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Tracking shifts in Atlantic mackerel (*Scomber scombrus*) larval habitat suitability on the Northeast U.S. Continental Shelf

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Abstract

Climate change has altered the oceanographic environment and subsequently the habitats of marine species. Fish and invertebrate populations' responses to habitat include movement with latitude and depth to remain within their fundamental niches. The northwest Atlantic mackerel (*Scomber scombrus*) population has fluctuated over the last century due in part to changes in the environment. We used species distribution models to understand the influence of the physical (temperature) and biological (zooplankton) environment on mackerel larval abundance, and how such relations have determined larval habitat suitability in the Northeast U.S. Shelf. Atlantic mackerel larval presence and abundance correlated with sea temperature and copepod abundances, suggesting that larval survival may be sensitive to specific temperatures and zooplankton prey. Predicted abundances were spatially interpolated to estimate Atlantic mackerel larval suitable habitat. Metrics for habitat quality indicate that the Mid-Atlantic Bight has become less suitable over time. Since the 1970s, the proportion of Northeast U.S. Shelf suitable habitat located in the Mid-Atlantic Bight has decreased, as southern New England and the western Gulf of Maine regions have become more suitable. Habitat suitability within the Northeast U.S. Shelf has shifted northeast: from the Mid-Atlantic Bight-southern New England border towards the northeast portion of southern New England. While total Northeast U.S. Shelf habitat suitability has decreased since the 1970s, the decline in the time series trend was not statistically significant. Thus, while select ecoregions have decreased in habitat suitability, larval habitat does not appear to be the only contributor to decreases in the U.S. Atlantic mackerel contingent.

KEYWORDS

Atlantic mackerel, habitat suitability, larvae, Northeast U.S. Shelf, sea temperature, species distribution models, zooplankton

1 | INTRODUCTION

Climate change has altered the physics and chemistry of marine ecosystems including ocean temperature, dissolved oxygen, pH, and ocean circulation (Poloczanska et al., 2016). These environmental changes have also transformed available habitat for marine fish and invertebrates. Climate change has been linked to changes in marine fish distribution through population shifts poleward, or to new depths (Nye, Link, Hare, & Overholtz, 2009). These distribution shifts reflect adjustments by species to remain within their optimal habitat (Anderson, Gurarie, Bracis, Burke, & Laidre, 2013). Adult fish distributional shifts and associated environmental conditions have been

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extensively documented along the Northeast U.S. Continental Shelf Large Marine Ecosystem (hereafter Northeast U.S. Shelf) (Nye et al., 2009; Pinsky & Fogarty, 2012; Kleisner et al., 2016), as well as spatial and temporal shifts in adult and larval fish distributions (Walsh, Richardson, Marancik, & Hare, 2015).

Atlantic mackerel (*Scomber scombrus*) is one Northeast U.S. Shelf species identified as vulnerable and exposed to climate change (Hare et al., 2016). A schooling, pelagic, planktivorous fish, Atlantic mackerel is found on both sides of the North Atlantic: from Newfoundland to North Carolina in the west, and from Greenland to the Mediterranean Sea in the east (Sette, 1950; Astthorsson, Valdimarsson, Gudmundsdottir, & Oskarsson, 2012; Jansen et al., 2016). The northwest Atlantic stock comprises a northern contingent spawning in the Gulf of St. Lawrence from May into August, and a southern contingent spawning from the Mid-Atlantic Bight through the Gulf of Maine from mid-April through June (Figure 1; Anderson, 1982; Berrien, 1982). During late fall and winter, the southern contingent inhabits offshore waters along the continental shelf in the Mid-Atlantic Bight, and from spring through autumn migrates north and inshore along southern New England through the Gulf of Maine to spawn and feed (Sette, 1943, 1950). The northern contingent exhibits similar migratory patterns, moving from Georges Bank and the Scotian Shelf to the Gulf of St. Lawrence in the late spring through summer, and returning south in autumn (Berrien, 1982; Overholtz, 1989). Atlantic mackerel have historically supported large commercial and recreational fisheries (Anderson & Paciorkowski, 1980) and served as prey for marine fish, birds and mammals (Studholme et al., 1999). Therefore, climate influences on the Atlantic mackerel stock may have significant consequences for both commercial fisheries and ecosystem function.

Changes in ocean temperatures have implications for Atlantic mackerel available habitat over all life stages. Atlantic mackerel are susceptible to changes in sea temperature via growth and mortality rates, particularly during the larval stage (Ware & Lambert, 1985). Sea temperature has long been suspected to influence population size via thermal requirements over multi-decadal scales, causing alternating regimes between Atlantic herring (*Clupea harengus*) and mackerel in the northwest Atlantic (Skud, 1982). Increases in sea temperature have also been associated with northwest Atlantic mackerel spatial distributions by size-class, spring migrations, and spawning seasonality (Overholtz, Hare, & Keith, 2011; Radlinski, Sundermeyer, Bisagni, & Cadrin, 2013). In the northeast Atlantic, several studies have described temperature's influence on adult (Astthorsson et al., 2012) and egg (Beare & Reid, 2002; Bruge, Alvarez, Fontan, Cotano, & Chust, 2016) distributions, and seasonality of occurrence.

Zooplankton community composition shifts also influence suitable habitat for Atlantic mackerel larvae. Changes in physical conditions affect zooplankton abundance and distribution through species' physiological constraints, differential advective transport and changes in predator-prey interactions. Altering zooplankton species composition changes the prey available for early life stage fish (Friedland et al., 2013), affecting fish larvae that have prey-specific diets, such

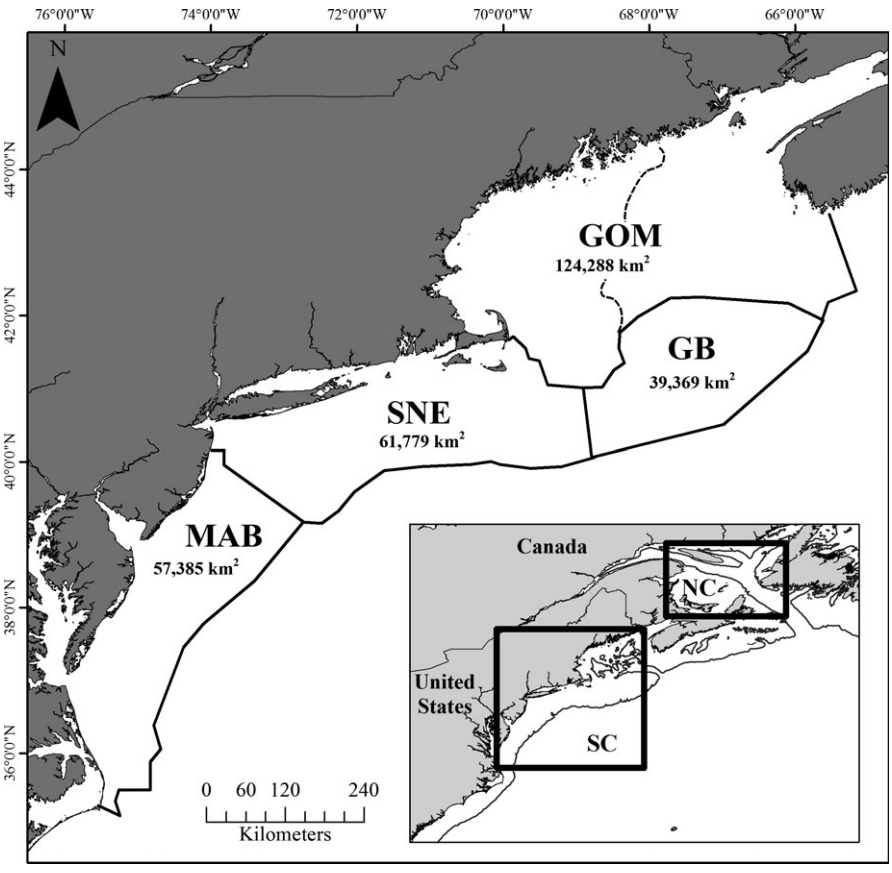

FIGURE 1 Regions of the Northeast U.S. Shelf examined for Atlantic mackerel larval habitat. Assessment was confined to the Mid-Atlantic Bight (MAB), southern New England (SNE), Georges Bank (GB), and the Gulf of Maine (GOM). The area (km^2) for each of these regions is provided. The dashed line through the Gulf of Maine delineates the western and eastern portions. Locus map illustrates the Northeast U.S. Shelf location within the northwest Atlantic, the southern (SC) and northern (NC) contingent spawning grounds, and the 200 m isobath (dark line)

as Atlantic mackerel. Early stage mackerel larvae prey primarily on copepods, including *Pseudocalanus* spp., *Temora longicornis*, and *Calanus finmarchicus* (Peterson & Ausubel, 1984; Ringuette, Castonguay, Runge, & Grégoire, 2002; Robert, Castonguay, & Fortier, 2008). Poor spatial-temporal match between larvae during the transition from yolk-sac to exogenous-feeding and their preferred prey can influence growth and mortality through increased starvation and susceptibility to predation (Takasuka, Aoki, & Mitani, 2003). In the northern contingent, Atlantic mackerel recruitment has been found to vary annually based on prey availability during the species' exogenous-feeding larval stage (Castonguay, Plourde, Robert, Runge, & Fortier, 2008; Plourde et al., 2015; Jansen, 2016). Changes in dominant zooplankton taxa could also influence future mackerel recruitment of the southern contingent.

While several studies have evaluated the environmental (e.g., temperature, larval prey field) influence on Atlantic mackerel recruitment and distribution patterns, such ecological relationships have yet to be used to describe and estimate suitable habitat available. Our work aims to understand the physical and biological habitat requirements for larvae of the northwest Atlantic mackerel southern contingent via ichthyoplankton, zooplankton, and oceanographic data. We used species distribution models to relate larval observations with environmental conditions and identify larval habitat (Hutchinson, 1957; Elith & Leathwick, 2009). The species distribution models were implemented to hindcast larval abundance spatially, quantify Atlantic mackerel larval habitat, and understand how the species' habitat suitability has changed over time. By quantifying larval habitat changes, our work provides a tool to understand influences of environmental shifts on Atlantic mackerel and evaluate possible mechanisms influencing observed Atlantic mackerel abundance trends.

2 | MATERIALS AND METHODS

2.1 | Field sampling

Ichthyoplankton, zooplankton, and oceanographic data have been collected over the last five decades in the Northeast U.S. Shelf through various long-term monitoring programs (Kane, 2003; Richardson, Hare, Overholtz, & Johnson, 2010). Data used in this study were derived from two programs conducted by the National Oceanic and Atmospheric Administration (NOAA): the Marine Resource Monitoring, Assessment, and Prediction (MARMAP) program and the Ecosystem Monitoring (EcoMon) program (Richardson et al., 2010). The MARMAP program operated from 1977 to 1987, and the EcoMon program has been active since 1992. Both programs were designed to describe and assess changes in oceanography and planktonic community structure of the Northeast U.S. Shelf. Surveys were performed four to eight times per year over the continental shelf, spanning from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (Richardson et al., 2010; Walsh et al., 2015).

MARMAP and EcoMon samples were taken throughout the year at both day and night. Deployments were performed with a 61 cm bongo net. Flowmeters were suspended in the bongo nets to measure the volume of water filtered. Bongo nets were towed at approximately 1.5 knots obliquely through the water column to within 5 m of the bottom, or a maximum of 200 m (Richardson et al., 2010; Walsh et al., 2015). Plankton samples collected by the bongo nets were processed for zooplankton or ichthyoplankton, with one net processed following one protocol (e.g., zooplankton) and the other net processed following the other protocol (e.g., ichthyoplankton). Over the years, plankton samples have been processed primarily by Morski Instytut Rybacki (Poland), with fewer samples processed by the Northeast Fisheries Science Center (United States), and the Atlantic Reference Center (Canada). However, the same protocols have been followed over the different programs. Zooplankton samples were reduced to 500 organism subsamples using a box splitter, and the subsample specimens were identified to the lowest possible taxon (Kane, 2008). Select zooplankton taxa were identified to specific life stages, with staging protocols varying by taxa. Ichthyoplankton were removed from the whole sample and identified to the lowest possible taxon (Walsh et al., 2015). Abundances were standardized to number per 10 m^2 based on the proportion of the sample processed, the volume filtered by the nets, and the depths the nets sampled. During the MARMAP period, surface and bottom oceanographic conditions were measured alongside plankton tows, and sea temperatures were measured with a thermometer or bathythermograph. During the EcoMon program, a CTD was used to collect depth discrete oceanographic measurements over the water column (Simpson et al., 2016). For further descriptions of the monitoring programs, please see Richardson et al. (2010) and Kane (2003).

Two differences in sampling between the MARMAP and EcoMon programs should be noted. First, the mesh size on the bongo nets for ichthyoplankton sampling differed between the MARMAP and EcoMon programs; the MARMAP program used a 0.505 mm mesh, whereas the EcoMon used a 0.333 mm mesh net. This discrepancy over time does not apply to zooplankton sampling, as zooplankton samples were taken with a 0.333 mm mesh net during both MARMAP and EcoMon programs. Second, the processing of the ichthyoplankton samples early in the EcoMon period (1992–1999) was inconsistent owing to budget constraints during the transition from MARMAP to EcoMon; the availability of zooplankton and oceanographic data is more consistent later in the EcoMon program (1999–present; Table S1).

Analyses incorporated May and June samples only, in order to model the typical Atlantic mackerel spawning period (Berrien & Sibunka, 1999). Additionally, only samples from the Mid-Atlantic Bight, southern New England, Georges Bank, and the Gulf of Maine were used; samples south of Cape Hatteras and off the shelf were excluded to focus analyses on the historical latitudinal range of the stock's southern contingent (Figure 1). Oceanographic, zooplankton, and ichthyoplankton data were available for various years from 1977 through 2013. Model development only incorporated data from years with adequate coverage of the Northeast U.S. Shelf during May and June: 1978–1984, 1986–1987, 2000–2002, 2004–2007,

and 2009–2013 (Table S1). In some years, weather or ship availability resulted in reduced spatial coverage of the shelf. Larvae were present in 11.87% of the May and June samples, with abundances as high as 10,819 larvae 10 m^{-2} and sizes ranging from 1.3 to 42 mm. Of larvae caught, 96.3% were 7 mm or less, representing those selecting zooplankton prey (Robert et al., 2008) and 99.6% were smaller than the post-larval stage, 11 mm, when individuals can actively avoid plankton nets (Sette, 1943).

2.2 | Species distribution models

Generalized additive models (GAMs) were implemented to describe the relationships between larval abundances and the environment (Venables & Dichmont, 2004). GAMs use several smooth additive functions, resulting in curvature or splines in the predictions (Hastie & Tibshirani, 1986). Atlantic mackerel larval abundances were modeled with a delta (or hurdle) model approach (Maunder & Punt, 2004). This method has two components, combining predictions from a presence/absence model with those from an abundance-when-present model. The approach is beneficial when analyzing species data with a large number of absences (or zero abundance), and is commonly used in the analysis of fisheries independent survey data (Grüss, Drexler, & Ainsworth, 2014; Lynch et al., 2015).

Several variables were tested to construct presence/absence and abundance GAMs for Atlantic mackerel larvae. Additionally, only variables previously found to influence larvae or catchability were considered. Sea surface and bottom temperatures were tested, as water temperatures influence time of spawning (Radlinski et al., 2013) and affects Atlantic mackerel larval growth and survival (Morse, 1989; Ware & Lambert, 1985). Several zooplankton species were considered to represent food available during the time of sampling. Zooplankton taxa that have been identified in mackerel larvae gut content, including *Pseudocalanus* spp., *T. longicornis*, *C. finmarchicus*, *Centropages typicus*, and *Oithona* spp. (Robert et al., 2008; Robert, Castonguay, & Fortier, 2009), were tested. Zooplankton abundances were transformed, ln(abundance + 1), prior to analyses. Water depth was also incorporated to identify regions over the shelf preferred for spawning.

Additional variables were tested in the models to account for catchability influences on the observed abundances. Information regarding light availability, such as solar zenith, photosynthetically active radiation (PAR), and a Day/Night categorical variable, were calculated for all samples using R statistical package "AstroCalc4R" to discern any diurnal variability in larval catchability (Jacobson, Seaver, & Tang, 2011). Mesh size of the bongo nets for ichthyoplankton sampling (0.333 mm versus 0.505 mm) was also included to account for larval extrusion differences between the gears over the time series (Johnson & Morse, 1994). GAMs were constructed using R statistical software package "mgcv".

Variables' significance in predicting larval presence and abundance were evaluated using a backwards stepwise selection approach (Wood, 2006). This process started by including all covariates in the model and then removing covariates that appeared to have little impact on the predictions one-by-one, and comparing the revised model's fit to the previous fit. The models' unbiased risk estimator (UBRE, presence/absence model) or generalized cross validation (GCV, abundance model) scores, and the variables' degrees of freedoms and *p* values were used to determine if the covariates did not significantly increase model fit and should be removed. To reduce model overfitting without degrading prediction error performance, models' degrees of freedom in UBRE/GCV scores were penalized by setting the gamma parameter to 1.4 (Wood, 2006). The best-fit presence/absence and abundance models differed in variables used in predicting Atlantic mackerel larvae. To maintain ecological consistency between the presence/absence and abundance models, variables found insignificant in one model, but significant in the other were reinserted into the former model. As a result, the models contained the same covariates. This approach has been used in several previous studies (Grüss et al., 2014; Lynch et al., 2015). Presence/absence and abundance were modeled as:

$$\begin{aligned} &\textit{Presence}/\textit{Absence} \text{ or } \ln(\text{Abundance}+1) \\ &= \text{s(Surface Temperature)} + \text{s(Bottom Temperature)} + \text{s(Depth)} \\ &+ \text{Mesh Size} + \text{s}(\textit{Calanus finmarchicus}) + \text{s}(\textit{Pseudocalanus} \text{ spp.}) \\ &+ \text{s}(\textit{Temora longicornis}) + \text{s}(\textit{Oithona} \text{ spp.}) + \text{s}(\textit{Centropages typicus}) \end{aligned} \tag{1}$$

Larval presence/absence was modeled using a binomial GAM with a logit-link function. The binomial model outputs were expressed as probability of larval occurrence between 0 and 1; however, such predictions do not allow for model validation given that observations are either absence (0) or present (1). Thus, a threshold was required to define binary presence/absence from continuous probability of occurrence. The threshold for conversion was set to the value that resulted in the greatest fraction of true positives (selectivity) and negatives (specificity), while minimizing false positives (commission errors) and negatives (omission errors) (Lobo, Jiménez-Valverde, & Real, 2008; Murtaugh, 1996). The kappa coefficient for the confusion matrix was calculated to quantify the agreement between the predictions and observations (Carletta, 1996). Larval abundances were transformed, ln(abundance + 1), prior to analysis, and modeled using a gamma GAM with an identity-link function. Presence/absence and abundance models were compared to models only using temperature and zooplankton covariates, separately, to assess the relative contributions of physical and biological factors to larval presence and abundance. These variants of the presence/absence and abundance models were compared using Akaike's information criterion (AIC; Akaike, 1973).

Predictions from the final presence/absence and abundance models were multiplied together to construct a zero-inflated adjusted abundance, representing the delta GAM results (Grüss et al., 2014). Predictions were made for all samples where zooplankton and hydrographic measurements were taken, including some years early in the EcoMon period that did not have ichthyoplankton data for use in model development. Predictions were interpolated over a 0.1° resolution grid encompassing the Northeast U.S. Shelf using inverse distance weighting with a power parameter of two.

Spatial autocorrelation was assessed prior to inverse distance weighting to determine and correct potential autocorrelation between predicted points (Dormann et al., 2007). Spatial autocorrelation was examined by incorporating latitude and longitude as covariates in spatial variograms (using ordinary and universal kriging). Only latitude and longitude were incorporated in the variogram and kriging trials given that the predictions were based on environmental data, and not all GAM inputs were available over the prediction grid. Annual variograms indicated that either spatial autocorrelation was not an issue with interpolations in space, or could not be resolved with variograms. Thus, kriging with variogram corrections were not used in the spatial interpolation between predicted points.

2.3 | Habitat suitability calculations

Habitat suitability was assessed for Northeast U.S. Shelf ecoregions where Atlantic mackerel are known to occur: the Mid-Atlantic Bight, southern New England, Georges Bank, and the Gulf of Maine. Habitat in the Gulf of Maine was evaluated for the western and eastern sides separately given the areas' contrasts in oceanography (Townsend, Thomas, Mayer, Thomas, & Quinlan, 2006), resulting in five distinct ecoregions. Trends in interpolated grid abundance predictions were evaluated to understand fine scale habitat changes within an ecoregion over time. An ecoregion's overall annual habitat (H) was assessed by summing predictions within an ecoregion and dividing by the regions' surface areas (km^2). Habitat suitability indices (HSI) were calculated with predicted abundances using two different metrics: (i) assessing habitat changes within a given ecoregion over time (HSI_E), and (ii) changes in ecoregions' contribution in overall habitat suitability within the Northeast U.S. Shelf (HSI_S).

$$HSI_E = H_{R,Y} \tag{2}$$

$$HSI_S = \frac{H_{R,Y}}{\sum H_Y} \tag{3}$$

$H_{R,Y}$ represents the estimated habitat (H) within a given ecoregion (R) and year (Y), and ΣH_Y is the sum of habitat over all regions in a given year. The first method aimed to identify absolute changes in suitable habitat available in each ecoregion. HSI_E values were also summed over ecoregions to evaluate total HSI_E for the Northeast U.S. Shelf. The second method assessed each region's relative contribution to the total suitable habitat within a given year, with all ecoregions in a given year summing to one. HSI_E indices were calculated for all years in which the respective ecoregions were sampled, resulting in differing HSI_E time series lengths by ecoregion (Table S1). HSI_S indices were only calculated if all ecoregions were adequately sampled within a year.

Along and across shelf changes in larval habitat suitability were calculated using HSI_S's to quantify directional habitat movement over the Northeast U.S. Shelf. Along and across shelf distances for ecoregion's center points were calculated as the distance north of Cape Hatteras, North Carolina and distance from the 200 m isobath, respectively (Nye et al., 2009). This method accounts for curvilinear dynamics of the continental shelf. Annual along and across shelf values were calculated by multiplying these center point positions by the ecoregions' HSI_S values, and summing results over ecoregions within a given year. Thus, the along and across shelf positions of larval habitat suitability represented positions weighted by the relative habitat suitability each ecoregion provided for each year. Annual along and across shelf habitat locations were then converted to latitude and longitude coordinates to understand geographical changes in suitable larval habitat.

3 | RESULTS

3.1 | Habitat model

Variability in larval presence and abundance was well explained by the biological and physical covariates. The presence/absence model explained approximately 58% of the variability in Atlantic mackerel occurrence, and the abundance model accounted for 69% of the variability in larval abundance (Table 1). Covariates used also indicated low collinearity (Table S2). When converting predicted probabilities of occurrences to binary presence/absence, a threshold of 0.111 maximized true positives and negatives. After applying the threshold to probability predictions, 86.2% of the observations from the validation dataset were accurately predicted: 75.5% true negative, 10.7% true positive (Table 2). The presence model accuracy was greater than random chance: the hypothetical probability of agreement was estimated at 0.70, and the kappa coefficient statistic for the confusion matrix was 0.53.

Presence/absence of Atlantic mackerel larvae was significantly affected by all covariates included. Sea surface temperatures between roughly 11 and 22°C had a positive influence on the presence of larvae, with temperatures above and below having a

TABLE 1 Model results for the presence/absence and abundance GAMs

	Presence/absence		Abundance	
Covariate	EDF	*p* value	EDF	*p* value
Surface temperature	**3.31**	**<.001**	**3.27**	**<.001**
Bottom temperature	**3.65**	**.006**	1.00	.709
Calanus finmarchicus	**3.82**	**<.001**	**2.69**	**<.001**
Temora longicornis	**4.23**	**<.001**	**3.00**	**.005**
Depth	**2.44**	**<.001**	1.14	.752
Pseudocalanus spp.	**1.00**	**.034**	**2.51**	**<.001**
Oithona spp.	**2.61**	**.009**	**1.87**	**.031**
Centropages typicus	**3.82**	**<.001**	**4.30**	**.012**
Mesh	**1.00**	**<.001**	**1.00**	**<.001**
R^2	0.58		0.69	
UBRE or GCV	−0.65		0.09	

Covariates are described in terms of their estimated degrees of freedom (EDF) and *p* values. Covariates with *p* values <.05 at an alpha of 0.05 are in bold. Model fitness is described using R^2 and unbiased risk estimator (UBRE, presence/absence model) and generalized cross validation (GCV, abundance model) scores.

TABLE 2 Confusion matrix describing the presence/absence model validation results

	Observed absence	Observed presence
Predicted absence	75.5%	1.7%
Predicted presence	12.1%	10.7%

negative impact on presence (Figure 2). Bottom water temperatures had a neutral effect on larval presence until roughly 15°C, with warmer bottom waters in May and June having a negative effect. Shallower depths (approximately < 65 m) had a positive influence on larval presence. Bongo nets equipped with a 0.505 mm mesh predicted higher larval presence probabilities than 0.333 mm mesh bongo nets. Significant zooplankton taxa had varying influences on larval presence at low zooplankton abundances, but all seemed to have similar positive influences at higher zooplankton abundance. At lower abundances, zooplankton taxa had neutral or negative influences on larval presence (Figure 2). Using only zooplankton covariates appeared to predict larval presence better than a model with only sea temperature (Table 3).

Abundance of Atlantic mackerel larvae was significantly related to surface water temperature, mesh size, and zooplankton taxa *C. finmarchicus*, *Pseudocalanus* spp., *T. longicornis*, *C. typicus*, and *Oithona* spp. (Figure 3). Sea surface temperatures between roughly 12 and 16°C had a positive influence on larval abundance, with temperatures above and below having a negative impact. Mesh sizes of 0.505 mm predicted higher mackerel abundances compared to 0.333 mm mesh. Relationships between significant taxa *C. finmarchicus*, *Pseudocalanus* spp., *T. longicornis*, *C. typicus*, and *Oithona* spp. and larval abundance were similar to those in the presence/absence model: at low larval abundance, the taxa had negative influences, and positive influences with greater copepod prey densities (Figure 3). As with the presence/absence model, zooplankton covariates were better predictors for abundance than sea temperature, but by a smaller margin (Table 3).

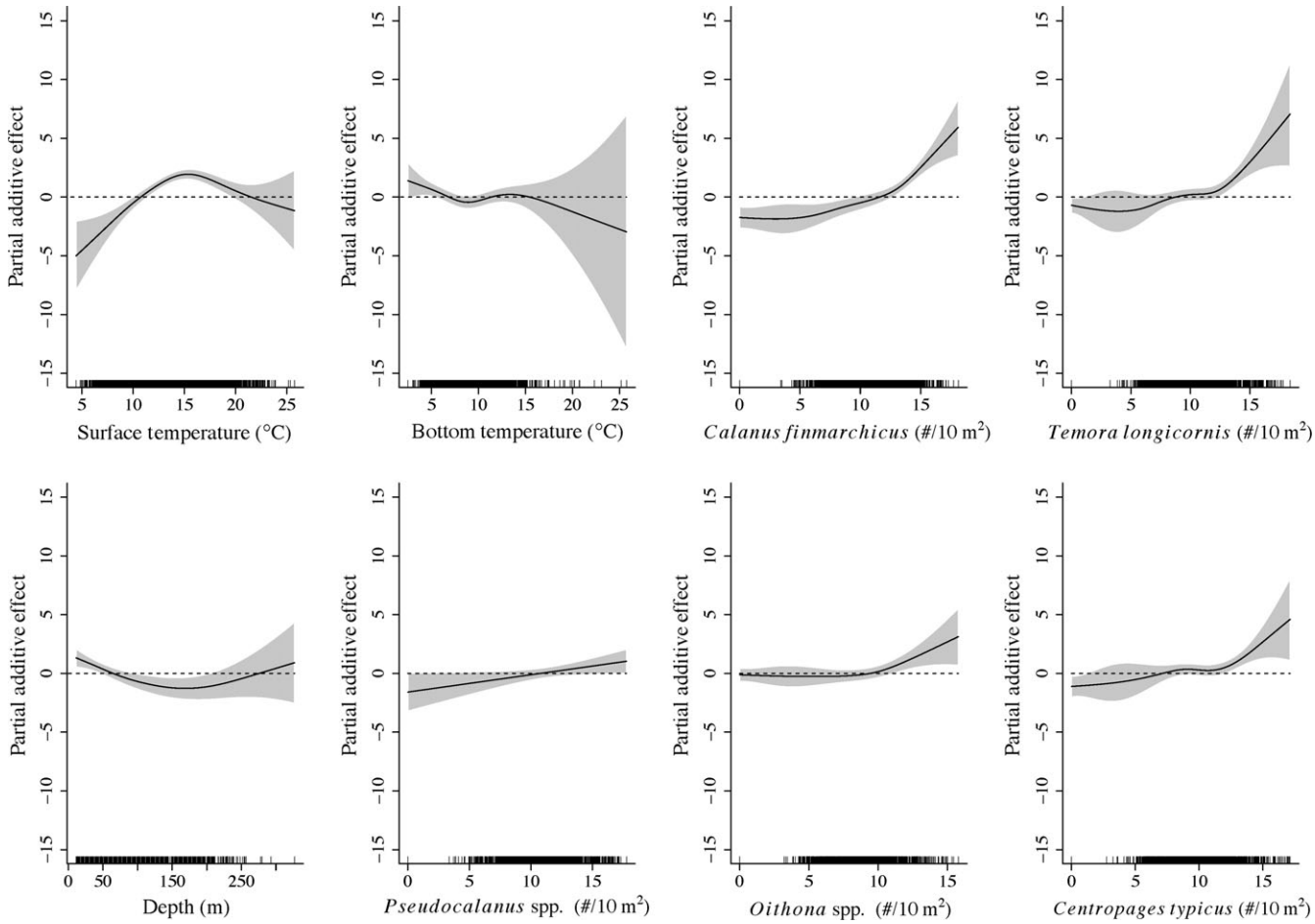

FIGURE 2 Partial additive effects for continuous variables used in the presence/absence GAM. Zooplankton abundances were transformed before modeling: ln(abundance + 1). Dark lines indicate the mean fit for each relationship, with grey bounds indicating the 95% confidence interval. The horizontal dashed lines represent a neutral effect on the presence/absence for the given covariate. Rug plots along *x*-axes indicate the values of independent variable observations, with fewer tick marks indicating fewer samples of that quantity of the covariate observed

TABLE 3 Relative model quality scores (represented as ΔAIC) of the presence/absence and abundance models used for these analyses (Final), only including temperature covariates from the Final model (Temperature) and only including zooplankton covariates from the Final model (Zooplankton)

	ΔAIC	
Model description	**Presence/absence**	**Abundance**
Final	0	0
Temperature	622	372
Zooplankton	416	351

3.2 | Temporal and spatial trends in larval habitat suitability

The amount of suitable habitat compared to observed abundances changed over space and time (Figure S1). Of the different ecoregions, habitat suitability trends within ecoregions (represented by changes in predicted abundances over time) decreased the greatest and most often for the Mid-Atlantic Bight and southern New England (Figure 4a). Greatest positive trends were in the western Gulf of Maine. Habitat suitability trends were most variable in the Mid-Atlantic Bight, southern New England and the western Gulf of Maine, representing the greatest changes in larval habitat suitability and heterogeneity within these ecoregions. Smaller variability in habitat suitability in Georges Bank and the eastern Gulf of Maine represent stronger homogeneity in habitat suitability for these ecoregions; these two regions remained fairly constant in suitable habitat over time (Figure 4a). Mean habitat suitability trends within ecoregions were greater than observed abundance trends, except in southern New England prior to the mid 1980s. Habitat suitability and observed abundances in southern New England have decreased over time, but observed larval abundances have decreased at a faster rate (Figure 4b). Mid-Atlantic Bight habitat suitability has been greater than observed abundances over the entire time series, with both decreasing. Georges Bank habitat suitability has increased slightly over time, with slight decreases in larval abundances. The eastern Gulf of Maine suitable habitat and observed abundances have slightly decreased since the late 1970s, whereas western Gulf

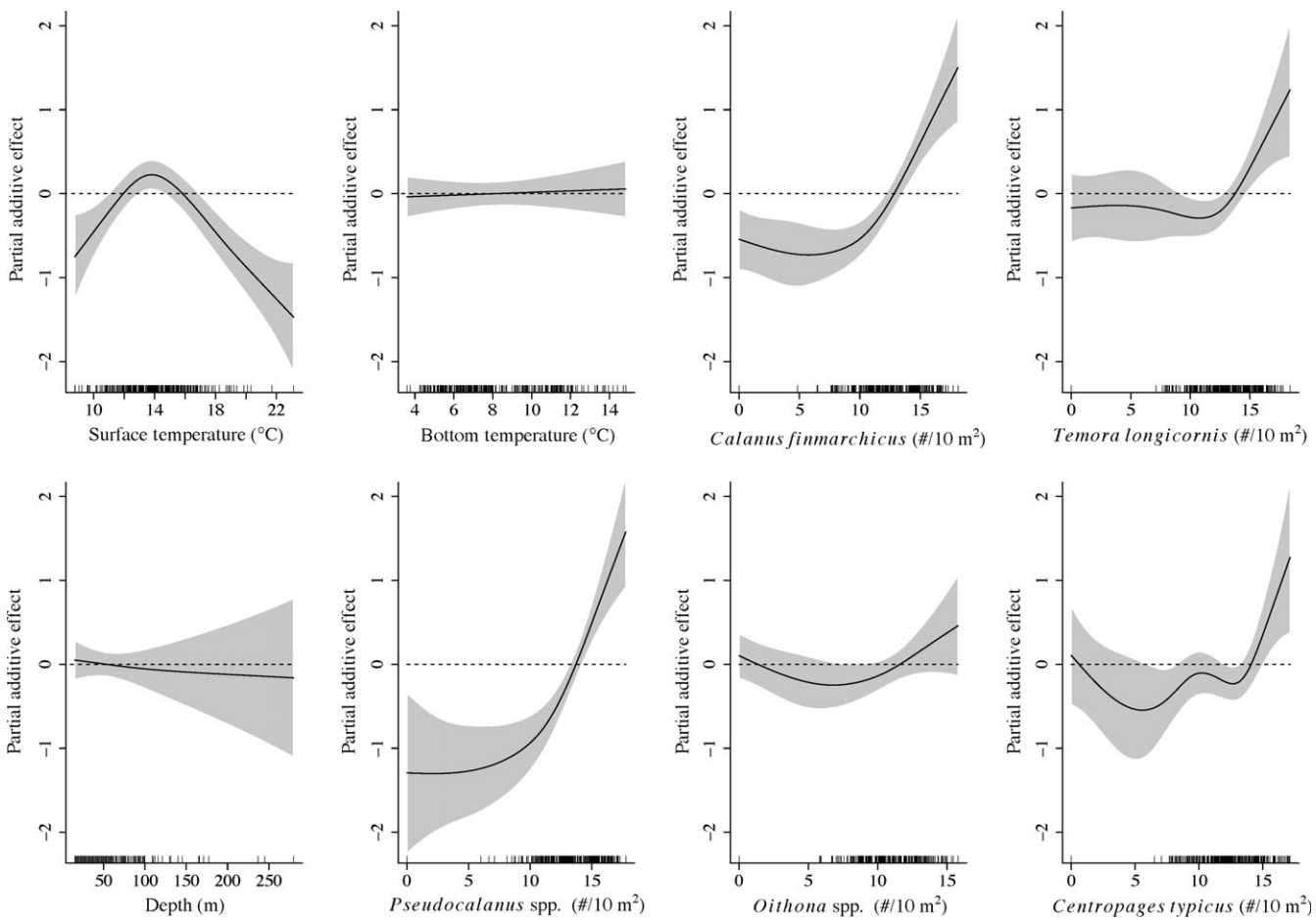

FIGURE 3 Partial additive effects for continuous variables used in the abundance GAM. Larval Atlantic mackerel and zooplankton abundances were transformed before modeling: ln(abundance + 1). Dark lines indicate the mean fit for each relationship, with grey bounds indicating the 95% confidence interval. The horizontal dashed lines represent a neutral effect on the abundance for the given covariate. Rug plots along *x*-axes indicate the values of independent variable observations, with fewer tick marks indicating fewer samples of that quantity of the covariate observed

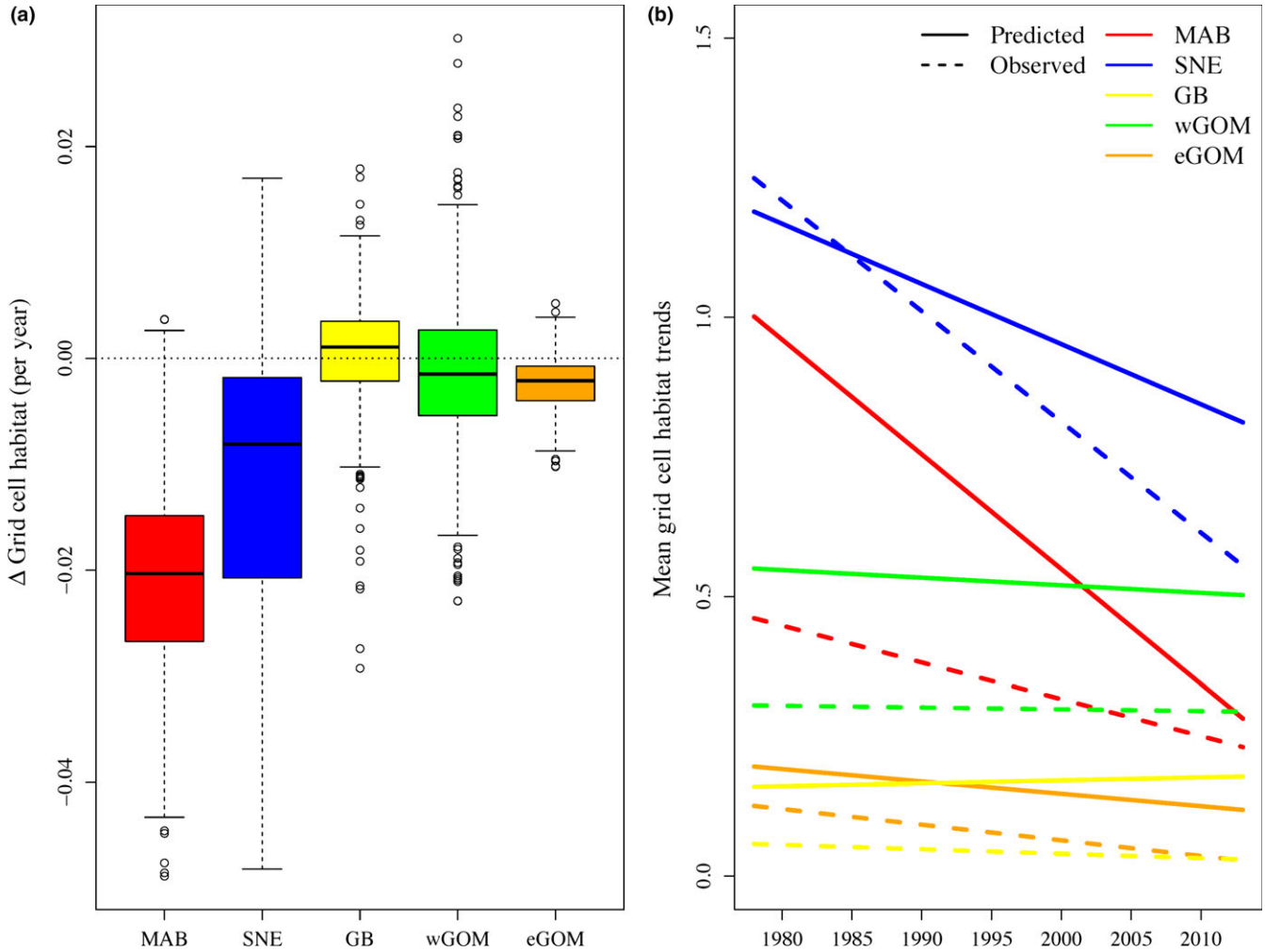

FIGURE 4 Grid cell trends in habitat for the five ecoregions: the Mid-Atlantic Bight (MAB, red), southern New England (SNE, blue), Georges Bank (GB, yellow), the western Gulf of Maine (wGOM, green), and the eastern Gulf of Maine (eGOM, orange) (a). Habitat grid cell linear trends (slopes) over time by ecoregion, with quartiles (lines) and outliers (points) presented. Horizontal dotted line represents no change in habitat. Mean grid cell trends (b) in interpolated abundance, representing habitat suitability (solid lines), and observed (dashed lines) abundance

of Maine suitable habitat has slightly decreased over time with marginal increases in the region's abundance (Figure 4b).

Trends in habitat suitability indices differed among ecoregions in the Northeast U.S. Shelf. HSI_E's were greatest for Mid-Atlantic Bight, southern New England, and western Gulf of Maine, with less habitat in Georges Bank and the eastern Gulf of Maine (Figure 5). HSI_E in the Mid-Atlantic Bight and southern New England have decreased over time, whereas habitat HSI_E in Georges Bank, western Gulf of Maine and eastern Gulf of Maine changed little. HSI_E for the entire Northeast U.S. Shelf decreased, but not significantly (Figure 5). Only Mid-Atlantic Bight HSI_E linear trends indicated a significant decrease (Table 4), while non-significant trends for other HSI_E's reflected high interannual variabilities in suitable habitat. When evaluating proportional habitat suitability shifts within the Northeast U.S. Shelf (HSI_S), the Mid-Atlantic Bight and southern New England have contained much of the suitable habitat for Atlantic mackerel larvae since the late 1970s (Figure 6). However, the Mid-Atlantic Bight contribution to Northeast U.S. Shelf suitable habitat has decreased significantly, while southern New England now contains the most suitable habitat for Atlantic mackerel (Figure 6). In the 2000s, the western Gulf of Maine surpassed the Mid-Atlantic Bight as the second largest contributor to total Northeast U.S. Shelf suitable habitat. Georges Bank and eastern Gulf of Maine contributions to total habitat suitability in the Northeast U.S. Shelf were low and changed little over the time series (Figure 6, Table 4).

The center of larval habitat suitability has remained within northern Mid-Atlantic Bight and southern New England since the late 1970s (Figure 7). Larval habitat suitability moved between the Mid-Atlantic Bight and southern New England ecoregions from the late 1970s through the 1980s, with suitable habitat from the mid 1990s through the early 2010s concentrated in southern New England (Figures 7a and c). Across and along shelf movement has been variable over the time series (Figures 7a and b), while geographical changes in the center of larval suitable habitat have moved north and closer to shore towards the southern New England-Gulf of Maine border (Figure 7c). While linear trends from the late 1978–2013 for across

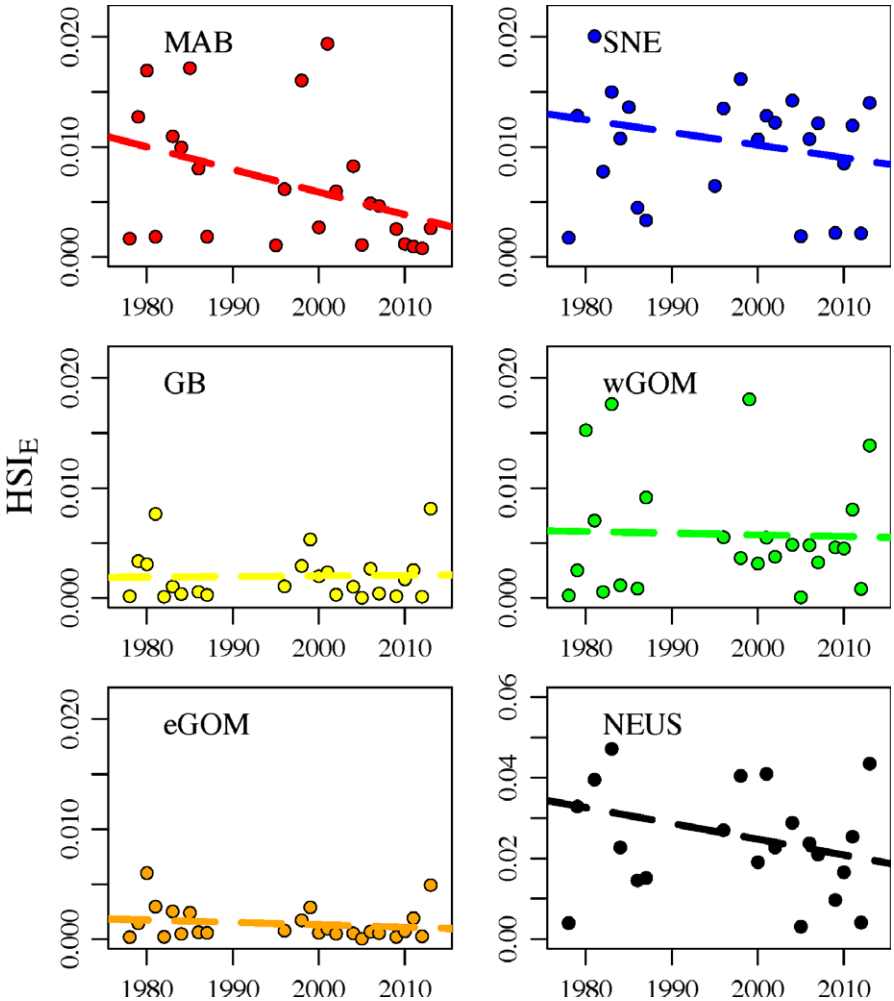

FIGURE 5 Habitat suitability indices within an ecoregion (HSI_E) for the Mid-Atlantic Bight (MAB, red), southern New England (SNE, blue), Georges Bank (GB, yellow), the western Gulf of Maine (wGOM, green), the eastern Gulf of Maine (eGOM, orange), and the Northeast U.S. Shelf (NEUS, black). Dashed lines represent linear fits of the indices over time. Index values are in units of ln(number + 1 1000-m^{-2})

and along shelf movement are insignificant, since 1995, the center of suitable habitat has moved significantly inshore (p value = .01) and north along the shelf (p value = .02) (Figures 7a and b). Since 1978, the geographical center of larval habitat suitability has moved north as much as 211 km, with relative distance changes between 119 and 175 km since 2009.

4 | DISCUSSION

Suitable Atlantic mackerel larval habitat in the Northeast U.S. Shelf has changed over the last 40 years. Habitat suitability indices indicate spatial shifts in the leading areas of suitable larval habitat (Figures 5 and 6). The Mid-Atlantic Bight has become less suitable over time (Figures 5 and 6), and been succeeded by northern regions such as southern New England and the western Gulf of Maine (Figure 6). Spatial variability in habitat suitability is also high within ecoregions. Areas increasing and decreasing in overall habitat suitability have strong heterogeneity in habitat changes over the time series (Figures 4a, 5 and 6). The Mid-Atlantic Bight habitat has varied in rate of habitat change, yet nearly the entire ecoregion has experienced decreased habitat suitability. While southern New England has experienced similar decreases (Figures 4a and 5), this region retains the most suitable habitat within the Northeast U.S. Shelf (Figure 6). The western Gulf of Maine has the greatest positive change in habitat suitability trends (Figure 4a) and is becoming a greater source of larval habitat for the stock's southern contingent. Areas that have historically had little suitable habitat, such as the eastern Gulf of Maine, have greater homogeneity in habitat suitability within their respective ecoregions (Figure 4a).

Latitudinal shifts in larval habitat suitability are consistent with other reports on Atlantic mackerel shifts in the northwest Atlantic. Overholtz et al. (2011) found that adult mackerel abundances in the Northeast U.S. Shelf have shifted approximately 250 km northeast and from deeper to shallower waters, which is of similar magnitude

TABLE 4 Linear slopes for habitat suitability index time series of each ecoregion

Ecoregion	HSI_S	HSI_E
Eastern Gulf of Maine	−1.0E-4	−2.2E-5
Western Gulf of Maine	2.2E-3	−1.5E-5
Georges Bank	3.3E-3	0.5E-5
Southern New England	2.2E-3	−1.2E-4
Mid-Atlantic Bight	−4.6E-3*	−2.1E-4**
Northeast U.S. Shelf	NA	−3.9E-4

Asterisks indicate degree of significance *p < .10, **p < .05.

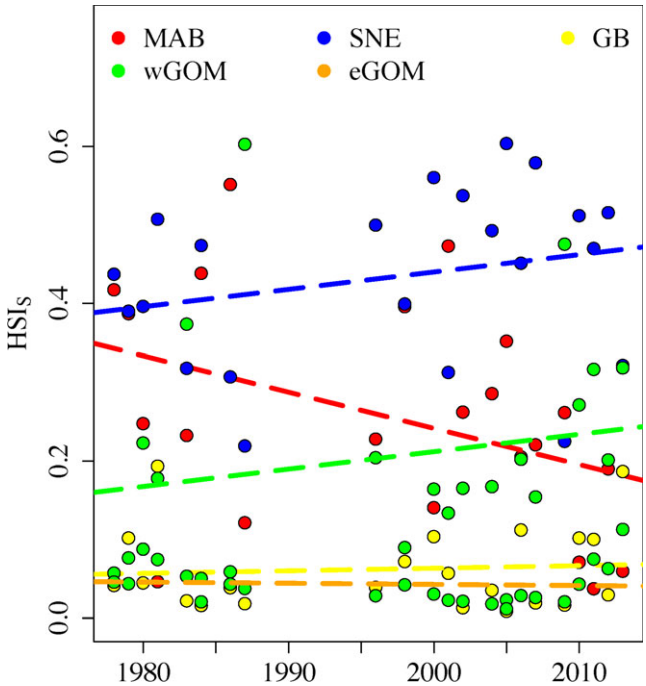

FIGURE 6 Habitat suitability indices within the Northeast U.S. Shelf (HSI_S) for the Mid-Atlantic Bight (MAB, red), southern New England (SNE, blue), Georges Bank (GB, yellow), the western Gulf of Maine (wGOM, green), and the eastern Gulf of Maine (eGOM, orange). Dashed lines represent linear fits of the indices over time

to the shift in larval habitat from the late 1970s to 2010s (Figure 7). Walsh et al. (2015) found that spring adult mackerel have shifted north and inshore, and during the spawning period (May–June), larval abundances have shifted inshore and appear later in the season. Suitable larval habitat changes across and along the shelf since the 1990s and geographical movement corroborate these findings, as the center of larval habitat has moved inshore and further north within southern New England (Figure 7c). A northwestward population expansion has been documented for the northeast Atlantic mackerel population. Northeast Atlantic mackerel spawning has shifted northward at a rate of 15.9 ± 0.9 km/decade from the early 1990s through early 2010s, and is projected to expand west and north up to 117 km and 328 km, respectively (Bruge, Alvarez, Fontán, Cotano, & Chust, 2016).

While larval habitat suitability has changed spatially over time, total suitable habitat available for the stock's southern contingent has not significantly decreased (Figure 5). Absolute changes in larval habitat (HSI_E) over the entire Northeast U.S. Shelf appear to have decreased, but strong interannual variability in habitat suitability persists (Figure 5f); thus, despite variability within and among ecoregions, habitat has been available over the ecoregions for spawning and larvae. Only Mid-Atlantic Bight suitable habitat has significantly decreased (Figure 5a). All ecoregions have provided habitat to support larval abundances greater than observed abundances for many decades (Figure 4b). Over the time series, spawning and larvae appeared to be habitat limited only in southern New England from the late 1970s through the 1980s (Figure 4b).

Latitudinal shifts in larval habitat suitability calculated with the species distribution models suggest the spatial movements are related to sea water temperature and zooplankton abundances (Table 1). Shifts in habitat over time coincide with warming sea waters in the Northeast U.S. Shelf (Friedland & Hare, 2007; Belkin, 2009). The influence of surface sea temperature on suitable larval habitat is not surprising, given adult Atlantic mackerel distributions, migrations and time of spawning are sensitive to sea temperature (Jansen & Gislason, 2011; Overholtz et al., 2011). Nye et al. (2009) and Astthorsson et al. (2012) found adult mackerel abundance and distribution metrics corresponded to sea temperatures and climate

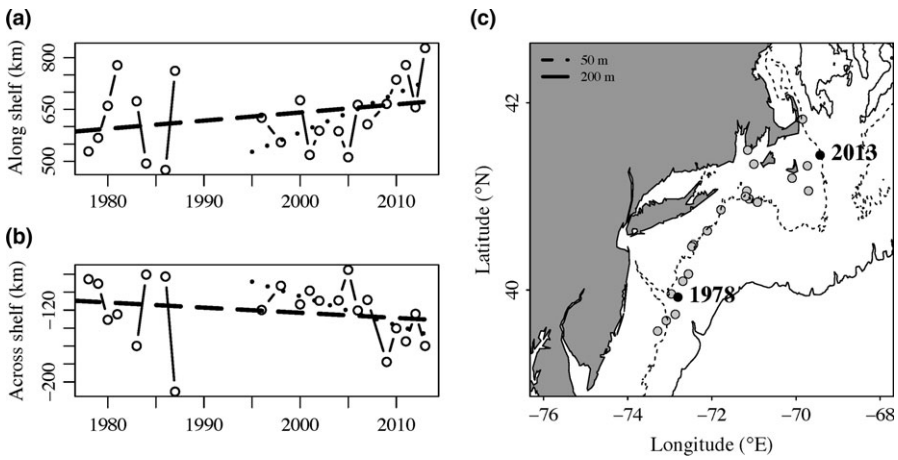

FIGURE 7 Along (a), across (b), and geographical (c) center positions of larval habitat over the Northeast U.S. Shelf. Along shelf distances (km) are relative to the 200 m contour off Cape Hatteras, North Carolina, with increase in values indicating further movement north. Across shelf movements (km) represent landward (negative) or seaward (positive) from the 200 m contour. For further description on the along and across shelf distance calculations, see Nye et al. (2009). Geographical center positions are represented in grey circles, except for start and terminal years (1978 and 2013, black circles). Along and across shelf trends since the late 1970s (dashed lines) and 1995 (dotted lines) are presented

oscillations that correlate to large-scale sea temperature patterns (such as the North Atlantic Oscillation and Atlantic Multidecadal Oscillation). Bruge et al. (2016) also found relationships between planktonic (egg) mackerel and sea temperatures in the northeast Atlantic. The authors noted that the thermal spawning niche for northeast Atlantic mackerel has moved north with thermal habitat changes at a rate of 28 ± 9 km/°C (Bruge et al., 2016). However, the variance explained with this thermal niche model is less than those found using these species distribution models for northwest Atlantic mackerel larvae (Table 1).

The species distribution models highlight the functional relationship between Atlantic mackerel larvae and sea temperature. The observed larval temperature range (Figure 2) agrees with previously reported ranges for spawning (9–14°C) and larval presence (6–22°C) in the northwest Atlantic, as well as the 9–14°C spawning temperature range in the northeast Atlantic (Beare & Reid, 2002; Jansen & Gislason, 2011; Studholme et al., 1999). The dome-shaped responses to temperature suggests an optimal thermal window for Atlantic mackerel larvae, theoretically driven by the bioenergetic and growth requirements (Buckley & Caldarone, 2004). Neutral influence of bottom sea temperature on larval presence and abundance suggests that surface environments are more influential, corroborating with reports of Atlantic mackerel larvae predominantly residing in surface layers (Fortier & Villeneuve, 1996).

Shifts in suitable larval habitat also coincide with oceanographic and climate oscillation induced changes in zooplankton community composition in the Northeast U.S. Shelf (Morse, Friedland, Tommasi, Stock, & Nye, 2017). However, there are two hypotheses for the significant relationship between larval presence and the abundance of specific zooplankton taxa: (i) spawning and higher larval survival occurs in areas where larval prey is abundant, and (ii) oceanographic processes concentrate egg and larval mackerel and zooplankton similarly. Both hypotheses are likely operating to varying degrees, given the planktonic nature of the larvae analyzed in this study. Some of the zooplankton taxa that significantly contributed to predicting larval presence and abundance likely represent true prey or habitat dependency for Atlantic mackerel larvae, such as *T. longicornis*, *Pseudocalanus* spp. nauplii, *Oithona* spp., and *C. finmarchicus* (Kane, 1984; Peterson & Ausubel, 1984; Robert et al., 2008; Paradis, Sirois, Castonguay, & Ploudre, 2012). *Centropages typicus* is highly abundant, yet a less frequent mackerel larval prey item, and may merely coexist with mackerel larvae due to similar habitat requirements and oceanographic processes. Stomach-content analyses of Atlantic mackerel larvae in the study area would better identify copepod species' contributions to mackerel larval diet.

Sizes and/or life stages of copepods sampled during the MARMAP and EcoMon cruises may also confound true relations between copepod and larval abundances. Atlantic mackerel less than 7 mm primarily eat copepod nauplii and copepodites (Fortier & Villeneuve, 1996; Robert et al., 2008, 2009), which are not sampled efficiently by 0.333 mm mesh nets (Runge, Castonguay, de Lafontaine, Ringuette, & Beaulieu, 1999). Copepods sampled during the MARMAP and EcoMon cruises with 0.333 mm mesh nets are older, typically stage IV through adults (Figure S2). Previous studies have used late-staged female copepods as proxies for egg production and nauplii abundances when evaluating available Atlantic mackerel larval prey and mackerel recruitment (Runge et al., 1999; Castonguay et al., 2008). However, given the multi-purpose nature of the MARMAP and EcoMon surveys, sex-specific zooplankton abundance information is not available for refined egg production estimates. Thus, analyses presented here use later stage abundances to represent fecund female copepods and subsequent nauplii production, and assumes that variability in the sampled zooplankton population corresponds to that of the female-specific population. Sampling and identifying smaller copepod nauplii with a finer mesh net, or identification of adult male and female copepods under the current sampling program for fecundity estimates may improve estimating the Atlantic mackerel larval prey field.

The depth influence on presence suggests that spawning primarily occurs within waters less than 60 or 70 m, corroborating historical recordings and observations of inshore spawning (Studholme et al., 1999). However, depending on the ecoregion, depth may act as a proxy for the physical environment influencing mackerel. For instance, years with warmer March sea temperatures in the Mid-Atlantic Bight corresponded to mackerel concentrated father inshore, while in colder years mackerel congregated further offshore (Radlinski et al., 2013). Additionally, mackerel have been shown to respond to tidal and shelf fronts as they move in response to advection and ocean circulation, which can displace them from their preferred habitat (Garrison, Michaels, Link, & Fogarty, 2000). Observed and predicted abundances in various years along the shelf-break (Figure S1) suggest that suitable spawning and larval conditions may exist beyond the historical shallow habitats. In the northeast Atlantic, mackerel spawn along the shelf-break from Portugal through the North Sea (Trenkel, Huse, MacKenzie, & Alvarez, 2014), with migrations to nursery areas correlated with the temporal patterns of the warm shelf edge current (Jansen et al., 2015). Additional shelf-break sampling would help clarify depth's confounding influence on Atlantic mackerel larvae in relation to thermal and prey preferences, and whether the hydrodynamics farther offshore can provide suitable habitat. Higher predicted larval presence and abundances with 0.505 mm mesh net compared with the 0.333 mm may be a temporal artifact given the changes in mesh over time: the coarser mesh may have predicted more larvae because more larvae were present during the 1980s when such gear happened to be used.

Higher predicted abundances than those observed (Figure 4b) and greater spatial discrepancies in predicted and observed abundances in recent years (Figure S1) suggest that temperature and prey described in the species distribution models are not significantly limiting available habitat for larvae over the entire Northeast U.S. Shelf (Figure 5). Other habitat features, such as additional oceanographic characteristics (e.g., fronts) or predator fields not represented in the GAMs may also be contributing to changes in larval abundance over time. While variables chosen to predict larval presence and abundance were based on known influences on larval survival and recruitment to assess changes in the fundamental niche, changes in the

adult stock also contribute to the abundance and distribution of larvae (Parker, 1985). Atlantic mackerel landings in the Northeast U.S. Shelf are currently the lowest in the last 40 years (Wiedenmann, 2016). Contradicting abundance indices and age structures in U.S. landings and bottom-trawl surveys have produced high uncertainty and significant retrospective patterns in stock assessment products (Deroba, Shepherd, Gregoire, Nieland, & Rago, 2010). As such, the U.S. declares the northwest Atlantic mackerel stock status as unknown (MAFMC, 2016). Gulf of St. Lawrence abundance indices based on egg survey data also reflect recent near time series lows in mackerel abundance (DFO, 2014). Canadian assessments have attributed recent reduced catches to overharvesting and recruitment overfishing, and indicate that the stock is at historic low levels (DFO, 2014; Plourde et al., 2015). Thus, lower stock abundances may also be contributing to the absence of larvae across ecoregions where they are expected based on the species distribution models.

Habitat suitability models for Atlantic mackerel larvae can be expanded upon. These results are influenced by the spatial interpolation of abundances where covariates were unavailable for predictions. Prediction spatial resolution can also influence the trends and patterns; Jones, Dye, Pinnegar, Warren, and Cheung (2015) found that species envelope models using different prediction grid sizes can affect the magnitude of trends and changes over time. As zooplankton distribution models become available for the northwest Atlantic (Albouy-Boyer, Plourde, & Pepin, 2016), oceanographic and zooplankton spatial predictions can be used to refine Atlantic mackerel habitat suitability.

Identifying essential fish habitat is critical in understanding key life history aspects (such as growth, survival, reproduction) and population trends, forecasting future abundances, and informing management regulations and quotas. Changes in habitat suitability have significant implications for marine fish species distribution shifts (Perry, Low, Ellis, & Reynolds, 2005), match-mismatches between spawning grounds and suitable early-life habitats (Cowen, Gawarkiewicz, Pineda, Thorrold, & Werner, 2007; Walsh et al., 2015), and changes in prey and predator fields (Mountain & Murawski, 1992; Murawski, 1993). Distributional shifts specifically pose challenges for future fisheries management. As evidenced in the northeast Atlantic, growing Iceland and Greenland mackerel fisheries and shifts in other European countries' harvest in response to northwestward expansion of northeast Atlantic mackerel will alter available fish for participating countries' fishery quotas (Astthorsson et al., 2012; Hughes, Dransfeld, & Johnson, 2015). Such changes will have direct effects on the revenue, employment opportunities, and food supply for local communities (Jansen et al., 2016). By identifying the relationships between fisheries and the environment, we can continue to anticipate how species distributions and abundance may shift in a changing marine environment and prepare for socioeconomic changes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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