

Modeling spatiotemporal variability of the bioclimate envelope of *Homarus americanus* in the coastal waters of Maine and New Hampshire



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ARTICLE INFO

Article history:

Received 13 August 2015

Received in revised form 11 January 2016

Accepted 12 January 2016

Keywords:

American lobster

Homarus americanus

Climate change

Habitat suitability index

Bioclimate envelope model

ABSTRACT

A bioclimate envelope model was developed to evaluate the potential impacts of climate variability on American lobster (*Homarus americanus*). Bioclimate envelopes were defined by season-, sex-, and stage-specific Habitat Suitability Indices (HSI) based on (1) bottom temperature, (2) bottom salinity, and (3) depth. The species' association to each of these three environmental attributes was expressed using Suitability Indices (SIs) calibrated by standardized lobster abundance derived from 14 years of fishery independent survey. A regional ocean model (Finite-Volume Community Ocean Model) was integrated with the HSI to hindcast spatiotemporal variability of bioclimate envelopes for American lobster in coastal waters of Maine and New Hampshire from 1978 to 2013. The model predictions indicated higher habitat suitability in inshore waters for both adult and juvenile lobsters. A statistically significant increasing trend in habitat suitability was observed for both sexes and stages (juvenile and adult) during the spring (April–June), while no significant trend in habitat suitability was observed in the fall (September–November). This study provides a modeling framework to reconstruct climatically suitable lobster ranges that can be used to formulate climate-based hypotheses for future studies of this species.

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1. Introduction

American lobster, *Homarus americanus*, is a large benthic crustacean present throughout coastal Northwest Atlantic waters, from Labrador, Canada to Cape Harettas, USA (Lawton and Lavalli, 1995; Wahle et al., 2013). The species is abundant in shallow coastal waters (<50 m) of the Gulf of Maine (GOM) and southern Gulf of St. Lawrence out to the canyons of the continental slope (Aiken and Waddy, 1986), but is often found in the intertidal zone at depths down to 700 m (Lawton and Lavalli, 1995). It prefers coarse rocky substrate often characterized by cobble and boulder, but can also be found on several other substrate types such as mud and sand base with rock (Lawton and Lavalli, 1995). *H. americanus* in the GOM supports one of the most valuable fisheries in the USA with an estimated ex-vessel value of \$460 million in 2013 (ASMFCa, 2015).

Due to its ectothermic nature, water temperature has a significant impact on *H. americanus* life history, especially when coupled with non-optimal dissolved oxygen and salinity conditions (Mercaldo-Allen and Kuropat, 1994). *H. americanus* can tolerate a wide range of temperatures and salinity, from 0–25 °C and

15–32 ppt, respectively, but the species exhibits affinity to a specific thermal (8–18 °C) and salinity (0–32 ppt) range to maximize its physiological functionality (Reynolds and Casterlin, 1979; Crossin et al., 1998; ASMFC, 2009). Adult *H. americanus* exhibit long distance seasonal movements (>100 km) between shallow and deep waters to pursue optimal water temperature for growth and egg development (Cobb and Wahle, 1994). Water temperature above 20.6 °C creates a stressful environment for *H. americanus* as the species is forced to spend more energy for respiration and less energy for growth and feeding (McLeese, 1958; Dove et al., 2005; Fogarty et al., 2007). Adult lobsters respond to even small changes in temperature (Crossin et al., 1998; Jury and Watson III, 2000) both behaviorally (e.g., movement) and physiologically (e.g., changes in cardiac cycle) (McLeese and Wilder, 1958; Worden et al., 2006).

The favorable habitat and spatial distribution of *H. americanus* vary with life stage and season (MacKenzie and Moring, 1985; Chang et al., 2010). Small juveniles typically remain inshore and within a home range of about 5–15 km, and do not exhibit large-scale seasonal movements (Cooper et al., 1975). Mature individuals exhibit an average annual range of 32 km (Campbell, 1986), and have a higher tolerance to deeper and cooler waters. In the GOM, adults migrate inshore and into estuaries during spring, and then migrate back offshore late fall (Watson III et al., 1999; Chen et al., 2006a). Differences in the spatial distribution of *H. americanus* with

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size composition suggest stage and season-specific responses to climate-driven variables such as bottom temperature and salinity (Jury et al., 1994; Factor, 1995).

Climate change is rapidly altering environmental conditions in the GOM. This could significantly impact *H. americanus* because its abundance appears to be primarily regulated by bottom-up forces (e.g., climate-driven changes in environment and resources) (Mills et al., 2013; Steneck and Wahle, 2013; Boudreau et al., 2015; Fernandez et al., 2015). Relationships between *H. americanus* distribution and climate variables have been well documented (Chang et al., 2010; Mills et al., 2013; Tanaka and Chen, 2015). Sea surface temperature in GOM shows an increase of 0.03 °C per year, resulting in a 1 °C increase in the mean temperature since 1982 (Mills et al., 2013). At the southern end of the species' range, summer sea surface temperature has increased approximately 0.09 °C per year since 1990 (Wahle et al., 2015). Such an abrupt increase in temperature is hypothesized to alter availability of suitable habitat for *H. americanus* and lead to a significant decline in the density and size composition in *H. americanus* nurseries (Tanaka and Chen, 2015; Wahle et al., 2015). While a northward shift in the species' distribution in response to climate variability has been observed (Pinsky et al., 2013), impacts of gradual and abrupt warming events on the spatiotemporal availability of suitable *H. americanus* habitat remain understudied. Such a knowledge gap restricts us from gaining a mechanistic understanding of the impacts of climate variability on the spatial dynamics of fish populations, which is crucial for implementation of effective ecosystem-based fishery management.

A bioclimate envelope model is a type of species distribution models, and has become a common ecological tool to hindcast/forecast species' responses to climatic variability (Pearson and Dawson, 2003; Araújo and Peterson, 2012; Watling et al., 2013). A bioclimate envelope is commonly defined as a set of physical and biological conditions that are suitable to a given species (Cheung et al., 2009, 2008). Bioclimate envelope models define climate-driven habitat suitability by using quantitative associations between climate variables and relative species abundance or occurrence, but do not incorporate predator-prey interactions or dispersal ability of a given species (Cheung et al., 2009, 2008). Thus, the utility of bioclimate envelope models lies in estimating realized niches of a given species, and is often applied to examine the spatial distribution of suitable environments as well as patterns and limiting factors for the species of interest (Stock et al., 2011; Araújo and Peterson, 2012; Watling et al., 2013).

In this study, an empirical bioclimate envelope model was developed based on season, sex and life history stage specific Habitat Suitability Indices (HSI) to evaluate spatiotemporal variability of a bioclimate envelope for *H. americanus* in the coastal waters of Maine and New Hampshire during spring (April–June) and fall (September–November) from 1978 to 2013. The HSI is an ecological index developed by the U.S. Fish and Wildlife Service (FWS) to facilitate habitat evaluation procedures (U.S. Fish and Wildlife Service, 1981). An HSI quantifies habitat suitability for a given species on a scale of 0–1 to represent "least suitable" to "most suitable" habitats, respectively (Franklin, 2010). It is a useful tool to describe the relationship between relative species abundance and ecological variables (Vinagre et al., 2006; Tian et al., 2009). The construction of an HSI is a repeatable technique, and the utility lies in enabling managers to predict where a species is likely to occur within a distributional range. In fisheries management, HSI is often combined with a geographic information system (GIS) to analyze the spatiotemporal variability in fish habitat preference, availability, and quality to make informed decisions (Terrell, 1984; Bovee and Zuboy, 1988; Morris and Ball, 2006; Chang et al., 2012). A HSI-based bioclimate envelope model was recently developed, in which spatial analysis was applied to analyze spatiotemporal variability of

suitable habitat for *H. americanus* in Long Island Sound, USA (Tanaka and Chen, 2015).

This study expands upon the modeling framework developed in Tanaka and Chen (2015) and adds an analytical component exploring the impact of changes in climate-driven *H. americanus* habitat suitability over 1978–2013 in the coastal waters of Maine and New Hampshire. Bioclimate envelopes were defined by habitat suitability based on bottom temperature, depth and bottom salinity. These three environmental attributes were chosen based on previous studies (Chang et al., 2010; Tanaka and Chen, 2015). A major advantage of the bioclimate model developed in this study is the incorporation of a regional ocean model for hindcasting impacts of climate change over 1978–2013. Such a contribution is important for understanding potential biome shifts in marine environments under changing climate (Harley et al., 2006). Although the model does not explicitly incorporate the effects of biological interactions and evolutionary process (Pearson and Dawson, 2003), the implications of these uncertainties are discussed.

2. Materials and methods

2.1. Maine–New Hampshire inshore bottom trawl survey

This study used 14 years of semi-annual fishery-independent survey data collected by the Maine–New Hampshire Inshore Bottom Trawl Survey for *H. americanus* from 2000 to 2013 conducted by the Department of Marine Resources (DMR) in spring (April–June) and fall (September–December). The total survey area spanned from 12,437 to 16,001 km² each year, and included 2,246 bottom-trawl samples in total ($n = 280,185$ lobsters; Sherman et al., 2005) (Fig. 1). The survey employed a stratified random design, with the coastal waters of Maine and New Hampshire being divided into five longitudinal areas based on abiotic and biotic features (Sherman et al., 2005; Cao et al., 2014). Each stratum is further separated into four depth classes (9–37 m, 37–64 m, 64–100 m, and >100 m with 12 km offshore limit), resulting in a total of 20 strata. Each survey targets 115 stations with a sampling density of 1 station for every 137.2 km². The number of tows in a given stratum is adjusted according to areas of each stratum size. The fishing gear is a modified shrimp net with 50.8 mm mesh in wings and 12.7 mm mesh liner in the cod end (Sherman et al., 2005). The targeted tow duration is 20 min at a velocity of 2.2–2.3 knots to cover approximately 1.48 km². A CTD profiler is deployed at each tow to record salinity, temperature and depth (Sherman et al., 2005).

2.2. Environmental data

The unstructured-grid Finite-Volume Community Ocean Model (FVCOM) was used to simulate monthly estimates of bottom temperature and salinity by location and time in the coastal waters of Maine and New Hampshire from 1978 to 2013. The FVCOM is a regional coastal ocean circulation model developed by the University of Massachusetts-Dartmouth and the Woods Hole Oceanographic Institution. It has a horizontal resolution ranging from 0.02 km to 10 km (Chen et al., 2006b). The unstructured FVCOM grid can capture complex and irregular coastal geometry, which makes FVCOM suitable for physical and biological studies in coastal regions and estuaries (Chen et al., 2006b; Huang et al., 2008). Bathymetry data were obtained from the U.S. Coastal Relief Model (CRM) (NGDC, 1999).

2.3. Data analysis and model development

This study is an extension of an earlier modeling effort for *H. americanus* in Long Island Sound (Tanaka and Chen, 2015). The

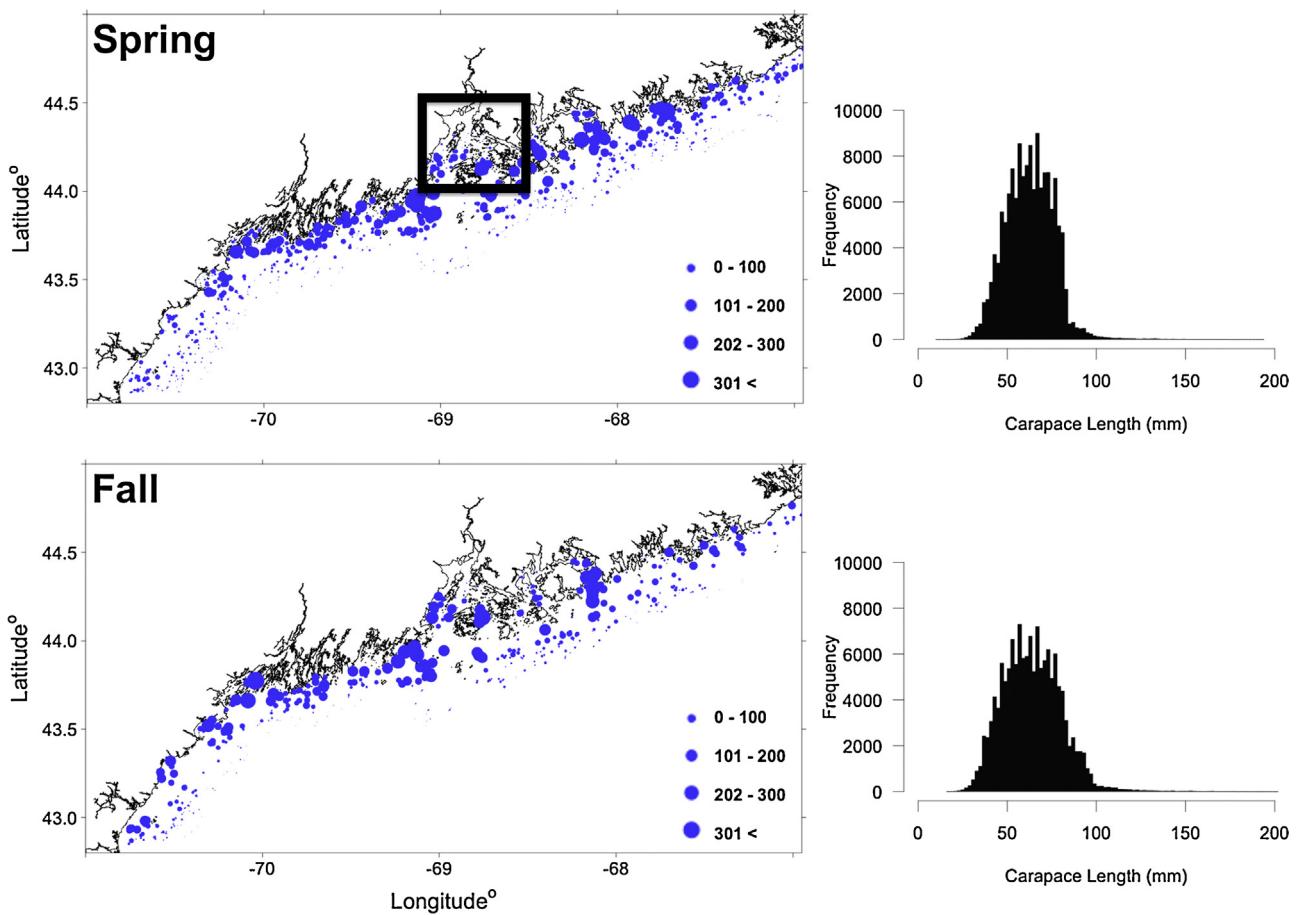


Fig. 1. Spatial distribution of standardized *Homarus americanus* abundance and observed size frequency based on spring and fall surveys during 2000–2013. The box on the map indicates the location of Penobscot Bay.

overall procedure for developing the HSI-based bioclimate envelope model (Fig. 2) was modified from Tanaka and Chen (2015). *H. americanus* exhibits season, size, and sex specific preferences to surrounding environment (Chang et al., 2010). For example, the species' response to change in temperature is determined by season or thermal history through acclimatization (Worden et al., 2006; Qadri et al., 2007; Jury and Watson III, 2013). The survey data were consequently analyzed separately by season (spring and fall), sex and for two *H. americanus* stage classes (adult: >60 mm carapace length, juvenile: ≤60 mm carapace length). The carapace length of 60 mm represents the minimum size at maturity defined by ASMFC (ASMFC, 2009).

The standardized *H. americanus* abundance index derived from the survey was used to develop suitability indices (SIs) for each environmental variable. The nominal abundance index was calculated as a survey catch per unit of sampling effort (CPUE) at station i, in season j, and year y (Chang et al., 2012; Tanaka and Chen, 2015);

$$\text{CPUE}_{ijy} = \left(\frac{\text{Count}_{ijy}}{\text{Tow Duration}_{ijy}} \right) \times 20 \quad (1)$$

where Count represents the total quantity of either adult or juvenile *H. americanus* caught and Tow duration is measured in minutes. Continuous environmental variables (temperature, salinity and depth) were delineated into 10 classes using Fisher's natural breaks classification method (Bivand, 2013). The SI of class k for environ-

ment variable i, $\text{SI}_{i,k}$, was calculated on a scale of 0.0–1.0 following (Chang et al., 2012; Tanaka and Chen, 2015):

$$\text{SI}_{i,k} = \frac{\text{CPUE}_{i,k} - \text{CPUE}_{i,\min}}{\text{CPUE}_{i,\max} - \text{CPUE}_{i,\min}} \quad (2)$$

where $\text{CPUE}_{i,k}$ represents the average CPUE over all the sampling stations falling within the class k of environmental variable i in each *H. americanus* group. $\text{CPUE}_{i,\min}$ and $\text{CPUE}_{i,\max}$ represents the minimum and maximum values of the average CPUEs of all the classes for environmental variable i, respectively. To analyze the relationships between each environmental variable and *H. americanus* abundance, estimated SI was assigned to each class of environmental variables in the form of a linear transfer function, where the most suitable class ($\text{SI} = 1$) and the least suitable class ($\text{SI} = 0$) were identified (Bayer and Porter, 1988).

Suitability Indices (SIs) were estimated using the histogram method (Vinagre et al., 2006; Chen et al., 2010), and a trimmed mean function was used to remove any missing values and 5% of the highest and lowest scores to eliminate outliers (Tukey, 1977; Crawley, 2007). Local polynomial regression fitting (LOESS) smoothing was applied to the SIs (R Core Team, 2014). Suitable ranges were identified as SI values above 0.8 (McMahon, 1983; Tanaka and Chen, 2015). The SIs were combined to form composite HSI also scaled from 0 to 1 following two mathematical equations (Franklin, 2010; Chang et al., 2012; Tanaka and Chen, 2015);

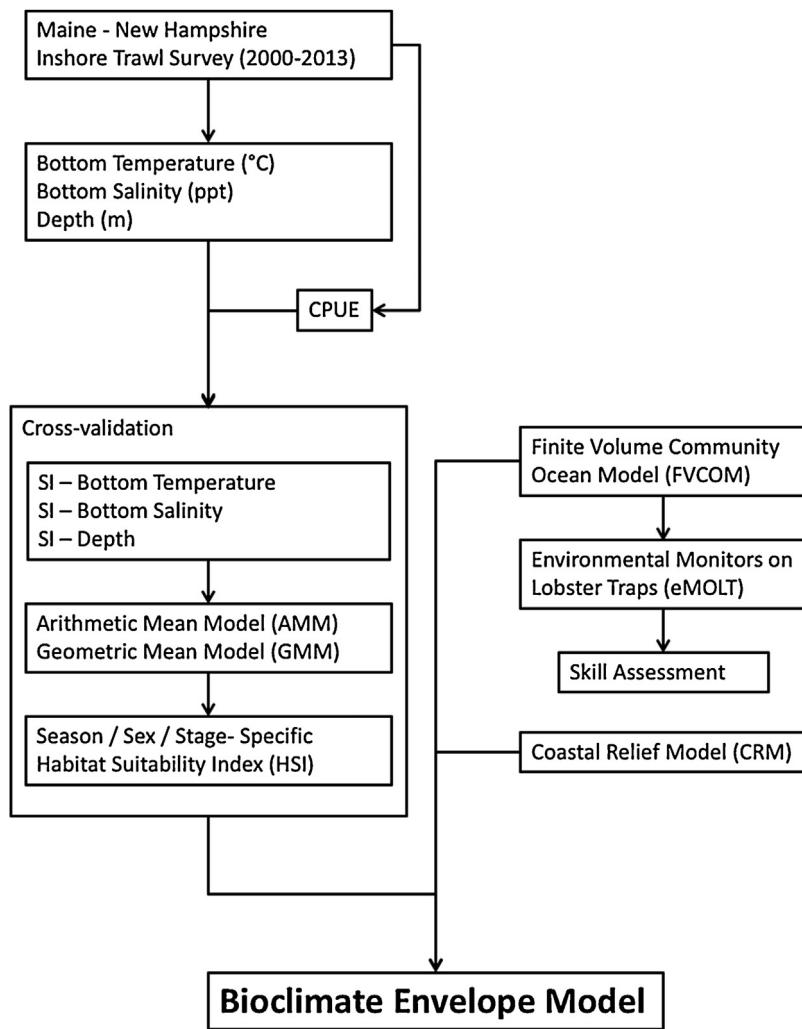


Fig. 2. Schematic representation of the structure of the bioclimate envelope model developed in this study, implemented in R programming environment.

Arithmetic Mean Model (AMM)

$$HSI = \frac{\sum_{i=1}^n SI_i}{n} \quad (3)$$

Geometric Mean Model (GMM)

$$HSI = \left[\prod_{i=1}^n SI_i \right]^{1/n} \quad (4)$$

where SI_i represents a SI value associated with the i^{th} environmental variable while n represents the number of environmental variables included in either AMM or GMM HSI.

2.4. HSI performance validation and FVCOM skill assessment

The predictive ability of HSIs was evaluated in a cross-validation study, which was conducted independently for each *H. americanus* group. A randomly selected subset representing 80% of all the data (training data set) was used for HSI development, while the remaining 20% (testing data set) was used for the evaluation of the HSI performance (Smith, 1994; Zuur et al., 2007; Tanaka and Chen, 2015). The predicted HSI values (based on the training data set) were compared against the observed HSI values (based on the testing data set), and linear regression analysis was performed to evaluate the predictive performance of the HSI. This

cross-validation procedure was repeated 100 times using random selection in each step to obtain 100 sets of liner regression parameters (intercept, slope, R^2 , and Akaike Information Criterion AIC). The results for both AMM and GMM were compared to determine which model had better predictive ability, which was quantified by an intercept (α) closest to 0, a slope (β) closest to 1, higher R^2 and lower AIC. The 95% conference intervals derived from the 100 runs of simulation were compared to evaluate the difference for each regression parameter between the AMM and GMM.

A collection of observed bottom temperatures provided by the Environmental Monitors On Lobster Traps (eMOLT) program was used to assess performance of FVCOM in the DMR bottom trawl survey area. The eMOLT provides a large collection of hourly bottom temperatures from lobster traps at more than 200 sites in the GOM and Georges Banks, and is ideally suited for skill assessment of coastal ocean circulation and regional ocean models (Manning and Pelletier, 2009). In a preliminary analysis, observed bottom temperatures from 64 eMOLT sites in the DMR survey area were compared to modeled FVCOM bottom temperature at hourly temporal resolution from 2001 to 2013 ($n=969,249$; Fig. 3). This univariate comparison of predicted (FVCOM) and observed (eMOLT) outputs were examined by six quantitative metrics; (1) correlation coefficient, (2) root mean squared error, (3) reliability index, (4) average error, (5) average absolute error, and (6) modeling efficiency (Stow et al., 2009). The results showed strong similarity between FVCOM and eMOLT outputs at an hourly resolution (correlation coeffi-

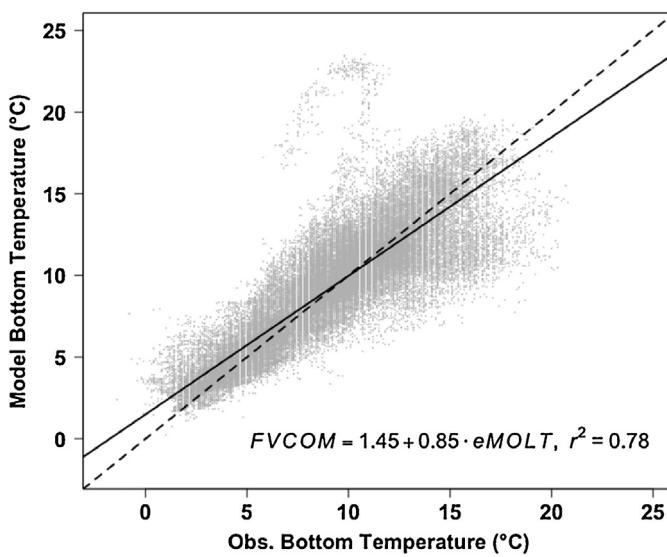


Fig. 3. A linear regression plot of the modeled bottom temperature (FVCOM) compared to the observed bottom temperature (eMOLT). The linear regression for the model versus predicted value is plotted (solid line) relative to the 1:1 line (dashed line).

cient = 0.877, reliability index = 1.062, average error = 0.156, root mean squared error = 1.704, average absolute error = 1.124, modeling efficiency = 0.759), demonstrating that modeled FVCOM bottom temperature can be used in this study.

2.5. Spatial and temporal HSI-based bioclimate envelope analysis

The model generated an HSI-based bioclimate envelope for every spring and fall season between 1978 and 2013 for both sexes and both stages of *H. americanus*.

A spatial interpolation technique using variogram modeling and ordinary kriging was implemented in the R programming environment to visualize the model outputs (Bailey and Gatrell, 1995; R Core Team, 2014). Semivariogram models were fitted with gaussian, exponential, and spherical variograms with non-linear least squares using R package "gstat". The model with the lowest mean squared error was used for kriging (Pebesma, 2004). Interpolated model outputs were mapped using "sp" R package (Pebesma and Bivand, 2005). The model outputs were first inspected visually. The interpolated surfaces for each modeled group were subtracted from one another to produce mean season, sex, and stage specific differences.

The distribution of median HSI over 36 years was evaluated for the spatial trend in the quality of bioclimate envelopes. In this study, an area with HSI value larger than 0.7 was designated as good habitat, while the area with HSI value below 0.3 as poor habitat (Brooks, 1997; Tian et al., 2009; Chang et al., 2012; Williams and Biggs, 2012).

Linear regression analysis was performed at every FVCOM grid and the slope (β) was used to evaluate temporal changes over 36 years in quality of *H. americanus* bioclimate envelopes. Annual median HSI was calculated with a fitted linear regression model to detect any statistically significant trend to evaluate temporal variation in climate driven habitat suitability in both seasons, sexes, and life-stages during 1978–2013.

Finally, as predicted HSI reflected one static variable (depth) and two dynamic variables (temperature and salinity), the HSI time series were cross-correlated with temperature and salinity time series to determine whether two variables are correlated with each other at different time lags in each season.

3. Results

3.1. Suitability index of each environmental variable

The highest SI for each environmental variable differed by sex, stage and season (Fig. 4; Table 1). Observed bottom temperature varied between 2.6–12.0 °C and 5.7–14.3 °C in spring and fall respectively. The suitable bottom temperature for adults varied from approximately 8.4–10.6 °C in spring and 11.6–14.3 °C in fall. Suitable temperature ranges for juveniles showed greater seasonal contrast, from approximately 6.6–10.1 °C in the spring, and shifted higher to 10.9–14.3 °C in fall. A broader suitable temperature range was observed for male juveniles compared to female juveniles.

Surveyed depth range varied between 3.3–121 m in spring and 2.5–121 m in fall. The range for male adults was 14.6–22.1 m and was 4.8–22.9 m for female adults in spring. The corresponding depth ranges shifted deeper to 12.2–40.3 m and 32.9–41 m in fall. For juveniles, spring suitable depth range was observed at 16.9–36.7 m in spring, and 16.5–27.7 for both males and females in fall.

Observed bottom salinity varied between 25.7–34.2 ppt in spring, and 26.7–34.6 ppt in fall. Male adults exhibited broader suitable salinity range in both seasons. Suitable salinity for female adults was between 30.7–31.9 ppt in spring, and 32.2–32.9 ppt in fall. For male adults, suitable salinity ranges were between 25.7–31.9 ppt in the spring, and 28.5–32.9 ppt in fall. For juvenile males, suitable salinity ranges were 31.2–31.8 ppt in spring, and 32–32.9 ppt in fall. For juvenile females, suitable salinity ranges varied between 27–28.5 ppt and 31.2–31.8 ppt in spring, and 32.5–32.9 ppt in fall.

3.2. Model validation

Table 2 shows a summary comparison of cross-validation results between AMM and GMM for eight modeling groups. AMM produced lower intercepts and higher slopes in 10 out of the 16 comparisons. AMM showed better predictive ability overall by showing smaller AIC values and higher R^2 for all the 8 modeling groups. Therefore, AMM was determined to be more appropriate than GMM in this study. Among the eight modeling groups, spring–female–adult showed the best predictive performance with the highest R^2 and the lowest AIC, while predictive performance for the fall–male–juvenile was the poorest with the lowest R^2 and the highest AIC.

3.3. Model prediction

The season, stage, and sex specific bioclimate envelopes for *H. americanus* were generated based on predicted HSI at every FVCOM grid in the DMR bottom trawl survey area (Fig. 5). Overall, high habitat suitability in inshore waters appeared to occur together while offshore areas were of low habitat suitability. Visual inspection revealed a higher propensity for suitable habitat (i.e., HSI > 0.7) for both juveniles in spring, while a greater area of suitable habitat in the fall was observed for adults. Adult bioclimate envelopes were more extensive than juvenile bioclimate envelopes in both seasons and sexes. Finally, the model predicted higher habitat suitability for female juveniles in the Penobscot Bay in fall, compared to male juveniles (Fig. 5). Season, stage, and sex specific comparison of interpolated model predictions showed larger mean differences between seasons (0.2058), compared to the differences between stages (0.0926) and between sexes (0.0982).

The changes in climate-driven habitat suitability during 1978–2013 are shown in Fig. 6. In the spring, there was greater change toward higher habitat suitability throughout coastal waters for both modeled stages and sexes. In the fall, the change was less

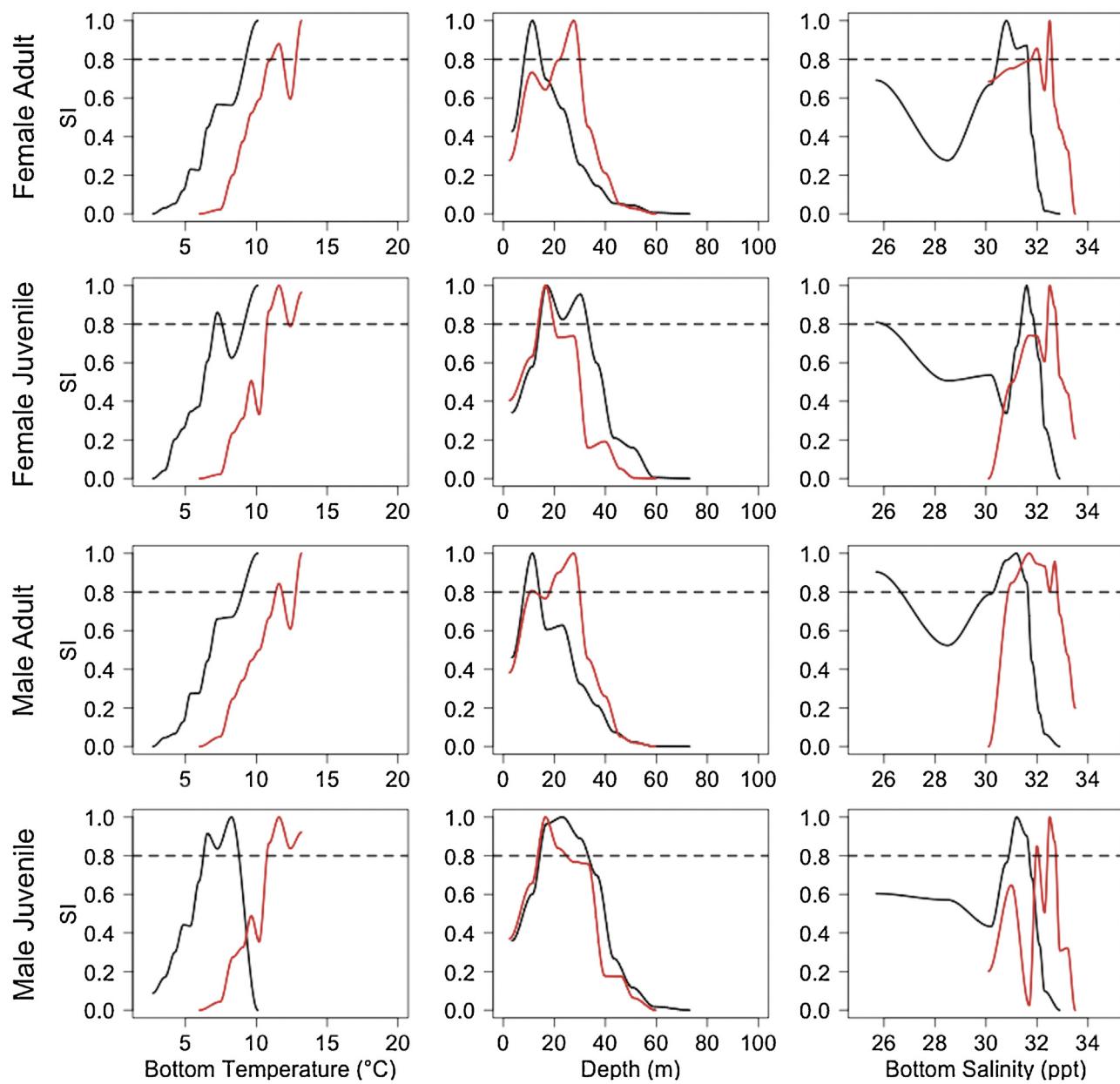


Fig. 4. Suitability Index (SI) curves of bottom temperature, depth, and bottom salinity for four groups of *Homarus americanus* (2 sexes × 2 life stages). Both spring (black line; April–June), and fall (red line; September–November) SI curves are plotted.

Table 1

Summary of season, sex, and stage specific suitable range of each environmental variable.

Season	Sex	Stage	Bottom temperature (°C)	Depth (m)	Bottom salinity (ppt)
Spring	Female	Adult	8.4–10.6	14.8–22.9	30.7–31.9
		Juvenile	6.8–9.6	17.1–36.2	27.0–31.8
	Male	Adult	8.4–10.6	14.6–22.1	25.7–31.9
		Juvenile	6.6–10.1	16.9–36.7	31.2–31.8
Fall	Female	Adult	11.6–14.3	32.9–41.0	32.2–32.9
		Juvenile	10.9–14.3	19.2–26.2	32.5–32.9
	Male	Adult	11.6–14.3	12.2–40.3	28.5–32.9
		Juvenile	10.9–14.3	16.5–27.7	32.0–32.9

significant in magnitude (fainter in color) for both sexes and stages. A declining trend in habitat suitability was observed in the upper Penobscot Bay in all eight modeled groups.

Temporal variation in climate driven-habitat suitability during 1978–2013 was observed for both seasons, stages and sexes of *H.*

americanus (Fig. 7). A significant increasing trend in habitat suitability was observed in all groups, except in the fall ($\beta = -0.0001$, $p = 0.806$). The cross-correlation analysis revealed significant relationships between HSI and both temperature and salinity in the

Table 2

Summary of linear regression results between the predicted and observed habitatsuitability index (HSI) for Geometric Mean Model (GMM) and Arithmetic Mean Model (AMM) based on 100 rounds of cross-validations.

Season	Sex	Stage	Sample size	Intercept				Slope			
				AMM mean	95% CI	GMM mean	95% CI	AMM mean	95% CI	GMM mean	95% CI
Spring	Female	Adult	38069	0.049	(0.040, 0.058)	0.023	(0.018, 0.028)	0.942	(0.923, 0.962)	0.959	(0.927, 0.991)
	Juvenile	31252	0.158	(0.146, 0.170)	0.101	(0.087, 0.114)	0.776	(0.755, 0.797)	0.848	(0.807, 0.888)	
	Male	Adult	43822	0.053	(0.041, 0.064)	0.054	(0.042, 0.065)	0.909	(0.893, 0.926)	0.826	(0.782, 0.870)
	Juvenile	29825	0.191	(0.177, 0.204)	0.166	(0.150, 0.183)	0.764	(0.741, 0.787)	0.747	(0.711, 0.783)	
Fall	Female	Adult	38069	0.235	(0.217, 0.254)	0.268	(0.241, 0.296)	0.690	(0.669, 0.712)	0.566	(0.539, 0.593)
	Juvenile	29686	0.261	(0.246, 0.275)	0.284	(0.262, 0.306)	0.636	(0.615, 0.658)	0.536	(0.511, 0.561)	
	Male	Adult	41350	0.280	(0.256, 0.303)	0.301	(0.276, 0.324)	0.667	(0.642, 0.693)	0.539	(0.560, 0.568)
	Juvenile	30122	0.206	(0.193, 0.219)	0.176	(0.160, 0.193)	0.621	(0.595, 0.647)	0.505	(0.452, 0.558)	
Season	Sex	Stage	Sample size	R-squared				AIC			
AMM mean	95% CI	GMM mean	95% CI	AMM mean	95% CI	GMM mean	95% CI	AMM mean	95% CI	GMM mean	95% CI
Spring	Female	Adult	38069	0.827	(0.813, 0.842)	0.817	(0.794, 0.840)	-557.18	(-577.60, -536.75)	-479.98	(-512.22, -477.74)
	Juvenile	31252	0.602	(0.580, 0.624)	0.544	(0.507, 0.580)	-287.93	(-297.56, -278.30)	-121.16	(-136.89, -105.44)	
	Male	Adult	43822	0.815	(0.799, 0.831)	0.657	(0.609, 0.704)	-550.42	(-569.86, -530.97)	-349.45	(-378.45, -311.45)
	Juvenile	29825	0.623	(0.599, 0.646)	0.462	(0.432, 0.493)	-303.62	(-313.63, -293.60)	-101.49	(-114.40, -88.00)	
Fall	Female	Adult	38069	0.569	(0.543, 0.595)	0.361	(0.333, 0.387)	-302.44	(-312.57, -292.31)	-124.22	(-135.76, -112.67)
	Juvenile	29686	0.522	(0.494, 0.551)	0.382	(0.358, 0.407)	-200.71	(-207.94, -193.45)	-110.15	(-117.12, -103.18)	
	Male	Adult	41350	0.561	(0.534, 0.588)	0.362	(0.330, 0.389)	-290.29	(-299.78, -280.80)	-123.01	(-133.75, -122.26)
	Juvenile	30122	0.451	(0.422, 0.479)	0.249	(0.211, 0.288)	-159.38	(-165.75, -153.01)	-37.829	(-46.459, -29.198)	

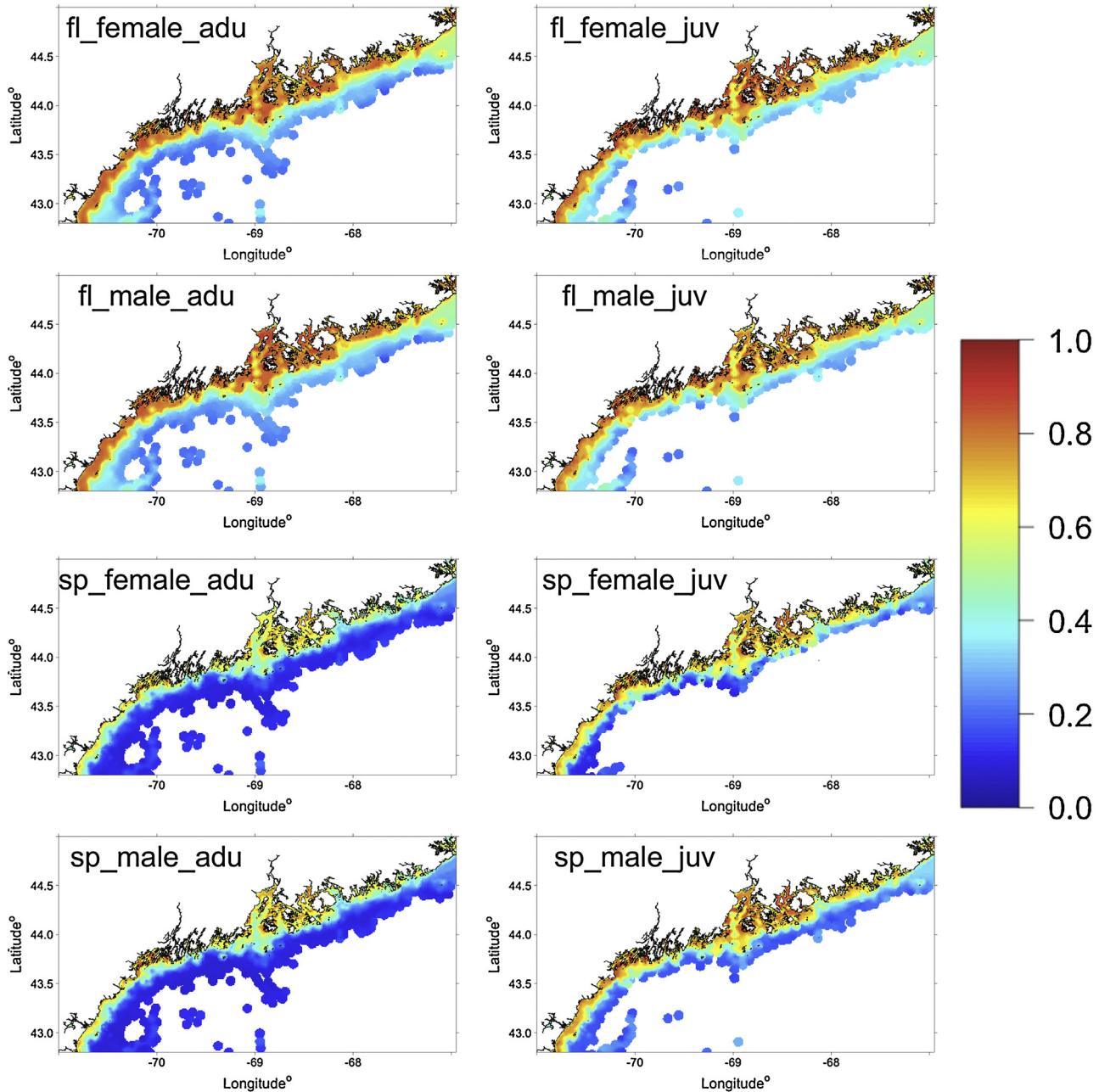


Fig. 5. Season, sex, and stage specific maps illustrating the spatial distribution of the median habitat suitability index (HSI) over 1978–2013 in the coastal waters of Maine and New Hampshire for *Homarus americanus*. fl: fall (September–November); sp: spring (April–June); adu: adult (>60 mm carapace length); juv: juvenile (<=60 mm carapace length).

spring, while the correlations between the variables were less significant in the fall (Fig. 8).

The relative proportion of poor, fair, and good habitat conditions ($\text{HSI} < 0.3$, $0.3 \leq \text{HSI} < 0.7$, and $0.7 \leq \text{HSI}$, respectively) was identified from 1978–2013 for both modeled stages, sexes, and seasons (Fig. 9). Proportion of habitat condition showed a similar trend between adult–juveniles and male–females; however, a larger proportion of good habitat was observed during the fall while a pronounced proportion of poor habitat was observed during the spring (Fig. 9).

4. Discussion

4.1. Variability of the bioclimate envelopes and suitability index of each bioclimatic attribute

The modeling results showed higher climate-driven habitat suitability during the fall, which was consistent with the field survey trends reporting higher lobster abundance during the fall survey (ASMFCB, 2015). The overall declining trend in habitat suitability in the upper Penobscot Bay suggests that contraction of *H. americanus* habitat is driven by the changes in bottom temperature and salinity. Empirical studies in the Great Bay Estuary, NH and Narragansett Bay, RI have shown the contraction of the species'

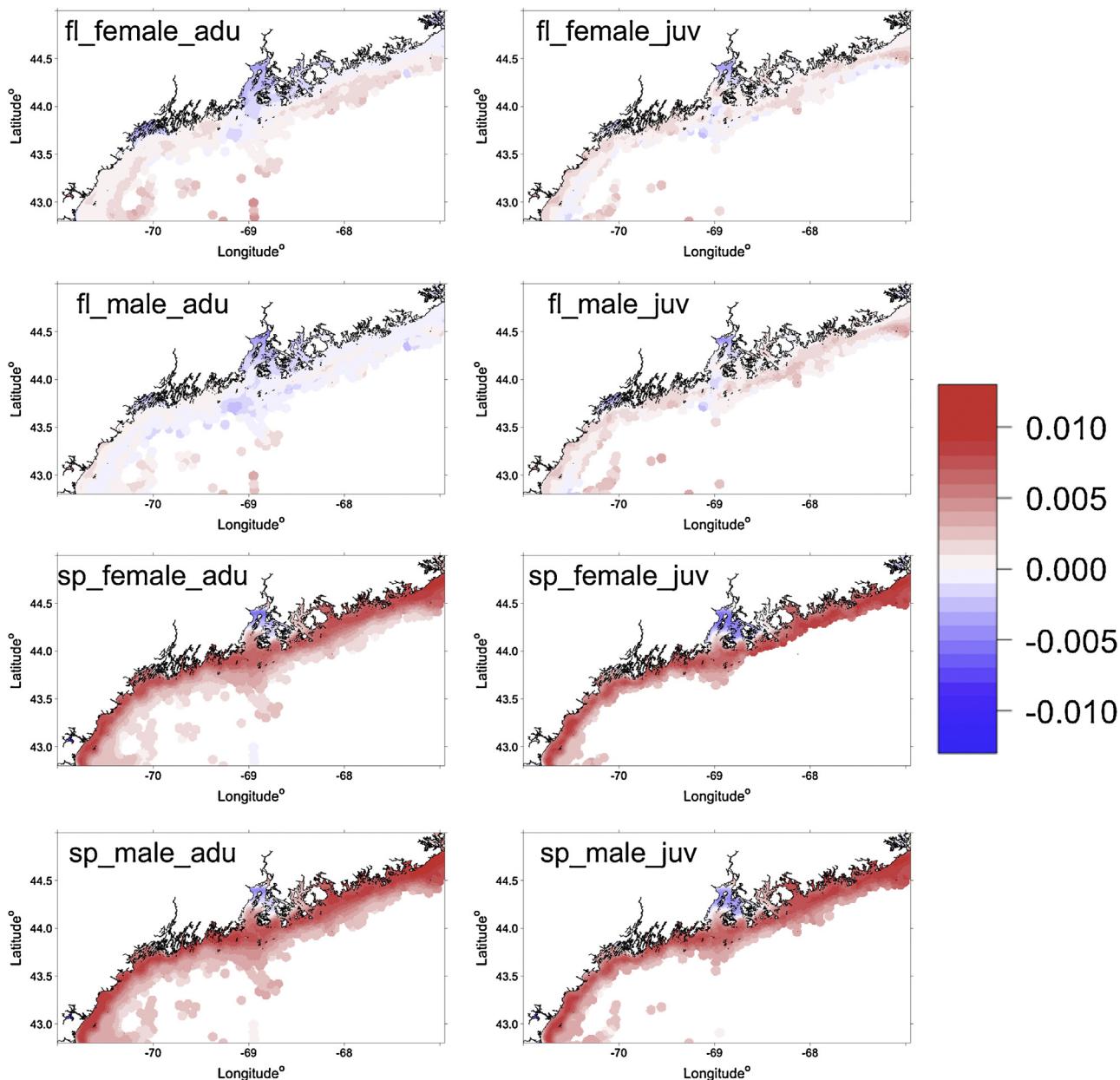


Fig. 6. Season, sex, and stage specific heat maps illustrating change in habitat suitability index (HSI) over 1978–2013 in the coastal waters of Maine and New Hampshire for *Homarus americanus*. fl: Fall (September–November); sp: Spring (April–June); adu: adult (>60 mm carapace length); juv: juvenile (<= 60 mm carapace length). Darker red indicates change toward higher habitat suitability at higher magnitude.

suitable habitat in estuarine systems where temperature and salinity become sub-optimal (Howell et al., 1999; Jury and Watson III, 2012). The greater propensity toward higher habitat suitability throughout coastal waters for both modeled stages and sexes during the spring indicates an increasing number of days that bottom temperature and salinity falls within the species' optimal range in this area. The modeling results show that the best predictive power was derived for adult females in spring (Table 2). This reflects adult females potentially exhibiting more significant behavioral thermoregulation compared to *H. americanus* of different stage, sex, and season (Campbell, 1986; Crossin et al., 1998). Hatching of eggs occurs in spring when bottom water temperature reaches approximately 15 °C, and completes within a relatively short time span of 10–14 days (Hughes and Matthiessen, 1962). Although few studies have focused on relationships between behaviors of adult females and surrounding environment, it has been proposed that

egg-bearing females seek to subject their eggs to a specific thermal regime during the spring to maximize degree-days required for egg development (Campbell, 1986; Ugarte, 1995; Goldstein and Watson III, 2015). This is plausible as *H. americanus* can detect very small changes in water temperature (Jury and Watson III, 2000), and the species' highly mobile and thermoregulated nature allow them to seek their preferred thermal regime (Crossin et al., 1998; Jury et al., 2013; Jury and Watson III, 2013; Reynolds and Casterlin, 1979). However, *H. americanus* also exhibits varying response and preference specific to changes in salinity, depth and other environmental factors depending on their physiological condition, sex, molt stage, and size (Mercaldo-Allen and Kuropat, 1994). Therefore, it is difficult to identify the extent to which environmental variables regulate the behavior of the species over others. In this regard, future bioclimate modeling efforts should actively incorpo-

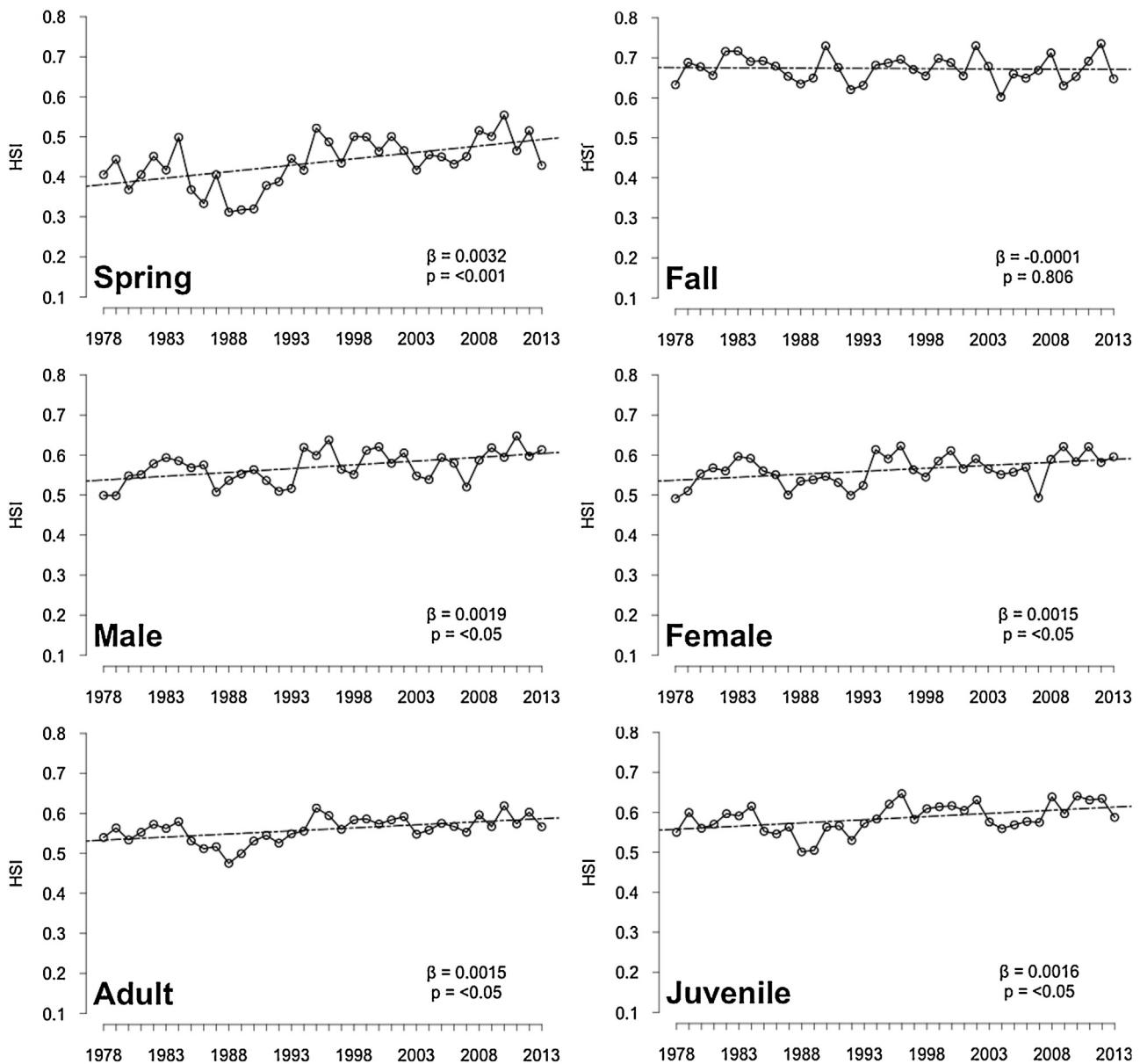


Fig. 7. Median habitat suitability index (HSI) for each year from 1978 to 2013 (solid line). The trend in both seasons–sexes, and stages was shown by the fitted linear regression model (dashed line).

rate mechanistic understanding of the species' metabolic response to each environmental variable.

The season- and stage-specific SIs for temperature, depth, and salinity were consistent with the existing literature of *H. americanus* habitat preferences. Seasonal shifts in SI curves likely reflect a composite result of interaction between different levels of temperature, light, oxygen concentration, salinity, food availability and predation dynamics exist at different water depths and seasons. The SI-temperature curves identified shifts in suitable thermal ranges between spring and fall for both adults and juveniles. Suitable temperature for *H. americanus* varied from 11.6–14.3 °C in the fall, and 8.4–10.6 °C in the spring. This was consistent with past findings reporting the species' avoidance of temperature below 5 °C and above 18 °C (Aiken and Waddy, 1986; Lawton and Lavalli, 1995; Crossin et al., 1998; Jury and Watson III, 2013). The SI-temperature curves generally did not show unimodal shape, and with the reported thermal preference of the species of 15.9 °C (Crossin et al., 1998) and 16.5 °C (Reynolds and Casterlin, 1979) suggests even

warmer bottom temperatures would be more suitable with no adverse effects. The significant shift in SI-depth curves for adults suggests a seasonal inshore/offshore migration, while a less significant shift in SI-depth curves for juveniles suggests a more localized migration along the coastal waters (Lawton and Lavalli, 1995). Adults exhibited a broader suitable salinity range in the fall, while juveniles showed a shift in suitable salinity ranges between spring and fall. The difference in suitable salinity ranges possibly reflected the juveniles actively moving to optimal salinity ranges due to their limited ability to osmoregulate (Charmantier and Aiken, 1987).

4.2. Model limitations and future improvements

Understanding climate-driven habitat suitability is a key component in the sustainable management of fishery resources (Chen et al., 2009; Cheung et al., 2008, 2009). However, there are limitations inherent to bioclimate envelope models.

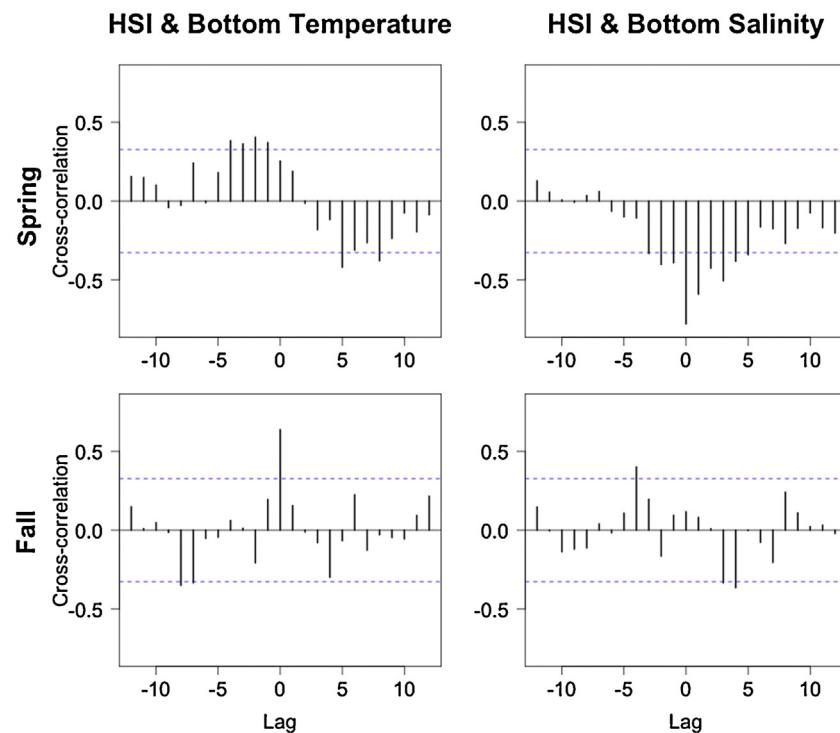


Fig. 8. Cross-correlation functions measuring correlations between two time series at different lags (years). Every vertical line shows the correlation between the two time series at each lag indicated along the x-axis. A correlation extending above or below the dotted lines shows statistical significance.

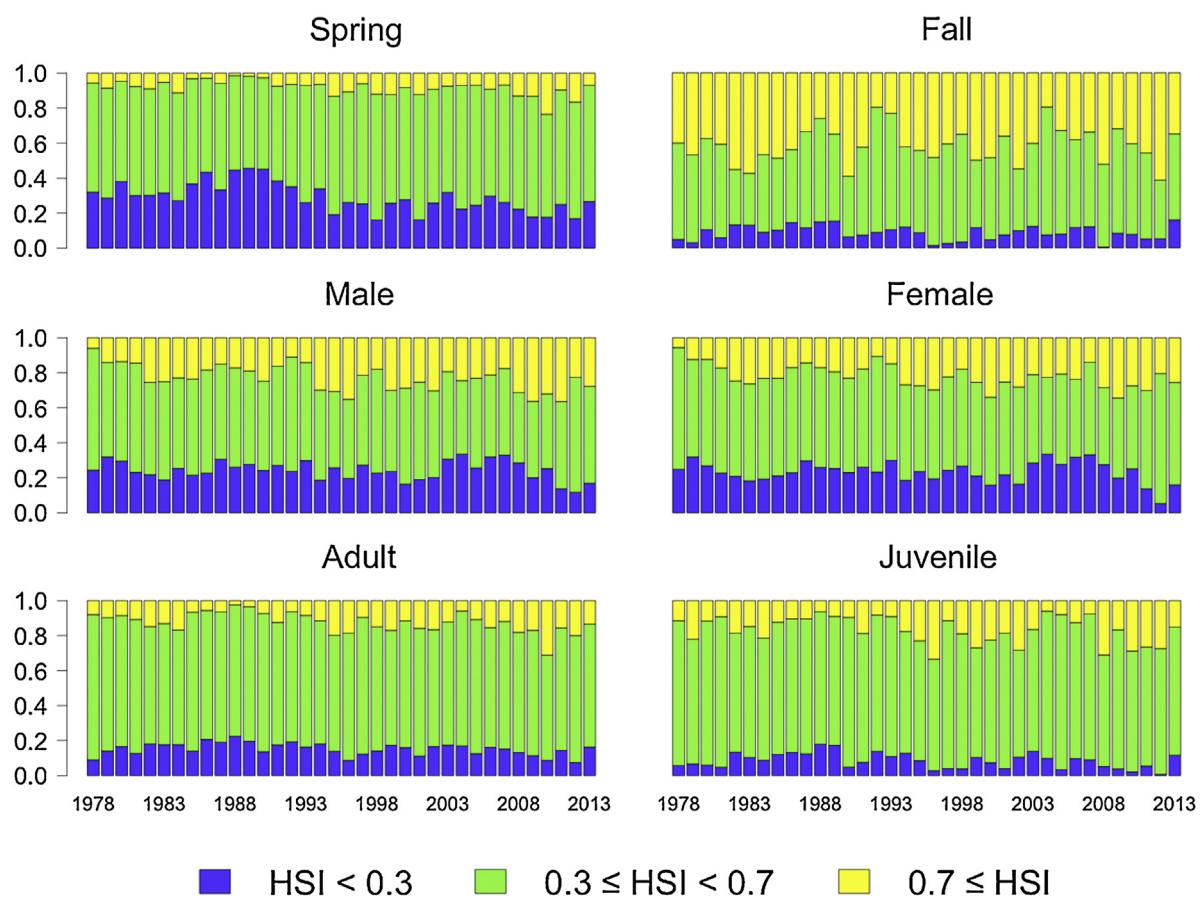


Fig. 9. Relative proportion of good (yellow), fair (green), and poor (blue) habitat for *H. americanus* in the coastal waters of Maine and New Hampshire (1978–2013). Upper panel represents fall (September–November), while lower panel represents spring (April–June). y-axis represents percentage of the study area.

4.2.1. Bottom substrate

This study initially considered bottom substrate type obtained from the Continental Margin Mapping (CONMAP) GIS database compiled by the U.S. Geological Survey (Poppe et al., 2005) as the fourth habitat variable. This variable was removed from the final bioclimate envelope model. It was determined that inclusion of the species' association to substrate based on bottom trawl survey would lead to biased results. Several reasons have been contributed to this decision.

First, contrary to previously documented substrate preferences by post-settled *H. americanus* for shelter-providing rocky and boulder landscape (Barshaw and Bryant-Rich, 1988; Wahle and Steneck, 1991; Lawton and Lavalli, 1995), none of the SI-bottom substrate results identified gravel as the most suitable substrate type for *H. americanus* (Appendix A). Based on the DMR Inshore Bottom Trawl Survey, clay–silt/sand was most frequently identified as the bottom type with highest habitat suitability, while gravel–sand was identified as the most suitable bottom substrate for adults in the spring. These results were likely artifacts of biased *H. americanus* abundance as rocky substrates are generally associated with poor trawl efficiency (Steneck and Wilson, 2001) and there are several areas that could not be towed due to complex bottom structure (Sherman et al., 2005; Cao et al., 2014).

Second, the CONMAP database did not distinguish between boulder or cobble as both substrates were included in the gravel category. The CONMAP categorized bottom substrate type in the study area as gravel (pebbles defined as 2.00–64.00 mm, cobbles defined as 64–256 mm, boulder defined as above 256 mm), gravel–sand (0.62–2.00 mm), sand–clay (0.001–0.004 mm), sand–clay/silt (0.004–0.062 mm), sand–silt/clay, and sand/silt/clay (Poppe et al., 2005). Although gravel, cobble, and boulder substrates are generally uncommon throughout the northeast coastal waters and only comprise 10–16% of the bottom type at depth less than 20 m along the coastline of Maine (Barnhardt et al., 1996; Hovel and Wahle, 2010), the overgeneralization of key substrates coupled with potentially biased *H. americanus* abundance and spatial patchiness of cobble/boulder substrates may have resulted in a biased estimation of SI-bottom substrate in this study.

Overall, SI-bottom substrate results were determined not to be meaningful as they were likely to be heavily biased by insufficient resolution of the substrate data and the limitation of the bottom trawl survey sampling design with key substrate type. The removal of bottom substrate type from the final model ignored the importance of shelter-providing gravel/cobble/boulder substrates as essential nursery substrates. While these data-driven biases and limitations cannot be quantified or ignored, the use of traditional ecological knowledge may be used as a qualitative correction criterion for these biases (Store and Kangas, 2001; Vincenzi et al., 2007). For future studies, the use of ventless trap based abundance index may be used to enhance the understanding of the species' association to temperature, salinity, depth and substrate (Maine DMR, 2006). A random stratified ventless trap survey can provide relative *H. americanus* abundance without the biases identified in conventional bottom trawl surveys. While data are available for the ventless trap survey for fewer years and it has smaller sampling coverage, this supplementary fishery-independent data can be used to compliment and validate the known sampling bias associated with the Maine–New Hampshire bottom trawl survey (Cao et al., 2014).

4.2.2. Assumptions and limitations inherent in bioclimatic envelope models

Calibration of bioclimate envelope model is often based on a restricted number of environmental variables, and forced to neglect food-web interactions, species dispersion, or ecosystem productivity because of the difficulty in obtaining reliable information

(Pearson and Dawson, 2003; Cheung et al., 2008, 2009; Stock et al., 2011; Jian et al., 2013; Watling et al., 2013; Tanaka and Chen, 2015).

The model developed in this study aimed to predict relative habitat suitability rather than actual species biomass or population level, and did not explicitly incorporate biotic interaction such as inter-specific or food-web interactions. It is likely that predators and prey of *H. americanus* respond differently to changes in climate-driven oceanographic conditions. For example, the increase in *H. americanus* abundance in the GOM may be correlated to changes in predators and prey abundance (Steneck and Wahle, 2013; Wahle et al., 2013). Integrating biotic interactions, multispecies population dynamics and species dispersal in predicting impact of climate variables would be the next modeling step and may address some of these limitations (Cheung et al., 2009, 2008).

Furthermore, the assumption that habitat preference of targeted species will remain unchanged with the shifting climatic conditions should be tested as evolutionary adaptations may yield factors that could affect the model outcomes (Pearson and Dawson, 2003; Stock et al., 2011; Araújo and Peterson, 2012). The model in this study was implicitly based on the niche conservatism. However, the extent to species to retain their ancestral traits and physiological thresholds is highly debated in a climate change context (Pearson and Dawson, 2003; Crisp et al., 2009). Some species may exhibit evolutionary adaptation to changing climates (e.g., increasing variety of habitat types and dispersal ability), while many species are susceptible to ecological change with a limited adaptive capacity to new biomes. Evolutionary changes may alter patterns of range-shifting of a targeted species. However, the rate of genetic changes in marine species with regard to climate change is poorly understood (Cheung et al., 2008), while a global trend toward the niche conservatism was observed as only 3.6% of the evolutionary divergences involved a biome shift (Crisp et al., 2009). Defining target species' physiological thresholds may address these problems in future applications.

A mismatch between prediction and observation is inherent and inevitable in modeling of open environmental systems (Oreskes et al., 1994; Araújo and Peterson, 2012). When a bioclimate envelope model evaluates a specific environment for a given species, prediction error is often due to potential species presence in unsampled areas or extrinsic factors not included in the modeling effort (Araújo and Peterson, 2012). Such commission error does not indicate model flaws, but simply indicates that the model needs further development (Oreskes et al., 1994).

For future studies, the model calibration process may incorporate additional procedures and variables to develop a more comprehensive bioclimate envelope model. For example, as species responses to the array of climate variables are neither gradual nor linear, the SIs may incorporate Cubic spline smoothing (e.g., Generalized Additive Model) to capture potential non-linear relationships between the response variable (CPUE) and key habitat variables (Chang et al., 2012). The three environmental variables had equal weight in the model, but the actual importance of different environmental variables may differ (Gong et al., 2012). This needs to be considered in the next modeling effort to reflect the relative influence of confounding variables on bioclimate envelope models.

The three environmental variables considered in this study were chosen based on perceived importance and data availability, but many other environmental variables can also greatly influence the species' habitat quality (Lawton and Lavalli, 1995). These variables may include more climate and ecological variables such as thermal fronts, latitude and longitude, coastal upwelling, regional climate forcing, change in pH level and dissolved oxygen concentration (Mercaldo-Allen and Kuropat, 1994; Boudreau et al., 2015). Alternatively, exclusion of certain habitat variables (e.g., depth) should be considered to allow greater change in the species' distribution as

a result of changes in other variables in future projection (Hare et al., 2013). While this study focused on climatic impacts on the species' realized niche, a mechanistic niche modeling to understand how environmental conditions affect the species' growth, survival and reproduction should be considered for future projection of climate change impact (Kearney, 2006).

4.3. Management implications

Commercial fish stocks including *H. americanus* often exhibit strong physiological responses to abrupt changes in the environment (Mills et al., 2013). Furthermore, sea surface temperature has increased significantly in the coastal waters of Maine and New Hampshire since the late 1990s, while the number of days that water temperature falls within the optimal range for the species has also increased (ASMFCb, 2015). Conventional stock assessments often neglect to address environmental variability (NMFS, 2010), but the modeling framework developed in this study can be used to characterize season-, sex-, and stage specific *H. americanus* habitat condition and provide several opportunities where climate variability can inform and improve stock assessments.

Recruitment in fish stocks often appears to be influenced by environmental conditions (Myers, 1998; Brander and Mohn, 2004; Keyl and Wolff, 2008). Recruitment in *H. americanus* stocks is generally modeled as a function of spawning stock, but inclusion of environmental covariates can potentially provide additional information about the annual recruitment variability (ASMFCb, 2015). The most recent *H. americanus* stock assessment incorporated a temperature recruit covariate (number of days with subsurface temperature above 20 °C measured by a local power station) to investigate the impact of increasing water temperature on the recent recruitment failure in southern New England (ASMFCb, 2015). While most studies have focused on linking recruitment to temperature and salinity (Myers, 1998), incorporating modeled HSI values as an alternative recruitment covariate captures the composite effect of climate variability on the species' recruitment dynamics. Alternatively, HSI-based bioclimate envelope models for the species in postlarval settlement and early benthic phase can be used to calculate a recruitment density index, while similar information for mature individuals is an important precursor to assessment of spawning stock biomass. Furthermore, while many fish stocks are affiliated with their relevant habitat variables, conventional bottom-trawl surveys are often stratified by geography, depth, and time (Horodysky et al., 2015). Differences between the nature of stratification by fishes and surveys can lead to flaws in inferences. Climate-driven change in species distribution and migration patterns may also affect survey catchability (NEFSC, 2014). Here, developing a species-specific bioclimate envelope models provide several advantages of (1) incorporating bioclimatic variables and climatic variability into stock assessments to improve the model fittings, and (2) avoiding fixed and subjective stratification to improve precision and accuracy of estimated stock status (Shelton et al., 2014).

As the rate of climate change is predicted to accelerate in the future, alongside the species' ongoing distributional shifts (Pinsky et al., 2013), there is a growing need to assess changes in *H. americanus* habitat condition. Under RCP 8.5 emissions scenario,

average bottom temperature in Northeast U.S. Continental Shelf system is expected to increase more than 1 °C by 2050 (IPCC, 2014; NOAA, 2015). While the projected increase in bottom temperature in the Gulf of Maine is not expected to exceed the species' maximum temperature tolerance and may even be considered favorable, management uncertainties at the southern range limits of the species can be addressed through scenario-based analysis (Hare et al., 2013; Shackell et al., 2014; ASMFCb, 2015). Bioclimate envelope models are valuable tools to; (1) evaluate climate impacts and aid implementation of ecosystem-based fishery management, and (2) generate hypotheses of large scale potential ecological changes in climate-driven marine environment (Cheung et al., 2009). Advancement in our understanding of climate-driven habitat suitability of *H. americanus* can play a critical role in the sustainability of the species' fishery.

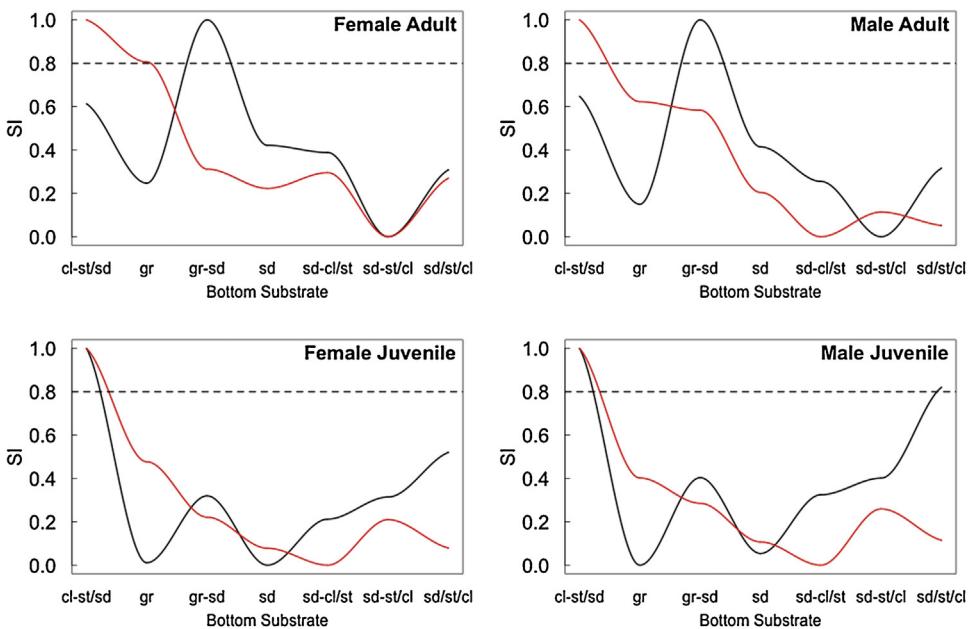
5. Conclusion

This study coupled a conventional habitat-suitability model (HSI) with a regional ocean model (FVCOM) to predict past and present bioclimate envelopes of *H. americanus*. The developed HSI-based bioclimate envelope model aimed to predict general patterns of potential responses of *H. americanus* to climatic variability. The model highlighted the impacts of climatic variables on the *H. americanus* fisheries at the regional scale. The results can be used to complement ongoing management efforts that focus on the analysis of the habitat needs and requirements of this species (ASMFC, 2014). For future analyses, appropriate downscaling of existing global climate models (GCMs) may enable resource managers to project the potential geographic shift of a given species' bioclimate envelopes, which will be a valuable addition to existing vulnerability assessment programs.

Acknowledgements

We thank Dr. Chongliang Zhang, Dr. Samuel Truesdell, Bai Li, Dr. Jie Cao, Katherine Thompson, and Michael Torre of University of Maine for their generous support, ideas, and perspectives. We would also like to thank Sally Sherman, Katherine Reardon, and Carl Wilson from the Maine Department of Marine Resources for providing survey data. We would like to thank Drs. Lawrence Jacobson, Richard Wahle, Andrew Pershing, and Damian Brady for insightful discussions and comments on this study. Three anonymous reviewers provided very thorough and constructive comments and the suggested changes greatly strengthened this manuscript. Financial support for this study was from NSF IGERT program, NSF Coastal SEES program and Maine Sea Grant College Program. This work uses the FVCOM model-predicted database created by Dr. C. Chen's research team at the Marine Ecosystem Dynamics Modeling Laboratory, University of Massachusetts Dartmouth.

Appendix A. : Suitability Index (SI) curve of bottom substrate type for four groups of *Homarus americanus* (2 sexes * 2 life stages). Both spring (black line; April - June), and fall (red line; September - November) SI curves are plotted. cl = clay, st = silt, sd = sand, gr = gravel.



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