Vol. 641: 159–175, 2020
https://doi.org/10.3354/meps13302
MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser
Published May 7

Predicting bycatch hotspots based on suitable habitat derived from fishery-independent data

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ABSTRACT: Bycatch remains a global problem in managing sustainable fisheries. A critical aspect of management is understanding the timing and spatial extent of bycatch. Fisheries management often relies on observed bycatch data, which are not always available due to a lack of reporting or observer coverage. Alternatively, analyzing the overlap in suitable habitat for the target and non-target species can provide a spatial management tool to understand where bycatch interactions are likely to occur. Potential bycatch hotspots based on suitable habitat were predicted for cusk *Brosme brosme* incidentally caught in the Gulf of Maine American lobster *Homarus americanus* fishery. Data from multiple fisheries-independent surveys were combined in a delta-generalized linear mixed model to generate spatially explicit density estimates for use in an independent habitat suitability index. The habitat suitability indices for American lobster and cusk were then compared to predict potential bycatch hotspot locations. Suitable habitat for American lobster has increased between 1980 and 2013 while suitable habitat for cusk decreased throughout most of the Gulf of Maine, except for Georges Basin and the Great South Channel. The proportion of overlap in suitable habitat varied interannually but decreased slightly in the spring and remained relatively stable in the fall over the time series. As Gulf of Maine temperatures continue to increase, the interactions between American lobster and cusk are predicted to decline as cusk habitat continues to constrict. This framework can contribute to fisheries managers' understanding of changes in habitat overlap as climate conditions continue to change and alter where bycatch interactions could occur.

KEY WORDS: Habitat modeling · Data limited management · Bycatch hotspots

1. INTRODUCTION

A critical aspect of species management or conservation is understanding the timing and spatial extent of species co-occurrence and how that changes over time due to changing habitat (Lewison et al. 2009) and climate (Ward et al. 2015). In the marine realm, understanding species co-occurrence is a critical aspect of managing bycatch (Ward et al. 2015), which remains a serious global threat to the conservation of endangered or overfished species (Alverson et al. 1996, Crowder & Murawski 1998, Morgan & Chuenpagdee 2003, Harrington et al. 2005). Typically, harvest data (e.g. observer or logbook data) are used to

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understand the spatio-temporal patterns of bycatch (Sims et al. 2008, Lewison et al. 2009). However, observer coverage, electronic monitoring, or catch and bycatch reporting programs are not always conducted for a fishery. Without directly observed fisheries-dependent data, the spatio-temporal trends of bycatch are often an unknown aspect of a management program that can lead to ineffective conservation of endangered or overfished bycatch species.

Concurrent habitat use can provide a method for understanding the potential spatial extent for persistent bycatch interactions (Lewison et al. 2009, Eguchi et al. 2017). The underlying ecological process of bycatch is shared habitat use, either seasonally or for portions of the species' life histories (Ward et al. 2015). Bycatch hotspots are evidence of concurrent habitat use by the target and non-target species (Sims et al. 2008). Fisheries-independent data may be useful in predicting where species are likely to co-occur, and thus provide a basis for understanding bycatch interactions in the absence of reliable fisheries-dependent data. For this approach to be successful, fisheries-independent data would need to capture the timing of the fishery and the bycatch interactions, in addition to having sufficient data for a model-based approach.

Habitat suitability indices (HSIs) assess relative habitat quality as a function of species density at a given location and the associated environmental conditions (Brooks 1997, Chen et al. 2009). HSIs provide a spatially explicit ranking, from 0 to 1, of habitat suitability, which allows for a direct comparison of suitable habitat across species, as opposed to comparing species density at a given location. Conventional HSIs typically utilize abundance indices derived from fisheries-independent surveys to evaluate the suitable range of environmental covariates (e.g. depth, bottom temperature, sediment type and salinity) within the survey coverage area (Terrell 1984, Terrell & Carpenter 1997, Morris & Ball 2006, Tanaka & Chen 2016). If fisheries-independent survey data have limited catches for a species or if catch rates have changed substantially over the time series, utilizing only one survey or data set to inform the HSI may not capture changes in habitat use. Instead, multiple surveys that sample different habitat types can be combined to derive model-based density estimates that account for changes in catchability to better inform HSIs (Runnebaum et al. 2018). Model-predicted density estimates can be derived from multiple fisheries-independent surveys using a spatio-temporal delta-generalized linear mixed model (delta-GLMM; Thorson et al. 2015, Thorson & Barnett 2017, Runnebaum et al. 2018). This approach can account for the differences in catch rates from multiple surveys, allowing for all available data to be fully utilized (Thorson & Ward 2014). Multiple surveys with different gear types can also be combined because of the ability to estimate catchability for each survey within the delta-GLMM (Runnebaum et al. 2018).

The objective of the present study was to use a modeling approach to predict areas where bycatch is likely to occur in a fishery based strictly on habitat suitability of the target and non-target species. As a case study, potential bycatch hotspots of cusk *Brosme brosme* were predicted for the American lobster *Homarus americanus* fishery. Cusk are known to be seasonally caught as bycatch in the Maine lobster fishery (Chen & Runnebaum 2014). American lobster supports the most valuable fishery in the United States (NMFS 2018) and cusk is a National Oceanic and Atmospheric Administration (NOAA) species of concern and currently under internal status review for the Endangered Species Act (72 FR 10710 2007).

2. MATERIALS AND METHODS

2.1. Survey and environmental data

Density estimates for cusk and American lobster were derived from multiple survey programs (Fig. 1, Table 1) that all operate in the spring and fall. All surveys used are stratified random surveys with different geographic regions, but have some overlap with each other. Data for cusk are available from the Northeast Fisheries Science Center (NEFSC) bottom trawl survey (1980–2015) and the NEFSC bottom longline survey (2014–2015). Survey data for American lobster are available from the NEFSC bottom trawl survey (1980–2015), the Maine–New Hampshire (ME–NH) bottom trawl survey (2001–2015) and the Massachusetts (MA) bottom trawl survey (1982–2015). The NEFSC bottom trawl survey operates from Cape Hatteras, North Carolina, to the Scotian Shelf in the Gulf of Maine (GOM). The NEFSC bottom longline survey operates in the western and central GOM to better sample demersal species in complex, rocky habitat not well sampled by the NEFSC bottom trawl survey (Hoey et al. 2013). The ME–NH inshore bottom trawl survey is conducted by the Maine Department of Marine Resources (Maine DMR) in the coastal waters of Maine and New Hampshire (Sherman et al. 2005). The MA bottom trawl survey is conducted by the Massachusetts Divi-

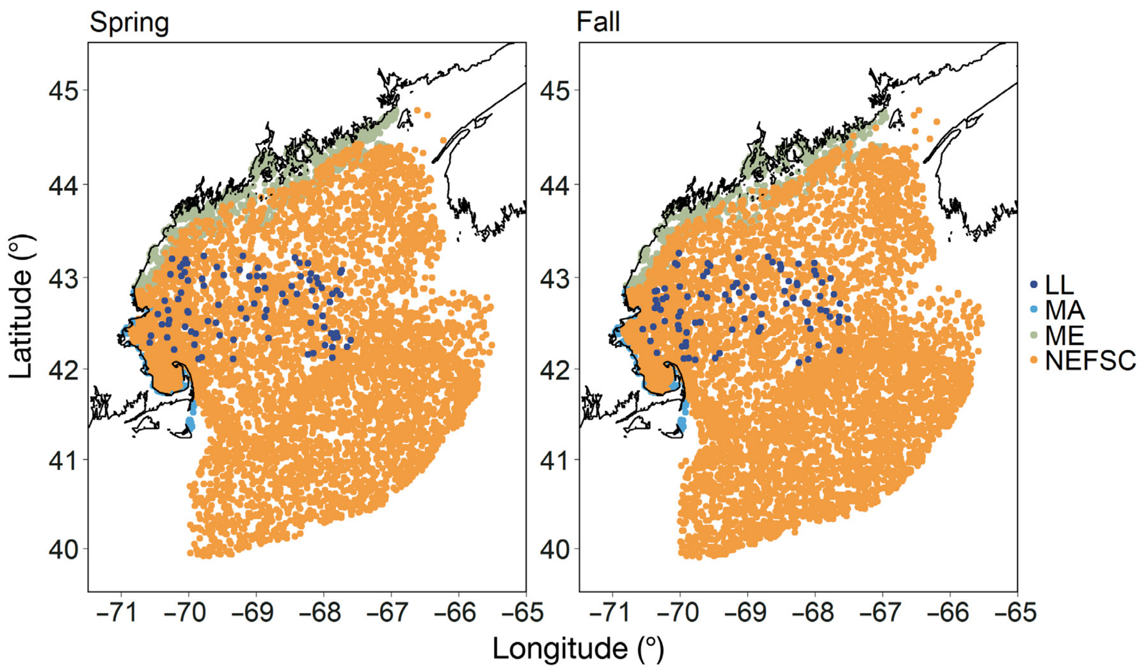

Fig. 1. Study area and survey data for overlap of cusk and American lobster. The Maine–New Hampshire (ME–NH), Massachusetts (MA) and Northeast Fisheries Science Center (NEFSC) are the bottom trawl surveys used for developing a model-based abundance index for American lobster. The NEFSC bottom trawl and longline (LL) surveys were used for developing the model-based abundance index for cusk

Table 1. Survey data. Includes sample size, depth coverage and which model the data were used for. NEFSC: Northeast Fisheries Science Center; ME: Maine; NH: New Hampshire; MA: Massachusetts; HSI: habitat suitability index

Data set	Sample size	Depth coverage (m)	Model used
NEFSC bottom trawl survey	25460	6 to 915	VAST cusk and lobster
NEFSC longline survey	179	29 to 272	VAST cusk
ME–NH Hampshire bottom trawl survey	3195	2 to 201	VAST lobster
MA bottom trawl survey	36761	4 to 86	VAST lobster
ME lobster sea sampling program	168	1 to 179	HSI qualitative validation

sion of Marine Fisheries (Massachusetts DMF) along the entire Massachusetts coast (King et al. 2010).

The Maine lobster sea sampling program provides spatially explicit fisheries-dependent data about the Maine lobster fishery (Maine DMR 2016), but is not a randomly designed observer program for bycatch. This program began sampling bycatch in 2006, when possible, and has inherent biases due to the lack of a random design for sampling and inconsistency in recording bycatch. However, these data were used to partially validate predicted bycatch hotspots.

Cusk habitat use is strongly influenced by depth, bottom temperature and sediment type (Hare et al. 2012, Runnebaum et al. 2018). Cusk have been documented in depths between 18 and 1000 m, and are thought to tolerate temperatures between 0°C and 14°C, with most cusk occurring between 6°C and 10°C in the GOM (Cohen et al. 1990, Collette & Klein-MacPhee 2002). Cusk are thought to prefer rock, gravel or pebble sediment, but are known to inhabit mud areas in the GOM, but not smooth sand (Cohen et al. 1990, Collette & Klein-MacPhee 2002). Environmental variables known to impact lobster habitat use are temperature, salinity and depth (Tanaka & Chen 2016). American lobsters are found in temperatures ranging from 0°C to 25°C, salinity ranging from 15 to 32 ppt (Reynolds & Casterlin 1979, Crossin et al. 1998, ASMFC 2015), and in a wide variety of sediment types. Juvenile and adult lobsters can be found in mud, cobble, bedrock inshore and in similar sediment types offshore as well as in clay (Lawton & Lavalli 1995). However, specific sediment preference is dependent on life history and molting stage (Lawton & Lavalli 1995). American lobsters are thought to be mainly found in depths up to 50 m but have been fished along the continental shelf in waters up to 700 m (Lawton & Lavalli 1995). Depth, temperature, sediment and salinity data were used to model habitat suitability for both species given the influence of these abiotic factors on habitat choice.

The American lobster stock boundary was the spatial extent over which monthly mean bottom temperature and salinity data (1980–2013) were used from the Northeast Coastal Ocean Forecast System (NECOFS) integrated atmosphere–ocean model forecast system for the GOM and Georges Bank (GB) regions. NECOFS data are generated over an unstructured Finite-Volume Community Ocean Model (FVCOM) G3 grid for these regions (Beardsley et al. 2013, NECOFS 2013). Seasonal means were taken for the predominant 3 mo in the spring (April, May and June) and the fall (September, October and November) when bottom trawl and longline surveys were conducted. Modeled depth data were extracted from the General Bathymetric Chart of the Oceans 30 arc-second interval grid (GEBCO 2014). Sediment data were extracted from the United States Geological Survey (USGS) East-Coast Sediment Texture Database (Poppe et al. 2014) using Geographic Information System (GIS). NECOFS bottom salinity, GEBCO depth and USGS sediment data were attributed to the centroid of the 0.05° × 0.05° grid cells spanning the GOM and GB statistical areas used as the spatial domain for this study.

2.2. Species density estimates

Cusk and American lobster density were separately estimated for the GOM and GB lobster stock areas using a delta-GLMM (VAST v7.0.0; Thorson et al. 2015). The present study is an extension of previous habitat suitability modeling efforts for cusk in the GOM that combined the NEFSC bottom trawl and longline surveys to estimate density fields for use in habitat mapping (Runnebaum et al. 2018). Previously published density field plots were developed for the cusk stock unit (i.e. statistical areas 464–465, 511–515, 521–522, 551 and 561), which would not capture the full extent of potential bycatch interactions in the state and federal lobster fisheries. In order to examine where cusk are likely to interact with the American lobster fishery, the defined GOM and GB lobster stock units, including statistical areas 464–465, 511–515, 525–526, 521–522, 551–552 and 561–562 (ASMFC 2015), were used in the present study (Fig. 1). Therefore, in this study, density estimates for cusk were re-estimated over the GOM and GB lobster stock areas using an improved version of VAST and lobster density estimates were newly developed.

The delta-GLMM is a 2-staged model that estimates catch in numbers (C) by estimating the probability (p) of encountering the target species (i.e. presence, Pr/absence):

$$\Pr\,[C > 0] = \mathrm{p}, \quad (1)$$

then estimating species density given the presence of a species (i.e. positive catches; Thorson et al. 2015):

$$\Pr[C = c \mid C > 0] = \mathrm{Gamma}(c, \sigma^{-2}, \lambda\sigma^{2})\ . \quad (2)$$

The second stage of the model assumes that the probability density function evaluated at value c follows a gamma distribution for both cusk and American lobster, where λ is the expected catch if encountered, and σ is the coefficient of variation for positive catches (Thorson & Ward 2014, Thorson et al. 2015).

Both stages of the model include 2 Gaussian Markov random fields to account for spatial (ω) and spatio-temporal (ε) autocorrelations (Thorson et al. 2015). The random fields are approximated at a prespecified number of knots that are generated over the defined domain (Thorson et al. 2015). In this study, 250 knots were preselected for both species and subsequently generated based on the proportional density of survey data over the study area for all years. Knot locations were determined by applying a k-means algorithm to survey location data. The area a_j of each knot j was then calculated using the Voronoi tool in the PBSmapping package (Schnute et al. 2018) in R version 3.5.1 (R Core Team 2018).

Encounter probability p_i and positive catch rates λ_i are approximated using linear predictors (Thorson et al. 2015):

$$\mathrm{p}_i = \mathrm{logit}^{-1}\left(d^{(\mathrm{p})}_{T_{(i)}} + Q^{(\mathrm{p})}_i + \omega^{(\mathrm{p})}_{J_{(i)}} + \varepsilon^{(\mathrm{p})}_{J_{(i)},T_{(i)}}\right)\ , \quad (3)$$

$$\lambda_i = w_i \exp\left(d^{(\lambda)}_{T_{(i)}} + Q^{(\lambda)}_i + \omega^{(\lambda)}_{J_{(i)}} + \varepsilon^{(\lambda)}_{J_{(i)},T_{(i)}}\right)\ , \quad (4)$$

where p_i and λ_i are the expected probabilities of an occupied habitat and positive catches given occupied habitat for sample i at a given location, respectively; $d_{T_{(i)}}$ is the average reference density (encounters/positive catch rates) in year T_i; Q_i is catchability for each survey; w_i is the area swept for sample i; J_i is the nearest knot to sample i; $\omega_{J_{(i)}}$ is a random field accounting for spatially correlated variability at knot

J_i that is persistent among years; and $\varepsilon_{J_{(i)},T_{(i)}}$ is the random field accounting for spatio-temporal correlation at knot J_i in year T_i (Thorson et al. 2015). Density estimates were extrapolated over a pre-specified survey area grid with 0.05° × 0.05° grid cells, resulting in a density estimate for each grid cell.

Multiple surveys were combined within the delta-GLMM to improve spatio-temporal coverage for both species (Runnebaum et al. 2018). Following the same approach used in Runnebaum et al. (2018), cusk density estimates were developed using the NEFSC bottom trawl and longline surveys to capture the full breadth of habitat distribution where cusk are found. Following similar methods, lobster density estimates were developed by combining the NEFSC bottom trawl survey, the ME–NH inshore bottom trawl survey and the MA bottom trawl survey.

For cusk, this study assumes that catchability needs to be estimated for the bottom trawl survey before and after the 2009 protocol changes that were instituted when the NEFSC replaced the research survey vessel. The protocol changes resulted in different catchabilities, which could not be estimated for cusk due to low catch numbers and low frequency of occurrence during the calibration studies, preventing the estimation of conversion coefficients (Miller et al. 2010). To account for these differences in the delta-GLMM, the NEFSC bottom trawl survey is considered as 2 separate surveys before and after the 2009 protocol change. A 3-column design matrix for cusk was built using the R package ThorsonUtilities with as many rows as observations and reduced to a 2-column matrix for identifiability (Runnebaum et al. 2018). The estimated intercepts for Q_i and $d_{T_{(i)}}$ are collinear when both are estimated in the model. To resolve this issue, a structure on temporal variation was defined for both stages of the cusk delta-GLMM. A random walk process was defined for $d_{T_{(i)}}$ for the first and second stages of the cusk delta-GLMM (Runnebaum et al. 2018). The random walk process can also account for time-varying catchability as a result of changes in species abundance (Wilberg et al. 2009).

The lobster delta-GLMM also required a 3-column design matrix for the 3 surveys included (i.e. ME–NH, MA and NEFSC bottom trawl surveys) and was reduced to a 2-column matrix. A random-walk process was defined for $d_{T_{(i)}}$ for the first and second stages of the lobster delta-GLMM. A random-walk process was also necessary to account for time-varying catchability of American lobster, as both species showed strong trends over time. While cusk population abundance has declined (Hare et al. 2012), the American lobster population abundance has steadily increased (ASMFC 2015), resulting in much higher catch rates of American lobster in more recent years.

2.3. Habitat suitability indices

HSIs evaluate a species' relative abundance for selected environmental variables to quantify habitat suitability at a given location (Terrell 1984, Terrell and Carpenter 1997). Suitability indices (SIs) are calculated for each environmental variable to describe the optimal range of environmental conditions (Terrell 1984, Terrell & Carpenter 1997, Morris & Ball 2006), which provides a ranking approach to evaluate suitability based on available data. The individual SIs are then averaged through a geometric mean or an arithmetic mean at each location to determine the cumulative HSI from most suitable (1) to least suitable (0) for each location (Chen et al. 2009, Tanaka & Chen 2016, Torre et al. 2019). Locations with the highest abundance are assumed to have the most suitable habitat for that organism.

Annual HSIs were derived for cusk and American lobster for the spring and fall to estimate habitat overlap over the defined spatial extent from 1980 to 2013. The HSI time series was truncated due to a lack of NECOFS modeled-temperature data being available at the time of analysis. The HSI model algorithm was developed by Tanaka & Chen (2016) for American lobster that previously utilized standardized catch-per-unit-effort from the ME–NH inshore bottom trawl survey. Density estimates derived from the delta-GLMM were used in the annual HSI models in place of sample-based abundance estimates for both species (Runnebaum et al. 2018). Using model-based density estimates provides spatially explicit density estimates in areas that were not directly sampled, and has shown improvement in HSI model performance (Runnebaum et al. 2018).

Mean density was estimated for each grid cell from the annual cell density derived in the delta-GLMM. The SI for bin k of environmental variable J, $SI_{J,k}$, was calculated on a scale of 0 to 1 (Chang et al. 2012, Tanaka & Chen 2015, 2016):

$$\mathrm{SI}_{J,k} = \frac{\overline{D_{J,k}} - \overline{D_{J,\min}}}{\overline{D_{J,\max}} - \overline{D_{J,\min}}}, \quad (5)$$

where $\overline{D_{J,k}}$ is the mean density over the entire study area within bin k for each environmental variable J. These SI values were then averaged as an arithmetic mean (AMM) and a geometric mean (GMM) for each cell:

$$\mathrm{HSI}_{\mathrm{AMM}} = \frac{\sum_{J=1}^{n} \mathrm{SI}_J}{n}\ , \qquad (6)$$

$$\mathrm{HSI}_{\mathrm{GMM}} = \prod_{J=1}^{n} \mathrm{SI}_J^{1/n}\ , \qquad (7)$$

where all SI_J represent equally weighted SI values associated for the Jth environmental variable for calculating annual HSI values, and n is the number of SI values included (i.e. the number of environmental variables; Tanaka & Chen 2015, 2016, Runnebaum et al. 2018, Tanaka et al. 2019). Annual $\mathrm{HSI}_{\mathrm{AMM}}$ and annual $\mathrm{HSI}_{\mathrm{GMM}}$ were each averaged over the time series to derive $\overline{\mathrm{HSI}}_{\mathrm{AMM}}$ and $\overline{\mathrm{HSI}}_{\mathrm{GMM}}$.

$\overline{\mathrm{HSI}}$ model performance in predicting species-specific habitat suitability at a given grid cell was cross-validated using a randomized test/train split approach. For this validation process, an $\overline{\mathrm{HSI}}$ model is built using a randomly partitioned 80% of the original data as the training data set to derive bin classifications for each environmental variable. The HSI values derived from the training data set (predicted HSI) were regressed against the HSI values derived from the test data set (observed HSI). This random-data partition process was applied to each year between 1980 and 2013. The resulting coefficients of determination (r^2) were used as an index of model performance based on runs using test data.

Changes in habitat suitability over the spatial domain were evaluated on an annual basis for cusk and American lobster. The vector of annual HSI values for each grid cell was linearly regressed by year to estimate the slope, or change. Slope was then extracted for each grid cell and mapped over the study area to evaluate where habitat for both species had changed positively or negatively over time for a given location (Tanaka & Chen 2016, Tanaka et al. 2019, Torre et al. 2019). A positive slope indicates an increase in habitat suitability while a negative slope indicates a decrease in habitat suitability over the time series.

2.4. Overlap of cusk and American lobster

Mean areas of overlap $\left(\overline{O_{T,i}}\right)$ were estimated for each year (T) at each grid cell (i) using mean cusk and American lobster HSI maps for areas where habitat suitability was >0:

$$\overline{O_{T,i}} = \overline{\mathrm{HSI}_{\mathrm{Lobster},T,i}} - \overline{\mathrm{HSI}_{\mathrm{Cusk},T,i}} \qquad (8)$$

Annual overlap maps were made for each season to extract the annual proportion of habitat suitability overlap. Grid cells with an $\overline{\mathrm{HSI}}_{\mathrm{AMM}} > 0$ were summed across the entire study area and extracted as a proportion of the total number of grid cells for each species. The changes in annual proportion of overlap were then correlated to NECOFS simulated mean seasonal bottom temperature to evaluate the relationship of temperature to the proportion of habitat overlap, using the cross-correlation function (CCF) from the tseries package (Trapletti & Hornik 2018). Temperature variability from year to year is hypothesized to drive the proportion of habitat suitability overlap for these 2 species with strong temperature preferences and dependences.

To validate the mean areas of overlap in habitat (Eq. 8) for cusk and American lobster, the positive cusk catches from the Maine DMR lobster sea sampling data (Maine DMR, unpubl. data) were mapped on top of the median overlap maps. This allows for a qualitative evaluation of the median overlap predictions.

3. RESULTS

3.1. Delta-GLMM density estimates

Spatially explicit density estimates for each grid cell over the spatial domain were extracted for use in developing the HSI. Model results from VAST are presented in Fig. A1 in the Appendix. All delta-GLMMs for cusk and lobster in both the spring and fall converged and parameter estimates were within bounds. The best model fit for both seasons and both species were produced with a random-walk process defined for $d_{T_{(i)}}$ for the first and second stages of the models to account for changes in species abundance over the time series. Pearson residual plots for both cusk and lobster did not demonstrate any spatial patterns in residuals (Fig. A1). Density field estimates for cusk show a contraction of the population further offshore while American lobster showed an expansion of the population throughout the GOM and GB regions with a predominant increase in the inshore area (Fig. A2).

3.2. Habitat suitability index models

Seasonal $\overline{\mathrm{HSI}}$ models were compared to determine the best method for estimating habitat suitability for cusk and lobster. The AMM HSIs performed better for both cusk and lobster based on cross-validation analyses (Table 2). Cross-validation for cusk indicated marginal differences in model performance between the AMM (e.g. cusk spring r^2 = 0.98) and GMM (e.g. cusk spring r^2 = 0.93; Table 2), with the AMM having slightly less variability in predictive performance (Fig. 2). Because the cross-validation analyses showed greater variability in predictive performance for both cusk and American lobster using the GMM HSI compared to the AMM HSI (Fig. 2), seasonal habitat maps for both species were based on AMM $\overline{\text{HSIs}}$ to preserve methodological consistency.

The resulting habitat distribution maps indicate that American lobster suitable habitat is predominately inshore on the northern and southern coastal shelves and on portions of GB and Browns Bank (Fig. 3). In the fall, suitable habitat for American lobster expands in the inshore areas and on GB (Fig. 3). The most suitable habitat for cusk is offshore in the central GOM, outside of the prominent basins in the region and on the edge of GB (Fig. 3). Suitable habitat locations for cusk and American lobster are almost the inverse of each other, with lobster preferring inshore habitat and cusk predominately preferring offshore habitat (Fig. 3).

American lobster habitat suitability in both the spring and fall increased over most of the study area. The most pronounced changes for American lobster were the inshore GOM, off the coast of Nova Scotia, Browns Banks and somewhat on GB (Fig. 4). For cusk, habitat suitability declined over most of the region, with a more pronounced decline in the spring than in the fall. The most pronounced changes were in the western GOM around Wilkinson Basin, off the coast of Nova Scotia and on GB (Fig. 4). There was some increase in habitat suitability for cusk in the spring around Georges Basin, Jordan Basin and the Northeast Channel to the east of GB (Fig. 4). In the fall, habitat suitability for cusk predominately decreased throughout the GOM and GB (Fig. 4).

Table 2. Evaluation of model fit. Coefficient of determination (r^2) for all HSI models based on a test/train validation approach to evaluate model performance. AMM: arithmetic mean; GMM: geometric mean

Model	Intercept	Slope	r^2
Cusk spring AMM	0.01	0.99	0.98
Cusk spring GMM	0.03	0.96	0.93
Lobster spring AMM	0.00	1.00	0.96
Lobster spring GMM	0.00	0.99	0.95
Cusk fall AMM	0.00	0.99	0.98
Cusk fall GMM	0.03	0.96	0.93
Lobster fall AMM	0.00	0.97	0.96
Lobster fall GMM	0.00	0.98	0.95

3.3. Overlap of cusk and lobster

There is inter-annual variability in the proportion of overlap for both seasons, with an overall decrease in the proportion of overlap in the spring and a slightly decreasing trend in the fall (Fig. 5). Time-series analysis indicates the proportion of overlap in habitat suitability was a non-significant relationship within a biologically reasonable time frame or at time 0 for the spring (r = 0.02) or the fall (r = 0.16).

Mean areas of overlap in suitable habitat for cusk and lobster are mostly in the nearshore regions along the northern coastal shelf (Fig. 6). Mean overlap in the spring months provides evidence of persistent areas of habitat overlap along the edge of the northern and southern coastal shelf, in the central GOM, where cusk habitat is highest, and on the southern portion of GB in both the spring and fall (Fig. 6). In the fall, areas of overlap are reduced and most persistent along the inshore northern and southern coastal shelf and on GB (Fig. 6). The mean overlap maps indicate a higher proportion of overlap in the spring than in the fall (Fig. 6). Mean overlap maps were partially validated by overlaying known locations where cusk bycatch in the Maine lobster fishery has occurred from 2006 to 2013, combined (Fig. 6).

4. DISCUSSION

4.1. Model-based bycatch hotspot inference

There are increasing efforts to understand bycatch hotspots without the need for fisheries-dependent data (Sims et al. 2008, Lewison et al. 2009, Eguchi et al. 2017, Hazen et al. 2018). If fisheries-dependent bycatch data are biased due to an observer effect or are not representative of the fishery, then the understanding of bycatch hotspots could also be biased. In the American lobster fishery, fisheries-dependent bycatch data from the Maine DMR are not designed to account for bycatch interactions. Observers record minimal bycatch data when the sampler thinks it will be possible to consistently collect data throughout the day. This sampling design assumes that a location without bycatch information had a true zero non-target catch.

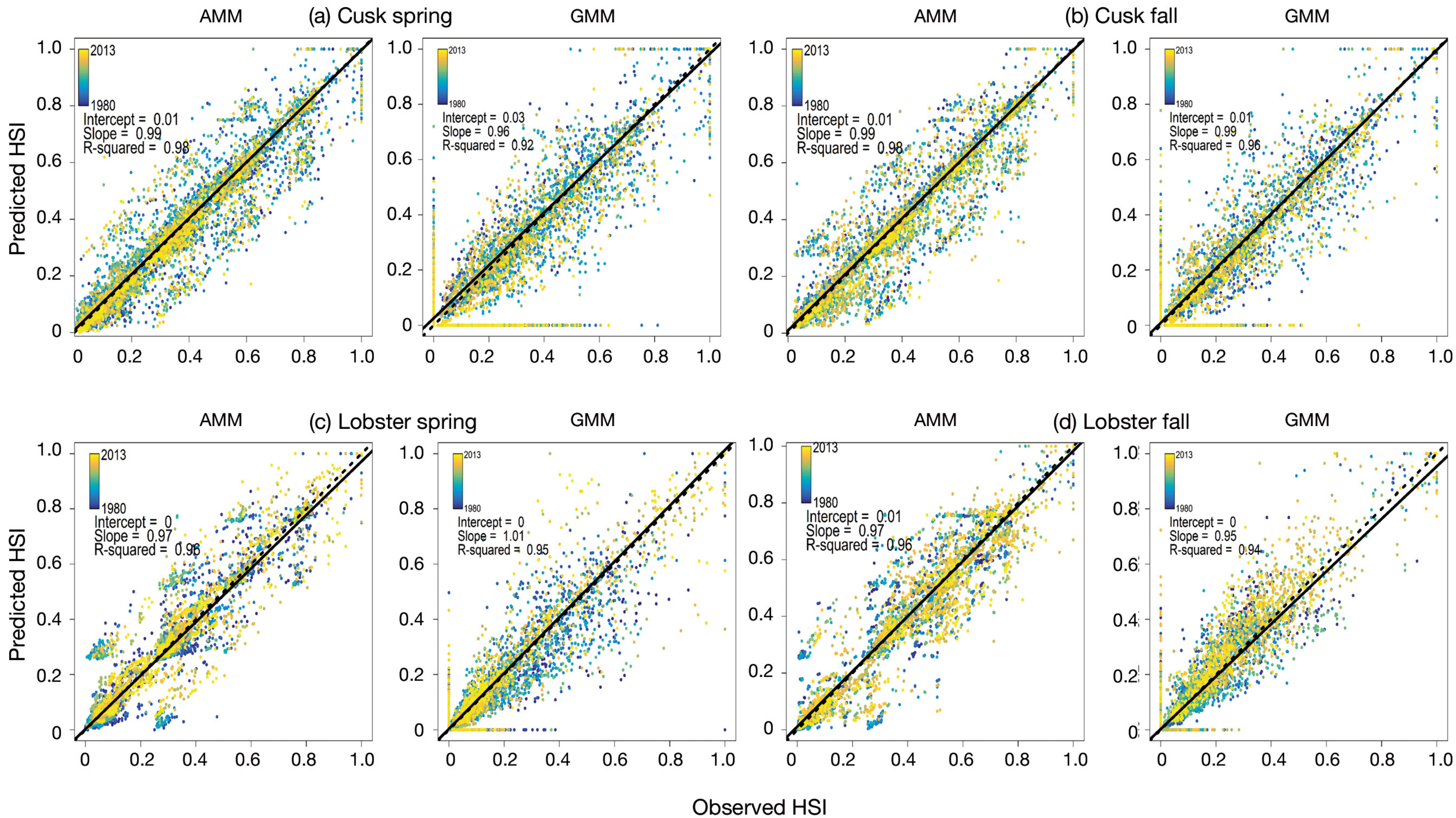

Fig. 2. Cross-validation of habitat suitability index (HSI) models. Test/train validation approach to evaluate HSI values derived from the training data set (predicted HSI) regressed against the HSI values derived from the test data set (observed HSI) for the arithmetic mean (AMM) and geometric mean (GMM) composite HSIs for cusk (A,B) and American lobster (C,D). Different colors indicate variability for each year of the time series 1980–2013

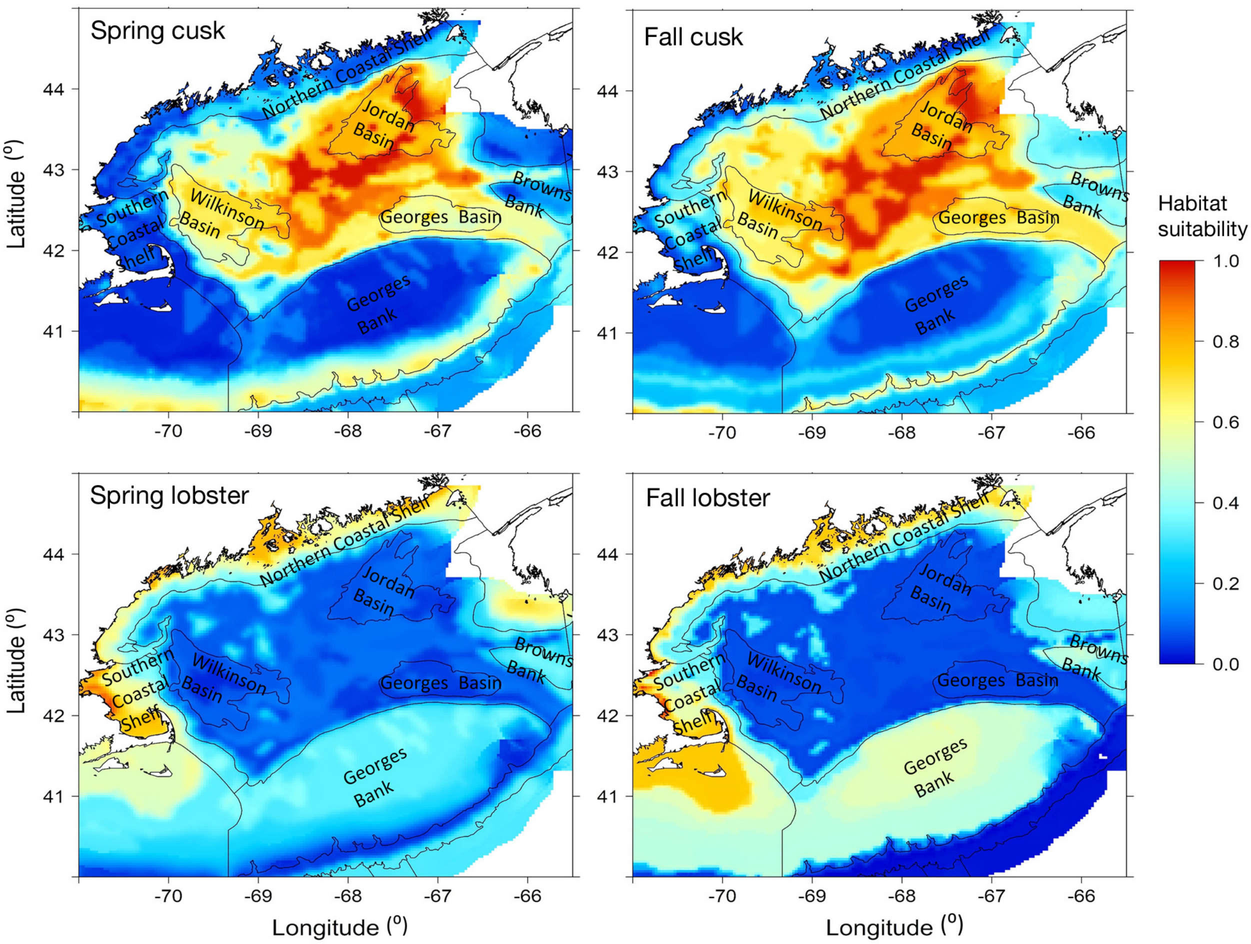

Fig. 3. Arithmetic mean habitat suitability maps, with prominent bathymetric features highlighted, for cusk and American lobster for the spring and fall between 1980 and 2013. Warm colors indicate high estimated habitat suitability (1.0) and cool colors indicate low estimated habitat suitability (0)

Instead, the framework developed in this study makes use of the data that are available from the long-standing NEFSC bottom trawl survey and the recently implemented NEFSC longline survey designed to sample complex habitat types of demersal groundfish species. By evaluating potential bycatch hotspots using this modeling framework, fisheries managers can evaluate the validity of the fisheries-dependent hotspots, understand potential bycatch hotspots for fisheries without reporting or observers, and understand how bycatch interactions may change with changing climate conditions. The general trends in overlap of suitable habitat match with the current understanding of where bycatch interactions occur (Fig. 6). For example, areas of habitat overlap are broader in the spring than in the fall, which matches when cusk bycatch is highest in the Maine lobster fishery because much of the fishing effort is offshore (Chen & Runnebaum 2014).

Managers currently do not have the tools to effectively implement any spatial management approaches without bycatch data from the fishery. Utilizing available fisheries-independent data to predict where and when bycatch interactions could occur provides state and federal managers with a new spatial tool. Cusk is one of the 4 main bycatch species in the Maine lobster fishery (Mateo et al. 2016). Cusk are susceptible to barotrauma when brought to the surface but can survive discarding if physical symptoms of barotrauma are not present or if they are recompressed shortly after being caught (Runnebaum 2017). However, conservation practices to reduce discard mortality are difficult to implement within the Maine commercial lobster fishery, potentially making avoidance practices a more feasible mechanism for reducing cusk bycatch mortality (Runnebaum 2017).

These spatially explicit locations should be interpreted with some caution since they are not known

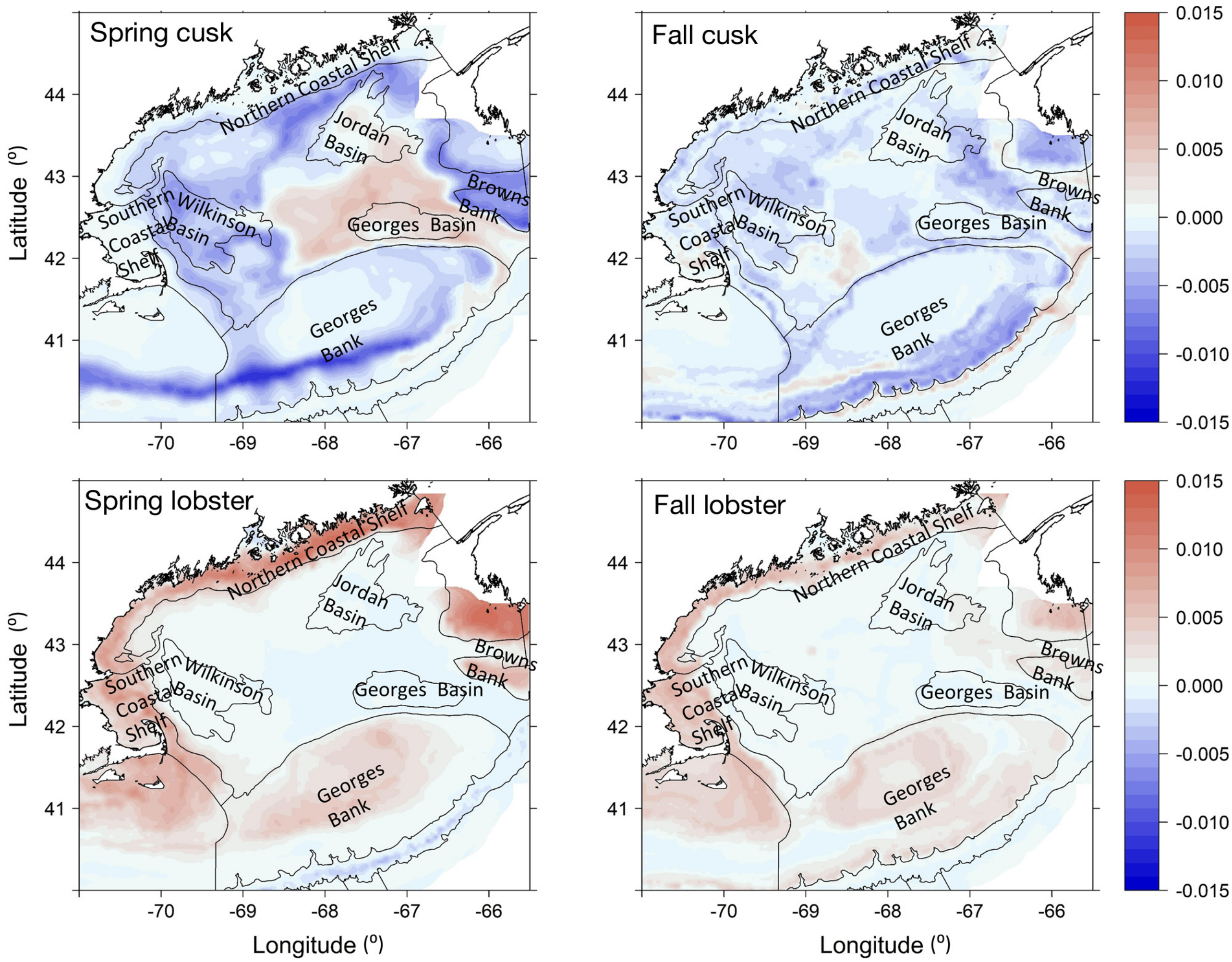

Fig. 4. Changes in habitat suitability for cusk and American lobster (1980–2013). The color ramp represents the relative change in habitat suitability over the time series, blue indicates a negative change in habitat suitability and red indicates a positive change in habitat suitability

locations of bycatch but are areas likely to experience bycatch based on habitat overlap during the spring and fall. HSI models do not necessarily align with realized species distributions, as they only provide data on habitat suitability relative to species density at a given location (Terrell 1984, Terrell & Carpenter 1997, Morris & Ball 2006). Additionally, HSI models are calculations of relative habitat importance and do not incorporate uncertainty in this empirical approach. While these models are useful in understanding habitat distribution and shifts, they are limited by the input data available (Guisan & Zimmermann 2000) and their lack of ability to incorporate uncertainty. Although the model-based density estimates improve the spatial distribution of information used in an HSI, this approach will also be limited by survey data availability. For instance, this analysis does not very well capture the overlap of cusk and lobster habitat suitability in the inshore western GOM and portions of the inshore eastern GOM (Fig. 6). The Maine lobster sea sampling data indicate several areas where cusk were caught as bycatch, but those locations fall outside of the predicted overlap areas (Fig. 6). The NEFSC bottom trawl has relatively few observations of cusk in the inshore areas, resulting in limited data available to fully inform the model-based density estimates for cusk. As more data become available for cusk in inshore areas, there may be better predictive capacity for the model-based density estimates to inform the habitat suitability. Additionally, future efforts could look to a robust analysis of incorporating uncertainty into HSI models as another means to improve this framework.

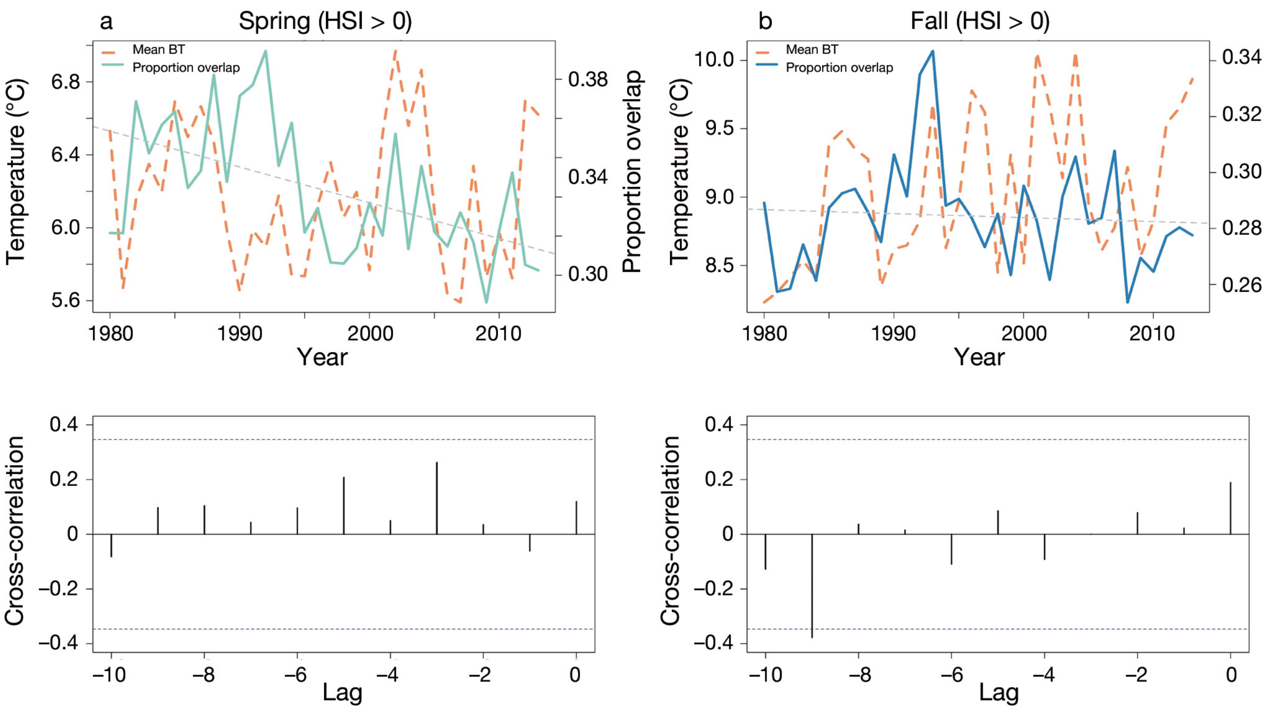

Fig. 5. Proportion of habitat overlap correlated to temperature. Proportion of overlap (solid line) relative to seasonal mean temperatures (dashed orange line) for spring (a) and fall (b) with associated cross-correlations between proportion overlap and seasonal mean temperatures. Dashed gray line on the top plots indicates a declining trend in the proportion of overlap in the spring and a slight decline in the proportion of overlap in the fall. Dashed blue lines on the time-series analysis (bottom plots) indicate a significant relationship

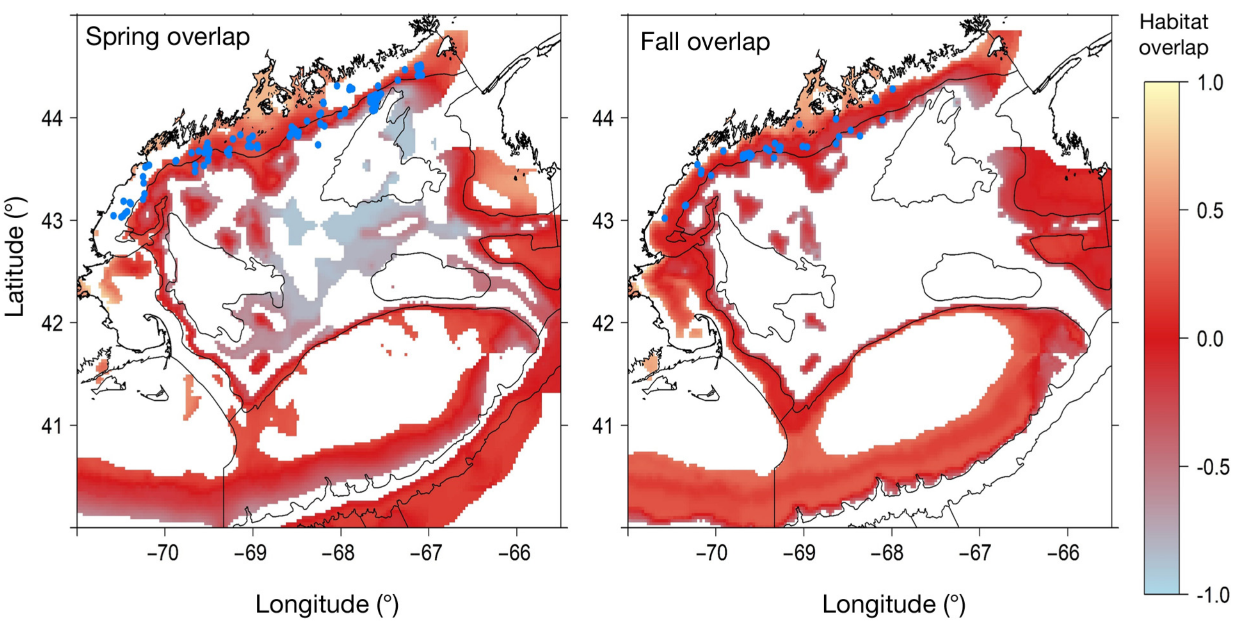

Fig. 6. Mean habitat overlap of cusk and American lobster. Spring and fall for HSI values greater than zero were used to capture the full range of habitat suitability overlap. Negative areas of overlap (i.e. −1.0) indicate areas of suitable habitat for cusk (gray) while positive values (i.e. 1.0) indicate areas of suitable habitat for lobster (yellow). Values close to zero (red) indicate similar cusk and lobster habitat suitability, either both low or both high. Blue circles indicate locations where cusk were observed as bycatch between 2006 and 2013 in the Maine lobster sea sampling program

4.2. Changes in habitat overlap

The Maine lobster fishery is a pursuit fishery (Scheirer 2003), where fishing behavior tends to mirror stock abundance and distribution (Pelletier & Magal 1996). Although HSIs do not show stock abundance, they show where a species is likely to occur at relatively higher densities. From this evidence, changes in fishing behavior can be somewhat predicted from changes in suitable habitat. For instance, the highest habitat suitability is inshore (Fig. 3) and most of the effort in the Maine lobster fishery is within 12 miles of the coast (ASMFC 2015). Evidence suggests that in recent years, lobster catches across all life history stages have increased in deeper waters (Goode et al. 2019). The present study shows that habitat quality for American lobster has increased in the offshore GOM (>12 miles offshore) and portions of GB in the spring and fall (Fig. 4). Offshore effort will be limited by the availability of federal permits that allow for a harvester to fish beyond 3 miles of the coastline. Based on habitat suitability alone, harvesters with federal permits may push further offshore, and lobster fishing effort could expand into areas with suitable cusk habitat. However, cusk habitat is also changing and is negatively impacted by warming temperatures in the GOM (Hare et al. 2012). Cusk habitat suitability in the spring increased around Jordan and Georges Basins (Fig. 4), indicating that this area could be of increasing importance to cusk, and reflecting a consolidation of habitat into the deeper portions of the GOM. However, habitat suitability remained relatively unchanged on most of GB (Fig. 4), an area where much of the Massachusetts American lobster fishing fleet's effort occurs (ASMFC 2015).

The changing habitat conditions found in this study could also reflect changing species abundance. However, there is the potential that species decline is still a confounding factor in understanding changing habitat suitability. Cusk habitat is thought to be negatively impacted by changing climate conditions (Hare et al. 2012), but there is the potential that shrinking suitable habitat reflects decreasing species abundance instead of decreasing suitable habitat (Bell et al. 2015). Conversely, expanding lobster habitat could reflect increased species abundance and the need for individuals to move into less suitable habitat due to density-dependent factors. Although it is difficult to know what came first, species decline or declining suitable habitat, it is evident that cusk decline and changing conditions in the GOM are impacting the distributions of both species (Hare et al. 2012, Goode et al. 2019). To address this confounding issue, the present study attempts to account for the impacts from changing species abundance in the density estimates from VAST by accounting for time-varying catchability as it may relate to a species' increasing or decreasing abundance (Runnebaum et al. 2018).

Over the time series, there was a decrease in the proportion of overlap in habitat between American lobster and cusk (Fig. 5). American lobster habitat suitability has increased throughout the GOM and GB in both the spring and fall, except around Georges and Jordan Basins (Fig. 4). Cusk habitat suitability, conversely, has increased in these deeper, offshore areas and somewhat along the edges of GB (Fig. 4), indicating a shift to cooler thermal environments closer to their optimal thermal range (8–10°C; Collette & Klein-MacPhee 2002). Previous habitat suitability analyses indicate that cusk prefer temperatures around 7°C in the spring and 8°C in the fall (Runnebaum et al. 2018). Climate projections for cusk estimate a 50–80 % loss of habitat due to warming ocean temperatures (Hare et al. 2012). The decrease in the proportion of habitat overlap between American lobster and cusk in the spring is likely a result of warming ocean temperatures and the resulting habitat suitability loss for cusk. Initial hypotheses predicted the proportion of overlap to be correlated to temperature; however, no statistically or biologically meaningful relationships emerged in the time-series analysis.

Lobster density has been shown to increase in the GOM when temperatures are over 5°C (Chang et al. 2010), and their distribution throughout the GOM is positively correlated with temperature (Chang et al. 2010, Tanaka & Chen 2016). American lobster in the GOM prefer slightly warmer temperatures in the fall (~11°C) than in the spring (8°C; Tanaka & Chen 2016). Although not significant, the present study indicates a potential relationship between temperature and the proportion of overlap in the spring, as some years show the proportion of overlap and temperature moving in the same direction. This could potentially be driven by the relationship between American lobster habitat distribution and temperature, with habitat distribution increasing as water temperature increases, but within their thermal range (Fig. 5). As the GOM continues to change, it will be important to explore these types of relationships with the other main bycatch species (Atlantic cod, yellowtail flounder and witch flounder; Mateo et al. 2016) to evaluate trade-offs of potential management measures to limit bycatch.

4.3. Study implications

Understanding the spatiotemporal dynamics of fisheries bycatch has been shown to support conservation measures (Becker et al. 2016) and limit bycatch without the need for broad-scale closures (Hobday et al. 2010, Maxwell et al. 2015). Although cusk bycatch interactions in the American lobster fishery predominately occur in the spring and fall (Chen & Runnebaum 2014), it is important for managers to understand that bycatch interactions are likely to be in discrete locations due to the patchy distribution of cusk (Hare et al. 2012). However, as future conditions change, the relationships observed through this current HSI can also change due to non-stationarity of environmental processes (Myers 1998).

In many fisheries, conservation of endangered species is a management priority, while climate-driven environmental changes often complicate existing management problems. Climate change can cause changes in species distribution and abundance that could lead to new 'choke' species limiting the prosecution of a fishery (Barange et al. 2018). Fisheries management in the coming decades is more likely to succeed if adaptive and spatially explicit ecosystem-based approaches are implemented with increasing flexibility and capacity for unexpected changes in biogeography of commercial stocks (Barange et al. 2009, Brander 2009, McIlgorm et al. 2010, Maxwell et al. 2015). Developing an ecological model that can predict the range of future bycatch trajectories is critical in order to enhance existing monitoring efforts and minimize bycatch risk and potential fishery closures. The framework used in this study can contribute to ongoing efforts to help reduce bycatch, which can assist the development of appropriate climate adaptation responses for fisheries managers.

Acknowledgements. We are grateful to Dr. Dave McLeroy at the NOAA Northeast Fisheries Science Center for collecting the longline survey data. We also thank Nancy McHugh from the Ecosystems Surveys Branch, NOAA Fisheries, for providing the NEFSC bottom trawl survey data. Thank you to the anonymous reviewers and editors, who provided helpful guidance on how to improve the manuscript. The NECOFS simulated temperature data in this study were from NERACOOS, Massachusetts Fishery Institution and MIT Sea Grant College programs. This research was funded by NOAA Saltonstall-Kennedy grant number NOAA NA14-NMF4270029.

LITERATURE CITED

72 FR 10710 (2007) NOAA Fisheries, Endangered and Threatened Species; initiation of a status review under the Endangered Species Act for cusk

Alverson DL, Freeberg MH, Pope JG, Murawski SA (1996) A global assessment of fisheries bycatch and discards. FAO Fisheries Technical Paper No 339. FAO, Rome

Atlantic States Marine Fisheries Commission (ASMFC) (2015) American lobster benchmark stock assessment and peer review report conducted on June 8–11, 2015, Woods Hole, MA. ASMFC, Arlington, VA

Barange M, Coetzee J, Takasuka A, Hill K and others (2009) Habitat expansion and contraction in anchovy and sardine populations. Prog Oceanogr 83:251–260

Barange M, Bahri T, Beveridge MCM, Cochrane KL, Funge Smith S, Poulain F (2018) Impacts of climate change on fisheries and aquaculture: synthesis of current knowledge, adaptation and mitigation options. FAO Fisheries and Aquaculture Technical Paper No 627. FAO, Rome

Beardsley RC, Chen C, Xu Q (2013) Coastal flooding in Scituate (MA): a FVCOM study of the 27 December 2010 nor'easter: FVCOM scituate December 2010 flooding study. J Geophys Res Oceans 118:6030–6045

Becker E, Forney K, Fiedler P, Barlow J and others (2016) Moving towards dynamic ocean management: How well do modeled ocean products predict species distributions? Remote Sens 8:149

Bell RJ, Richardson DE, Hare JA, Lynch PD, Fratantoni PS (2015) Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the Northeast US shelf. ICES J Mar Sci 72:1311–1322

Brander K (2009) Impacts of climate change on marine ecosystems and fisheries. J Mar Biol Assoc India 51:1–13

Brooks R P (1997) Improving habitat suitability index models. Wildlife Soc Bull 25:163–167

Chang J, Chen Y, Holland D, Grabowski J (2010) Estimating spatial distribution of American lobster *Homarus americanus* using habitat variables. Mar Ecol Prog Ser 420: 145–156

Chang YJ, Sun CL, Chen Y, Yeh SZ, Dinardo G (2012) Habitat suitability analysis and identification of potential fishing grounds for swordfish, *Xiphias gladius*, in the South Atlantic Ocean. Int J Remote Sens 33:7523–7541

Chen Y, Runnebaum J (2014) A preliminary study for improving survivability of cusk bycatch in the Gulf of Maine lobster trap. NOAA Contract EE1333F12SE2038

Chen X, Li G, Feng B, Tian S (2009) Habitat suitability index of chub mackerel (*Scomber japonicus*) from July to September in the East China Sea. J Oceanogr 65:93–102

Cohen DM, Inada T, Iwamoto T, Scialabba N (1990) Gadiform fishes of the world (Order Gadiformes). FAO Fisheries Synopsis No 125, Vol 10. FAO, Rome

Collette BB, Klein-MacPhee G (2002) Bigelow and Schroeder's fishes of the Gulf of Maine. Smithsonian Institution, Washington, DC

Crossin GT, Al-Ayoub SA, Jury SH, Howell WH, Watson WH III (1998) Behavioral thermoregulation in the American lobster *Homarus americanus*. J Exp Biol 201:365–374

Crowder LB, Murawski SA (1998) Fisheries bycatch: implications for management. Fisheries 23:8–15

Eguchi T, Benson SR, Foley DG, Forney KA (2017) Predicting overlap between drift gillnet fishing and leatherback turtle habitat in the California Current Ecosystem. Fish Oceanogr 26:17–33

GEBCO (2014) The GEBCO_2014 Grid, version 20150318, www.gebco.net

Goode AG, Brady DC, Steneck RS, Wahle RA (2019) The brighter side of climate change: how local oceanography amplified a lobster boom in the Gulf of Maine. Glob Change Biol 25:3906–3917

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Modell 135:147–186

Hare JA, Manderson JP, Nye JA, Alexander MA and others (2012) Cusk (*Brosme brosme*) and climate change: assessing the threat to a candidate marine fish species under the US Endangered Species Act. ICES J Mar Sci 69:1753–1768

Harrington JM, Myers RA, Rosenberg AA (2005) Wasted fishery resources: discarded by-catch in the USA. Fish Fish 6:350–361

Hazen EL, Scales KL, Maxwell SM, Briscoe DK and others (2018) A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. Sci Adv 4:eaar3001

Hobday AJ, Hartog JR, Timmiss T, Fielding J (2010) Dynamic spatial zoning to manage southern bluefin tuna (*Thunnus maccoyii*) capture in a multi-species longline fishery: improvement in dynamic spatial management for tuna. Fish Oceanogr 19:243–253

Hoey J, O'Brien L, Natanson L, McMlroy D, Manderson J, Borggaard D, Silva R (2013) Development of a bottom longline survey for stocks associated with complex rocky habitat in the western and central Gulf of Maine, including several data poor stocks that are ESA species of concern. NEFSC & NERO PROPOSAL 2013 Cooperative Research Solicitation. National Marine Fisheries Service, Woods Hole, MA

King JR, Camisa MJ, Manfredi VM (2010) Massachusetts Division of Marine Fisheries trawl survey effort, lists of species recorded, and bottom temperature trends, 1978–2007. Technical Report. Massachusetts Division of Marine Fisheries. www.mass.gov/eea/docs/dfg/dmf/publications/tr-38.pdf

Lawton P, Lavalli KL (1995) Postlarval, juvenile, adolescent, and adult ecology. In: Factor JR (ed) Biology of the lobster *Homarus americanus*. Academic Press, San Diego, CA, p 47–83

Lewison RL, Soykan CU, Franklin J (2009) Mapping the bycatch seascape: multispecies and multi-scale spatial patterns of fisheries bycatch. Ecol Appl 19:920–930

Maine Department of Marine Resources (Maine DMR) (2016) DMR lobster sea sampling program. https://www1.maine.gov/dmr/science-research/species/lobster/research/seasampling.html (accessed 11 March 2020)

Mateo I, Ennis J, Criquet G, Dunne E (2016) Marine Stewardship Council full assessment final report and determination Gulf of Maine lobster fishery (*Homarus americanus*). Report Code MSC 017. SAI Global Assurance Service, Dundalk

Maxwell SM, Hazen EL, Lewison RL, Dunn DC and others (2015) Dynamic ocean management: defining and conceptualizing real-time management of the ocean. Mar Policy 58:42–50

McIlgorm A, Hanna S, Knapp G, Le Floc'H P, Millerd F, Pan M (2010) How will climate change alter fishery governance? Insights from seven international case studies. Mar Policy 34:170–177

Miller TJ, Das C, Politis PJ, Miller AS and others (2010) Estimation of Albatross IV to Henry B. Bigelow calibration factors. Northeast Fisheries Science Center Ref Doc 10-05. NEFSC, Woods Hole, MA

Morgan LE, Chuenpagdee R (2003) Shifting gears: addressing the collateral impacts of fishing methods in US waters. Pew Science Series, Washington, DC

Morris L, Ball D (2006) Habitat suitability modelling of economically important fish species with commercial fisheries data. ICES J Mar Sci 63:1590–1603

Myers RA (1998) When do environment–recruitment correlations work? Rev Fish Biol Fish 8:285–305

National Marine Fisheries Services (NMFS) (2018) Fisheries economics of the United States 2016. Economics and Sociocultural Status and Trends Series. NOAA Technical Memorandum NMFS-F/SPO-187

NECOFS (2013) The Northeast Coastal Ocean Forecasting System. http://fvcom.smast.umassd.edu/research_projects/NECOFS

Pelletier D, Magal P (1996) Dynamics of a migratory population under different fishing effort allocation schemes in time and space. Can J Fish Aquat Sci 53:1186–1199

Poppe LJ, McMullen KY, Williams SJ, Paskevich VF (2014) USGS east-coast sediment analysis: procedures, database, and GIS data (ver. 3.0, November 2014): US Geological Survey Open-File Report 2005-1001. http://pubs.usgs.gov/of/2005/1001/

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/

Reynolds WW, Casterlin ME (1979) Behavioral thermoregulation and activity in *Homarus americanus*. Comp Biochem Physiol 64:25–28

Runnebaum JM (2017) Improving management and conservation of cusk (*Brosme brosme*): habitat distribution, bycatch interactions, and conservation practices. PhD dissertation, University of Maine, Orono, ME

Runnebaum J, Guan L, Cao J, O'Brien L, Chen Y (2018) Habitat suitability modeling based on a spatiotemporal model: an example for cusk in the Gulf of Maine. Can J Fish Aquat Sci 75:1784–1797

Scheirer KM (2003) Analysis of the spatial dynamics of the American lobster (*Homarus Americanus*) fishery along the coast of Maine. Masters thesis, University of Maine, Orono, ME

Schnute JT, Boers N, Haigh R (2018) PBSmapping: mapping fisheries data and spatial analysis tools. R package version 2.70.5. https://cran.r-project.org/web/packages/PBSmapping/PBSmapping.pdf

Sherman S, Stepanek K, Sowles J (2005). Maine-New Hampshire Inshore Groundfish Trawl Survey: procedures and protocols. https://www.maine.gov/dmr/science-research/projects/trawlsurvey/reports/documents/proceduresandprotocols.pdf

Sims M, Cox T, Lewison R (2008) Modeling spatial patterns in fisheries bycatch: improving bycatch maps to aid fisheries management. Ecol Appl 18:649

Tanaka K, Chen Y (2015) Spatiotemporal variability of suitable habitat for American lobster (*Homarus Americanus*) in Long Island Sound. J Shellfish Res 34:531–543

Tanaka K, Chen Y (2016) Modeling spatiotemporal variability of the bioclimate envelope of *Homarus americanus* in the coastal waters of Maine and New Hampshire. Fish Res 177:137–152

Tanaka KR, Cao J, Shank BV, Truesdell SB, Mazur MD, Xu L, Chen Y (2019) A model-based approach to incorporate environmental variability into assessment of a commercial fishery: a case study with the American lobster fishery in the Gulf of Maine and Georges Bank. ICES J Mar Sci 76:884–896

Terrell JW (1984) Proceedings of a workshop on fish habitat suitability index models. Biol Rep, 85:393

Terrell JW, Carpenter J (1997) Selected habitat suitability index model evaluations. Information and Technology Report, USGS/BDR/IT 1997-0005, Springfield, VA

Thorson JT, Barnett LAK (2017) Comparing estimates of abundance trends and distribution shifts using single- and multispecies models of fishes and biogenic habitat. ICES J Mar Sci 74:1311−1321

Thorson JT, Ward EJ (2014) Accounting for vessel effects when standardizing catch rates from cooperative surveys. Fish Res 155:168−176

Thorson JT, Shelton AO, Ward EJ, Skaug HJ (2015) Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. ICES J Mar Sci 72:1297−1310

Torre MP, Tanaka KR, Chen Y (2019) Development of a climate-niche model to evaluate spatiotemporal trends in *Placopecten magellanicus* distribution in the Gulf of Maine, USA. J Northwest Atl Fish Sci 50:37−50

Trapletti A, Hornik K (2018) tseries: time series analysis and computational finance. R package version 0.10-46. https://cran.r-project.org/web/packages/tseries/tseries.pdf

Ward EJ, Jannot JE, Lee YW, Ono K, Shelton AO, Thorson JT (2015) Using spatiotemporal species distribution models to identify temporally evolving hotspots of species co-occurrence. Ecol Appl 25:2198−2209

Wilberg MJ, Thorson JT, Linton BC, Berkson J (2009) Incorporating time-varying catchability into population dynamic stock assessment models. Rev Fish Sci 18:7−24

APPENDIX. Supplemental VAST outputs for cusk and American lobster

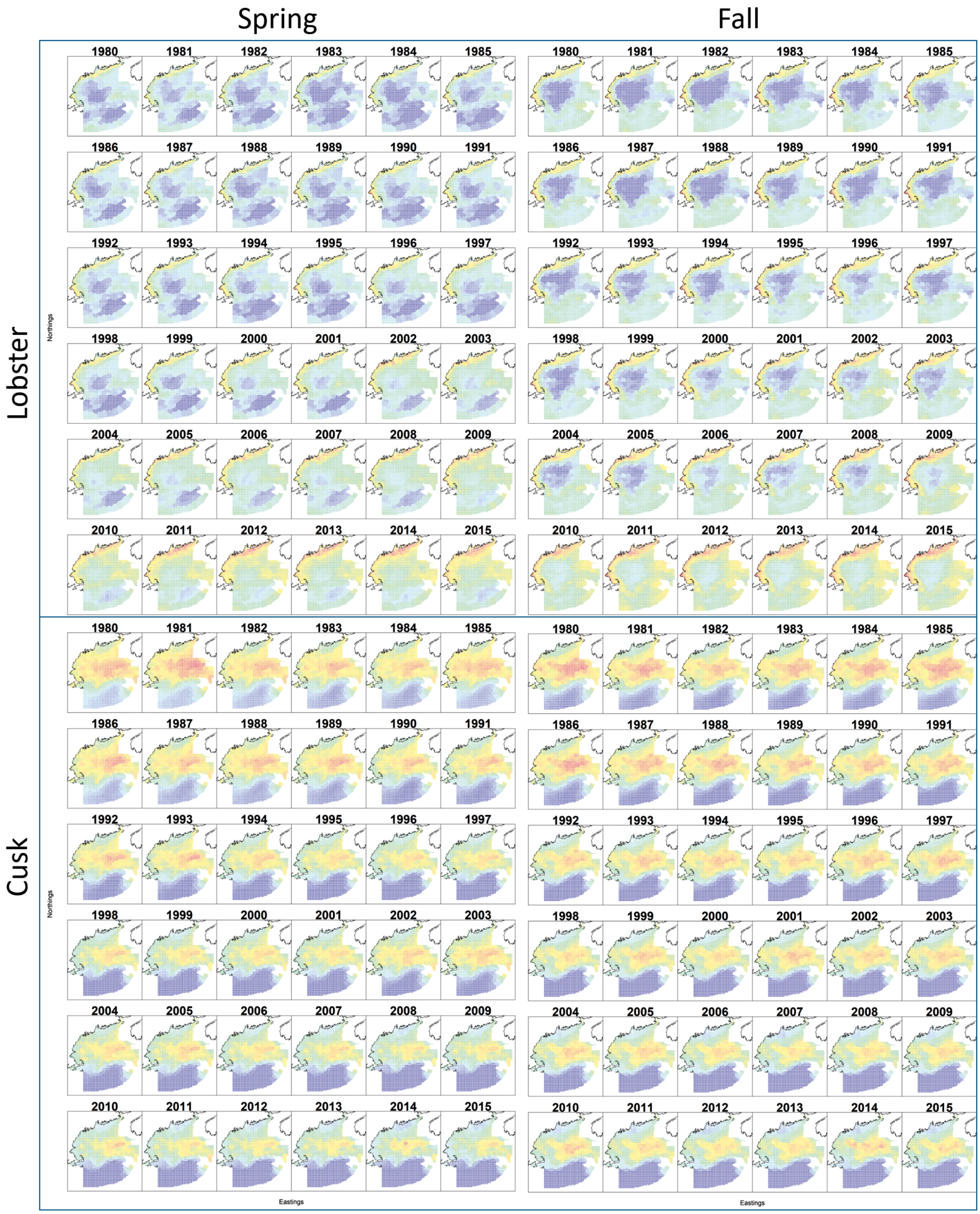

Fig. A1. VAST density plots for cusk and American lobster. Warm colors indicate areas of high density, with red being the highest density areas, and cool colors indicate areas of low density, with blue being the lowest density

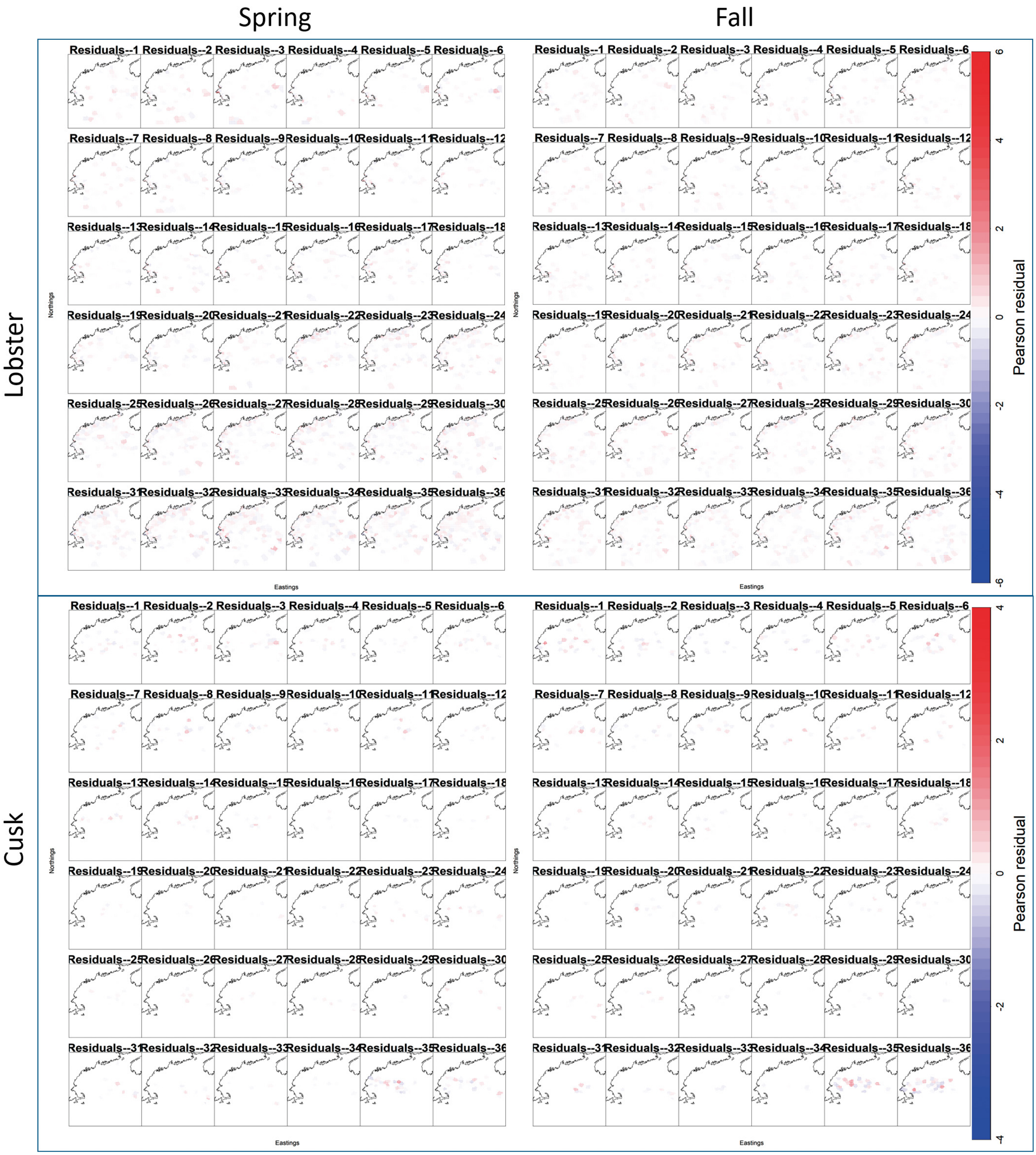

Fig. A2. Pearson residual plots for cusk and American lobster in spring and fall. Red indicates positive residuals and blue indicates negative residuals

Editorial responsibility: Franz Mueter, Juneau, Alaska, USA

Submitted: August 13, 2019; Accepted: March 18, 2020
Proofs received from author(s): May 1, 2020