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Mesoscale climatic impacts on the distribution of *Homarus americanus* in the US inshore Gulf of Maine

Kisei R. Tanaka¹,², Jui-Han Chang³, Ying Xue⁴, Zengguang Li⁴, Larry Jacobson³ and Yong Chen¹,².

1. School of Marine Sciences, University of Maine, Orono, ME USA
2. Climate Change Institute, University of Maine, Orono, ME USA
3. Northeast Fisheries Science Center, National Oceanic and Atmospheric Administration, Woods Hole, MA USA
4. Fisheries College, Ocean University of China, Qingdao, China

Abstract

American lobster (*Homarus americanus*) supports one of the most valuable fisheries in the United States. Spatial distributions of *H. americanus* are hypothesized to be influenced by climate-driven environmental factors but such effects have not been quantified. We developed a Tweedie-generalized additive model (GAM) to quantify environmental effects on season, sex- and size-specific distributions of *H. americanus* in the inshore Gulf of Maine. Tweedie GAMs were coupled with regional circulation model output to predict spatiotemporal changes in distribution of *H. americanus* due to mesoscale climate variability. GAM results indicated that bottom temperature and salinity impacts on *H. americanus* distribution were more pronounced during spring. The coupled climate-niche model predicted significantly higher *H. americanus* abundance under a warm climatology scenario. This study provides a predictive climate-niche modelling framework that may be useful for planning
fishery investments and anticipating management challenges given ongoing climate driven changes in the Northwest Atlantic.

Keywords: *Homarus americanus*, biogeography, generalized additive model, climate variability
1 Introduction

American lobster (*Homarus americanus*) supports the most economically valuable single-species commercial fishery in the northeast USA and Atlantic Canada ($618 million ex-vessel value in the US during 2015; ACCSP 2016). Over the last three decades, lobster landings increased dramatically in the US portion of the Gulf of Maine where abundance is at record high levels (ASMFC 2015). Commercial fishing activities for lobster in the Gulf of Maine are predominantly in near-shore waters because lobsters recently molted to legal size are found mainly in inshore waters less than 50 m depth (Maine DMR 2014). Growth in both catch and production of the lobster fishery has led many coastal communities to become increasingly dependent on the fishery, leaving the coupled natural and human system vulnerable to environmental change (Steneck et al. 2011).

Lobster movement and abundance in the coastal waters are closely tied to changes in water temperature (ASMFC 2015a). Lobsters are cold blooded and tend to move to areas with more optimal water temperatures (Caputi et al. 2013) and climatic variability has been recognized as a key driver of seasonal changes in distribution (Mills et al. 2013; Pinsky et al. 2013; Boudreau et al. 2015). Lobsters are found across a wide range of water temperature, from -1 to 26 °C (Lawton and Lavalli 1995; Quinn 2016), but several laboratory studies have demonstrated that the species prefers a narrower temperature range by 12-18 °C and avoids temperature below 5 °C and above 19 °C (Crossin et al. 1998). Warmer water temperatures within its preferred range allow lobsters to be more active and to utilize shallow nearshore areas with low salinity (Jury 1994). Therefore, changes in thermal regime may influence lobster movements, migrations, and seasonal distribution patterns (Crossin et al. 1998; Lawton and Lavalli 1995; Phillips 2006; Caputi et al. 2013).
Water temperatures in the Gulf of Maine have increased over the last 30 years and further increases are likely (Fernandez et al. 2015; Pershing et al. 2015; Kleisner et al. 2016; Saba et al. 2016). Rising water temperatures are expected to result in behavioral and phenological changes in lobster (e.g. early and more frequent molting) and ecological changes including increased seasonal migrations and shifts in distribution (Fogarty et al. 2007; Pinsky et al. 2013). Mean bottom temperature on the northeast U.S. Continental Shelf system is expected to increase more than 1 °C by 2050 according to the Intergovernmental Panel on Climate Change Representative Concentration Pathway (IPCC-RCP) scenario with highest greenhouse gas emissions (RCP 8.5: IPCC 2013; NOAA, 2015). This projected increase in bottom temperatures in the Gulf of Maine is not expected to exceed the species’ maximum physiological tolerance and it is possible that quality of lobster habitat will actually increase in the inshore Gulf of Maine (Tanaka and Chen 2016).

While the Gulf of Maine have experienced the long-term effect due to change in climate, the region’s inshore waters have also experienced short term natural variability within the climate system. Climatic variability such as water temperature anomalies can trigger many ecological processes in marine ecosystems and affect abundances and distributions of many fish and shellfish species through habitat range expansions and contractions (Tian et al. 2009). In the case of American lobster, the species’ habitat condition was greatly affected by the 2012 northwest Atlantic heat wave, which generated abrupt and unexpected ecological and economic changes in the U.S. lobster fisheries (Mills et al. 2013). The ecological and economic impacts of the 2012 ocean heat wave raised the need to develop a tool that can better understand the associations between lobster abrupt climate variability events and lobster catch density, and development of a predictive tool to facilitate climate adaptation planning within fisheries management in the Gulf of Maine.
In the coastal US Gulf of Maine, fixed management boundaries divide the lobster fishery into seven coastal management zones (A-G: Acheson, 2013; ASMFC 2015b). The lobster fishery management plan established in 1995 allows license holders in nearshore zones to operate a trap fishery which is independent of fishing in offshore areas for relatively large lobsters. Changes in lobster distribution inside these zones could lead to management issues stemming from population size increases in some zones and decreases in others while fishermen cannot easily reallocate their fishing effort between zones (Caputi et al. 2013). As the rate of climate variability is predicted to accelerate in the future (IPCC 2013), there is a growing need to (1) evaluate the relative importance and impacts of environmental drivers of the lobster distribution, (2) develop the capacity for predicting spatiotemporal changes in the lobster distribution under different climatology, and (3) address management uncertainty due to potential changes in lobster distribution (Hare et al. 2012; ASMFC 2015b).

In this study, a statistical climate-niche model was developed to predict spatiotemporal changes in lobster distribution in the inshore Gulf of Maine. A climate-niche model is a type of species distribution model that is useful for predicting distributional responses to climatic variability (Cheung et al. 2009; Franklin 2010; Stock et al. 2011; Hare et al. 2012; Tanaka and Chen 2016). We used Tweedie-generalized additive models (GAMs) to quantify association between season, stage, and sex specific lobster catch density and key environmental variables. Fitted GAMs were coupled with the output from a regional circulation model to predict lobster distribution in a climatically altered environment. This study provides a step towards an adaptive ecosystem-based management of the commercially important lobster fishery in the US Gulf of Maine (ASMFC 2014).
2 Materials and Methods

2.1 Study area

The study area covers the inshore US waters in the Gulf of Maine between Nova Scotia, Canada and Massachusetts, USA (42.85°-44.80° N and 70.80°-66.95° W) where depth ranges 4.6-221.3 m (Fig. 1). It is characterized by rough terrain, tidally-mixed coastal waters, and high biological productivity capable of supporting large productive fisheries (Townsend et al. 2006). The inshore Gulf of Maine is influenced by nutrient-rich deep waters transported by winter convective mixing and cross-isobath water fluxes. Rivers and streams contribute freshwater (Townsend et al. 2006). From 2000-2014, bottom temperatures as measured by the Maine-New Hampshire (ME-NH) Inshore Trawl survey in the study area increased at the average rate of 0.12 yr\(^{-1}\) in spring and 0.08 yr\(^{-1}\) in fall (Fig. 1). The analysis was structured around Maine’s seven lobster management zones (LMZs A-G: Fig. 1) to incorporate a spatial scale of management interest and to avoid focus on very small areas where model predictions could be less interpretable (Incze et al. 2010; Xue et al. 2008; Chang et al. 2016;).

2.2 Data

Season, size, and stage specific lobster survey data used in modeling were collected by ME-NH Inshore Trawl surveys during 2000-2014 (Sherman et al. 2005). This fishery-independent otter bottom trawl survey program is conducted biannually, covers ~16,000 km\(^2\) per season, and targets about 115 random stations (Sherman et al. 2005). The survey is stratified by depth and position along the coast. Tows of 20 minutes at 2.5 knots are made at each station to cover a mean distance of 1,509 m with average swept area of about 15,853 m\(^2\) per tow. The otter trawl is a modified shrimp net that can effectively capture...
bottom dwelling species such as lobster. The trawl net has a 21.34 m head rope, 6.35 cm mesh size in the front end, 5.08 cm in the belly and a codend with a 1.27 cm mesh codend linear. A CTD profiler attached to the trawl net records depth, bottom salinity, and bottom temperature at each station. Observed depth ranged 4.57-221.29 m, bottom temperatures 2.6-14.9 °C, and salinity 25.8-34.6 ppt.

A tow was considered satisfactory and used in analysis if it contained relevant biological information (carapace length, sex) for each lobster as well as all environmental (e.g. bottom water temperature, salinity and depth) and spatial (e.g. latitude and longitude) information. A precautionary analysis was applied to minimize spatial autocorrelation, and stations that remained stationary within a 1 nm² grid (a designated survey grid size) between 2000-2014 were removed. The data for modeling was from 2,142 tows (Spring: n = 1312, Fall: n = 830) and 252,262 lobsters with carapace lengths (CL, mm) that ranged 10-203 mm (median 63 mm). The distribution of lobster differs by season, sex, and size class (Lawton and Lavalli 1995; Chang et al. 2010; Tanaka and Chen 2016), therefore the lobster catches were compiled separately for adults (> 60 mm CL) and juveniles (≤ 60 mm CL) and by season (spring: April-June and fall: September-November) and sex (male and female). Lobster catches were standardized as numbers caught per 792 m² min⁻¹ of area swept (Chang et al. 2010: hereafter referred as lobster catch density).

Following the 2015 benchmark assessment, both spring and fall surveys were assumed to have a linear catchability relationship that remained constant during 2000-2014 (ASMFC 2015a). Therefore, lobster catch density in this study was used as a proxy for distribution and abundance, which assumed that lobster catches reflected the presence/absence and density of the species at a given location within the study area, and not confounded by bias associated
with sampling efficiency and environmental variability (Chang et al. 2010; ASMFC 2015a; Tanaka and Chen 2016; Xue et al. 2017).

### 2.3 Generalized additive models

A generalized additive model (GAM) was used to study the impact of climatic variation on lobster distribution. A GAM is a nonlinear extension of generalized linear models (Zuur et al. 2007). Environmental variables used to predict catch density (e.g. depth and temperature) are often correlated. Variance inflation factors (VIF) were therefore calculated and variables with VIF value > 3 were removed to minimize collinearity and improve model performance (Table 1; Zuur et al. 2007; Tanaka et al. 2017). Following Sagaresse et al. (2014), boosted regression tree (BRT) analysis was used to identify potentially significant bivariate interaction terms, which were incorporated in the GAM fitting process. In this study, the general GAM formulation to estimate lobster catch density $\eta$ can be expressed as:

$$g(\eta) = \alpha + \sum_{j=1}^{p} s_j(x_j) + \epsilon$$

where $g(\eta)$ represents the log link function between $\eta$ and each additive predictor; $\alpha$ denotes the intercept term; $s_j(\cdot)$ denotes a cubic spline function that might be linear or nonlinear; $x_j$ is a single or pair of additive predictor; $\epsilon$ is the residual error. Smooth terms with a pair of predictors were used to model interactions. Maximum degrees of freedom for smooth terms was set at 5 ($k = 5$) for univariate smooth functions and 30 ($k = 30$) for bivariate smooth functions to prevent model over-fitting (Zuur et al. 2009; Sagarese et al. 2014; Rooper et al. 2014). Model fitting and variable selection were carried out separately for each of the eight combinations of size, season and sex (Chang et al. 2010). All statistical analyses were conducted in the R programing environment (R Core Team, 2016). VIF and BRT procedures
used the *fmsb* and *dismo* packages (Hijmans et al. 2015; Nakazawa 2015). GAMs were fitted using *mgcv* package (Wood 2011).

The likelihood used to measure GAM fit was based on a Tweedie distribution to account for the large proportion of zero-catch tows and skewness in the catch data (Fig. 2). A Tweedie distribution model is a type of exponential dispersion model (Jørgensen 1997; Shono 2008). The Tweedie distribution has three parameters: mean, dispersion and a power parameter $p$ that ranges from 1 for the Poisson distribution to 2 for Gamma distribution to 3 for inverse Gaussian distributions (Shono 2008; Wood 2011). The Tweedie distribution in this study was assumed to be a compound Poisson-Gamma distribution with $1 < p < 2$ (Wood 2011). This assumption was shown to be appropriate with analysis of zero-catch fishery data (Shono 2008; Li et al. 2011), where a Tweedie distribution for $1 < p < 2$ can support all non-negative real numbers with a point mass in zero (Berg et al. 2014). Tweedie GAMs were fitted by optimizing its profile likelihood and power parameter $p$ was estimated within the range of $1 < p < 2$ during model fitting process (Candy 2004; Shono 2008; Wood 2011; Berg et al. 2014). Shono (2008) and Li et al. (2011) showed that this Tweedie model as an extension of compound Poisson–Gamma distribution model performs well with zero-inflated fisheries data. Its ability to handle zero inflated data uniformly along with the skewed positive data has shown to outperform the traditional non-Tweedie approaches such as quasi-Poisson, negative binomial, delta (two-stage) distributions and log transformation with an additive constant where the estimation results are sensitive to the choice of the constant and combining two sub-models can complicates the model interpretation (Tweedie 1984; Candy 2004; Berg et al. 2014).
2.4 Model selection and validation

Stepwise backward selection using chi-square statistical tests and Akaike’s information criteria (AIC) was used to reduce a full model (with univariate and bivariate terms identified through VIF and BRT analyses) to a parsimonious final model with lowest AIC and only significant variables (Tanaka et al. 2017). The stepwise model selection procedure was repeated as long as the removal of the variable with the lowest significant $p$-value reduced AIC. The best-fitting models were used to provide a spatiotemporal measure of the probability of lobster catch density (numbers caught per 792 m$^2$ min$^{-1}$ of area swept). The proportion of deviance explained was used for model comparisons and to measure how well the final models explain the variance in the observation. Diagnostic plots using random-quantile residuals (Miller et al. 2017) were examined to identify lack of fit and evaluate model assumptions.

The predictive performance of final models for each group of lobsters was evaluated externally through a 100-fold manual cross-validation procedure. In this procedure, 80% of the original data was randomly partitioned for model calibration (training set), while the remainder was used for model validation (testing set). The final model was fit to each training set and used to predict the corresponding testing set (Miller and Franklin 2002; Brotons et al. 2004; Tanaka and Chen 2016; Tanaka et al. 2017). The cross-validation procedure was repeated with random partition of testing and training data in each iteration. The predictive power of a final model was evaluated by regressing model predictions on the validation data and comparing the distributions of regression intercepts ($\alpha$), slopes ($\beta$), and adjusted $R^2$ to expectations for a precise and unbiased model with $\alpha = 0$, $\beta = 1$, and $R^2 = 1$. The intercept coefficient indicates systematic bias in prediction while the slope coefficient not
significantly different from 1 indicates that observation and prediction have similar spatial patterns (Chang et al. 2010).

2.5 Environmental data

Finite-Volume Community Ocean Model (FVCOM) runs configured for Northwest Atlantic Shelf region were used to estimate monthly bottom temperature and salinity in the study area during 1982 to 2013. The FVCOM is an advanced regional ocean circulation model developed by University of Massachusetts Dartmouth and Woods Hole Oceanographic Institution (Chen et al. 2006; Li et al. 2017). The horizontal resolution of FVCOM in the study area ranges between ~0.02 km in inshore waters to ~10 km offshore waters (Chen et al. 2006). Bathymetry of the study area was derived from the Coastal Relief Model (CRM) with horizontal resolution of 3 arc-seconds (~90 m: NGDC 1999). To assess the skill of FVCOM and CRM in the study area, modeled bottom temperature, salinity and depth data were compared to spatially and temporally corresponding in situ data recorded in the ME-NH survey. To evaluate agreement between observed and modeled data, each variable was assessed using (1) a bivariate observation versus prediction plot and a set of linear regression coefficients such as the coefficient of determination ($r^2$), slope ($\alpha$), and intercept ($\beta$) and (2) a graphical summary based on standardized Taylor diagrams (Taylor 2001; Stow et al. 2009; Li et al. 2017).

2.6 Mesoscale climatic impacts on lobster distribution

Final GAMs were used to predict lobster catch density at every ME-NH survey station in the study area during 2000-2014. Spatiotemporal changes in lobster distributions due to mesoscale climatic variability was analyzed using the following approaches. Spatial centroids for predicted and observed lobster catch densities were compared to evaluate the proportion
of climatic effects on changes in lobster distribution (Broennimann et al. 2007; VanDerWal et al. 2013). The purpose of this approach was to determine how well model predictions based on climate data (bottom temperature and salinity variables) predicted recent changes in lobster distribution. Longitudinal and latitudinal centroids were calculated:

\[
\text{Lon}_{s,y} = \frac{\sum_{i=1}^{K} (\text{Lon}_i \times D_i)}{\sum_{i=1}^{K} D_i}
\]

\[
\text{Lat}_{s,y} = \frac{\sum_{i=1}^{K} (\text{Lat}_i \times D_i)}{\sum_{i=1}^{K} D_i}
\]

where \(\text{Lon}_i\) and \(\text{Lat}_i\) are for ME-NH survey station \(i\); \(D_i\) denotes the predicted or observed lobster catch density at ME-NH survey station \(i\); \(K\) is the total number of ME-NH survey stations in the study area.

Final GAMs were also used to project how lobster distribution may change under two thermally contrasting climatologies (Sagarese et al. 2014). Predictive fields were interpolated using ordinary kriging to describe spatial variability in lobster catch density (Froeschke and Froeschke 2016; Tanaka et al. 2017). Ordinary kriging procedures were conducted via the automap package (Hiemstra et al. 2008) and kriged maps were prepared at 0.03 × 0.03 latitude/longitude grid. Model prediction using FVCOM outputs made projections under two hypotheses about climate variability possible. Hypothetical “cold” and “warm” climatology scenarios for the study area were constructed by averaging FVCOM bottom temperature and salinity fields during the five warmest and coldest modeled spring and fall survey periods (April-June & September-November) during 1982-2013 (Fig. 3). The purpose of this analysis was to investigate how two contrasting modes of regional climatology influences the relative lobster abundance. Average bottom temperatures were 5.1 °C during the spring and 7.3 °C during fall in the “cold” climatology scenario and 9.7 °C during spring and 11.9 °C during...
fall in the “warm” climatology scenario. Predicted lobster density in each cell in the warm
and cool scenarios were subtracted to highlight potential differences in lobster distributions
due to change in bottom temperature and salinity (Jones et al. 2016).

3 Results

3.1 GAMs

Latitude (°) and depth (m) with VIF values > 3 were omitted before fitting all GAMs
(Table 1). Bottom temperature (°C) and distance offshore (m) were included as significant
predictor variables in all final models (p < 0.001). Two-dimensional smooth terms for salinity
and longitude were included in all final spring models and for adult models in fall because
BRT analysis identified two-way interactions between salinity and longitude (Table 2).
Univariate salinity and longitude terms were included in fall models where statistically
significant (Table 2). Percent deviance explained ranged from 47% to 56% and was
somewhat higher for spring (Table 2). The cross validation result suggested that the final
models can predict lobster catch density well. The slope coefficients (β) in cross-validation
analysis ranged from 0.96 to 1.08, while the intercept coefficients (α) ranged from -0.10 to
0.04, indicating that the model performance was close to being ideal (1:1 slope; Table 3).
However, variability in model accuracy increased at higher lobster catch density in every
modeled group (Fig. 4).

Response curves for lobster catch density as a function of bottom temperature during
spring were dome-shaped with highest lobster catch density between 6-10 °C (Fig. 5). In
contrast, during the fall lobster catch densities increased across the range of bottom
temperature but plateaued at higher temperature. The two-dimensional terms for interaction
between salinity and longitude were significant in spring models and for male juvenile
lobsters during fall (A1). Response curves for distance offshore were similar in all models
(Fig. 5), where lobster catch densities increased with increasing distance from coastline and peaked around ~4,000-4,500 m. Longitude was a part of significant interaction term in 6 out of 8 lobster models (Table 2). Longitude response curves for female and male juvenile models in fall were similar, and indicated that study area between ~68.5°-69° W had the lowest effect on abundance of both male and female juvenile lobster groups in fall (Fig. 5).

3.2 **FVCOM and CRM skill assessment**

FVCOM and CRM predictions for bottom temperature and depth were similar to observations but predicted and observed bottom salinities were less so (Fig. 6). Regression coefficients showed that FVCOM and CRM predictions were almost unbiased for depth and bottom temperature, but biased for bottom salinity. Standardized Taylor diagrams indicated the FVCOM showed a higher skill in modeling bottom temperature, while the modeled data showed smaller variability overall (A3). Despite these shortcomings, FVCOM salinity estimates were used because they provided best bottom salinity prediction in the study area and captured general spatial and temporal trends in the observations.

3.3 **Mesoscale climatic impacts on lobster distribution**

During 2000-2014, the spring centroids of observed and modeled lobster distribution were mainly between 69.3°-68.6° W, while observed and modeled fall centroids were farther east between 69.4°-68.8° W (zones C and D: Fig. 7). All observed spring centroids shifted northeast, while this unidirectional northeastward shift was generally captured by spring GAMs based on changes in bottom temperature and salinity. Observed and modeled centroids for adult lobster during fall initially shifted in different directions. Modeled fall centroids first shifted southwest then shifted northeast, while the corresponding observed centroids shifted east. Spatial discrepancies between modeled and observed centroids were
larger during fall, and centroids of observed juvenile lobster distribution showed larger
changes. Magnitude of spatial discrepancies between observed and modeled centroids were
generally within 20 km (Fig. 7).

Median predicted lobster catch density in the study area ranged from 0.53 to 1.58 (Fig. 8). Predicted lobster catch density was higher inshore, for adults, and during fall (Fig. 8). Lobster catch density was projected to increase more under the warm climatology scenario than in the cold climatology scenario across the study area in both seasons and for all size groups (Figs. 9-10). Median predicted lobster catch density ranged from 0.32 to 1.22 under the cold climatology scenario and 0.65 to 2.02 under the warm climatology scenario (Fig. 9). Differences in lobster catch density were pronounced inshore, and largest for male adults in spring (0.89) and smallest for juvenile males in spring (0.33). Differences between the two climatology scenarios were generally larger mid-coast (zones B-F/G), and more pronounced during spring except for male juveniles (Fig. 10). Lobster catch density was projected to increase more across the Gulf of Maine under the warm climatology scenario than the cold climatology scenario by 65.3% (fall adult male) to 119.8% (fall juvenile male) (Fig. 10).

4 Discussion

4.1 GAMs

The GAMs with Tweedie distributions for zero-inflated survey catch data were useful prediction tools based on cross-validation results (Table 3 & Fig. 4), and this study recommend the Tweedie models to be considered as a candidate modeling approach for similar future studies. Model results indicate that nonlinear relationships between lobster catch density and environmental variables were common in the ME-NH Inshore Trawl survey data. For example, the GAM response curves captured nonlinear lobster responses to bottom
temperature and salinity within the specie’s known tolerable temperature and salinity ranges (Fig. 5; Harding 1992; Mercaldo-Allen and Kuropat 1994; Lawton and Lavalli 1995).

Lobsters are found across a wide range of water temperature (-1 to 26 °C; Lawton and Lavalli 1995; Quinn 2016) and salinity (10-32 ppt), but modeled nonlinear lobster responses likely reflect the species’ abilities to detect local environmental variabilities associated with temperature and salinity and demonstrate the species’ sensory-based adaptive behaviors to avoid suboptimal habitats (Jury et al. 1994; Crossin et al. 1998).

Bottom temperature was included in all final GAMs as a univariate term, indicating that this variable alone significantly influenced lobster catch density regardless of season, stage, or sex. Lobsters are capable of behavioral thermoregulation and actively seek seasonal optimal thermal habitats over others to maximize its growth or reproductive benefits (Ennis 1984; Crossin et al. 1998; Jury and Watson III 2013). Water temperature is considered to have a pervasive influence on the behaviors of ectothermic lobsters, and high lobster densities have been observed in the range of 8-18 °C (Aiken and Waddy 1986; Cooper and Uzmann 1980; Ennis 1984; Jury and Watson III 2013). Season-specific temperature response curves likely reflect their responses to changes in water temperature that is dependent on the season or their thermal history (i.e. acclimation). Sex-and stage-based differences were not apparent in the final GAMs outputs; however, discrepancies concerning the sex and stage-specific responses to temperature reported in different studies may be due to the (1) spatial scale of this study area, (2) the range and timing of temperature data recorded by ME-NH survey that varied between 2.6-12 °C in spring and 5.7-14.3 °C in fall, and (3) potential unmeasured underlying ecological processes present in the in-situ survey data.

The significance of univariate bottom salinity terms for juveniles but not adults in the fall models may be due to ontogenetic differences and water temperatures (Jury et al. 1994).
For example, juvenile and adult lobsters are limited osmoregulators restricted to coastal waters, but juveniles have less salinity tolerance compared to adults and are more susceptible to osmotic stress (Lawton and Lavalli 1995; Mercaldo-Allen and Kuropat 1994; Watson III et al. 1999). Furthermore, interactive effects of temperature and salinity on lobsters have also been observed such that low salinity causes higher osmotic stress at higher water temperature (McLeese 1956; Mercaldo-Allen and Kuropat 1994). Therefore, the significant univariate bottom salinity terms included in the final fall juvenile models potentially reflect the combination of ontogenetic differences and interactive effects of temperature and salinity.

With the exception of the model for juvenile lobsters in fall, all final GAMs included an interaction between bottom salinity and longitude (Table 2). The bivariate interactive terms indicate that bottom salinity exerted varying magnitude of influence on local lobster abundance along the coastline (i.e. longitude axis), especially when the study area was characterized by lower bottom salinity during spring (Table 2 & A2). Furthermore, the effect of longitude shown in both univariate and bivariate terms slightly decreased around ~69° W where the Penobscot bay is located (Fig.1 & A2). This localized salinity-longitude effect is likely linked to the changes in bottom salinity in the area around Penobscot Bay, and the GAMs may have captured the systematic ecological response of lobsters.

Distance offshore significantly influenced season, stage, and sex specific lobster catch density (Table 2). However, unlike bottom temperature and salinity that have direct influence on lobsters, distance offshore should be considered as an indirect variable (i.e. substitute or proxy) for unmeasured but more influential variables such as magnitude of both salinity and temperature variabilities or availability of prey or nesting opportunities. While these indirect variables are often not considered as key ecological niche constraints of lobsters, the feasibility of the correlative modeling approach can implicitly reflect the unmeasured

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ecological interactions and predict the abundance of lobster within the “observed” range of environmental conditions.

All four predictor variables (bottom temperature, bottom salinity, distance offshore, and longitude) were included in the final GAMs that explained 47-56% of the total deviance. Spring GAMs explained more deviance than fall GAMs, suggesting that the contribution from the predictor variables, especially the two more direct and dynamic temperature and salinity variables were less significant during fall (Table 2). Boudreau et al. (2015) suggest that the effects of bottom-up forcing in regulating lobster abundance are likely higher at thermal range boundaries. Bottom temperature in the inshore Gulf of Maine varied between 2.6-12 °C in spring and 5.7-14.3 °C in fall, where mean spring and fall bottom temperature were 5.5°C and 9.9 °C respectively. Several studies reported that the species preferred thermal range is in between 8-18 °C (Reynolds and Casterlin 1979; Crossin et al. 1998; ASMFC 2009; Tanaka and Chen 2016), which suggest that the spring bottom temperature was closer to the lobsters’ lower thermal range boundary and lobsters were likely experiencing stronger bottom-up temperature control during spring. While not to the same extent, reduced bottom salinity during spring also likely resulted in stronger bottom-up salinity control on lobster distribution as lobsters generally prefer higher salinity over lower salinity (A2; McLeese 1956; Mercaldo-Allen and Kropat 1994).

4.2 Assumptions and limitations of correlative species distribution models in predictive context

The GAMs exhibited higher performance for predicting occurrence (presence/absence) rather than density (Fig. 4). A plausible explanation is that modeled lobster catch density was likely a proxy for “habitat suitability” as opposed to actual lobster abundance, given that measured catch was affected by some niche dimensions and processes not explicitly
included in the predictors (e.g. territorial occupancy occurring at smaller scales). For example, increased variability in model accuracy at higher lobster density indicates that the actual lobster density differed under similar habitat suitability in different areas. Nonetheless, our GAMs matched lobster distribution and density well even when some variables likely influencing the species are not included. This suggests that the variables included in our GAMs were likely collinear to the influencing ones. Furthermore, the data were collected at random locations and factors not included in the best-fitting GAMs were sampled randomly, which allowed the model outputs to reflect average habitat conditions at given lobster abundance within the general area of sampling.

Our study objective was to describe the patterns, not mechanism, in the association between lobster abundance distribution and environmental data. The cross-validation results suggested that the GAMs were acceptable for its intended use. However, it is important to note that the quantified associations between lobster distribution and selected environmental data are the “indirect” consequences of relationships between the species and its niche dimensions (Kearney and Porter 2009). In correlative species distribution models, the true effects of bottom-up and top-down forcing on species’ behavioral mechanisms often remain unknown (Kearney and Porter 2009). Unlike process-based mechanistic models built with explicitly defined behavioral mechanisms and life history parameters, parameters in correlative models have no explicit ecological interpretation and processes are implicit (Dormann et al. 2012). The use of indirect variables often leads to limited model interpretability and transferability. While the use of correlative species distribution models presents new conservation and management platforms, its assumptions and limitations when used in predictive context should be considered carefully.
Predictions based on present realized niches assume stationarity in how environmental processes affect behavior of American lobster. For example, a time-constant linear catchability assumption was used to interpret the ME-NH survey data as the relationship between survey swept-area and lobster catch density (ASMFC 2015a). The assumption was assumed to be reasonable as trawls are an active fishing gear and its catchability does not entirely depend on the movement of lobster that have relatively stable and high survey catchability in the inshore Gulf of Maine (ASMFC 2015a). However, bottom trawl surveys might be subject to potential biases related to density and environment-dependent catchability (Thorson et al. 2013). For example, water temperature is speculated as a factor that can influence lobster catchability (ASMFC 2005), and the inshore ME-NH survey area may have been relatively saturated such that any observed changes in lobster abundance may have been influenced by the changes in offshore lobster abundance (ASMFC 2015a). There is little supporting empirical evidence around uncertainty for lobster catchability by active gears in the inshore Gulf of Maine, and exact mechanisms are unknown as water temperature affects lobster behavior in many ways (Aiken and Waddy 1986; Mercaldo-Allen and Kuropat 1994; Lawton and Lavalli 1995; Wahle et al. 2013). Future studies should incorporate the potential nonlinear catchability relationships (e.g. saturating or exponential) to explore the impact of density-dependent and time-varying active gear efficiency on the ME-NH survey indices.

4.3 Drivers of lobster distribution and abundance

Changes in bottom-up (e.g., climate and temperature) and/or top-down (e.g. fishing and predation) forcing are both important mechanisms regulating the ecology of lobster (Grabowski et al. 2009; Steneck and Wahle 2013; Boudreau et al. 2015). This study quantified partial bottom-up effects on changes in lobster distribution arising from bottom temperature and salinity. The inter-seasonal difference in the magnitude of bottom-up
temperature and salinity control likely resulted in the difference in precision of GAM outputs. Seasonal changes in the GAM performances can be used to estimate inter-seasonal variability in the magnitude of bottom-up temperature and salinity forcing on lobster distribution in the inshore Gulf of Maine. Spring GAMs showed higher skill as larger spatiotemporal discrepancies between observed and modeled lobster centroids were found during fall. A unidirectional northeastward shift was exhibited by all observed centroids except by fall adult lobsters, and spring GAMs were able to capture general trend in lobster distribution shift based on changes in bottom temperature and salinity. Larger spatiotemporal discrepancies between observed and modeled lobster centroids during fall suggest reduced bottom temperature and salinity controls on changes in lobster distribution, where the observed lobster centroids during fall initially shifted in the different direction from that expected on the basis of the bottom temperature and salinity controls (Fig. 7). It is likely that the bottom-up temperature and salinity control was stronger during spring when the bottom temperature and salinity were below the species’ preferred temperature and salinity ranges (Boudreau et al. 2015), and the bottom-up temperature and salinity control played a weaker role in regulating lobster distribution during fall when temperature and salinity were near optimum for lobsters.

This study showed spatiotemporal changes in lobster catch density in the inshore Gulf of Maine were not fully dictated by bottom-up temperature and salinity control but also driven by the number of top-down/bottom-up factors that were not considered in our modeling approach. For example, lobster in this region experienced several major ecological changes through the (1) demographic diffusion (e.g. intraspecific habitat competition), (2) decline in the predatory pressure from groundfish (e.g. Atlantic cod) and (3) an increase in fishing effort (e.g. number of traps) (Steneck 2006; McMahan et al. 2013; Steneck and Wahle 2013; Boudreau et al. 2015). Lobsters show strong agonistic behavior and seek more space as
they grow larger. Due to high population density, habitat competition among lobsters is considered intense and widespread in the inshore Gulf of Maine (Lawton and Lavalli 1995; Steneck 2006; Steneck and Wahle 2013). Larger lobsters avoid area of highest population densities (e.g. western inshore Gulf of Maine), which results in “demographic diffusion” (Steneck 2006). Furthermore, as temperatures warmer than 12 °C facilitate settlement, increasing bottom water temperature will likely open new nursery grounds and contributing to the increase of juvenile/legal-sized lobsters in the colder (i.e. northeastern) side of the study area (Maine DMR 2016). Several studies have shown that decline in both abundance and body size of inshore predators has effectively removed predatory constraints on lobster population growth, while increasing fishing efforts have exerted a positive influence on lobster abundance due to its significant trophic contribution to lobsters from trap bait (Saila et al. 2002; Steneck and Wahle 2013; Boudreau et al. 2015). Grabowski et al. (2009) indicated that a high proportion of the lobsters’ diet is now supplemented by herring bait used in the lobster trap, and substantial quantities of baits used in traps are luring and fueling lobster abundance in the inshore Gulf of Maine where fishing effort is extremely high. It is also noted that undersized lobsters benefit from a high-energy substance every time they are caught and released, further enhancing their growth (Saila et al. 2002; Grabowski et al. 2009). Furthermore, the center of lobster fishing efforts in the inshore Gulf of Maine has shifted northeast due to increased number of traps from zones A-D over the last 20 years (Dayton and Sun 2012; Maine DMR 2016). The increase in number of traps in zones A-D is likely due to lobster fishermen experiencing higher profit-per-trap in these zones where the fishery resource is not fully exploited, and also concerns among fisherman that maximum rates in zones E-G have already been achieved especially with regard to gear density in the near-shore fishing areas (Dayton and Sun 2012). It is likely that the amount of bait subsidies...
increased faster in the northeastern portion of study area (Zones A-D) during 2000-2014, resulting in spatial heterogeneity of the effect of fishing effort. Therefore, the general northeastward shift exhibited by the observed lobster centroids is likely driven by the composite effect of (1) seasonal difference in the magnitude of bottom-up temperature and salinity control (2) demographic diffusion due to increase in lobster abundance by the depletion of their predators and subsequent intraspecific habitat competition (3) and geographically uneven changes in fishing effort (i.e. number of traps) enhancing lobster population growth in eastern portions of the study area through bait subsidies.

4.4 Changes in lobster distribution and abundance

The characterization and modeling of climate-driven fish and shellfish response in the marine ecosystem has become the central research topic within the coupled climate–fisheries discipline (Hollowed et al. 2015). Many climate impact investigations to date have focused on the 30+ year time frame, but it has long been recognized that commercial fish stocks can also show abrupt response to climate variability (Lehodey et al. 2006), with some of the most notable examples of climate variability effects on commercial fish stocks found in crustaceans and pelagic species (Lehodey et al. 2006; Finney et al. 2010; Mills et al. 2013). For example, lobsters showed unexpectedly quick biogeographical response to the intense 2012 warming, which resulted in an economic crisis within the U.S. lobster fishery.

This study provided a regional projection of changes in lobster abundance distribution under two contrasting hypothetical climatology scenarios, which were separated by more than 2 °C in the average bottom temperature for both spring and fall (Fig. 4). The spring and fall bottom water temperature increased across the study area over the course of the time
series (Fig.1: Tanaka and Chen 2016). While the bottom temperature in this area is expected to increase over the foreseeable future, the magnitude of the temperature anomalies through 2060 (~1.5–3 °C) was observed during the 2012 heat wave within the study area (Herbert et al. 2012; Shackell et al. 2014). The biogeographical response of lobsters to the 2012 Gulf of Maine heat wave demonstrates how changes in water temperature can lead to significant changes in lobster abundance in the inshore Gulf of Maine (Mills et al. 2013). Given the highest temperature extracted by the ME-NH bottom trawl survey was 14.3 °C and well above the hypothetical warm climatology scenario, further increase in bottom water temperature may have a further positive influence on lobster abundance in this study area. However, the species’ climate-driven biogeographical response will more likely be determined by the interactions between ecological, environmental, and evolutionary factors (Kingsolver 2009). A rate of climate change that determines whether it has a positive or negative overall effect on the species may be mediated by the capacity for individuals/meta-populations to adapt to changes in local climate conditions (Angilletta 2009).

Our projections are based on quantified response of lobster to limited niche-requirements and subject to process-based uncertainties. However, our simple statistical climate-niche modelling framework can provide local lobster resource managers appreciable ‘first cut’ approximations of biogeographical responses of lobsters to major modes of climate variability in the inshore Gulf of Maine. The climatology scenario-based approach developed in this study can provide an initial triage to gauge the magnitude of impact of climate-driven thermal environment on the local lobster distribution. Such information could (1) assist stakeholders to make an educated guess about the consequences of abrupt climate variability events and, (2) reduce potential marine resource management uncertainty influenced by climate anomalies (e.g. warm vs cold years) (Sagarese et al. 2014; Shackell et al. 2014). Viewed at appropriate scales, the statistical climate-niche modeling
framework presented in this study offers a flexible climate risk management tool for the stakeholders.

4.5 Utility of climate-niche models within management context

Within the context of climate adaptation strategies, application of climate-niche models has emerged as a useful tool to quantify the magnitude of bottom-up forcing and project the likely consequences of climatic variability on a species’ distribution (Cheung et al. 2009; Hare et al. 2013; Tanaka and Chen 2016). The statistical climate-niche modeling approach developed in this study can be used to better understand the relationship between commercially important fish stocks and climatically-altered environment in the Gulf of Maine. The first signs of these changes might appear in coastal areas, where temperature gradients are more extreme.

The lobster fisheries in the inshore Gulf of Maine waters are managed through fixed management boundaries and the Maine lobster fishery is regulated through a system that limits the number of commercial licenses within each zone. Therefore, geographically uneven change in lobster catch (i.e. abundance increases in some zones and decreases in others) could lead to a potential management issue as lobster fishermen cannot easily reallocate their fishing effort between zones (Dayton and Sun 2012). While this study did not identify clear “winners” among the lobster management zones, the impact of climatic forcing on lobster catch was more pronounced in the mid-coast, suggesting that the mid-coast zones are more likely to experience an increase in lobster catch density under the environment characterized by the warm climatology scenario (Fig. 10). Further modeling effort focusing on long term climate change effect on lobster fisheries can facilitate evaluation of management policy issues such as whether to maintain the current zone structure based on historical equity, or
adjust the boundaries recognizing that there could be a significant long-term spatial change in
lobster biomass.

This study showed that the assumptions that poleward distribution shifts should be
expected in response to climate variability is not always expected at a regional scale. The
assumption of climate-driven unidirectional distribution shifts generally does not account for
complex species-environment tolerances and interactions (VanDerWal et al. 2013) as well as
geographically uneven bottom-up and top-down forcing (Steneck and Wahle 2013). While
our statistical climate-niche modelling approach did not consider variables other than bottom
temperature and salinity, the model outputs can be used to generate hypotheses about the role
of additional factors affecting the spatiotemporal changes in lobster catch density for future
investigation. It is also important to acknowledge that covariates in our best-fitting GAMs
were meant to capture the empirically-defined lobster-environment relationships within the
MENH-survey data and area, which may not necessary represent conditions outside of
space-time frame of the data. Therefore, the model outcomes in the other areas or sampling
seasons outside of MENH survey data should not be considered. A simpler model fitted only
with proximal (causal) factors will be able to provide more general but robust spatiotemporal
extrapolation and statistical foundation for mechanistic modeling approaches that can
simulate underlying processes necessary to address the uncertainty in climate-driven species
distribution shift (Franklin 2010; Hare et al. 2012).

While lobsters may initially respond to climatic variation by tracking optimum
temperature and changing distribution, changes in population dynamics, fishing pressure,
physiological adaptation, and predator-prey interactions may have a more significant impact
in the long-term (Cheung et al. 2008; Hale et al. 2011; Simpson et al. 2011; Shackell et al.
2014). This study should be viewed as a first order approximation of changes in lobster
abundance and subject to future refinement. The future efforts should focus on advancing
ensemble climate-niche modeling (Thuiller et al. 2016) or including the incorporation of the
mechanistic linkage between a species’ fitness and environment (Zurell et al. 2016) as well as
downscaling of ensemble global climate models (Kearney 2006; Wiens et al. 2009), which
would enable the evaluation of the physiological consequences of a species under more
robust climate change projections and trim the projections toward more probable outcomes.
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Table 1. Candidate variables used generalized additive modeling of American lobster biannual Maine/New Hampshire bottom trawl survey catches in the inshore Gulf of Maine during 2000-2014. Variance Inflation Factors (VIF) listed in the table are final VIFs, where NA indicates that the variable was omitted from generalized additive modeling efforts.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Description</th>
<th>VIF - Spring</th>
<th>VIF - Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude (°)</td>
<td>Measurement of latitude trawl was conducted (mid trawl point)</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Longitude (°)</td>
<td>Measurement of longitude trawl was conducted (mid trawl point)</td>
<td>1.3</td>
<td>1.1</td>
</tr>
<tr>
<td>Distance Offshore (m)</td>
<td>Measurement of distance between a trawl location and coastline</td>
<td>1.5</td>
<td>1.8</td>
</tr>
<tr>
<td>Depth (m)</td>
<td>Observed depth at a trawl location</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Bottom Temperature (°C)</td>
<td>Observed bottom temperature at a trawl location</td>
<td>1.5</td>
<td>1.3</td>
</tr>
<tr>
<td>Bottom Salinity (ppt)</td>
<td>Observed bottom salinity at a trawl location</td>
<td>1.5</td>
<td>1.6</td>
</tr>
</tbody>
</table>
Table 2. Best-fitting generalized additive models for season-, stage-, and sex specific American lobster catch densities in the Maine/New Hampshire bottom trawl survey with deviance explained by the model (Dev. Exp.) and Akaike Information Criteria (AIC). The terms in models are distance offshore (Do), bottom temperature (Te), bottom salinity (S) and longitude (Lo). edf; estimated degree of freedom.

<table>
<thead>
<tr>
<th>Season</th>
<th>Sex</th>
<th>Stage</th>
<th>Model</th>
<th>edf</th>
<th>Dev.Exp</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>Female</td>
<td>Adult</td>
<td>(s(Do) + s(Te) + s(S, Lo))</td>
<td>4.49, 4.21, 23.75</td>
<td>0.50</td>
<td>3370.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>(s(Do) + s(Te) + s(S, Lo))</td>
<td>4.68, 4.45, 24.88</td>
<td>0.56</td>
<td>3115.12</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>Adult</td>
<td>(s(Do) + s(Te) + s(S, Lo))</td>
<td>4.21, 4.28, 24.08</td>
<td>0.53</td>
<td>3643.39</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>(s(Do) + s(Te) + s(S, Lo))</td>
<td>4.53, 4.14, 25.24</td>
<td>0.56</td>
<td>3017.63</td>
</tr>
<tr>
<td>Fall</td>
<td>Female</td>
<td>Adult</td>
<td>(s(Do) + s(Te) + s(S, Lo))</td>
<td>4.92, 3.98, 19.87</td>
<td>0.47</td>
<td>2594.94</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>(s(Lo) + s(Do) + s(Te))</td>
<td>4.42, 4.33, 3.45</td>
<td>0.48</td>
<td>2334.61</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>Adult</td>
<td>(s(Do) + s(Te) + s(S, Lo))</td>
<td>4.47, 3.24, 19.58</td>
<td>0.47</td>
<td>2800.67</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>(s(Lo) + s(S) + s(Do) + s(Te))</td>
<td>4.46, 3.87, 5.01, 3.51</td>
<td>0.50</td>
<td>2334.91</td>
</tr>
</tbody>
</table>

Spring: \(n = 1312\), Fall: \(n = 830\)

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Table 3. Summary of regression analyses from 100 runs of cross-validations for the season, stage and sex specific lobster generalized additive modelling (GAM) effort.

<table>
<thead>
<tr>
<th>Season</th>
<th>Sex</th>
<th>Stage</th>
<th>Intercept</th>
<th>Slope</th>
<th>R-squared</th>
<th>GAM</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>95% CI</td>
<td>Mean</td>
<td>95% CI</td>
</tr>
<tr>
<td>Spring</td>
<td>Female</td>
<td>Adult</td>
<td>-0.10</td>
<td>(-0.42 , 0.15)</td>
<td>1.08</td>
<td>(0.85 , 1.38)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>0.04</td>
<td>(-0.16 , 0.26)</td>
<td>0.98</td>
<td>(0.70 , 1.20)</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>Adult</td>
<td>0.00</td>
<td>(-0.27 , 0.24)</td>
<td>1.00</td>
<td>(0.78 , 1.24)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>0.04</td>
<td>(-0.17 , 0.28)</td>
<td>0.96</td>
<td>(0.70 , 1.27)</td>
</tr>
<tr>
<td>Fall</td>
<td>Female</td>
<td>Adult</td>
<td>0.07</td>
<td>(-0.32 , 0.42)</td>
<td>0.96</td>
<td>(0.72 , 1.26)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>0.03</td>
<td>(-0.21 , 0.27)</td>
<td>0.98</td>
<td>(0.75 , 1.26)</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>Adult</td>
<td>0.07</td>
<td>(-0.32 , 0.42)</td>
<td>0.96</td>
<td>(0.72 , 1.26)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>0.03</td>
<td>(-0.21 , 0.27)</td>
<td>0.98</td>
<td>(0.75 , 1.26)</td>
</tr>
</tbody>
</table>
Figure 1. Top: Study area in the inshore Gulf of Maine covered by Maine/New Hampshire (ME-NH) inshore bottom trawl surveys with station locations during spring (blue, n = 1312) and fall (red, n = 830). The polygons A-G are lobster management zones. Bottom: Bottom temperature trends in the ME-NH bottom trawl survey for spring (0.12 °C year$^{-1}$, $R^2 = 0.34$, $p < 0.05$) and fall (0.08 °C year$^{-1}$, $R^2 = 0.24$, $p < 0.05$). The gray land lines represent major river systems.
Figure 2. Frequency histograms of season, stage and sex specific standardized lobster catch (per 792 m²) from Maine/New Hampshire bottom trawl survey (2000-2014). Lobster catch larger than 15 was truncated as a plus group to enhance readability.
Figure 3. Bottom temperature and salinity distributions in the study area for hypothetical cold and warm climatology scenarios from Finite Volume Community Ocean Model. The scenarios were based on five coldest and warmest springs and falls during 1982-2013. Temperatures averaged 9.7 °C (median 9.5 °C) during cold falls (1987, 1992-1993, 1998, 2007), 11.9 °C (median 11.5 °C) during warm falls (2002, 2010-2013), 5.1°C (median 5.5 °C) during cold springs and 7.3°C (median 7.7 °C) during warm springs (2000, 2010-2013). Salinity averaged 29.7 ppt (median 32.1 ppt) during cold falls, 29.8 ppt (median 32.1 ppt) during warm falls, 28.9 ppt (median 31.7 ppt) during cold springs and 29.1 ppt (median 31.5 ppt) during warm springs.
Figure 4. Observed versus predicted plots complemented by the graphical summary of regression analyses from 100 runs of cross-validations for the season, stage and sex specific lobster generalized additive modelling effort. The light gray lines represent 100 linear regression lines. The black line represents the mean of 100 linear regression lines. The dashed line represents the 1:1 line and an ideal model performance.
Figure 5. Plots describing the partial effect of significant univariate explanatory variables in the best-fitting generalized additive models for lobster catches in Maine/New Hampshire bottom trawl surveys with 95% confidence intervals for the fitted line. The y-axis represents the degree of smoothing with its range showing the relative importance of the explanatory variable. Tick marks on the x-axis denote observations.
Figure 6. Bivariate observed versus predicted plots illustrating the similarity between modeled and observed environmental data. Total 2,982 modeled-observed match-ups were used to assess Coastal Relief Model (CRM) and Finite-Volume Community Ocean Model (FVCOM) skills in depth, bottom salinity, and bottom temperature.
Figure 7. Changes in the centroids of predicted (red arrows) and observed (blue arrows) lobster catch densities in the Maine/New Hampshire bottom trawl survey (2000-2014). The observed and modeled shifts in centroids were aggregated to 3-time blocks for ease of visual interpretation (2000-2005, 2006-2010, and 2011-2014). The arrows represent the direction of change in the annual centroids. SP-Spring, FL-Fall, ADU-Adult, JUV-Juvenile, M-Male, F-Female.
Figure 8: Average predicted season-, stage-, and sex-specific lobster catch densities in inshore Gulf of Maine during 1982-2013. The color key indicates predicted number of lobsters per $792\,m^2$. SP-Spring, FL-Fall, ADU-Adult, JUV-Juvenile, M-Male, F-Female.
Figure 9. Predicted lobster catch densities under warm (1st & 2nd rows) and cold (3rd and 4th rows) climatology scenarios. The 5th and 6th row shows difference in catch density between warm and cold climatology scenarios derived through cell-by-cell map subtraction. The rainbow color key indicates predicted number of lobsters per 792 m², while the red-blue color key indicates changes in lobster catch per 792 m².
Figure 10. Difference (top row) and percentage difference (bottom row) in predicted season, stage, and sex specific lobster catch density per 792 m² between warm and cold climate scenarios in Maine Lobster Management Zones A–G.
A1. Partial generalized additive model (GAM) plots describing the significant interactive effect of bivariate bottom salinity-longitude variable in the best-fitting GAM.
A3. Standardized Taylor diagrams for modeled bottom temperature and salinity. The black square on the x-axis represents the standardized observation. The position of each dot represents the correlation (angular distance from the x-axis), root mean square error (radial distance from the standardized observation), and standard deviation (radial distance from the origin) of modeled data comparing with standardized observed data.