated fewer small lobsters and more large lobsters in all seasons for both sexes but more so in the winter and spring (Figs. II-5 and II-6). Also, in the summer and fall, the IBLS simulated more male lobsters just above the legal minimum size (Fig. II-6). Before tuning, the simulated size composition better matched the size composition from the stock assessment (Figs. II-5 and II-6). The biggest differences in size composition before and after tuning were in the winter and spring (Figs. II-5 and II-6).

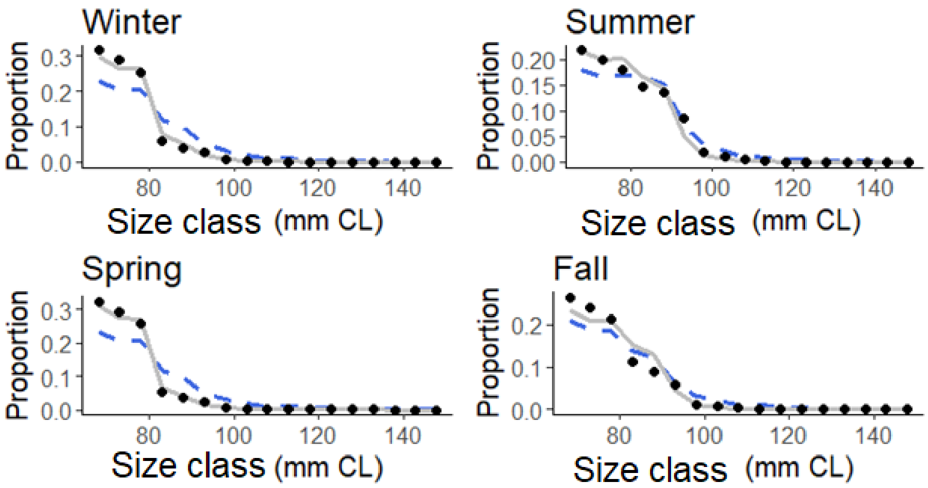


Figure II-5. Simulated mean seasonal female size composition. Observed = black dots, simulated with coefficients = dashed blue lines, and simulated without coefficients = grey lines.

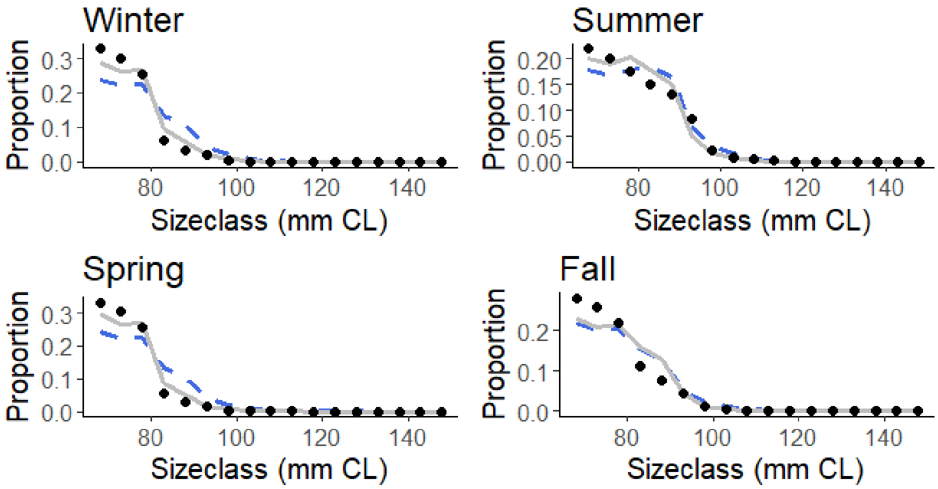


Figure II-6. Simulated mean seasonal male size composition. Observed = black dots, simulated with coefficients = dashed blue lines, and simulated without coefficients = grey lines.

II-3-2. Application

With high recruitment (average of highest five years of recruitment), reference abundance remained steady and well above the abundance target reference point (124 million) from 2014 to 2023 (Fig. II-7). With intermediate recruitment (average of historical recruitment), reference abundance declined below the abundance target reference point but remained above the abundance limit reference point (60.7 million) (Fig. II-7). With low recruitment (average of lowest five years of recruitment), reference abundance declined below the limit reference point (Fig. II-7). The rate of decline was larger with low recruitment and decreased over time in both the low and intermediate recruitment scenarios (Fig. II-7).

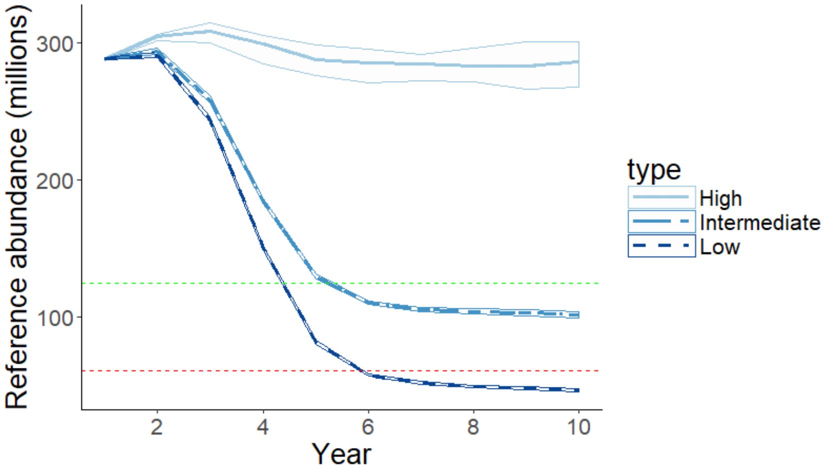


Figure II-7. Reference abundance from 2014 to 2023 with low, intermediate, and high recruitment. The horizontal dotted green line represents the target abundance reference point (124 million) (75th percentile of reference abundance). The horizontal dotted red line represents the limit abundance reference point (60.7 million) (25th percentile of reference abundance).

Exploitation rate remained steady and above the exploitation rate limit (0.352) with high recruitment (Fig. II-8). With intermediate recruitment, exploitation rate declined to around the limit and then increased (Fig. II-8). With low recruitment, exploitation rate declined to below the target (0.332) and then increased to just above the target (Fig. II-8). Exploitation rates were similar across all recruitment levels until the fifth year of the projection (Fig. II-8).

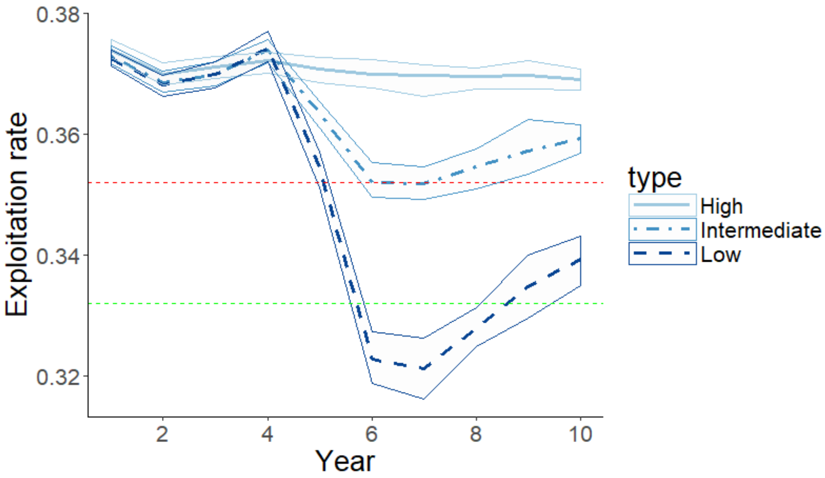


Figure II-8. Exploitation rate from 2014 to 2023 with low, intermediate, and high recruitment. The horizontal dotted green line represents the target exploitation rate reference point (0.332). The horizontal dotted red line represents the limit exploitation rate reference point (0.352).

With high recruitment, landings only slightly declined (Fig. II-9). With intermediate recruitment, landings declined to about half of the amount in the first year of the projection (Fig. II-9).

Landings declined even more and at a faster rate with low recruitment (Fig. II-9). With both intermediate and low recruitment, the landings leveled off around year 6 of the projection (Fig. II-9).

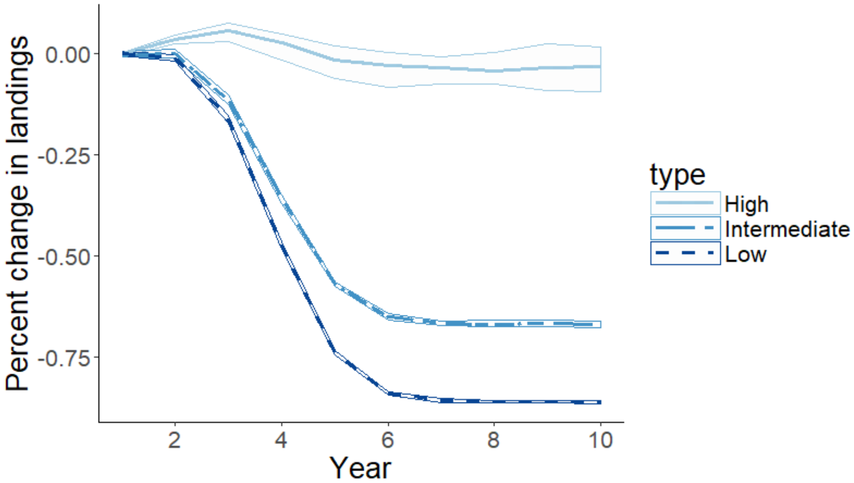


Figure II-9. Percent change in landings from 2014-2023 with low, intermediate, and high recruitment.

II-4. Discussion

In this study, an individual-based simulation tool that can be used to evaluate fisheries management is described, modified, parameterized, tuned, and applied. In this section, we discuss the lessons learned from calibrating the IBLS, the management implications for the American lobster fishery, and the applicability of this simulator in other crustacean fisheries.

II-4-1. Lessons from calibrating the IBLS

One of the main goals posed by the present study was to tune the IBLS by identifying appropriate values of coefficients for the IBLS parameters. Because fisheries are complex, variable, and difficult to observe, there is substantial uncertainty in fisheries models (Hill et al. 2007). Complex fisheries result in complex models and many assumptions, and data are frequently inadequate for evaluating complex models (Hill et al. 2007). Calibrating a model includes tuning the model by determining a set of parameters that fit the model to its data and can provide insights into the uncertainty of input data, model parameters, and model structure. This is different from estimating model parameters in a statistical model. Results from a simulation model are based on many initial parameter estimates, which are not known. Coefficients can be applied to inputs that are not as certain, and once the simulator is tuned, the more the coefficients deviate from 1, the more uncertainty can be expected from that input or model structure.

In this study, there are discrepancies between results obtained before and after calibrating the IBLS. The large coefficients, or scalers, represent either inaccuracies of the input data or the IBLS structure. Interestingly, the simulated size composition matched the historical size composition better before tuning the model, which may be a result of the model catching more small lobsters to better fit the historical landings. Additionally, structural differences between the stock assessment model (ASMFC 2015) and the simulator may result in bias (Hill et al. 2007). Potential bias may be apparent in the size composition of male lobsters in the summer and fall. The IBLS simulates more male lobsters just above the legal minimum size in these seasons, which may be a result of the IBLS simulating less catch of male lobsters overall to match the catch from the stock assessment. Tuning the IBLS highlights some uncertainties in the lobster stock assessment. The GOM lobster stock assessment model underestimated the amount of large lobsters (ASMFC 2015), and the tuned simulations produced more large lobsters than there were in the stock assessment output data, especially in the winter and spring, when migration to offshore waters occurs. In the IBLS, lobsters cannot migrate, so the large lobsters are kept within the system unless they die. Moving forward, the Atlantic States Marine Fisheries Commission (ASMFC) will combine the GOM lobster stock with the Georges Bank lobster stock because of the migration of large lobsters between the two stocks (ASMFC 2015).

Tuning the IBLS addresses the uncertainty in the fishing effort, as well as other parameters. In this study, fishing effort was estimated from harvester data as trap haul set over days. Simulated landings are sometimes underestimated with no coefficients, which indicates that this may not be the best estimate of fishing effort. The effort data used in this study were obtained from fishing vessels that only target lobster. However, misreporting by lobster fishers is possible, and logbooks are only filled out by 10% of Maine lobster fishers which may not be representative of the fishery. Also, the stock area includes New Hampshire and Massachusetts fishery areas, and fishing effort data from those states were not included in this study. Additional factors such as lobster fisher skill and bait may also play a role. Future research should consider changes in skill and bait over time.

As a result, the simulated annual, spring, and summer landings before calibration were all lower than the landings from the stock assessment, which indicates that the trap haul set over days from the harvester data may be an underestimation of fishing effort. The simulated landings in the winter and fall are higher than the landings from the stock assessment, which suggests that in those seasons, the harvester data may be an overestimation of fishing effort. The values of coefficients for the encounter probabilities had a much higher magnitude in the winter and spring than in the summer and fall, indicating that the harvester data are more reliable in the summer and fall than in the winter and spring. The same amount of trap haul set over days applied in the summer and fall can result in a larger catch than that of the winter and spring because of the differences in spatial distribution of lobster (Chang et al. 2010).

However, the lack of fit to the observed catch and size composition may be an effect of inappropriate model structure and assumptions instead of the data input. For example, the IBLS is structured so that lobsters are only allowed to be caught once in a time step, when in reality, they could be caught and released several times in a time step. This affects the encounter-rate calculation, hence another reason to tune the encounter probabilities. Also, the lobsters and fishing effort are assumed to be distributed evenly across the area, which is not realistic. Lobsters are also assumed not to migrate out of or into the stock. Additionally, natural mortality is assumed to occur before growth and fishing. The response of lobster fishers to changes in the system was not incorporated into the simulator either.

II-4-2. Management implications for the American lobster fishery

The simulations in this study indicate that the robustness of Maine lobster fishery management regulations is dependent upon recruitment. However, the recruitment levels in these simulations are much different from each other because they are based off the historical recruitment, which has a wide range of values. Future studies should include different levels of recruitment that are closer in magnitude.

Nevertheless, according to the simulations, even if recruitment declines to a third of the current recruitment, abundance will still be above the limit abundance. Also, if recruitment were to decline to a tenth of the current recruitment, then exploitation rate would decline to below the target, which indicates that current management regulations allow for a reduction in exploitation rate with low recruitment. Current management regulations also allow for a reduction in exploitation rate with intermediate recruitment. Although catch declines dramatically with low recruitment, it only declines to a level similar to the historical catch in the mid-1990s.

The tuned IBLS replicates the historic data well and therefore can be used to evaluate management regulations in the GOM lobster fishery. Simulators for fisheries management combine the best available data and can evaluate a variety of management scenarios (Grant et al. 1981). The simulator in this study can be a useful tool for management of the American lobster fishery and other lobster and crab fisheries by evaluating management strategies with consideration of varying biological factors.

The simulator used in this study can be adapted to serve as an operating model within a management strategy evaluation (MSE) context. MSE is an emerging approach that can improve fisheries management because it is an adaptable framework for modeling a fishery management system instead of just the fish stock (Cochrane et al. 1998; Smith et al. 2008). MSE uses a simulator as a realization of the truth and can be used to identify management strategies that will fail at meeting objectives before deciding the final management measures (Harwood and Stokes 2003). However, to work towards a complete MSE, future studies should identify management objectives for the GOM lobster fishery with information from stakeholders. Failure in fisheries management is often due to lack of clearly defined management objectives. Future MSE work should involve lobster fishers early in the process. MSEs allow precautionary management to be implemented thoroughly and scientifically (Harwood and Stokes 2003).

Not only can the simulator evaluate management strategies, but it can also be used to identify which factors influence the current lobster abundance and landings. In the GOM lobster fishery, fishers and scientists believe that both conservation measures and environmental factors have led to changes in the Maine lobster fishery and population (Acheson and Gardner 2010; Acheson and Steneck 1997). Future studies should use simulations to help identify the degree to which conservation measures and biological factors have influenced the fishery.

Before the simulator can be used to test management scenarios, it is important that the assumptions of the simulator be understood. Because the conclusions may be incorrect if some of the numerous restraining assumptions are changed, the best performing management scenarios should be viewed with consideration of these assumptions. Some of these assumptions include no variation of population dynamics over space, no migration between stocks, constant natural mortality, and constant size at maturity. For the most part, the simulator is based on similar assumptions and the same equations as those in the stock assessment. Natural mortality and maturity equations used in the simulator are assumed to be known in the stock assessment, which is usually not true.

Additionally, an important assumption of this simulator is that the behavior of the lobster fishers is a response to present management. The response of lobster fishers to new management measures are not considered, although it is important for policy performance (Sanchirico and Wilen 2001). Parameterization of the response of lobster fishers to new management measures is difficult. Currently, the stock assessment also does not consider responses of lobster fishers to management measures (ASMFC 2015). In the stock assessment, no stock–recruitment relationship is assumed, which is why the simulator has multiple options for simulating recruitment. Future work with the simulator should focus on sensitivity analyses to evaluate the robustness of the results by varying these assumptions.

In this study, recruitment is not affected by changes in SSB that result from changes in management because there is no relationship between recruitment and SSB. The stock–recruitment relationship, which is often important in identifying the effects of long-term management scenarios, is difficult to quantify for American lobster. In general, the stock–recruitment relationship and the impact of environmental variability and biological factors on this relationship are unclear (Punt et al. 2014). Although the simulator is based on single-species population dynamics, it can consider some effects of ecosystem variability when simulating recruitment. Rather than trying to identify a single best recruitment estimation method, uncertainty in recruitment can be explicitly and formally accounted for by incorporating a wide range of biologically plausible recruitment scenarios into the tuned IBLS. Other fishery simulators have included a range of structures for recruitment relationships (Punt and Smith 1999). Recruitment can be designated as a function of SSB and bottom-water temperature. Otherwise, recruitment can be drawn from theoretical distributions derived from historical recruitment that correspond to high and low SSBs.

Future studies on simulations of the Maine lobster fishery should not only focus on recruitment estimation, but also on growth and fishing behavior changes. The GOM is experiencing rapid water temperature changes (Le Bris et al. 2018; Mills et al. 2013) and an aging Maine lobster fleet (Johnson and Mazur 2018). Temperature changes may influence lobster population dynamics, as temperature has a large effect on the life history of American lobster, especially on recruitment and growth (Aiken and Waddy 1986). This can be incorporated into the simulator by creating a relationship between temperature and recruitment and a relationship between temperature and growth matrices. An aging lobster fishing fleet may also impact the effectiveness of existing management because fishing behavior may begin to change, as different generations of fishers may have different perceptions of the resource (Nemec 1972; Silva 2016). For example, the percentage of compliance of v-notching may change over time. These changes could be incorporated by testing scenarios with different v-notching ratios. Incorporation of other information such as temperature changes and lobster fishing fleet dynamics may potentially improve the calibration of the IBLS. Incorporating temperature into the development of an SSB and recruitment relationship may improve the calibration of the IBLS and projection of the population. In addition, changing growth may result in changes in the effectiveness of existing size-related management.

II-4-3. Applicability of the IBLS in other crustacean fisheries

IBMs are useful alternatives to statistical models for crustacean management. Although statistical models work well for crustacean population dynamics, IBMs can also accurately simulate crustacean fisheries and can even be used to validate statistical model results. IBMs can be used to supplement stock assessments and inform fisheries management. As the IBLS is flexible, it can be modified for the use of a simulator in other crustacean fisheries as well. Numerous biological and management scenarios can be simulated with small alterations of the parameters.

The IBLS can be especially useful for any lobster or crab fishery, as they have similar life history and fishery processes to American lobster. With an IBM approach, a variety of biological and fishery processes is included in the simulator. Crustacean life history processes such as molting, molting mortality, and bearing eggs are included. The individual-based approach can capture the non-continuous molting processes that vary among individuals.

The results from the present study are encouraging for the simulation of crustacean fisheries; however, additional explorations are needed. The simulator can integrate enhanced knowledge about the fishery and changes in some model assumptions, including changes in size at maturity or natural mortality over time. The IBLS also has functionality that allows uncertainties in recruitment to be addressed, which should be used in future studies.

Management measures that are common in crustacean fisheries such as legal sizes and protection of egg-bearing individuals are included in the simulator. IBMs are useful because they can treat each of the many complex management measures as separate processes rather than one combined selectivity. This differs from models in which total allowable catches or fishing effort levels are the only management measures included. An important feature of the IBLS is that it does not have fishing mortality as a parameter; instead, it is estimated. Using encounter probabilities as a proxy for fishing effort is important for the American lobster fishery, which does not have harvest control rules, so in testing management regulations, there should be no predetermined fishing mortality. Additionally, v-notching is not practiced in all lobster fisheries. This simulator can be used as a tool to test this conservation measure in other fisheries. In the simulator, the compliance of v-notching can be set at different rates, which is important to consider for a management measure that cannot be fully enforced, as it occurs on the boat. Maximum size is another management measure not used in all lobster fisheries and can be tested with the simulator as well. In the IBLS, the number of fisheries and management measures is not a limitation. Many different management measures can be simulated alone and in combinations within the simulator such as marine protected area, total allowable catch, and different legal sizes. A combination of numerous management measures is more realistic. The seasonality of the simulator also allows evaluation of seasonal management measures.

New knowledge can be easily integrated and updated in the simulator without recompiling the code. Economic variables, including price and price decreasing with landings, can also be incorporated into the fishery dynamics. Many bioeconomic models have been developed for crustacean fisheries and could be linked with the simulator (Clarke et al. 1992; Maynou et al. 2006; Holland 2011; Chang 2015). Currently, the IBLS is only parameterized for one area, but this is not fixed. Additional areas can be designated according to the data available. With the necessary data, IBMs have the flexibility to include multiple areas (Grimm 1999). Adaptive management simulations are also a valuable ability of the simulator, as management can be simulated as more conservative or less conservative when the fishery or fish population passes a reference point. Another innovation in this model is the inclusion of the ability to select different compliance rates for conservation measures. Another advantage that IBMs have over statistical models is the process-based design. This allows for easier communication to stakeholders about how the model works. A flowchart (such as in Fig. II-1) may be easier for stakeholders to understand than mathematical equations.

Lobster fishery management can have effects that extend past the species and into the ecosystem. Future studies should address potential missing ecosystem processes in the simulator. Because of modeling limitations, not all effects of fisheries management can be examined with a single simulation tool. In many cases, adding extra details into the model to address these limitations may not be essential; as Walters et al. (1997) describe, we should not "go to too much detailed models without stopping to ask whether the extra is necessary". The results from simulations will become less useful if additional uncertainties are integrated (Grant et al. 1981; Somers and Wang 1997). This may cause managers to not implement management measures that would have positive influences on the fishery (Grant et al. 1981). Adding multiple areas would require all of the input data for each area and the migration of lobsters among areas, which are often not available or difficult to quantify. Spatially explicit models are often not developed because of the sensitivity of fishery dynamics to migration coefficients and the difficulty of estimating the coefficients (Pelletier and Mahévas 2005). Because there is usually not enough detailed data compared with model complexity, parameter estimation for spatially explicit models is difficult (Pelletier and Mahévas 2005). Here, a trade-off between parsimony and complexity must be made.

In this study, an individual-based approach captures the necessary details of the life history and fishery processes of the American lobster. With the simulation tool that has been modified, parameterized, and calibrated in this study, the GOM American lobster fishery can be simulated. The process of tuning the IBLS highlights the uncertainty in the input data and model structure. This study begins to evaluate the robustness of current management regulations with variability in recruitment, but the simulator has the potential to explore more questions. This simulator can be used to evaluate the robustness of management regulations not only in the GOM lobster fishery but can also be modified for use in other lobster and crab fisheries.

III. Evaluating V-notching on its impacts on the lobster fishery

III-1. Introduction

The lack of understanding of v-notching calls for a careful evaluation of this conservation measure and dissemination of results to the industry if v-notching is critical to the sustainability of the fishery. When conducting such a study, variability in fishing behavior, v-notch definitions, and lobster recruitment dynamics should be considered. Because the v-notch conservation measure is voluntary, it is important to consider variability in compliance rates (i.e., the percent of lobsters caught with eggs that will be v-notched by a lobster fisher). Also, different American lobster management areas have different v-notch definitions; some areas have less strict v-notch definitions, while other areas have strict v-notch definitions. Additionally, stock-recruitment dynamics are often difficult to define in a changing environment, which adds the uncertainty in our effort to evaluate the effectiveness of v-notching (ASMFC 2015).

Given the changing environmental conditions in the GOM which may greatly influence the lobster recruitment and growth dynamics (ASMFC 2015; Mcmahan et al. 2016; Tanaka and Chen 2016), an improved understanding of the effectiveness of v-notching in regulating the lobster population dynamics becomes urgent and necessary. However, no systematic and comprehensive study has been done to evaluate and quantify the measure’s contribution to the improved lobster stock and landings with consideration of multiple stock-recruitment relationships, variability among individual lobsters, variation in management compliance, and variation in v-notch definitions.

III-2. Methods

In this chapter, the IBLS conditioned in this project was used to simulate the Maine lobster fishery.

III-2-1. Recruitment dynamics

Four different recruitment scenarios were considered, including scenarios with no relationship between recruitment and SSB, because the American lobster stock-recruitment relationship is not clear. In the first recruitment simulation scenario, recruitment was drawn from estimated historical recruitment of the corresponding year from the stock assessment (ASMFC 2015), assuming no stock-recruitment relationship. Under the assumption that estimated historical recruitment from the stock assessment has some uncertainty, recruitment was drawn from a normal distribution with the estimated historical recruitment value of the corresponding year from the stock assessment as the mean and a coefficient of variation (CV) of 10%.

Recruitment is estimated annually in the stock assessment and divided into summer and fall portions (ASMFC 2015); therefore, in all the recruitment simulation scenarios, annual estimated recruitment values are used and then the resulting recruitment values are divided into summer and fall portions. Around 66% of recruitment occurs in the summer, and 33% of recruitment occurs in the fall (ASMFC 2015).

The second recruitment simulation scenario was to randomly assign recruitment values from normal distributions, with means and standard deviations estimated from the stock assessment output, that correspond to five levels of SSBs (ASMFC 2015; Fig. III-1 and Table III-1). Higher recruitment values correspond with more recent years (Fig. III-2). This approach partially considered the possible relationships between SSB and annual recruitment. SSB was the SSB in the summer, because this is when lobster eggs hatch (Ennis 1995). SSB was lagged by six years, which is considered as the average time a young of the year lobster takes to reach size at recruitment (Campbell and Robinson 1983; Fogarty and Idoine 1986). To simulate recruitment of a given year, a random number was drawn from the normal distribution of recruitment values that corresponded with the SSB from six years before. For the first six years (1982-1988), the first recruitment simulation scenario, in which recruitment values are drawn from a normal distribution with a mean of the estimated historical recruitment of the corresponding year from the stock assessment, was used. Historical recruitment was assumed for the first six years, because a change in v-notching would not affect recruitment until six years later; therefore, these scenarios simulate a change in v-notching in 1982. As this approach incorporates a relationship between recruitment and SSB, but not a theoretical stock-recruitment relationship, from here on, these scenarios are referred to as weak stock-recruitment relationship scenarios.

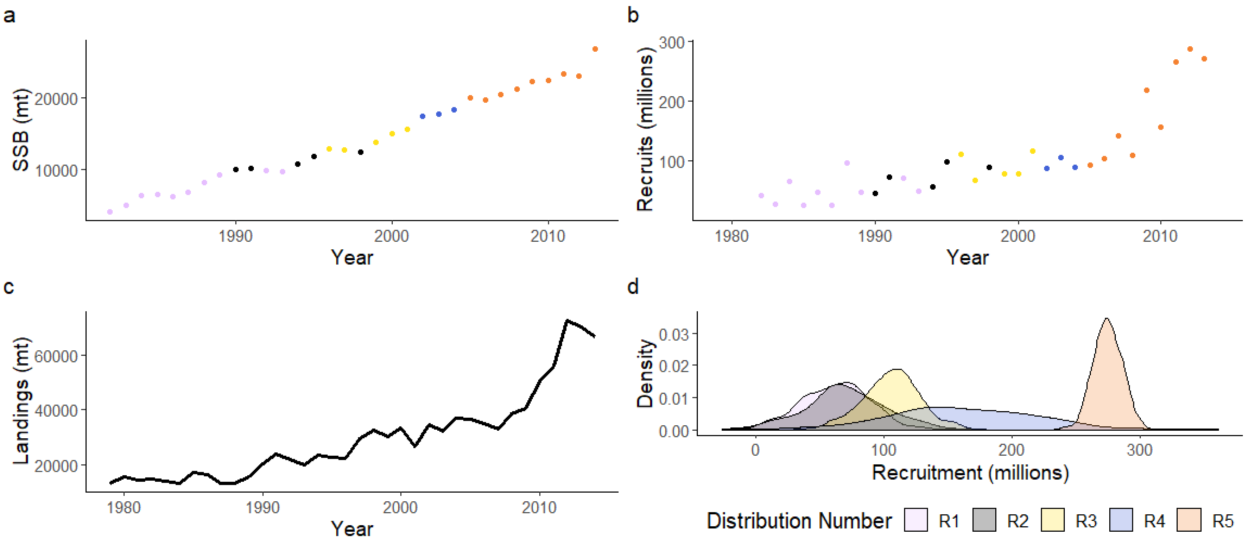


Figure III-1. Time series of spawning stock biomass, recruitment, and landings and the weak stock-recruitment relationship (SRR) distributions. a) Simulated spawning stock biomass (SSB) over time. Colors correspond to the distributions in the weak SRR. b) Estimated recruitment from the stock assessment over time. Colors correspond to the distributions in the weak SRR. c) Estimated landings from the stock assessment over time. d) The normal distributions of recruitment from the stock assessment that correspond to five different SSB levels. R1 corresponds to SSB that is below 10,000 mt, R2 corresponds to SSB that is above 10,000 mt but below 12,500 mt, R3 corresponds to SSB that is above 12,500 mt but below 16,000 mt, R4 corresponds to SSB that is above 16,000 mt but below 19,000 mt, and R5 corresponds to SSB that is above 19,000 mt.

Table III-1. Recruitment and spawning stock biomass (SSB) means and SDs of the normal distributions of recruitment values that correspond to five levels of SSB.

SSB level (mt)	**Recruitment mean (millions)**	**Recruitment SD (millions)**	**SSB mean (mt)**	**SSB SD (mt)**
<10000	62.05	25.84	7232.45	1968.92
>10000 <12500	69.32	32.57	11050.11	1025.5
>12500 <16000	107.18	21.18	14061.74	1308.39
>16000 <19000	161.67	55.15	17831.86	436.64
>19000	274.67	10.97	20035.9	394.27

The third recruitment simulation scenario was to use a stock-recruitment model, because stock-recruitment models are commonly used to predict recruitment. To define a stock-recruitment model, the SSB lagged by six years and recruitment data from the stock assessment were fit to a variety of Ricker and Beverton-Holt models (Chang et al. 2016). With a stock-recruitment model, recruitment continuously increases with SSB. This differs from the weak stock-recruitment relationship scenarios, which suddenly switched recruitment distributions with increasing SSB. To find the best stock-recruitment model, four different stock-recruitment models were developed: Ricker and Beverton-Holt models with no temperature and with average bottom water temperature in the summer and fall. The model with the lowest Akaike information criterion (AIC) was chosen for this recruitment simulation scenario. The temperature was the annual average GOM bottom water temperature in the summer and fall months (July- December) from 1982 to 2013 from Finite-Volume Community Ocean Model (FVCOM) stations (Chen et al. 2006). Bottom water temperature was chosen, as it has a large role in driving lobster distribution (Chang et al. 2010). Temperature from the summer and fall was chosen, because recruitment occurs in these seasons (ASMFC 2015).

The Ricker model with no temperature was $R = \alpha S e^{-\beta S} e^{\varepsilon}$ (Ricker 1954, 1958), and the Ricker model with temperature was $R = \alpha S e^{-\beta S} e^{\gamma T} e^{\varepsilon}$ (Penn and Caputi 1986). The Beverton-Holt model with no temperature was $R = \frac{S}{\alpha + \beta S} e^{\varepsilon}$ (Beverton and Holt 1957), and the Beverton-Holt model with temperature was $R = \frac{S}{\alpha + \beta S} e^{\gamma T} e^{\varepsilon}$ (Quinn and Deriso 1999). R is the number of recruits, S is the SSB, T is the average bottom water temperature of the GOM in the summer and fall months, α is the density-independent parameter proportional to fecundity, β is the density-dependent parameter, γ is a coefficient expressing the magnitude of the effect of temperature, and ε is the multiplicative error term. The parameters: α, β, and γ had a range of values, based on 90% confidence intervals determined by bootstrapping. In the v-notching scenarios, these parameters were chosen for each iteration by randomly selecting the parameters from these ranges of values. For the first six years (1982-1988), the first recruitment simulation scenario was used. The fourth recruitment simulation scenario was a stock−recruitment model with an increased density dependence effect. The purpose of this recruitment simulation scenario was to determine how sensitive the results were to density-dependence effects. This recruitment scenario followed the same methods as the third recruitment scenario, except the distribution of the β parameter was modified so that all values were several orders of magnitudes larger those in the bootstrapped β distribution.

III-2-2. V-notching scenarios

Within the IBLS, we addressed effect of v-notching on lobster landings and biomass. We simulated different v-notching conservation compliance levels (0, 50, and 100%) and different numbers of molts until a v-notch grows out (1 or 2 molts) with the 4 different recruitment simulation scenarios from 1982−2013 (Table III-2). These simulations focused on the long-term effects of different notch definitions and compliance regimes.

Table III-2. The different v-notching scenarios.

Scenario	Compliance rate (%)	Definition	Time until a v-notch grows out (years)
Reference	90	Strict	4
0	0	N/A	N/A
50-S	50	Strict	4
100-S	100	Strict	4
50-L	50	Less strict	2
100-L	100	Less strict	2

Tully (2004) pointed out that determining the contributions of v-notching and other conservation measures would be impossible if the measures were concurrent. However, with the IBLS, it is possible to identify the contribution of concurrent conservation measures, because each conservation measure is simulated as a separate process. Indeed, many conservation measures can be applied concurrently to the fishery. This approach may lend itself to handling more complex management problems in situations involving varying compliance rates and enforcement criteria.

Conservation measures can be evaluated with different enforcement criteria with the IBLS. This is realistic for measures that are not easily and consistently enforced, such as v-notching. In this case, the size of a notch that is considered a v-notch can differ, so considering different criteria or v-notch definitions is necessary for understanding the measure's impact on the fishery and population.

The number of molts until a v-notch grows out depends on how strict the v-notch management definitions are; from here on, 2 molts will be referred to as a strict definition and 1 molt will be referred to as a less strict definition. With a strict definition, more molts are needed for the v-notch to grow out because any size notch is considered a v-notch. Lobster fishers can keep the lobsters after approximately 2 yr with a less strict definition and 4 yr with a strict definition, since mature female lobsters tend to molt every other year. The state of Maine currently has a zero tolerance v-notch definition, meaning that a lobster with any notch depth is illegal to land; however, in other lobster management areas a lobster with a notch of less than 1/4th to 1/8th of an inch (3− 6 mm) can be landed.

When evaluating conservation measures, a benefit of using the IBLS is that different compliance rates can be applied in the simulation. Instead of only considering scenarios of implementing a conservation measure or not, conservation measures can be implemented with varying degrees of compliance, which is more realistic. Compliance may differ based on fishermen's reactions to management measures, so consideration of the response of fishermen is necessary when evaluating the impact of management. Maintaining varying degrees of compliance is especially realistic in cases where the conservation measure is difficult to enforce.

In these simulations, the probability of a legal sized lobster being v-notched by a lobster fisher if it is caught with eggs represents the v-notching compliance rate, meaning that 0, 50, or 100% of legal sized lobsters caught with eggs are v-notched. If the lobster is v-notched, it is released back to the population and protected from harvest for 1 or 2 molts. If the lobster is not v-notched, it is released back to the population and can be harvested in the next timestep. Simulations were performed 50 times for each scenario from 1982−2013 due to computational demands.

The results from these simulations were compared with those for the reference scenario, which is the historical scenario. The reference scenario simulates what occurred in the fishery using the first recruitment scenario, or historical recruitment. Historically, there was a 90% v-notching compliance rate and a strict v-notching definition (Mazur et al. 2018), and these were implemented in the reference scenario as well.

Because changes in the v-notching compliance and v-notch definition may not always have a detectable effect on the fishery and population, we used independent samples t-tests to determine if the final SSBs and cumulative landings were significantly different ($\alpha < 0.05$) between scenarios.

III-3. Results

In general, v-notching positively affected American lobster SSB, but more so with a stock−recruitment relationship (Fig. III-2). V-notching positively affected cumulative landings with a stock−recruitment relationship but negatively affected cumulative landings without a stock−recruitment relationship (Fig. III-2). Both high compliance and a strict definition increased the positive effect of v-notching (Fig. III-2). Because the Ricker models did not predict recruitment well (Fig. A21; Mazur 2021), determining the effect of v-notching from these scenarios was difficult.

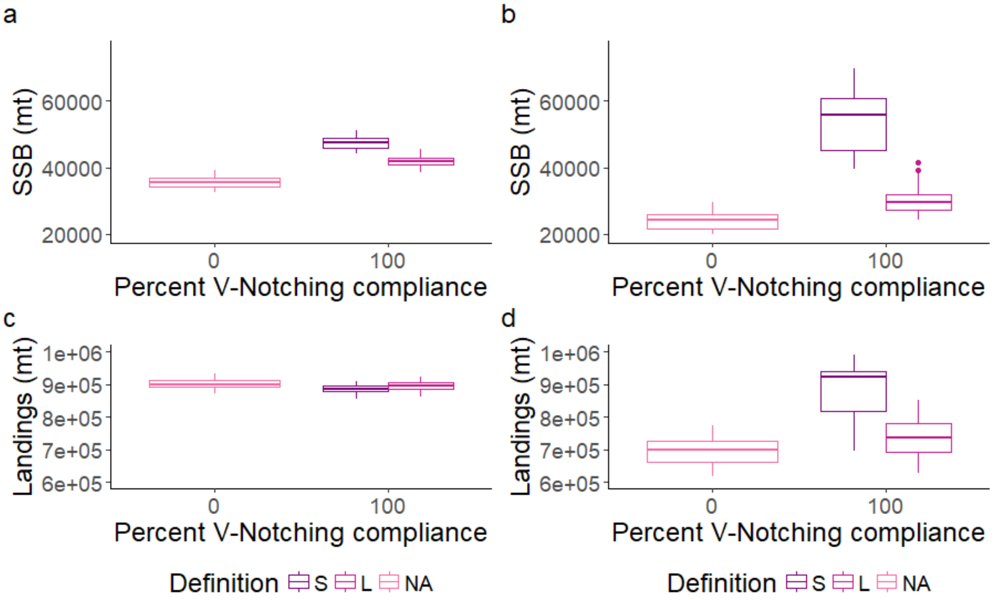


Figure III-2. American lobster v-notching scenario results. (a,b) Spawning stock biomass (SSB) in the last year of simulations (2013) of 0% and 100% v-notching compliance rates with different definitions and with (a) historical recruitment and (b) recruitment from the weak stock−recruitment relationship. (c,d) Cumulative landings of scenarios with 0% and 100% v-notching compliance rates with different definitions and with (c) historical recruitment and (d) recruitment from a weak stock−recruitment relationship. S: strict; L: less strict; NA: no v-notch definition because there was 0% compliance. Box midline = median; upper box limit = 75% quartile, upper hinge; lower box limit = 25% quartile, lower hinge; lower whisker: smallest observation greater than or equal to lower hinge – 1.5 × interquartile range (IQR); upper whisker = largest observation less than or equal to upper hinge + 1.5 × IQR. These are the same for all boxplots in the figure.

III-3-1. Results with fixed, historical recruitment

With the historical recruitment scenario, higher v-notching compliance and a stricter v-notch definition significantly (p-values < 1.60 × 10–5) positively affected SSB (33% higher with 100% compliance and a strict definition than with 0% compliance) (Fig. III-3, Table III-3). However, the difference in SSB between the 100% compliance with a strict definition scenario and the reference scenario (i.e. what occurred in the fishery) was negligible (p = 0.79) (Fig. III-3). The SSBs with 100% v-notching compliance with a less strict definition were slightly less than the SSBs with 50% v-notching compliance with a strict definition (Fig. III-3, Table III-3).

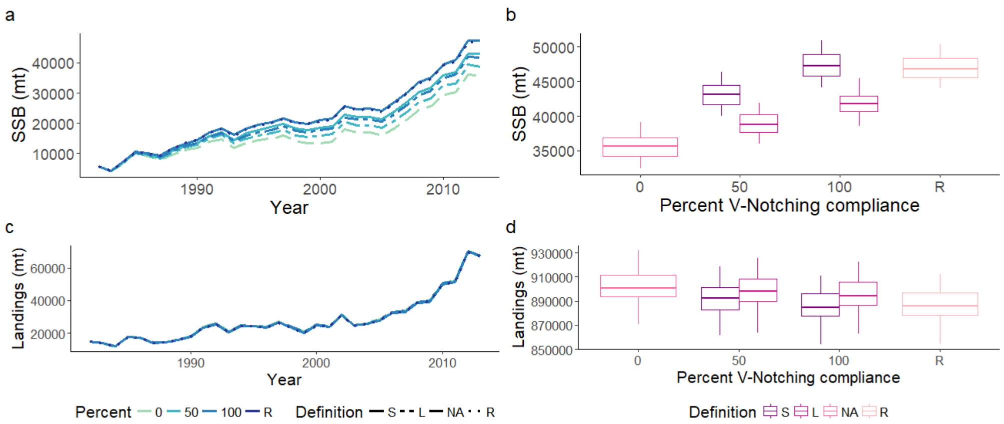


Figure III-3. V-notching scenarios with historical recruitment. Median American lobster (a) spawning stock biomass (SSB) and (c) landings from 1982−2013 with 0, 50, and 100% v-notching probabilities, with strict (S) and less strict (L) definitions, and with historical recruitment. (b) SSB and (d) cumulative landings in the last year of the simulations (2013) of 0, 50, and 100% v-notching compliance rates with different definitions and with historical recruitment. Results from the reference or historical scenarios are also included. NA: no v-notch definition because there was 0% compliance; R: reference scenario with 90% compliance and a strict definition.

Table III-3. The median, lower confidence interval (C.I.) (80%), and upper confidence interval (C.I.) (80%) of the spawning stock biomass (SSB) in metric tonnes from the last year of each of the recruitment, V-Notching compliance, and V-Notch definition scenarios.

Scenario	**Median (mt)**	**Lower C.I. (mt)**	**Upper C.I. (mt)**
Reference Scenario (90% compliance with a strict definition)	46868	44863	48991

Historical recruitment			
0%	35600	33273	37698
50% with a strict definition	43096	40924	45715
100% with a strict definition	47316	44920	49262
50% with a less strict definition	38755	36592	40905
100% with a less strict definition	41817	39653	44202
Weak stock-recruitment relationship			
0%	13674	11455	15555
50% with a strict definition	24321	21621	29264
100% with a strict definition	52616	33188	59172
50% with a less strict definition	18026	14865	21115
100% with a less strict definition	22192	20016	25773
Ricker model recruitment			
0%	4049	4671	5314
50% with a strict definition	19141	16787	21522
100% with a strict definition	29631	27161	32844
50% with a less strict definition	10769	9202	12269
100% with a less strict definition	15733	14633	18212
Ricker model recruitment with increased density-dependence			
0%	4266	3794	5103
50% with a strict definition	16250	14861	17873
100% with a strict definition	24224	22534	26945
50% with a less strict definition	9578	8755	11104
100% with a less strict definition	14085	12681	15469

The landings of the different scenarios did not notably differ from each other over time in the historical recruitment scenarios (Fig. III-3). However, v-notching had a negative effect on cumulative landings (1.9% higher with 0% compliance than with 100% compliance and a strict definition). Most of the cumulative landings of the various scenarios differed significantly (p-values < 0.04), except for the cumulative landings of the strict definition scenarios and reference scenario (p-values > 0.05), the 50% compliance with a strict definition and the 100% compliance with a less strict definition scenarios (p = 0.228), and the less strict definition scenarios (p = 0.348) (Table A25 in Mazur 2020). The scenario with no v-notching had the highest cumulative landings, followed by the scenarios with less strict definitions, then the scenario with 50% compliance with a strict definition, and then the 100% compliance with a strict definition and reference scenarios (Fig. III-3, Table III-4).

Table III-4. The median, lower confidence interval (C.I.) (80%), and upper confidence interval (C.I.) (80%) of the cumulative landings in metric tonnes of each of the recruitment, V-Notching compliance, and V-Notch definition scenarios.

Scenario	**Median (mt)**	**Lower C.I. (mt)**	**Upper C.I. (mt)**
Reference Scenario (90% with a strict definition)	885641	866906	902586
Historical recruitment			
0%	900705	881989	920561

50% with a strict definition	892349	872429	1176305
100% with a strict definition	884293	867689	903623
50% with a less strict definition	897743	877295	913353
100% with a less strict definition	894253	877563	913492
Weak stock-recruitment relationship			
0%	700318	645521	741212
50% with a strict definition	753058	674208	812215
100% with a strict definition	928331	742080	995844
50% with a less strict definition	709219	644956	782125
100% with a less strict definition	736278	667777	801478
Ricker model recruitment			
0%	347086	332866	366472
50% with a strict definition	525284	502732	563015
100% with a strict definition	624020	605157	675085
50% with a less strict definition	440004	416481	468897
100% with a less strict definition	494312	468181	529320
Ricker model recruitment with density-dependence			
0%	279149	264276	290662
50% with a strict definition	431833	408764	458245
100% with a strict definition	515884	488519	548969
50% with a less strict definition	362657	341657	379928
100% with a less strict definition	403271	385252	435226

III-3-2. Simulation results for weak stock-recruit relationships

For the weak stock−recruitment relationship scenarios, v-notching positively affected SSBs (285% higher with 100% compliance and a strict definition than with 0% compliance) (Fig. III-4, Table III-3). The SSBs from the reference scenario (i.e. what occurred in the fishery) were slightly below the SSBs from the 100% compliance with a strict definition scenario (Fig. III-4, Table III-3). The final SSBs were highest with the 100% v-notching compliance with a strict definition (Fig. III-4, Table III-3). Scenarios with strict definitions resulted in an increase in SSB that was not observed in the less strict definition scenarios (Fig. III-4). Also, the final SSBs in each of the scenarios differed significantly (p-values < 4.17 × 10–5), except for the difference between the 100% compliance with a strict definition and reference scenarios (p = 0.79) (Table A22 in Mazur 2020).

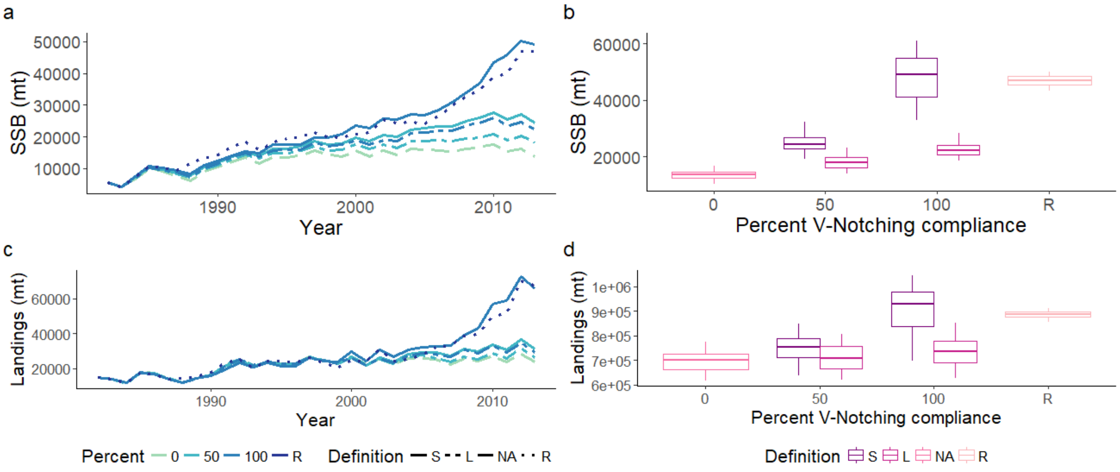


Figure III-4. Same as Fig. III-3, but showing the results of the simulations with the weak-stock recruitment relationship.

For the weak stock–recruitment relationship scenarios, v-notching had a positive effect on cumulative landings (33% higher with 100% compliance and a strict definition than with 0% compliance) (Fig. III-4, Table III-4). The landings of the 100% compliance and strict definition and reference scenarios increased dramatically after 2005, unlike the landings from the other scenarios (Fig. III-4). Like the SSBs, the landings were highest with 100% compliance and a strict definition, followed by the reference scenario landings, landings with 50% compliance and a strict definition, landings with 100% compliance and a less strict definition, landings with 50% compliance and a less strict definition, and then landings with 0% compliance (Fig. III-4, Table III-4). The landings from the reference and the 100% compliance and strict definition scenarios were similar throughout the time series (Fig. III-4). In the scenarios with 100% compliance and a less strict definition and 50% compliance and a strict definition, the landings were similar (Fig. III-4, Table III-4). Most of the cumulative landings differed significantly (p-values < 0.04), except for the cumulative landings from the 100% compliance with a strict definition and reference scenarios ($p = 0.74$), from the 50% compliance with a strict definition and 100% compliance with a less strict definition scenarios ($p = 0.33$), and from the 50% compliance with a less strict definition and 0% compliance scenarios ($p = 0.08$) (Table A26 in Mazur 2020).

III-3-3. Simulation results with strong stock-recruit relationships

When theoretical stock–recruitment models estimated recruitment, the best model was the Ricker model without temperature. The AIC value for the Ricker model without temperature was the lowest (57.6), followed by the AIC value for the Beverton-Holt model with temperature (58.9394), and the Ricker model with temperature (58.9396). The Beverton-Holt model without temperature did not converge. The predicted recruits from the best model overall followed the same trend as the historical recruits; however, the model tended to overestimate recruits at intermediate levels of SSB and underestimate recruits at high and low levels of SSB (Fig. A21 in Mazur 2020). The bootstrapped β parameters were all small negative numbers close to zero, so the modified β parameter distribution for increased density-dependence was the positive transformation of the bootstrapped distribution.

Because the Ricker model could not accurately estimate lobster recruitment at low and high SSBs, the SSBs in all scenarios with recruitment estimated from the Ricker model and the Ricker model with an increased density-dependence effect were lower than the reference SSB (Figs. III-5 & III-6, Table III-3). With the Ricker models, v-notching had a positive effect on SSB (468–632% higher with 100% compliance and a strict definition than with 0% compliance) (Figs. III-5 & III-6, Table III-3); 100% compliance with a strict definition most positively affected SSB, and the SSBs with no v-notching decreased over time (Figs. III-5 & III-6). The SSBs in the other scenarios did not increase drastically over time (Figs. III-5 & III-6). With an increased density-dependence effect, the results were similar to that of the regular Ricker model, but the differences between the compliance and definition scenarios were smaller (Fig. III-5, Fig. III-6, Table III-3). All the final SSBs significantly differed from each other (p-values < 2.71 × 10–13) (Tables A3 and A4 in Mazur 2020).

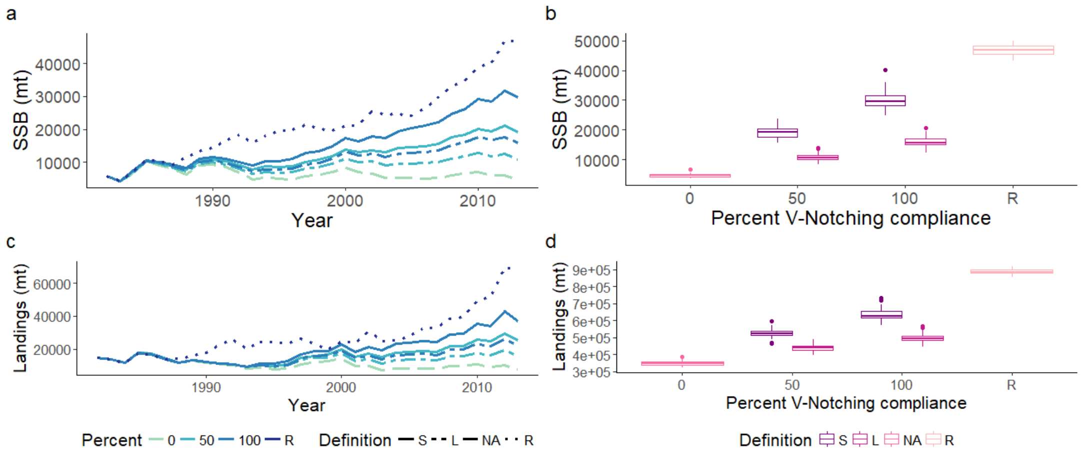


Figure III-5. Same as Fig. III-3, but showing the results of the simulations with the Ricker stock-recruitment model.

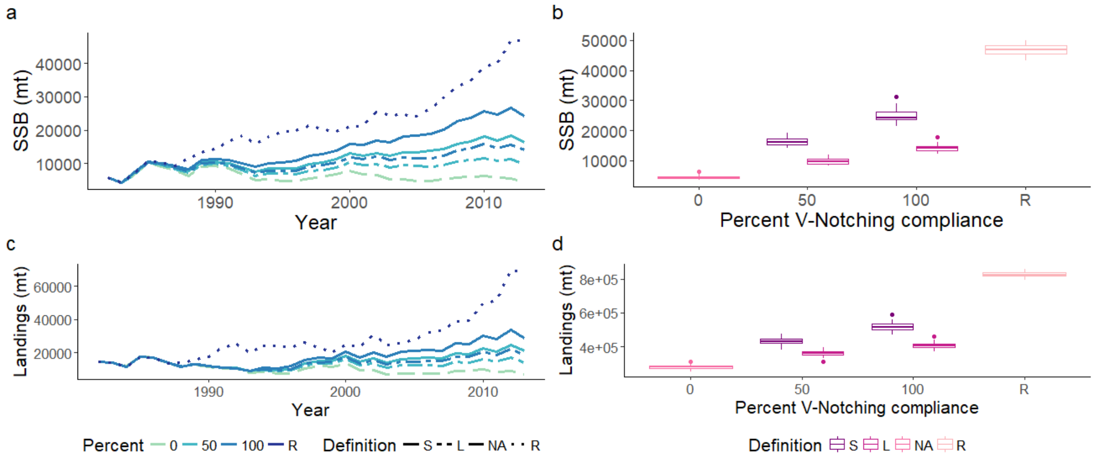


Figure III-6. Same as Fig. III-3, but showing the results of the simulations with the Ricker stock-recruitment model with an increased density-dependence effect.

Like the SSBs, cumulative landings were positively affected by v-notching with recruitment from the Ricker models (80–85% higher with 100% compliance and a strict definition than with 0%

compliance) (Figs. III-5 & III-6, Table III-4). Cumulative landings from the reference scenario were higher than that of all the different v-notching scenarios with recruitment estimated from the Ricker models (Figs. III-5 & III-6, Table III-4). Regardless, the landings increased with 100% compliance (Figs. III-5 & III-6). Similar to the SSBs with recruitment from the Ricker model, the landings also decreased with no compliance (Figs. III-5 & III-6). V-notching significantly positively affected landings (p-values < 4.10 × 10–8) (Tables A7 & A8 in Mazur 2020). There were no large differences between the cumulative landings of the regular Ricker model and the Ricker model with an increased density-dependence effect, but there were larger differences between the compliance and definition scenarios with the regular Ricker model than with the Ricker model with an increased density-dependence effect (Figs. III-5 & III-6, Table III-4).

III-4. Discussion

The results of this study support the consensus among lobster fishers (Acheson and Gardner 2010) that the protection of spawning female American lobsters, in this case by v-notching, has had a positive impact on the GOM lobster population and fishery. The magnitude of the positive impact of v-notching depended on the assumptions of the stock−recruitment relationship, compliance rate, and v-notch definition. V-notching always had a positive impact on SSB, and the impact on cumulative landings depended on the stock−recruitment relationship.

In all scenarios, v-notching preserved SSB, which can act as a buffer if there were a downturn in the fishery or population. With historical recruitment, even if only half of the egg-bearing lobsters that were caught were v-notched, there would still be a significant positive impact on the population (21% larger with 50% compliance and a strict definition than with 0% compliance). With the assumption of a weak stock−recruitment relationship, v-notching had even greater impacts on the population, as the protected spawning stock contributed recruits into the fishery (285% larger with 100% compliance and a strict definition than with 0% compliance). Under this weak stock−recruitment relationship recruitment scenario, there were even more advantages to a higher v-notch compliance rate and strict v-notch definition. SSB did not experience such a dramatic increase without high compliance rates and a strict definition. With the assumption of a stock−recruitment model, a higher v-notch compliance and a strict v-notch definition had a significant large positive impact as well (468–632% higher with 100% compliance and a strict definition than with 0% compliance). Preserving SSB becomes increasingly important in the face of climate change, since warming waters may have deleterious effects on the lobster population. Le Bris et al. (2018) projected the American lobster fishery with warming water temperatures and found that management measures for conserving the reproductive potential can help mitigate the negative effects of climate change.

The impact of v-notching on landings depended on the compliance, definition, and recruitment scenario. In historical recruitment scenarios, no v-notching produced the highest cumulative landings (1.9% higher with 0% compliance than with 100% compliance and a strict definition). With the assumption of a stock−recruitment relationship, v-notching had a positive impact on landings (33–85% higher with 100% compliance and a strict definition than with 0% compliance).

The results from these simulations also suggest that the v-notch definition had an important role. In all recruitment simulation scenarios, even 100% compliance with a less strict definition did not produce more SSB than 50% compliance with a strict definition. In the weak stock−recruitment relationship scenarios, even with 100% compliance rate but with a less strict definition, the SSB and landings would not have experienced a dramatic increase. However, this does depend on the assumptions in this study. One assumption is that the lobsters v-notched stay in the GOM stock area. If they were to go to another area, they could be landed with a less strict v-notch definition. Also, if egg production were used as a metric instead of SSB, there is the possibility that a lobster could be v-notched and never contribute more eggs under a less strict assumption, because mature lobsters bear eggs every other year.

A strict definition of a v-notch only benefits SSB and does not reduce landings with a stock−recruitment relationship, suggesting that all areas should use a strict definition of a v-notch (i.e. takes at least 2 molts to grow out). Without high compliance and a strict definition, there is a risk of a negative impact on the fishery. The state of Maine has the strictest definition of a v-notch, but other US states and Canada currently have a less strict definition of a v-notch.

The v-notching conservation measure sustained viable levels of fishery activity and is appropriate assuming that one objective of management is to maximize yield, under sustainability restraints. With conservation of biomass and an increase in landings, v-notching can be considered a tool for community-based conservation, in which both conservation and development are achieved (Berkes 2004). These results suggest that input controls, such as v-notching, can significantly benefit fish populations and fisheries.

However, v-notching compliance has decreased in recent years in the Maine lobster fishery. In this study, we simulated constant compliances to determine the effect of v-notching; currently, the magnitude of the change in compliance and when this change began to occur is unknown. Future studies should focus on lobster fishers' behavior regarding v-notching—more specifically, when the v-notching compliance began to decrease and how v-notching compliance changes with the status of the lobster population.

Future studies should also focus on understanding lobster recruitment, as the model results are dependent upon recruitment assumptions. This is especially important in understanding the effects of a conservation measure that protects the spawning stock with the long-term objective of increased recruitment. It was difficult to compare the results from the Ricker model recruitment scenarios to the reference scenario, because the Ricker model did not accurately capture historical recruitment. In general, the Ricker models were unable to represent the observed data, especially at high and recent SSBs. As a result, the results from the Ricker model scenarios could not be easily used to determine the effect of v-notching. However, if there were no stock−recruitment relationship, regulations that protect the spawning stock would not be important for the future of the fishery. In reality there is a stock−recruitment relationship that the data cannot show because of possibly large measurement errors, spatial differences in stock− recruitment relationships, and influences from environmental factors aside from temperature (Hilborn and Walters 1992). Chang et al. (2016) found that different stock−recruitment relationships existed at different spatial scales for the American lobster, possibly resulting from retention of pelagic larvae by oceanic circulations in the GOM (Xue et al. 2008), and the best model was at a medium spatial scale. Additionally, the productivity of American lobsters in the GOM may be changing due to increasing water temperatures which has caused an increase in suitable habitat (Tanaka and Chen 2016). In this study, the average temperature of FVCOM stations was used, but FVCOM stations are not distributed evenly throughout the GOM, which could have led to bias in the temperature averages. Temperature can also affect the stock-recruitment process at many different stages. At the larval stage, sea surface temperature may impact larval survival by increasing larval growth and therefore shortening the length in the water column (Incze and Naimie 2000) and decreasing larval vulnerability to predation. At the settlement stage, if waters are above 12°C, settlement habitat expands (Steneck and Wahle 2013). Increasing water temperatures also cause lobsters to molt more frequently (Comeau and Savoie 2001), which could decrease the lag between SSB and recruits, but it could also increase the number of recruits entering the fishery each year, as more lobsters are molting. This partially explains why a stock−recruitment relationship was difficult to find at a large spatial and temporal scale, such as the whole GOM from 1982−2013.

III-5. Conclusions

The IBLS model results showed that v-notching has a significant positive impact on the GOM lobster SSB (33–632% higher with 100% compliance and a strict definition than with 0% compliance) regardless of the stock−recruitment assumption and a significant positive impact on landings (33–85% times higher with 100% compliance and a strict definition than with 0% compliance) with a stock−recruitment relationship. The higher the compliance rate and the stricter the v-notch definition, the greater the positive impact on the fishery and population. The stock− recruitment relationship assumed in the model can influence the magnitude of the positive effect of v-notching. The framework proposed in this study can be extended to evaluate conservation and management measures in other fisheries.

IV. Evaluating impacts of legal sizes on lobster population dynamics

IV-1. Introduction

It is now widely acknowledged that in fisheries management it is necessary to account for both environmental change and human impacts on the population dynamics of a fishery resource (Jul-Larsen et al., 2003). There is a growing body of literature exploring environmental impacts such as effects of climate change on population productivity or distribution (Brander, 2010). However, simulation studies that quantify the contribution of fishery management regulations to population dynamics remain scarce (Chavez et al., 2003; Stewart et al., 2016). Management strategy evaluation involves using simulation to compare the relative effectiveness of alternative management regulations and determine the performance of existing regulations (Punt et al., 2016). Fisheries management with efficient conservation regulations can lead to positive development of a fishery with increased landings and abundance of a fisheries resource (Wormet al 2009). Therefore, simulation studies provide an effective framework for evaluating the trade-offs among alternative conservation regulations and for assessing the consequences of uncertainty for achieving management goals (Punt et al., 2016).

The American lobster (*Homarus americanus*) fishery is the most commercially important fisheries in the United States with a dramatic boom in landings in the Gulf of Maine (GOM) since the 1980s (Acheson and Steneck, 1997; Tanaka and Chen, 2016). The dramatic increase in landings and abundance have been attributed to changes in the environment such as warming temperature, reduced predation, and improved habitat (Wahle et al., 2013; Tanaka and Chen, 2016; Pinsky, 2018). In spite of various environmental impacts, effects of conservation measures on the lobster population have also been explored. For example, Le Bris et al. (2018) used a simulation model to evaluate "what if" scenarios and suggested that about half of the increase in lobster abundance can be attributed to the conservation measures. Gendron (2005) has also suggested that an increase of 1 mm carapace length per year in minimum legal size would lead to a doubling of egg-per-recruit production of American lobsters in the Canadian Magdalen Island after seven years. However, some of these studies do not include recruitment variability or the simulation work is hard to validate (Sundelof et al., 2014; Pinsky, 2018). The models used in previous simulation may not be able to realistically capture lobster population and fisheries dynamics because of the complexity in the life history and fishery process (Chen et al., 2005). It is thus necessary to explore a more flexible and powerful modeling framework, such as an individual-based model, to more realistically quantify the lobster life history and fishery processes and evaluate different conservation measures (Butler, 2003; Chen et al., 2005; ASMFC, 2009; Kanawai et al., 2010; Chang et al., 2011).

Conservation measures, which have been implemented in the American lobster (Homarus americanus) fishery for over 140 years, are likely to have contributed to the dramatic increase in the GOM lobster abundance (ASMFC 2015; Le Bris et al., 2018). The most important conservation measures include minimum and maximum legal sizes, v-notching (i.e. put a v- shaped notch cut in the tail of lobsters) egg-bearing female lobsters, and prohibition on taking egg-bearing or v-notched females (Acheson and Gardner, 2011). Minimum and maximum legal sizes are the most common conservation measures that set the smallest and largest carapace lengths that a lobster can be legally retained if caught (Hill, 1992). The minimum legal size ensures that the lobsters spawn at least once in their life span (Acheson and Reidman, 1982). The maximum legal size protects the larger and more fecund females. It allows the larger females to spawn more than once and increases the numbers of eggs per spawning (Hill, 1992). The lobster population is likely to fluctuate if there is a change in minimum or maximum legal size. It is important to quantify the impact of legal sizes on the lobster population with size explicit simulation scenarios.

The value of implementing minimum legal size in the lobster fishery has been well recognized while the effectiveness of maximum legal size on lobster fisheries has been debated for years. The ICES Homarus Working Group has shown that an increase in minimum legal size along with a decrease in fishing mortality would lead to an increase in stock biomass and reduce the risk of fishery-induced recruitment failure (Bennett and Edwards, 1981). However, it is difficult to decide how large a stock of breeding females is required for adequate recruitment to the fishery since no clear stock-recruitment relationship has been defined in the lobster fishery (Thomas, 1965; ASMFC, 2015). Therefore, it is important to apply different stock-recruitment relationships to the lobster data and verify how the choice of the stock-recruitment relationship may influence the management policy (Bannister and Addison, 1986).

This study used an individual-based lobster simulator to assess the impact of current legal sizes and potential effects of alternatives on the American lobster population in the GOM. We considered four types of stock-recruitment relationships in order to project reasonable variations in recruitment after changing legal sizes. We examined 25 different legal size scenarios based on combinations of 0, 1, and 2 mm increment and decrement in the current minimum and maximum legal sizes. The potential changes in lobster landings, abundance, and size composition in each scenario were quantified and evaluated in this study. The developed simulation framework may be also suitable for other fisheries with similar conservation measures.

IV-2. Materials and methods

IV-2-1. Individual-based lobster simulator and input data

We explored specific legal sizes simulation scenarios using an individual-based lobster simulator to evaluate alternative management strategies. The individual-based lobster simulator was originally described in Chen et al. (2005), ASMFC (2009), and Chang (2015). It models lobsters from 53 mm to 223+ mm carapace length (CL) in the GOM (Figure 3.1). The simulator mimics the life history and fishery processes a lobster experiences. The life history section determines the molt, maturity, and egg-bearing conditions of a lobster. It also tracks the lobster through time and determines whether it is dead due to natural mortality or it is available to the fishery. A live lobster may then be caught by the fishery and landed if it is not v-notched, is not bearing eggs, and is within the legal sizes during the fishery processes. The simulator summarizes landings, abundance, biomass, population size composition, spawning stock biomass, and recruitment at each season (Chang, 2015). The reference scenario was determined by tuning the simulator to minimize the difference between predicted catch and observed catch.

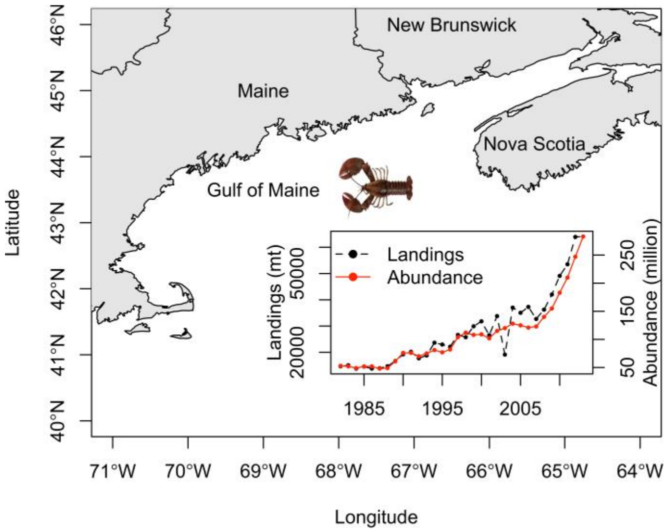


Figure IV-1. Map of study area and the historical landings and abundance of lobsters from 1982 to 2013.

IV-2-2. Stock-recruitment relationships

The historical simulation of the lobster population and fishery does not require a defined stock-recruitment relationship because we used the recruitment estimates from the stock assessment as input data to the simulator. However, the projected recruitment varies by season with changes in spawning stock biomass that results from changing the legal sizes. Therefore, a season-specific stock-recruitment relationship for summer and fall following the stockassessment settings was built into the projection function of the simulator.

Four types of stock-recruitment relationships were explored in this study and the one that produces best fits of recruitment was used for further simulations. These stock-recruitment relationships estimate recruitment by season through (1) sampling recruitment from the historical recruitment with a coefficient of variation (CV) of 50%, (2) Beverton-Holt model, (3) Ricker model, and (4) sampling recruitment from the recruitment distributions at different spawning stock biomass levels (Quinn II and Deriso, 1999). The spawning stock biomass and recruits used to estimate the relationship were the estimated spawning stock biomass and recruitments fromthe historical simulation of the individual-based lobster simulator. For the type 4 relationship, dividing the spawning stock biomass into 6 levels produced the least root mean square error between predicted recruitment and the observed recruitment from the simulator. The recruits ranged from 53 mm to 73 mm CL and they were recruits to the fishery. It takes a lobster an estimated 5 to 7 years to grow into this size range, depending on water temperature (ASMFC, 1997; Wahle et al., 2004). Therefore, we tried different time lags between stock spawning biomass and recruitment in the stock-recruitment relationship assessment. A time lag of 5 years was used for further simulations with least disagreement between predicted and observed recruitment.

$$(3.1)\ R \sim N(HR, HR \times CV)$$

$$(3.2)\ R = \frac{\alpha_1 S}{1+\beta_1 S} e^{\varepsilon}$$

$$(3.3)\ R = \alpha_2 S e^{-\beta_2 S + \varepsilon}$$

$$(3.4)\ R \sim \begin{cases} N(R_1, SD_1) & S \leq S_1 \\ N(R_{i+1}, SD_{i+1}) & S_i < S \leq S_{i+1},\ 1 \leq i \leq 5 \\ N((^{R}/_{S})_6, SD_6) \times S & S \geq S_6 \end{cases}$$

where *R* is the predicted recruitment in each season, *N* represents normal distribution, *HR* is the historical recruitment from the 2015 stock assessment report, *S* is the spawning stock biomass, α_1 and α_2 represents the number of recruits per spawner at the low number of spawners, β_1 and β_2 controls the levels of density dependence and is proportional to fecundity and density-density dependent mortality (Quinn II and Deriso, 1999), ε is the error with mean of zero and variance of σ2, R1, Ri+1, SD1, and SDi+1 represent the mean recruitment and standard deviation at spawning stock biomass level 1 (S1) and i+1 (Si+1), (R/S)6 and SD6 is the recruitment to spawning stock biomass ratio and standard deviation at spawning stock biomass level 6 (S6) or above.

The performances of the four types of stock-recruitment relationships were compared using Pearson’s correlation (Li et al., 2017). The performances of type 2 and 3 were further compared with the linear regression model that has an assumption of density independence between recruits and spawners using ANOVA test (Ogle, 2015). For each type of stock- recruitment relationships, we repeat the simulation process 50 times to account for the variability in predicted recruitment. We compared the mean of the 50 predicted recruitments with the estimated historical recruitment to estimating the performance of different types of stock- recruitment relationships.

IV-2-3. Legal sizes simulation scenarios

We explored 25 simulation scenarios that included all possible combinations of 5 minimum and 5 maximum legal sizes. Each legal size scenario was iterated 50 times. These legalsizes represented changes of -2, -1, 0, +1, +2 mm CL on the reference minimum and maximum legal sizes respectively. The scenario with no change in minimum and maximum legal sizes was the reference scenario. The reference scenario used the minimum (1982-1987: 81 mm CL, 1988: 82

mm CL, and 1989-2013: 83 mm CL) and maximum (1982-2013: 127 mm CL) legal sizesfrom the 2015 stock assessment report. Other scenarios used the same values from the reference scenario for other parameters besides the minimum and maximum legal size. We summarized therelative changes in landings, abundance, and size composition observed from the other scenarios.We used an ANOVA test to compare the mean values from 2013 estimates under different scenarios and tested the significance of minimum and maximum legal sizes impact on the lobsterpopulation.

IV-3. Results

IV-3-1. Stock-recruitment relationships

The recruitment projected from using different stock-recruitment relationships showed various degrees of correlation with the estimated recruitment from the simulated population (Figure IV-2). The estimation in summer exhibited less discrepancy with the observations and variations compared with the projection in fall (Table IV-1). The usage of the historical recruitment type relationship (type 1) produced the highest correlation between estimated and observed recruitments. However, the type 1 relationship had a tendency of overfitting the recruitment without a functional link to predict recruitment reliably under different management strategies.

The predicted recruitment in response to different spawning stock biomass levels(type 4) yields the second highest correlation. The predictions with Beverton-Holt (type 2) and Ricker (type 3) types of relationships showed relatively similar trends. The magnitude of correlation between predictions and observations for the type 2 and 3 were lower than othertypes of relationships. The fits of the stock-recruitment relationship from type 2 and 3 were no better than the fits from the density independent models according to the ANOVA test ($p > 0.05$).

Table IV-1. Correlation between predicted and observed recruitment using four types of stock-recruitment relationships with a five-year lag.

	Summer	**Fall**
Type 1	0.99	0.99
Type 2	0.85	0.68
Type 3	0.85	0.67
Type 4	0.96	0.83

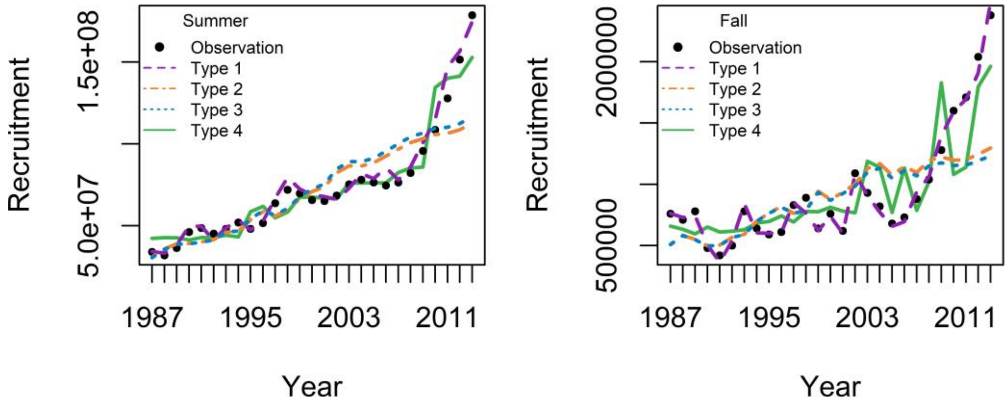


Figure IV-2. Temporal trends of the predicted recruitments from the reference scenario and scenarios using four types of stock-recruitment relationship.

IV-3-2. Changes in landings, abundance, and size composition

The 25 legal size scenarios were then explored using the type 4 stock-recruitment relationship with a 5-year lag since the type 4 relationship showed a relatively good performancein predicting the recruitment. We summarized the simulation results in terms of relative changes in landings, abundance, and size composition.

IV-3-3. Landings

Minimum legal size showed a greater impact on lobster landings than maximum legal size. The predicted landings in 2013 were up to 279.92% higher than the reference landingswhen change only happened in minimum legal size (Table IV-2). Given the same minimum legal size, the predicted landings showed a similar trend when there was a -2 mm CL change in maximum legal size compared with no change in maximum legal size (Figure IV.3). The predictedlandings from different scenarios showed similar trends over 1982 to 1989 and the variability in predictions occurred after 1990. Overall, the predicted landings were lower than the mean of the reference landings after 1990 while there was a decrease in minimum legal size and vice versa (Figure IV-3). The positive change in landings was greatest in 2013 when there was a 2 mm CL increase in minimum legal size. The greatest negative change occurred when there was a 2 mm CL increase in maximum legal size and a 2 mm CL decrease in minimum legal size (Table IV-2). For the scenario that produced the highest positive change in 2013 landings, the landings experienced a fluctuation around the reference landings for the first 7 years and the landings produced only positive changes after 1989.

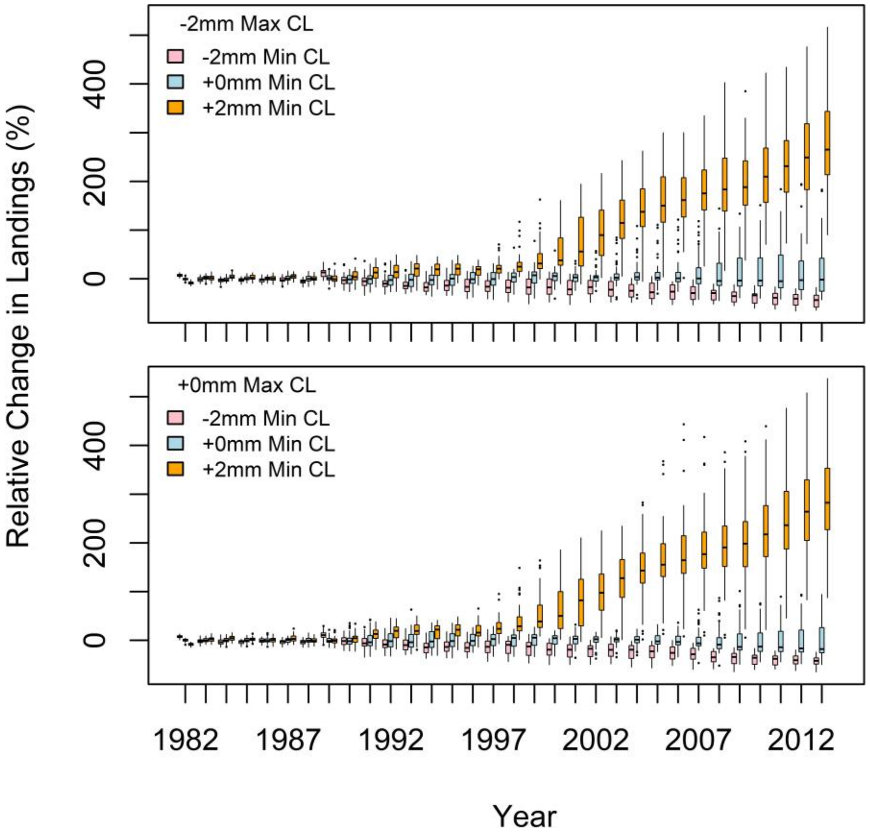


Figure IV-3. The boxplot of relative change in landings (%) from 50 iterations of 6 legal sizes scenarios. The reference value was the mean landings from the scenario with no change in minimum and maximum legal sizes.

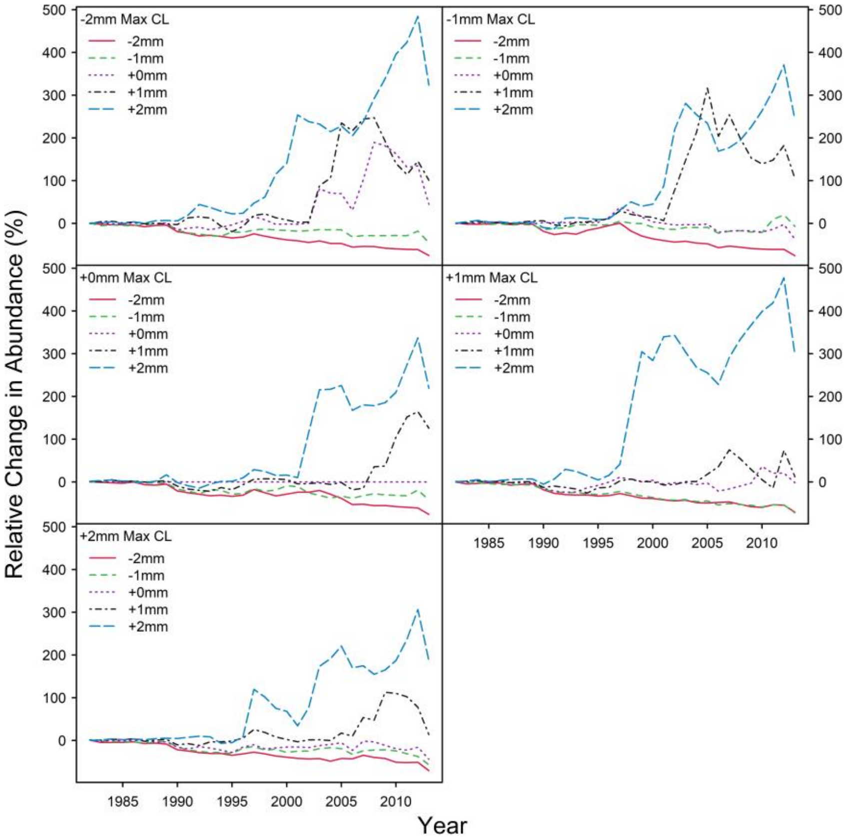
Table IV-2. Relative changes in lobster landings (t) and abundance in 1997 and 2013.

Min Legal Size	Max Legal Size	Landings (%)		Abundance (%)	
		1997	2013	1997	2013
-2	-2	-15.11	-45.23	-17.74	-47.75
-1	-2	-11.35	-29.17	-11.51	-30.65
0	-2	-0.93	12.77	2.02	12.91
1	-2	7.76	81.28	11.55	92.58
2	-2	21.56	276.97	32.28	316.34
-2	-1	-18.68	-44.51	-21.62	-47.81
-1	-1	-11.53	-30.40	-11.01	-33.16
0	-1	0.10	0.22	0.65	1.73
1	-1	10.73	90.03	13.13	93.87
2	-1	22.52	255.25	32.41	288.91
-2	0	-13.22	-43.68	-16.27	-46.21
-1	0	-11.41	-29.06	-12.55	-31.33
0	0	0.00	0.00	0.00	0.00
1	0	8.99	89.76	12.30	96.19
2	0	26.66	279.92	41.63	319.68
-2	1	-21.52	-45.97	-23.94	-48.39
-1	1	-6.87	-25.21	-7.63	-27.73
0	1	0.99	3.63	2.22	4.39
1	1	10.50	106.60	15.38	117.70
2	1	21.68	239.09	33.10	263.05
-2	2	-17.94	-46.29	-20.18	-49.29
-1	2	-11.21	-31.89	-12.69	-33.63
0	2	-3.05	-4.41	-2.03	-3.14
1	2	11.80	96.09	15.88	104.92
2	2	21.33	251.48	31.46	285.32

IV-3-4. Abundance

The relative change in abundance showed a similar temporal trend compared with the relative change in landings (Figure IV-4). The scenario with a 2 mm CL increase in the minimum legal size showed the highest positive change in 2013. The scenario with a 2 mm CL increase in maximum legal size but a 2 mm CL decrease in minimum legal size produced the most negative changes in abundance in 2013. The lobster abundance was more sensitive to changes in minimum legal size than maximum legal size. Any increase in minimum legal size leaded to a positive change of abundance in 2013 while a decrease in minimum legal size produced negative change in abundance. However, given no changes in minimum legal size, the abundance slightly increased with decreased maximum legal size. A 1 mm CL increase in maximum legal size resulted in 4.39% increase in abundance during 2013 while a 2 mm CL increase leaded to 3.14% decrease in abundance (Table IV-2). The impact of changing minimum legal size ($p < 2e-16$) was significant according to the ANOVA test while the maximum legal size ($p = 0.36$) showed no significant impact on the lobster abundance.

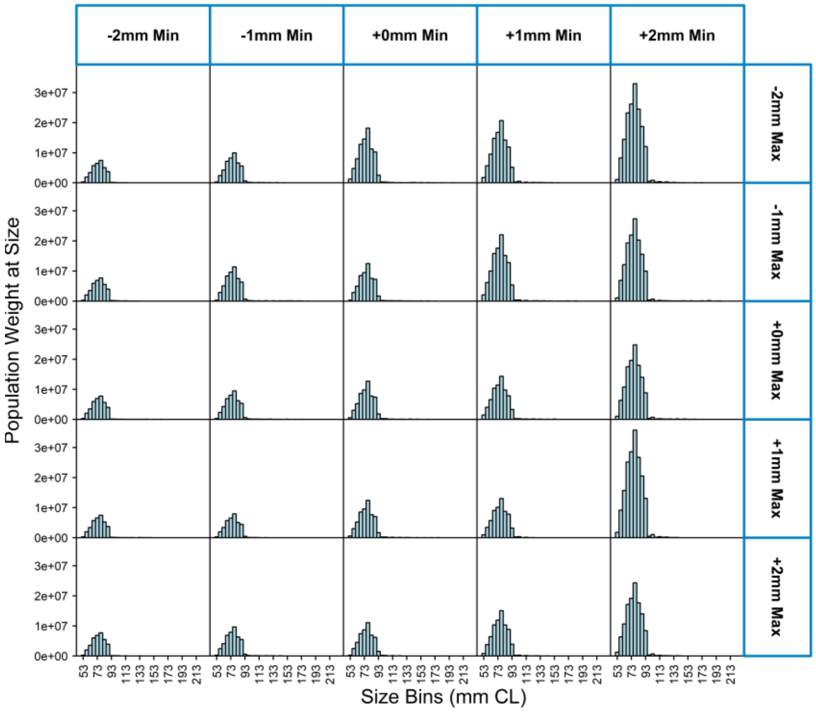
Figure IV-4. Relative changes in abundance (%) from the 25 scenarios compared with the scenario with no changes in minimum and maximum legal sizes.



IV-3-5. Size composition

Given the same maximum legal size, increasing minimum legal size produced increased lobster weight at different size bins (Figure IV-5). There was no clear pattern on changes in size composition at a fixed minimum legal size (Figure IV-5). Besides the scenario with a 2 mm CL increase in minimum legal size, other scenarios produced comparable size composition under different levels of maximum legal size. Under a 2 mm CL increase in minimum legal size scenario, the size composition slightly decreased over size bins when there was an increase in maximum legal size (Figure IV-5). With a 2 mm CL increase in minimum legal size, a 1 mm CL decrease in maximum legal size produced less lobster weight per size bin, but a 2 mm CL decrease in maximum legal size could lead to a small increase in the lobster weight per size bin (Figure IV-5).

Figure IV-5. The size distribution of population weight (t) at size from 25 simulation scenarios.



IV-4. Discussions

American lobster studies tend to focused on the improvement of understanding environmental effects alone on the abundance and distribution of the lobsters, whereas quantification on the impact of conservation measures has received relatively less attention until recently (Le Bris et al., 2018; Pinsky, 2018). Most of the research has quantified the impact of conservation measures based on yield-per-recruitment assessment that lack the consideration of recruitment variability, size-dependent mortality, maturity and growth (Sundelof et al., 2014). Along with the scarce model simulation and validation, there is little study to evaluate the effect of a maximum legal size on the population dynamics when double-gauge regulation is developed for the fishery. This study quantifies the impact of both minimum and maximum legal sizes on the American lobster fishery in the GOM using simulations. The simulation model was validated by comparing predicted and observed catches. The assessment incorporated the recruitment variability by consideration of four types of the stock-recruitment relationships. The results derived from this study would improve our understanding of the contribution of legal size regulations to the dramatic increase of lobster landings and abundance in the GOM.

This study has considered recruitment variability when quantifying the impact of legal sizes on the lobster population by exploring four different types of stock-recruitment relationships. The relationship using sampled recruitments from customized recruitment distribution from different spawning stock biomass levels provided the best projection of recruitments. The historical recruitment with a large CV could not reveal the variability in recruitment due to the lack of a functional link between recruitment and spawning stock. The recruitment does not respond to the variations in spawning stock biomass that result from changes in legal sizes because there is no functional link between the recruitment and the stock. The classic stock-recruitment models could not fit the observations well (Chang et al., 2015). The performance of these classic models is no better than a density-independent model. Sampling recruitment from recruitment distributions that developed for different spawning stock biomass levels has produced the best predictions in this study. The objective of the study has not been to define the stock-recruitment relationship for American lobster, but to use simulations to see which stock-recruitment relationship could be applied to the lobster data for further management strategy evaluation. Further exploration on estimating the lobster stock-recruitment relationship is necessary since the landings are likely to be governed by the shape of the stock-recruitment relationship (Bannister and Addison, 1986).

It is urgent to quantify the effect of different stock-recruitment relationships on the lobster stock assessment so that the population projections under different conservation strategies can be carried out accurately. Bannister and Addison (1986) have described how various stock- recruitment relationships affect the relation between yield and different management strategies. They have suggested that a highly overcompensatory stock-recruitment curve tends to reduce the benefits of increasing minimum legal size or of setting a maximum legal size. Chang et al. (2016) has quantified the stock-recruitment relationships for American lobsters in the inshore GOM. The recruitment in their study is newly settled young-of-year lobster (around 10 mm CL) and they found that the functional stock-recruitment relationship could vary by area and spatial scales. The recruitment in this study is the recruitment to the fishery and it is an essential component in the lobster stock assessment (ASMFC, 2015). A thorough study on estimating the stock-recruitment relationship is vital to understand the population dynamics of the lobster and would improve our studies on quantifying the impact of different conservation measures on the lobster fishery (Wahle, 2003).

The minimum and maximum legal sizes have been implemented in the Gulf of Maine lobster fishery with a long history but the strength of their impacts on the lobster population are different. The responses from fishermen showed that 90.4% of the fishermen expect minimum legal size to be very effective but the expectation on maximum legal size is lower (Acheson and Gardner, 2011). The results from this study further indicate that changes in minimum legal size showed greater influence on the lobster landings, abundance, and size composition than changes in maximum legal size. For example, at the fixed maximum legal size situations, changes in minimum legal sizes could result in almost a three-fold difference in relative changes in 2013 landings. However, given a fixed minimum legal size, changes in maximum legal size only produce a lesser difference in relative changes in landings. This may be one of the reasons that there were more changes in minimum legal size than in maximum legal sizes in the lobster fishery (Acheson and Steneck, 1997). Minimum legal size is expected to be more effective for achieving goals such as a doubling egg per recruitment (Gendron 2014).

The effects of minimum and maximum legal sizes on the lobster population are not a one-way trip. An increase in minimum legal size may produce increased landings but increasing maximum legal size may create a mixed picture. The results from this study suggested that a 1 mm increase in maximum legal size with no change in minimum legal size may result in a small increase in landings but a 2 mm increase would lead to negative changes in landings. The current maximum legal size supports relatively good performance in lobster landing and abundance. To produce large changes in lobster landings, abundance, and size distribution, a greater change (e.g. ±5 or ±10 mm CL) in maximum legal size may be required.

The impact of maximum legal size on the lobster population depends on how it is combined with the minimum legal size and other conservation measures. Therefore, this simulation study with different combinations of minimum and maximum legal sizes greatly improve our view on the effect of maximum legal size on the lobster population in the GOM. However, the views on effectiveness of maximum legal size remain controversial. The maximum legal size is developed to protect the large lobsters that are particularly valuable not only because they carry more eggs, but also because they can extrude eggs twice after a molt (Waddy and Aiken, 1986). However, some observers think the maximum legal size is biologically unsound because Massachusetts and New Hampshire do not have the maximum legal size measure but still experienced the boom of lobsters in the 1990s (Acheson and Steneck, 2011). The results from this study also imply that the lobster population is not sensitive to 1 or 2 mm CL change in maximum legal size.

There is a tendency that the lobster landings increase steadily with a 1 mm CL increase in minimum legal size after a very short term loss and a medium term fluctuation (e.g. 13 years). This is similar with the real patterns in Maine lobster fishery. The minimum legal size has been increased 1 mm CL in 1989 (Acheson and Steneck, 1997). The catch per unit effort fluctuated from 1990 to 2007 but had a two-fold increase from 2007 to 2013 (Steneck et al., 2017). The relatively good match between prediction and history highlights the benefits of using the individual-based lobster simulator for the management strategy evaluation. The increase in lobster landings and abundance may not be only influenced by the increased minimum legal size, but also other conservation measures such as v-notch practice, no-take egg bearing lobsters, reduced trap limits, and limited entry (Steneck and Wahle, 2003; Steneck et al., 2017). Evaluating the effectiveness of these conservation measures would greatly improve our understanding of the lobster population dynamics.

The quantified impact of minimum and maximum legal size on the lobster population provides numerous management implications. The effect of difference in legal sizes by stock area on the lobster population may require further exploration, given the climate-change induced changes in lobster maturation and growth. The American lobster is managed with different legal sizes by different stock areas (ASMFC, 2015). It is necessary to apply the simulation approach developed in this study to other areas and to quantify the impact of difference in legal sizes on the lobster population. The difference in legal sizes by stock area would be necessary if the species shows different size at maturity by stock area (Hill, 1992). Depending on the size at maturity along the coast, a minimum legal size that is lower than the size at maturity may result substantial loss of catch in local fishery.

Examinations on impact of different sizes by sex and season may provide us a better understanding of the current conservation measures. The minimum and maximum legal sizes in the lobster fishery are developed to primarily protect female lobsters (Steneck et al., 2017). Inappropriate size measures such as same legal size for both female and male lobsters may induce adverse sex ratio in the lobster population. Furthermore, lobsters experience seasonal migration from offshore to inshore. There is a need to quantify the impact of legal sizes on the lobster population using a finer spatial-temporal resolution (e.g. inshore/offshore- and season- specific legal sizes).

In conclusion, current conservation measures, such as minimum and maximum legal sizes, have made a great contribution to the dramatic increase in the American lobster fishery in the GOM. The effect of minimum legal size is greater than the effect of maximum legal size on the lobster landings, abundance, and population weight at sizes. A 2 mm CL increase in minimum legal size with no changes in maximum legal size would produce the largest positive relative change in landings in 2013, but more studies are needed to evaluate climate-induced changes in size at maturity and growth (Khalsa et al. in preparation). Further estimation on the effect of different stock- recruitment relationship on the lobster population would improve the reliability of the predicted landings, abundance, and size distribution. Developing a simulation approach with a finer spatial-temporal resolution would further improve our understanding of the legal size effects on the lobster population.

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Evaluate effectiveness of ventless trap,

in monitoring sublegal lobster stock in a changing Gulf of Maine

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Summary

The stock assessment of American lobster (Homarus americanus) plays an important role in managing the fishery in the Gulf of Maine (GOM). Various fishery-dependent and fishery-independent data are required in the stock assessment to estimate key fisheries parameters that define the population dynamics of American lobster. In the 2015 benchmark stock assessment, ventless trap survey (VTS) data were included for the first time to provide information about the sublegal lobster (carapace length < 83 mm) dynamics. However, the effectiveness of VTS data in monitoring sublegal lobsters has not been evaluated and we have little information on whether the VTS sampling design can capture sublegal lobster dynamics. The primary goal of this project was to evaluate and determine whether the data collected from the Maine VTS provide robust estimation of design-based sublegal lobsters abundance index in the inshore GOM. To achieve this goal, we conducted the following four-step analysis: (1) estimate and evaluate variations in catch rates derived, respectively, from the first, second, and third ventless trap per site; 2) predict sublegal lobster population at a high spatial resolution using generalized additive models (GAMs); (3) sample the simulated sublegal lobster population following the sampling protocol used in the VTS program to derive a simulated VTS abundance index; and 4) compare the simulated VTS abundance index with the predicted population abundance index in the simulated sublegal lobster population. The spatial scale of the study was defined by the National Marine Fisheries Service (NMFS) statistical areas in Maine, areas 511, 512, and 513. The lobster data used to develop the GAMs were from the Maine-New Hampshire Inshore Bottom Trawl Survey (BTS) from years 2006-2016. The VTS data from 2006-2016 were sourced as the observed VTS abundance index. VTS catch rate per trap was considered during the step of sampling the simulated sublegal lobster population using the VTS sampling protocol, and the predictive variables considered included depth and temperature. This study suggests that there were no significant differences in abundance, sex ratio, and size composition of the juvenile lobsters caught by the three traps in a trawl used in a VTS and that the correlation between abundance indices from subsampling scenarios and corresponding observed abundance indices were all greater than 0.99. We conclude that the VTS provides a robust estimation of sublegal American lobster abundance index in the inshore GOM.

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I. Project Introduction

The American lobsteris a bottom-dwelling crustacean distributed along the coast of northeastern United States, The Gulf of Maine (GOM) and Georges Bank (GBK) stock yield more than 90% of the American lobster (*Homarus americanus*) harvested in the U.S. (ASMFC, 2020). More than 96 million pounds of American lobster were landed in Maine in 2020, which was worth over $400 million (DMR, 2021). There are an estimated 5,000 license holders, accounting for approximately 55% of all commercial fishing licenses held in the state (DMR 2016). Such dependence on the lobster fishery leaves the coupled natural and human system vulnerable to environmental and regulatory changes.

Studies suggest that the population dynamics of American lobster experience both top-down (e.g., fishing pressure) and bottom-up (e.g., climate and resources) controls (ASMFC 2015; Boudreau et al. 2015). For sustainable management of this species, it is critical to (1) evaluate the relative importance and synergistic impacts of these environmental drivers, (2) maximizing the efficiency and accuracy of the existing stock monitoring and assessment program, and (3) to develop the capacity for predicting changes in ecology, biogeography and phenology of American lobster which potentially can limit the lobstering grounds in future.

Climate-driven changes in the GOM ecosystem structure have been identified as a likely primary stressor to population dynamics of this species within its whole geographic distribution (Dove et al. 2005; Jacobson et al. 2009). The American lobster is an ectothermic species, thus its physiology is regulated by the surrounding water temperature (Hamilton et al. 2007). Lobsters prefer a thermal range between 12 and 18 °C, and avoid temperatures above 19 °C (Crossin et al. 1998). Increasing water temperature forces lobsters to use more energy for respiration, leaving diminished energy reserves for feeding, growth, immune response, and reproduction and also influence the regulation of hormones, specifically those that control the molting cycle (Gilgan and Burns 1977; Butler and Taylor 1978; Qadri et al. 2007). The water temperature in GOM has increased over the last 40 years (Nye et al. 2009; ASMFC 2015). Sea surface temperature in GOM shows an increase of 0.03 °C per year, resulting in a 1 °C increase in the mean temperature since 1982 (Mills et al. 2013).

As the rate of climate change is predicted to accelerate in the future, alongside the species' ongoing distributional shifts (Pinsky et al. 2013), there is a growing need to assess changes in lobster distribution and possible impacts of such a change on the existing lobster monitoring programs. Under the latest Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathways (RCP) 8.5 emissions scenario, average bottom temperature in Northeast U.S. Continental Shelf system is expected to increase more than 1 °C by 2050 (IPCC 2014; NOAA 2015). While the projected increase in bottom temperature in the GOM is not expected to exceed the species' maximum temperature tolerance and may even be considered favorable, management uncertainties at the southern limits of the species' range can be addressed through scenario-based analysis (Hare et al. 2012; Shackell et al. 2014, ASFMC 2015).

Climate-driven changes in GOM ecosystem structure will likely alter the spatio-temporal availability of suitable habitats for the GOM lobster stock (Tanaka and Chen 2016). Warmer temperatures are likely to cause lobsters to move toward higher latitudes, deeper water or to areas cooled by tidal mixing and exhibit behavioral changes, such as early and more frequent molting (Templeman 1936; Fogarty et al. 2007). *Consequently, thermal changes in GOM lobster habitat may have great impacts on current lobster monitoring (e.g., whether current monitoring* *program will still be effective?). This calls for a thorough evaluation of the effectiveness of the current monitoring programs in quantifying the dynamics of lobster fisheries in the GOM.*

The impact of spatio-temporal shifts in lobster distribution resulting from environmental changes may decrease the effectiveness of current sampling programs. Effective sampling designs provide scientists a representative view of lobster population with limited effort (Cao et al. 2014). The data from multiple surveys have been used to calibrate the stock assessment model for the lobster population in the GOM (ASMFC 2015). Initially the proposal was developed to evaluate ventless trap and trawl survey programs, but we were provided 1/3 level of requested funding and was suggested to focus on the evaluation of ventless trap survey because it has not be evaluated in previous studies. Thus, this project evaluates the performance of ventless trap survey in capturing sublegal lobster stock dynamics in a changing GOM.

II. Project Objectives

The overarching goal of this study is to ***evaluate effectiveness of ventless trap surveys in monitoring sublegal lobster stock in a changing Gulf of Maine.*** The simulation framework developed in this study are a continuation of ongoing research in the Chen Lab in collaboration with NOAA, ASMFC and Maine Department of Marine Resources (DMR) to improve our understanding of how lobster population dynamics may respond to climate changes.

Section I. Evaluating the catch rates of different trap positionings in American lobster (*Homarus americanus*) ventless trap survey in the Gulf of Maine

The American lobster resource is assessed by many surveys. Each survey has its own insufficiencies. Atlantic States Marine Fisheries Commission (ASMFC) implemented the Ventless Trap Survey (VTS) in 2006 to complement existing survey programs and to better capture sublegal lobster abundance dynamics (Watson et al., 2019). Although the implementation of the VTS follows a scientifically rigorous approach and rarely encounters obstacles in both the natural environment and management, a comprehensive study of the survey design and the performance of the VTS in monitoring sublegal lobster abundance is needed. One of the most important steps in evaluating the performance of the VTS is to identify the potential differences between the individual ventless traps in the same linked trawl.

There are common perceptions that positioning of traps in a linked trawl set at a sampling site results in different catch rates of lobster because of gear saturation, which would affect the estimation of lobster abundance index (Pickering et al., 2010). In this study, we derived a design-based sublegal lobster (< 83 mm carapace length) abundance index at each of Maine's National Marine Fisheries Service (NMFS) Statistical Areas using the observed VTS data from 2006-2017. We then derived design-based abundance indices using data from the first, the second, and the third ventless trap per site. The correlation between abundance indices from three traps and the true abundance index in each statistical area was then examined. Finally, the sex ratio and size composition of subsamples were compared with the samples collected from the three traps per trip.

I-1. Materials and Methods

I-1-1. Study Area and Data Used

The data used in this study were from the DMR VTS, which were collected in and divided by the NMFS statistical areas 511, 512, and 513 along the Maine coast (Figure I- 1).

Three depth strata were deployed in the survey—0-20 m, 21-40 m, and 41-60 m. The potential sampling station locations are shown in Figure I- 1 . (Thompson, 2019).

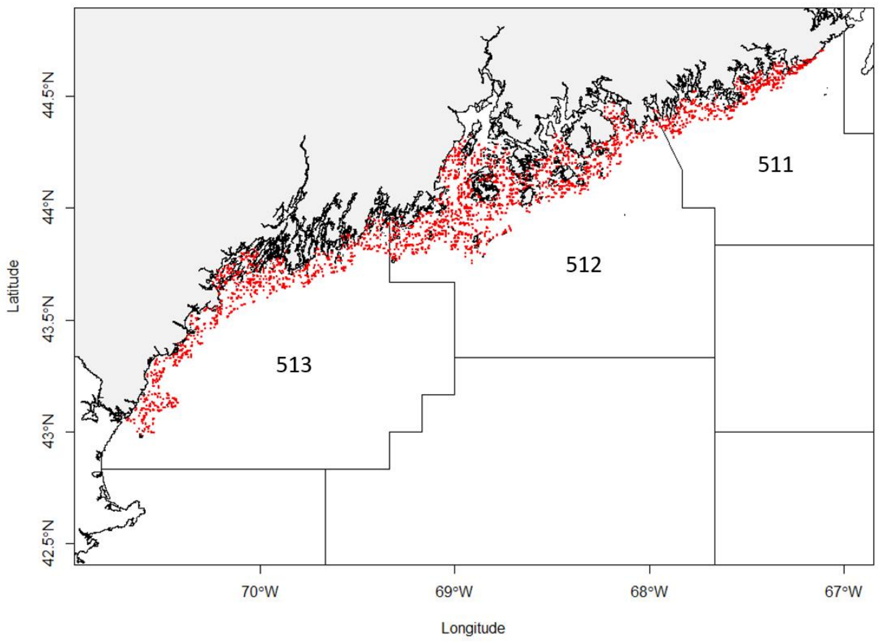

Figure I- 1 . Potential survey station locations in NMFS statistical areas 511, 512, and 513 along Maine coast.

The data sourced from DMR VTS ranged from 2006-2016 with surveys conducted in June, July, and August every year. The surveys collect lobster biological data, such as carapace length, sex, fecundity, shell status, cull status, and external gross pathology, and survey logistical information, such as number of lobsters in each trap, number of traps, trap soak time, trap type, and bait type. The detailed number of sampling stations each year were selected randomly (me of three days (ASMFC, 2020).

Table I-1), and the target sampling frequency of each station was twice a month with a trap soaking time of three days (ASMFC, 2020).

Table I-1. The detailed number of stations selected since 2006 for each depth stratum in statistical areas 511, 512, and 513. *Note.* Reprinted from "ME Survey Design" by Thompson. K, 2019, Unpublished manuscript. Copyright 2019 by K. Thompson.

	Statistical Area									
Depth Stratum (m)	511			512			513			**Total stations**
	0-20	21-40	41-60	0-20	21-40	41-60	0-20	21-40	41-60	
2006	9	8	8	8	8	9	7	11	6	74
2007	8	7	8	19	23	19	12	13	14	123

2008	8	9	7	23	24	24	14	15	15	139
2009	9	9	6	25	17	26	15	16	14	137
2010	8	9	7	23	24	22	13	16	14	138
2011	8	9	7	25	21	23	14	17	14	138
2012	7	9	8	23	24	22	14	15	16	138
2013	8	8	8	22	23	24	15	15	15	138
2014	8	8	8	22	24	23	15	16	14	138
2015	16	17	15	47	49	42	30	29	31	276
2016	16	16	16	46	46	46	30	30	30	276
2017	16	16	16	45	44	49	30	30	30	276

Before 2015, each trawl included six traps, with three vented traps and three ventless traps positioned alternately (Figure I-２). The selectivity difference between vented traps and ventless traps can be studied with nine years of data existed. Therefore, to expand the sampling area and improve efficiency, only ventless traps were kept in the survey, and thus, starting in 2015, the number of VTS sample stations were doubled (Courchene & Stokesbury, 2011; Thompson, 2019).

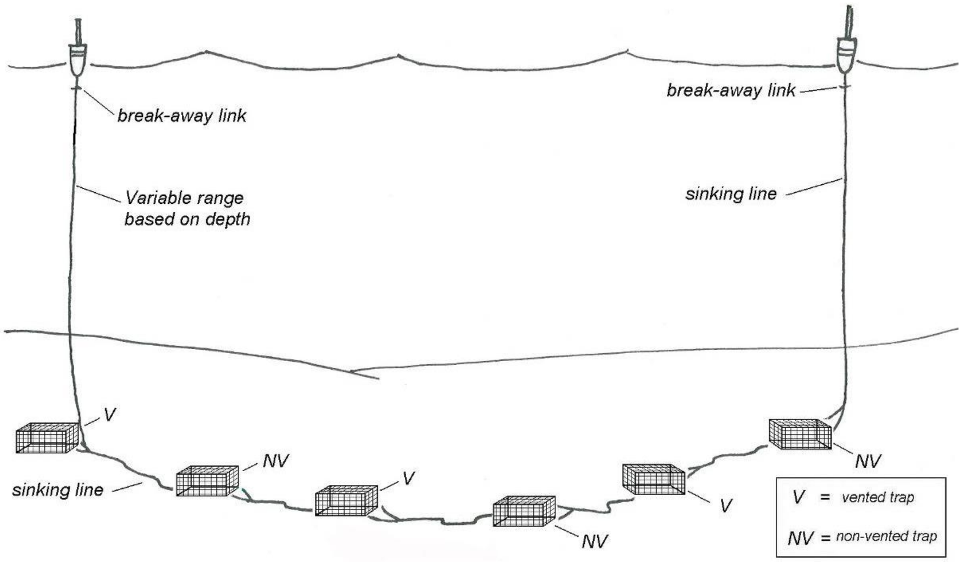

Figure I-２. Diagram of VTS traps deployment before 2015. Adapted from “ME Survey Design,” by Thompson (2019), *Unpublished manuscript.*

I-1-2. Design-based abundance index

When calculating sublegal lobster abundance index with information from the VTS, only the data collected by the ventless traps are used. Because the survey months for the VTS are

June, July and August, which are also popular months for various agencies to conduct other surveys, sometimes the target soaking time (i.e., three days) for the VTS is not met due to lack of manpower, overlapping routes, or needs of vessels. However, due to the assumed linear relationship between trap soak time and lobster catch, soak time needed to be standardized to three days. Therefore, when exploring these data, VTS soak time outliers (i.e., one day and six days) were discarded and the rest were used to divide lobster catch number for catch per day, and then multiplied by the target soaking time (i.e., three days). The equation is shown as:

$$Catch = \frac{Catch_n}{t} \times s$$

where $Catch$ is the standardized lobster catch per trap, $Catch_n$ is the observed lobster catch per trap, t is the recorded soak time, and s is the target soaking time.

The design-based abundance index in each survey area in a survey season was calculated as:

$$Catch_y = \frac{\sum_{str} \frac{\sum_s Catch_{s,str,y}}{N_{str,y}} \times A_{str}}{\sum_{str} A_{str}}$$

where $Catch_{s,str,y}$ is the mean catch at site s in stratum str and year y, $N_{str,y}$ is the number of sites in stratum str and year y, and A_{str} is the number of sites in stratum str.

The abundance index variance was calculated as:

$$Variance = \frac{\sum_{str} A_{str} \times (A_{str} - N_{str,y}) \times (\frac{(\sum_{AD} Sub_{AD,y} / (N_{str,y} - 1))}{N_{str,y}})}{A_{total}^2}$$

Where A_{str} is the area of stratum str, A_{total} is the area of the sum of all strata, $N_{str,y}$ is the number of sites in stratum str and year y, and $Sub_{AD,y}$ is the mean catch in each area designation in year y.

The mean catch in each area designation was calculated as:

$$Sub_{AD} = (\frac{Catch_{str,y}}{n_{str,y}} - \frac{Catch_{AD,str,y}}{n_{AD,str,y}})^2$$

Where $Catch_{str,y}$ is the mean catch at stratum str and year y, $n_{str,y}$ is the number of traps deployed in stratum str and year y, $Catch_{AD,str,y}$ is the mean catch in each area designation in stratum str and year y, and $n_{AD,str,y}$ is the number of traps deployed in each area designation in stratum str and year y.

The sampling area in each depth stratum in a statistical area is shown in Table I-2 (ASMFC, 2020).

Table I-2. The number of sites sampled in each depth stratum in a statistical area.

	Depth stratum 1 (0-20m)	Depth stratum 2 (21-40m)	Depth stratum 3 (41-60m)	Total
SA511	122	82	92	296
SA512	566	395	420	1381
SA513	315	338	198	851

I-1-3. Subsampling

The three ventless traps deployed at a site might have different catch rates due to their unique positioning, and therefore different abundance indices. In order to evaluate this hypothesis, we calculated the abundance index of sublegal lobster (carapace length < 83 mm) for the first, second, and third trap individually, as well as the correlation of each trap's abundance index to the sublegal lobster abundance index derived from the three traps combined.

The abundance index of a trap in a statistical area was calculated as:

$$Catch_{T,sa,y} = \frac{A_{sa,str} \times \sum_{str} \frac{\sum_{T} Catch_{T,y,sa,str,}}{n_{T,y,sa,str}}}{\sum_{str} A_{sa}}$$

where $A_{sa,str}$ is the area of stratum str in statistical area sa, A_{sa} is the area of the sum of all sampling stations in statistical area sa, $Catch_{T,y,sa,str}$ is the mean catch by trap T in stratum str in statistical area sa and year y, and $n_{T,y,sa,str}$ is the number of traps T in stratum str, statistical area sa and year.

The abundance index variance of a trap was calculated as:

$$Variance_{T} = \frac{\sum_{str} A_{str,sa,y} \times (A_{str,sa,y} - N_{str,sa,y}) \times (\frac{(\sum_{s} Sub_{T,s,y} / N_{str,sa,y})}{N_{str,sa,y}})}{A_{sa}^{2}}$$

where $A_{str,sa,y}$ is the area of stratum str in statistical area sa and year y, A_{sa} is the area of the sum of all surveys area in statistical area sa, $N_{str,sa,y}$ is the number of sites in stratum str in statistical area sa and year y, and $Sub_{T,s,y}$ is the mean catch at site s by trap T in year y.

The mean catch in site s by trap T in year y was calculated as:

$$Sub_{T,s,y} = (\frac{Catch_{T,str,sa,y}}{n_{T,str,sa,y}} - \frac{Catch_{T,s,str,sa,y}}{n_{T,s,str,sa,y}})^{2}$$

where $Catch_{T,str,sa,y}$ is the mean catch at stratum str caught by trap T in statistical area sa and year y, $n_{T,str,sa,y}$ is the number of trap T deployed in stratum str in statistical area sa and year y, $Catch_{T,s,str,sa,y}$ is the mean catch by trap T in site s in stratum str in statistical area sa and year y, and $n_{T,s,str,sa,y}$ is the number of trap T deployed in site s in stratum str in statistical area sa and year y.

The calculations of abundance index and variance for each statistical area were similar to the calculation used for each trap but included data from all three traps combined.

I-1-4. Sex ratio and size composition

The sex ratio of sublegal lobster caught in trap 1, trap 2, and trap 3 were calculated, as well as the sex ratio calculated using data from all three traps combined. The female ratios were calculated as the number of female sublegal lobsters caught by trap T divided by all sublegal lobsters caught by trap T times 100. The male ratios for trap T were calculated as 100-female ratio. The size composition was generated by assigning the VTS mean catch per trap of lobsters by 20 mm carapace length size bins. The size bins are intercepted at the 85 mm size bin as the threshold of sublegal lobster carapace length is 83 mm.

I-1-5. Statistical analysis

To determinate if there are any differences related to trap positionings in sublegal lobster catch between all three traps combined and trap 1, trap 2, and trap 3 respectively, a one-way ANOVA was applied.

I-2. Results

I-2-2. Abundance indices

The derived abundance indices from one trap per site showed a similar trend compared to the abundance indices derived from all three traps per site (Figure I-３). The correlation between abundance indices from subsampling scenarios and corresponding true abundance indices are all greater than 0.99 (Table I-3).

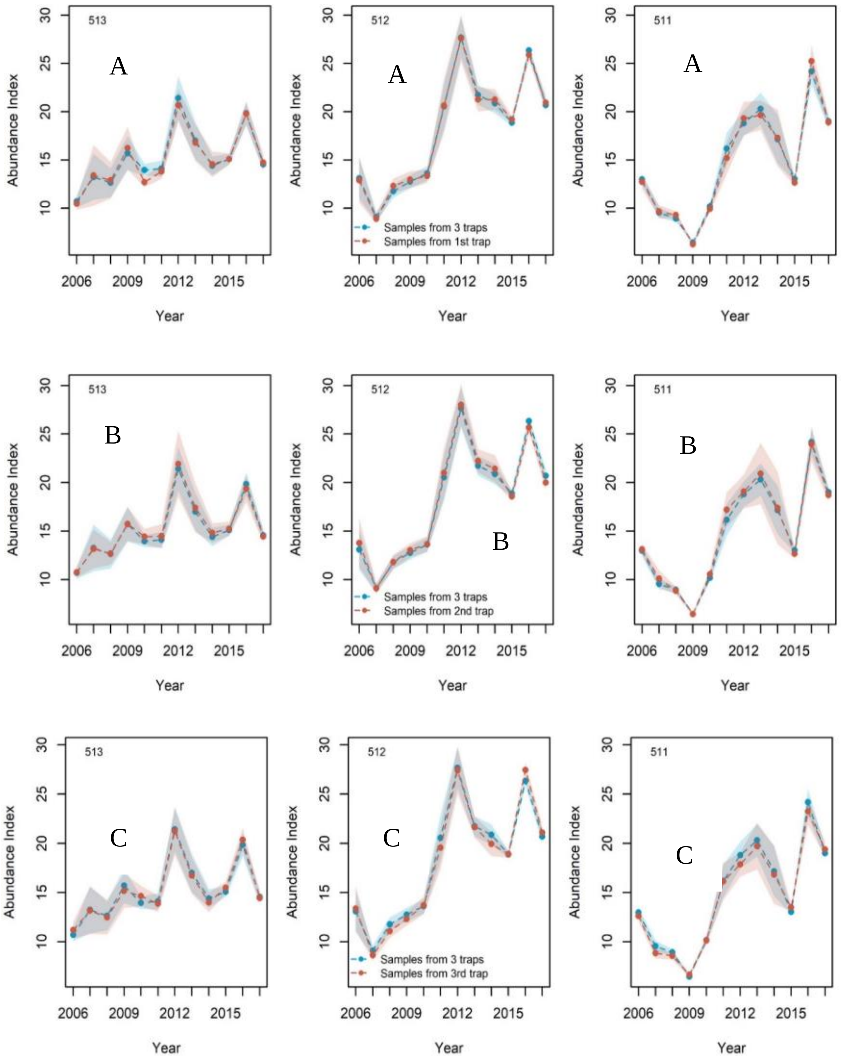

Figure I-３. Abundance indices of sublegal lobsters caught by the first (A), second (B), and third trap (C) compared to abundance indices of sublegal lobsters caught by all three traps combined in statistical areas 511, 512, and 513 from right to left, respectively from 2006 to 2017.

Table I-3. The correlation between the abundance indices calculated using all three traps in each statistical area and the abundance indices calculated for trap 1, trap 2, and trap 3 from all statistical area individually.

	SA511 All three traps	SA512 All three traps	SA513 All three traps
Trap 1	0.995614	0.9984942	0.986705
Trap 2	0.9970937	0.9970475	0.9950832
Trap 3	0.996536	0.99563	0.9910384

I-2-2. Sex ratio

The sex ratio between female and male sublegal lobsters obtained from all three traps per site showed similar trends to samples collected from one trap per site (

Figure I-4). The sex ratio remained stable over time, slightly skewed to females.

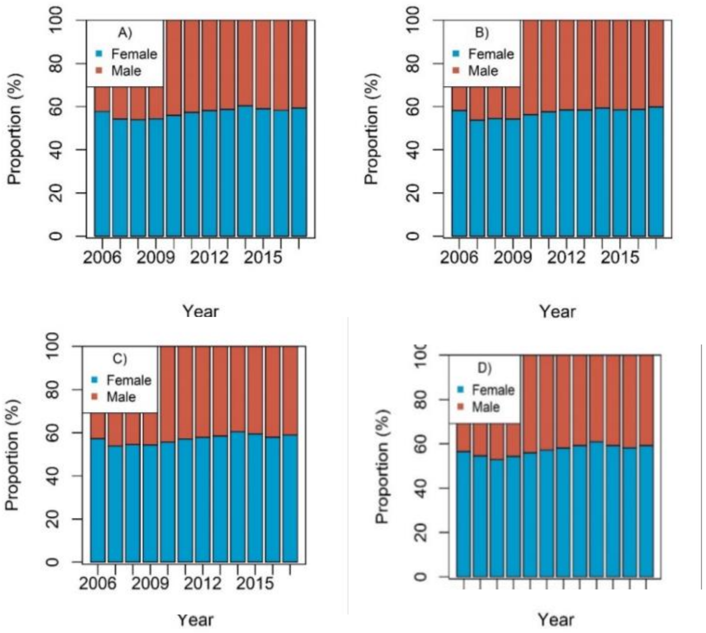

Figure I-4. Sex ratio of sublegal lobsters derived from all three traps per site combined (A) and from the first trap per site (B), second trap per site (C), and third trap per site (D).

I-2-3. Size composition

The size composition of sublegal lobsters showed nearly identical patterns when using data collected from all three traps per site combined and data from only one trap per site (Figure I-5). The results from this study indicated that the positions of traps hauled from a linked set did not appear to result in much variation in sublegal lobster catch rates.

I-2-4. The differences of catch

Examining the mean catch between all three traps combined and trap 1, trap 2, and trap 3, the one-way ANOVAs results showed no significant difference (Table I-4).

Table I-4. The p-value resulted from ANOVAs between the mean catch calculated using all three traps in each statistical area and the mean catch calculated for trap 1, trap 2, and trap 3 from all statistical area individually.

	SA511 All three traps	SA512 All three traps	SA513 All three traps
Trap 1	0.982034392	0.994855382	0.917681136
Trap 2	0.934157133	0.967874803	0.905698655
Trap 3	0.898878934	0.948007084	0.993623784

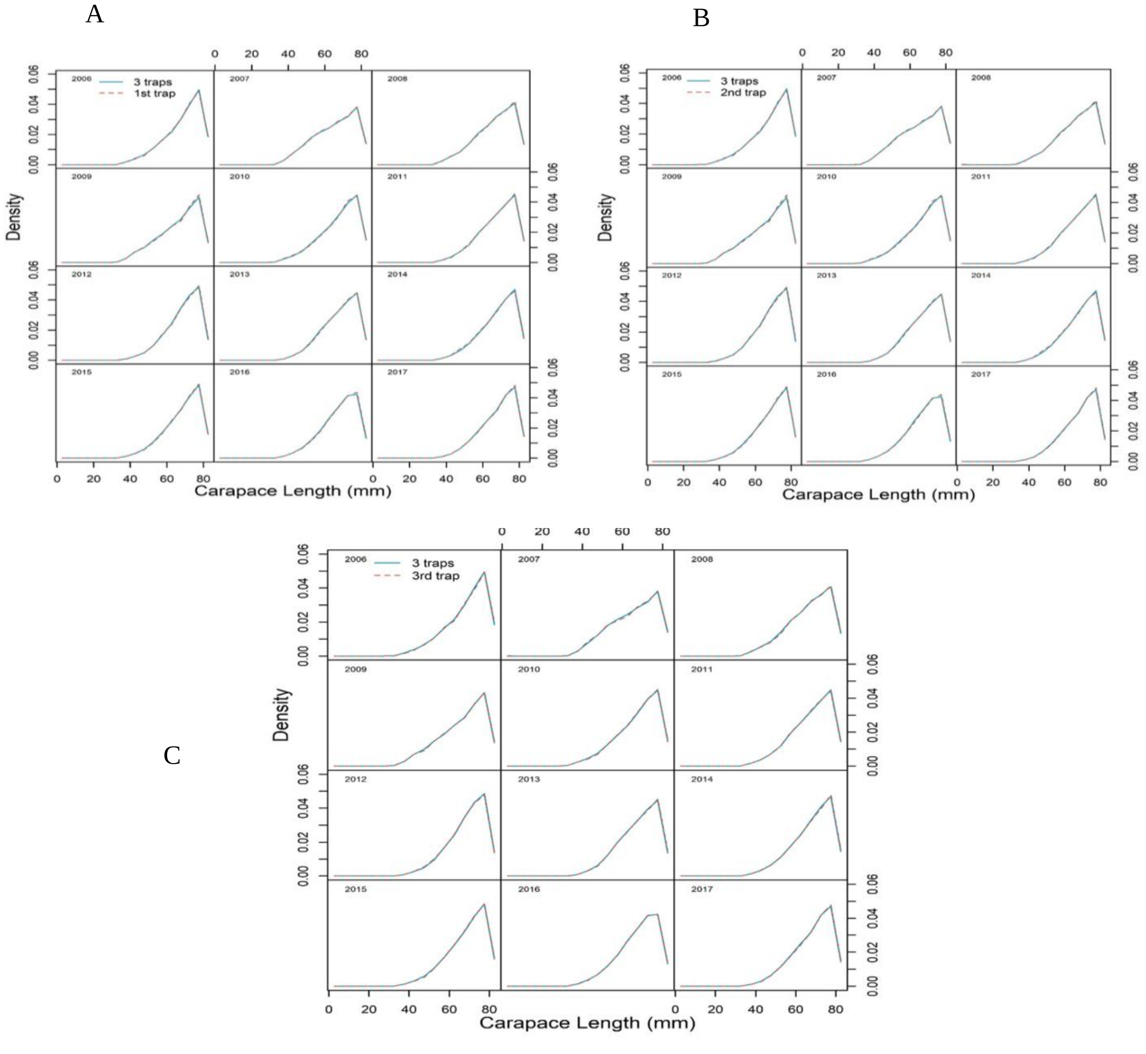

Figure I- ５. Size composition of sublegal lobsters derived from all three traps per site combined, and from the first (A), second (B), and third (C) trap per site individually from 2006-2017.

I-3. Discussion

Incorporating VTS data into the American lobster stock assessment is becoming more and more important due to its significance on investigating sublegal lobster population distribution, making it vital to evaluate if or how the settings of traps in the survey influence sublegal lobster abundance estimates. An improved understanding of how trap positioning in the VTS affects catch rate would greatly reduce the risk of misrepresenting data related to stock assessment. In this study, we compared the abundance, sex ratio, and size composition of sublegal lobsters caught in the three traps used in the sampling design of the VTS.

The results from this study showed that subsampling from the first, second, or third trap per site produced similar abundance indices, sex ratios, and size compositions of sublegal lobsters in the inshore GOM when compared to those metrics derived using data collected from all three traps per site combined. In 2007, Pickering et al. (2010) conducted a field study to investigate the catch differences between individual commercial lobster traps set in a trawl and found similar results. They set up four-trap trawls in Malpeque Bay (Prince Edward Island, Canada), with 14.6 m between traps, and 944 traps were hauled daily over four consecutive weeks. In weeks two and four, each second trawl was fitted with an intermediate buoy designed to reduce the wind-driven fluctuation of the first trap. They found no significant differences or relationships in these analyses (Pickering et al., 2010), and therefore, the positioning of commercial lobster traps and the wind speed may not affect the catch rate.

We found similar results in this study with the ventless lobster traps such that no significant differences were found between trap 1, trap 2, and trap 3, or when each trap was individually compared to metrics calculated using all three traps combined. This indicates that different positionings of ventless traps at VTS sites result in similar sublegal lobster catch rates, and subsequently do not affect the estimation of sublegal lobster abundance index. The result suggests that the ventless traps deployed in each VTS site can be reduced and resources and efforts can be shifted to increase survey sites and expand survey depth to cover more survey area. This would enhance the understanding of sublegal American lobster population dynamics, which is especially important in the context that catch rate offshore can be largely impacted by the change of temperature resulted by climate changing. Reducing ventless traps in VTS sites can also reduce the risk of misrepresenting data since the amount of data demanded can be lessened.

Section II. Simulation and comparison: sublegal American lobster population dynamics in the inshore Gulf of Maine and the effectiveness of ventless trap survey quantifying sublegal lobster abundance

The stock assessments have relied heavily on fishery-dependent at-sea sampling data, as well as data from fishery-independent trawl surveys and SCUBA-based air-lift suction sampling (ASMFC 2000, 2006, 2009, 2015 and 2020). In 2015, data from a new gear type and survey, the ventless trap survey (VTS), were included for the first time in the stock assessment. The data from the VTS provides information on sublegal sized lobsters (i.e., < 83 mm carapace length), but its effectiveness of monitoring sublegal lobsters has not been evaluated (ASMFC, 2015).

The data from fishery-dependent and fishery-independent monitoring programs provide valuable information for the lobster stock assessment, but each program has its own unique advantages and disadvantages in monitoring lobster populations (Courchene and Stokesbury, 2011). The fishery-dependent at-sea sampling data provide catch, fishing effort, size, weight, fecundity, and discard information of commercial catch for the stock assessment, but it may have biases associated with the non-random nature of selected traps (Scheirer et al., 2004; Comeau et al., 2009; Li et al., 2019). The data from bottom trawl surveys have been used to provide indices of relative lobster abundance in the stock assessment. The trawl gears, however, are not suitable for surveying areas with rocky bottoms, which are the preferred habitat for lobsters, and are not suitable for highly productive areas of the fishery with existing lobster traps (Smith and Tremblay, 2003; Henry et al., 2020). SCUBA-based air-lift suction sampling collects important young-of-year lobster data and provides future recruitment information, but it is difficult to dive and collect data from deeper water if the depth range of young-of-year lobsters expands (Smith and Tremblay, 2003; Wahle et al., 2012). To supplement data collected from existing monitoring programs and describe important sublegal lobster populations, the Atlantic States Marine Fisheries Commission (ASMFC) developed the coast wide VTS in 2006 (Watson et al., 2019).

An increasing number of field studies have examined the performance of VTS in capturing lobster size composition and abundance compared with other monitoring programs (Clark et al., 2015). Recently, several efforts have been made for understanding the catch rates and saturation of ventless traps (Tremblay 2006; Clark et al., 2018; Watson et al., 2019). However, rigorous evaluation of the VTS sampling design on capturing sublegal lobsters' abundance through a simulation approach remains scarce. Such work requires comprehensive evaluation with a wide temporal-spatial range and high resolution of observed data collected from the VTS.

The primary goal of this study was to determine if the data collected from the Maine VTS provides robust estimation of a design-based sublegal lobster abundance index in the inshore GOM. In order to accomplish the goal, we compared the estimated VTS abundance index with the "true" abundance index from simulated sublegal lobster populations. The spatial distribution of sublegal lobsters from June to August was simulated by a generalized additive model (GAM) to provide the "true" abundance index using the 2006-2016 Maine/New Hampshire inshore bottom trawl survey (BTS) and environmental data. The GAM-simulated population was then used to evaluate the effectiveness of the VTS design when estimating sublegal lobster abundance indices. The "estimated" VTS abundance indices per National Marine Fisheries (NMFS) statistical area in Maine were derived by modeling the VTS sampling process based on the simulated population. By detecting the correlations between these abundance indices generated by different strategies, we evaluated the reliability of the VTS survey, and thus endorse its importance in the American lobster stock assessment.

II-1. Materials and Methods

II-1-1. Study Area and Data Used

The data used to develop GAMs to predict the sublegal lobster population were sourced from the 2006-2016 BTS data. The strata in the BTS were aggregated from five longitudinal regions and four depth strata (Figure II-６). However, in order to match the spatial divisions of the VTS, we assigned the BTS data to their correspoding NMFS Statistcal Area in Maine, either 511, 512, or 513 (Figure II-2).

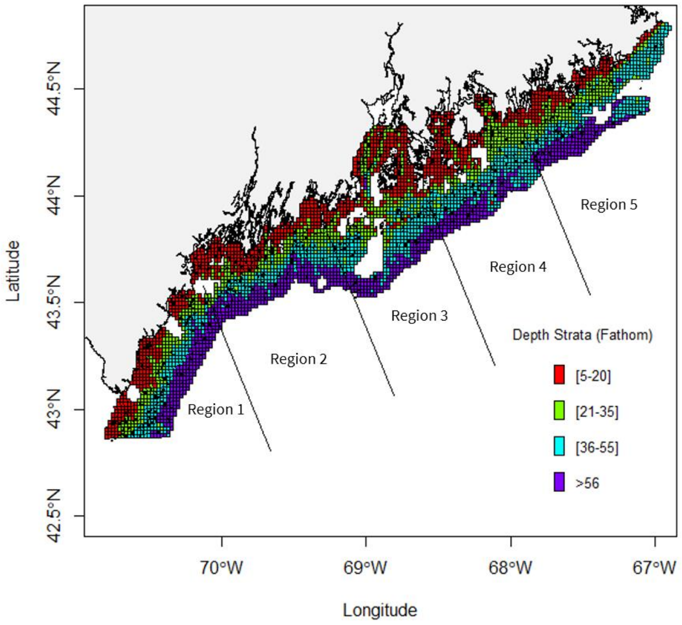

Figure II- 6 . The map of Maine/New Hampshire Inshore Bottom Trawl Survey with four depth strata and five latitudinal regions sampled in Maine.

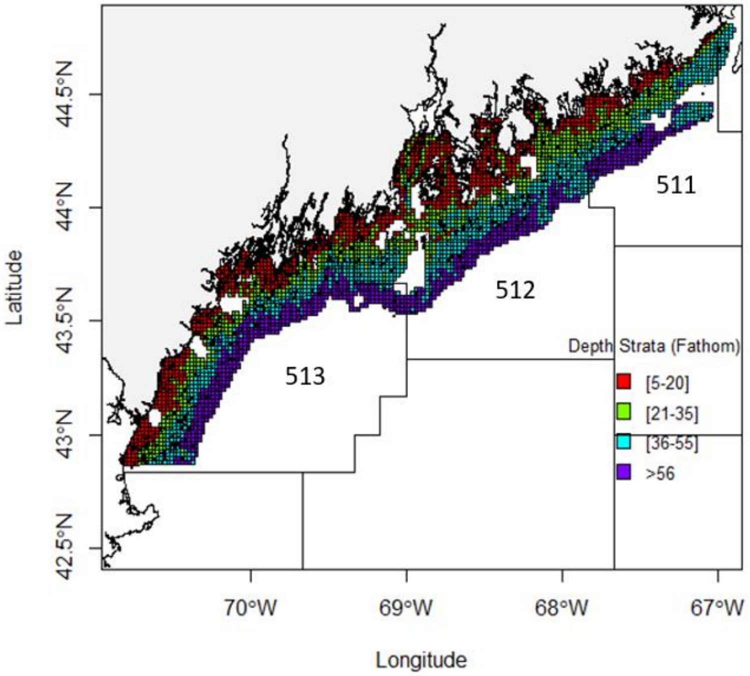

Figure II- 7 . The map of Maine/New Hampshire Inshore Bottom Trawl Survey with four depth strata and three NMFS statistical areas for Maine.

For the observed VTS abundance indices, the data were sourced from the 2006-2016 Maine VTS, which was conducted every summer (i.e., June, July, and August). The survey used a random stratified sampling design based on depth and the NMFS statistical area (i.e., 511, 512, and 513). The three depth strata (i.e., 0-20 m, 21-41 m, and 41-60 m) of interest were defined based on the range of depths in which sublegal lobsters are commonly fished in inshore waters. Potential sampling stations were generated along a one-minute latitude and longitude grid.

The June to August bottom water temperature data and bottom water salinity data from 2006-2016 used for prediction were obtained from the Finite-Volume Community Ocean Model (FVCOM), which was created by the Marine Ecosystems Dynamics Modeling Laboratory at the University of Massachusetts-Dartmouth. The unstructured grid used by FVCOM provides it the ability to depict complex sea topography and coastal regions (Chen et al., 2006; Li et al., 2017).

II-1-2. Model development

The spatial distribution of sublegal lobsters from June to August is influenced by many biotic and abiotic factors (Steneck and Wahle, 2013; Boudreau et al., 2015). A generalized additive model (GAM) with a Tweedie distribution has been recommended and widely used to quantify the relationships between lobsters and environmental variables in the inshore GOM (Chang et al., 2010; Tanaka et al., 2019). A GAM can be considered as in the middle range between linear models and machine learning models—a good balance between flexibility and interpretability (Hastie & Tibshirani, 1987, 1990). GAMs can be fit to spline functions to predict complex relationships with a relatively understandable method (Yee & Mitchel, 1991; Wood, 2017). In addition to a link function that builds the connection between dependent and independent variables, a smooth function is applied upon each independent variable, allowing the relationship between the dependent variable and the smoothed independent variables to be flexible, and thus to avoid over- or under-fitting and leading to better predictions. Generally, the determination of independent variables is estimated by a penalized regression method when building the model where all potential independent variables are included but adjusted according to their significance (if the p-value < 0.05, the variable is remained) or the model's Akaike's information criterion and deviance explained (Zuur et al., 2009; Wood, 2017; Liu et al., 2019). We used a GAM model with a Tweedie distribution to estimate lobster density and to predict sublegal lobster population at a high spatial resolution. Here, the predictor variables used in the GAM that had significant p-values included longitude, latitude, depth, and bottom water temperature.

The data used to develop a GAM are from the BTS survey (2006-2016). There are no fishery-independent surveys that have been conducted in summer with a wide spatial coverage in the inshore waters, and the best available data we could use are these BTS data. The density of sublegal lobsters per trawl, along with the trawl position and other environmental data (i.e., depth and bottom water temperature) were used in the GAM. In order to find the best combination of data to predict sublegal lobster population and also to account for the spatially varied relationships between lobster density and environmental variables, a series of data with different temporal and spatial ranges was used to build GAM models. We then compared these GAM predicted population indices with the observed BTS abundance indices. The predicted population with the strongest correlation to the observed BTS abundance indices were using June and Fall BTS data and the spatial ranges were classified by statistical areas (511, 512, and 513).

The design-based BTS and VTS abundance index of a year was calculated as:

$$Catch_y = \frac{A_{str} \times \sum_{str} \frac{\sum_s Catch_{s,y,str}}{N_{y,str}}}{\sum_{str} A_{str}}$$

Where A_{str} is the area of stratum str, $Catch_{s,y,str}$ is the mean catch in site s in stratum str and year y, and $N_{y,str}$ is the number of traps sites in stratum str and year.

The general GAM formulation to estimate sublegal American lobster (size < 83mm) abundance in each statistical area was expressed as:

$Catch_{SA}$ = s(depth)+s(temperature)+s(latitude)+s(longitude)

where s is the spline smoother.

We predicted the sublegal lobster population in the inshore GOM at a higher spatial resolution with quantified relationships between lobster densities and environment from the GAM. The FVCOM produced bottom water temperature and salinity data. However, the FVCOM data stopped in 2017 and a different mesh was used in 2017. Thus, in order to limit uncertainty, our prediction ranged from 2006-2016. We then modeled the VTS sampling process based on the predicted population. During the modeling process, we also considered the catch rate of VTS traps when estimating the catch of lobsters per trap at each station. The catch rate was assumed related to monthly water temperature (i.e., June, July, and August temperatures from 2003-2016) and depth. The catch rate per station was calculated as follow:

$$\overline{q}_{T,D} = \frac{1}{n}\sum_{i=1}^{n}\frac{C_{i,T,D}}{S_{i,T,D}}$$

where T is the monthly mean temperature classes obtained from FVCOM at VTS sampling areas; D is the depth classes (1-20m, 21-40m, and 41-60m); $\overline{q}_{T,D}$is the mean catch rate per temperature and depth class; n is the number of sampling sites at a specific temperature and depth class; $C_{i,T,D}$ is observed real number of lobsters per ventless trap at site i, temperature class T, and depth class D; and $S_{i,T,D}$ is simulated lobsters per site i within a temperature class T and depth class D. Mean catch rate was assigned to each VTS site ($\overline{q}_{i,T,D}$) based on the real temperature and depth at each VTS site. The simulated numbers of lobsters caught per ventless trap with consideration of catch rate ($C'_{i,T,D}$) was calculated as:

$$C'_{i,T,D} = \overline{q}_{i,T,D} \times S_{i,T,D}$$

The simulated abundance indices per statistical area based on the predicted population were derived from VTS catch with and without consideration of catch rate respectively. These abundance indices were also compared with the trend of the predicted population.

The population abundance indices were normalized based on the equation below:

$$z_{i=}\frac{C_i - min(C)}{max(C) - min(C)}$$

where C = (C_{2006},…, C_{2016}) is the population abundance indices from 2006 to 2016, and z_i is the i^{th} normalized population index.

II-2. Results

II-2-1. GAMs result

The GAMs resulted in reasonable fitting performances. The final and significant predictor variables included in the GAMs for the three different statistical areas were the same and included longitude, latitude, depth, and bottom water temperature. The deviance explained by the GAMs was 56.2%, 48.2%, and 75.8% for statistical areas 511, 512, and 513, respectively.

II-2-2. VTS Simulation

The calculated catch rate (dividing the observed number of lobsters per trap by simulated lobsters per trap in the same depth and temperature class) of sublegal lobsters (Table II-5) varied by monthly temperature classes and depth stratum. The calculated mean catch rate for a specific temperature and depth class ranged from 0.03 to 0.22. The mean monthly bottom temperature classes ranged from 7.41 to 12.89 °C. Catch rate is generally higher in depth class 1-20m compared to depth class 21-40m and depth class 41-60m. The trendlines in three depth classes show that the catch rate is decreasing while the temperature increases (Figure II-3; Figure II-4).

Table II-5. Mean simulated catch rate within temperature and depth classes.

Temperature Class	**Depth Class (1-20m)**	**Depth Class (21-40m)**	**Depth Class (41-60m)**
7.41	0.165229	0.203397	0.130009
8.32	0.177642	0.11234	0.119457
8.38	0.157372	0.0986	0.105305
8.6	0.146586	0.097894	0.115344
8.65	0.186053	0.15436	0.150728
8.68	0.186616	0.156801	0.162654
8.71	0.214351	0.124656	0.13334
8.81	0.156143	0.111592	0.066976
9.1	0.143041	0.100969	0.067175
9.48	0.19501	0.139526	0.154656
9.66	0.13522	0.081533	0.070784
9.84	0.130875	0.114986	0.103069
10	0.12628	0.064078	0.060372
10.19	0.125102	0.102981	0.132579
10.28	0.195167	0.12077	0.127152
10.84	0.115887	0.072516	0.037574
11.07	0.2068	0.099733	0.091975
11.09	0.118871	0.056421	0.064739
11.12	0.081903	0.091893	0.072815

11.28	0.178303	0.084968	0.074344
11.45	0.122053	0.035875	0.037184
11.5	0.123813	0.042738	0.036075
11.68	0.160801	0.053865	0.06724
11.98	0.109726	0.066764	0.051355
12.31	0.130854	0.0568	0.045478
12.76	0.193038	0.05418	0.029098
12.89	0.100833	0.064087	0.064087

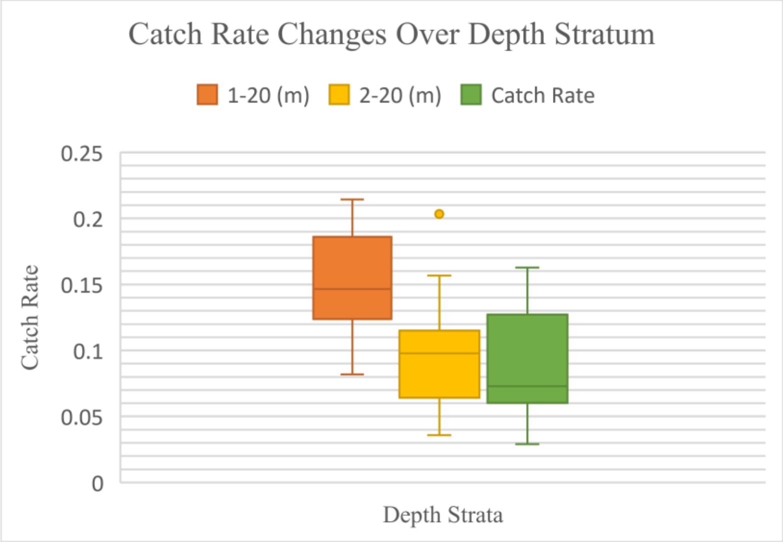

Figure II- 8 . Catch rate changes over depth stratum 1-20 (m), 21-40 (m), and 41-60 (m).

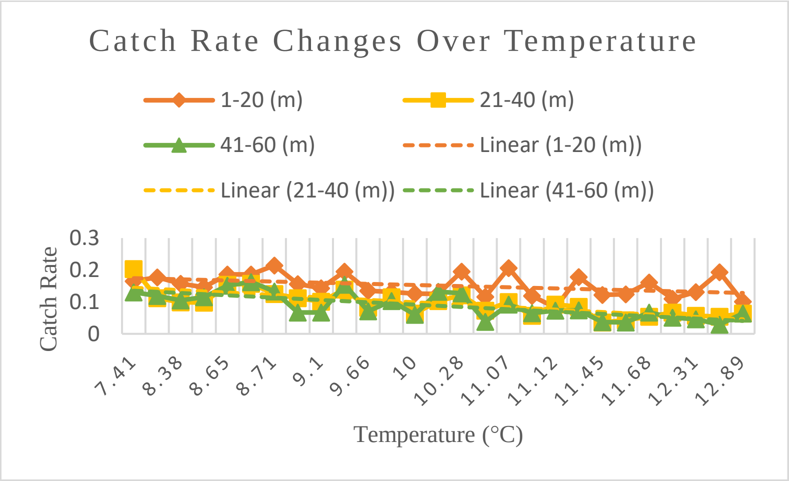

Figure II- 9 . Catch rate changes over annual mean water temperature (°C).

The predicted population index, simulated VTS index, the observed VTS abundance index, and the simulated VTS index with the consideration of catch rate all fluctuated largely from 2006-2016 with a generally increasing trend until after the year 2012 when there was dramatic decline in all the statistical areas (Figures II-5, 306). The abundance indices in statistical areas 511, 512 and 513 bounced back after the huge decline. The observed VTS is more overlapped with the simulated VTS index with the consideration of catch rate (similar increasing and decreasing tendency) than the simulated VTS index without the consideration of catch rate (Figure II-6). After considering the catch rate in the simulation work, the correlation between simulated VTS abundance indices and observed VTS abundance indices improved by 0.26, 0.26, and 0.64 at statistical areas 511, 512, and 513, respectively (Table II-6). The predicted population index is more overlapped with the simulated VTS index without the consideration of catch rate (nearly identical increasing and decreasing tendency in statistical areas 511, 512, and 513 after year 2011) than the simulated VTS index with the consideration of catch rate (Figure II-5). The correlation between predicted population indices and simulated VTS population abundance indices was 0.92, 0.98, 0.84 for statistical areas 511, 512, and 513, respectively. The correlation between predicted population indices and simulated VTS abundance indices with considerations of catch rate was 0.84, 0.73, and 0.39 for statistical areas 511, 512, and 513, respectively (Table II-6). The correlation results indicated that there was a discrepancy between simulated VTS abundance indices with consideration of catch rate and the predicted population indices (**Error! Reference source not found.**). The correlation coefficients between observed VTS and BTS abundance index were 0.82, 0.70, and 0.67 (Table II-6) in statistical areas 511, 512, and 513 respectively. The trend is shown in **Error! Reference source not found.** that although the general tendency increased until 2012 followed by a decrease in abundance index and a reboot afterward, the two indices have seldom overlapped.

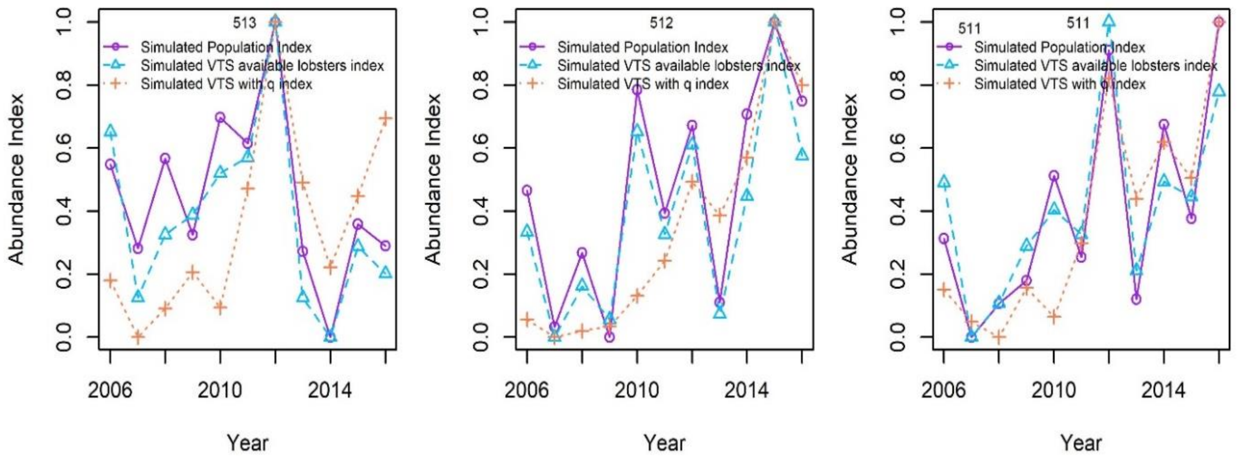

Figure II-１０. The relationship between the normalized predicted population index, which is the purple line with circle symbol, simulated VTS index, which is the blue line with triangle symbol, and simulated VTS index with the consideration of catch rate, which is the yellow line with the cross symbol for statistical areas 511, 512, and 513 from 2006 to 2016.

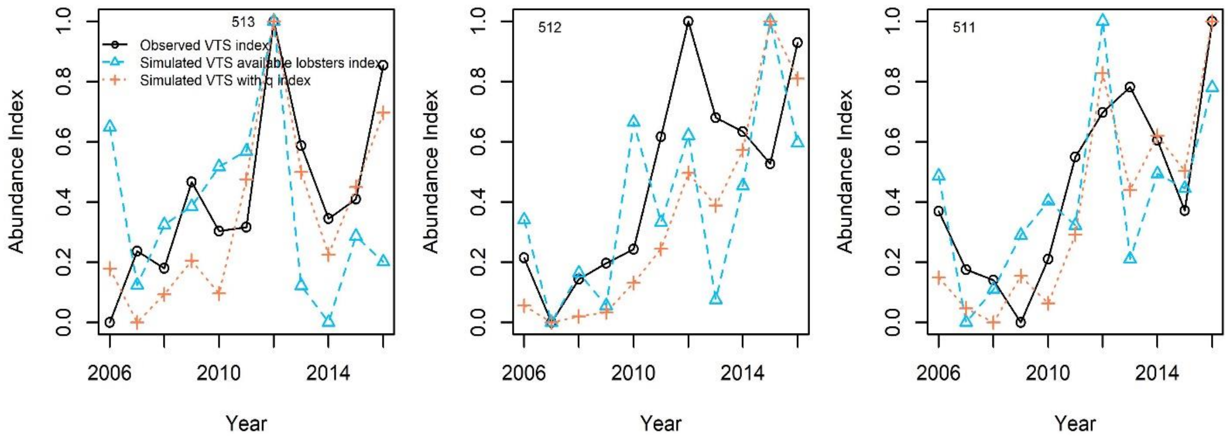

Figure II-１１. The relationship between the normalized observed VTS abundance index, which is the black line with circle symbol, simulated VTS index, which is the blue line with the triangle symbol, and simulated VTS index with the consideration of catch rate, which is the yellow line with the cross symbol for statistical areas 511, 512, and 513.

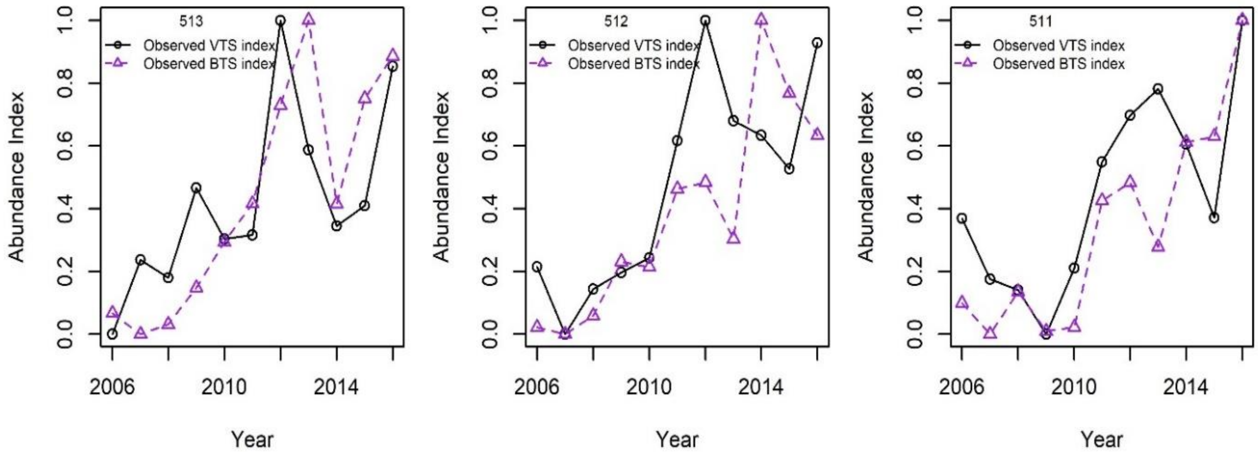

Figure II-１２. The relationship between normalized observed VTS abundance index which is the black line with circle symbol and normalized observed BTS abundance index which is the purple line with the triangle symbol for statistical areas 511, 512, and 513.

Table II-6. Correlations of various indices calculated in the study across statistical areas 511, 512, and 513. The comparison column states which indices and under which circumstances (i.e., whether or not catch rate was considered) were compared for each statistical area.

Comparison	Statistical area 511	Statistical area 512	Statistical area 513
Observed VTS population index/ Simulated VTS index	0.61	0.46	0.23
Observed population index/ Simulated VTS index with catch rate	0.87	0.72	0.87

Predicted population index/ Simulated VTS index	0.92	0.98	0.84
Predicted population index/ Simulated VTS index with catch rate	0.84	0.73	0.39
Observed BTS abundance index/ Observed VTS abundance index	0.81	0.69	0.76
Observed BTS abundance index/ Simulated VTS index	0.63	0.61	-0.05
Observed BTS abundance index/ Simulated VTS index with catch rate	0.90	0.84	0.79

II-3. Discussion

In this study, we quantified the evaluation of the VTS sampling design on the performance of capturing sublegal American lobster abundance in the GOM. GAMs were developed to predict the sublegal lobster population in a high spatial resolution. A simulated VTS abundance index based on the predicted population with and without the consideration of VTS trap catch rate were compared to the predicted population index. Strong correlations were detected between the comparisons, indicating that the current sampling design of the VTS is able to produce a robust abundance index of sublegal lobsters in the inshore GOM.

However, although the correlation coefficients of observed BTS and VTS abundance indices showed strong correlations, there is little overlap in the timing of the BTS and the VTS sampling periods. Additionally, the BTS survey is sequentially conducted from southwest to northeast while the VTS survey is conducted in all survey areas during the same time period. Therefore, uncertainty exists when using BTS data to test the effectiveness of VTS sublegal lobster abundance. The introduction of catch to ventless traps during the step of sampling the predicted lobster population using the VTS program sampling protocol helped rectify the availability of lobsters to a ventless trap.

Considering catch rate of ventless traps in the sampling process reproduces population indices that fit observed VTS abundance indices better. Nevertheless, the simulated VTS abundance indices with consideration of catch rate show lower correlation with predicted population abundance indices using BTS data compared with the situation that no catch rate was considered. These findings showed that it is difficult to incorporate catch rate into the analysis and much remains unknown about the factor that could affect the catch rate of ventless traps. Both density-dependent and density-independent factors could affect the probability of sublegal lobsters encountering and being caught by a ventless trap. For example, catch rates of a ventless trap could increase with substrate complexity and decrease when temperature is high (Clark et al., 2015). Although the trap soak time was standardized to three days in the VTS (ASMFC, 2020), a plateau in lobster catch may also occur 24 hours after the VTS traps are deployed. This could lead to a reduction of catch rate as lobsters accumulate in traps, inhibiting entry of additional lobsters and accelerating escapements. The loss of bait attractiveness could also reduce catch rates (Watson et al., 2019). Given the discrepancy between the simulated VTS abundance indices with consideration of catch rate and the predicted population indices, it is urgent to have more studies to understand how catch rate of ventless traps changes over time and space. With a better understanding of the factors that could affect the catch of lobsters using ventless traps, the stock assessment of American lobster could be improved by incorporating the catch rate information in the estimation.

Although the uncertainty of catch rate makes the study difficult to simulate VTS abundance index of sublegal lobsters, the similar trend between predicted population index and the simulated VTS abundance index without consideration of catch rate verified that the stratified random sampling design helps produce robust estimates of American lobster population abundance index. Smith and Tremblay (2003) also suggested that stratified random design of the VTS is more efficient than other sampling designs. The stratified random design helps reduce 10-31% variance of the stratified mean compared with a simple random design (Smith and Tremblay, 2003). It is important to understand changes in catch rate and the movement of lobsters in response to changes in the environment to improve the precision of abundance estimates.

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DEVELOPING INDICATORS OF HABITAT AND ECOSYSTEM CHANGE IN THE GULF OF MAINE

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Background

American lobster currently supports the most valuable single species fishery in the United States (NOAA 2019). Maine lobstermen harvest most of these landings, and the fishery represents over 79% of the value of all marine commercial fishery landings in the state (ME DMR 2020). Processing and sales of lobsters, as well as industries that support the lobster fishery, add further value to the economy. This income is important statewide and is central to the economies of many small coastal communities.

The Maine lobster fishery is situated within a rapidly changing ecosystem. The Gulf of Maine has been warming rapidly over the past 30 years, and particularly in the past decade (Pershing et al. 2015), and this warming trend was punctuated by ocean heat waves throughout much of 2012, 2016, 2018, 2020, and 2021 (Mills et al. 2013, ongoing GMRI research). The warming trend has been linked to changes in lobster populations. Temperature influences molting and growth (Aiken and Waddy 1986), size at maturity (Le Bris et al. 2017, Waller et al. 2021), fecundity (Koopman et al. 2015), larval survival (i.e., settlement) (Pershing et al. 2012, Goode et al. 2019, Oppenheim et al. 2019), and shell disease (Castro et al. 2012). These rates ultimately affect population outcomes. As waters have warmed, the southern New England population has declined but the Gulf of Maine population has increased (Le Bris et al. 2018, ASMFC 2020). Fisheries in each region were affected by these population impacts, leading to a decimation of the southern New England fishery and recent record landings in the Maine fishery (ASMFC 2020). The Maine fishery has also been affected by short-term temperature events such as the 2012 heat wave, which altered the timing of the summer uptick in fishery landings, leading to a glut of product and a price collapse (Mills et al. 2013).

Temperature is not the only factor changing in the Gulf of Maine ecosystem. The region is characterized by high levels of seasonal and interannual variability in physical conditions such as currents and winds, which may also affect lobsters (Incze et al. 2010, Xue et al. 2010, Pershing et al. 2012). In addition, physical changes affect other species in the ecosystem that interact with lobsters. For example, changes in the abundance of the zooplankton *Calanus finmarchicus* appear correlated with changes in larval lobster survival (Carloni et al. 2018). Further, traditional predators such as cod have declined in abundance and size in the Gulf of Maine, reducing predation on lobsters (Steneck et al. 2011, Wahle et al. 2013), but alternative predators may be moving into the region as waters warm (Wahle et al. 2013, Selden et al. 2018).

Given this nexus of a rapidly changing ecosystem and high coastal community dependence on the lobster fishery, there is a clear need to understand how ecosystem changes are affecting lobster biology, population dynamics, and ultimately, the Maine lobster fishery. As our contribution to the Lobster Research Collaborative, we developed and tested a suite of ecosystem indicators to identify changes in the ecosystem and draw connections to lobster biological and fishery responses.

Services Provided

As members of the Lobster Research Collaborative, we developed a suite of ecosystem indicators that represent changes in physical and ecological conditions in the Gulf of Maine. We evaluated these indicators against lobster biological and population parameters to identify associations with lobster population processes and trends. These indicators can be used by others in the Collaborative as co-variates in models of ecosystem-lobster relationships. They will also be available for consideration in the stock assessment process. Relationships between point-location temperatures and lobster population parameters have been reported in the benchmark stock assessment (ASMFC 2020), and the indicators we developed provide an ability to look at a broader set of changes in ecosystem conditions at multiple nested temporal and spatial scales.

1. Development of habitat and ecosystem indicators

As participants in the Lobster Research Collaborative, we developed indicators of habitat and ecosystem conditions to help characterize how the Gulf of Maine is changing in space and time. These indicators included sea surface temperature (SST), bottom temperature, salinity, stratification, Maine Coastal Current strength, predator indices, and zooplankton indices. Data source details and rationale for inclusion of each indicator are provided in Table 1. The focused study area included NOAA statistical areas 511, 512, and 513, as well as a coastal area defined for the Maine Coastal Current (Figure 1).

We assessed relationships between these indicators and lobster biological attributes. The lobster data we used included the American Lobster Settlement Index (ALSI), ME DMR’s ventless trap survey’s sublegal lobster catch, ME/NH inshore trawl survey, NEFSC trawl survey, and Maine lobster landings. We evaluated ways in which ecosystem changes affect the lobster population and identified drivers that may be most important for integrating environmental considerations into lobster population models.

Code for indicator development can be found in the Gulf of Maine Research Institute’s GitHub repository Ecosystem Indicators (https://github.com/gulfofmaine/Ecosystem_Indicators). Each indicator has its own R Markdown sheet that includes the data sources, information on how to access the data, and processing code.

2. Analysis and evaluation of indicators

For each indicator, we analyzed its trend over the entire length of the time series using a linear model. We performed a segmented regression to find breakpoints in the slope using R package segmented (Muggeo 2021) and performed a changepoint analysis to find changes in the mean of the data using R package mcp (Lindeløv 2020). Analyses were run on yearly values averaged over the entire domain of the study area. We entered a subset of the indicators into a principal component analysis (PCA) and cluster analysis. The subset includes bottom temperature, bottom salinity, Maine Coastal Current index, NEFSC predator abundance, NEFSC predator size spectra, and the Continuous Plankton Recorder Calanus index. We selected this suite of indicators after investigating collinearity between the same variables of different sources or depths, and the longest time series within groups of similar indicators was selected. The significant components of the PCA were entered into a principal component regression with the lobster variables. Generalized additive models (GAM) were used in instances where the best model fits were non-linear. For each GAM, the relationship to each principal component was informed by the breakpoints found in the lobster biological data, and period was included as a grouping variable. For each GAM, year was included as a random variable.

3. Participation in Lobster Research Collaborative (LRC)

Throughout the duration of this project, we participated in meetings of the LRC, shared updates, and solicitated feedback on the indicators. We worked with other members of the LRC to use relevant lobster indicators and biological data sets.

Results

1. Individual indicators and lobster datasets

Results for individual indicators are summarized in Table 2 and time series plots are shown in Figure 2. Detailed results can be found in the Ecosystems Indicators GitHub repository. All three temperature indicators show significant warming trends and have a breakpoint in the mean at the year 2009, where the mean temperature stepped up about one degree C after the breakpoint. Additionally, both sea surface temperature (SST) indicators have a breakpoint in the slope in the early 1990's, that show slight cooling in the 1980s then warming from 1990 through present. Surface and bottom salinity, and Maine Coastal Current do not have significant linear trends, but have a breakpoint in the trend in 2007.9, 2005.2, and 2008, respectively. Salinity and the Maine Coastal Current are negatively correlated. During the years when the Maine Coastal Current is positive, salinity is lower. Each shows similar breakpoints in the mean around the years 1992 and 2010. Salinity shifts from a more saline regime to fresher water then back to more saline waters. The Maine Coastal Current shifts from a weaker and slightly offshore current, to a strong current crossing Penobscot Bay, and back to a weaker current. The stratification index is one of the shorter indices and does not have a significant linear trend, does not have a breakpoint in the slope, but does show a breakpoint in the mean around the year 2005, indicating a shift to a more stratified water column.

The NEFSC species-based predator index shows a significant increasing trend in biomass and abundance and has a breakpoint in the mean in 2000 and 2010, respectively, with the trend increasing at a faster rate after the breakpoint. The NEFSC size-based predator indices show significant decreasing trends in size spectrum slope, with a breakpoint mean near 2010. The decreasing size spectrum slope indicates a greater proportion of smaller fish relative to larger fish. The ME/NH inshore trawl survey shows a linear increase in predator biomass and abundance, with a breakpoint in the slope in 2006 and 2005, respectively. Prior to the breakpoint, there is a decrease in predators, followed by an increase after the breakpoint. The ME/NH inshore trawl survey predator size spectrum shows a similar pattern in slope as the NEFSC survey, indicating a greater proportion of smaller fish relative to larger fish.

The small zooplankton index is negatively correlated to small zooplankton abundance, so a negative index indicates a greater number of small zooplankton. The small zooplankton index shows a significant decreasing trend, indicating a greater number of small zooplankton. There are mean breakpoints around 1990, shifting to a regime of more small zooplankton, and then in 2001, shifting to a period of fewer small zooplankton. The Calanus index, which is positively correlated to Calanus abundance, shows a mildly significant increasing linear trend through the late 1980s.

Results for individual lobster biological data are summarized in Table 3 and time series are shown in Figure 3. Detailed results can be found in the Ecosystems Indicators GitHub repository.

NEFSC trawl survey abundance and biomass data have significant positive linear trends with breakpoints in the trend in 2006, shifting from a positive slope to a steeper positive slope, and breakpoints in the mean in 2010, shifting to greater biomass and abundance. Similarly, the ME/NH lobster biomass and abundance data have significant positive linear trends with a breakpoint in its trend in 2016, changing direction from a positive slope to a negative slope, and a breakpoint in the mean around 2010, shifting to a period of greater biomass and abundance. The sublegal lobster data have a significant positive linear trend but had no breakpoints estimated in either its mean or slope. Lastly, the ALSI index had a borderline significant negative linear trend, with a breakpoint in slope in 2005, changing from a positive slope to a negative slope, and a breakpoint in mean in 2011, shifting to a period of lower settlement.

2. Multivariate analysis

The first three principal components had eigenvalues greater than one and explained 34.5%, 24.8%, and 14.4% of the variability in the data, respectively (Table 4, Figure 4). Bottom temperature, bottom salinity, and predator abundance are strongly positively correlated with PC1 (Table 5, Figure 5, Figure 6). The small zooplankton index is strongly negatively correlated to PC2, and the Maine Coastal Current is strongly positively correlated to PC2 (Table 5, Figure 5, Figure 6). PC3 is most strongly correlated to bottom temperature and the size-based predator index (Table 5). PC1 and PC3 do not have a significant linear trend, and PC2 has a moderately increasing trend (Table 6, Figure 4). Breakpoints in the trend were detected in PC1 in 2009 and 2012, and in PC2 in the year 1996. Breakpoints in the mean were detected in PC1 in 2001 and 2010, and in PC2 in 1990 and 2001 (Table 6).

Each lobster dataset, except ALSI, was strongly positively correlated to PC1, and ALSI was strongly negatively correlated with PC1 (Table 7). PC2 and PC3 were uncorrelated to moderately correlated to the lobster data (Table 7). The results of the stepwise linear regression showed highly significant models for each lobster dataset (Table 8). The model with the lowest AIC changed depending on the source of the lobster data and ranged from a model only including Year or PC1 to models containing all three PCs and Year (Table 8). The results for the breakpoint-informed GAMs generally improved upon the stepwise regression models (Table 9). For most of the lobster datasets, PC1 and Year were included in the best model selected through AIC.

The cluster analysis revealed which years grouped together based on the status of the ecosystem indicators in each year (Figure 7). The years 2011-2016 clustered together and loaded most strongly on the positive PC1 dimension. 1993-2001, 2008 and 2010 grouped together and loaded most strongly on the positive PC2 dimension. The remaining years (1981-1992, 2002-2007, 2009) grouped together generally along the negative PC1 and negative PC2 dimensions.

Discussion

The physical and biological indicators developed through this project provided insights into conditions in the Gulf of Maine ecosystem that are associated with changes in multiple lobster life stages.

Ocean temperature has been increasing over the past thirty years, with a particularly steep increase in temperature from about 2005 to 2016. The breakpoint in the mean of all the physical indicators around the year 2010 indicates the coastal ocean system may have entered a new regime at this time. After 2010, the study system was on average warmer and saltier, with a weaker disconnected coastal current, than the preceding twenty years. Additionally, after 2010 lobster predators increased in biomass and abundance at a greater rate than in the preceding decades.

Multivariate analyses help elucidate ways in which these variables act jointly to shape Gulf of Maine ecosystem conditions. Our results indicate linkages between the Maine Coastal Current and bottom salinity in the Gulf of Maine. In years when the Maine Coastal Current is stronger and crosses Penobscot Bay, bottom waters are less salty. The mean breakpoints in these indicators may indicate different oceanographic regimes. Prior to 1993, the coastal regions were salty and water movement was more offshore. From 1993 to 2010, the coastal region was less salty, and the coastal current was more strongly connected across Penobscot Bay. After 2010, the region shifted back into a saltier state with a weak or offshore coastal current. Stratification may have historically followed this same pattern of salinity, although the short time series available from buoy observations we used for this project only follows half of the cycle. Stratification is a function of salinity and temperature. Since temperature is increasing rapidly and salinity seems to follow a more cyclic pattern, overall stratification may be increasing with periods of highly stratified waters during the less saline periods.

The species-based lobster predator complex has been increasing in biomass and abundance over the length of the time series, with a faster rate of increase in the past 10 years (Table 2). The years around 2010 came out as a breakpoint in the mean across all species-based indicators. The size-based indicators show a decreasing trend in the size spectra slope, indicating a greater proportion of smaller fish relative to larger fish. This pattern aligns with the trends in the biomass and abundance indicators, where abundance is increasing at a faster rate than biomass, particularly in the past 10-15 years. An increase in lobster predators across all size classes may lead to decrease in lobster abundance.

The lobster biological data sets were chosen to represent different life stages of a lobster's life history, from larval settlement into recruitment into the fishery. The biomass and abundance indicators represent both the inshore ME/NH trawl survey and offshore NMFS trawl survey and capture possible inshore-offshore dynamics. Lobster biomass and abundance indices, including the Maine landings time series, all show very similar patterns with no trends prior to the late 1980s, moderately positive trends from the 1980s to the mid 2000s, strongly positive trends from the mid 2000s to the mid 2010s, peaking around 2016, and then sharply declining to 2020 (Table 3). The sublegal dataset is too short and contains a strong linear trend so no breakpoints could be estimated. The ALSI index shows a strong positive trend in larval settlement to the year 2005, then exhibits a strong negative trend.

The results of the multivariate analyses provide insights into how ecosystem conditions have aligned with different states of the lobster population. Long-term lobster population trends are associated with changes in the strength and direction of the Maine Coastal Current, bottom temperature, bottom salinity, zooplankton and predators. The early years of our analysis period (1981-1992) as well as 2002-2007 and 2009 were characterized by a weaker and less connected Maine Coastal Current, cooler and saltier water, and fewer small zooplankton (Figure 7). Subsequent years (1993-2001, 2008, and 2010) experienced a stronger and more connected Maine Coastal Current, fresher water, and more small zooplankton (Figure 7). Both these sets of years aligned with positive trends in lobster biomass and abundance, with particularly strong increases in the lobster population in later years. However, in the most recent years (2011-2016), the ecosystem has been characterized by warmer and saltier waters and higher predator abundance (Figure 7), and these conditions align with declines in lobster biomass and landings.

Conclusion

Many features of the Gulf of Maine ecosystem that may influence habitat suitability, biological processes, and population dynamics for American lobster have changed over time. Many ecosystem conditions—including the Maine Coastal Current, surface and bottom temperature and salinity, and predator indices—showed particularly distinct shifts around 2010. Over the observed time period, most size stages of lobster experienced increasing abundance or biomass, and landings also rose substantially; these changes were also concentrated after 2010. The larval stage showed with a counter-acting trend, with young-of-year settlement showing a declining trend in the American Lobster Settlement Index; these declines have been further exacerbated after 2010. Our findings indicate circulation, oceanographic, and biological changes around 2010 transformed the Gulf of Maine ecosystem to a state that favors growth of the lobster population and fishery. These changes appear to have benefitted later lobster life stages, and the paradoxically counter-acting trends in abundance at the larval stage versus later stages leaves open questions regarding the likelihood that the observed ecosystem-lobster patterns will continue driving a highly abundant state of the lobster population.

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Table 1: Habitat and ecosystem indicators developed as contribution to the Lobster Research Collaborative, including data sources, general processing, and relevance of the indicator to American lobster.

Indicator	**Data source**	**Data processing**	**Rationale: relevance to American lobster**
Sea surface temperature	NOAA OISST (0.25°x0.25° grid, daily 1982-2020) and Finite Volume Unstructured Grid Model (FVCOM) as provided through the Northeast Coastal Ocean Forecast System (1978-2020)	Create time series or gridded spatial layers of temperature, anomalies, or degree days at multiple scales of spatial (e.g., lobster zone, statewide) and temporal (e.g., daily, annual) resolution	Widely available and correlated to bottom temperature in most portions of Gulf of Maine; many documented relationships between temperature and lobster biology
Bottom temperature	Finite Volume Unstructured Grid Model (FVCOM) as provided through the Northeast Coastal Ocean Forecast System (1978-2020)	Create time series or gridded spatial layers of temperature, anomalies, or degree days at multiple scales of spatial (e.g., lobster zone, statewide) and temporal (e.g., daily, annual) resolution	Many documented relationships between temperature and lobster biology
Salinity	Finite Volume Unstructured Grid Model (FVCOM) as provided through the Northeast Coastal Ocean Forecast System (1978-2020)	Create time series of salinity at multiple temporal scales and water column depths	Relationship to metabolism (Jury et al. 1994) and spatial distribution of lobsters (Tanaka and Chen 2015) and incidence of shell disease (Tanaka et al. 2017)
Stratification index	NERACOOS buoys (point locations, 2001-present)	Create time series of density gradient between surface and depth	Reflects large-scale circulation and seasonal hydrographic conditions; relationship to *Calanus* prevalence in zooplankton community (Head and Sameoto 2007), which has been associated with YoY lobster recruitment (Carloni et al. 2018)
Strength of Maine Coastal Current	FVCOM NECOFS model (1978-present)	Create time series of strength of Eastern and Western portions of the coastal current system	Influences larval distribution, development time, settlement rates, and

			population connectivity (Xue et al. 2010, Incze et al. 2010)
Predator index: species-based	ME/NH trawl survey (2000-present) and NEFSC trawl survey (1970-2019)	Create time series of relative abundance of suite of lobster predators (identified in stock assessment)	Predation release identified as contributor to lobster success in Gulf of Maine (Steneck et al. 2011, Wahle et al. 2013)
Predator index: size-based	Size-based model of predation pressure (Le Bris et al. 2018) ME/NH trawl survey (2000-present) and NEFSC trawl survey (1970-2019)	Create time series of lobster predator size spectra slope at seasonal, or annual time steps	Smaller-bodied predators prey on smaller size classes of lobsters (Wahle et al. 2013, Le Bris et al. 2018)
Zooplankton index	Continuous plankton record	Time series index of zooplankton community that captures changes in small zooplankton abundance and Calanus abundance	Potential food for larval lobster and associated with YoY recruitment (Carloni et al. 2018)

Table 2. Habitat and ecosystem indicators: linear trend, changepoint in regression slope, changepoint in intercept, and sparkline showing the general pattern in the time series.

Indicator	**Linear trend**	**Changepoint in slope**	**Changepoint in intercept**	**Sparkline**
Sea surface temperature_OISST	0.039 deg C/yr $R^2=0.46$ $p << 0.05$	1992	2009	
Sea surface temperature_FVCOM	0.032 deg C/yr $R^2=0.32$ $p<<0.05$	1990.9	2009	
Bottom temperature	0.014 deg C/yr $R^2=0.11$ $p=0.03$	No changepoint estimated	2009	
Surface salinity	NS	2007.94	1992, 2008	
Bottom salinity	NS	2005.18	1992.5, 2010.6	
Maine Coastal Current Index	NS	2008	1993.4, 2010.6	
Stratification	NS	No changepoint estimated	2005	
ME/NH predator biomass	$R^2=0.33$ $p << 0.05$	2011	2014	
ME/NH predator abundance	$R^2=0.3$ $p << 0.05$	2003	2011	
NEFSC predator biomass	$R^2=0.13$ $p = 0.024$	1998	2009.4	

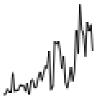
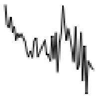
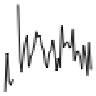
NEFSC predator abundance	R^2=0.57 p<<0.05	2007	1990, 2009.5	
NEFSC size spectra slope	R^2=0.28 p=0.00018	No changepoint estimated	2009	
ME/NH size spectra slope	R^2=0.46 p=0.00096	No changepoint estimated	2010.85	
Small zooplankton index	R^2=0.17 p=0.002	No changepoint estimated	1989.69, 2001.5	
Calanus index	R^2=0.16 p=0.002	1987	1975.42	

Table 3. Lobster biological attributes and data sources, and their associated linear trends, changepoint in regression slope, changepoint in intercept, and sparkline showing the general pattern in the time series.

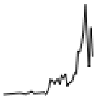
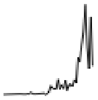
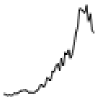
Lobster biological attribute and data source	Linear trend	Changepoint in trend	Changepoint in mean	Sparkline
Juvenile lobster density, American Lobster Settlement Index (ALSI)	$R^2 = 0.21$, $p=0.046$	2005	2011.8	
Sublegal (70-80mm) lobster CPUE, ME DMR ventless trap survey	$R^2 =0.73$, $p<<0.05$	No changepoint estimated	No changepoint estimated	
Lobster biomass, ME/NH trawl survey	$R^2 =0.71$, $p<<0.05$	2004, 2016	2009.7	
Lobster abundance, ME/NH trawl survey	$R^2 = 0.71$, $p <<0.05$	2004.1, 2016	2009.6	
Lobster biomass index, statistical areas 511-513, NEFSC trawl survey	$R^2 = 0.59$, $p<<0.05$	1989.2, 2006.3	1995.2, 2010.5	
Lobster abundance index, statistical areas 511-513, NEFSC trawl survey	$R^2 = 0.49$, $p<<0.05$	1990.1, 2006.3	2010.6	
Maine lobster landings, ME DMR	$R^2 =0.68$, $p<<0.05$	1987.6, 2008.7, 2012.6	1996.5, 2009.5	

Table 4. Variance explained by first four principal components in analysis of habitat and ecosystem indicators.

	PC1	**PC2**	**PC3**	**PC4**
Standard deviation	1.55	1.32	1.00	0.90
Proportion of Variance	0.34	0.25	0.14	0.12
Cumulative Proportion	0.34	0.59	0.74	0.85

Table 5. Loading of each habitat and ecosystem indicator on first three principal components.

Indicator	**PC1**	**PC2**	**PC3**
Bottom temperature	0.45	-0.075	0.54
Bottom salinity	0.45	-0.44	0.043
Maine Coastal Current	-0.35	0.48	0.27
NEFSC predator abundance	0.49	0.33	0.3
NEFSC size spectrum slope	-0.34	-0.11	0.69
Small zooplankton index	-0.19	-0.62	0.031
Calanus index	-0.30	-0.27	0.27

Table 6. Breakpoint of principal components.

Indicator	**Linear trend**	**Breakpoint in trend**	**Breakpoint in mean**
PC1	NS	2009, 2012	2001.7, 2010.5
PC2	R^2=0.18 p = 0.012	1996.9	1990.2, 2001.6
PC3	NS	No breakpoint detected	No breakpoint detected

Table 7. Correlation table between PC1, PC2, PC3 and each lobster data set.

	PC1	**PC2**	**PC3**
ALSI	-0.69	-0.21	0.034
Sublegal_CPUE	0.72	0.13	-0.052
ME/NH biomass	0.74	0.015	-0.35
ME/NH abundance	0.74	-0.014	-0.35
NEFSC biomass	0.60	0.20	-0.021
NEFSC abundance	0.62	0.16	-0.10
ME_landings	0.55	0.27	0.22

Table 8. Stepwise regression results

	R^2	**p**	**Model**
ALSI	0.47	0.0022	lob_index~PC1
Sublegal_CPUE	0.78	0.00034	lob_index~Year
ME/NH biomass	0.89	2.07E-6	lob_index~PC1+PC2+Year
ME/NH abundance	0.90	8.73E-07	lob_index~PC1+PC2+Year
NEFSC biomass	0.80	1.8E-09	lob_index~PC1+PC2+PC3+Year
NEFSC abundance	0.77	1.83E-08	lob_index~PC1+PC2+PC3+Year
ME_landings	0.95	6.03E-19	lob_index~PC1+PC2+Year

Table 9. Results for breakpoint period-based GAMs relating lobster indices to PC1, PC2, and year. Models were chosen based on AIC and only best models are shown. In each model, PC1 and/or PC2 is grouped by period based on the breakpoint years of the lobster index of interest and year is a random variable.

	R^2	**Deviance explained**	**Model**
ALSI	0.58	70%	lob_index ~ s(PC1, by = period)+s(year)
Sublegal_CPUE	0.75	77.6%	lob_index ~ s(year)
ME/NH biomass	0.94	95.5	lob_index ~ s(PC1, by = period)+s(year)
ME/NH abundance	0.95	96.7%	lob_index ~ s(PC1, by = period)+s(year)
NEFSC biomass	0.96	96.9%	lob_index ~ s(PC1, by = period)+s(PC2, by = period)+s(year)
NEFSC abundance	0.86	90%	lob_index ~ s(PC1, by = period)+s(PC2, by = period)+s(year)
ME_landings	0.98	98%	lob_index ~ s(PC1, by = period)+s(year)

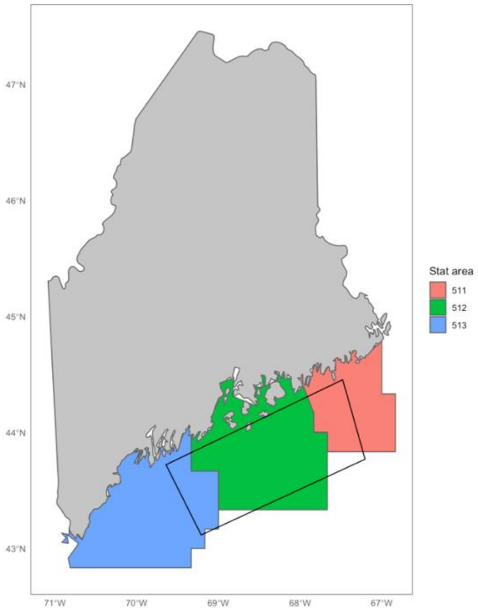


Figure 1. Study region. NOAA statistical areas are indicated as colored polygons. The region used for calculating the Maine Coastal Current index is indicated by the black outlined open polygon.

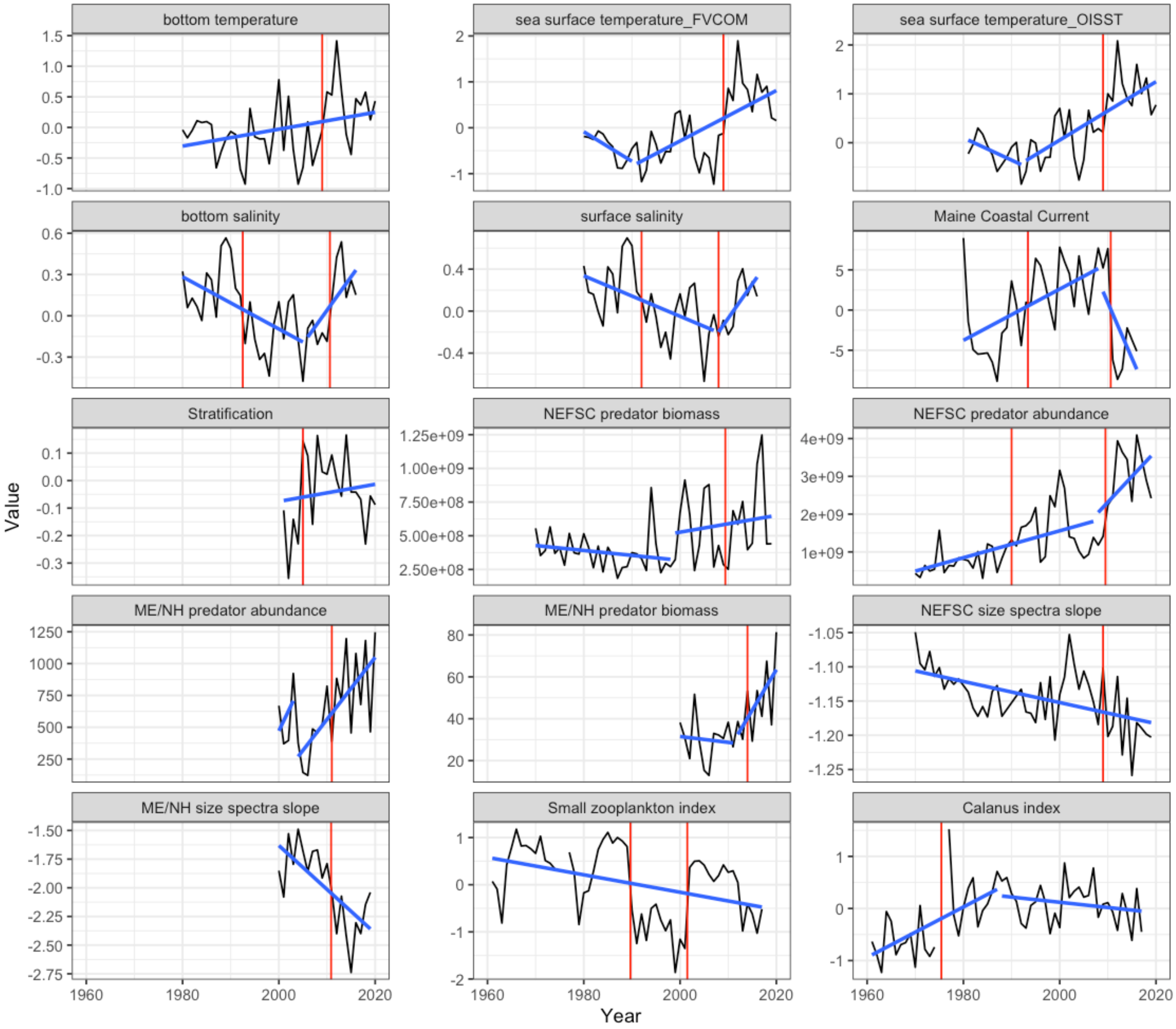


Figure 2. Time series plots of ecosystem indicators. Blues line shows the breakpoint regression for each indicator. Red lines show the breakpoints in the mean.

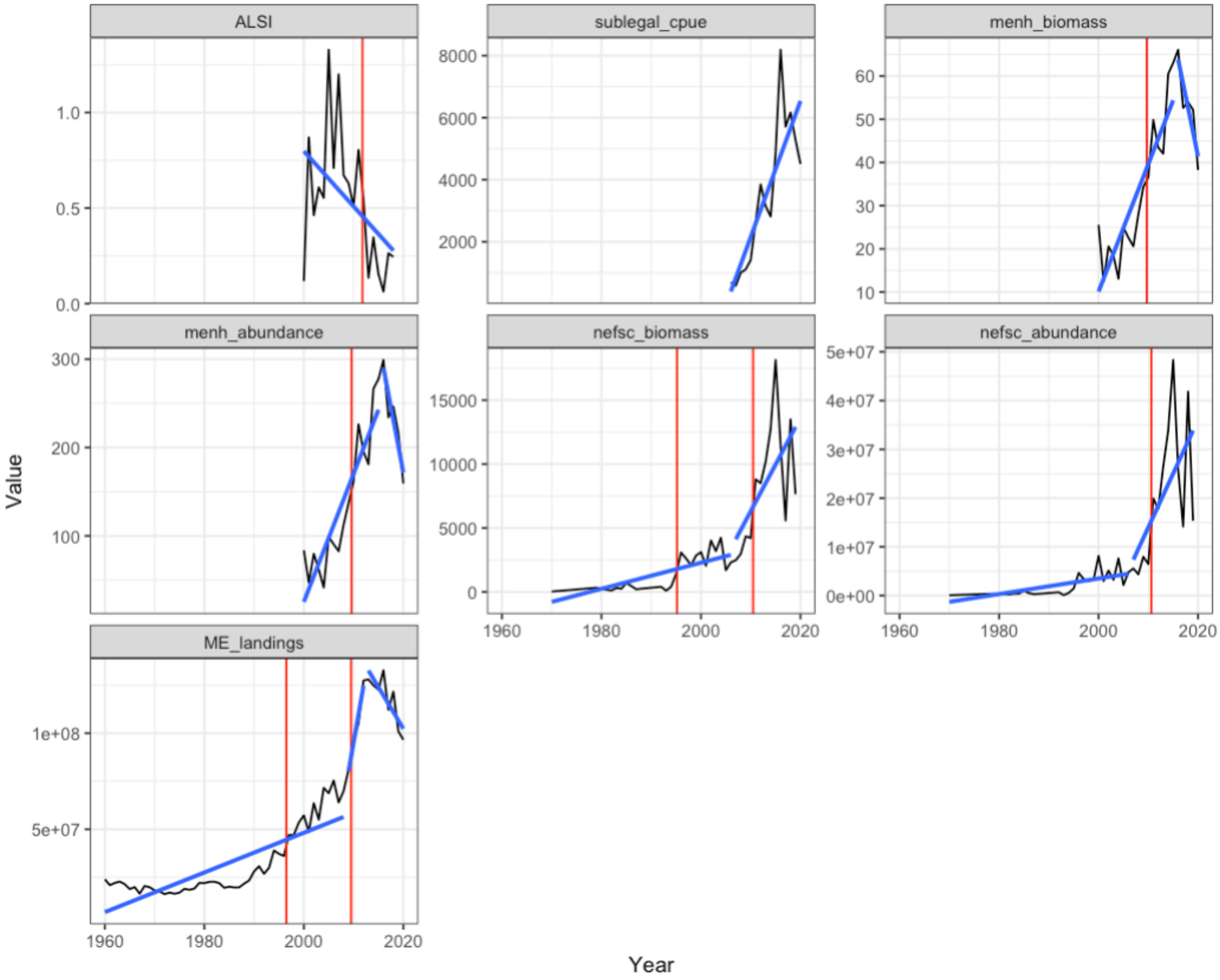


Figure 3. Time series plots of lobster data. Blues line shows the breakpoint regression for each indicator. Red lines show the breakpoints in the mean.

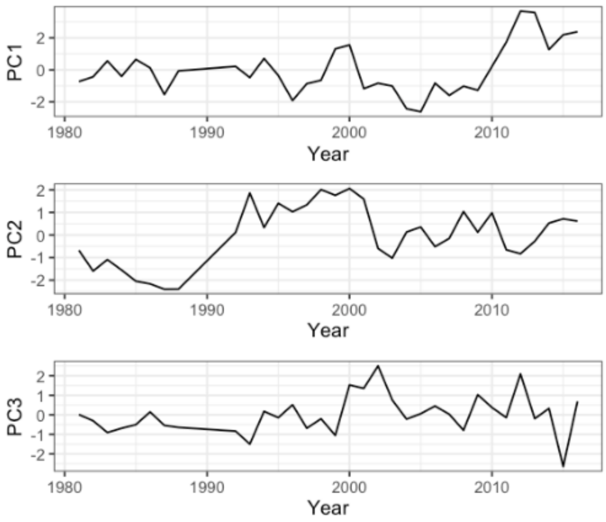


Figure 4. Time series of PC1, PC2, and PC3

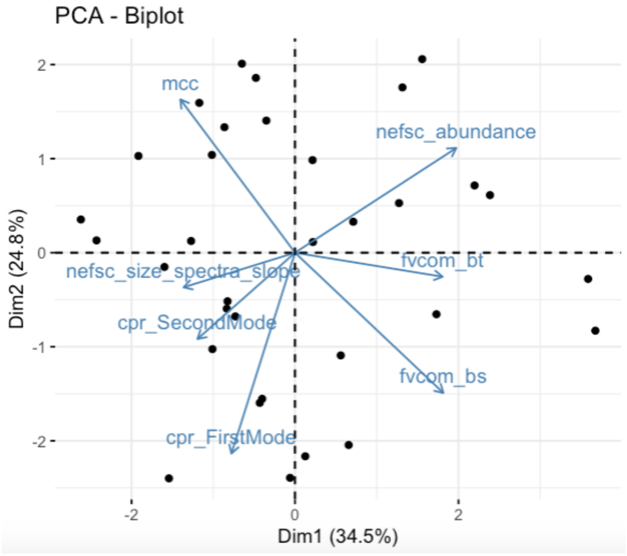


Figure 5. Biplot of indicator scores on Principal Components 1 and 2. Line length and direction represents each variable's loading to PC1 and PC2. The dots are scores for each year along the PC1 (Dim 1) and PC2 (Dim 2) axis. The percentage in the parentheses in the axis labels is the amount of variability explained by each PC. Cpr_SecondMode is the Calanus index. Cpr_FirstMode is the small zooplankton index

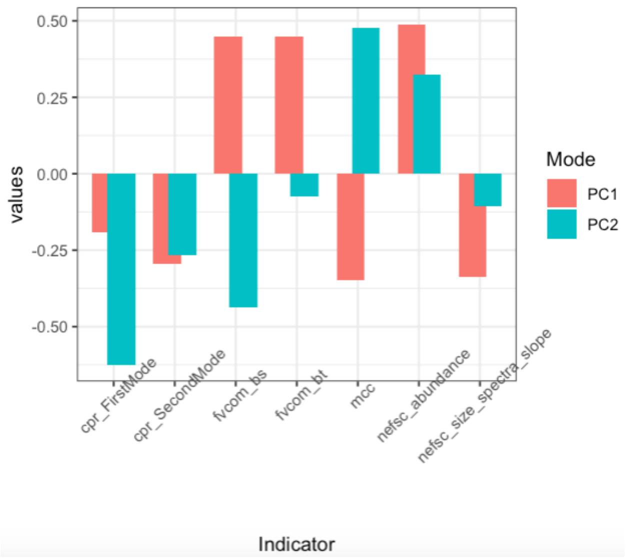


Figure 6. Loadings plot of PC1 and PC2 for each indicator. Cpr_SecondMode is the Calanus index. Cpr_FirstMode is the small zooplankton index

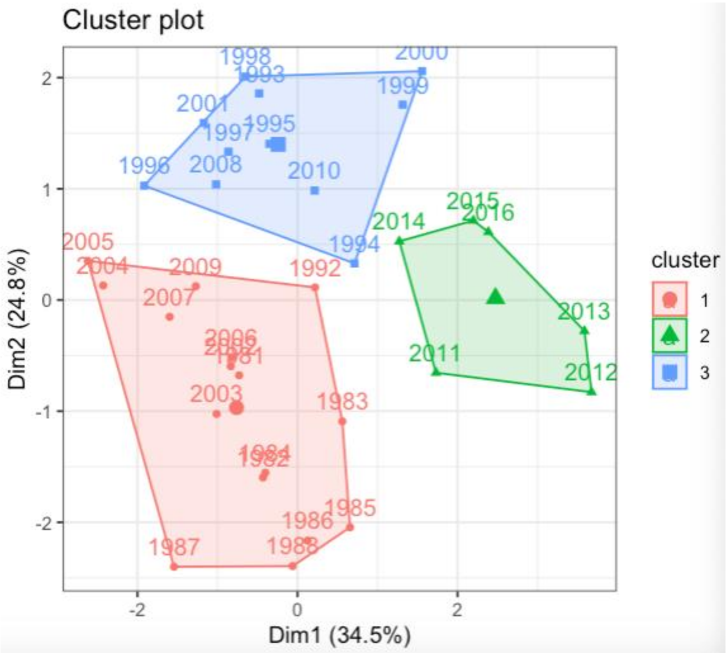


Figure 7. Groupings of years based on a cluster analysis of the indicators. Colored years and polygons represent each cluster.

Maine Department of Marine Resources

Lobster Research Collaborative

Final Project Report

September 5, 2021

BRIDGING THE SPAWNER-RECRUIT DISCONNECT II: REVEALING BASIN-SCALE CORRELATIONS AND PHENOLOGY SHIFTS BETWEEN ZOOPLANKTON AND LOBSTER SETTLEMENT DYNAMICS IN THE GULF OF MAINE

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ABSTRACT

This project builds on previous research describing correlative links between changes in the abundance of the copepod *Calanus finmarchicus,* a foundational zooplankton species of the pelagic food web, and recruitment of young-of-year lobster to benthic nursery habitats in the Gulf of Maine. We addressed two novel objectives: (1) To evaluate how local- and basin-scale zooplankton dynamics and oceanographic indicators in the Gulf of Maine correlate with lobster settlement indices and each other since the late 1980s; and (2) To evaluate changes in larval lobster and *C. finmarchicus* phenology over the period. Under objective 1 we report that lobster settlement trends in southwestern Gulf of Maine study areas, from Midcoast Maine to Cape Cod Bay, tend to be significantly correlated with basin-wide *C. finmarchicus* dynamics and the strength of the Labrador Slope Water index, whereas lobster settlement in the northeastern Gulf, from Penobscot Bay to the Bay of Fundy, tended to link more strongly to *C. finmarchicus* variability in the Fundy region, and less with changes in the Labrador Slope Water. As for phenological shifts, we found significant correlation between warming ocean temperature and the earlier onset of the lobster egg hatch and the first appearance of Stage I larvae. Consequently, Stage I larvae have appeared about two-weeks earlier than they did in the 1980s, but their last appearance has been delayed by than two weeks, while the onset, end and length of the postlarval season has varied without trend. Since 2010, the *C. finmarchicus* season has been ending before the peak abundance of stage I lobster larvae, with the net effect being an increasingly mismatched phenology of the two species in recent years. Our results are consistent with the hypothesis that the combined effect of climate-related declines in abundance and phenological shifts of *C. finmarchicus* over the past decade have contributed to declines in lobster settlement over the past decade, and justify further research into the mechanisms of this interaction. These

changes also align with the weakening influence of cold Labrador Slope Water and strengthening effects of warm Gulf Stream waters that precipitated an ecosystem-wide regime shift in the Gulf of Maine over the past decade and may have greater implications for lobster recruitment than previously suspected.

INTRODUCTION

There are clear signs that the changing ocean environment is directly and indirectly impacting Maine's, and the nation's most valuable fishery – the American lobster, *Homarus americanus*. In 2018 Maine's Department of Marine Resources (DMR) initiated a Lobster Research Collaborative (LRC) that solicited proposals to address aspects of the lobster fishery and ecology that would lead to a better understanding of environmental factors and interactions driving change in the lobster population. In response to that call, we assembled a team representing academic, non-governmental, state and private organizations that, together with Maine DMR, are well positioned to address one of the least understood aspects of American lobster ecology and population dynamics – trophic interactions of larvae with the Gulf of Maine's (Gulf) pelagic food web. The project builds on a previously published benchmark study (Carloni et al. 2018), describing correlative links between changes in the abundance of the copepod *Calanus finmarchicus,* a keystone species of the pelagic food web (Pershing and Stamiezskin 2020), and recruitment of young-of-year (YoY) lobster to benthic nursery habitats in the Gulf. As with the Carloni et al. paper, this project capitalizes on more than three decades of zooplankton and benthic lobster settlement monitoring in the coastal Gulf. We continue to investigate the links between lobster recruitment and zooplankton assemblages over a broader geographic and taxonomic scope to better evaluate potential explanatory mechanisms behind Gulf-wide settlement and fishery recruitment declines (Oppenheim et al., 2019). We also, again, take advantage of the three-decade zooplankton and larval lobster time series collected on the New Hampshire coast to evaluate changes in phenology. This project therefore entailed two primary objectives: (1) *To evaluate how local- and basin-scale zooplankton dynamics and oceanographic* *indicators in the Gulf of Maine correlate with lobster settlement indices and each other; and (2) Quantify changes in larval lobster and zooplankton phenology over the three decades of seasonal sampling along the New Hampshire coast from 1988 to 2018.*

Under Objective 1, we reasoned that if coherent relationships existed between basin-scale zooplankton dynamics, coastal zooplankton dynamics, and lobster settlement patterns, we would have a compelling evaluation of the environmental factors influencing lobster recruitment success within the Gulf of Maine.

As for Objective 2, long-term (1988-2018) zooplankton and larval lobster monitoring conducted along the New Hampshire coast provide a unique opportunity to assess phenological changes of lobster larvae and zooplankton over the past three decades. Surveys of egg-bearing female lobsters indicate that seasonal onset of the larval hatch has been earlier in recent years (ASMFC 2020). Lobster larval development is well known to be responsive to temperature change and to be subject to delay under starvation (Templeman 1936, Anger et al. 1985). What remains unclear is whether changes in these environmental factors have altered the phenology of either the predator or their putative prey, *C. finmarchicus*. However, if the zooplankton assemblage is an important prey item for larval lobster, a divergent phenology between the two would be consistent with the hypothesis of Carloni et al. (2018) that lobster larvae have become more food limited recently and would also be a further indication of the linkage between the Gulf's larval lobster population dynamics and the pelagic food web.

METHODS

Objective 1: Local and basin-scale correlations of zooplankton, lobster settlement and oceanographic indicators

We compared time trends across five data sets from the Gulf of Maine (Fig. 1): the American Lobster Settlement Index (ALSI) from southern Nova Scotia to Cape Cod Bay; the abundance of *C. finmarchicus* in coastal seasonal surveys in (2) New Hampshire and (3) the mouth of the Bay of Fundy; (4) the abundance of *C. finmarchicus* and associated zooplankton from NOAA's Gulf-wide Ecosystem Monitoring (EcoMon) cruises, and (5) the relative advection index of Labrador Slope Water (LSW) entering the Gulf through the Northeast Channel. Details of each time series follow.

Lobster Settlement time series: The time series for lobster settlement was based on suction sampling conducted by contributors to the American Lobster Settlement Index from 1989-2020 (ALSI, https://umaine.edu/wahlelab/american-lobster-settlement-index-alsi/). The data were constrained to individuals with a carapace length of 17 mm or less except for Massachusetts study areas where the constraint was set at 24 mm to account for a somewhat warmer regime with faster growth rates. These size bins are estimated to correspond to Young-of-Year (YoY) and 1-Year-Olds, in effect capturing two years of settlement, and serving our intent to characterize long-term trends and reduce observation errors rather than characterizing finer-scale inter-annual variability (Harrington et al. 2018). We further constrained the data to study areas within the Gulf, from southern Nova Scotia through Cape Cod, and study areas with a minimum of six years of data. This resulted in a data set consisting of 14 study areas, each comprised of 4-10 study sites and collectively totaling 70 study sites.

ALSI suction-sampling surveys at established fixed sites have a hierarchical sampling design with study areas containing multiple representative study sites and multiple quadrats sampled per study site and year. We applied a hierarchical model-based method rather than a designed survey index, such as nested random-stratified, because study areas did not encompass all the coastline in the study region and study sites represent selected habitats. Observations of young lobsters in quadrats were converted to densities, based on quadrat size, then averaged across quadrats at a study site and sampling event. For time-series trajectories of individual study areas, means across study sites with respective study areas were simply averaged together on a yearly basis.

To estimate a region-scale Gulf-wide lobster settlement index, we used the Template Model Builder platform (TMB, Kristensen et al. 2016) to fit a state-space model that finds a common trajectory of lobster settlement through time that best describes all study areas.
Each study area's influence on this common trajectory is proportional to the length of its time series. Because some locations naturally have more lobsters than others, we estimate a "study area effect" (likely a function of larval supply, habitat quality, predation rates, etc.), which is simply a multiplier that scales abundance for each study area up or down to account for this effect. To obtain a predicted settlement time series from this model, we applied the study area effect for a single study area to the estimated common trajectory among all study areas. The choice of study area is inconsequential for our purposes because our primary interest is in relative change over time, and they give the same result when the estimated temporal trend is correlated against another data set, such as an environmental index.

Because prior analysis suggested differences in trajectories among study areas in the northeastern and southwestern end of the Gulf (Pershing et al. 2012, Goode et al. 2019), we also split the region and fit two separate models; one to northeastern study areas from Penobscot Bay through Nova Scotia, and a second model including southwestern study areas from Midcoast Maine to Cape Cod (Fig. 1).

Coastal New Hampshire and Bay of Fundy copepod time series: We constructed coastal copepod abundance time series based on a zooplankton monitoring study conducted off New Hampshire (Normandeau 2016) and lower Bay of Fundy (Casault et al. 2020). In New Hampshire macrozooplankton were sampled at two stations using oblique tows with a pair of 1-m diameter plankton hoop nets (505 µm mesh) (Fig. 1 and Fig. S-1). Nets were fitted with depressors and flow meters and towed for 10 minutes under variable speeds to allow nets to sample the majority of the water column with each tow sampling a volume of about 500 m^3. Samples were collected monthly from 1988-2018 and fixed in buffered formalin before enumeration. Annual geometric mean *C. finmarchicus* abundances were then calculated for each site. Because values for both sites were not available for all years, we merged the time series for the two sites into a single time series by fitting a linear model with year effects and offsets for different sites and then extracting the calculated year effects. We then fit a local-level model to the merged time series.

Sampling for zooplankton at the mouth of the Bay of Fundy began in 1999 by Fisheries and Oceans Canada fixed station “Prince 5” (Fig. 1) near Grand Manan Island (Casault et al. 2020). Monthly vertical tows were conducted year-round with ring net (202 µm mesh net) for biomass (wet and dry weights) and numerical abundance. Samples were fixed in buffered formalin. Numerical abundance data were log transformed, expressed as standardized anomalies relative to the time series mean, and smoothed prior to conducting correlation analyses described below.

EcoMon Regional zooplankton time series: We used zooplankton data collected on NOAA, Northeast Fishery Science Center (NEFSC) Ecosystem Monitoring (EcoMon) cruises between 1988 and 2018 to examine regional dynamics of the zooplankton assemblage and specifically, *C. finmarchicus*, across the Gulf of Maine (Fig. 1). EcoMon sampling uses two 60 cm diameter Bongo nets with different mesh sizes: 333 and 505 µm. While these surveys occurred year-round, we constrained the analysis to samples collected during the summer and fall survey periods, (i.e., between August 7th and November 20th, Fig. S-2). The summer period best corresponded to the time that lobster larvae were present, but sampling rates for this season were low and inconsistent across years. However, the fall period had more consistent sampling and exhibited similar temporal patterns to the summer data, so was also included to stabilize abundance indices. All calculations were performed on zooplankton densities per meter squared.

We explored cohesive time trends among groups of zooplankton species represented in the EcoMon database for summer and fall using a principal components analysis (PCA). This analysis was chosen both to understand if there were significant temporal shifts in community composition and with some expectation that dynamics across multiple correlated species may be more stable than for individual species, partially mitigating observation error. The PCA included the 21 most common species, occurring in >20% of plankton samples, as well as three less common species groups (*Calanus minor*, Ostracods and Protozoa) that exhibited strong temporal patterns. Abundances from individual tows for each species were log+1 transformed before aggregating by survey stratum and year. We then transformed the resulting mean abundances to z-scores within species and stratum across years to effectively perform a PCA on sample correlations, which gave each species and stratum equal influence in the analysis regardless of absolute abundances or frequency of observation. Finally, we selected a limited set of the resulting principal components based on the variance explained by each component and the plankton species groups that were closely correlated with each component. For each retained component, we averaged the PCA score for each year across strata and plotted this mean time series for the PCA.

To examine if there were spatially distinct trajectories for *C. finmarchicus* in different areas of the EcoMon sampling domain, we log-transformed and averaged copepod densities within strata and years, then calculated z-scores within each stratum across years, and conducted another cluster analysis on the standardized data. This analysis did not support splitting the Gulf into sub-areas with distinct dynamics, so we calculated a stratified-mean survey index for the region as a whole. This survey index was then log-transformed and fitted to a local-level model.

Labrador Slope Water Index: Water enters the Gulf of Maine primarily through the northeast channel and surface waters south of Nova Scotia (Fig. 1; Runge et al. 2015). As part of the State of the Ecosystem Report (https://noaa-edab.github.io/tech-doc/), the NOAA-NEFSC maintains and updates a time series on the composition of water entering through the Northeast Channel, based on CTD data collected from a defined region encompassing the channel (Fig. 1) and a three-point mixing algorithm developed by Mountain (2012). Here we used data between 1988 and 2018 publicly available for download through the R ‘ecodata’ library. Of the three potential water types observed here, most water is either Labrador Slope Water (LSW) or Warm Slope Water (WSW), with a third small fraction being Scotian Shelf Water. LSW is essentially derived from the cold, low salinity, and nutrient rich Labrador Current flowing from the north, whereas the WSW is warm, high salinity, nutrient poor Gulf Stream water flowing from the south. Thus, the LSW index is essentially an indicator for the temperature, salinity, and nutrient composition of water entering the Gulf of Maine, as well as the zooplankton community associated with these waters. We extracted the time series of the proportion of LSW entering the Gulf and fit a local-level model.

Correlation Analysis: We first performed Pearson's correlations of *C. finmarchicus* from both the Gulf-wide EcoMon and Bay of Fundy to the raw lobster settlement time series for 14 individual ALSI study areas, including lagging lobster settlement behind plankton dynamics by one year.

We then used the aggregated Gulf-wide, northeast and southwest lobster settlement indices described above, to perform Pearson's correlations for all combinations of the biological and environmental indices to include raw and smoothed *C. finmarchicus* indices from coastal New Hampshire, Bay of Fundy, the Gulf-wide EcoMon domain, as well as Labrador Slope Water index area (Fig. 1).

Objective 2: Changes in zooplankton and lobster larval phenology

Study Area: Changes in phenology were assessed for American lobster and *C. finmarchicus* using the following long-term monitoring programs: (1) Commercial lobster sea sampling; (2) lobster larval neuston tows: and (3) oblique macrozooplankton tows. Sampling for all three of these monitoring programs were conducted off the coast of New Hampshire (Fig. 1, inset).

Data Sources:

Commercial Sea Sampling: New Hampshire Fish and Game Department conducted monthly sampling of the commercial lobster catch from NOAA Statistical Area (SA) 513 from May through November at three areas along the New Hampshire coastline from 2002 through 2017 (Fig. 1). Sampling was conducted during day trips on commercial lobster boats fishing in NH waters. During each trip, lobsters were sampled from a majority of trawls hauled. The following biological data were collected for each lobster: sex, presence and developmental stage of eggs, presence of v-notch, cull condition, molt stage, shell disease, and carapace length (mid-dorsal carapace length to the nearest millimeter (mm). A full description of the egg staging technique used in this study can be found online (https://www.youtube.com/watch?v=cJogiaAofCg)

Zooplankton and larval lobster sampling: Normandeau has conducted zooplankton and larval lobster monitoring off the New Hampshire coast since 1978 as part of ongoing environmental impact studies. Methods for the zooplankton surveys are described above under Objective 1. To sample lobster larvae, a neuston net (1000 micron) was deployed with depressor and flow meter to sample 0.5 m of the surface. Thirty-minute tows were made during the day, sampling an average area of ~3730 m^2 (a volume of 1865 m^3). Tows were conducted weekly from May through October. In our analysis, we used mean values for stage I and postlarval (stage IV) indices from 1988 through 2018 due to consistency in sampling during that time period. We did not analyze trends in stage II and stage III larvae as these stages are primarily found at greater depths than can effectively be sampled by neuston net (Harding et al. 1987).

Statistical Analysis: We used Pearson's correlation coefficient (r) to assess linear relationships between variables. In cases where variables violated the normality assumption (as assessed via Shapiro Wilk test), Spearman's rank test was used to assess correlations. Trends in time series were assessed using Mann-Kendall, and deemed significant at the 0.05 level. Because if differences in sampling frequency, changes in phenology of lobster larvae were assessed on a weekly basis, whereas trends in *C. finmarchicus* were assess by two-week blocks, which are expressed as time periods (e.g., time period 1 = first two weeks of January). We defined the start of *C. finmarchicus* season as the time period where the 25th percentile of the cumulative annual index was reached, the end of the season as the 75th percentile and duration as 25th to the 75th percentile.

We also evaluated the degree of overlap between the larval lobster and *C. finmarchius* season. To do that we created a mismatch index modeled after Burthe et al. (2012), assessing the difference in time between peak stage I lobster larval abundance and the end of the *C. finmarchicus* season as defined above. Peak stage I abundance was used because we presumed that for larvae to advance through the stages, it would be critical for stage I larvae to have an ample supply of food.

RESULTS

Objective 1: Local and basin-scale correlations of zooplankton, lobster settlement and oceanographic indicators

Lobster dynamics: The smoothed index for YoY and 1-year old lobsters indicates a period of moderate settlement density between 1990-1995, a drop to a period of low densities from 1996-2000, followed by a sharp rise to high settlement levels from 2003-2011, followed by another drop to low levels from 2013-2020 (Fig. 2a). Splitting the study areas into northeastern and southwestern sectors reveals distinct trajectories for the two areas (Fig. 2b). The trend for the northern area is consistently lower in the first half of the study period, followed by a sharp rise in

2005 to match and exceed the southwestern study areas. The two sub-regions show remarkably cohesive dynamics for the second half of the period.

Zooplankton Assemblage Dynamics: Our more taxonomically inclusive evaluation of aggregate time trends among the EcoMon zooplankton assemblage indicated complex trends in the first three Principal Components (Fig. 3). PC1 accounted for 21% of the total variance and was primarily associated with five diverse taxonomic categories (*Oithona* spp., Siphonophora, Gastropoda, Protozoa, and Chaetognatha). This PC shows strong temporal trends, broken into three time periods, first increasing prior to 2000, dropping to a low level through 2011, then jumping to a high level thereafter. PC2 accounted for 15% of the variance and was primarily associated with four copepod groups (*Temora longicornis*, *Acartia* spp., *Centropages hamatus*, *Pseudocalanus* spp., and bryozoan larvae). This PC exhibited a gradual decline throughout the time series with a potential regime shift around 2000. PC3 accounted for 8% of the variance and comprised four copepod taxa: *C. finmarchicus, Pseudocalanus* spp., *Metridia lucens and Nannocalanus minor,* the first three of which are positively correlated with the component, while *N. minor* was negatively correlated with the component. It is noteworthy that of the four species *N. minor* is associated with warmer water and has the most southern distribution (WORMS 2021). PC3 exhibits three stable regimes, starting above the time series mean prior to 2002, then hovering close to the mean through 2010, before dropping in 2011, ending at time-series lows in 2016 and 2017.

Calanus finmarchicus Dynamics: The *C. finmarchicus* index from coastal New Hampshire shows a high-density regime from 2001-2009 with low densities before and after this period

(Fig. 4a). Similarly, the *C. finmarchicus* index from the EcoMon survey was low prior to 2001, increases through 2005, followed by a decline through the remainder of the time series, ending at or near record low values (Fig. 4b). The *C. finmarchicus* time series for the coastal Fundy region did not begin until 1999, but it is similarly low in its initial year and increases dramatically in the early 2000s to a time series peak in 2006 after which it declines monotonically through 2018 (Fig. 4c). The volume of Labrador Slope Water advected into the Gulf of Maine has been declining in recent years: while there has been much interannual variability, the smoothed index was generally high, approaching 30%, until the late 2000s followed by a decline to less than 10% in the most recent years (Fig. 4d).

Correlations: The Gulf-wide, smoothed EcoMon *C. finmarchicus* index from 1989 to 2018 tended to correlate more strongly with lobster settlement trends in the southwestern Gulf of Maine. EcoMon's copepod index significantly correlated with the raw lobster settlement trends in six of the 14 study areas when unlagged and eight of the 14 when lagged by one year, with all of them restricted to the southwestern end of the Gulf, southwest of Penobscot Bay when unlagged, and all but one when lagged by one year (Fig. 5). By contrast, the Bay of Fundy smoothed *C. finmarchicus* index tended to correlate more strongly with lobster settlement dynamics in the northeastern Gulf. This copepod index correlated with the raw lobster settlement trends in five of the 14 study areas when unlagged, and seven when lagged by one year (Fig. 6). Three of the five significant unlagged correlations, and five of the seven lagged correlations, were with lobster study areas in the northeastern Gulf, from Penobscot Bay to Beaver Harbour. In short, this analysis suggests lobster settlement trends in the southwestern Gulf of Maine to be more strongly linked to basin-scale *C. finmarchicus* dynamics, while those in the northeastern sector may be more strongly tied to coastal dynamics in the Bay of Fundy and eastern Maine.

Figure 7 and Table 1 provide a comparison of the correlation statistics for the aggregated and smoothed state-space lobster settlement time series (Fig. 3; north, south and combined study areas) with the smoothed New Hampshire, Bay of Fundy and EcoMon *C. finmarchicus* time series (Fig. 4a-c), as well as the smoothed Labrador Slope Water index (Fig. 4d). Correlations involving smoothed time series performed better than raw time series in virtually all cases. For brevity and clarity only correlations for the smoothed time series are given in Table 1. Sixteen of the of 18 correlations presented in Table 1 were significant at $p<0.05$, and no correlations were negative. The coastal New Hampshire and Gulf-wide EcoMon *C. finmarchicus* time series, and the Labrador Slope water most strongly correlated with the ALSI lobster combined and southern time series, whereas *C. finmarchicus* trends in the Bay of Fundy correlated more strongly with lobster trends in the north. Moreover, we observed that *C. finmarchicus* dynamics in coastal New Hampshire are more highly synchronized with the Gulf-wide (EcoMon) *C. finmarchicus* dynamics than those in the Bay of Fundy. Similarly, variability in the Labrador Slope Water was strongly tied to *C. finmarchicus* trends in both New Hampshire and EcoMon, but not to the Bay of Fundy. In short, as with our finer spatial scale correlations depicted in Fig. 5 and 6, lobster settlement trends in the southwest Gulf of Maine appear to be generally correlated with basin-wide *C. finmarchicus* dynamics and the Labrador Slope Water index, whereas lobster settlement in the north tends to link more strongly to *C. finmarchicus* variability in the Fundy region, which also does not appear to be as strongly tied to changes in the Labrador Slope Water.

Objective 2: Changes in zooplankton and lobster larval phenology

The proportion of lobster eggs hatching in June has tripled on average since these data have been collected, beginning in 2002 (Fig. 8, Mann Kendall: P=0.021). This trend correlates well with mean spring temperatures (April through June) over the same period (Pearson's: r=0.7013, P=0.0025, time series not shown). Accordingly, the first appearance of stage I larvae advanced on average two weeks earlier over the time series (Fig. 9a, Mann Kendall: P=0.070), which also correlates well with spring bottom water temperature (Spearman's -0.5567, P=0.0011, time series not shown). Last appearance of stage I ranged from week 26 to 40 and trended significantly upward (Fig. 9b, Mann Kendall: P=0.037). First appearance, last appearance, and season duration of postlarvae, has varied without trend, however, over the time series (Mann Kendall >0.05). But because of the earlier appearance of stage I larvae, total season duration to last appearance of postlarvae has increased over the time series (Fig. 9c, Mann Kendall: P=0.009), resulting in a significant inverse correlation between first appearance of stage I and total larval season duration (Pearson's r=-0.5004, P=0.0067).

Although the onset of the *C. finmarchicus* season has varied without trend over the 30 year time series (Mann Kendall P>0.05), the season end has tended to come earlier in recent years, resulting in a generally shorter season (Figs. 10a & b; Mann Kendall: P<0.05). We found the strongest correlation between monthly counts of *C. finmarchicus* and annual abundance of postlarval lobster to occur in July and August (Table 2), suggesting these months to be especially important to postlarval success. The *C. finmarchicus* season duration has not only become shorter, but since 2012 it has ended before July 1 in six of the seven years (Fig. 10). This has only occurred five other times in the 30-year time series.

Differences in the timing of peak stage I lobster larvae and the *C. finmarchicus* season were integrated into a mismatch index (Fig.11), which depicts a significant downward trend (i.e., reduced overlap) over the time series (Mann Kendall P=0.039). That is, between 2000-2009 stage I larvae peaked well before the end the *C. finmarchicus* season, but in six of the nine years since 2010 stage I larvae peaked after the *C. finmarchicus* peak.

DISCUSSION

Lobster - zooplankton linkages in the Gulf of Maine

Our retrospective three-decade time series analysis reinforces our understanding of correlative linkages between American lobster recruitment and changes in the Gulf of Maine's pelagic food web, as might have resulted from warming temperatures and changing oceanography over the past few decades since relevant long-term environmental monitoring time series have become available. Specifically, by virtue of NOAA's EcoMon database, we have extended the correlations reported for the New Hampshire coast (Carloni et al. 2018) to include a larger geographic scope of biological and oceanographic indicators.

The significant correlation between the local scale New Hampshire data set and the Gulf-wide scale EcoMon time series for *C. finmarchicus* indicate that time trends measured in coastal New Hampshire strongly reflect basin-scale dynamics for this species. This is important because, to date, evidence of larger scale coherence was only suggested by correlations between local *C. finmarchicus* variability measured in coastal New Hampshire and lobster settlement time series along the southwestern Gulf coast (Carloni et al. 2018). Similarly, in the present study we found that EcoMon's Gulf-wide *C. finmarchicus* index most strongly correlated with lobster settlement trends at study areas in the southwestern Gulf of Maine, but only weakly with those in the northeast. Conversely, we have found lobster settlement dynamics measured in the northeastern sector of the Gulf to more strongly correlate with *C. finmarchicus* variability measured there, by virtue of the new biological monitoring data from the Fundy region (Casault et al. 2020). The biological implications of contrasting physical oceanographic conditions and dynamics in the northeast and southwest Gulf have long been recognized, especially as regards the lobster fishery (Huntsman 1923, Steneck and Wilson 2001, Pershing et al. 2012, Goode et al. 2019). From the present analysis it is clear that the large surge in juvenile lobster observed in the northeast Gulf lagged a few years behind the smaller magnitude surge in the southwest, but over the last decade the two regions have been declining precipitously in tandem. One interpretation for the lag in the northeast lobster settlement surge, advanced by Goode et al. (2019), is that until the northeastern Gulf warmed sufficiently, larval settlement was suppressed by the relatively cool temperatures in that region. They argued that the relatively recent boom in lobster settlement in the northeastern Gulf in the mid-2000s was triggered by warming above a critical thermal threshold for larval developmental at approximately 12°C (MacKenzie et al. 1988, Annis 2005).

We caution that the spatial coverage of the ALSI settlement time series was relatively sparse prior to 2000 and the state-space model may not fully capture regional dynamics in the earlier years. Nonetheless, the state-space time series extrapolated back to the 1990s is grounded in an understanding of the scale of spatial coherence and justifies dividing the Gulf into northeastern and southwestern recruitment cells (e.g., Pershing et al. 2012, Goode et al. 2019), even if they may have become more convergent in recent years. In addition, the trends in early benthic phase lobster abundance are also robust to the selection of size definitions used for age 0+ and 1+ year lobsters. The size ranges we selected are based on previous analyses shared with Maine DMR (e.g., Harrington et al. 2017, Morin and Wahle 2019) and remain the subject of continuing refinement and interpretation.

Especially noteworthy is the finding that *C. finmarchicus* is not unique among the zooplankton in its downward trajectory over the past decade. The EcoMon database reveals a significant decline over the past decade of a taxonomically diverse segment of the zooplankton assemblage including protozoans, siphonphores, chaetognaths and copepods, as well as *C. finmarchicus*. Concurrent with these declines are dramatic oceanographic changes in the Gulf of Maine that have diminished primary and secondary productivity over the past decade, and may further be driven by environmental changes occurring in the Arctic that transfer to the Gulf of Maine along the Scotian Shelf (Friedland et al. 2020, Gonçalez-Neto et al. 2021, Seidov et al. 2021). These reports, along with the declines in the Labrador Slope Water index trend reported here, suggest a weakening influence of the cold, nutrient rich waters of the Labrador Current and a concurrent strengthening effect of warm, nutrient poor waters from the Gulf Stream on the Gulf of Maine (Townsend et al. 2015, Pershing et al. 2021). These results reinforce our previous work suggesting that the drivers of lobster recruitment may be linked to still poorly understood trophic interactions of lobster larvae in the pelagic food web.

Changing Phenology

By virtue of weekly sampling on the New Hampshire coast during the larval lobster season over 30 years, we have gained a deeper understanding of phenological changes in both larval lobster and *C. finmarchicus* at this single well-studied location at the center of coastal Gulf of Maine. To our knowledge this study represents the first attempt to evaluate changes in the relative phenology of lobster hatch and larval occurrence with *C. finmarchicus*. We found correlative links between warming ocean temperature and timing of egg hatch, as well as first and last appearance of stage I larvae and postlarval lobster that indicate that the timing of critical developmental events is shifting. From these data we quantified the shift in temporal overlap of larval lobster and *C. finmarchicus* over the years using a match/mismatch index (Cushing 1990). This study provides evidence that temporal overlap has declined in recent years: with increasing frequency since 2010, the *C. finmarchicus* season has been ending before the peak abundance of stage I lobster larvae. We speculate that in addition to declines in abundance of *C. finmarchicus* reported above, this reduced overlap between planktonic larval lobsters and their prey may have exacerbated recent declines in lobster recruitment.

From our combined results we infer that it is not only the declines in abundance of *C. finmarchicus*, but also the widening temporal mismatch that may adversely affect recruitment success of lobster. Similarly, in Western Australia, Lestang et al. (2015), found consecutive low years of western rock lobster, *Panulirus cygnus*, recruitment were more strongly linked to timing of spawning relative to favorable environmental conditions for larval development than to the volume of egg production. Although the mechanisms may differ, our analysis also suggests the thermally controlled timing of the egg hatch is likely an important factor determining the co-occurrence of larvae with their planktonic foods. The temporal overlap of American lobster larvae with *C. finmarchicus* remains poorly understood on a wider geographic scale because of the lack of larval lobster sampling. Recently initiated larval sampling by Maine Department of Marine Resources and the Atlantic Offshore Lobstermen's Association will dramatically increase our understanding of larval lobster dynamics in the future.

Conclusions, Implications and Future Research:

The Gulf of Maine is warming at an alarming rate, and although we are beginning to understand the effects of these changes on fisheries in this region (Pershing et al. 2015, 2021, Richards 2016, Gonçalez-Neto et al. 2021), our understanding of the mechanisms at work behind these changes remain largely correlative. The disconnect identified by Carloni et al. (2018) between lobster spawning stock biomass and postlarval abundance, despite the strong quantitative link between spawners and stage I larvae, narrowed the likely timing of decoupling of the spawner-recruit relationship to the early larval stages. With this report we provide supporting evidence that declines in *C. finmarchicus*, and perhaps other members of the zooplankton assemblage may be linked to that decoupling. In the analysis of the coastal New Hampshire data, Carloni et al. (2018) found little evidence of a correlation between postlarval lobster variability and potential plankton predators, such as gelatinous zooplankton, chaetognaths or ichthyoplankton. The rising abundance of some of these planktonic carnivores evident in the EcoMon time series suggest we cannot entirely rule out the potential role of top-down mechanisms as a driver of larval lobster survival. The gelatinous zooplankton warrant more attention as they are especially difficult to sample, and few long-term time series exist. Increases in some planktonic species, on the other hand, may reflect northwardly shifting ranges of warmer water species, such as the copepod, *Nannocalanus minor,* for example.

The significant correlation between declines in both the Labrador Slope Water and *C. finmarchicus* begin to link changes in potential oceanographic drivers to subsequent changes in the zooplankton assemblage, and specifically the abundance and phenology of *C. finmarchicus* that may have important implications for lobster larval survival. While the evidence presented here remains correlative, it poses testable hypotheses for continued analysis regarding the mechanisms driving trends in lobster settlement, subsequent fishery recruitment and landings over the past decade.

Recent low levels of YoY lobster recruitment in the Gulf of Maine have been a cause for concern to fishery managers, and although adult abundance is still at or near time series highs, signs of a decline in larger size classes have emerged in recent years. Additionally, the Coastwide Ventless Trap Survey and the Maine-New Hampshire groundfish trawl survey have begun to show declines in sublegal lobster in coastal Maine (NOAA Statistical Areas 513 and 514), with significant correlations to YoY indices (ASMFC 2020). Further, commercial landings have recently begun to decline after reaching historic highs in 2016, as projected by Oppenheim et al. (2019). This rate of decline in recruitment may be tempered to some degree by increased suitable thermal habitat in deep water and in the eastern Gulf (Goode et al. 2019), however, there is agreement among several surveys of initial signs of declining biomass. In response to these concerns, Atlantic States Marine Fisheries Commission is developing an addendum to provide additional resiliency to the Gulf of Maine-Georges Bank lobster stock. The research presented here adds further support to the hypothesis that environmental changes impacting the pelagic food web and larval food abundance may be a key factor affecting lobster recruitment. Le Bris et al. (2018) noted that conservation measures implemented in the Gulf of Maine to protect spawning stock biomass set the stage for the fishery to capitalize on favorable conditions for recruitment during the boom years, and may help stave off fishery collapse in the event of a downturn.

There is significant need for further research to elucidate trophic linkages and test hypotheses advanced in this study. Maine DMR's Lobster Research Collaborative and the National Sea Grant's Lobster Research Initiative are contributing resources that will provide new insights into the physical and biological drivers of recruitment to this iconic fishery. Field sampling and experiments will further improve our understanding of the mechanisms behind observed correlations between lobster larval dynamics and the pelagic food web that we suspect may play a key role in lobster benthic recruitment.

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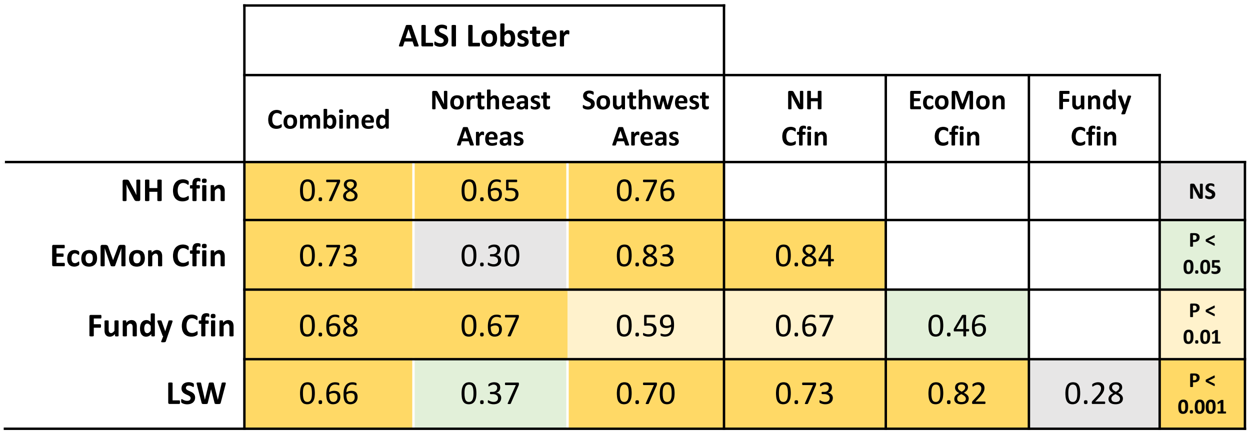
Table 1. Pearson coefficients for correlations among constructed time series. Colors indicate statistical significance. See Table S-1 for full comparison of correlations for raw and modeled indices.



	ALSI Lobster						
	Combined	Northeast Areas	Southwest Areas	NH Cfin	EcoMon Cfin	Fundy Cfin	
NH Cfin	0.78	0.65	0.76				NS
EcoMon Cfin	0.73	0.30	0.83	0.84			P < 0.05
Fundy Cfin	0.68	0.67	0.59	0.67	0.46		P < 0.01
LSW	0.66	0.37	0.70	0.73	0.82	0.28	P < 0.001

Table 2. Correlation statistics by month between *Calanus finmarchicus* and postlarval lobster abundance in New Hampshire waters.

Month	Spearman's r	p
May	0.25	0.1887
June	-0.15	0.4311
July	**0.64**	**0.0002**
August	**0.58**	**0.0007**
September	0.25	0.1751
October	0.25	0.1806

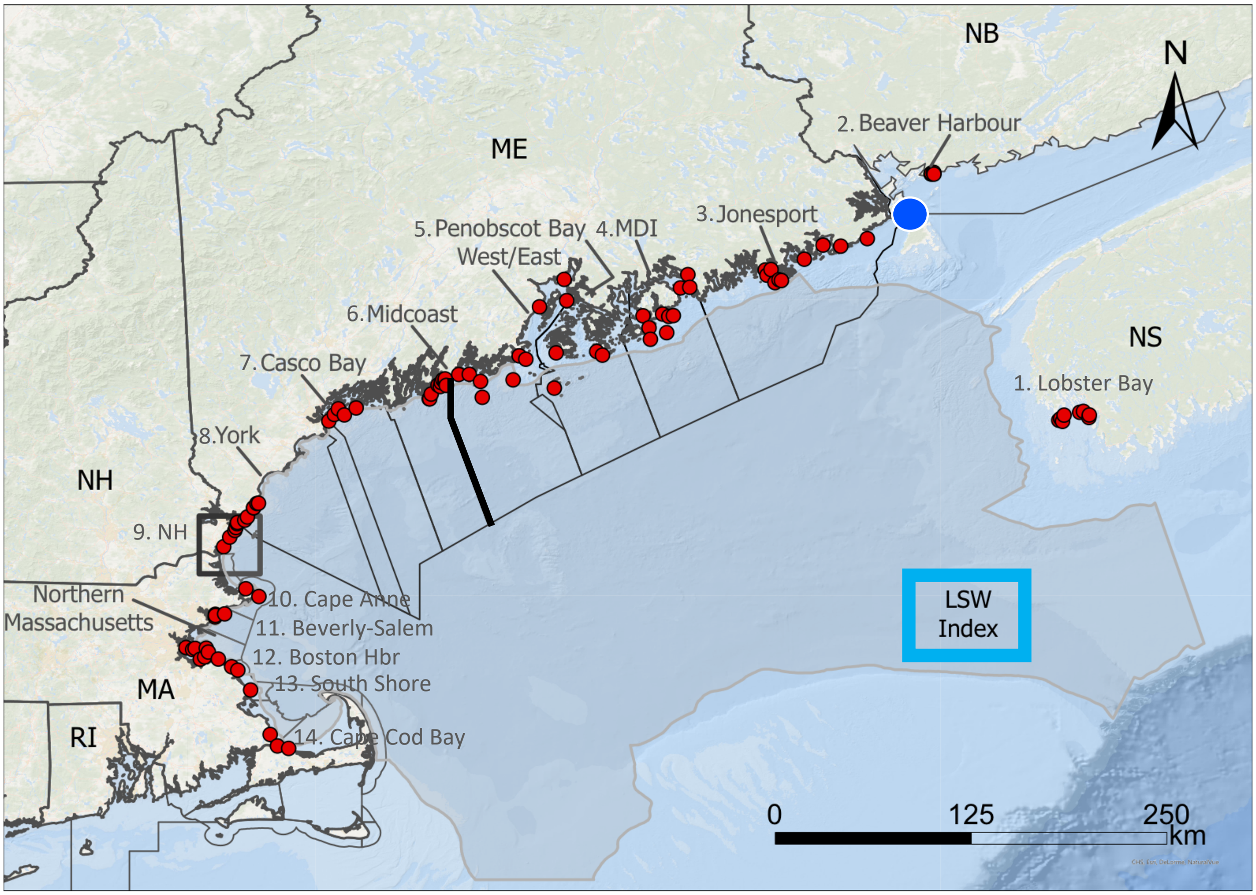


Figure 1. Gulf of Maine region depicting ALSI study sites (red dots) within the 14 respective study areas (black boundaries; bold black line denotes boundary between northeast and southwest study areas); coastal New Hampshire larval lobster and zooplankton sampling sites (black box; see Fig. S-1 for detail); DFO coastal Bay of Fundy zooplankton sampling station (blue dot); NEFSC basin-wide EcoMon sampling domain (darkened); and study area of the Northeast Channel used to calculate the Labrador Slope Water (LSW) index (blue box).

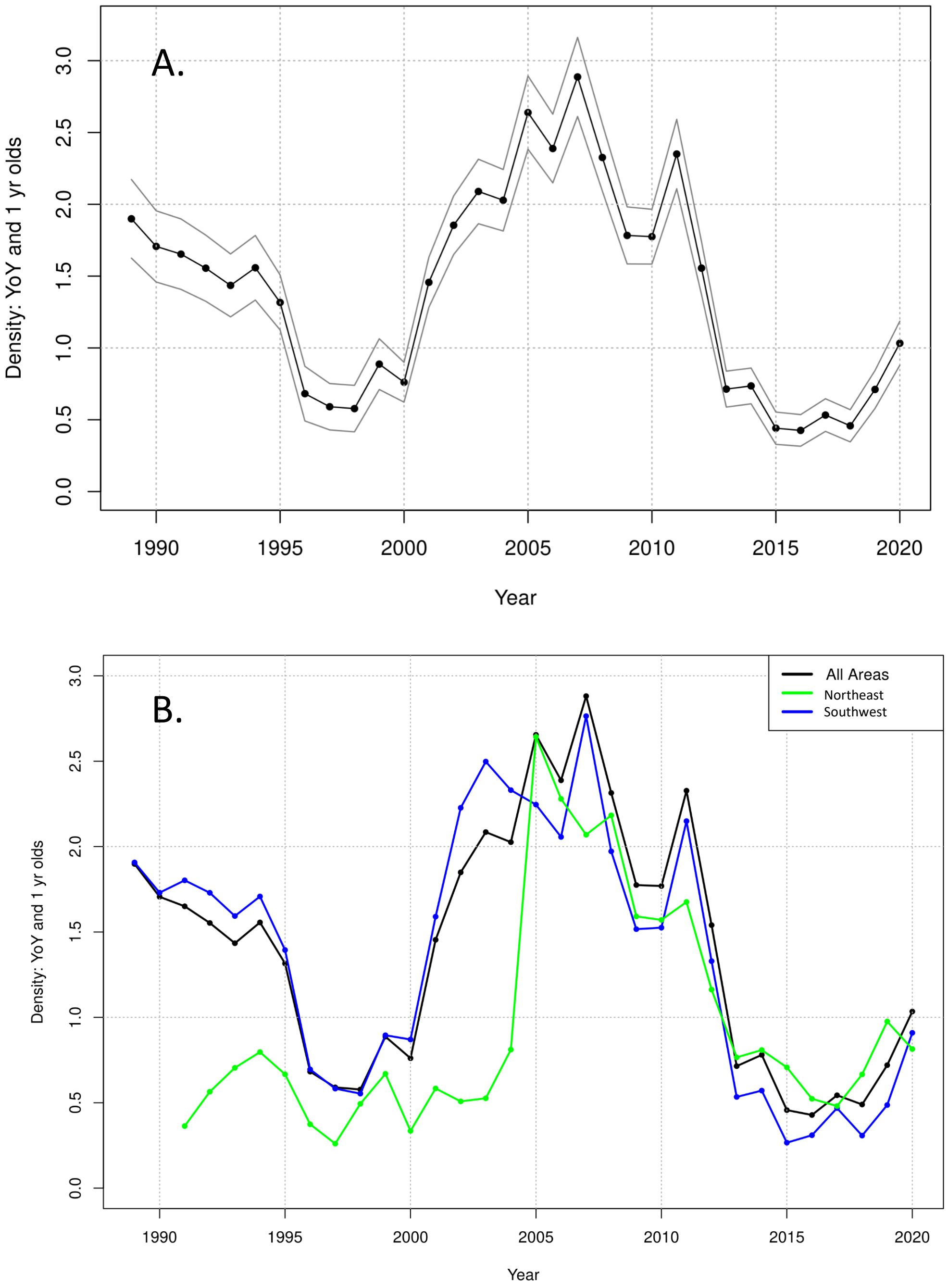


Figure 2. A. Modeled ALSI settlement trends (+/- 2SE) for all combined study areas in the Gulf of Maine. B. Modeled ALSI settlement trends for all combined study areas, as in A, and separate trends for southwestern and northeastern study areas.

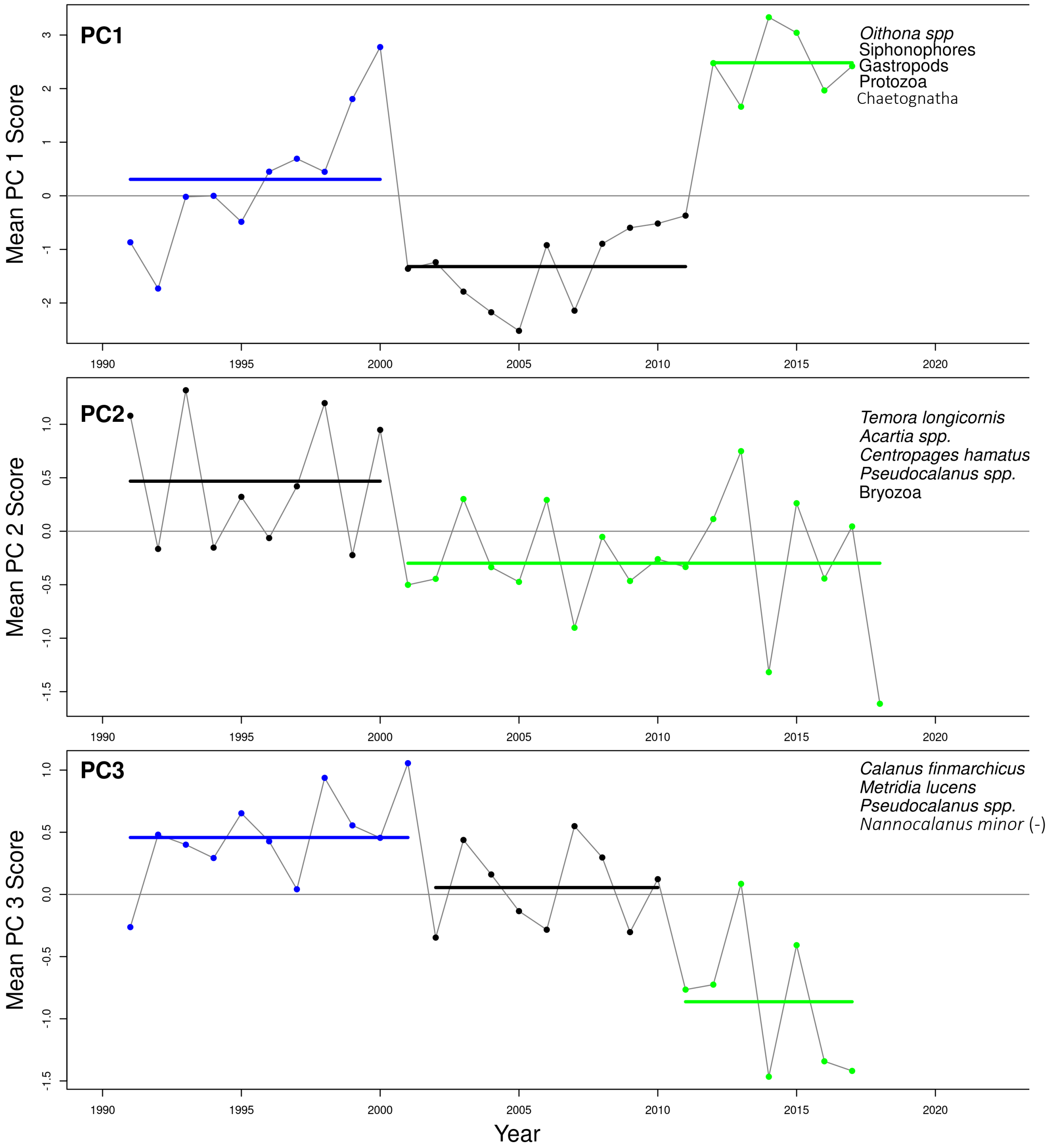


Figure 3. Principal component (PC) analysis depicting three PCs of the zooplankton assemblage with differing dynamics. Horizontal bars indicate mean for the corresponding time series. Note precipitous increase in PC1 and decline in PC3 after 2010. Species listed comprise those correlating most strongly, either directly or inversely with the PC at a threshold value above 0.25 or below -0.25. In all cases species meeting these criteria correlated positively with their PC, with the exception of *Nannocalanus minor* in PC3.

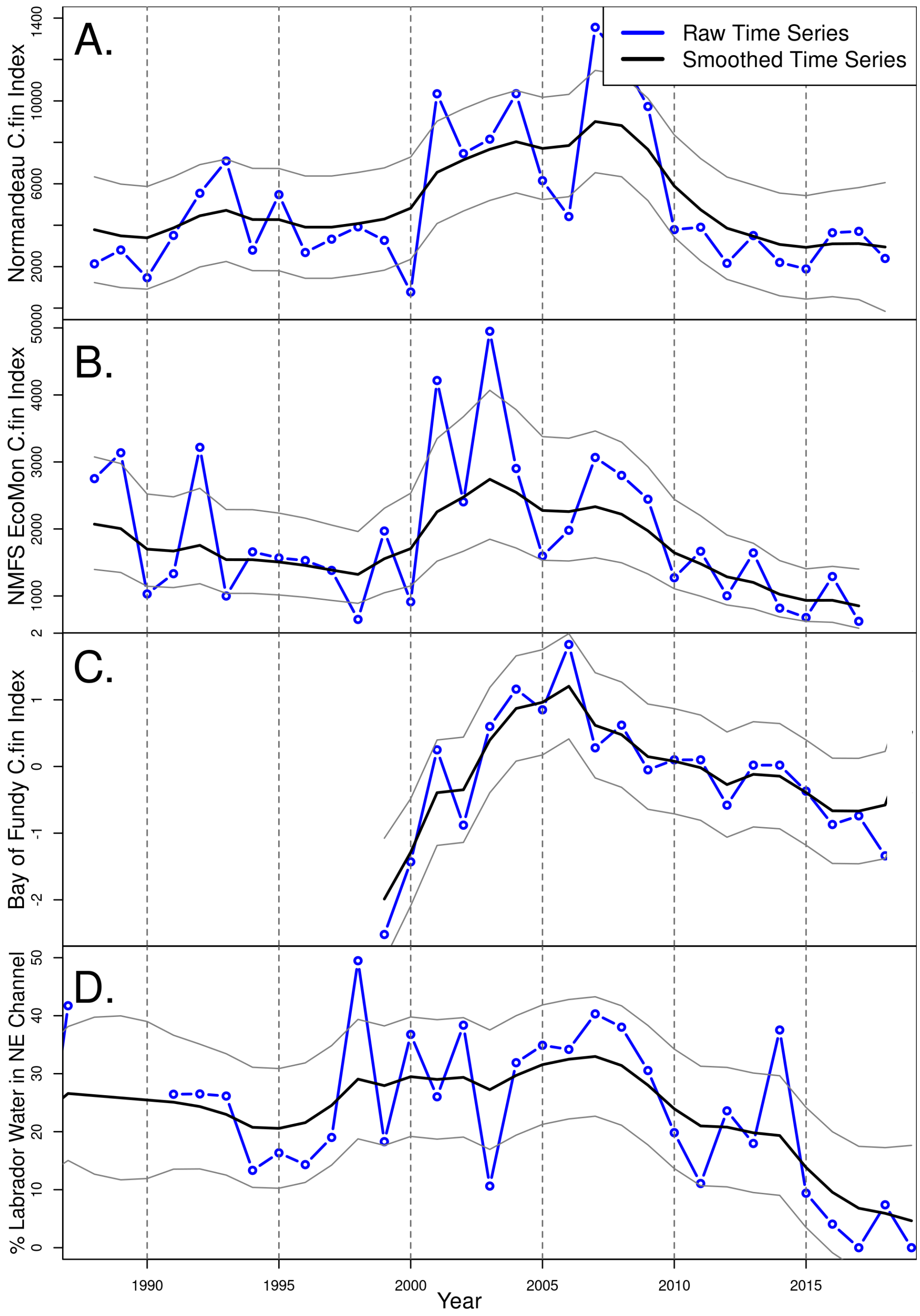
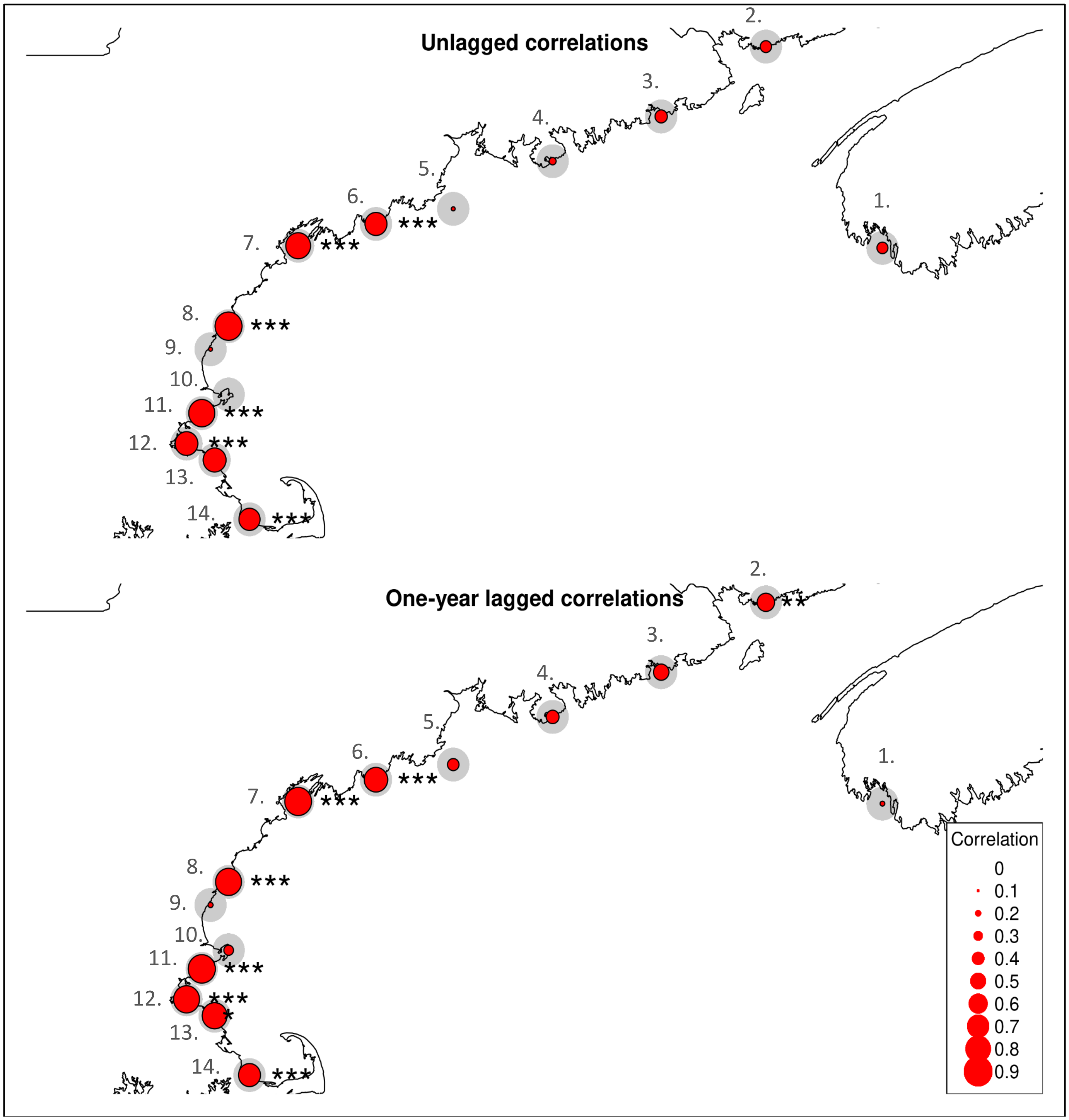


Figure 4. *Calanus finmarchicus* indices for (A) coastal New Hampshire, (B) Gulf-wide EcoMon domain, and (C) Bay of Fundy. (D) Labrador Slope Water index measured at the Northeast Channel of the Gulf of Maine. Raw annual data (blue); smoothed (black) (+/- 2SE). See Fig. 1 for sampling locations.



Unlagged correlations

One-year lagged correlations

Figure 5. Mapped correlations between raw settlement time series (YoY + 1Year Olds) for individual study areas and the smoothed EcoMon *C. finmarchicus* index for the period 1988 to 2018. Significant correlations are noted as * - $p<0.05$, ** - $p<0.01$, *** - $p<0.001$. Some higher correlations do not achieve the significance criteria due to shorter time series. Study area labels as in Fig. 1.

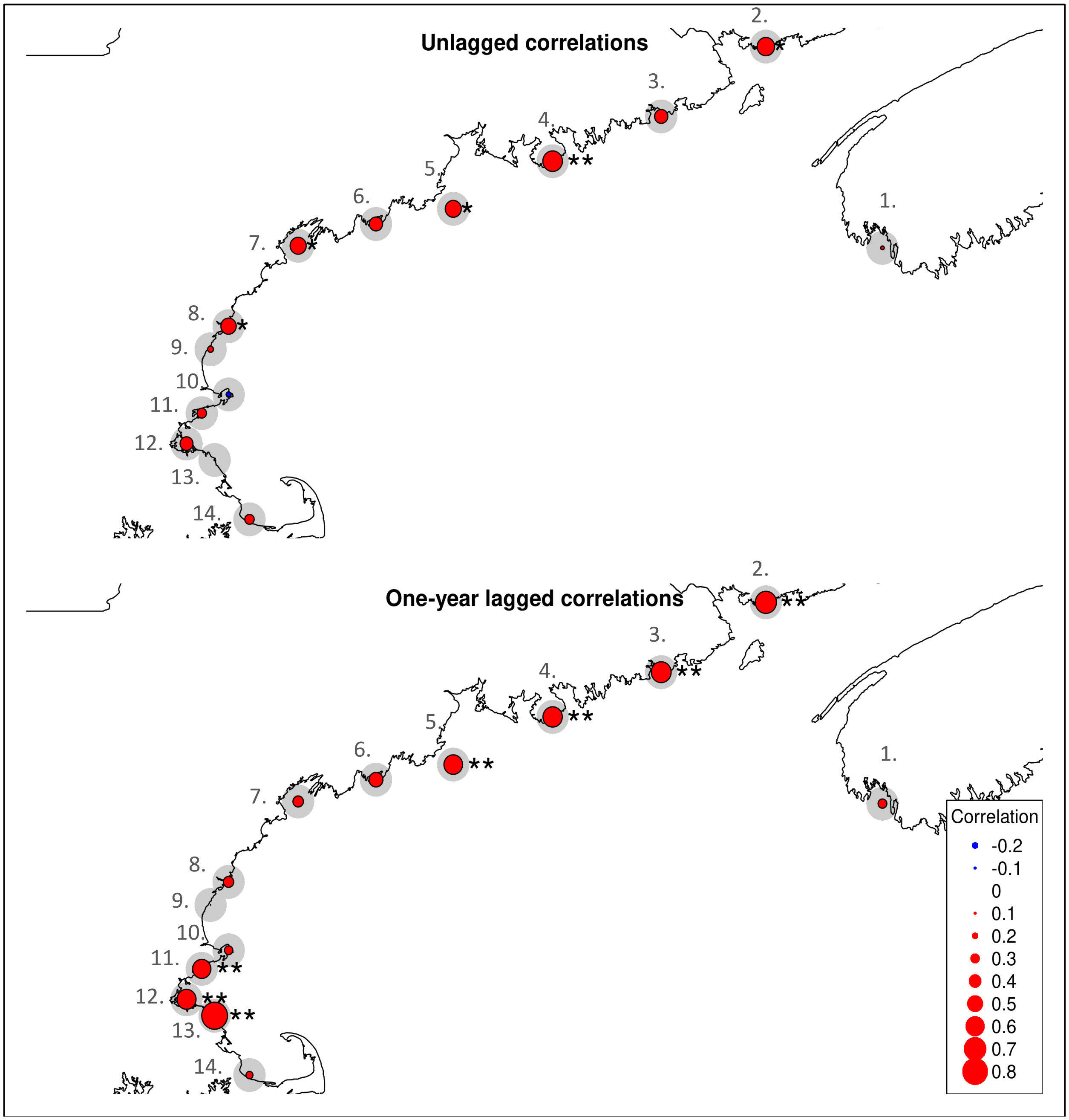


Figure 6. Mapped correlations between raw settlement time series (YoY + 1Year Olds) for individual study areas and the smoothed *Calanus finmarchicus* index for the period 1999 to 2019 from Casault et al. (2020). Significant correlations are noted as * - p<0.05, ** - p<0.01, *** - p<0.001. Some higher correlations do not achieve the significance criteria due to shorter time series. Study area labels as in Fig. 1.

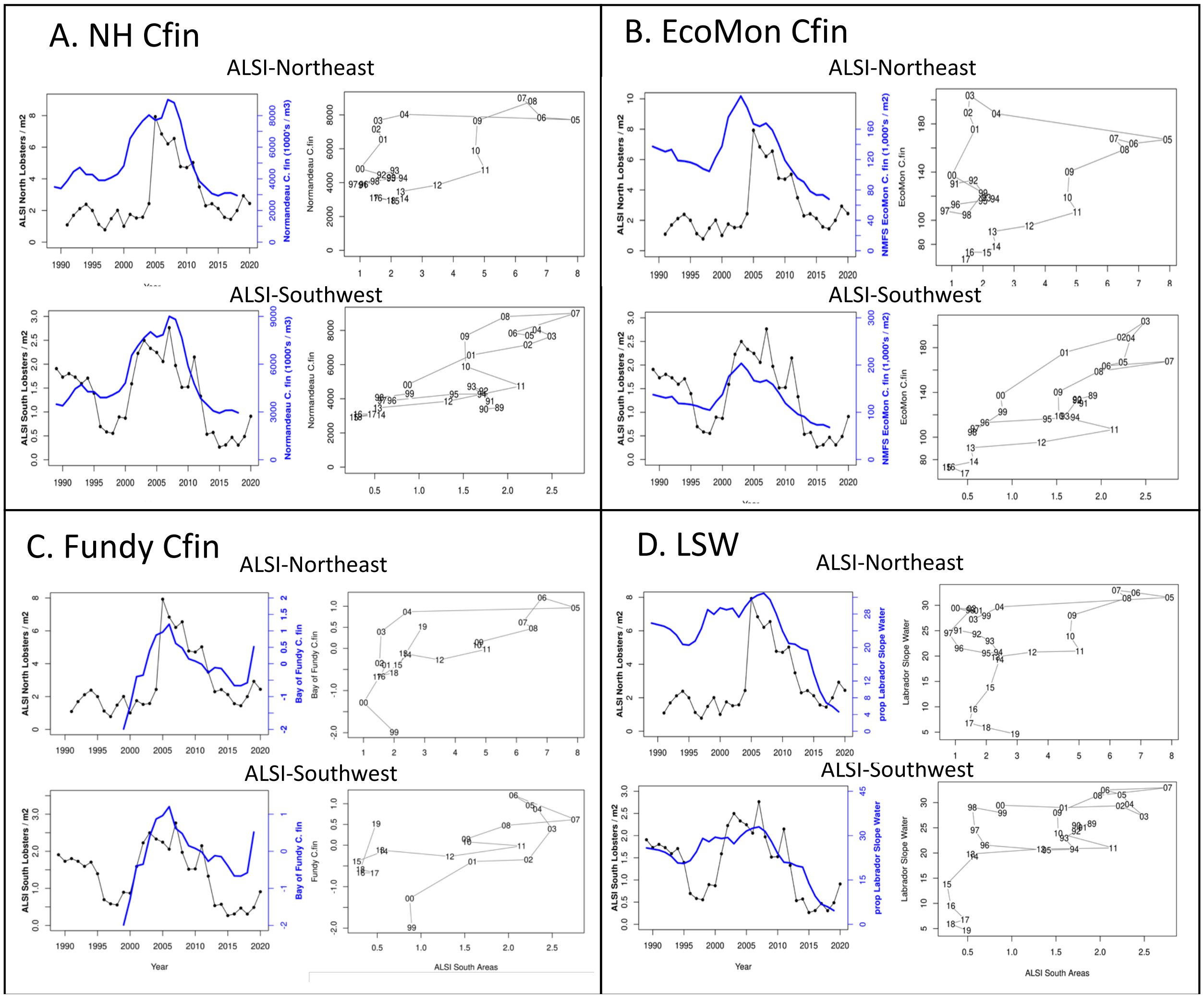


Figure 7. Time series (left) and scatterplots (right) of northeast and southwest Gulf of Maine lobster settlement indices with (A) New Hampshire *C. finmarchicus* index, (B) NEFSC EcoMon *C. finmarchicus* index, and (D) Labrador Slope Water index. Points on scatterplots denote sampling year; lines connect consecutive years. See Table 1 for correlation statistics.

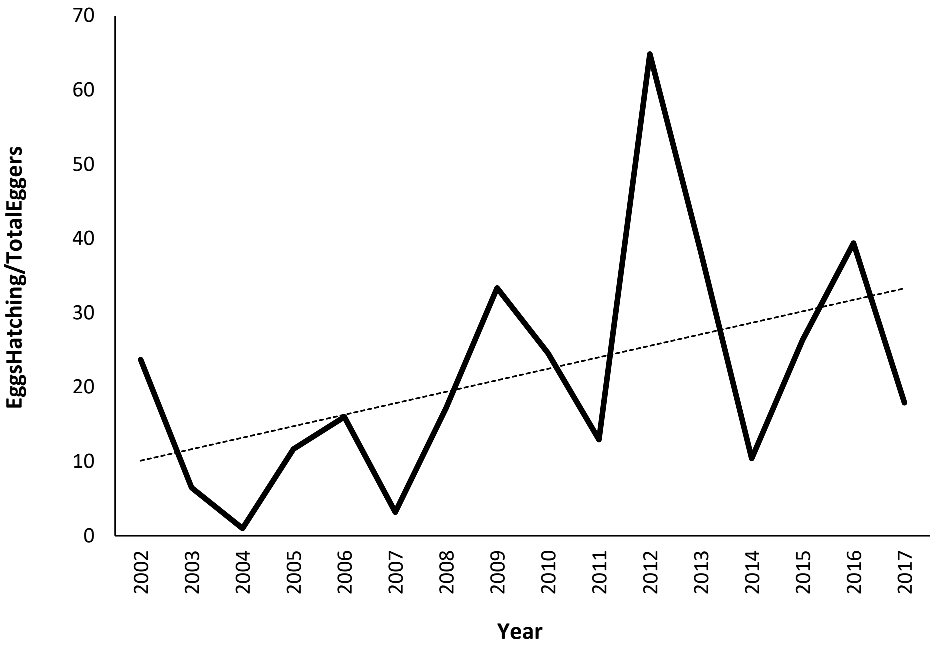


Figure 8. Proportion of egg bearing lobsters with eggs in the process of hatching in the month of June, from commercial lobster sea sampling in New Hampshire coastal waters from 2002 through 2017. See text for trend line statistics.

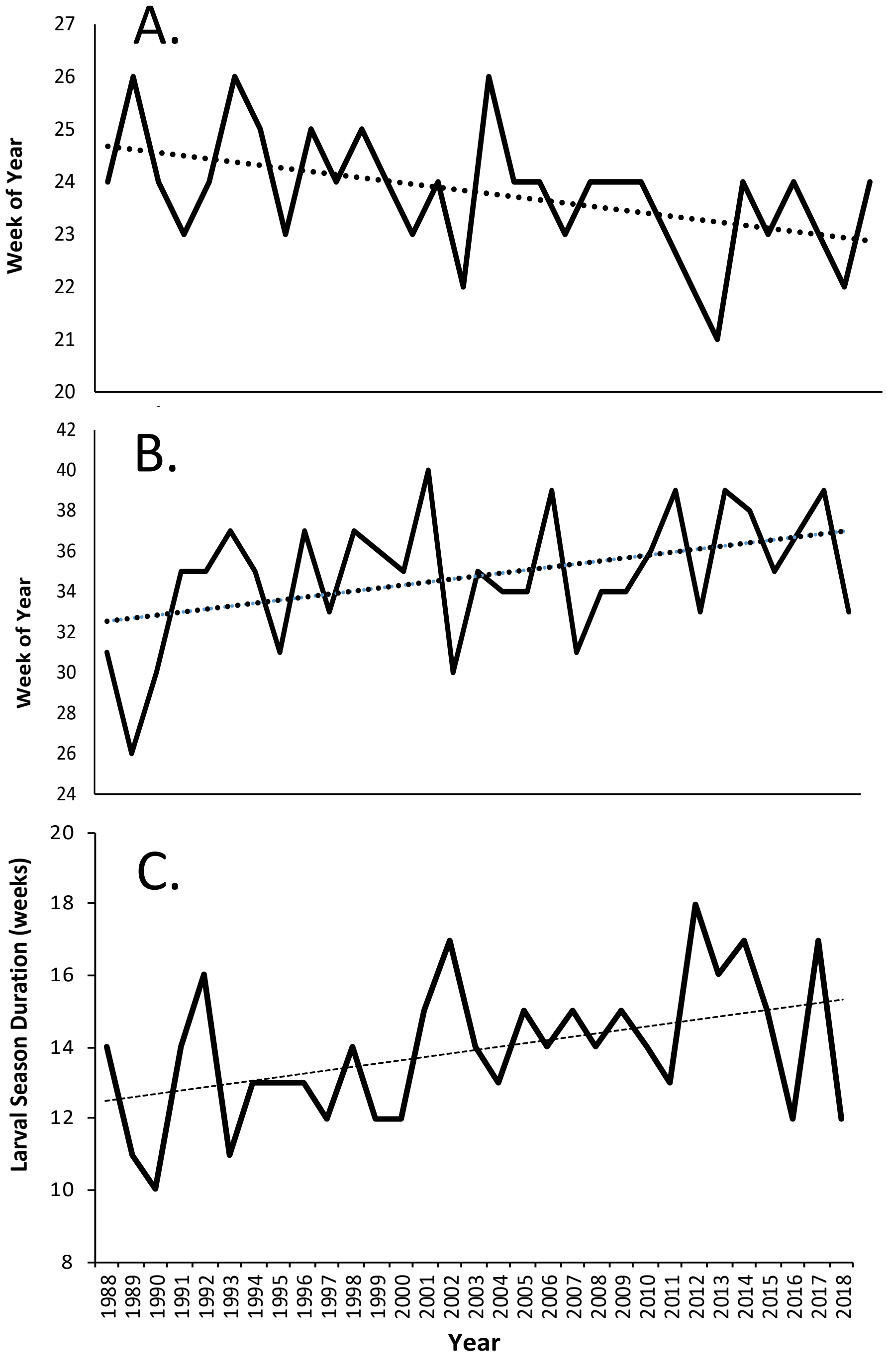


Figure 9. First appearance (A) and last appearance (B) of stage I lobster larvae, and total larval season duration from stage I through postlarva (C) from neuston net sampling along the New Hampshire coast, 1988 through 2018.

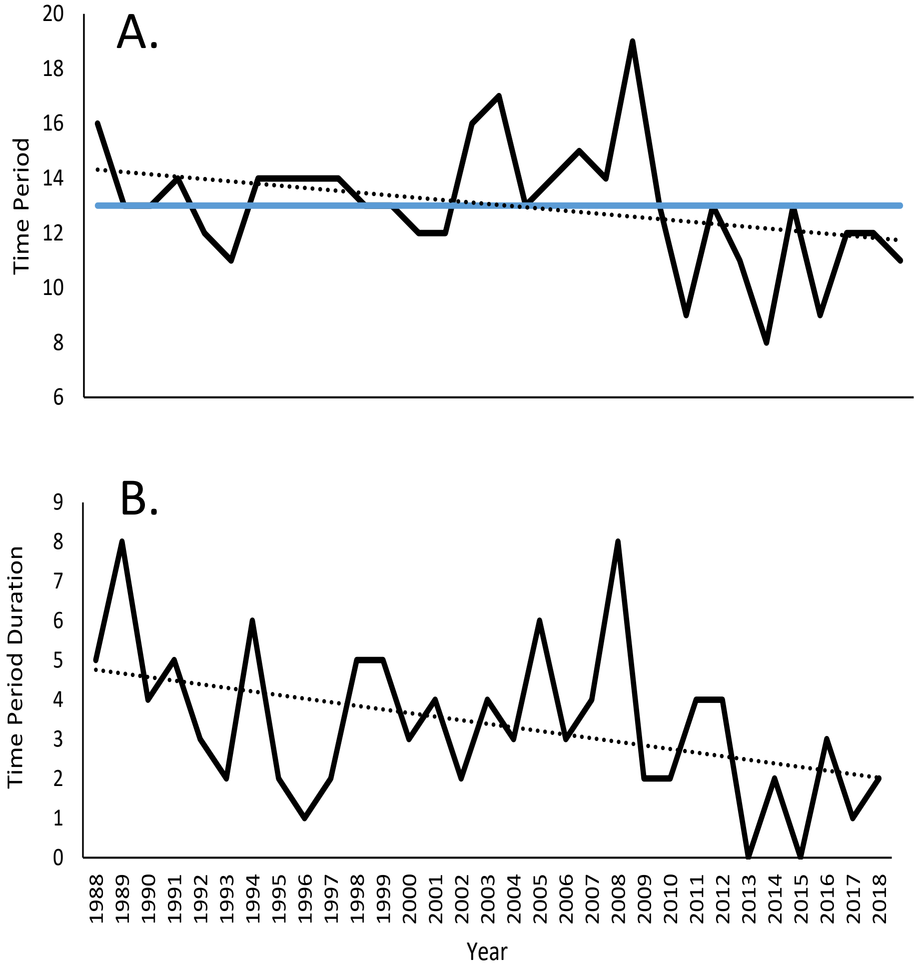


Figure 10. Shifts in *C. finmarchicus* phenology. (A) End of season, and (B) Season duration by year from 1988 through 2018. "Time periods" correspond to two-week blocks. Note, blue horizontal line in A denotes July 1 (time period 13); since 2009 the season has ended on or before that date.

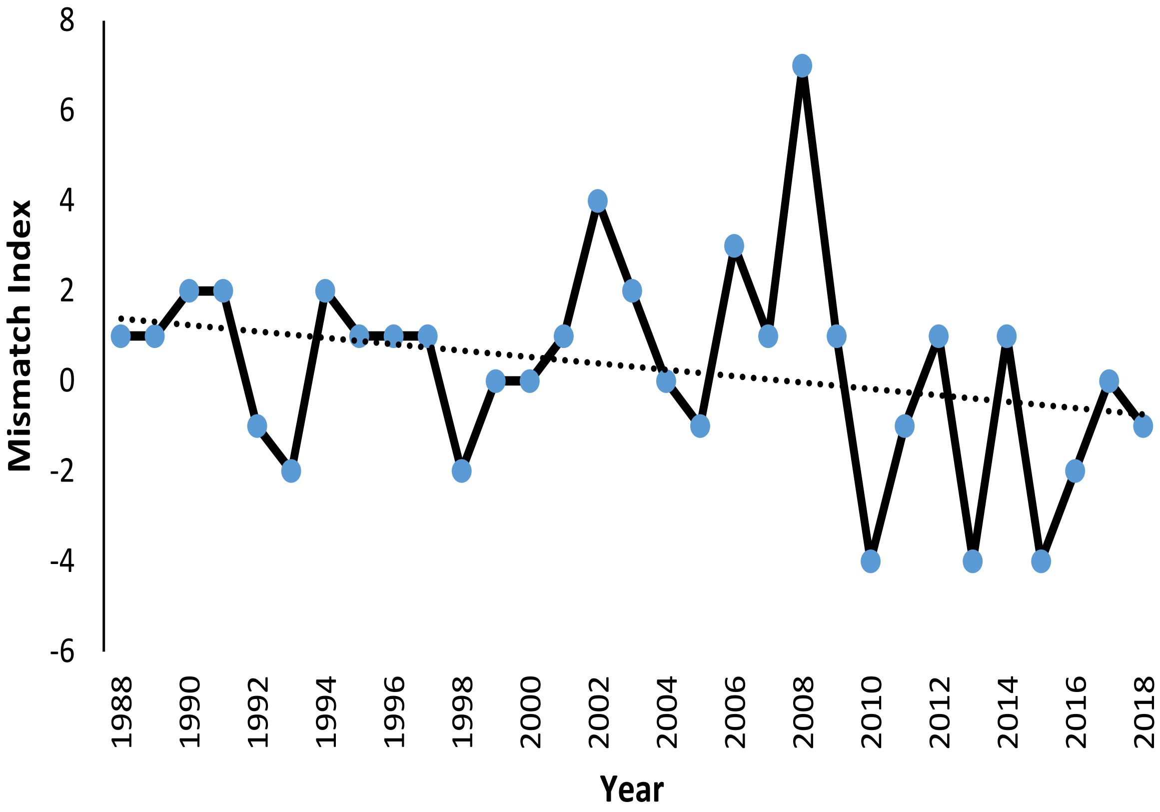
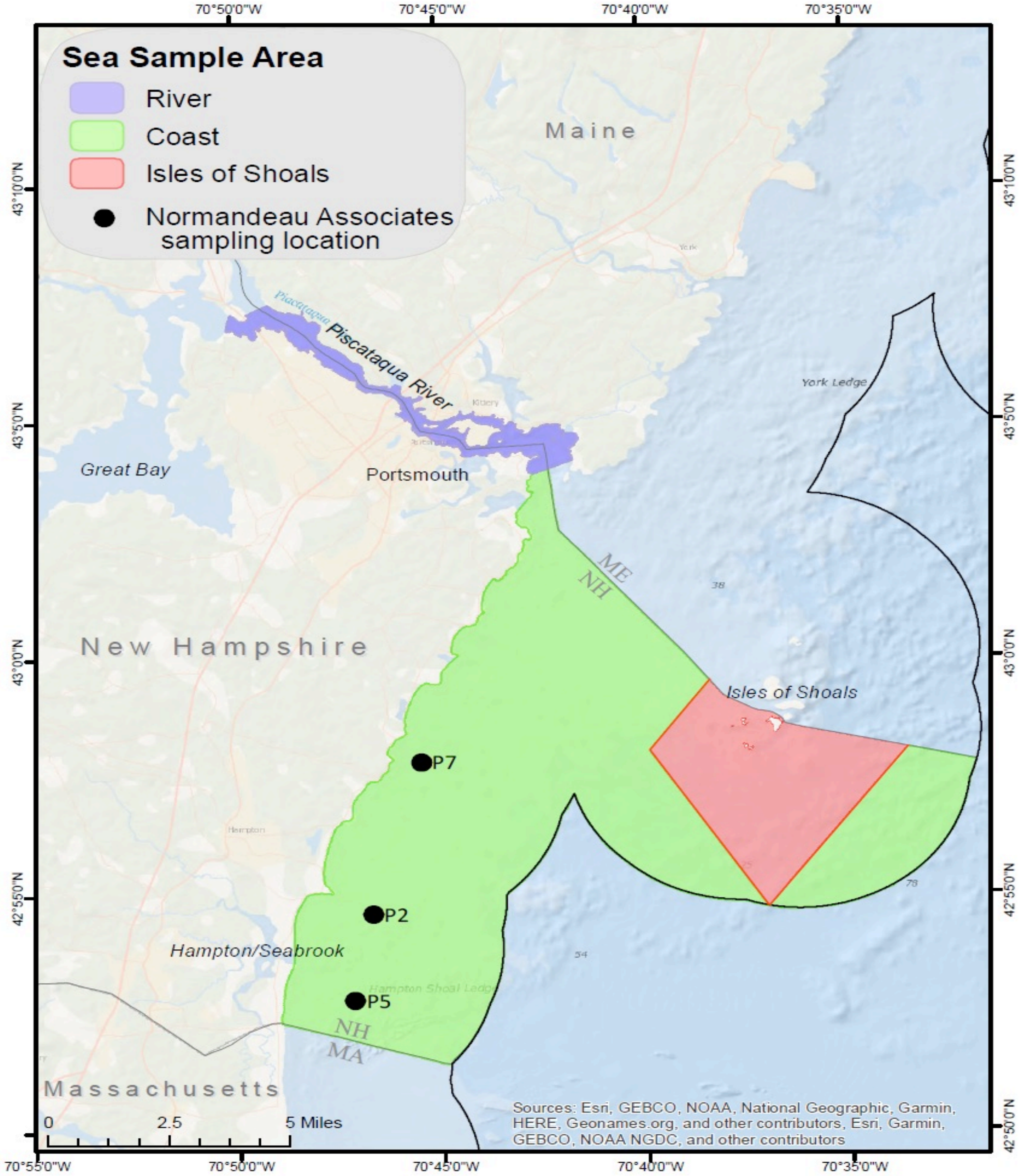


Figure 11. Mismatch index-illustrating the decreasing overlap between peak stage I larval lobster and the end of the *C. finmarchicus* season. A negative index indicates that peak stage I occurred after the end of *C. finmarchicus* season. The downward trend is statistically significant (Mann-Kendal P=0.039).

SUPPORTING MATERIAL



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure S-1. Study areas for New Hampshire Fish and Game's lobster sea sampling and Normandeau Associates lobster larval neuston tows and oblique macro-zooplankton tows.

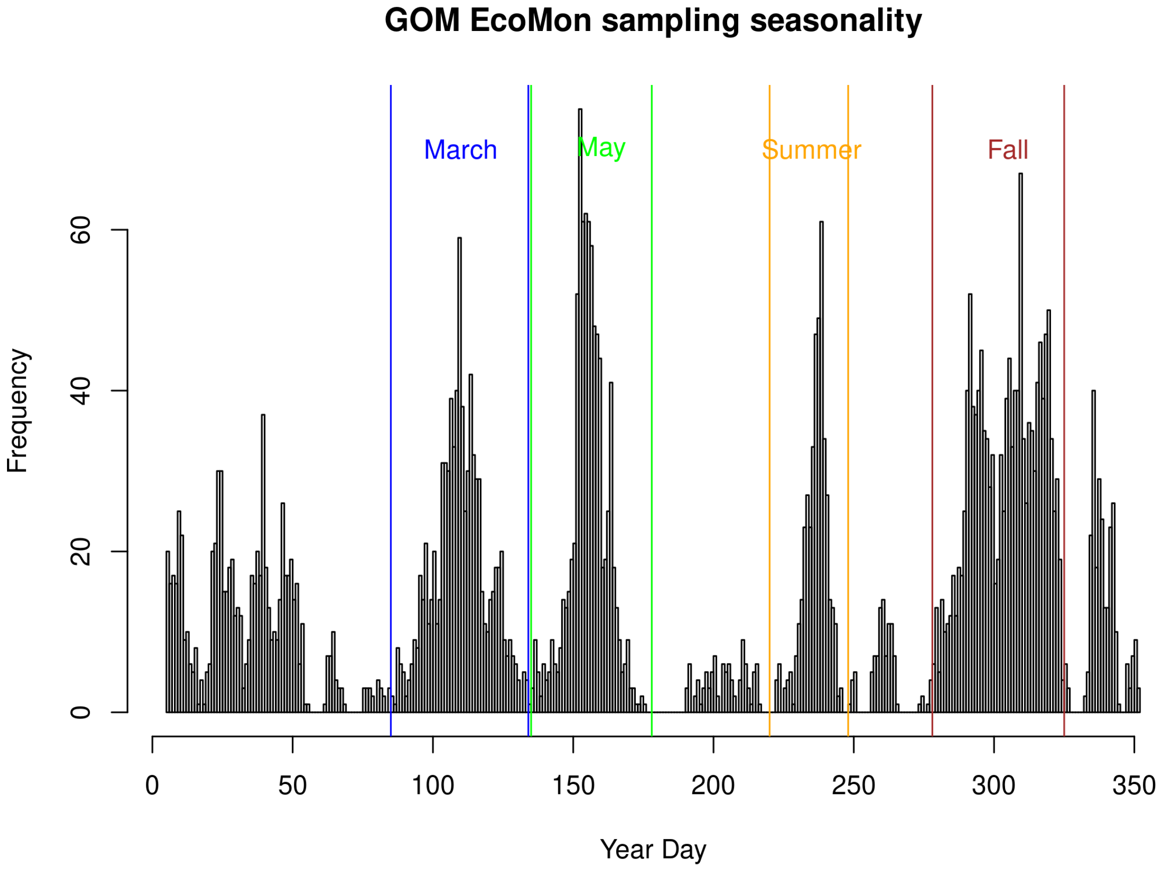


Figure S-2. Seasonal sampling rates for the NEFSC Ecosystem Monitoring surveys. Zooplankton dynamics were assessed for the combined Summer and Fall time periods.