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Dynamic changes in American lobster suitable habitat distribution on the Northeast U.S. Shelf linked to oceanographic conditions

Running Title: Change in American lobster suitable habitat

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Abstract

American lobster (*Homarus americanus*) supports one of the most valuable regional fisheries in the United States, with its abundance and distribution profoundly influenced by environmental conditions. To explain how lobster distribution has changed over time and assess the role of environmental variables on these changes, we used random forest classification and regression trees models to estimate occupancy and biomass in two seasonal periods. The occupancy models were fit to static and dynamic variables, which yielded model fits with AUC scores of 0.80 and 0.78 for spring and fall, respectively. Biomass models were fit with the same data and resulted in models explaining 61 and 63% of the spring and fall biomass variance, respectively. Significant variables scored in the formation of the regression trees were secondary productivity (i.e. zooplankton), bathymetry characteristics, and temperature. American lobster suitable habitat has changed regionally; habitat has increased in the Gulf of Maine and declined in Southern New England. There is also evidence of declining habitat along the inshore margin of the Gulf of Maine, which has been accompanied by a shift in occupancy probability offshore. Habitat suitability results from the random forest models provide insights on the structure and function of lobster habitat and context to understand recent population trends.

Key words: American lobster, Random Forest, suitable habitat, temperature, secondary productivity, front, Northeast U.S. Shelf

Introduction

American lobster (*Homarus americanus*) is widely distributed over the Northeast U.S. Continental Shelf (hereafter referred to as the Northeast U.S. Shelf) where it supports the most valuable single-species fishery in the United States (NOAA, 2017). A recent assessment highlighted the disparity between the two separate lobster stocks, with the Gulf of Maine-Georges Bank (GOM/GBK) stock reaching record high abundances while the Southern New England (SNE) stock declining to all-time low abundances (ASMFC, 2015). While commercial harvest has influenced population abundances through time, environmental and ecosystem changes have contributed to the recent stock dynamics (ASMFC, 2015). A combination of conservation measures and favorable environmental conditions lead to dramatic increases in landings in the GOM/GBK lobster fishery, but deficient conservation measures and unfavorable environmental conditions led to a collapse of the SNE lobster fishery (Le Bris et al. 2018). To effectively provide advice on sustaining lobster populations and maintaining the viability of the commercial lobster fishery, understanding the environmental impacts on American lobster and its habitat are imperative.

Temperature is perhaps the most prominent environmental forcing factor on American lobster and in defining its habitat. American lobster migration has been linked to water temperatures, which contributes to a lobster's ability to successfully molt, mate, and extrude eggs (Cooper & Uzmann, 1971; 1980). Increased temperatures have been associated with more frequent molts, reduced intermolt increments, smaller sizes to reach sexual maturity (Little and Watson, 2005; McMahan et al., 2016), and faster and earlier egg development and hatching (Goldstein and Watson, 2015). Lobsters partition spatially by size and sex (Karnofsky et al., 1989; Campbell, 1990), with these segregations attributed to their differing responses to environmental factors such as temperature and depth (Chang et al., 2010).

In the Northeast U.S. Shelf, ocean temperatures have increased significantly over the last several decades (Friedland and Hare, 2007; Pershing et al., 2015; Kavanaugh et al., 2017). The change in temperature is associated with changes in American lobster population size and distribution, with both centers of lobster biomass and fisheries landings shifting northeast since the 1970s (Pinsky and Fogarty, 2012). Projections of increasing temperatures over the next century (Saba et al., 2016) suggest that temperature will continue to have an impact on critical American lobster life history traits and the anticipated distribution of thermal habitat for lobster (Fogarty et al., 2007; Chang et al., 2010; Tanaka and Chen, 2015; Tanaka and Chen, 2016;

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Georgas et al., 2016; Rheuban et al., 2017; Goode et al., 2019). Warming water conditions may have a disproportionate effect on lobster at the southern end of their latitudinal range due to impacts on their life history. At temperatures nearing 20ºC, increased physiological stress, increased prevalence of lobster epizooitic shell disease, and decreased immune function can lead to increased rates of natural mortality (Steenbergen et al., 1978; Dove et al., 2005; Pearce and Balcom, 2005; Glenn and Pugh, 2006; Wahle et al., 2009; Steneck et al., 2011; Barris et al., 2018).

Several other environmental and oceanographic factors affect lobster life history and contribute to the definition of lobster habitat. Lobsters are associated with benthic structure including rocks, cobble, boulders, and ledge that they use to shelter, particularly during larval settlement and following life stages (Lawton and Lavalli, 1995). Suitable settlement habitat has often been considered a significant contributor to recruitment success and may impose limitations on year class size (Wahle and Steneck, 1991; Wahle and Steneck, 1992).

Productivity variables, which are not often accounted for in habitat evaluations, may also serve an important role in defining lobster habitat and influence recruitment. The Northeast U.S. Shelf ecosystem has undergone decadal changes in zooplankton community composition and spatial structure (Pershing et al., 2010; Morse et al., 2017), with zooplankton abundance variability linked to finfish stocks' recruitment (Perretti et al., 2017) and larval habitat suitability (McManus et al., 2018). For adult marine fauna, correspondence between their abundance and zooplankton often highlight the reliance on productive regions and the oceanographic conditions that support them (Sheldon et al., 1977). Ocean fronts associated with water temperature and density may play an important role in structuring lobster habitat (Belkin et al., 2014) through defining regions of enhanced productivity and pelagic to benthic coupling that support increased growth and foraging opportunities (Bakun, 2006). Fronts likely contribute to suitable habitat for a range of species and subsequently increasing prey-predator interactions and feeding opportunities for lobster (Mugo et al., 2014). This interaction may be reflected in the diet of adult lobsters, which includes prey such as mussels, gastropods, macroalgae, polychaetes, and amphipods (Sainte-Marie and Chabot, 2001). To date, food availability for older lobsters has not been considered a limiting factor in their abundance and distribution.

Species distribution models (SDMs) have been useful tools for identifying an organism's potential habitat range, prioritizing areas for conservation and management decisions, and

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evaluating survey designs (Guisan & Thuiller, 2005; Elith and Leathwick, 2009; Bacheler et al., 2016). American lobster life history and habitat have been the subject of hindcast and forecast models for various portions of the Northeast U.S. Shelf using bioclimate envelope models, generalized additive models, and additional analytics (Chang et al., 2010; Tanaka and Chen, 2015; Tanaka and Chen, 2016; Kleisner et al., 2017; Tanaka et al., 2017; Morley et al. 2018; Tanaka et al., 2018). However, previous studies have evaluated a rather narrow scope of variables and, aside from Kleisner et al. (2017) and Morley et al. (2018), isolated their inferences to fine scale areas that do not evaluate change over the entire Northeast U.S. Shelf. Furthermore, prior studies have not provided a comparative analysis of variable contribution.

We implemented random forest (RF) ensemble models (Cutler et al. 2007) to identify the environmental factors that correspond to lobster presence and abundance. The RF models were then used to predict spatio-temporal lobster distribution to understand how lobster suitable habitat has changed through time for both U.S. stocks. The resulting time series habitat indices describe changes in the lobster abundance through time and help guide future ecosystem considerations for lobster fishery management. Using a suite of marine ecosystem descriptors, we aimed to help form hypotheses for future studies focusing on mechanistic relationships between lobsters and their habitat.

Methods and Materials

This study is based on a series of SDMs, created with RF models, for dominant species in the U.S. Northeast Shelf (Friedland et al. 2020). Details for sources of variables in this study are provided in the respective sections below.

Data collection

Lobster data

The response variables were occurrence and catch-per-unit-effort of American lobster from the Northeast Fisheries Science Center's (NEFSC) fishery-independent bottom trawl survey within federal waters of the Northeast U.S. Shelf. The survey has been conducted in the spring since 1968 and the fall since 1963 using a stratified random design, which provides both spatial and temporal depictions of fish and macroinvertebrate abundances (Grosslein, 1969). Catches were standardized for various correction factors related to vessels and gears used in the time series (Miller et al. 2010), following the methods of Friedland et al. (2020). These data are from

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the NEFSC fishery-independent bottom trawl survey available from the InPort NMFS Data Management Program (https://inport.nmfs.noaa.gov/inport/).

Explanatory variables

The independent or explanatory variable set included bathymetry, productivity, and climate variables (Table A1). Several explanatory variables were used to describe lobster habitat and develop hypotheses that can be tested in future studies focusing on mechanistic relationships in lobster habitat. Static variables were kept constant over all years, whereas dynamic variables varied annually. Station data included observations made contemporaneously to survey stations.

Prior to fitting the models, the independent variable set was first tested for multicollinearity among the explanatory variables (R package rfUtilities, version 2.1-3), and strongly correlated covariates were removed from the analysis (threshold: p=0.1), following the methods of Murphy et al. (2010). From the reduced set of explanatory variables, the final model variables were selected utilizing the model selection criteria of Murphy et al. (2010) as implemented in ‘rfUtilities’. This includes removing multivariate redundant variables using qr matrix decomposition. Removing redundant variables improves the biological interpretability and predictive power.

Climate

Surface and bottom water temperature and salinity were used as dynamic abiotic variables in the analysis. These data were collected contemporarily to each tow with Conductivity/Temperature/Depth (CTD) instruments. The data are from the NEFSC survey temperature and salinity data from the National Center for Environmental Information (https://www.nodc.noaa.gov/oads/stewardship/data_assets.html).Temperature and salinity data for model predictions were based on an interpolation procedure described in Friedland et al. (2019). This procedure combines a kriged interpolation of the annual data with climatological data to estimate complete temperature and salinity fields. This approach was favorable since it preserved the observational nature of the data and kept it as close as possible to the data used in the habitat model fits.

Sea surface temperature (SST) from remote sensing sources were summarized as monthly means with their associated gradient magnitude or frontal fields, and applied in the habitat models as static variables. There are many methods used to identify oceanographic fronts (e.g. Belkin and O'Reilly, 2009) that often apply a focal filter to reduce noise and then identifies

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gradient magnitude with a Sobel filter. These calculations were conducted in R using the raster package (version 2.6-7) by applying a three by three mean focal filter and a Sobel filter to generate x and y derivatives, which were then used to calculate gradient magnitude. This indexes the annual cycle, and all the available monthly variables, after removing collinear and redundant variables, were used in each of the seasonal models. These monthly variables were averages of the monthly concentrations or fronts from all years in the time series. Monthly SST fields were based on the 4 km MODIS Terra sensor data. These data are from the Ocean Color website (https://oceancolor.gsfc.nasa.gov/).

Bathymetry

Bathymetry variables represented a series of static variables that reflect the shape and complexity of the benthic environment. Depth of the station (in meters) was used as a static variable in the analysis. The observed depth made with each survey tow was used in model fitting, whereas model predictions were based on depths from the ETOPO1 (https://www.ngdc.noaa.gov/mgg/global/) dataset, which provided Northeast U.S. Shelf bathymetry at a resolution of 0.0167° (Fig A1).

Most of the other bathymetry variables were based on depth measurements, including the complexity, bathymetry position index (BPI), vector ruggedness measure (VRM), profile curvature at 2, 10, and 20 km, slope at 2, 10, and 20 km, slope of the slope at 2, 10, and 20 km, rugosity, and seabed topography variables (Table A1). Complexity represented the difference in elevation values from a center cell and the eight cells immediately surrounding it. Each of the different values were squared and then averaged. The index was the square root of this average (Riley et al., 1999). BPI was a second order derivative, which compares the depth and slope values at a location to those at neighboring locations, of the bathymetry using the Nature Conservancy Northwest Atlantic Marine Ecoregional Assessment (NAMERA) data with an inner radius of 5 and an outer radius of 50 (Lundblad et al., 2006). VRM measured terrain ruggedness as the variation in three-dimensional orientation of grid cells within a neighborhood based on the TNC NAMERA data (Hobson, 1972; Sappington et al., 2007). Rugosity measured small-scale variation of amplitude in the height of a surface, the ratio of the real to the geometric surface area (Friedman et al., 2012). Seabed topography is a measure that combines seabed position and slope (Anderson et al., 2010). Benthic profile curvature, slope, and slope of slope at 2 km, 10 km and 20 km spatial scales were also derived from depth data (Winship et al., 2018). The vorticity

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variable was based on benthic current estimates and is at a 1/6 degree (approximately 19 km) spatial scale (Kinlan et al., 2016). Soft sediment was based on grain size distribution from the USGS usSeabed: Atlantic coast offshore surficial sediment data (Anderson et al., 2010). Aside from the bathymetry variables derived from depth, these variables' data were from Northeast Ocean Data (http://www.northeastoceandata.org/), or National Centers for Coastal Ocean Science (https://coastalscience.noaa.gov/project/statistical-modeling-marine-bird-distributions/).

Productivity

Productivity was incorporated into the model as both primary and secondary levels of production in the marine ecosystem. Chlorophyll concentration from remote sensing sources were summarized as monthly means with their associated gradient magnitude or frontal fields and applied in the habitat models as static variables. These chlorophyll concentration and frontal field variables represented seasonal primary productivity cycles. After removing collinear and redundant variables, all the available monthly chlorophyll variables were tested in each of the seasonal models. Chlorophyll concentration measurements were based on the 4 km data from the Sea-viewing Wide Field of View Sensor (SeaWiFS), Moderate Resolution Imaging Spectroradiometer on the Aqua satellite (MODIS), Medium Resolution Imaging Spectrometer (MERIS), and Visible and Infrared Imaging/Radiometer Suite (VIIRS) sensors during the period 1997-2016. These data represented a merged product using the Garver, Siegel, Maritorena Model (GSM) algorithm obtained from the Hermes GlobColour website. These four sensors provided an overlapping time series of chlorophyll concentration during the period and were combined based on a bio-optical model inversion algorithm (Maritorena et al., 2010). From these data, mean monthly fields were generated for chlorophyll. Gradient magnitudes of these data were calculated in the same manner as with the habitat data as described above. These data are from the Hermes GlobColour website (http://hermes.acri.fr/index.php).

Zooplankton abundance was used as a dynamic variable measured by the NEFSC Ecosystem Monitoring Program (EcoMon), which conducts shelf-wide bimonthly surveys of the Northeast U.S. Shelf ecosystem (Kane, 2007), and the MArine Resources Monitoring, Assessment, & Prediction program (MARMAP), which conducted similar surveys before EcoMon (data available at https://accession.nodc.noaa.gov/0187513). Zooplankton and ichthyoplankton were collected throughout the water column to a maximum depth of 200 m using paired 61-cm Bongo samplers equipped with 333-micron mesh nets. Sample location in

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this survey was based on a randomized strata design, with strata defined by bathymetry and along-shelf location. Plankton taxa were sorted and identified. In this study, zooplankton represents a proxy for secondary productivity as opposed to representing a direct relationship between zooplankton and adult and juvenile lobsters. This is because lobsters at the life stages represented in the trawl survey catch do not feed on zooplankton, because they are not in early life stages. We used the log of the abundance (number per 100m^3 of water filtered) of each of the 18 most abundant taxonomic categories as potential explanatory variables, and we also used the total bio-volume of all taxa (displacement volume in ml per 100m^3 of water filtered) as a potential explanatory variable. Biovolume is the settled volume of plankton per water volume sampled (mm^3/m^3). It is measured by estimating the total volume of plankton in the sample jar. The zooplankton sample time series had some missing values which were ameliorated by summing data over five-year time steps so that the current year is centered and interpolated into a complete field using ordinary kriging, following the methods from Friedland et al. (2020). For example, the data for spring 2000 would include the available data from 1998-2002 tows.

Data analysis

Random forest approach

RF is an ensemble model approach based on combinations of large sets of decision trees (Breiman et al., 1984). Tree models such as RF provide powerful predictive power with many explanatory variables (Cutler et al., 2007), yet perhaps the greatest benefit of these models is they largely ignore non-informative predictors, but predictor selection is still important given redundant predictors increase variance and reduce model performance (Elith et al., 2008). Other benefits of tree models include resistance to overfitting, ability to identify interactions, and overall flexibility (Elith et al., 2008). In this technique, the learning sample is divided in two by maximizing the homogeneity in the two resulting child nodes, which is done with an algorithm known as binary recursive partitioning. RF trees are grown by selecting a random bootstrap subset of the original dataset and a random set of explanatory variables (Liaw and Wiener, 2002), which is different from the process in standard decision trees, where all explanatory variables are used. Within the subset, the partitioning starts with the most important variable and ends with the least important variable.

Occupancy and biomass habitat models

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Occupancy and biomass habitats for lobster were estimated with RF decision tree models using the aforementioned static and dynamic explanatory variables. The effect of bathymetry, productivity, and climate factors on variation in species presence or absence and biomass were tested. Models were constructed separately for spring and fall seasons. The spring and fall seasons were based on the timing of the offshore survey, which varied slightly over time. The modeling domain focused on the Northeast U.S. Shelf and upper slope, latitudinally extending from the states of North Carolina to Maine. Occupancy models were fit as two-factor classification models (absence as 0; presence as 1) using the 'randomForest' R package (version 4.6-14). Biomass models were also fit using the same package with $\log_{10}$ transformed biomass-per-unit-effort plus one (fall biomass: mean=0.228, sd=0.4, spring biomass: mean=0.180, sd=0.353) as the response variable and the same starting set of explanatory variables as in the occupancy models. The number of trees was set to 200, and the number of variables randomly sampled as candidates at each split was the square root of the total number of variables for the occupancy models, and the total number of variables divided by three for the biomass models.

Habitat was estimated from the model fits over a standard 0.1° grid, which circumscribes the range of ecosystem assessment areas in the region (Figure 1) and a wide range of habitats with varying oceanographic conditions (Townsend et al., 2006). The grid represented limited extrapolation into the inshore areas of the Northeast U.S. Shelf not exceeding one grid cell beyond the observed data. The length of the time series of model fits was constrained by the shortest dynamic variable time series to meet the requirement of complete cases in the RF fitting. As such, the fitting time series was constrained to 1992 – 2017, corresponding to the length of the station salinity data.

Model selection criteria and variable importance

The habitat models were evaluated for fit based on out-of-bag classification accuracy. For occupancy model accuracies, AUC (Area Under the Receiver Operating Characteristic Curve) and Cohen's Kappa were calculated using the "irr" R package (version 0.84) (Gamer et al., 2012). The AUC assumes a threshold of classification probability of 0.5. For biomass models, the variance explained by the model, mean absolute error, root mean square error, and bias were calculated using the "Metrics" R package (version 0.1.3). To evaluate variable importance in both occupancy and biomass models, the number of times a variable was the root variable, or the variable at which the whole sample is divided into two (the first variable in the tree), were

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plotted against the mean minimum node depth for the variable, highlighting the top 10 important variables ("randomForestExplainer" R package, version 0.9). For occupancy models, Gini index decreases were plotted against accuracy decreases, whereas node purity increases versus MSE increases were plotted for the biomass models, highlighting the top 10 most important variables. These presentations allowed for calculating and visualizing variable importance under different criteria.

Visualizations

Three types of visualizations were created from the model output. The first visualization provided the average probability of occupancy over the ecosystem, accompanied by the rate of change in occupancy probability as a Sen slope, which represented the median of the slopes of all lines through pairs of points. The nonparametric Sen slope is less vulnerable to single values. The second visualization provided the gradient magnitude of occupancy probability over the ecosystem, or frontal strength of this habitat measure, also accompanied by the rate of change in occupancy gradients as a Sen slope. Gradient magnitudes of these output data were calculated in the same manner as with the habitat data as described above. The third visualization provided average biomass habitat over the ecosystem, also accompanied by the rate of change in biomass habitat as a Sen slope. Trends in total occupancy habitat area in each ecoregion (GOM, GBK, and SNE), delimited by threshold occupancy probabilities of 0.25, 0.50, and 0.75 over time, were calculated, as well as the sum of the area with occupancy probabilities above each probability during each year.

Results

Model diagnostics

Although both occupancy models were accurate, the spring model was better fitting than the fall model (Table 1). The AUCs indicated that all models performed better than random classifications. The spring model had a better rate of successful classification than the fall model. The Kappa statistics indicated that spring and fall occupancy models showed substantial and moderate agreements, respectively. For biomass, the RF models explained between 60.9% to 63% of the variance (Table 2). The spring biomass model had a smaller error and bias than the fall biomass model.

Variable importance

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A variety of climate, bathymetry, and productivity variables were significant and included in the spring and fall models (Table A1). Bottom water temperature, BPI, depth, several secondary productivity variables, and SST fronts were important variables (Figure 2; Figure 3). Bottom water temperature was a highly important variable for fall, and more for the occupancy model than for the biomass model. In the spring, SST fronts were more important than in the fall, especially for occupancy (Figure 2 a and b and Figure 3 a and b). Bathymetry variables were more important for occupancy in the spring than in the fall. Chlorophyll fronts were more important than SST fronts in the fall, and SST fronts were more important than chlorophyll fronts in the spring. Zooplankton taxa Chaetognaths, *Centropages typicus, Paracalanus parvus,* and *Calanus finmarchicus* were particularly important for occupancy and biomass models in the spring, followed by bathymetry variables (Figure 2 c and d). Secondary productivity was consistently more influential and significant than primary productivity in the spring. Secondary productivity variables were also important in the fall occupancy model, followed by bathymetry variables (Figure 3 a and b). *Metridia lucens,* Appendicularians, *Pseudocalanus spp.,* and *Centropages hamatus* had especially strong influences in the fall. Productivity variables were also very important for fall biomass, while bathymetry variables were not as important for fall biomass as they were for fall occupancy (Figure 3 c and d).

Of the most important variables, lobster occupancy was negatively related to depth, slope at 2 km, and *Metridia lucens*. Lobster occupancy had nonlinear relationships and optimal ranges with values of November SST front, December SST front, BPI, March chlorophyll concentration, Chaetognatha, *Paracalanus parvus, Calanus finmarchicus, Pseudocalanus spp.,* Gastropoda, Appendicularians, and bottom water temperature. Lobster occupancy was positively related to *Centropages typicus* and Salpa (Fig. A1 - A10; A21- A29). Lobster biomass decreased with SST, December SST front, Chaetognatha, *Paracalanus parvus, Calanus finmarchicus,* Appendicularians, and *Centropages typicus.* Lobster biomass had nonlinear relationships and optimal ranges with values of November SST front, December SST front, BPI, September chlorophyll concentration, *Penilia spp.,* and Gastropoda. Lobster biomass increased with depth, June chlorophyll concentration, July chlorophyll concentration, October chlorophyll front, *Temora longicornus, Centropages hamatus,* and *Pseudocalanus spp.* Lobster biomass increased and then decreased with bottom water temperature (Fig. A11- A20; A30- A41). Values of these important dynamic variables varied overtime (Fig. A42- A54).

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Predicted area occupied and biomass

Lobster distribution varied across space, with greater occupancy and biomass predicted for GOM and GBK than SNE. Lobster habitat occupancy probabilities were greatest (probability > 0.50) for inshore GOM, off the coast of southern Nova Scotia, and offshore SNE (Figure 4 a and c). All models predicted low occupancy in offshore southern GOM. In the fall, the occupancy was concentrated near inshore areas, whereas it was more diffused into offshore areas in the spring. However, the occupancy probability area in offshore SNE was higher in the fall than in the spring. Off the coast of Massachusetts, more areas were predicted to be found with lobster in the fall than in the spring as well.

Occupancy habitat scores increased through time in most of the offshore GOM and some portions of SNE and declined in the inshore GOM and most of SNE (Figure 4 b and d). The greatest negative change in occupancy was in the northern and inshore region of SNE. The greatest positive change in occupancy was in the offshore GOM. In the spring, there was more of a positive change in the center of the GOM than in the fall. The greatest negative change in occupancy for the fall was in the northern part of SNE and GBK. More of the inshore GOM had a negative change in occupancy in the fall than in the spring.

The total area with 25% or greater probability of occupancy varied over time and regions (Figure 5 a and b). In the GOM, the total area with 25% or greater probability of occupancy increased in the fall and varied with no trend in the spring. In GBK, the total area with 25% or greater probability of occupancy varied with no noticeable trend. In SNE, the total area with 25% or greater probability of occupancy varied with no noticeable trend in the spring and decreased in the fall. The total area with 50% or greater probability of occupancy increased greatly over time in the GOM and increased slightly in GBK (Figure 5 c and d). In SNE, the total area with 50% or greater probability of occupancy varied with no trend in the spring and decreased in the fall. At the beginning of the time series, the total area with 50% or greater probability of occupancy was lowest in the GOM compared to the other regions, but by the end of the time series, the total area was highest in the GOM. The total area with 75% or greater probability of occupancy increased greatly in the GOM but declined in recent years (Figure 5 e and f). In GBK and SNE, the total area with 75% or greater probability of occupancy varied over time in the spring and slightly decreased in the fall.

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Habitat frontal strength, or occupancy gradient magnitude, was large off the inshore GOM, around GBK, and in offshore SNE near the shelf break (Figure 6 a and c). In the fall in SNE, there was a larger shift in habitat front towards offshore near the shelf break than in the spring. The linear trend in the occupancy fronts was most positive in the offshore GOM and the most negative in the inshore GOM, indicating that the habitat front was moving offshore (Figure 6 b and d).

Spatial predictions of the models highlighted strikingly area-specific differences in biomass (Figure 7 a and c). Lobster biomass was predominantly concentrated near inshore GOM, including off the coast of southern Nova Scotia, and most of the predicted lobster biomass was off mid-coast Maine. The predicted biomass of the inshore GOM was much higher than the predicted biomass in any other area, with the highest predicted biomass in other areas being almost half of that in the inshore GOM. Biomass was much less in the offshore GOM and the whole area of SNE, although in SNE much of the lobster biomass was predicted to be offshore near the shelf break. There was more biomass in the offshore GOM in the spring than in fall, and biomass off Cape Cod and in GBK was greater in the fall than the spring.

Changes in biomass were not necessarily aligned with changes in occupancy. Positive changes in biomass were pervasive in the GOM, especially off mid-coast Maine, and most of the negative change in biomass was in SNE (Figure 7 b and d). There were also some patches of positive changes in biomass in the southern region of SNE. In the spring, the most positive change in biomass was off midcoast Maine. In the spring, the rate of change was more similar over space in the GOM than it was in the fall. The most positive change the fall biomass was off the coast of Maine and Nova Scotia. There were also some negative changes in biomass on GBK and in some parts of the inshore GOM in the fall, as well as positive changes in biomass in the greater GOM region. These changes differ from the spring, in which there was less negative change on GBK and positive change in most of the inshore GOM.

Habitat fronts produced from spatial predictions of the occupancy and biomass models corresponded to SST fronts (Figure 8). Strongest SST front probabilities in the spring and fall were most pronounced along the shelf break in SNE, followed by the inner shelf regions of SNE and GOM, and southwest GBK. Habitat fronts were strongest in the inner GOM and SNE, and offshore SNE, but spatially mismatched with SST front probabilities in GBK.

Discussion

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Trends in lobster habitat suitability

The RF models accurately described the changes in American lobster habitat over the Northeast U.S. Shelf. The models provide information on both lobster distribution and the environmental conditions associated with lobster occupancy. The habitat trends estimated for ecoregions corresponded to the declining and increasing population trends for the SNE and GOM-GBK stocks, respectively (ASMFC, 2015). Separating the GOM and GBK into two regions, as opposed to the unified stock region, allowed for acknowledging the oceanography differences between the two areas, as well as their differences in habitat suitability trends. Since 1992, lobster habitat has declined and shifted offshore in SNE, and shifted offshore into deeper water in GOM-GBK. These patterns agree with previously reported decreasing habitats in SNE (Rheuban et al., 2017; Tanaka and Chen, 2015), offshore transitioning thermal habitats in the GOM-GBK (Rheuban et al., 2017), increased habitat suitability in the GOM (Tanaka and Chen, 2016; Chang et al., 2010), and regional landings increasing in the north (NMFS, 2018).

Occupancy and biomass patterns differed in both the spring and fall, possibly indicating density-dependent habitat selection of American lobster. Both occupancy and biomass were highest off the coast of the GOM, peaking off the coast of the mid-Maine region, but there was a greater change in occupancy in the offshore GOM and even a negative change in occupancy in the inshore GOM, unlike the change in biomass. Lobsters are moving into areas that were previously less occupied or unoccupied, which may be attributed to the increase in biomass in the inshore GOM or an offshore shift in optimal thermal conditions (Tanaka and Chen, 2016), causing lobsters to spread out into more offshore areas. It has been repeatedly demonstrated that the spatial distribution of marine species expands with increases in abundance (Marshall and Frank, 1994; Petitgas, 1998; Anderson and Gregory, 2000), indicating density-dependent habitat selection where increases in population size lead to increases in competition, reduced habitat suitability and ultimately an expansion of occupied area (Fretwell and Lucas, 1970; MacCall, 1990). The ideal free distribution theory describes that mobile individuals will select habitats that maximize their fitness (Fretwell and Lucas, 1970). Population abundance can affect demographic and life history characteristics of populations, such as dispersal (Fauchald et al., 2006), survival (Bjornstad et al., 1999; Hails and Crawley, 1992), and reproductive success (Burgess et al., 2011). Future research should consider including a density-dependent variable into analyses of spatial distributions of lobster.

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Environmental drivers in predicted habitat

Although American lobster distribution has been extensively studied, the RF models provided additional insight on the effects of environmental factors on lobster abundance and distribution. Spatial-temporal variability in lobster abundance and distribution corresponded to both biological and physical oceanographic conditions. Although climate variables were important drivers of American lobster habitat, productivity and bathymetry variables had the greatest significance on lobster presence and biomass. These results suggest that productivity fronts, which correspond with SST fronts, are important for lobster habitat. To date, biotic variables such as chlorophyll concentration and zooplankton have not been included in lobster habitat models. Additionally, bathymetry variables have largely not been included.

Environmental drivers

Climate drivers

Exact mechanisms driving habitat occupancy change are unclear but have been associated with increasing ocean temperatures. Ocean warming has led to a northward center of biomass shifts for many taxa (Pinsky et al., 2013), and the results for lobster biomass in this study agrees with this. Increased prevalence and severity of epizootic shell disease in the warming habitats of SNE (Steneck et al., 2011; Castro et al., 2006) have contributed to the collapse of southern lobster populations, which suggests that temperature has a large effect on habitat.

The influence of temperature was stronger and significant in the fall, with secondary productivity variables relevant in both seasons. Temperature’s profound impact on lobster life history makes it surprising that it was not the leading contributor to habitat suitability in the RF models in the spring. However, this finding should not negate or lessen the impact of temperature on lobster behavior, physiology and distribution, as temperature is anticipated to have further ramifications for the population in the future (Fogarty et al., 2007; Pinsky et al., 2013). The variability of temperature during the spring trawl surveys may contribute to the model results. Additionally, during the timeframe of the spring trawl surveys, lobsters may not be actively migrating or moving since temperature may not have increased enough to stimulate movement.

Bathymetry drivers

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Bathymetry, especially depth and BPI, played a large role in lobster habitat. However, the importance of bathymetry variables was often less than that of productivity and climate variables. Although shelter is important for lobsters, bathymetry may play a role more for smaller lobsters for refuge from predators than larger lobsters. As lobsters grow larger, they become more active and use shelter less often (Lawton and Lavalli, 1995).

Productivity drivers

Although zooplankton taxa have been found to directly impact larval survival and recruitment for several fish stocks in the study region (Peretti et al., 2017), the importance of zooplankton taxa for lobster likely represents another important environmental condition that also relates to zooplankton. This study focuses on juvenile and adult lobster and not earlier life stages that may feed directly on zooplankton. Zooplankton biomass varies dynamically during a given year, which makes it difficult to relate zooplankton biomass collected at the time of the zooplankton surveys to lobsters in the spring and fall. However, averaging zooplankton biomass can be a proxy for productivity over time, as the chlorophyll variables were static. The zooplankton variables represent overall ocean productivity as opposed to a true predator-prey relationship. The relationship between adult and juvenile lobsters and zooplankton is probably not a direct relationship but lobster habitat is most likely dictated by productivity and oceanography. For example, ocean fronts are key components to the ecosystem within the Northeast U.S. Shelf through vertical mixing of nutrients that can affect the onset and duration of phytoplankton blooms (Mann and Lazier, 2006). Ocean fronts occur over various spatial and temporal scales (Belkin et al., 2014) and support multiple trophic levels and fisheries (Tseng et al., 2014).

We hypothesize that the significance of zooplankton in describing lobster habitat is associated with the role of physical oceanography, specifically frontal transition zones, in creating these productive, ecologically rich features, as has been described for other species (Le Fevre et al., 1986). The link between water column productivity in supporting demersal fish and invertebrate species via benthic-pelagic coupling has been noted within the Northeast U.S. Shelf (Friedland et al., 2008), and may serve as a major mechanism in providing lobster habitat in these dynamic regions. Broad changes in the GOM may be reflected by changes in zooplankton abundances (Pershing et al., 2005). Zooplankton community composition has undergone distinct regime shifts over the previous decades (Morse et al., 2017). In this study, breaking zooplankton

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into small taxonomic levels was beneficial, because individual taxonomic levels are spatially varied. Plankton biovolume was not used in any of the models, probably because it is not as spatially varied as individual taxonomic levels. Some individual taxonomic levels tend to line up with production zones and fronts, which further supports our hypothesis that productive waters are important for lobster habitat. Some plankton species are more dominant within fronts, whereas others are more dominant outside of fronts (Moisander et al. 1997; Taylor et al. 2012; Roy et al. 2015). In Georges Bank, different taxonomic levels are associated with different water mass types (Ashjian et al. 2001). In the Northeast U.S. Shelf, anomalies of several copepod taxa are associated with changes in frontal zones (Pershing et al. 2010). Therefore, the model results are most likely suggesting general correlations among organisms within high productivity waters.

Nonetheless, these results can be used to develop hypotheses to test in future studies that focus on the role of zooplankton in lobster habitat. Another future research topic can be the effect of broad scale changes in productivity on American lobster. This study suggests productivity has a large effect on lobster distribution, even more so than temperature.

Modelling limitations

The results from this modeling effort are limited by both the survey design and the covariate data available. The trawl survey data capture the broader population movements and abundance trends through time; trawl surveys are unable to sample near rocky bottom or ledge or where fixed gear is set (Smith and Tremblay, 2003), a known habitat preference and high abundance regions of lobsters (Wahle, 1992; Lawton and Lavalli, 1995). The significance of bathymetry and ruggedness in the RF models suggests that this preference for lobsters is at least partially accounted for, but both sampling in these areas and covariate information at finer scales and descriptions (e.g. cobble, rock, ledge, boulder) may improve results.

The NEFSC trawl survey also occurs in federal waters offshore and samples larger lobsters, while a notable portion of the population, particularly smaller lobsters, reside within inshore waters from spring through fall. Additionally, the large proportion of adult lobsters in the trawl survey data may be a result of exploitation of the young lobsters. Thus, these results are specific to larger lobsters, and may not represent the habitat requirements of younger, pre-recruit lobsters. Other trawl surveys that cover inshore waters should be considered. Once catchability differences between the NEFSC and states' trawl surveys are calibrated, other trawl data sources

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can be included to allow for fully modeling the regions. Additionally, although correction factors were applied, changes in vessels and gears in the trawl survey can introduce biases.

A key assumption in this study is that relationships between lobster and environmental variables are stationary across space and time. Li et al. (2018) modeled lobster spatial distribution allowing relationships to vary among space and found that the relationships between lobster and environmental variables were different in the western and eastern GOM. Similarly, the relationship between bathymetry variables and lobster may have changed overtime with fluctuations in the abundance of predators and therefore, the need for sheltered habitat.

In this study, the RF models were used to describe American lobster realized niche using bottom-up forcing covariates, and do not account for top-down controls on the population. Predation on lobsters also influences their spatial distribution, most prominently at the extreme ends of the range of lobsters (Boudreau et al., 2015). Changes in top-down controls related to ground fish predation have been postulated to have influenced lobster abundance in the coastal GOM area. Following intense fishing on cod and haddock in the coastal GOM during the 1930s, lobster abundance and landings increased in the following decades with the contemporary increased abundance consistent with a predation release effect (Acheson and Steneck, 1997; Steneck, 2006; Steneck and Wahle, 2013). Predators, notably cod, have long been noted to influence lobster abundance and distribution (Boudreau et al., 2015). The decline in cod abundance has been thought to explain part of the increase in lobster abundance (Hanson & Lanteigne, 2000). Li et al. (2018) found a significant relationship between temperature and lobster habitat in the eastern GOM, but not in the western GOM, with the operating hypothesis that predators may have a greater effect on lobsters than temperature in the western GOM. Predation risk on lobsters is lower in the GOM than in SNE, which may affect lobster habitat (Wahle et al., 2013). Changes in top down controls (i.e. predators) may have also allowed lobster to persist on previously unsuitable substrates (i.e. mud). Other top down controls, including fishing pressure, may also contribute to discrepancies between our predictions and empirical observations and should be further evaluated.

Additionally, RF models have limitations. Interpreting the relationships between the response and explanatory variables can be difficult with many decision trees. Furthermore, variable importance from RF models tend to be biased towards correlated variables, continuous

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variables, and variables with many categories (Strobl et al. 2007; 2008).

Conclusions

These habitat suitability results advanced current understanding on lobster habitat distribution, change, and the various environmental factors influencing American lobster presence and biomass. Of note, the role of lower trophic level productivity appears to be an important consideration in defining lobster habitat, which previous studies have not investigated. Furthermore, previous studies have examined finer spatial scales for lobsters (Chang et al., 2010; Tanaka and Chen, 2015; Tanaka and Chen, 2016; Tanaka et al., 2017; Tanaka et al., 2018), whereas this work provides a more holistic view of the changes in lobster habitat since 1992 that better correspond to the migratory species' stock bounds.

These results may prove valuable as inputs to the lobster stock assessment (i.e. tuning recruitment deviations). Furthermore, these results can provide insights into the environmental variables that have strong influences on distribution, and hence, population dynamics. Including such estimates and information in the stock assessment model may better account for ecosystem changes that have impacts on lobster life history and abundance, a common call often included in assessments' terms of references. As these results suggest, a holistic approach using various levels of oceanography should be incorporated into the assessment and management of American lobster to ensure sustainable harvests. With the marine ecosystem expected to continue changing, understanding of the environmental drivers for America's largest fishery are imperative now more than ever.

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Conflict of interest statement

There is no conflict of interests to state in this research.

Data sharing statement

The data that support the findings of this study can be available upon reasonable request from the corresponding author.

Author Contribution Statement

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M.D.M. wrote the manuscript along with K.D.F., M.C.M., and A.G.G. K.D.F. conceived the presented idea and performed the random forest modelling. M.D.M. and K.D.F. analyzed the modelling results. All authors discussed the results and contributed to the final manuscript.

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Tables

Table 1. Diagnostics for occupancy models including accuracy, area under the curve (AUC) and Cohen's Kappa.

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Season	**Accuracy**	**AUC**	**Cohen's Kappa**
Spring	0.85	0.80	0.62
Fall	0.79	0.78	0.56

Table 2. Diagnostics for biomass models including variance explained, Mean Absolute Error (MAE), Root Mean Squared Error (RMSE), and bias (logarithmic scale).

Season	**Variance explained**	**MAE**	**RMSE**	**Bias**
Spring	60.9	0.059	0.15	-0.0048
Fall	63.0	0.096	0.17	-0.0054

Figures

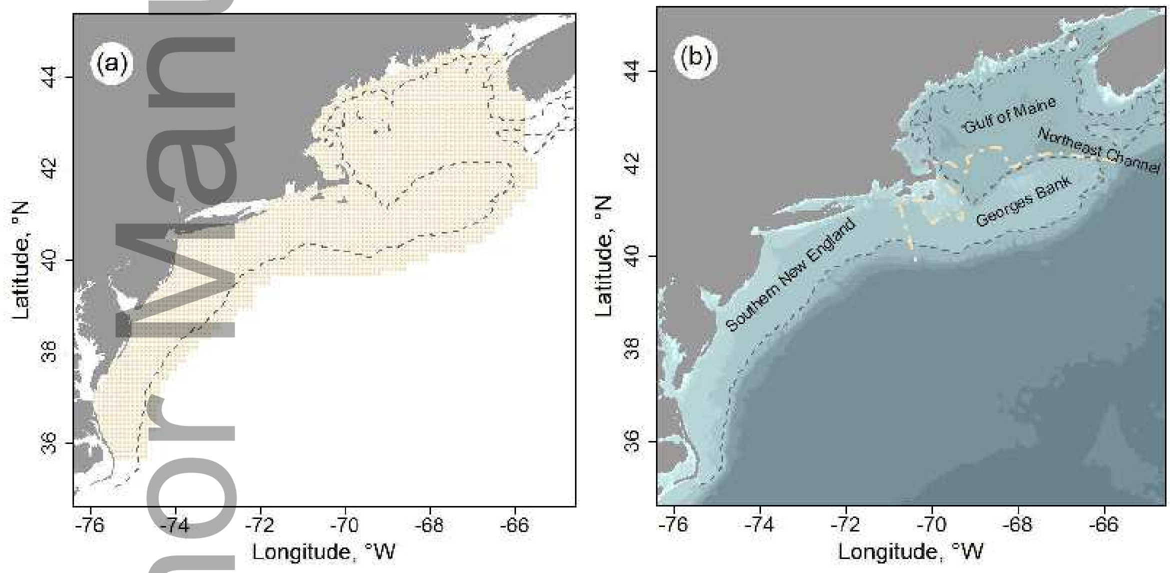

Figure 1. Northeast U.S. shelf with the estimation grid (a). Boundaries between Gulf of Maine, Georges Bank and Southern New England regions demarked with yellow lines (b). Grey dashed lines denote 100 m depth contour.

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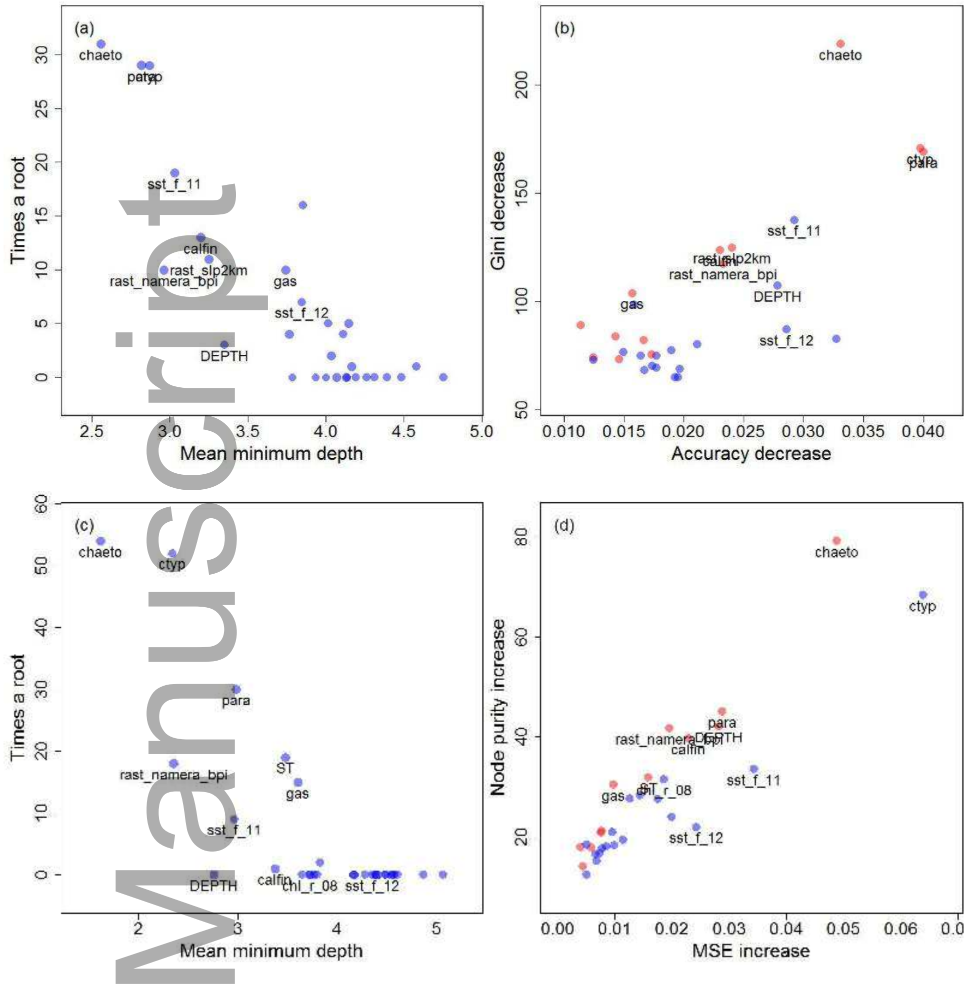

Figure 2. The number of times a variable was the root node variable versus the mean minimal depth of a variable in a tree in spring occupancy (a) and biomass (c) models. The mean decrease in the Gini index of node impurity by a variable versus the mean accuracy decrease if a variable were to be removed from the spring occupancy model (b); red circles indicate that the variable is significant. The mean node purity increase by a variable versus the mean increase of mean squared error (MSE) if a variable were to be removed from the spring biomass model (d); red circles indicate that the variable is significant. The variables are significant if the number of nodes in which the variable was used for splitting is greater than the theoretical number of successes if they were random. The explanations of the abbreviations are in Table A1.

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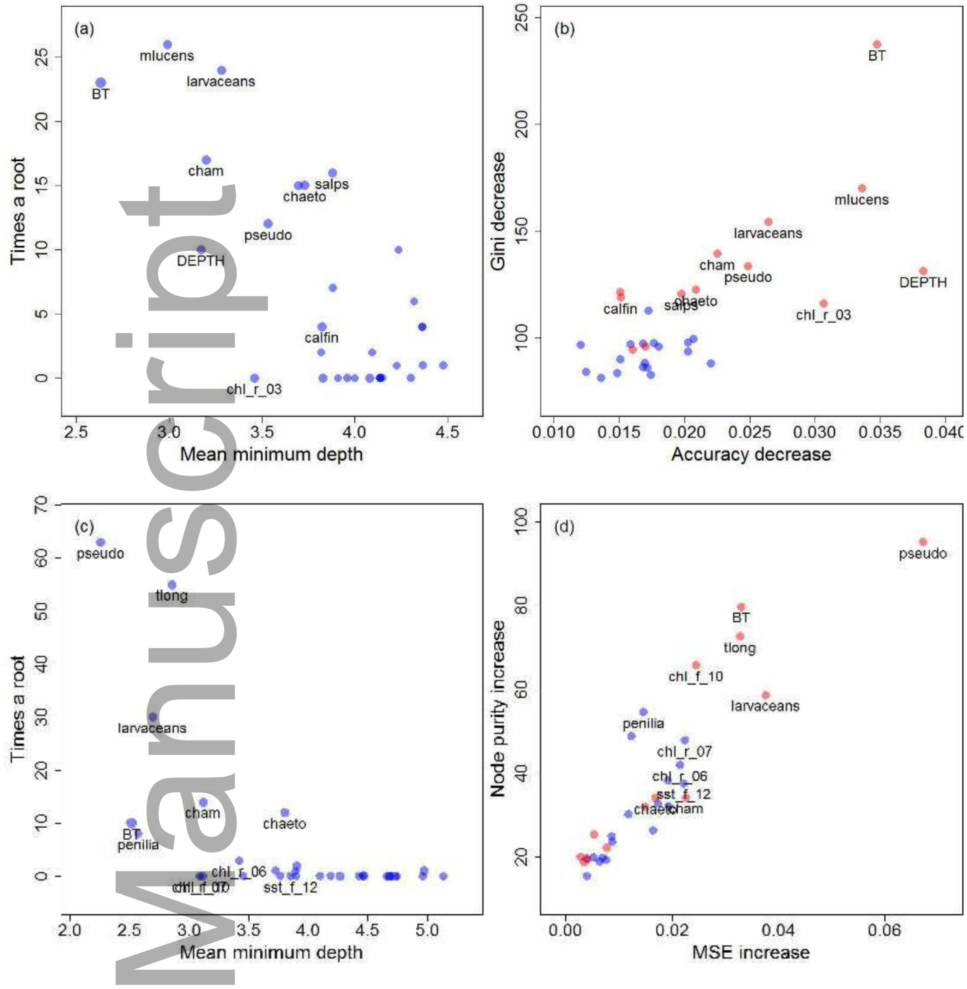

Figure 3. The number of times a variable was the root node variable versus the mean minimal depth of a variable in a tree in fall occupancy (a) and biomass (c) models. The mean decrease in the Gini index of node impurity by a variable versus the mean accuracy decrease if a variable were to be removed from the fall occupancy model (b); red circles indicate that the variable is significant. The mean node purity increase by a variable versus the mean increase of mean squared error (MSE) if a variable were to be removed from the fall biomass model (d); red circles indicate that the variable is significant. The variables are significant if the number of nodes in which the variable was used for splitting is greater than the theoretical number of successes if they were random. The explanations of the abbreviations are in Table A1.

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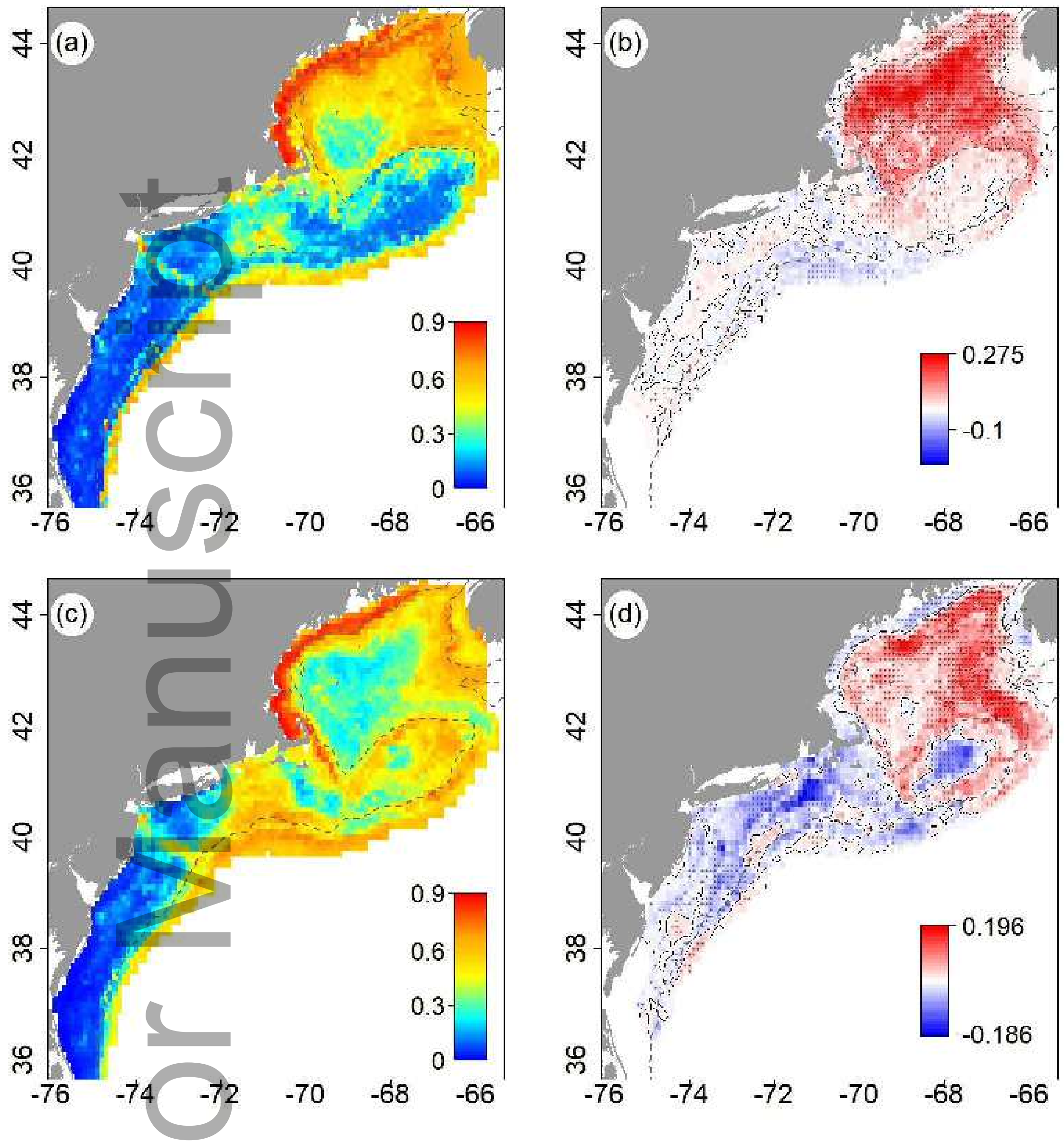

Figure 4. Time series mean predicted occupancy probability for American lobster in the spring (a) and fall (c) using the RF model with the annual rate of change (Sen slope) in occupancy probability (b and d, spring and fall, respectively). Black crosses in rate of change panels indicate significant slopes (p<0.01).

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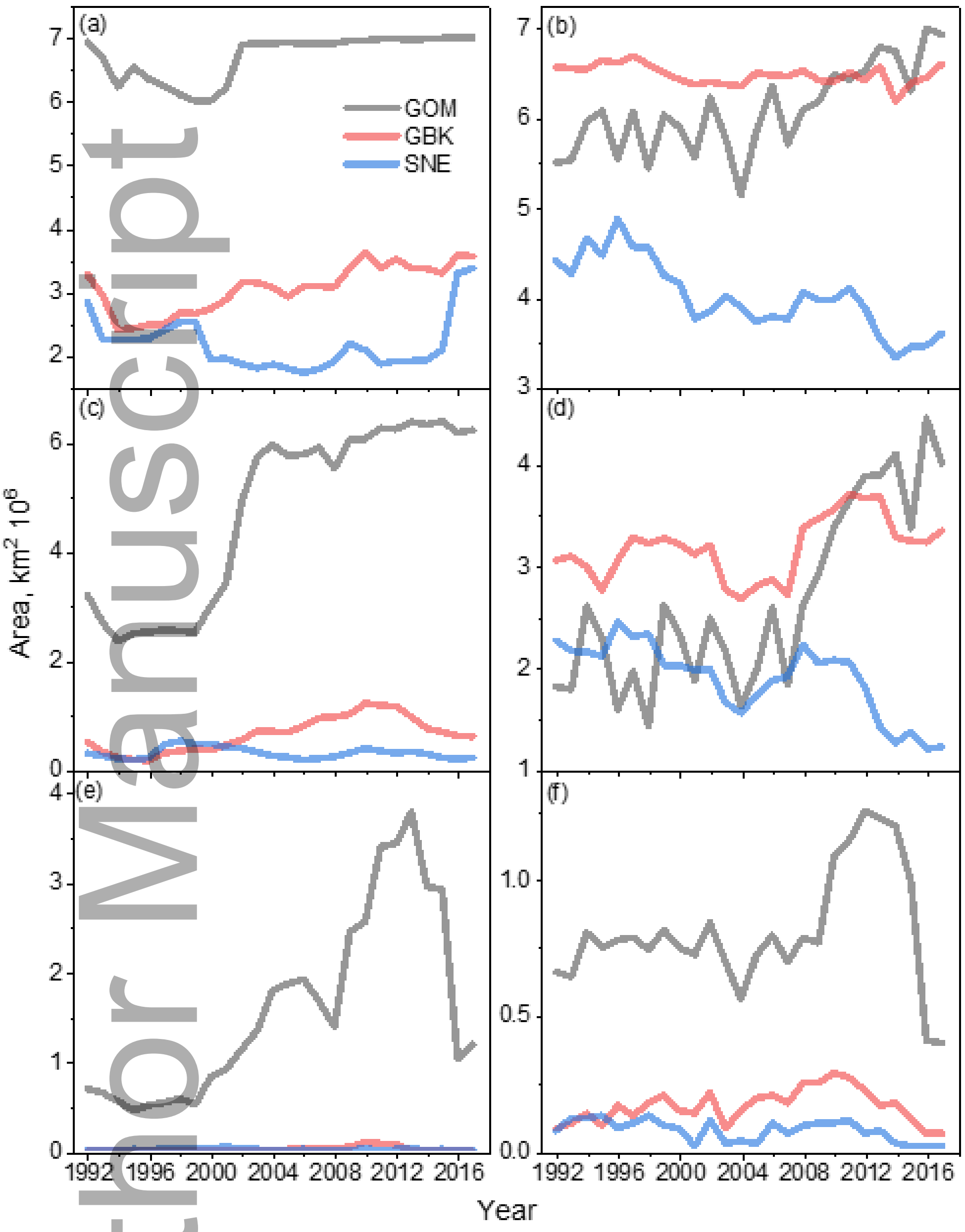

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Figure 5. Habitat areas in each region (Gulf of Maine, Georges Bank, and Southern New England) with minimum occupancy probabilities of 25%, 50%, and 75% for spring (a, c, and e, respectively) and fall (b, d, and f, respectively) for the years 1992 to 2017 predicted from the RF models.

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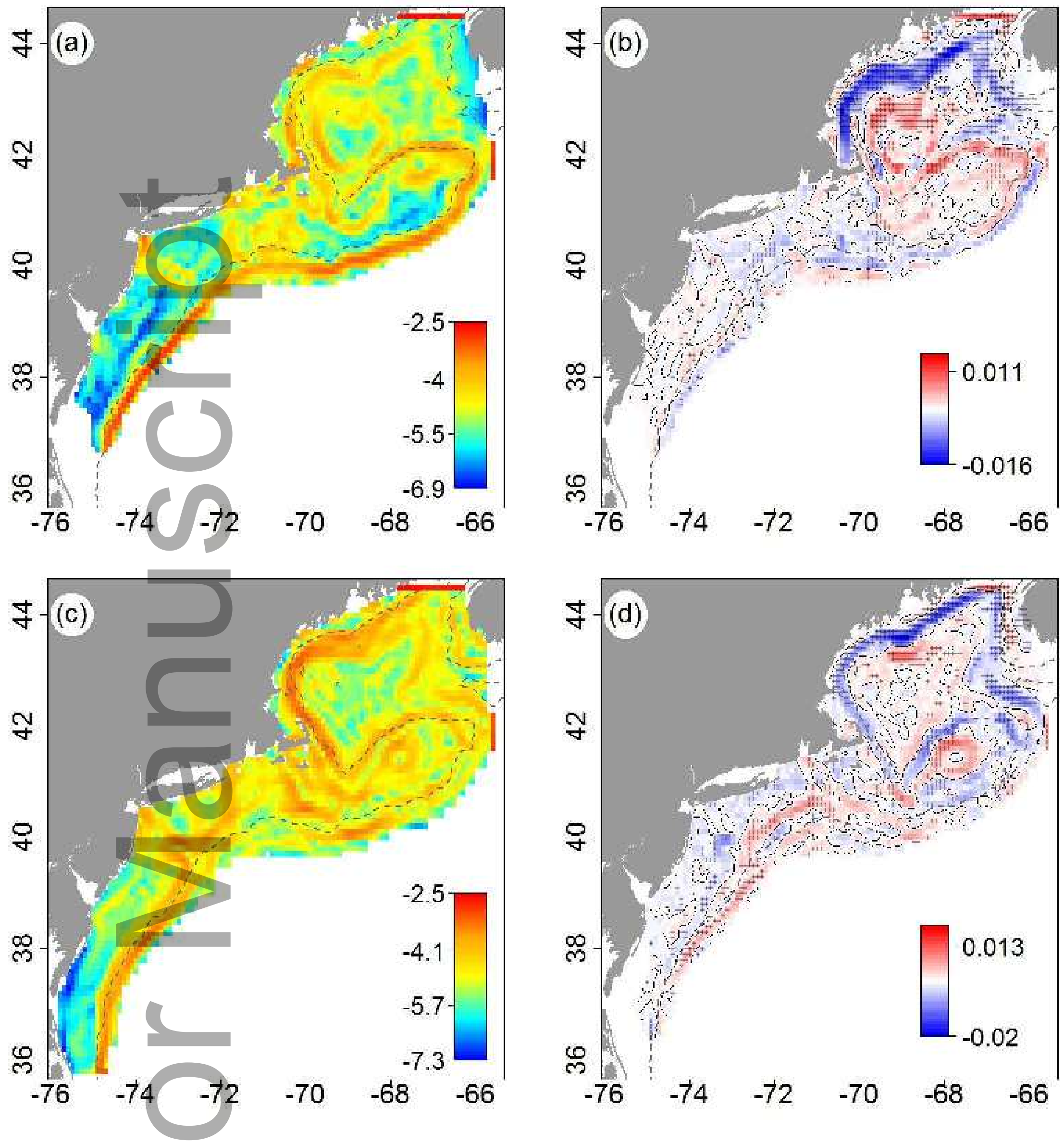

Figure 6. Time series mean occupancy probability gradient magnitudes (frontal strengths) predicted in the spring (a) and fall (c) with the rates of change (Sen slope) in occupancy gradient magnitudes (b and d, spring and fall, respectively). Black crosses in rate change panels indicate that the slopes are significant (p<0.01).

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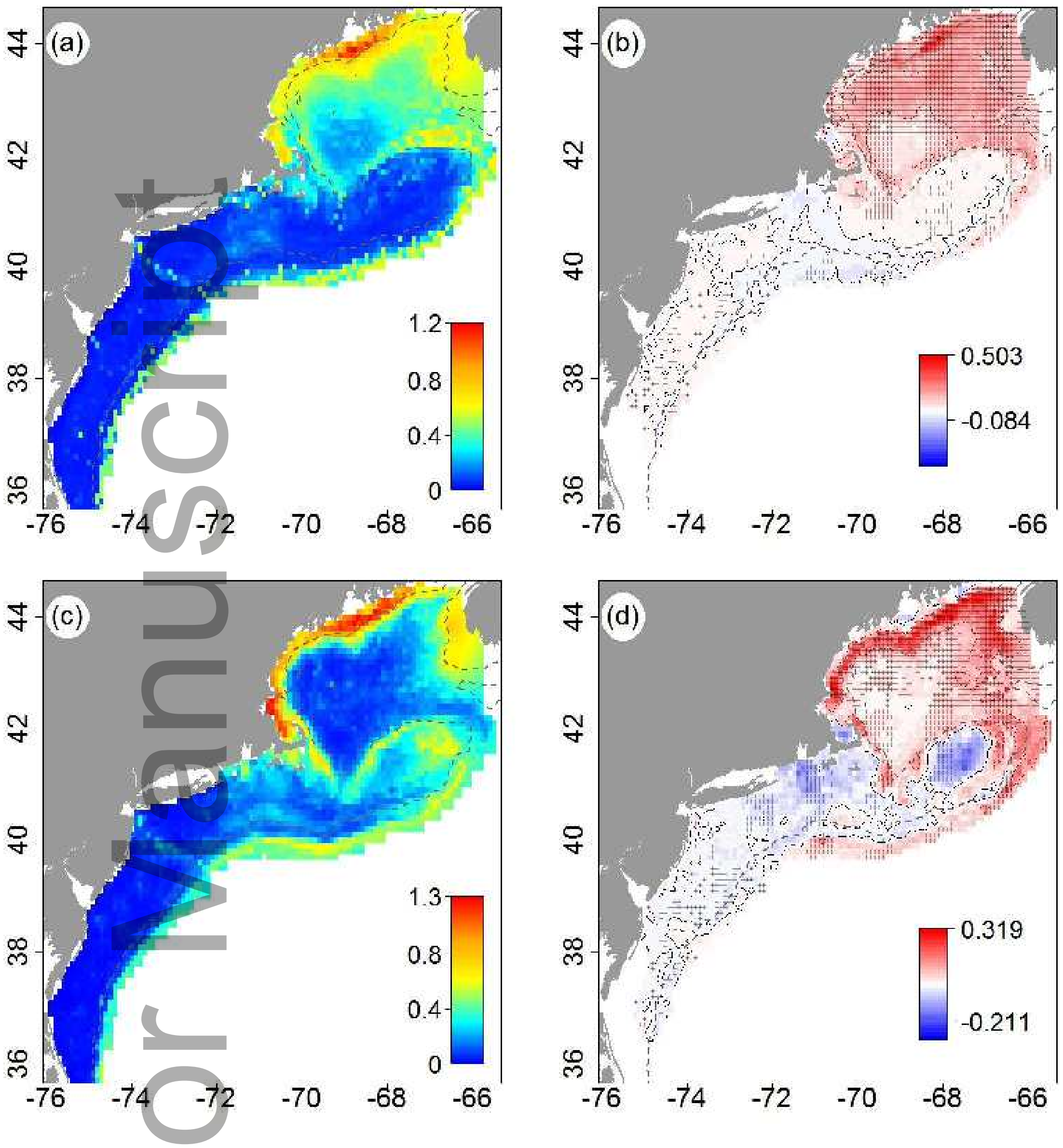

Figure 7. Time series mean predicted biomass for American lobster in the spring (a) and fall (c) using the RF model with the annual rates of change (Sen slope) in biomass (b and d, spring and fall, respectively). Black crosses in rate of change panels indicate significant slopes ($p<0.01$).

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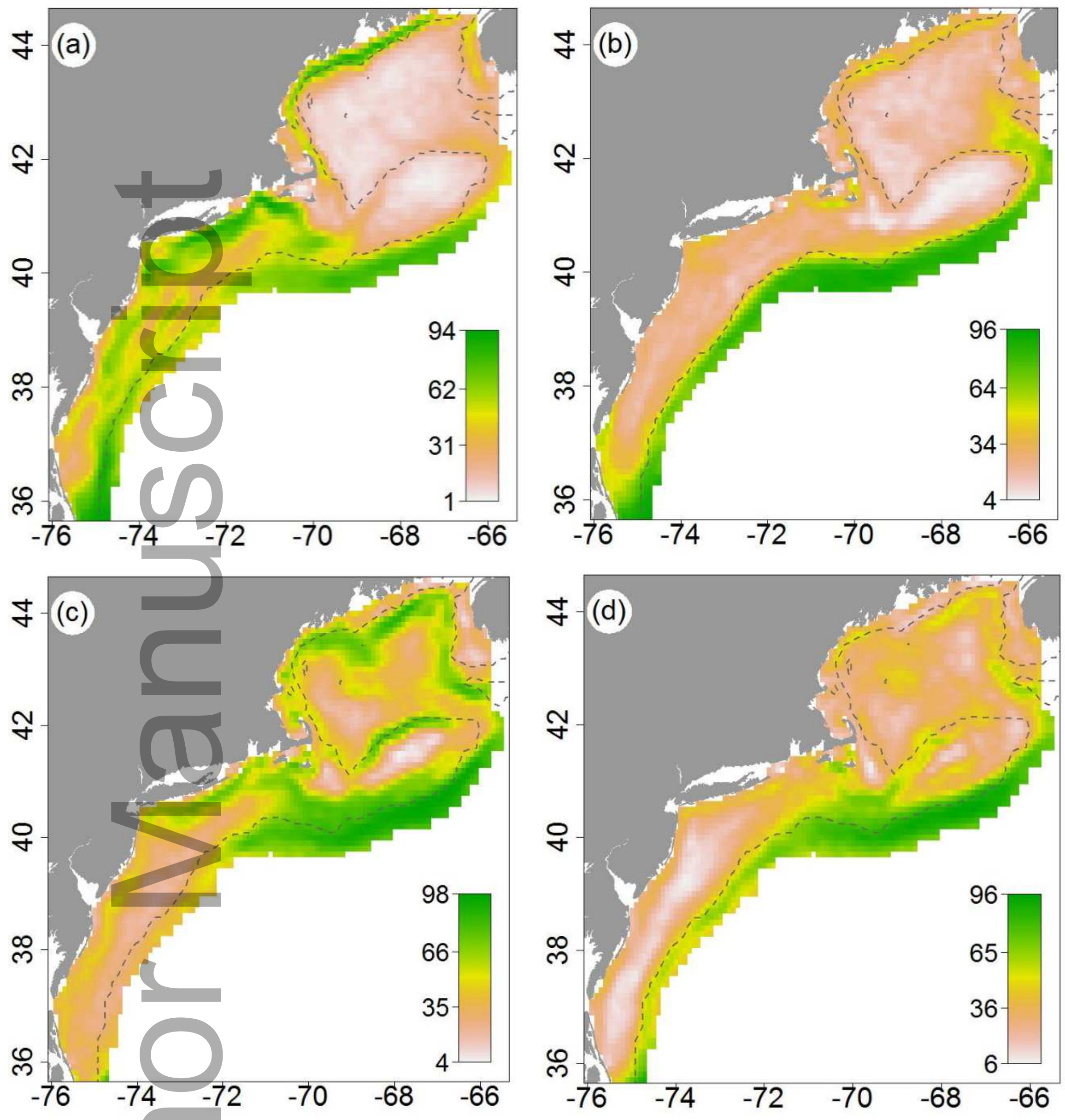

Figure 8. Sea surface temperature frontal probabilities (expressed as percent) for winter (a), spring (b), summer (c), and fall (d). Sea surface temperature frontal probabilities were taken from Winship et al. (2018) and represent the likelihood of a front forming during the four seasonal time periods.

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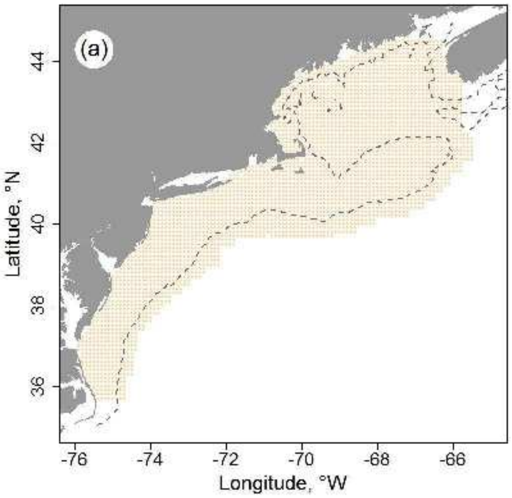

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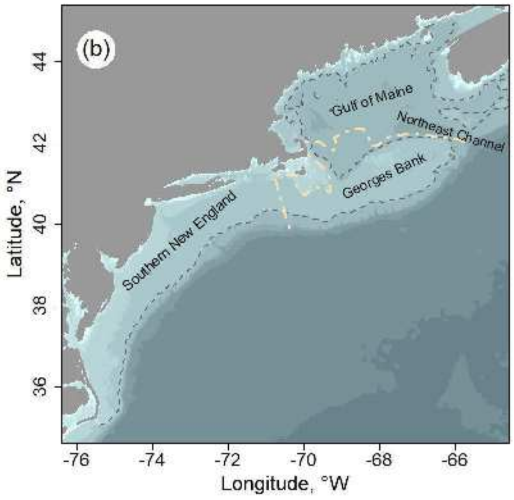

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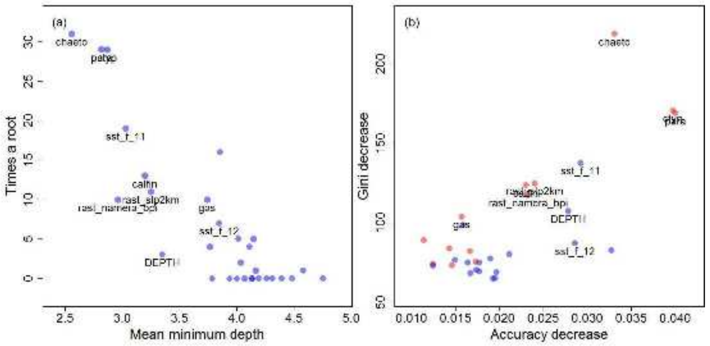

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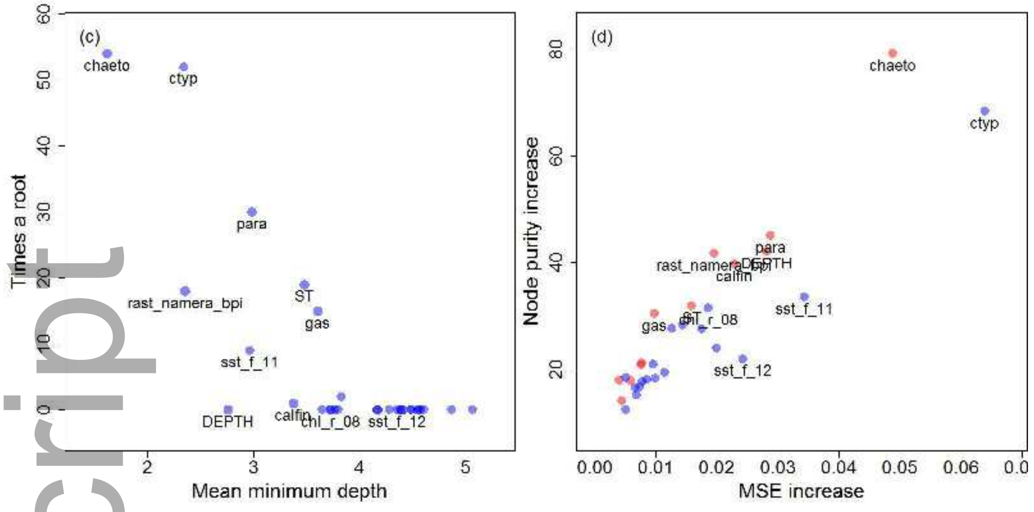

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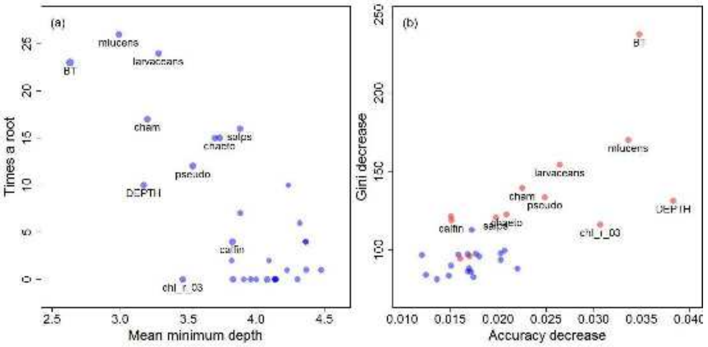

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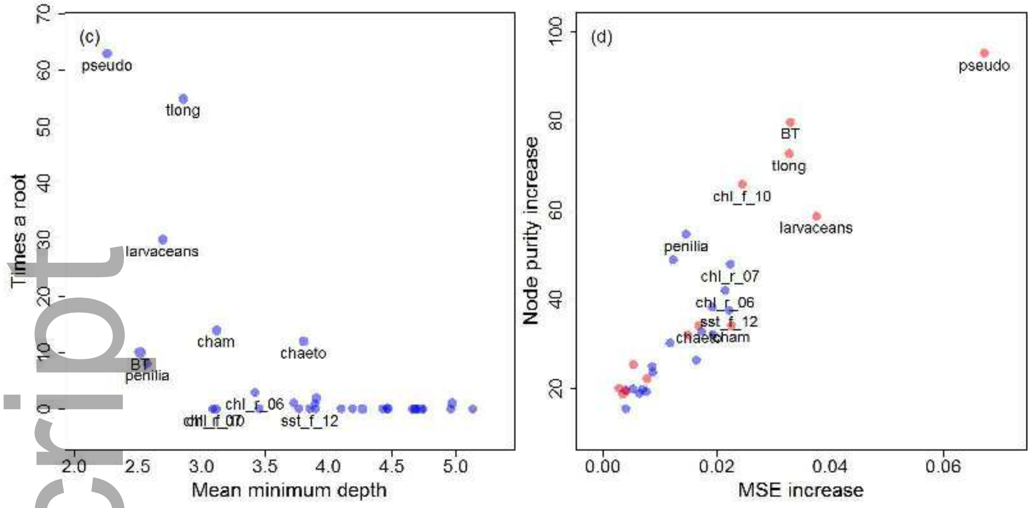

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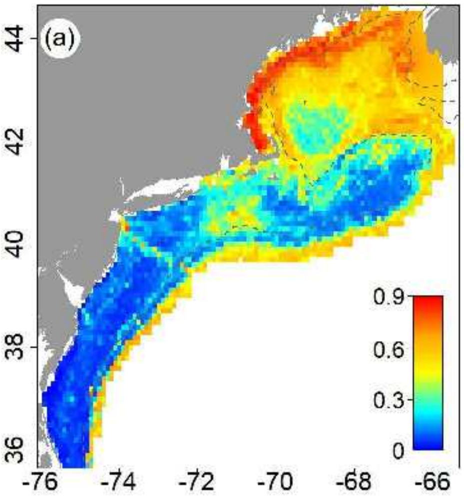

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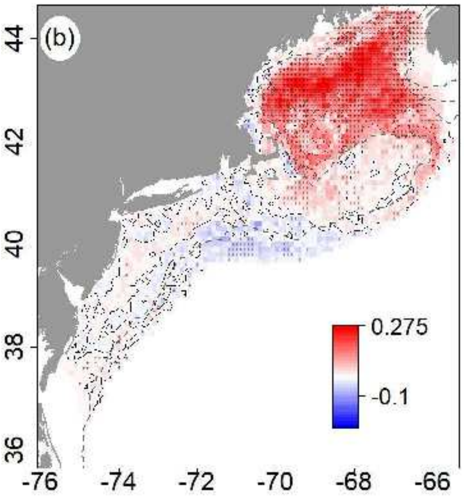

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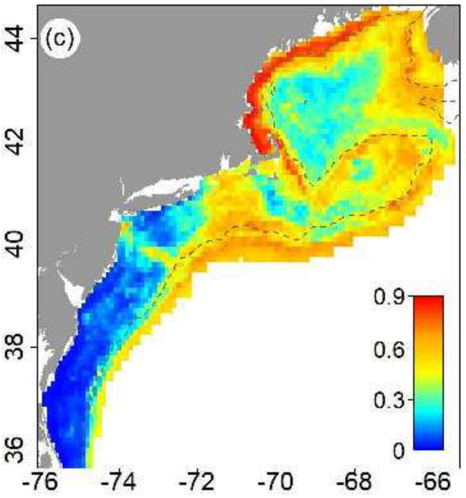

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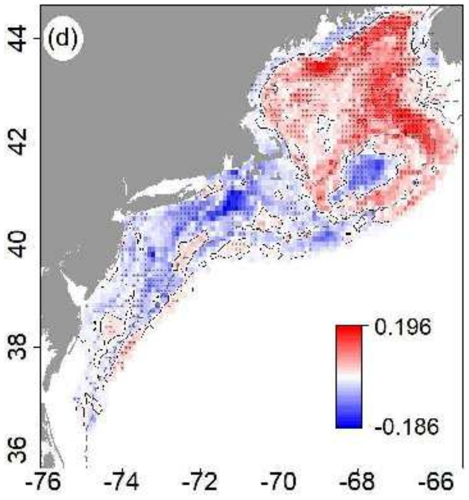

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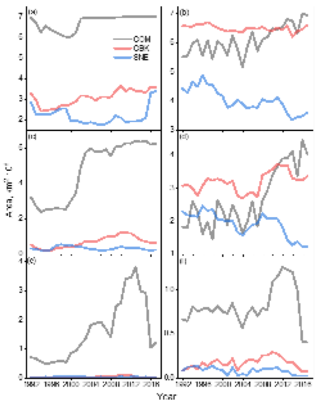

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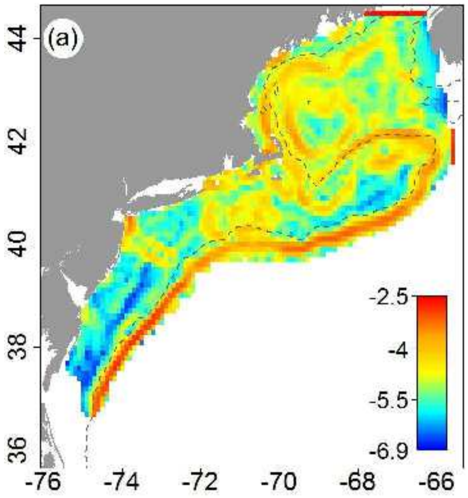

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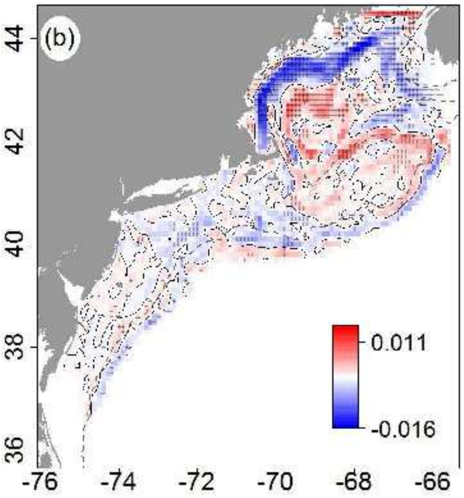

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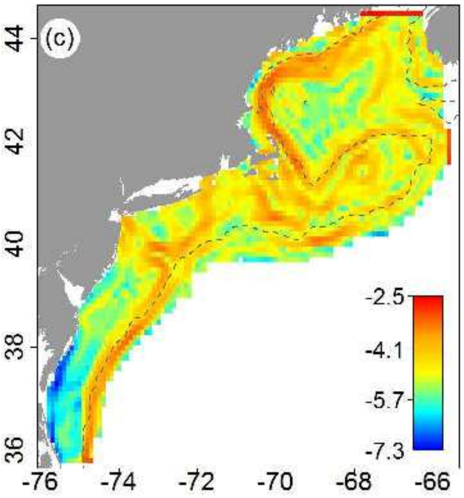

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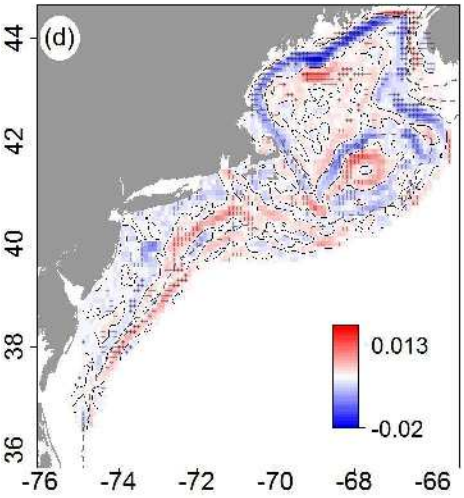

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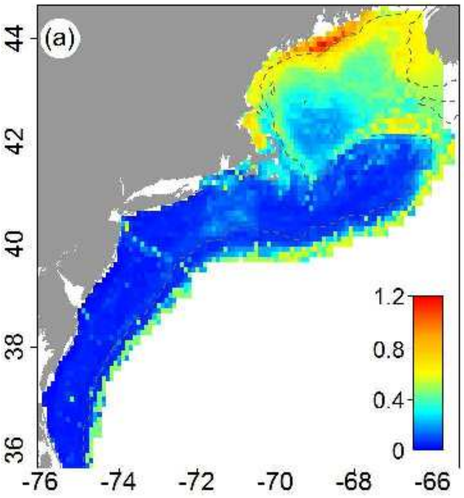

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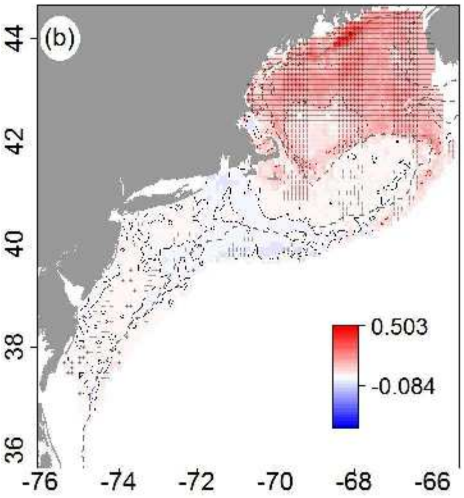

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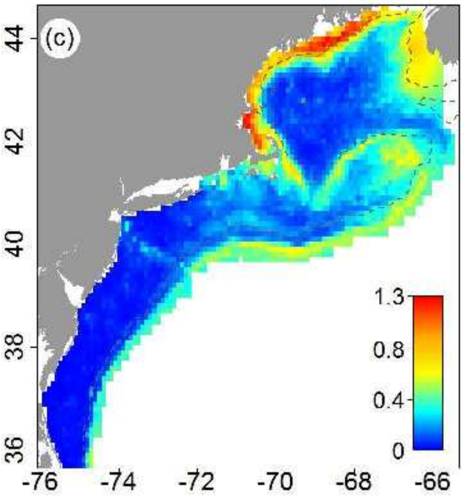

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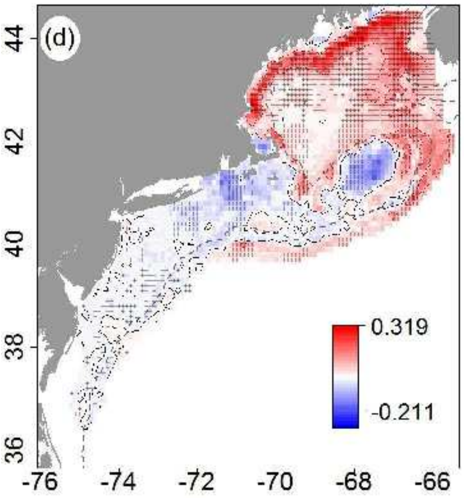

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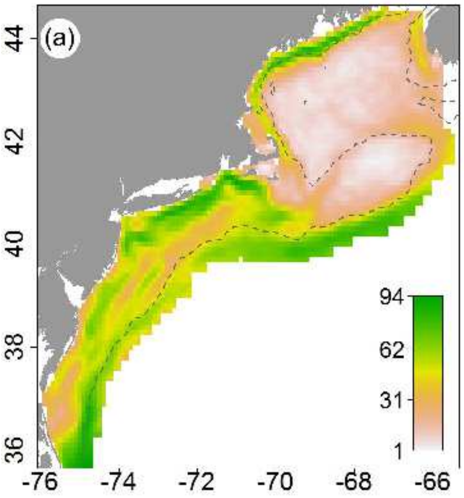

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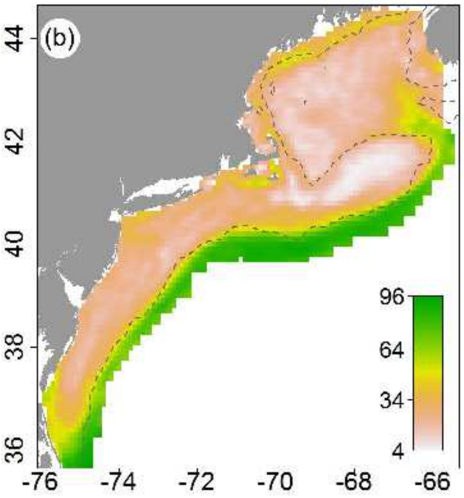

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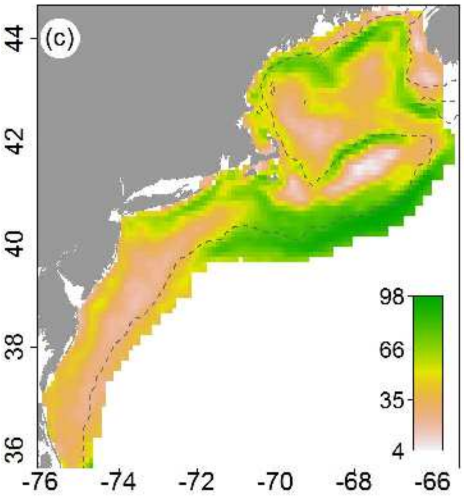

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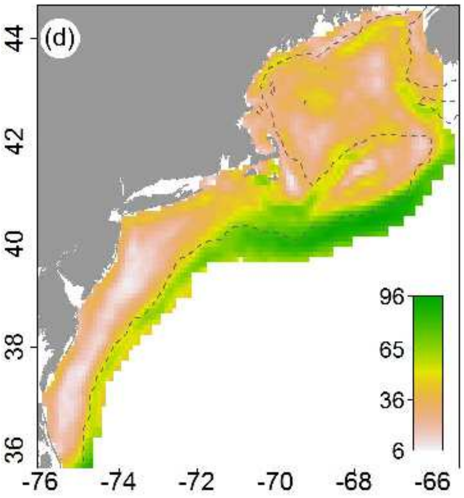

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