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ARTICLE

# A spatiotemporal Evaluation of Atlantic Sea Scallop *Placopecten magellanicus* Habitat in the Gulf of Maine Using a Bioclimate Envelope Model

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***Abstract***
**A bioclimate envelope model was developed to evaluate the impacts of climate variability on spatiotemporal availability of suitable habitat for the Atlantic sea scallop *Placopecten magellanicus* in the Gulf of Maine (GOM). Bioclimate envelopes were established through habitat suitability indices (HSIs) based on bottom temperature, bottom salinity, current velocity, depth, and bottom composition. The relationship between Atlantic sea scallop abundance and each environmental variable was quantified using suitability indices, which were generated based on standardized scallop abundance sampled over 10 years of dredge survey data. Boosted regression tree models were used to determine the relative importance of each environmental variable to scallop abundance, thereby establishing a weighting scheme within the HSI. A regional circulation model was coupled with the weighted HSI to hindcast spatiotemporal dynamics of suitable habitat for Atlantic sea scallop in coastal and offshore waters of the GOM from 1978 to 2013. Higher habitat suitability was found along inshore areas compared with offshore areas. Model predictions indicated an increasing trend in habitat suitability in inshore waters since 1978 and decreasing habitat suitability in offshore waters. This research provides a novel modeling framework with which to enhance research and management of commercially valuable Atlantic sea scallop stocks over broad spatiotemporal scales in the climatically altered GOM.**

The Atlantic sea scallop *Placopecten magellanicus* is a bivalve mollusk of the family Pectinidae. The species occurs on the continental shelf, and its distribution extends from the Gulf of St. Lawrence to Cape Hatteras, North Carolina (Shumway and Parsons 2006). The Atlantic sea scallop supports a highly valuable fishery overall in the United States. However, the scallop fishery in the Gulf of Maine (GOM) is depleted, having bottomed out in 2005, when landings of only 14,969 kg (33,000 lb) were reported, compared with over 1.36 million kg (3 million lb) landed in the early 1990s (Kelly 2012). Recent data show an increasing trend in Atlantic sea scallop abundance, which provides an ideal opportunity to establish a persistent, valuable fishery through focused research and management efforts (Kelly 2012).

The distribution and abundance of many benthic species are closely tied to their surrounding environment, which fluctuates over space and time (Dickie 1955; Slacum et al. 2010). The abundance and distribution of the Atlantic sea scallop are influenced by a multitude of habitat characteristics, such as depth, bottom composition, currents, temperature, and salinity (MacDonald and

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Thompson 1985a, 1985b; Macdonald et al. 1987; Thouzeau et al. 1991; Wildish and Saulnier 1992; Stokesbury and Himmelman 1995; Hart and Chute 2004). Atlantic sea scallops occur mainly at depths ranging from 15 to 110 m throughout the species' geographic range, but they can be found in shallower water in the northern part of the range, where they have been reported at depths up to 2 m (Naidu and Anderson 1984). Both juveniles and adults of this species are generally found on sand, gravel, shells, or small rock substrate, with gravel typically holding the highest abundances (Thouzeau et al. 1991). Adult Atlantic sea scallops show optimal growth at temperatures between 10°C and 15°C, with temperatures above 21°C being lethal, and they prefer full-strength seawater (~35‰), with salinities of 16.5‰ or lower being lethal (Stewart and Arnold 1994). Atlantic sea scallops are usually found in environments with strong currents (Hart and Chute 2004), and flow velocity has been shown to be a key factor controlling waste removal, oxygen uptake, feeding, and growth rates (Stewart and Arnold 1994; Shumway and Parsons 2006). The feeding response of most suspension-feeding bivalves to increases in unidirectional flow velocity is expected to follow a unimodal function where, at low flow rates, increases in velocity enhance filtration up to an optimal rate beyond which further increases result in feeding inhibition (Wildish and Kristmason 1993; Pilditch and Grant 1999). Optimal growth for this species occurs at a velocity of around 0.1 m/s (Wildish and Saulnier 1992). Pilditch and Grant (1999) observed inhibition of feeding at 0.25 m/s. Despite the clear influence of habitat quality on bivalve ecology, evaluations of Atlantic sea scallop–habitat relationships and spatiotemporal trends in suitable habitats remain scarce (Shumway and Parsons 2006; Mendo et al. 2014).

The GOM has warmed faster than the majority of the world's oceans, with temperatures increasing an average rate of 0.026°C per year since 1982 (Mills et al. 2013; Pershing et al. 2015). Both bottom temperature and bottom salinity are also increasing (Saba et al. 2016). Rapidly increasing temperatures are impacting the abundance and distribution of numerous marine species (Overholtz et al. 2011; Howell and Auster 2012; Hollowed et al. 2013), and many fish stocks are exhibiting a poleward shift in their center of biomass and/or an increase in depth (Nye et al. 2009). Atlantic sea scallop distribution and abundance have been shown to be impacted by climatic variability (Frank et al. 1990; Kurihara 2008). Dickie (1955) and Caddy (1979) showed that fluctuations in Atlantic sea scallop abundance in the Bay of Fundy was correlated with bottom water temperature, with higher temperatures leading to increases in scallop abundance. The influence of increased temperature is thought to result in rapid larval development and improved survival of juveniles and adults (Dickie 1955; Caddy 1979). In light of a changing GOM ecosystem (Mills et al. 2013; Pershing et al. 2015), it is becoming increasingly critical to document the importance and synergistic effects of climate forcing on the dynamics of species abundance and distribution.

A bioclimate envelope model was developed in this study through coupling of empirical habitat suitability indices (HSIs) with a regional ocean circulation model to evaluate the climate-driven changes in habitat suitability for Atlantic sea scallops from 1978 to 2013. Bioclimate envelopes are generally referred to as a multivariate space defined by a set of key climatic and environmental variables that best describe the physical and/or biological conditions of observed species distribution (Cheung et al. 2009; Araujo and Peterson 2012). The HSI is an ecological index that can quantify the relationships between environmental variables and species abundance and can predict where a species is likely to persist (Giannoulaki et al. 2011; Araujo and Peterson 2012). Habitat suitability-based bioclimate envelope models are increasingly used to quantify the impact of climatic variation on the spatiotemporal availability of suitable habitat for a given species (Pearson and Dawson 2003; Araujo and Peterson 2012; Tanaka and Chen 2016).

Bioclimate envelopes for Atlantic sea scallops were defined by HSIs derived from bottom temperature, depth, bottom composition, flow velocity, and bottom salinity. This HSI-based bioclimate envelope model has been adapted to incorporate the largely sedentary nature of adult Atlantic sea scallops through temporal aggregation of dynamic environmental variables (temperature, salinity, and flow velocity) to reflect an annual range of conditions in a given location. The modeling effort developed in this study establishes the ability to evaluate spatiotemporal changes in bioclimate envelopes due to the incorporation of a regional ocean circulation model. Spatiotemporal trends in bioclimate envelopes are discussed in relation to potential climate-driven changes in Atlantic sea scallop abundance and distribution. This research is novel, as it is the first bioclimate envelope model developed for Atlantic sea scallops and provides a framework that can facilitate ecosystem-based management of commercially valuable GOM stocks.

## METHODS

*Study area.*— This modeling effort covers the inshore (<5.56 km [<3 nautical miles] from shore) and offshore (>5.56 km from shore) waters within the GOM from Cape Cod, Massachusetts, to Downeast Maine, USA (Figure 1). The GOM is characterized by a mixture of oceanic influences directly affected by the Labrador Current, the Gulf Stream, and the freshwater discharge from the St. Lawrence River (Sutcliffe et al. 1976). As such, water temperature follows a gradient moving up the coast and also offshore.

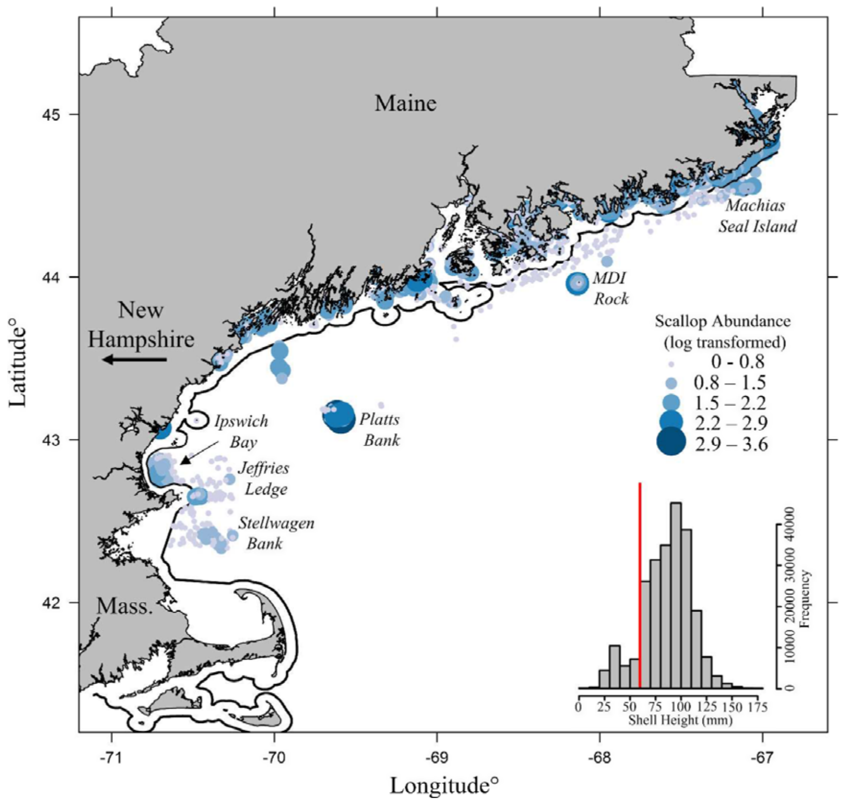


FIGURE 1. Spatial distribution of $\log_e$ standardized Atlantic sea scallop abundance within the study area in the Gulf of Maine from Cape Cod, Massachusetts, to the Maine–Canada border is shown along with observed scallop size frequency (shell height). The vertical red line indicates the size cutoff (65 mm shell height) below which Atlantic sea scallops were not included in the model; MDI Rock = Mount Desert Island Rock.

Within the study area, Atlantic sea scallops were found in areas with maximum yearly temperature ranging from 8°C in deeper areas to 16°C in shallow areas. Salinity ranged from 26‰ in inshore areas subject to freshwater inputs to full seawater (35‰) in offshore locations. This study covered depths to approximately 60 m since Atlantic sea scallops are known to be uncommon in areas deeper than this depth range (Hart and Chute 2004).

*Survey data.*— This study incorporated 10 years of dredge-based, fishery-independent surveys of Atlantic sea scallops in the inshore and offshore waters of Maine and Massachusetts conducted by the Maine Department of Marine Resources (2005–2014; Figure 1; Kelly 2012). Sections of this total area were sampled intermittently throughout the study period. An annual spring survey covered alternating portions of inshore Maine waters and followed a stratified random design. An annual systematic survey covering select coastal areas occurred each fall. Offshore areas were surveyed in 2009 and 2012 using an adaptive two-stage, random stratified design. The gear used for all surveys was an unlined, 2.13-m (7-ft), New Bedford-style drag with 5.08-cm (2-in) rings, 4.45-cm (1.75-in) head bale, 8.89-cm (3.5-in) twine top, 25.4-cm (10-in) pressure plate, and rock chains. Since Atlantic sea scallops less than 65 mm in shell height were not efficiently sampled with the 5.08-cm rings (Kelly 2012), these were excluded from all analyses. Tows were conducted at 6.482–7.408 km/h (3.5–4.0 knots) and lasted from 2.5 to 5 min depending on the location, bottom type, and amount of fixed fishing gear in the area. All combined surveys yielded a total of 2,469 tows and captured 235,111 samples (Figure 1).

*Environmental data.*— The unstructured-grid Finite-Volume Community Ocean Model (FVCOM) configured in the northwest Atlantic shelf region was used to simulate monthly estimates of bottom temperature, salinity, and current velocity from 1978 to 2013 throughout the entire study area. The FVCOM is a regional ocean circulation model developed by the University of Massachusetts–Dartmouth and the Woods Hole Oceanographic Institution (Chen et al. 2006). It has a horizontal resolution ranging from 0.02 to 10 km (Chen et al. 2011). The unstructured FVCOM grid captures complex and irregular coastal geometry, making this model suitable for physical and biological studies in coastal regions and estuaries (Chen et al. 2011). Since the survey did not measure temperature, salinity, or current velocity, the FVCOM predictions were matched to survey tows from the nearest

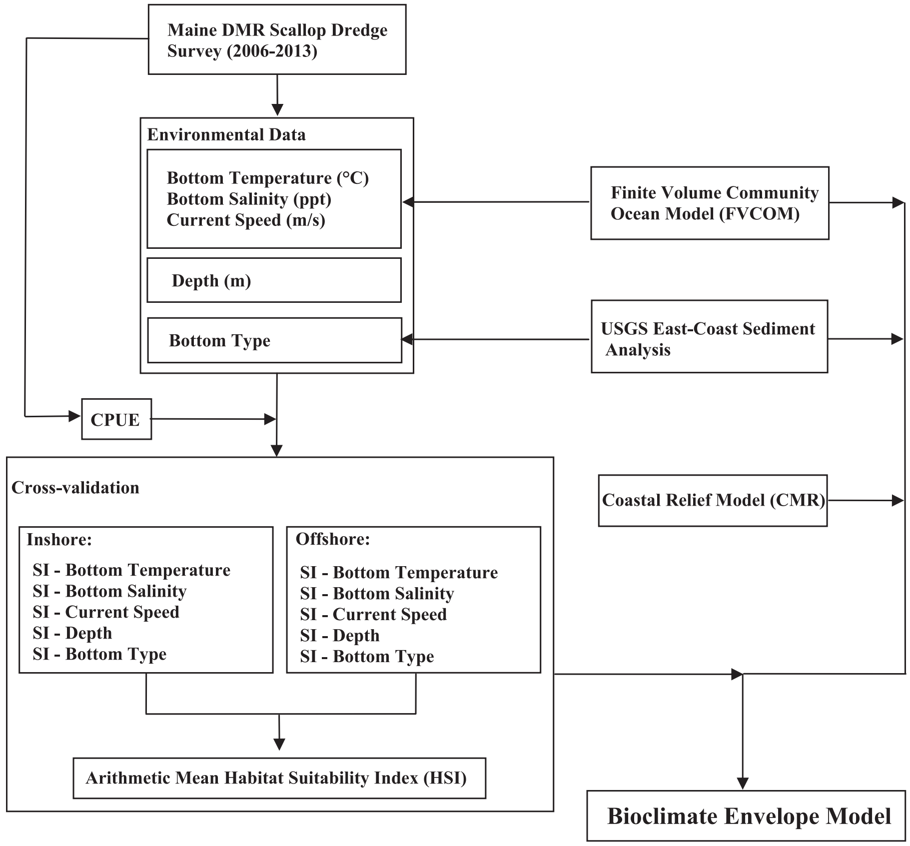


FIGURE 2. Schematic diagram of the bioclimate envelope modeling effort implemented in this study (Maine DMR = Maine Department of Marine Resources; USGS = U.S. Geological Survey). All data exploration and modeling procedures were conducted in the R programming environment.

neighboring FVCOM point during the time of sampling (Figure 2). The absolute value of two-dimensional current velocity was taken to approximate the magnitude of water flow at a given location. Current velocity ($C$) was estimated at station $i$ and year $y$ from FVCOM predictions using the following equation:

$$C_{i,y} = \sqrt{u_{i,y}^2 + y_{i,y}^2}, \tag{1}$$

where $C$ is the magnitude of the predicted current velocity; and $u$ and $y$ are the $x$- and $y$-vector components of the velocity (Chen et al. 2011).

Bathymetry and substrate data were obtained from the U.S. Coastal Relief Model and the Continental Margin Mapping (CONMAP) GIS database, respectively (NGDC 1999; Poppe et al. 2005). Substrate type in the study area included gravel (pebbles: 2.00–64.00 mm; cobbles: 64–256 mm; boulder: >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).

*Model development.*— The modeling approach used in this study to develop the HSI-based bioclimate envelope model (Figure 2) for Atlantic sea scallops is an extension of previous modeling efforts for American lobsters *Homarus americanus* in Long Island Sound and coastal New Hampshire to Maine (Tanaka and Chen 2015, 2016). Adult Atlantic sea scallops are known to be largely sedentary, with little to no movement reported from previous studies (Posgay 1981; Carsen et al. 1995). Additionally, any movement that does happen is thought to be random in distance and direction, and any net movement over time is likely the result of tidal currents as opposed to active habitat selection (Posgay 1981). Given this, the distribution of Atlantic sea scallops corresponds to both successful settlement in an area and survival until capture. Consequently, temporally dynamic environmental variables (bottom temperature, bottom salinity, and current velocity) in this model were incorporated as yearly aggregates (mean bottom temperature, mean salinity, and mean current speed across the 12 months prior to capture) in order to better reflect the range of conditions that an individual would experience in its location over time.

The standardized Atlantic sea scallop abundance derived from the dredge surveys was used to develop suitability indices (SIs) for each environmental variable. The nominal abundance index was calculated as survey catch per unit of sampling effort (CPUE) at station $i$ and in year $y$ (Chang et al. 2012; Tanaka and Chen 2015, 2016),

$$\mathrm{CPUE}_{iy} = \left(\frac{\mathrm{Count}_{iy}}{\mathrm{Tow\ Duration}_{iy}}\right) \times 2.5, \quad (2)$$

where Count represents the total abundance of all captured Atlantic sea scallops greater than 65 mm in shell height. Tow Duration (min) varied from 2.5 to 7.0 min depending on location, bottom type, and amount of fixed fishing gear in the area and was standardized to 2.5 min at each station. In this study, Atlantic sea scallops inhabiting offshore waters (>5.56 km [<3 nautical miles] from shore) were found to exhibit different habitat preferences relative to those inhabiting inshore waters (<5.56 km from shore). Thus, separate sets of SIs were developed for inshore and offshore areas to more accurately reflect an optimal (SI > 0.8) range for each environmental variable.

All continuous environmental variables were binned using Fisher's natural breaks classification method (Bivand 2013). The number of bins ranged from 6 to 10 to ensure an adequate sample size in each data grouping. Each SI of class $k$ for environment variable $i$ ($\mathrm{SI}_{i,k}$) was calculated on a scale of 0.0 to 1.0 as follows (Tanaka and Chen 2015, 2016):

$$\mathrm{SI}_{i,k} = \frac{\mathrm{CPUE}_{i,k} - \mathrm{CPUE}_{i,min}}{\mathrm{CPUE}_{i,max} - \mathrm{CPUE}_{i,min}}, \quad (3)$$

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

Inshore and offshore SIs were estimated using the histogram method (Tanaka and Chen 2016). Local polynomial regression fitting (i.e., LOESS) smoothing was applied to the SIs (R Development Core Team 2008). Suitable ranges were identified as SI values above 0.8 (Tanaka and Chen 2015, 2016). Boosted regression tree

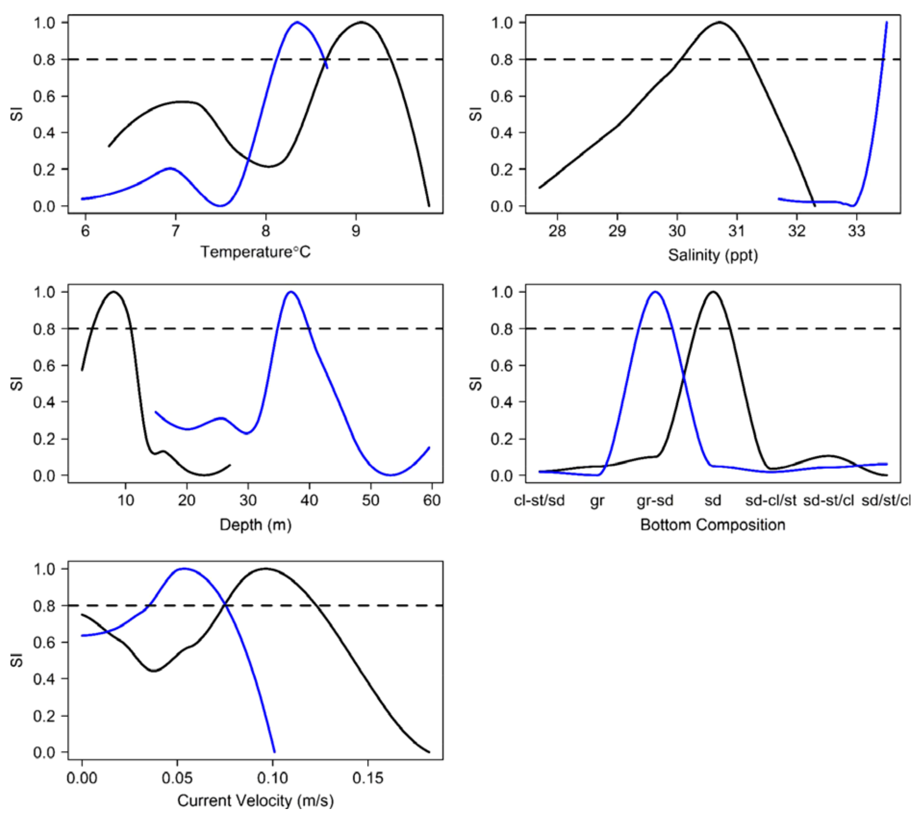


FIGURE 3. Inshore (black line) and offshore (blue line) suitability index (SI) curves showing the relationship between Atlantic sea scallop (>65 mm shell height) abundance and bottom temperature, depth, bottom salinity, current velocity, and bottom composition (cl = clay; st = silt; sd = sand; gr = gravel). Horizontal dotted lines represent the cutoff above which the suitability of a given habitat variable was considered high.

TABLE 1. Summary of location-specific suitable ranges (suitability index > 0.8) of each environmental variable examined for the Atlantic sea scallop models.

| Location | Mean bottom temperature (°C) | Mean bottom salinity (‰) | Mean flow velocity (m/s) | Depth (m) | Bottom composition |
|---|---|---|---|---|---|
| Inshore | 8.6–9.4 | 30.1–31.3 | 0.04–0.07 | 5–12 | Sand |
| Offshore | 8.1–8.7 | >33.0 | 0.07–0.13 | 35–41 | Gravel–sand |

TABLE 2. Relative contribution (%) of all environmental variables used in inshore and offshore Atlantic sea scallop habitat suitability index models to the deviance explained by the boosted regression tree.

| Location | Mean bottom temperature | Mean bottom salinity | Mean flow velocity | Depth | Bottom composition |
|---|---|---|---|---|---|
| Inshore | 28.18 | 32.30 | 16.25 | 8.39 | 14.86 |
| Offshore | 29.47 | 34.32 | 13.12 | 15.83 | 7.24 |

(BRT) models were used to identify the relative importance of environmental variables for the response variable (Elith et al. 2008; Xue et al. 2017). Using this method, weights were assigned to each environmental variable corresponding to its relative contribution (%) to the deviance explained in the BRT model (Xue et al. 2017). The BRTs were developed with the "gbm.step" function within the R package "gbm" (Ridgeway 2015). The SIs were then combined to form a composite HSI (also on a 0–1 scale) using an arithmetic mean model (Xue et al. 2017),

$$\mathrm{HSI} = \frac{1}{\sum_{i=1}^{n} w_i} \times \sum_{i=1}^{n} \mathrm{SI}_i w_i, \quad (4)$$

where $\mathrm{SI}_i$ represents an SI value associated with the $i$th environmental variable; $w_i$ represents the weight of variable $i$ based on BRT results; and $n$ represents the number of environmental variables included in the arithmetic mean model (AMM). In this study, only the AMM was used to generate HSI predictions, as previous studies have shown consistently better performance of this model over a geometric mean model (Tanaka and Chen 2015, 2016).

*Model validation.*— A cross-validation study was implemented to evaluate the performance and predictive ability of weighted HSIs. A randomly selected subset representing 80% of all data (training data) was used for HSI development, while the remaining 20% (testing data) was used for the evaluation of HSI performance (Smith 1994; Zuur et al. 2007; Tanaka and Chen 2015, 2016). The predicted HSI values based on the training data were compared against the observed HSI values based on testing data, and linear regression analysis was performed to evaluate the predictive performance of the HSI. This cross-validation procedure was repeated 100 times using random data selection in each round to obtain 100 sets of linear regression parameters (intercept, slope, and $R^2$). Good model performance was indicated by an intercept parameter close to zero, a slope close to 1.0, and an $R^2$ close to 1.0. This process was carried out separately for inshore and offshore stations.

*Spatiotemporal habitat suitability index-based bioclimate envelope evaluation.*— The weighted HSI model coupled with the FVCOM was used to predict spatiotemporal variability of the bioclimatic envelope for Atlantic sea scallops (>65 mm in shell height) in inshore and offshore GOM areas between 1978 and 2013. A spatial interpolation technique using ordinary kriging with a semivariogram function was used to produce continuous model outputs (Bailey and Gatrell 1995; R Development Core Team 2008). The HSI values were aggregated temporally by obtaining the median HSI value over the 36-year study period at each FVCOM node. Median HSI values were used instead of means because medians provided a clearer interpretation of the tendency over the 36 years (i.e., they were not susceptible to skewing in rare cases of outliers). The distribution of median HSI over 36 years was evaluated for the spatial distribution in the quality of bioclimate envelopes. In this study, an area with an HSI value larger than 0.8 was designated as highly suitable habitat, while an area with an HSI value below 0.3 was considered poor habitat (Tanaka and Chen 2015, 2016). Linear regression analysis was performed at every FVCOM node, and the derived slope (β) coefficient was used to evaluate temporal changes in the quality of Atlantic sea scallop bioclimate envelopes over 36 years.

## RESULTS

### Suitability Indices

Highest yearly bottom temperature ranged from approximately 9°C to 16°C inshore and from about 7°C to 12°C offshore. Lowest yearly bottom salinity ranged from approximately 26‰ to 31.5‰ inshore and from about 30.5‰ to 33‰ offshore. Depth ranged from about 2 to 25 m inshore and from about 15 to 57 m offshore. Average current speed ranged from close to 0 to 0.1 m/s for both inshore and offshore areas (Figure 3). Substantial differences in SI curves were found between Atlantic sea scallops located within inshore areas and those in offshore areas (Figure 3). Peak SIs for each environmental variable were as follows: for highest yearly bottom temperature, approximately 15°C inshore and about 10°C offshore; for lowest yearly bottom salinity, about 31‰ inshore and about 33‰ offshore; for depth, approximately 10 m inshore and about 37 m offshore; and for average current speed, about 0.05 m/s inshore and about 0.1 m/s offshore (Table 1; Figure 3).

## Variable Weighting and Model Validation

The BRT-based variable weighting showed that bottom salinity, bottom temperature, and flow velocity were the most important variables inshore, while bottom salinity, bottom temperature, and depth were the most important variables offshore (Table 2).

The performance (i.e., predictive ability) of the AMM, as tested through cross validation, was better within inshore stations relative to those offshore. Median values from linear regression showed that inshore stations had a median intercept of 0.14, a slope of 0.88, and an $R^2$ of 0.81. Offshore stations had a median intercept of 0.14, a slope of 0.57, and an $R^2$ of 0.35.

## Spatiotemporal Habitat Suitability Index-Based Bioclimate Envelope Evaluation

Projected HSI-based bioclimate envelopes for Atlantic sea scallops showed higher habitat suitability inshore compared with most offshore areas (Figure 4). However, offshore shoal areas displayed high habitat suitability on par with inshore areas. Cobscook Bay appeared to have the highest habitat suitability over the study area (Figure 4).

Changes in climate-driven habitat suitability over the 36 years (1978–2013) were apparent throughout the study area. Overall, inshore areas showed a trend of increasing habitat suitability (Figure 5). Offshore areas exhibited a decreasing trend in general, with the exception of shoal areas, which showed an increasing trend (Figure 5).

During 1978–2013, the proportion of total habitat with at least moderate habitat suitability (HSI > 0.5) for Atlantic sea scallops in the GOM ranged from 14.49% (1980) to 46.66% (2001). Total habitat with an HSI greater than 0.5 from the median over the 36-year study period was 26.16%. Proportion of total habitat with high habitat suitability (HSI > 0.8) for Atlantic sea

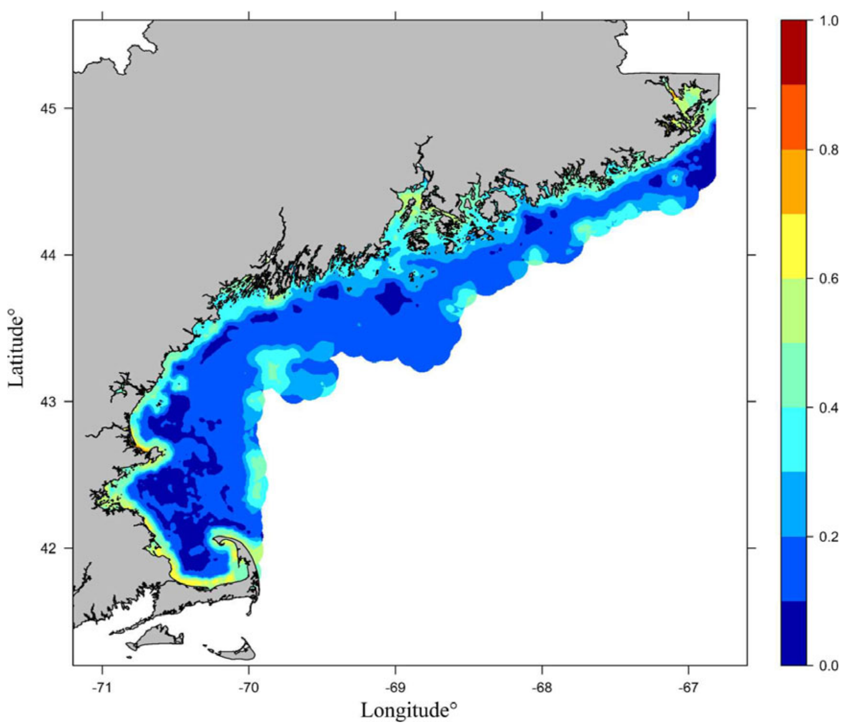


FIGURE 4. Map showing the spatial distribution of median habitat suitability index (HSI) values over the study period (1978–2013) for Atlantic sea scallops (>65 mm shell height) from Massachusetts to Maine. The HSI values larger than 0.8 are designated as good habitat, while HSI values below 0.3 are considered poor habitat. The color ramp corresponds to predicted HSI value, where blue indicates poor habitat and red indicates good habitat.

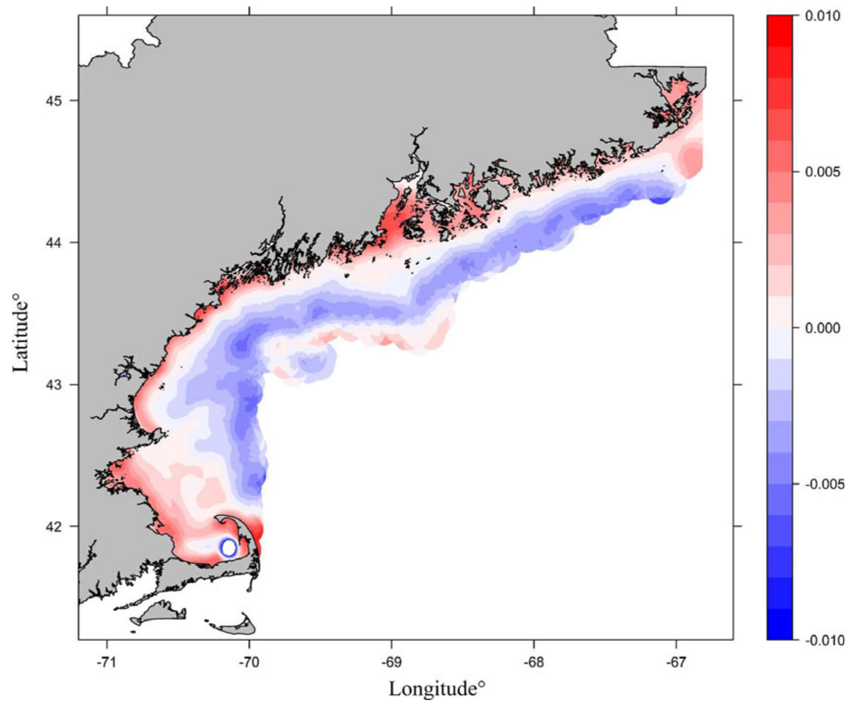


FIGURE 5. Map showing the temporal change in habitat suitability index (HSI) values for Atlantic sea scallops (>65 mm shell height) from Massachusetts to Maine over the study period (1978–2013). The color ramp corresponds to the linear regression slope (β) coefficient. Red areas have a positive slope, and blue areas have a negative slope.

scallops in the GOM ranged from 0.03% (1988) to 6.04% (2012) during the period of interest. Total habitat with HSI greater than 0.8 from the median over the 36-year period was 0.02%.

## DISCUSSION

A dominant spatial trend made apparent by this modeling approach was a decline in habitat suitability moving from inshore to offshore locations. It is likely that decreased habitat suitability in offshore areas is largely driven by increases in depth and decreases in temperature. This finding corresponds with habitat suitability being higher among offshore shoal areas relative to adjacent deep areas. Previous studies sampling Atlantic sea scallops along a depth gradient (10–30 m) have observed decreases across a range of ecological energetics (shell growth, somatic growth, somatic production, gonad production, gonad output reproductive effort, and residual reproductive value) in deeper waters (MacDonald and Thompson 1985a, 1985b; Macdonald et al. 1987). These differences are attributed to deteriorating food availability and temperature conditions with increasing water depth, which is thought to represent a natural gradient of habitat quality (Sarro and Stokesbury 2009; Hennen and Hart 2012).

Modeled nonlinear responses of the SIs reflect larval supply coupled with the species' ability to survive the environmental variability present in a given area. The SI curves for bottom temperature, depth, bottom salinity, current velocity, and bottom composition fell within known habitat ranges for Atlantic sea scallops (Naidu and Anderson 1984; Thouzeau et al. 1991; Wildish and Kristmason 1993; Stewart and Arnold 1994; Pilditch and Grant 1999; Hart and Chute 2004). However, within these broad ranges, the present study identified considerable differences in habitat preference between Atlantic sea scallops inhabiting inshore and offshore areas. Inshore Atlantic sea scallops were most abundant in shallower areas with stronger currents, higher temperatures, and lower salinities relative to offshore scallops. Abundance of inshore Atlantic sea scallops was highest on sand substrate as opposed to offshore, where gravel–sand was preferred. Inshore–offshore differences in dispersal and retention patterns of Atlantic sea scallop larvae were found by Tremblay and Sinclair (1991), which may factor into differences in habitat selectivity observed during the present study. Additionally, Beyer et al. (2010) speculated that habitat selection is context-dependent, with functional responses in preference resulting from changing availability. Although Atlantic sea scallops inhabiting both inshore and offshore areas were within known, broad ranges of physiologically suitable environmental conditions, they were still subject to a different composite of habitat variables. Thus, it is possible that perceived habitat preference may partially reflect given habitat availability rather than the species' physiologically preferred habitat range. Furthermore, interactive effects of multiple habitat variables could have resulted in the observed difference in inshore and offshore SI curves. For example, the higher optimal flow velocity observed for inshore Atlantic sea scallops may reflect a required higher feeding rate due to an increased metabolic rate resulting from higher temperatures in these areas. Such complex interactions among key habitat variables highlight a benefit of evaluating habitat quality in a holistic manner as opposed to analyzing each variable in isolation.

Total suitable habitat coverage (HSI > 0.8) in the model showed large interannual variations ranging from 0.03% to 6.04%, which reflect changes in dynamic environmental variables (bottom temperature, current velocity, and bottom salinity). The mean proportion of total suitable habitat (HSI > 0.8) for Atlantic sea scallops in the GOM over the 36-year study period was 0.02%. Brown et al. (2000) developed HSI models for eight fish and invertebrate species in Casco Bay and Sheepscot Bay, Maine. Total suitable habitat (HSI > 0.84; note the difference in "suitable" habitat cutoff between the Brown et al. [2000] study and the current study) for these species ranged from 6% (American Sand Lance *Ammodytes americanus*) to 95% (adult American lobsters). Coverage of suitable habitat for Atlantic sea scallops in the current study was low relative to the species modeled by Brown et al. (2000); however, consideration should be given to the spatial scale at which these models were applied. Brown et al. (2000) confined their model to a much smaller coastal area, while the present model was applied over a large portion of the GOM. Applying the current model over a large spatial scale increased the likelihood that a gradient in habitat quality would be covered, effectively lowering the percent of suitable habitat coverage. Environment–biota relationships can include a hierarchy of factors operating at different scales (Willis and Whittaker 2002; Pearson and Dawson 2003; Hattab et al. 2014). This study highlights spatial effects in the relationships between Atlantic sea scallops and habitat variables. Thus, bioclimate envelope models may perform differently if applied over different spatial scales. In the current study, this was addressed through the individual development of both inshore and offshore SIs to reflect the perceived change in habitat preference between these areas. Future refinement of the model could include an evaluation of Atlantic sea scallop–habitat relationships over even smaller spatial scales to further explore the scale at which each environmental variable operates.

An increasing temporal trend in climate-driven (i.e., bottom temperature and salinity) habitat suitability was observed for inshore areas, with a decreasing trend in offshore areas (Figure 5). Any change in habitat suitability over time resulted from changes in dynamic habitat variables (bottom temperature, bottom salinity, and current velocity), suggesting that the composite of these three factors from 1978 to 2013 has changed favorably for Atlantic sea scallops in inshore areas and has remained relatively stable in offshore areas. These trends assume that the habitat preference of Atlantic sea scallops did not change over the study period (Pearson and Dawson 2003; Crisp et al. 2009; Catullo et al. 2015).

Model validation revealed that offshore areas had lower predictive ability relative to inshore areas. Higher inshore performance likely corresponds to having approximately 4.5 times more tows conducted in these areas. Future iterations of this model can include more data in both inshore and offshore areas, potentially increasing the predictive ability in offshore areas. However, it is also possible that predicting the distribution of offshore Atlantic sea scallop habitat is more difficult due to possible complex or de-coupled interactions between Atlantic sea scallops and habitat variables in these areas, as described above (Beyer et al. 2010).

Modeling methodology in ecological research has historically been largely quantitative (Bradbury et al. 1986). However, qualitative models effectively capture ecological patterns and have the advantage of avoiding the data-driven biases to which quantitative models are subject (Bradbury et al. 1986; Store and Kangas 2001; Tanaka and Chen 2016). This HSI-based bioclimate envelope modeling approach can be applied to a number of different research areas, such as modeling potential species distribution and evaluating the effects of climate-driven changes in habitat suitability on this distribution through hindcasting/forecasting analyses (Pearson and Dawson 2003; Araujo and Peterson 2012; Tanaka and Chen 2016). However, there are intrinsic limitations to this approach that should be considered when evaluating model results (Pearson and Dawson 2003; Luoto et al. 2005). The FVCOM predictions used as inputs for all dynamic habitat variables in this study provided the highest resolution and broadest spatial coverage for temperature, salinity, and current velocity data available in the study area; however, Atlantic sea scallop beds can frequently occur over relatively small spatial scales. Due to the inherent resolution of this environmental data set, it is unlikely that the modeling approach used here would be able to resolve fine-scale patches of habitat with the potential to support Atlantic sea scallop beds. Instead, the bioclimate envelopes developed here are more useful for exploring spatiotemporal trends in meso-scale climate-driven habitat suitability.

Development of bioclimate envelope models relies upon environmental data, and as with any environmental data, there are several possible sources of error that could cause misrepresentation of model predictions. Since all data obtained through FVCOM are outputs from model simulations as opposed to directly measured values, prediction accuracy needs to be taken into account. To evaluate the performance of FVCOM within the study area, Tanaka and Chen (2016) and Li et al. (2017) used a set of observed bottom temperatures collected by the Environmental Monitors on Lobster Traps (eMOLT) program to compare with FVCOM predictions. They found that although some variability occurred in FVCOM outputs relative to eMOLT observations, FVCOM adequately captured the general spatial and temporal trends in bottom temperature and salinity. These findings add validity to the quality and accuracy of FVCOM predictions over broader scales. Another important consideration is the bottom composition data obtained from the CONMAP GIS database (Poppe et al. 2005). This GIS layer provides a relatively coarse resolution of bottom type, which may be insufficient to resolve potential fine-scale Atlantic sea scallop habitat. However, the CONMAP GIS database provides the most comprehensive coverage of bottom composition and was useful here as a key component to identifying large-scale spatial trends in habitat suitability.

In this study, the bioclimate envelopes were defined based upon five environmental variables when in reality, a large number of physical, biological, and chemical conditions likely factor into the life history and distribution of Atlantic sea scallops. As more comprehensive environmental data become available in the future, studies to develop a further detailed bioclimate envelope model could include additional variables, such as pH, dissolved oxygen, predator–prey interactions, and other food web interactions, to capture a more comprehensive representation of Atlantic sea scallop ecology (Araújo and Luoto 2007). Additionally, environmental predictors in this study were selected based on availability and their assumed correlation with habitat quality. However, as is generally the case with species–environment modeling, the variables used to build this model may be operating as surrogates for factors that directly control species distribution through physiological mechanisms (Austin 2007; Araujo and Peterson 2012). From the associations between variables, we can infer the relationship between spatiotemporal variability of environmental factors and habitat quality. For instance, salinity in these models may act as a proxy for broad spatial patterns in Atlantic sea scallop distribution coupled with—and driven by—the origin of the water mass existing in a given area. An additional example is that temperature and depth likely correspond to gradients in food availability (MacDonald and Thompson 1985a, 1985b; Macdonald et al. 1987).

An important assumption to consider in this modeling framework is that predicted habitat quality is directly related to observed Atlantic sea scallop density, whereas in reality, a number of other factors collectively act on the ecology of this species. For instance, Atlantic sea scallop density is highly influenced by larval supply (Shumway and Parsons 2006); this modeling approach also did not account for spatiotemporally variable fishing pressure, which acts directly on adult Atlantic sea scallop density. Thus, certain areas with quality habitat may still have low Atlantic sea scallop density, which could impact modeled nonlinear responses of SIs. However, although this is an important point to consider as a result of the large spatiotemporal extent of Atlantic sea scallop observations used to calibrate this model, it is likely that collectively, the SIs accurately reflect this species' preferred ranges of environmental variability in the given area.

In light of recent abrupt warming events as well as long-term warming trends within the GOM ecosystem, it is becoming increasingly important to view resource management from within the context of climate change (Mills et al. 2013; Pershing et al. 2015). Effective management of marine resources requires knowledge of population distribution and dynamics (Langton et al. 1995); however, fisheries managers must frequently base their decisions on limited information (Brown et al. 2000). Even when intensive sampling efforts are conducted, they sometimes fail to provide adequate spatial or temporal coverage to capture an entire range of available habitat, which can result in misinformed management decisions (Brown et al. 2000). Additionally, many stock assessments fail to incorporate environmental variability (NMFS 2010). The bioclimate envelope model developed in this study provides a unique tool to visualize the extent of available habitat for Atlantic sea scallops as well as to evaluate the potential impacts of a changing ecosystem on the distribution of available habitat in the GOM. Our study sheds new light on spatiotemporal trends in habitat suitability that could potentially inform and improve stock assessments and the management of Atlantic sea scallops. Other potential management applications for this modeling framework could include the development of habitat maps in poorly sampled areas (Brown et al. 2000), refinement of fisheries-independent surveying efforts, and prioritization of areas for conservation actions.

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