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Incorporating Environmental Variability Into Assessment and Management of American Lobster (Homarus americanus)

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INCORPORATING ENVIRONMENTAL VARIABILITY INTO ASSESSMENT AND MANAGEMENT OF AMERICAN LOBSTER (*HOMARUS AMERICANUS*)

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A Dissertation

Submitted in Partial Fulfillment of the

Requirements for the Degree of

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(in Ecology and Environmental Sciences)

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Dissertation Adviser: Dr. Yong Chen

An Abstract of the Dissertation Presented
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The American lobster (*Homarus americanus*) support one of the most valuable fisheries in the United States. A growing body of literature recognizes the importance of environmental variables in regulating this species’ biogeography and population dynamics. However, the current lobster stock assessment and management do not explicitly consider the impact of environmental variables such as water temperature and assumes spatiotemporal variabilities in the lobster environment as random background noises. Furthermore, while climate-induced changes in marine ecosystems continue to impact the productivity of lobster fisheries, studies that model lobster response to altered environmental conditions associated with climate change are lacking. As such, evaluating changes in lobster biogeography and population dynamics, as well as explicitly incorporating quantified lobster response to altered environmental conditions into the specie’s stock assessment will be critical for effective lobster fisheries management in a changing environment.

This dissertation research developed a modeling framework to assess and incorporate environmental variability in assessment and management of American lobster stocks in the Gulf of Maine, Georges Bank, and southern New England. This modeling framework consists of: 1) a qualitative bioclimate envelope model to quantify the spatiotemporal variability in availability of suitable lobster habitat; 2) a statistical climate-niche model to

quantify spatiotemporal variability of lobster distribution; and 3) a process-based population size-structured assessment model to incorporate the effect of environmental variable such as water temperature in lobster population dynamics. The developed modeling framework was used to predict climate-driven changes in lobster habitat suitability and distribution, as well as to determine whether incorporating the environmental effects can better inform historical recruitment especially for years when recruitment was very low or very high.

The first component of the framework provides a qualitative bioclimate envelope model to evaluate the spatiotemporal variability of suitable lobster habitat based on four environmental variables (bottom temperature, bottom salinity, depth, and bottom substrate type. The bioclimate envelope model was applied to lobsters in Long Island Sound and inshore Gulf of Maine waters. In the Long Island Sound, an examination of the temporal change in annual median habitat suitability values identified possible time blocks when habitat conditions were extremely poor and revealed a statistically significant decreasing trend in availability of suitable habitat for juveniles during spring from 1978 to 2012. In the Gulf of Maine, a statistically significant increasing trend in habitat suitability was observed for both sexes and stages (juvenile and adult) during the spring (April–June), but not during the fall (September–November).

The second component of the framework provides a statistical niche model to quantify the effects of environmental variables on lobster abundance and distribution. The statistical niche model was used to estimate spatiotemporal variation of lobster shell disease in Long Island Sound, and to quantify environmental effects on season, sex- and size-specific lobster distributions in the Gulf of Maine. In the Long Island Sound, the statistical niche model found that spatial distribution of shell disease prevalence was strongly influenced by the interactive latitude and longitude effects, which possibly indicates a geographic origin of shell disease. In the Gulf of Maine, the statistical niche model indicated that bottom

temperature and salinity impact on lobster distribution were more pronounced during spring, and predicted significantly higher lobster abundance under a warm climatology scenario.

The third component of the framework provides a size-structured population model that can incorporate the environmental effects to inform recruitment dynamics. The size-structured population model was applied to the Gulf of Maine/Georges Bank lobster stock, where climate-driven habitat suitability for lobster recruitments was used to inform the recruitment index. The performance of this assessment model is evaluated by comparing relevant assessment outputs such as recruitment, annual fishing mortality, and magnitude of retrospective biases. The assessment model with an environment-explicit recruitment function estimated higher recruitment and lower fishing mortality in the early 2000s and late 2010s. Retrospective patterns were also reduced when the environmentally-driven recruitment model was used.

This dissertation research is novel as it provides the comprehensive framework that can quantify impacts of environmental variability on lobster biogeography and population dynamics at high spatial and temporal scales. The modeling approaches developed in this study facilitate the need to invoke assumptions of environment at non-equilibrium and demonstrate the importance of considering environmental variability in the assessment and management of the lobster fisheries. This dissertation is dedicated to increase the breadth of knowledge about the dynamics of lobster populations and ecosystems and renders a novel first step towards sustainable management of this species given the expected changes in the Northwest Atlantic ecosystem.

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CHAPTER 1 - INTRODUCTION AND BACKGROUND

1.1 Status of American lobster fisheries in the United States

This doctoral dissertation at the University of Maine aims to enhance the adaptive capacity of management efforts for the American lobster (*Homarus americanus*) fishery in the United States. The American lobster supports one of the economically valuable fisheries in the United States with landings over $666 million in 2016 (ACCSP, 2017). The U.S. lobster fishery has experienced significant expansion in both effort and landings over the last 60 years (ASMFC, 2015a). Lobster landings were generally around 25 million pounds until the early 1950s, increasing to roughly 150 million pounds in 2012 (ASMFC, 2015b). Approximately 94 % of total U.S. landings came from the Gulf of Maine in 2012 (ASMFC, 2015b). The 2015 benchmark stock assessment showed record high stock abundance and recruitment in the Gulf of Maine and Georges Bank; however, the southern New England lobster stock was found to be in poor condition due to prolonged low abundance and persistently poor recruitment (ASMFC, 2009, 2015a). Changes in water temperature, salinity, and dissolved oxygen coupled with continued high fishing mortality had been identified as principal causes of low recruitment and poor stock condition (ASMFC, 2009, 2015a). Because of the specie's economic value, improving the accuracy and reliability of the specie's stock assessment is critical (ASMFC, 2015a); however, its complex life cycle, physiological characteristics that make its population dynamics likely to be influenced by environmental variability, and the spatial complexity of the fishery offer many challenges to scientists and managers (Factor, 1995; Butler et al., 2006; Wahle et al., 2013; ASMFC, 2015b) .

1.2 Ecology of juvenile and adult American lobster

American lobster is a large benthic crustacean widely distributed along the Atlantic coast of North America (Fig. 1.1). American lobster is an ectothermic species sensitive to changes in environmental conditions (Reynolds and Casterlin 1979). Water temperature has a significant impact on the physiology of juvenile and adult lobsters especially in non-optimal dissolved oxygen and salinity conditions (Mercaldo-Allen and Kuropat 1994), and plays an important role in regulating this species' behavior, movement, recruitment dynamics and growth (Factor 1995; Butler et al., 2006; Wahle et al., 2013). Lobsters have been found in waters temperatures ranging from 0-25 °C and with salinities ranging from 15-32 ppt, but prefer a thermal range between 12 °C and 18°C (Crossin et al. 1998) and salinities of 20-32 ppt (ASMFC, 2009; Harding, 1992; Jury et al., 1994). Increasing water temperature forces lobster to use more energy for respiration, leaving less energy for feeding, growth, immune response, and reproduction (Butler et al. 2006; Lawton and Lavalli 1995; Wahle et al. 2013). As water temperatures rise abosve 20.6 °C, lobster show various physiological stress responses such as increased respiration rates and depression of immunocompetence (Dove et al. 2005; Fogarty et al. 2007).

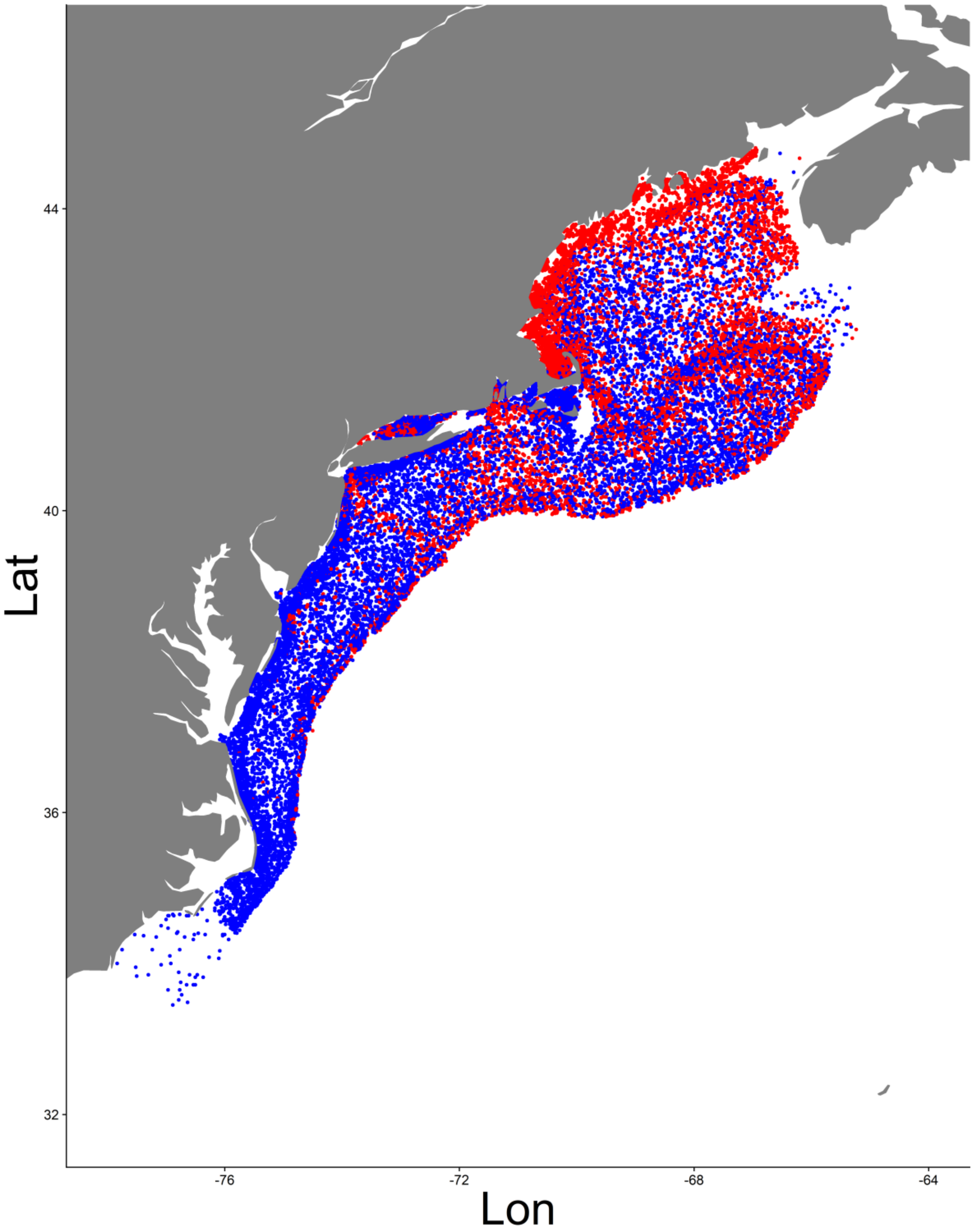

Figure 1-1: Known distribution of *Homarus americanus* within US waters based on fishery-independent bottom trawl surveys (1984-2016). Red dots represent where the species was caught.

American lobster can be found in waters ranging from the inter-tidal zone to depths of up to 700 m, but tend to be most abundant in coastal waters shallower than 50 m (Lawton and Lavalli 1995; Wahle et al. 2013). American lobster prefer rocky substrate, but can be found on other several substrate types including bottoms covered with mussel shells, eelgrass, or algae (Lawton and Lavalli 1995). American lobsters typically remain within a home range of about 5-15 km^2, but the spatial distribution of lobster is known to vary by sex, size, and season (Lawton and Lavalli 1995; Chang et al., 2010). Large adults are more likely to be found in deeper, cooler waters, but migrate to shallow coastal waters during spring to reproduce. Large mature lobsters in the Gulf of Maine move inshore and into estuaries in spring (Jury et al., 1994) and often remain close to shore in the summer, then move back offshore in late fall to escape winter turbulence (Chen et al., 2006). Small juvenile lobsters are more likely to be found inshore at depths of less than 10 meters and do not make seasonal migrations offshore in winter (Cooper et al., 1975). These differences in spatial distribution suggest size-specific responses to environmental variables such as bottom temperature and salinity (Jury et al., 1994; Lawton and Lavalli, 1995).

American lobster generally requires 5-8 years to reach minimum legal size of 82.5 mm CL and enter the fishery (ASMFC, 2015b, 2009). While many abiotic factors can influence the biological processes of lobster, temperature is speculated to be one of the most significant environmental factors influencing the embryonic and larval development, progression of the molt cycle, and subsequent recruitment to the fishery (Aiken and Waddy, 1986; ASMFC, 2015b; Wahle et al., 2013). Water temperature regulates recruitment of postlarvae to the benthic habitat by controlling their vertical movement (Annis 2005; Cobb and Wahle 1994). Seasonal variations of temperature regulates oocyte maturation and timing of spawning (Aiken and Waddy 1986). American lobster grow incrementally by molting, and the growth rate show a proportional relationship to temperature within a thermal range of 8-

25 °C (Waddy and Aiken 1995); however, region-specific stepwise growth models show clear differences in growth trajectories between thermally contrasting Gulf of Maine and southern New England regions (Bergeron 2011). In warmer southern New England, juvenile lobsters show higher growth rate compared to the cooler Gulf of Maine, but mature at a smaller size than Gulf of Maine lobster (Bergeron 2011). The U.S. lobster fishery largely depends on lobster newly recruited to the fishery, and environmental variability such as shift in thermal regime can have a significant impact on fishery recruitment and productivity.

1.3 Climate-driven changes in the Northwest Atlantic marine system

Shift in thermal regimes as a result of climate change is speculated to alter the lobster biogeography and population dynamics (Caputi et al. 2013). The water temperature in many parts of the Northwest Atlantic coastal waters has increased over the last 40 years (ASMFC, 2009; Mills et al., 2013; Nixon et al., 2004). The 31-year time series recorded at inshore (20 m depth) eastern Long Island Sound shows a significant warming trend of 0.04 degrees per year (ASMFC, 2009). A 49-year time series for sea surface temperature (SST) from Narragansett Bay and Rhode Island Sound show a larger warming trend at 0.05 °C per year (ASMFC, 2009). The number of days when the average bottom water temperature remains above 20 °C has increased substantially (ASMFC, 2009). These warming trends were also observed in SST recorded at Woods Hole, and bottom water temperatures recorded at Buzzards Bay and eastern Long Island Sound (ASMFC, 2009). The average SST in the Gulf of Maine increased at 0.03 °C per year since 1982 (Fernandez et al. 2015; Mills et al. 2013)(Fig. 1.2). The abrupt warming trend in the Gulf of Maine SST is particular evident as the rate of warming has intensified to 0.23 °C per year since 2004. The recent findings indicated that this abrupt warming trend in the Gulf of Maine is faster than 99% of the world oceans (Fernandez et al. 2015).

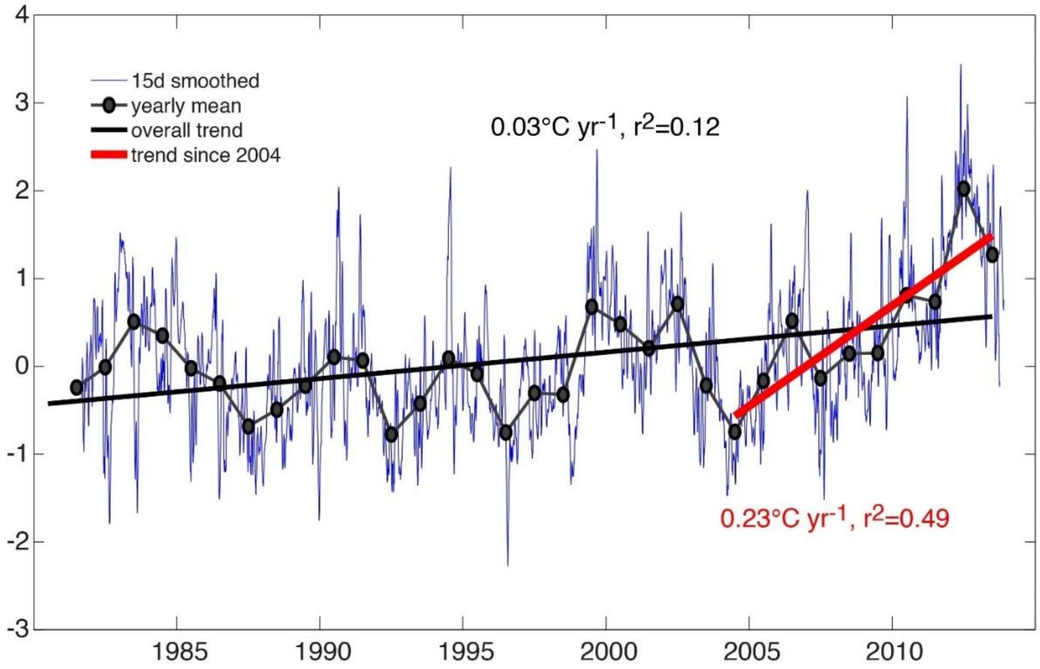

Figure 1-2: Trends in Gulf of Maine Sea Surface Temperature (SST) since 1982 (Mills et al., 2013).

Climate change has been identified as a likely primary stressor to the U.S. American lobster fisheries (Caputi et al. 2013; Dove et al. 2005; Mills et al. 2013). In 1999, a combination of above average water temperature, low levels of dissolved oxygen, the toxic impacts of ammonia and sulfides in western Long Island Sound led to a massive die-off of lobsters, which effectively eliminated the $100 million lobster industry in the region (Pearce and Balcom 2005). The 2012 Northwest Atlantic Heat Wave did not result in population collapse in the Gulf of Maine, but contributed to early inshore migration and molting of lobsters. This led to unusually high and early landings of lobsters in June and July, and overwhelmed the processing capacity, ultimately led to a 17 % price drop and a decline in total value of the U.S. lobster fishery (Mills et al. 2013). Furthermore, specific climatic factors have been tied to increasing epizootic shell disease (ESD) prevalence since the first outbreak was documented in 1996 in the southern New England (Cawthorn 2011; Gomez-Chiarri and Cobb 2012). The prevalence of ESD is positively correlated to the number of days with water temperature above 20 °C (ASMFC, 2009). The prevalence of ESD has been speculated to cause the collapse of lobster populations south of Cape Cod (Bell et al. 2012). As warming of the northwest Atlantic Ocean continues, the disease has spread northward and become a threat to the sustainability of the Gulf of Maine lobster fishery (Homerding et al. 2012). These findings indicate the impact of climate change on American lobster and reveal the importance of incorporating key environmental variables into the assessment and management of the species. Furthermore, the Northwest Atlantic marine ecosystems are especially susceptible to abrupt shifts in environment as the stability of these systems has been long compromised by biodiversity losses due to overfishing (Acheson 2006).

1.4 Dissertation structure

A growing body of literature is recognizing the impacts of environmental variability on many aspects of this species' population dynamics and ecological processes (e.g. Caputi et al., 2013; Chang et al., 2016; Tanaka and Chen, 2016). Furthermore, climate change has been identified as a catalyst for increased uncertainty in the traditional management paradigm of American lobster (ASMFC, 2015b; Pinsky et al., 2013; Tanaka and Chen, 2016). While climate-induced changes in marine ecosystems will continue to impact ecological processes and population dynamics of American lobster, studies that model lobster population dynamics and altered climatological conditions are lacking. Current management and assessment of American lobster stocks do not incorporate environmental variability (ASMFC, 2015b), while many coastal communities continue to be heavily dependent on the lobster fishery, leaving the coupled natural and human system vulnerable to environmental changes (Steneck et al., 2011). For sustainable management of the U.S. lobster fisheries, it is critical to (1) evaluate the relative importance and synergistic impacts of environmental variability, and (2) maximize the efficiency and accuracy of the existing stock assessment program.

To this end, my dissertation research presents a coupled qualitative-statistical-population modeling framework that incorporates environmental variability into the assessment and management of the U.S. lobster fishery. The following two research objectives outline the overall structure of my modeling framework; (1) develop the capacity for predicting spatiotemporal changes in the biogeography of American lobster, and (2) incorporate environmental variability into the current lobster assessment to better evaluate the status of U.S. lobster stocks in a changing environment. The modeling capacity developed in my dissertation research will improve our understanding of the impact of climate-driven environmental changes on the U.S. lobster fishery resources, and will be critical to effective management of this species given the inevitable changes in the northwest Atlantic marine ecosystems. The dissertation will consist of the following chapters;

Chapter 2 & 3 will present the qualitative-modeling component of this framework, which consists a bioclimate envelope model that can hindcast spatiotemporal variability of suitable American lobster habitat for more than 30 years (Tanaka and Chen, 2015, 2016). The bioclimate envelope model utilizes empirical Habitat Suitability Index (HSI) that is a numerical index that describes the capacity of a given habitat to support a given species, scaled from 0 (least suitable habitat) to 1 (most suitable habitat) based on key environmental variables (e.g., temperature; Franklin (2010). Tanaka and Chen (2015, 2016) coupled a qualitative HSI and a regional circulation model to quantify the spatiotemporal variability of bioclimate envelope (a species' habitat suitability with boundaries defined by physical and climatic variables) for American lobster in the Long Island Sound and coastal waters of Maine and New Hampshire from 1978 to 2013. Tanaka and Chen (2016) found a statistically significant increasing trend in the species' habitat suitability during the spring.

Chapter 4 & 5 will present the statistical-modeling component of this framework, which consists a generalized additive model (GAM) that can forecast changes in lobster abundance and distribution under different climatic scenarios. Studies suggest that the population dynamics of American lobster experience strong bottom-up (e.g., climate and temperature) controls (Boudreau et al. 2015). Using bottom temperature and salinity fields generated by a regional ocean circulation model, this statistical-modeling component of the framework provides a hindcasting and forecasting tool that can enhance adaptive management in changing ecosystems. Tanaka et al., (2017) applied two-stage GAM approach to predict spatial distribution of American lobster shell disease in Long Island Sound to improve the efficiency and precision of existing lobster shell disease monitoring programs. Tanaka et al., (In Review) developed a Tweedie-GAM to quantify such effects on season, sex- and size-specific distribution of American lobster in the inshore Gulf of Maine.

Chapter 6 will present the population-modeling component of this framework consist of a size-structured assessment model for the U.S. lobster stocks that incorporates the effect of key environmental variables (e.g., bottom water temperature) in lobster recruitment dynamics. The performance of this assessment model is evaluated by comparing relevant population and fishery parameters from the current assessment model that neglects environmental variability. This population-modeling component of the framework specifically focuses on determining if including environmental variability can improve precision and robustness of the existing lobster assessment model relative to changes in stock production and recruitment (Tanaka et al., In Prep).

To date, the management advice for the U.S. lobster fishery has been predominantly based on a “single species equilibrium” paradigm (ASMFC, 2015b). On the other hand, climate change and the resulting ecosystem shifts will continue to impact American lobster and the socioeconomic benefits provided by the lobster fishery. Overall, through the proposed modeling framework, my dissertation research aims to provide the necessary pillars of ecosystem-based approaches to the assessment and management of the U.S. lobster fishery. The research outcome can be used to facilitate and operationalize ecosystem-based fisheries assessment and management and provide a better understanding of how American lobster will respond to changing marine ecosystems. Developing a modeling framework to incorporate environmental variability into assessment and management of resilient fish stock and fisheries in a changing ecosystem will be critical for sustainable fisheries management.

CHAPTER 2 - SUITABLE HABITAT FOR LOBSTER IN LONG ISLAND SOUND

2.1 Abstract

A Habitat Suitability Index (HSI) model was developed using four environmental variables (bottom temperature, bottom salinity, depth, and bottom substrate type) and 28 years of spring and fall lobster surveys for evaluating the spatio-temporal variability of suitable lobster habitat in Long Island Sound (LIS). The suitability indices (SIs) calculated for the four environmental variables were combined to form a composite HSI using an arithmetic mean model (AMM) and geometric mean model (GMM). A cross-validation study was conducted to evaluate the predictive performance of the HSI models. Annual GIS maps of estimated HSI values were produced using kriging interpolation for adult and juveniles in spring and fall from 1978 to 2012. The overall spatial distribution of suitable habitat for lobster was mainly concentrated in the western-central part of LIS during spring (April-June), but showed clustering patterns throughout LIS during fall (September-October). An examination of the temporal change in annual median HSI values identified possible time blocks when habitat conditions were extremely poor and revealed a statistically significant decreasing trend in availability of suitable habitat for juveniles during spring from 1978 to 2012. Spatio-temporal variability in availability of suitable habitat may imply changes in carrying capacity of LIS for the American lobster.

2.2 Introduction

The American lobster (*Homarus americanus*) is a benthic crustacean distributed throughout coastal Northwest Atlantic waters, most commonly from Newfoundland, Canada through North Carolina, USA (Thunberg 2007). The species can be found in waters ranging from the intertidal zone to depths of up to 700 m, but tend to be most abundant in coastal waters shallower than 50 m (Lawton and Lavalli 1995; Meeren et al. 2010). Coarse rocky substrates (cobbles and boulders) are the most common habitat, but lobsters can also be found on several other substrates including mud, sand base with rock, shell, eelgrass, or algae (Lawton and Lavalli 1995).

The American lobster is an ectothermic species with a specific preferred thermal range for optimum physiological functionality (Reynolds and Casterlin 1979). Water temperature has a significant impact on the physiology of juvenile and adult lobsters especially in non-optimal dissolved oxygen and salinity conditions (Mercaldo-Allen and Kuropat 1994). Lobsters have been found in waters temperatures ranging from 0-25 °C and with salinities ranging from 15-32, but lobsters prefer a thermal range between 12 °C and 18 °C (Crossin et al. 1998) and salinities of 20-32 (ASMFC, 2009; Harding, 1992; Jury et al., 1994). Lobsters use more energy for respiration in warmer water conditions leaving less energy for feeding, growth, immune response, and reproduction (Qadri et al. 2007). As water temperatures rise above 20 °C, lobster show various physiological stress responses such as increased respiration rates and decrease in immunocompetence (Dove et al. 2005; Fogarty et al. 2007).

The spatial distribution of lobster is known to vary by sex, size, and season (Chang et al., 2010). American lobsters typically remain within a home range of about 5-15 km^2 (Lawton and Lavalli 1995). Large adults are more likely to be found in deeper, cooler waters, but migrate to shallow coastal waters seasonally to reproduce. Large mature lobsters in the Gulf of Maine (GOM) move inshore and into estuaries in spring (Watson III et al. 1999) and often remain close to shore in the summer, then move back offshore in late fall to escape winter turbulence (Chen et al., 2006). Small juvenile lobsters are more likely to be found inshore at depths of less than 10 meters and do not make seasonal migrations offshore in winter (Cooper et al., 1975). These differences in spatial distribution suggest size-specific responses to environmental variables such as bottom temperature and salinity (Jury et al., 1994; Lawton and Lavalli, 1995; Mercaldo-Allen and Kuropat, 1994).

The American lobster fishery in the northeastern U.S.A. has experienced significant expansion in both effort and landings over the last 60 years (ASMFC, 2015c). Lobster landings were generally around 25 million pounds until the early 1950s, increasing to roughly 150 million pounds in 2012 (ACCSP, 2017). Approximately 94% of total U.S. landings came from the GOM (ASMFC, 2015c). The 2009 benchmark stock assessment showed record high stock abundance and recruitment in the GOM and Georges Bank (GBK); however, the Southern New England (SNE) lobster stock was found to be in poor condition due to prolonged low abundance and persistently poor recruitment (ASMFC, 2009). Changes in water temperature, salinity, and dissolved oxygen coupled with continued high fishing mortality have been identified as principal causes of low recruitment and poor stock condition (ASMFC, 2009).

The lobster population in Long Island Sound (LIS) is a part of the SNE lobster stock. With ex-vessel values over $40 million, the LIS lobster fishery accounted for over 90% of the value of commercial landings in the region and remained the third largest lobster fishery in the United States until 1998 (Shields 2013). The LIS lobster stock has experienced a substantial decrease in abundance over the last 20 years due to deteriorating habitat and heavy exploitation (ASMFC, 2015b, 2009). Triggered by the major mortality event possibly caused by stress from warm temperatures, pollutants and decreasing oxygen concentrations, landings declined by 89% in 1999 with cumulative landings from 1999 - 2010 only reaching 0.42 million pounds (CTDEP, 2014). Epizootic shell disease has also become an increasing threat to the stability of the LIS lobster fishery (Bell et al., 2012; Castro and Somers, 2012). As climate change continues to alter Northwest Atlantic coastal ecosystems (Mills et al. 2013), the poorly adapted LIS lobster stock is under increasing stress caused by changes in suitable habitat availability. In order to illustrate the extent that habitat deterioration has influenced the American lobster's decline in LIS, it is necessary to quantify changes in suitable lobster habitat over time.

Habitat suitability index (HSI) models are widely utilized in wildlife management to describe the relations between species abundance and ecological variables (Chang et al., 2012; Franklin, 2010; Morrison et al., 2012). An empirical HSI model is derived from observations of the species in the field, and reflects the impacts of multiple habitat variables given the input data (e.g., abundance index or relative biomass) (Ahmadi-Nedushan et al., 2006; Chen et al., 2009, 2010; Dettki et al., 2003). HSI models standardize habitat suitability a target species on a scale from 0-1, representing "least suitable" to "most suitable" habitat qualities respectively (Schamberger et al. 1982). Oftentimes evaluation of habitat suitability is based on a limited number of habitat variables that influence organism abundance and distribution. Therefore, HSI implies relative habitat quality rather than actual population levels (Jian et al. 2013). HSI modeling results in combination with GIS provide an effective means of evaluating spatio-temporal variability in habitat conditions of a target species and produce habitat maps that can be used by managers and policymakers to make informed decisions (Bovee and Zuboy 1988; Terrell 1984). In fisheries management, the HSI model is often used to characterize fish habitat preference, availability, and quality (Morris and Ball 2006). For the lobster fishery, the HSI model can evaluate variability of suitable lobster habitat considering all key environmental variables for different life history stages.

The objective of this study is to develop an HSI model for evaluating the spatio-temporal variability of suitable habitats for LIS juvenile and adult lobsters in spring (April-June) and fall (September-October) from 1978 to 2012. The model is used to describe how the proportion and spatial trend of suitable habitat have changed over time. Finally, HSI model results were used to identify possible periods when lobster habitat conditions were extremely poor in LIS in order to determine whether habitat conditions have influenced the decline of lobsters in this region.

2.3 Materials and methods

2.3.1 Study area

The LIS is an estuary 181.9 km long and 33.8 km wide at its widest and covers approximately 3,419 km^2 in the area (Fig. 2.1). The depth of LIS varies from 4.6-60.4 m, averaging 22.6 m. Salinity ranges from 23 at the western end to 35 at the eastern end (Gottschall 2013).

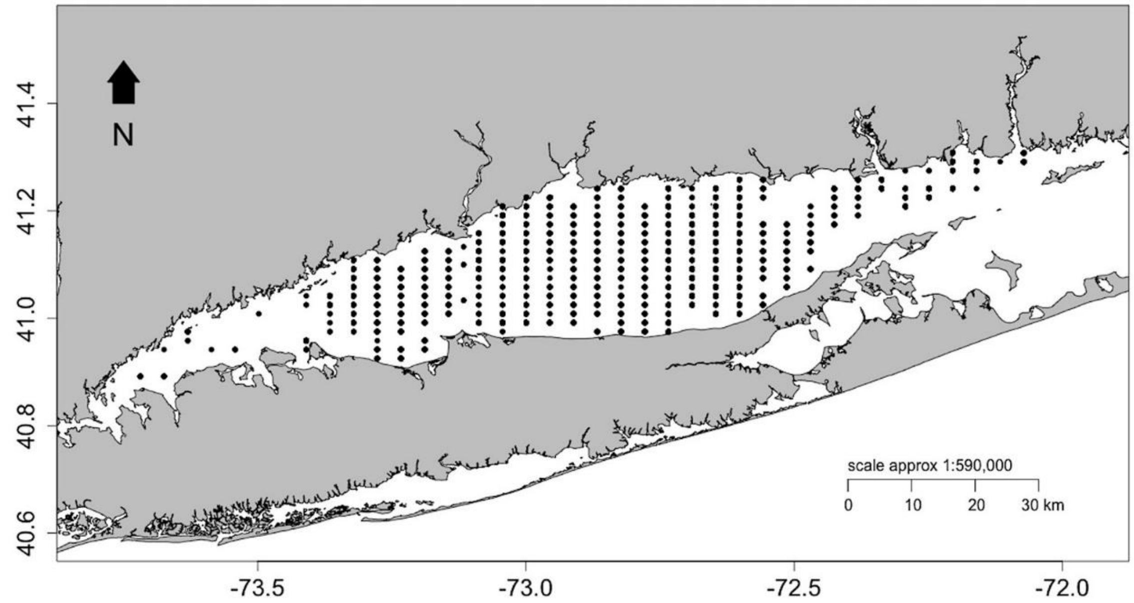

Figure 2-1: Map of Long Island Sound and sampling locations for the bottom trawl survey used in this study (1984-2012). Each sampling site is 1.85 x 3.7 km.

2.3.2 Fishery Data

Fisheries-independent data tend to provide a better representation of species distribution and abundance than fisheries-dependent data as they are normally collected using standardized gear and sampling methods with a clearly defined spatiotemporal scale (Tian et al., 2009). Bottom trawl survey data collected from LIS by the Connecticut Department of Energy and Environmental Protection (CTDEP) from 1984 to 2012 were used to develop the HSI models in this study (Fig. 2.2).

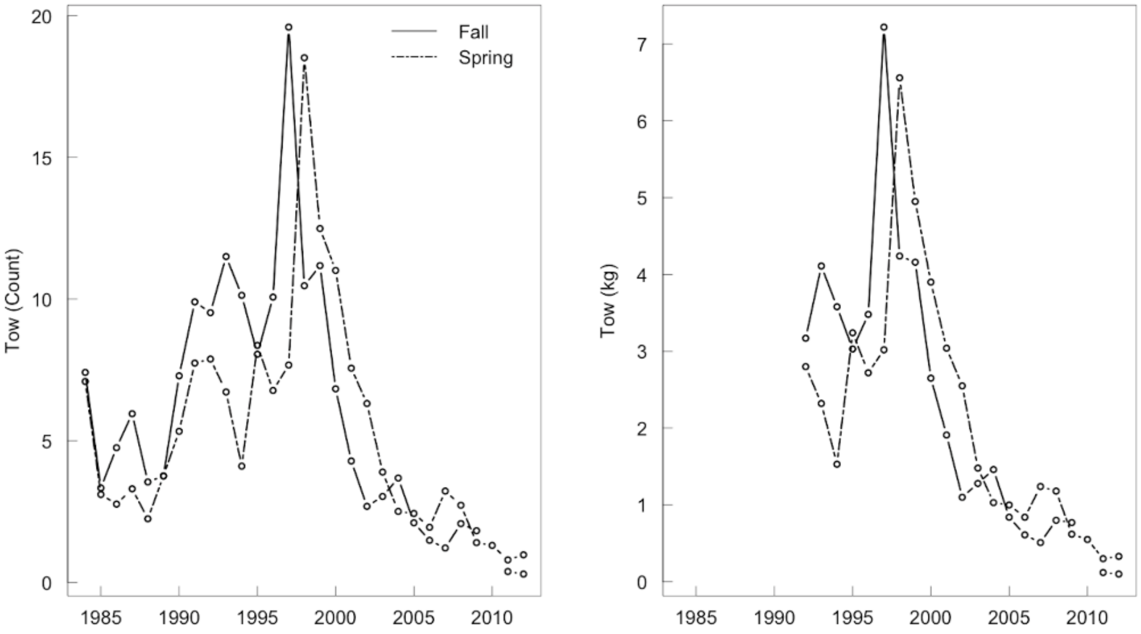

Figure 2-2: Geometric means of selected bottom trawl survey data for American lobster in Long Island Sound (1984 - 2012).

The LIS trawl survey is a semi-annual fishery-independent survey operated by the CTDEP. The survey encompasses an area from longitude 72^o 03' (New London, Connecticut) to longitude 73^o 39' (Greenwich, Connecticut), and includes both Connecticut and New York state waters from 5 to 46 m in depth over mud, sand and transitional (mud/sand) substrate types. The survey is based on a stratified-random sampling design, and the survey area is divided into 1.85 x 3.7 km sites assigned to 12 strata classified by depth (0-9 m, 9.1-18.2 m, 18.3-27.3 m, and 27.4 + m) and bottom substrate type.

The survey was conducted in the spring, from April through June, and during the fall, from September through October, with 40 sites sampled monthly for a total of 200 sites annually. It was done during daylight hours with a 14-m otter trawl with a 51 mm codend sampling gear to reduce the sampling bias associated with diurnal variability in catchability (Sissenwine and Bowman 1978). Target tow duration was 30 min at 3.5 knots to cover a mean distance of 3,241 m at each site (CTDEP, 2013). At each site, tow date, tow location (latitude and longitude), tow duration, environmental variables (e.g. bottom temperature, bottom salinity, and depth) and biological information of the catch (e.g. carapace length, weight, cull condition, and shell disease presence) were recorded (Gottschall 2013).

No information with regards to measure of area swept was available before 2012 (CTDEP, 2013, 2012). The size specifications for the trawl net and associated gear remain unchanged as far as since 1992 (Reid et al. 1999). The standardized survey design allows for temporal comparisons of lobster catch and distribution. In this study, a total of 5,353 tows that sampled 156,202 lobsters between fall 1984 and spring 2012 were analyzed. Lobster carapace length (CL) ranged between 16.1 and 112 mm and between 16 and 117 mm for the spring and fall surveys, respectively.

2.3.3 Environmental data

The Finite-Volume Community Ocean Model (FVCOM) was used to produce bottom temperature and bottom salinity estimates by depth, time, and location in LIS from 1978 to 2012. This regional coastal ocean circulation model was developed by UMASSD-WHOI joint efforts and is suited for forecasting and hindcasting the ecosystem dynamics for areas characterized by complex coastlines and inter-tidal zones (Chen et al., 2006). Additionally, data on distribution of surficial substrate (resolution: 0.00001 decimal degrees or 1.11m) throughout LIS was obtained from the U.S. Geological Survey Poppe and Seekins, 2000). Bottom substrate types in LIS include gravel (pebbles defined as 2.00-64.00 mm, cobbles defined as 64-256 mm, boulder defined as above 256 mm), gravel-sand (0.62-2.00 mm), sand-clay (0.001-0.004 mm), silt (0.004-0.062 mm) /sand, sand- clay/silt, sand-silt/clay, and sand/silt/clay Poppe and Seekins, 2000). Bathymetry data were obtained from the U.S. Coastal Relief Model - Northeast Atlantic by the NGDC-NOAA (NGDC, 1999).

2.3.4 Habitat Suitability Index (HSI) model

HSI is a numerical index based on suitability indices (SIs) that can quantify the habitat conditions from 0 (least suitable habitat) to 1 (most suitable habitat) for key habitat variables. The SIs can be calibrated from presence/absence data, presence only data, or using expert knowledge (Franklin 2010). Development of HSI model requires: 1) selection of habitat variables to include in the model, 2) development of SIs for each habitat variable, and 3) combination of those SIs via a mathematical equation to produce a composite HSI (Schamberger et al. 1982). Based on the literature on American lobster ecology and behavior (ASMFC, 2009; Chang et al., 2010), the following four environmental variables were chosen for their potential influence on American lobster habitat: bottom temperature (°C), bottom salinity, depth (m), and bottom substrate type.

2.3.5 Data analysis and processing

Bottom trawl survey data for American lobster in LIS from 1982 to 2012 were used in this study. To depict behavioral difference throughout lobster life stage, the dataset was divided into two size classes, juveniles (≤ 60 mm carapace length) and adults (> 60 mm carapace length), as 60 mm represents the minimum size at maturity defined by ASMFC (ASMFC, 2009). The spring and fall survey data were analyzed separately. This approach resulted in four groups of lobster (2 size classes × 2 seasons). Each lobster group was modeled independently.

The abundance index derived from LIS bottom trawl survey was considered a good indicator of lobster abundance in developing SIs and HSI models in this study (Chang et al., 2010). The nominal abundance index, calculated as a survey catch per unit of sampling effort (CPUE) at sampling station i, in season j, and year y, was calculated as;

$$CPUE_{ijy} = \left(\frac{Count_{ijy}}{TowDuration_{ijy}}\right) * 20 \qquad \textit{Eq. 2-1}$$

where Count is the total number of either adult or juvenile lobsters caught. Tow Duration is towing time duration measured in minutes, which usually varied from 20 to 30 minutes but was standardized to 20 minutes at each sampling station.

The relationship between lobster CPUE and habitat variables from 1984 to 2012 was identified. For each habitat variable, a suitability index (SI) based on species abundance (CPUE) was first developed. The SIs were estimated using a common approach known as the histogram method (Chen et al., 2010; Vinagre et al., 2006). The three continuous habitat variables (bottom temperature, bottom salinity and depth) were delineated into 10 classes using Fisher's natural breaks classification method (Bivand, 2013), while the categorical habitat variable bottom substrate was classified into seven substrate types (Poppe et al., 2000). For class k of habitat variable *i* in each lobster group, the average CPUE over all the sampling stations falling within the class was calculated as $CPUE_{i,k}$. The SI value of class *k* for habitat variable *i*, $SI_{i,k}$, was then calculated on a scale of 0.0 - 1.0 using the following formula (Chang et al., 2012)

$$SI_{i,k} = \frac{CPUE_{i,k} - CPUE_{i,min}}{CPUE_{i,max} - CPUE_{i,min}} \qquad \textit{Eq. 2-2}$$

where $CPUE_{i,min}$ and $CPUE_{i,max}$ are the minimum and maximum values of the average CPUEs of all the classes for habitat variable d. Thus, the SI for the most suitable class should have a value of 1, while the SI for the least suitable class should have a value of 0. An SI value was assigned to every class of the habitat variables in the form of a linear transfer function to qualitatively analyze the relationships between the habitat variable and lobster abundance. As a result, a total of sixteen SIs were calculated (i.e. four SIs corresponding to the four environmental variables for four lobster groups including two seasons and two stages).

For the purpose of sensitivity analysis, the SI curves were first drawn by mean function, and then re-drawn by trimmed mean function to remove any missing values and 5% of the highest and lowest scores (Crawley 2013; Tukey 1977). The suitable ranges were identified as area under both SI curves. The SI values derived from each habitat variable were then combined to form composite HSIs also scaled 0 - 1 and proportional to habitat quality. The following two empirical HSI models were developed in this study (Cooperrider et al. 1986) (Fig. 2.3);

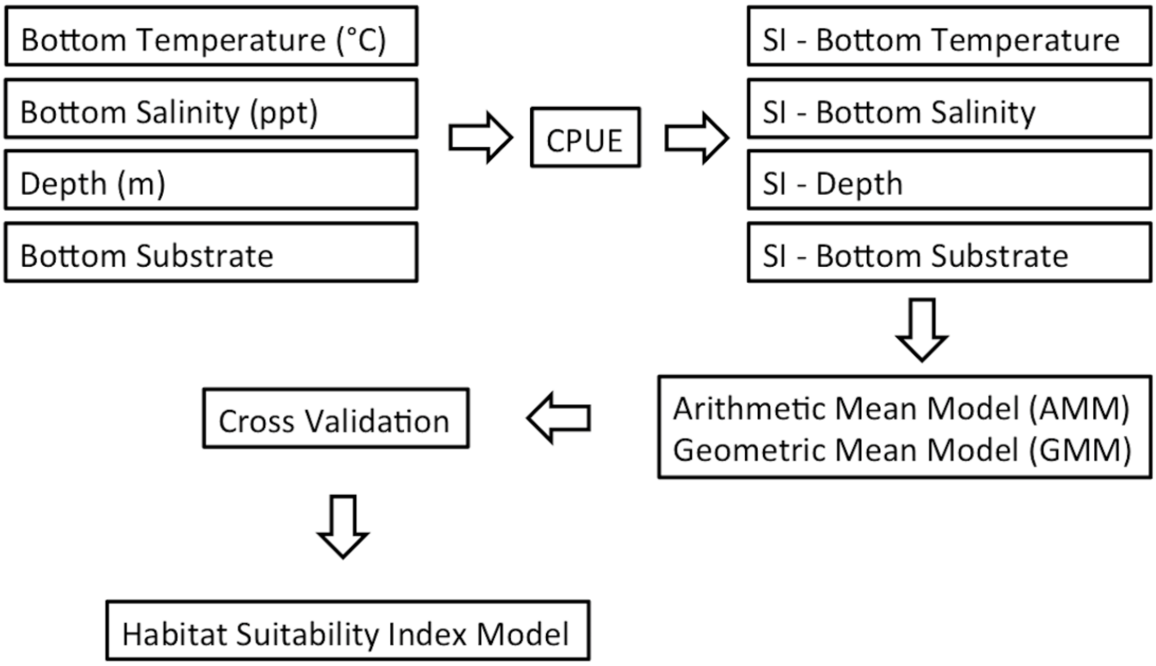

Figure 2-3: Flow chart of modeling procedure for estimating the habitat suitability index (HSI) of American lobster in Long Island Sound

Arithmetic Model (AMM):

$$HSI = \frac{\sum_{i=1}^{n} SI_i}{n} \qquad \text{Eq. 2-3}$$

Geometric Model (GMM):

$$HSI = \left[\prod_{i=1}^{n} SI_i\right]^{1/n} \qquad \text{Eq. 2-4}$$

where SI_i is a value of SI associated with the i^{th} habitat variable and n is the number of habitat variables included in the HSI model.

2.3.6 Model validation

A cross-validation approach was applied for evaluating the predictive performance of the HSI models. Models were developed independently for each lobster group (e.g. spring-adult, spring-juvenile, fall-adult and fall-juvenile) using a randomly selected subset of data representing 80% of all the data, referred to as training data. The remaining 20% of the data, referred to as testing data, were set aside for the cross-validation to assess the predicting ability of models developed from training data (Zuur et al. 2007). The predicted HSI values were compared against the observed HSI values. Linear regression analysis was performed on predicted versus observed HSI values, and the regression intercept, slope, r-squared value, and the Akaike information criterion (AIC) score were used to evaluate the predictive performance of the HSI model. An unbiased prediction should have an intercept parameter not significantly different from 0, a slope not significantly different from 1, and a high R^2. One hundred rounds of cross validation were conducted using random selection in each round to obtain 100 sets of regression parameters. This validation process was conducted for both AMM and GMM HSI models to determine which model performed better.

2.3.7 Mapping HSI values

The predicted HSI values were assigned to every FVCOM grid in LIS, and this procedure was conducted for every year that was available in the FVCOM dataset between 1978 and 2012. The ordinary Kriging method using the exponential semivariogram function was applied to create continuous HSI maps. The area with the highest class of HSI (e.g. 0.6 - 1.0) was designated as good habitat and correspondingly the area with the lowest HSI (e.g. 0 - 0.2) as poor habitat. The spatial distribution of median HSI values for a total of 34 years was mapped to observe the overall spatial trend in suitable habitat distribution for each group of lobsters. The median HSI maps were then compared to spatial trends in CPUE from the survey to verify the model. Finally, a median HSI value for each year was calculated with a fitted linear regression model to analyze whether there was any statistically significant trend in suitable habitat. The following R packages were used to implement this analysis; *sp* (E. Pebesma et al. 2014), *maptools* (Koh et al. 2014), *rgdal* (Bivand et al., 2014), *gstat* (E. J. Pebesma 2004), *maps* (Becker et al. 2014), and *fields* (Douglas et al. 2014).

2.4 Results

2.4.1 Suitability indices

The highest SI for bottom temperature differed by season and lobster size. The suitable thermal range (i.e., bottom temperature with SI > 0.8) for spring-adult lobsters was found to be 11.1-12.4 °C (Fig. 2.4A), while the suitable thermal range for spring-juvenile lobsters was 8.45-9.55 °C (Fig. 2.4B). In spring, the suitable depth range for adult and juvenile lobsters was similar at 31.9-37.2 m (Fig. 2.4C) and 31.9-37.3 m (Fig. 2.4D), respectively. The suitable salinity range for spring-adult lobsters was 21-23.7 (Fig. 2.4E), while the spring-juvenile lobsters had a suitable salinity range of 21.9-24.4 (Fig. 2.4F).

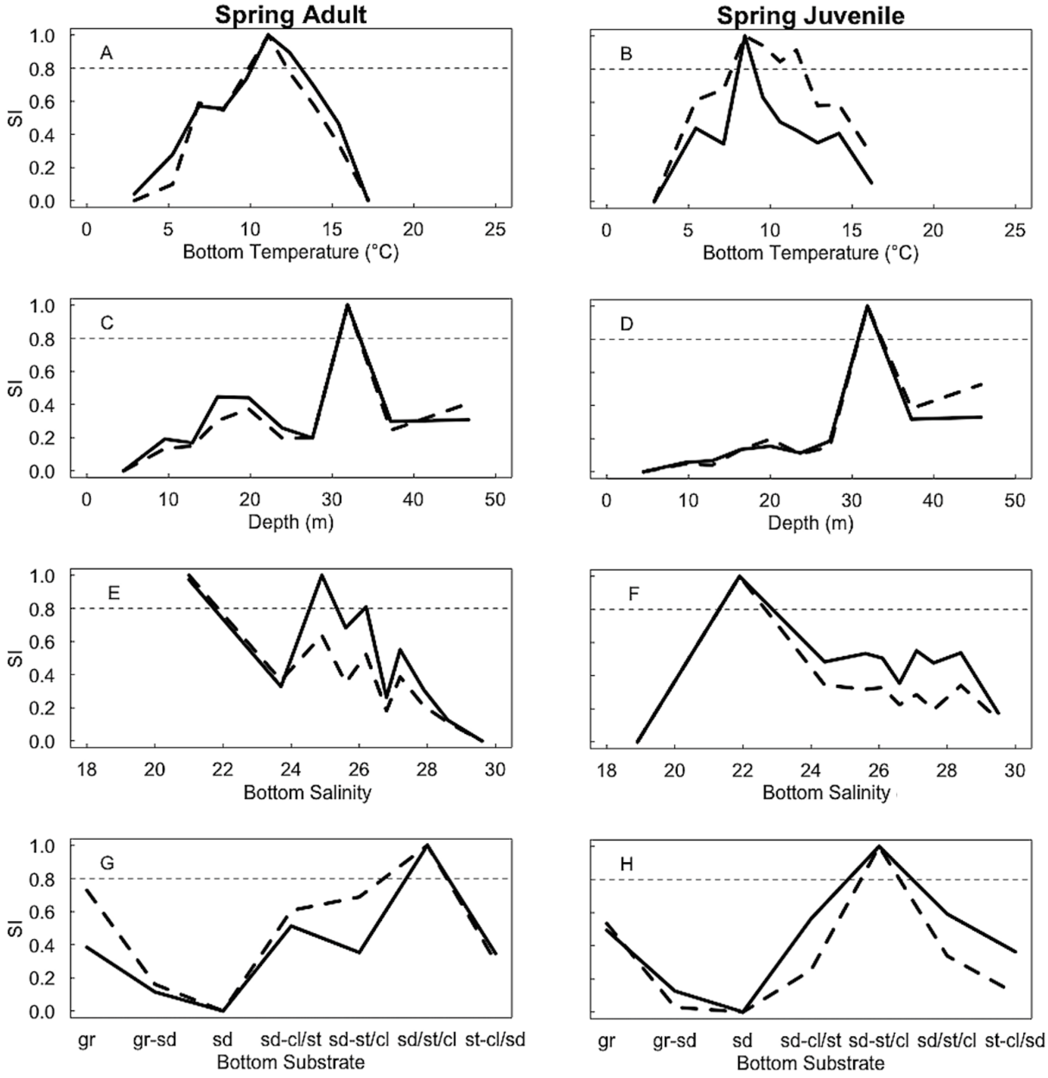

Figure 2-4: Suitability index (SI) graphs of bottom temperature, depth, bottom salinity and bottom substrate for juvenile and adult lobsters in spring. Both mean SI (solid line) and trimmed mean SI (dashed line) are plotted.

The suitable thermal range for fall-adults was 17.9-19.2 °C (Fig. 2.5A), and 15.6-16.6 °C as well as 17.4-18.4 °C for fall-juveniles (Fig. 2.5B). The suitable depth range for fall-adult lobsters was between 14.8-17.9 m and 31.9-37.3 m (Fig. 2.5C), while the suitable depth range for fall-juvenile lobsters was 15-17.9 m (Fig. 2.5D). Higher suitable salinity ranges were observed in fall for both size groups: 27.6-28.1 for adults (Fig. 2.5E) and 26.6-27.4 and 29.4-30.4 for juveniles (Fig. 2.5F).

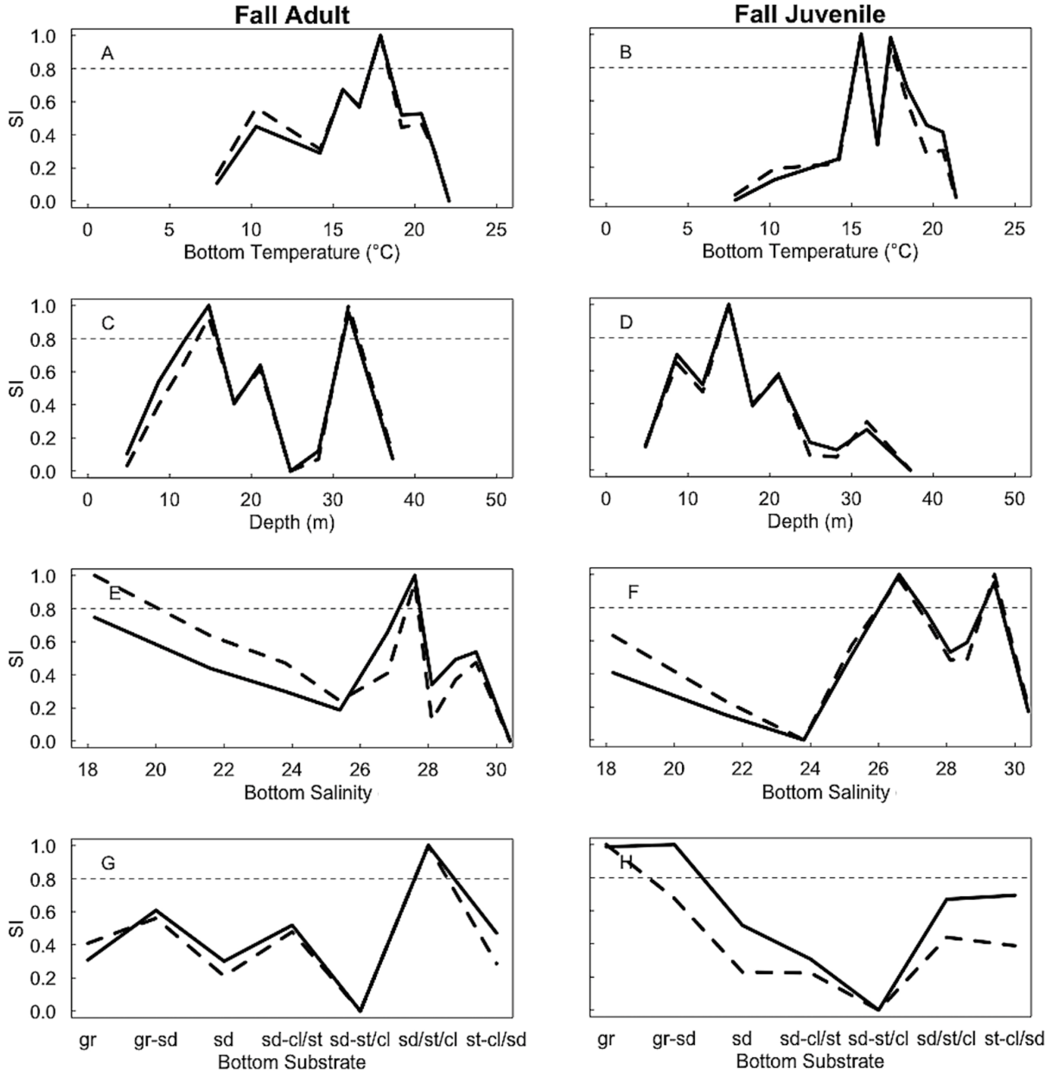

Figure 2-5: Suitability index (SI) graphs of bottom temperature, depth, bottom salinity and bottom substrate for juvenile and adult lobsters in fall. Both mean SI (solid line) and trimmed mean SI (dashed line) are plotted.

Sand/silt/clay was found to be the substrate type with the highest SI values for adult lobsters in both seasons (Fig. 2.4G & Fig. 2.5G). For the spring-juvenile group, sand-silt/clay showed the highest SI values, while gravel appears to be the most suitable substrate type for fall-juveniles (Fig. 2.4H & Fig. 2.5H).

2.4.2 Model validation and selection

The GMM model showed intercepts (α) closer to 0, while the AMM model showed slopes (β) closer to 1 in the regression between predicted and observed HSI values in cross validation. However, the AMM-HSI models showed higher R^2 values in all four groups. When compared with an ideal model without prediction bias (i.e., $\alpha = 0$, $\beta = 1$, and $R^2 = 1$), predictive performance for the spring-adult lobster was found to be the best ($\alpha = 0.145$, $\beta = 0.732$, $R^2 = 0.611$), and predictive performance for the spring-juvenile lobster was the poorest ($\alpha = 0.212$, $\beta = 0.595$, median $R^2 = 0.456$). The AMM model also predicted HSI values better, since AIC values were smaller in all modeling groups (Table 2.1). Finally, due to the nature of geometric mean algorithm, GMM-HSI model yielded a “0” HSI value when the model included an SI value of 0. Thus, the AMM can better distinguish subtle differences in areas of low SI values, and was determined to be more appropriate than the GMM for estimating lobster HSI in LIS.

Table 2-1: Summary of regression analyses from 100 runs of cross validations. The table shows model parameters for the linear regression between the predicted and observed habitat suitability index (HSI) values and Akaike information criterion (AIC) for the two HSI models - arithmetic mean model (AMM) and geometric mean model (GMM).

Model	Life Stage	Season	Intercept (α)				Slope (β)				R^2		AIC	
			Mean	Median	(95% C.I.)		Mean	Median	(95% C.I.)		Mean	Median	Mean	Median
AMM	Adult	Spring	0.145	0.143	0.042	0.266	0.732	0.732	0.529	0.922	0.594	0.611	-533	-539
	Juvenile	Spring	0.212	0.212	0.082	0.368	0.594	0.595	0.397	0.797	0.458	0.456	-357	-351
	Adult	Fall	0.161	0.168	0.007	0.271	0.682	0.676	0.493	0.949	0.495	0.492	-274	-273
	Juvenile	Fall	0.179	0.183	0.075	0.291	0.683	0.681	0.465	0.867	0.549	0.550	-199	-194
GMM	Adult	Spring	0.128	0.124	0.012	0.280	0.750	0.746	0.484	1.123	0.536	0.541	-306	-298
	Juvenile	Spring	0.136	0.136	0.036	0.284	0.680	0.669	0.343	1.194	0.441	0.448	-194	-181
	Adult	Fall	0.161	0.166	0.001	0.305	0.628	0.615	0.341	0.954	0.384	0.358	-94	-84
	Juvenile	Fall	0.152	0.162	0.052	0.247	0.679	0.673	0.470	0.910	0.507	0.512	-148	-144

2.4.3 Spatial and temporal variability in HSI values

Using the AMM-HSI model, the spatial distribution of estimated HSI values in LIS was mapped for each lobster group. A visual examination of HSI maps revealed that the suitable habitats (i.e. HSI > 0.6) are concentrated in western-central LIS in spring for both size groups of lobster, but showed clustering patterns throughout LIS in fall (Fig. 2.6). The season and size-specific distribution of suitable habitats predicted by the AMM-HSI model generally coincides with high and low lobster catch on the bottom trawl survey (Fig. 2.6).

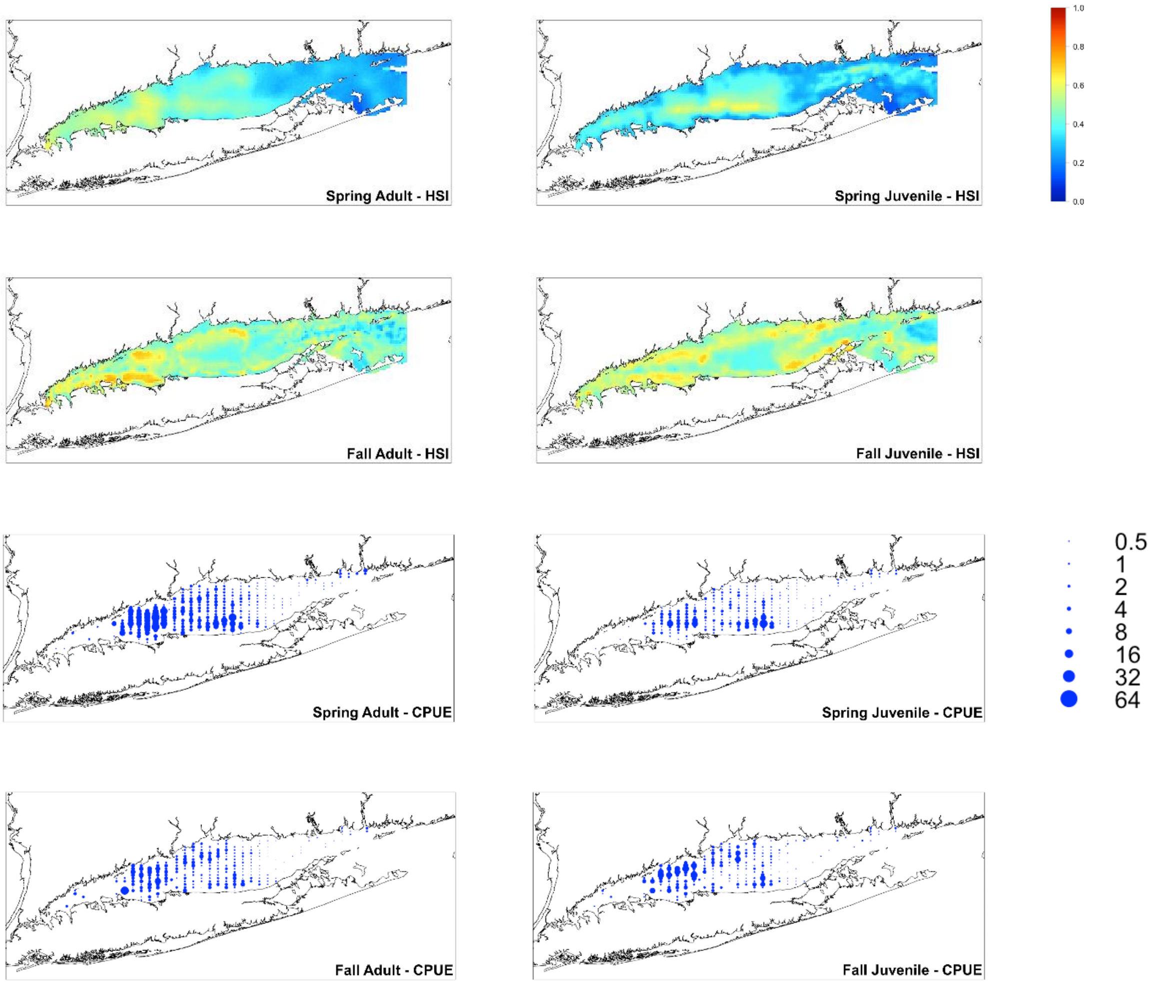

Figure 2-6: Comparison of spatial distribution of the median habitat suitability index (HSI) values over 1978-2012 (upper 4 panels), and average Catch Per Unit Effort (CPUE) from bottom trawl survey over 1984-2012 (lower 4 panels) in Long Island Sound.

Temporal variation in proportion of suitable habitat was observed in all four groups over the 34-year time series (Fig. 2.7). There were no statistically significant temporal trends in suitable habitat change for adult lobsters in spring (*p* = 0.317) and fall (*p* = 0.609). For juvenile lobsters, a significant declining trend in proportion of suitable habitat was found in spring (β = -0.003, *p* = 0.016), and a significant increasing trend was found in fall (β = 0. 002, *p* = 0.015) (Fig. 2.8).

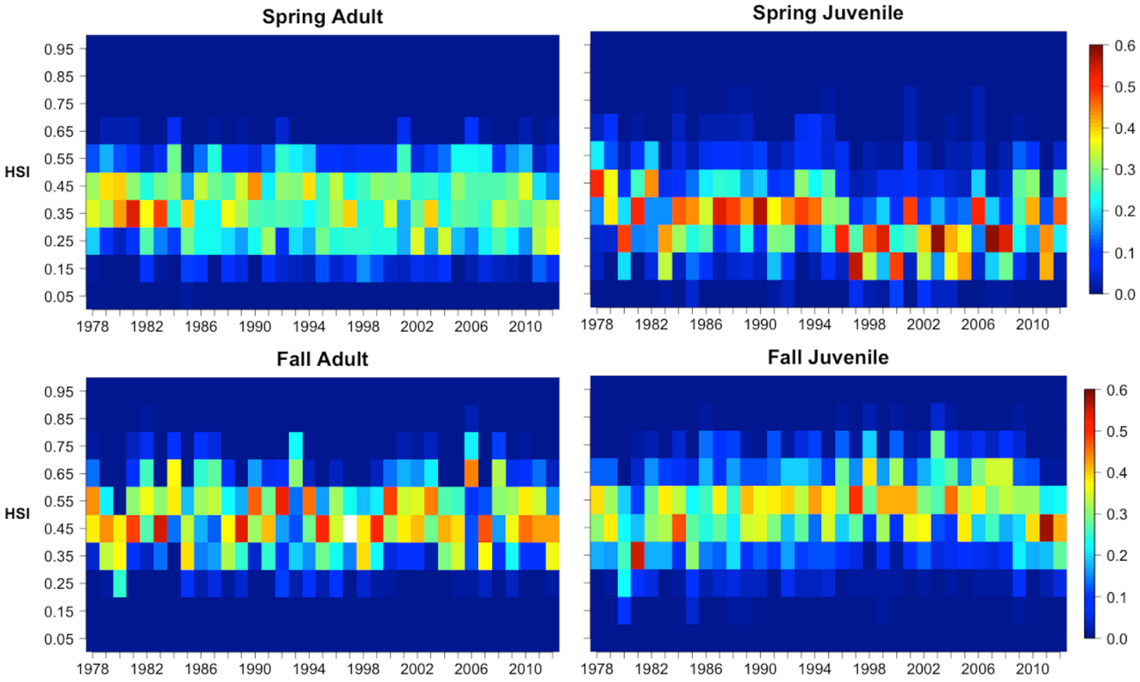

Figure 2-7: Temporal variation in habitat suitability index (HSI) values. The color scale bar on the right indicates the percent area for each year, with dark gray being the largest percent area and light gray is the lowest percent area.

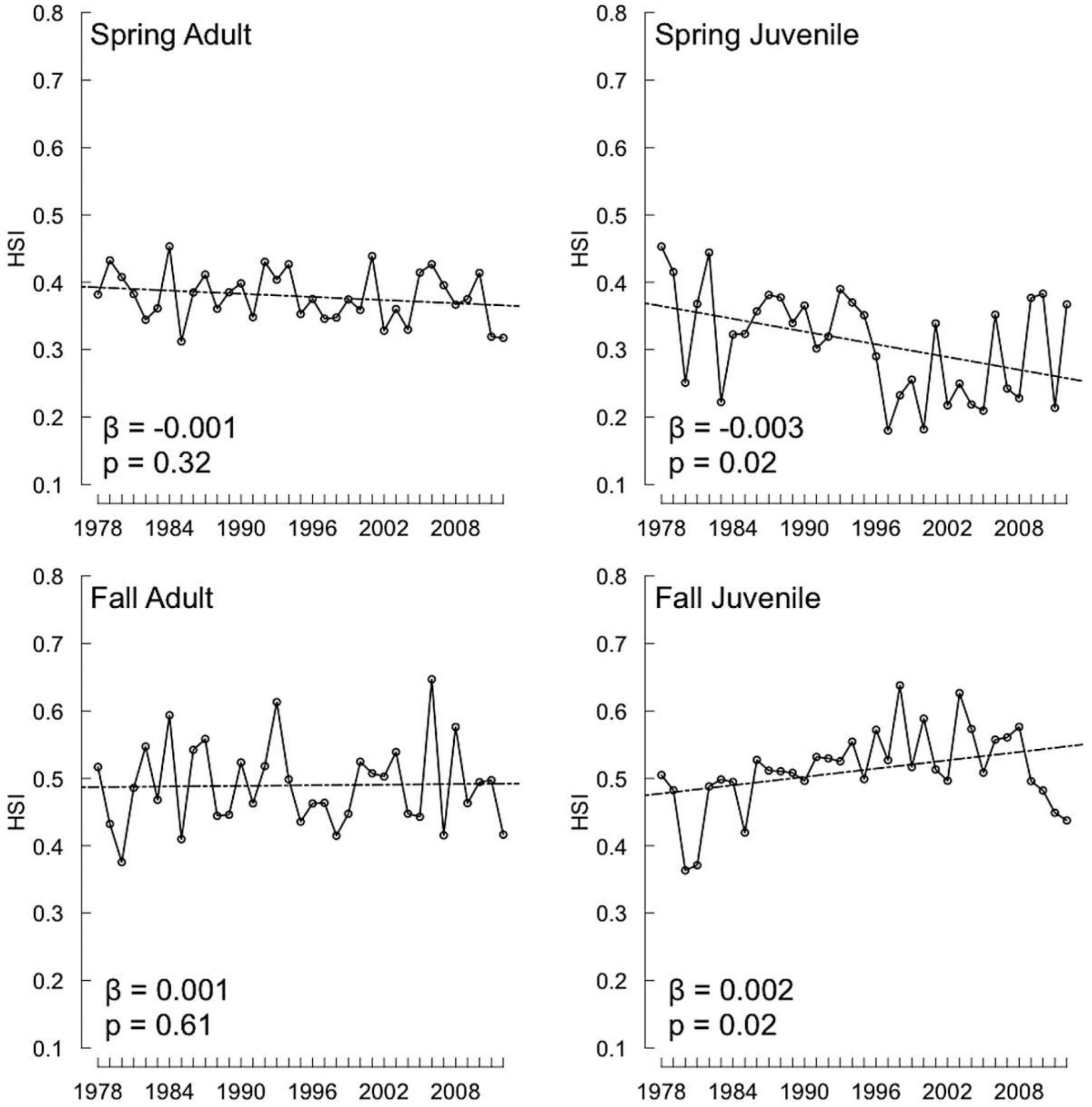

Figure 2-8:Median habitat suitability index (HSI) score for each year from 1978 to 2012 (solid line). The trend in each group was shown by the fitted linear regression model (dashed line).

In the HSI model, depth and substrate type are static components, while bottom temperature and bottom salinity are dynamic components. However, no relationships were observed between temporal trends in temperature, salinity and availability of suitable habitat (Fig. 2.9). Possible periods of extremely poor habitat conditions (such as a year when both seasons had an HSI value above 0.6 in less than 10% of the studied area) were identified. For adult lobsters, poor habitat conditions were observed in 1979-1980, 1983, 1985, 1988-1989, 1994-1999, 2004-2005, 2007, and 2009. For juvenile lobsters, poor habitat conditions occurred in 1980, 1983, 1985, 1997, 1999, 2002, 2004-2005, and 2011(Fig. 2.10).

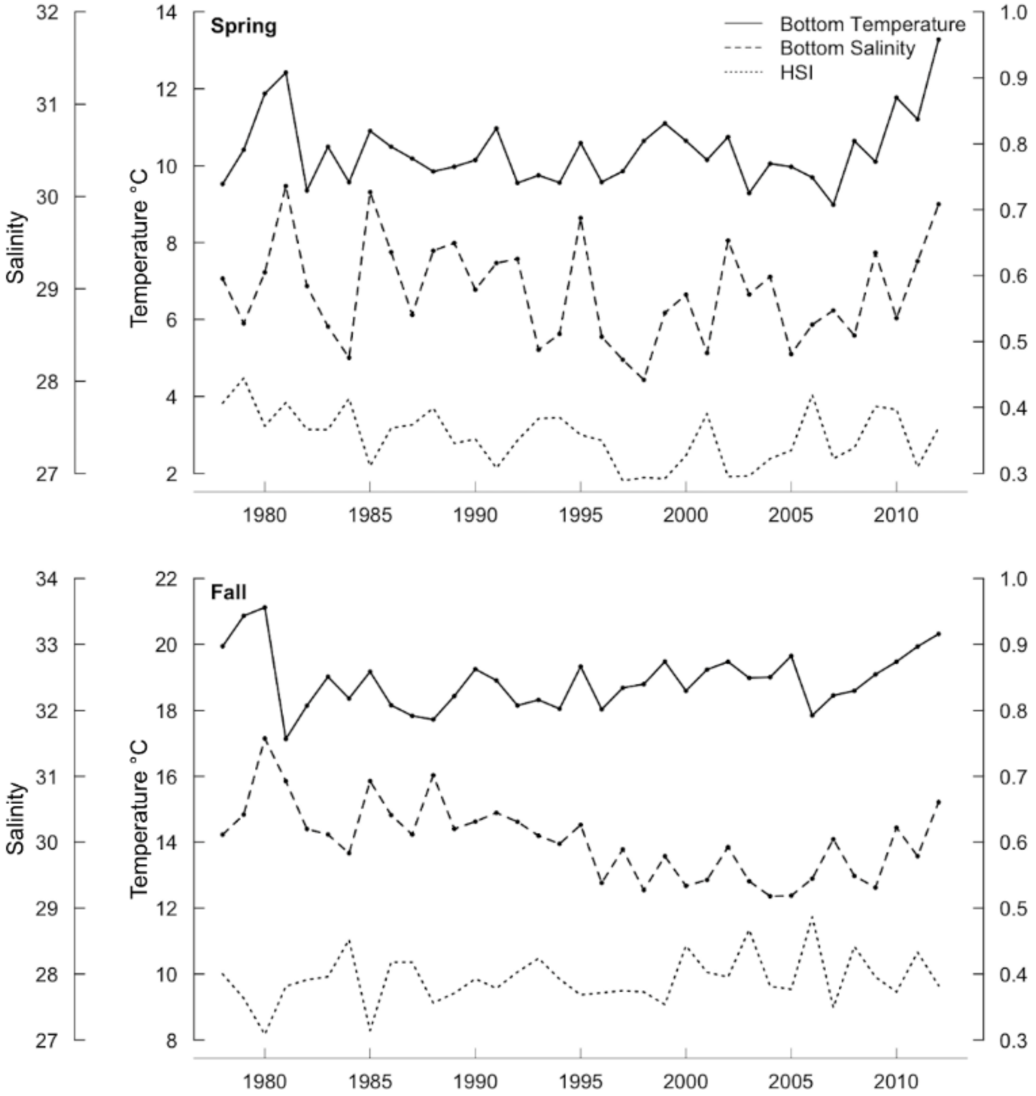

Figure 2-9: Mean bottom temperature, mean bottom salinity and mean Habitat Suitability Index (HSI) values for spring (April-June) and fall (September-October) from 1978 to 2012 in Long Island Sound. The mean HSI values represent both adult and juvenile lobsters.

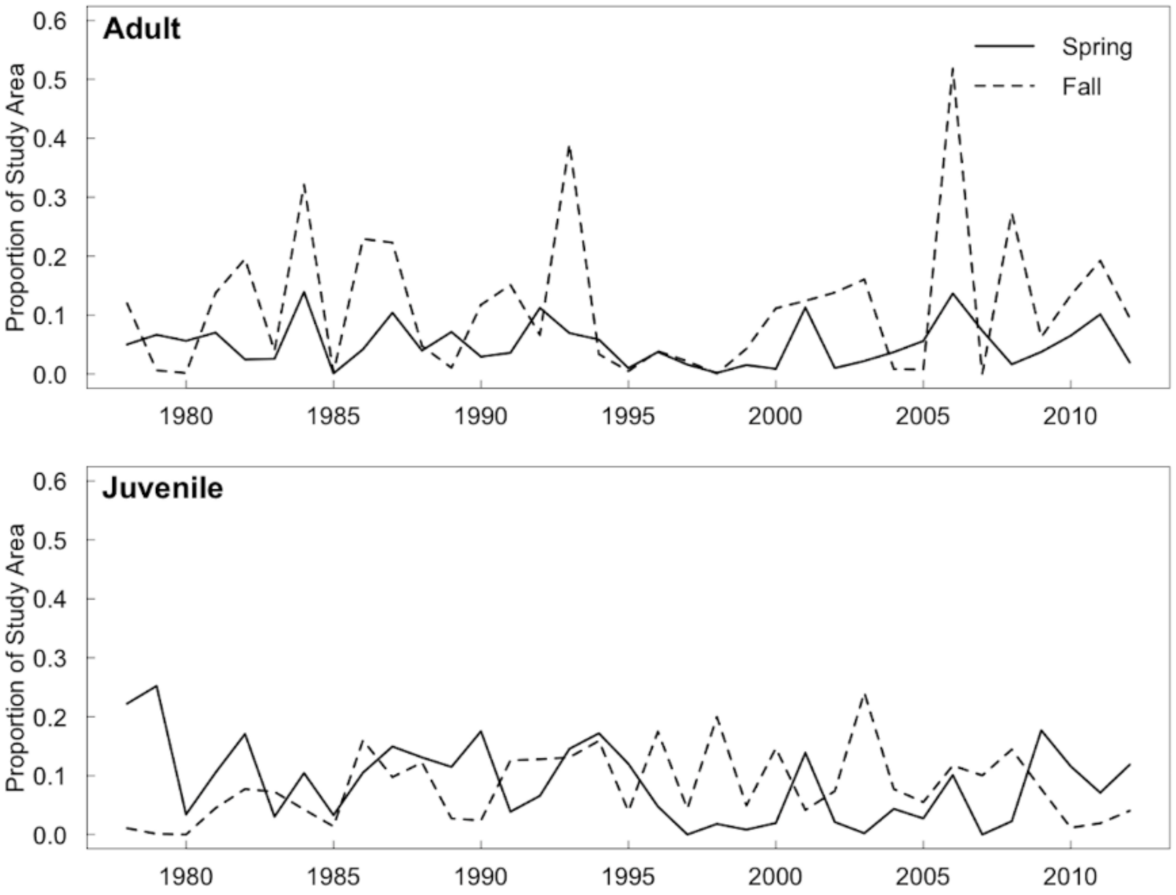

Figure 2-10: Change in proportion of suitable habitat with habitat suitability index (HSI) values above 0.6.

2.5 Discussion

This study developed a modeling approach to analyze the spatio-temporal variability of suitable habitat as a function of bottom temperature, bottom salinity, depth, and substrate for lobster in LIS.

The SI results for bottom temperature, bottom salinity and depth were consistent with past observations of preferential lobster habitat. The SI for bottom temperature identified different suitable thermal ranges between spring and fall for both size classes of lobsters. Adult lobsters showed a slightly higher and broader suitable thermal range compared to juveniles. In spring, the suitable thermal range for adults appeared to be considerably warmer than that of juveniles, while the difference in thermal range between the two size classes was less in fall. Overall, the suitable thermal range for lobsters in fall appears to be greater than that in spring. Water temperatures above the thermal threshold were avoided in both seasons (Crossin et al. 1998). Finally, two separate suitable thermal ranges were identified for juveniles in fall. These distinctive suitable thermal ranges between two seasons and two life history stages may be due to differences in behavioral thermoregulation as lobsters mature. It is generally accepted that lobster behavior is strongly regulated by water temperature (Crossin et al. 1998), and that the relationship between lobster density and bottom temperature is dome-shaped with a peak somewhere between 14-19 °C (Chang et al., 2010). In this study, the suitable thermal range (SI > 0.8) varied from 8.45-18.4 °C. This is consistent with a previous study in the GOM where lobster concentrations observed in areas with water temperature greater than 5 °C in spring and 8 °C in fall (Chang et al., 2010).

The SI for depth showed differences in suitable depth ranges across all groups. In fall, the suitable depth range for adult lobsters was between 14.8-17.9 m and 31.9-37.3 m, which might reflect a skewed spatial distribution by sex caused by migrations of ovigerous lobsters and sex-specific responses to different salinity ranges (ASMFC, 2009; Chang et al., 2010). Contrary to previous findings suggesting that small juveniles are more likely to remain inshore at depths of less than 10 meters (Cooper et al., 1975), both adult and juvenile lobsters in spring showed a deeper suitable depth range when compared to depths in fall. These findings agree with the in-situ observations of seasonal lobster movements in Bonavista Bay, Newfoundland (Ennis 1984) and suggest possible seasonal shift in suitable depth ranges for both life stages of lobster.

Model results indicate a suitable salinity range of 21-30.4, which is consistent with lobster salinity tolerance observed in past studies of 20-32 with occasional tolerance as low as 15 (ASMFC, 2009; Harding, 1992; Jury et al., 1994). The bottom salinity SI identified relatively constant suitable salinity ranges between adults and juveniles. However, higher suitable salinity ranges were observed in fall for both age groups, which may indicate different salinity tolerance of lobsters under different thermal regimes (Ennis and Fogarty, 1997; Jury et al., 1994; Mercaldo-Allen and Kuropat, 1994). There were two separate suitable salinity ranges identified for fall juveniles. This may indicate differential distribution of male and female juveniles in the fall. Since females are more sensitive to low salinities, males are generally more dominant in inshore waters and females dominant in offshore waters (Jury et al., 1994; Chang et al., 2010).

This study identified sand/silt/clay as the most suitable bottom substrate type for adult lobsters in both spring and fall. Sand-silt/clay was the substrate with the highest SI for juveniles in spring, but was the least suitable substrate for juveniles in fall. Gravel yielded the highest SI for fall juveniles. These findings are relatively inconsistent with the previously documented post-settled lobster habitat preferences of shelter-providing rocky and boulder substrates (Barshaw and Bryant-Rich 1988; Wahle and Steneck 1991). Several factors have been identified as the potential source of this inconsistency. First, the U.S.G.S. substrate data used in the HSI models did not differentiate boulder or cobble substrate, since the category of gravel includes grain size greater than 2 mm in diameter Poppe and Seekins, 2000). This over-generalization of bottom substrate type may have affected SI values derived from the histogram method and may have resulted in underrepresentation of bottom substrate as a habitat variable in the HSI model. Second, the CTDEP bottom trawl survey may have shown biased lobster density as rocky substrate could sometimes interrupt a tow (CTDEP, 2013) and boulder and rocky substrates are generally associated with lower trawl capture efficiency (Steneck and Wilson, 2001). While the lack of trawl survey data with certain key substrates cannot be quantified or ignored, these data-driven biases can be potentially corrected by the use of expert knowledge as quantitative assessment criteria (Store and Kangas, 2001;

Vincenzi et al., 2007). Furthermore, while shelter-providing rocky/cobble/boulder substrates are generally considered to be preferred habitat by both newly-settled and older lobsters (Cooper and Uzmann, 1980; Steneck, 2006), preference for specific substrates diminishes as lobsters grow out of the early benthic phase (Wahle and Steneck 1991). This inconsistency in substrate preference between lobster life stages was also observed in the Gulf of Maine, where substrate type affected the probability of juveniles, but not adult, presence (Chang et al., 2010). Similarly, mud base (particle size < 0.06 mm) with burrows is known to be a preferred substrate by adult lobsters in inshore and in estuaries where lobsters can create shelters by excavating soft substrate (Lawton and Lavalli 1995). This literature supports the result that sand/silt/clay is the most suitable substrate type for adults in both spring and fall. Overall, despite insufficient resolution of the substrate data and trawl survey bias, agreement of the seasonal size-specific suitable lobster habitat predictions by the HSI model and patterns in survey catch suggest the robustness of modeling results.

While cross-validation of the AMM-HSI model suggested reasonable predictive performance, the SIs derived from the spline smooth regression method can be used to deal with possible non-linear relationships between covariate and response variables in a semi-parametric manner for further analysis (Chang et al., 2012; Maunder and Punt, 2004).

The type and number of habitat variables to be inacluded in the calibration of an HSI model is critical to the successful identification of suitable habitats (Tian et al. 2009). Distribution and abundance of lobster can be influenced by many other environmental variables such as availability of prey, presence of predators, thermal fronts, latitude and longitude, time of the day, light levels, and dissolved oxygen concentration (Wahle and Steneck 1992; Mercaldo-Allen and Kuropat 1994; Crossin et al., 1998; Chang et al., 2010). Consequently, more habitat variables may need to be incorporated and evaluated in future analyses. While these variables are likely to be correlated, application of dimension reduction technique such as principal component analysis can be incorporated to develop more comprehensive HSI model (Daskalov 1999).

Furthermore, while equal weight was assigned to each habitat variable for the empirical HSI model in this study (Vayghan et al. 2013), the relative importance of different habitat variables in regulating lobster spatio-temporal distribution is likely to be variable, which could significantly influence the predictive performance of HSI models (Gong et al. 2012). For the existing HSI models to better predict spatio-temporal distribution of suitable lobster habitat, the impact of differential weighing of habitat variables should be carefully analyzed based on relative contribution to the spatial distribution of lobsters (Chang et al., 2010). The selection and weighting of habitat variables in an empirical HSI model should be further studied to improve the model's hindcasting or forecasting ability. This will be important in promoting the use of HSI models in fishery management and could be particularly useful when considering shifts in the marine environment due to climate change.

Most stock assessments neglect to incorporate habitat information into the assessment models, but habitat data are important to many aspects of the stock assessment process. The SI and HSI modeling results for juvenile lobsters have implications for lobster recruitment, while results for adult lobsters have implications for spawning stock biomass. For example, periods of low habitat suitability, such as years when both seasons had an HSI value above 0.6 in less than 10% of the studied area (Fig 2.10), partially overlap with periods of estimated low recruitment abundance (2003 - 2007) and low spawning stock abundance (2004 - 2007) from the 2009 benchmark assessment (ASMFC, 2009). Further analysis may (1) reveal statistically significant correlations between habitat suitability and recruitment or spawning stock abundance, and (2) link availability of suitable habitat to carrying capacity of LIS for American lobsters. Also, change in habitat availability could potentially be related to the recent collapse of LIS lobster stock.

Application of HSI models can improve lobster stock assessment by allowing us to (1) hindcast and forecast periods of distinct lobster productivity and recruitment dynamics in LIS, and (2) define and compare different modeling time periods with respect to these processes. Traditional stock assessment models focus on the context of commercial fishing, where natural mortality is relegated to a single, typically time-invariant parameter that is often not related to lobster ecology. The recent management shift towards Ecosystem-Based Fisheries Management (EBFM) requires scientists and managers to develop useful, quantitative measures to illustrate the history of stock fluctuations in an ecological context. Incorporating habitat availability modeling into stock assessments will aid in effective implementation of ecosystem-based management.

CHAPTER 3 - THE BIOCLIMATE ENVELOPE OF AMERICAN LOBSTER

3.1 Abstract

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

3.2 Introduction

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

Due to its ectothermic nature, water temperature has a significant impact on *H. americanus* life history, especially when coupled with non-optimal dissolved oxygen and salinity conditions (Mercaldo-Allen and Kuropat, 1994). *H. americanus* can tolerate a wide range of temperatures and salinity, from 0 – 25 °C and 15 – 32 ppt, respectively, but the species exhibits affinity to a specific thermal (8 – 18 °C) and salinity (0 – 32 ppt) range to maximize its physiological functionality (Reynolds and Casterlin, 1979; Crossin et al., 1998; ASMFC, 2009). Adult *H. americanus* exhibit long distance seasonal movements (>100 km) between shallow and deep waters to pursue optimal water temperature for growth and egg development (Cobb and Wahle, 1994). Water temperature above 20.6 °C creates a stressful environment for *H. americanus* as the species is forced to spend more energy for respiration and less energy for growth and feeding (McLeese, 1958; Dove et al., 2005; Fogarty et al., 2007). Adult lobsters respond to even small changes in temperature (Crossin et al., 1998; Jury and Watson, 2000) both behaviorally (e.g., movement) and physiologically (e.g., changes in cardiac cycle) (McLeese and Wilder, 1958; Worden et al., 2006).

The favorable habitat and spatial distribution of *H. americanus* vary with life stage and season (MacKenzie and Moring, 1985; Chang et al., 2010). Small juveniles typically remain inshore and within a home range of about 5 – 15 km, and do not exhibit large-scale seasonal movements (Cooper et al., 1975). Mature individuals exhibit an average annual range of 32 km (Campbell, 1986), and have a higher tolerance to deeper and cooler waters. In the GOM, adults migrate inshore and into estuaries during spring, and then migrate back offshore late fall (Watson et al., 1999; Chen et al., 2006a). Differences in the spatial distribution of *H. americanus* with size composition suggest stage and season-specific responses to climate-driven variables such as bottom temperature and salinity (Jury et al., 1994; Factor, 1995).

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

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

In this study, an empirical bioclimate envelope model was developed based on season, sex and life history stage specific Habitat Suitability Indices (HSI) to evaluate spatiotemporal variability of a bioclimate envelope for *H. americanus* in the coastal waters of Maine and New Hampshire during spring (April – June) and fall (September – November) from 1978 to 2013. The HSI is an ecological index developed by the U.S. Fish and Wildlife Service (FWS) to facilitate habitat evaluation procedures (FWS, 1981). An HSI quantifies habitat suitability for a given species on a scale of 0 – 1 to represent "least suitable" to "most suitable" habitats, respectively (Franklin, 2010). It is a useful tool to describe the relationship between relative species abundance and ecological variables (Vinagre et al., 2006; Tian et al., 2009). The construction of an HSI is a repeatable technique, and the utility lies in enabling managers to predict where a species is likely to occur within a distributional range. In fisheries management, HSI is often combined with a geographic information system (GIS) to analyze the spatiotemporal variability in fish habitat preference, availability, and quality to make informed decisions (Terrell, 1984; Bovee and Zuboy, 1988; Morris and Ball, 2006; Chang et al., 2012). A HSI-based bioclimate envelope model was recently developed, in which spatial analysis was applied to analyze spatiotemporal variability of suitable habitat for *H. americanus* in Long Island Sound, USA (Tanaka and Chen, 2015).

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

3.3 Materials and Methods

3.3.1 Maine - New Hampshire Inshore Bottom Trawl Survey

This study used 14 years of semi-annual fishery-independent survey data collected by the Maine-New Hampshire Inshore Bottom Trawl Survey for *H. americanus* from 2000 to 2013 conducted by the Department of Marine Resources (DMR) in spring (April – June) and fall (September – December). The total survey area spanned from 12,437 to 16,001 km2 each year, and included 2,246 bottom-trawl samples in total (n = 280,185 lobsters; Sherman et al., 2005) (Fig. 3.1). The survey employed a stratified random design, with the coastal waters of Maine and New Hampshire being divided into five longitudinal areas based on abiotic and biotic features (Sherman et al., 2005; Cao et al., 2014). Each stratum is further separated into four depth classes (9 – 37 m, 37 – 64 m, 64 – 100 m, and >100 m with 12 km offshore limit), resulting in a total of 20 strata. Each survey targets 115 stations with a sampling density of 1 station for every 137.2 km2. The number of tows in a given stratum is adjusted according to areas of each stratum size. The fishing gear is a modified shrimp net with 50.8 mm mesh in wings and 12.7 mm mesh liner in the cod end (Sherman et al., 2005). The targeted tow duration is 20 minutes at a velocity of 2.2 – 2.3 knots to cover approximately 1.48 km2. A CTD profiler is deployed at each tow to record salinity, temperature and depth (Sherman et al., 2005).

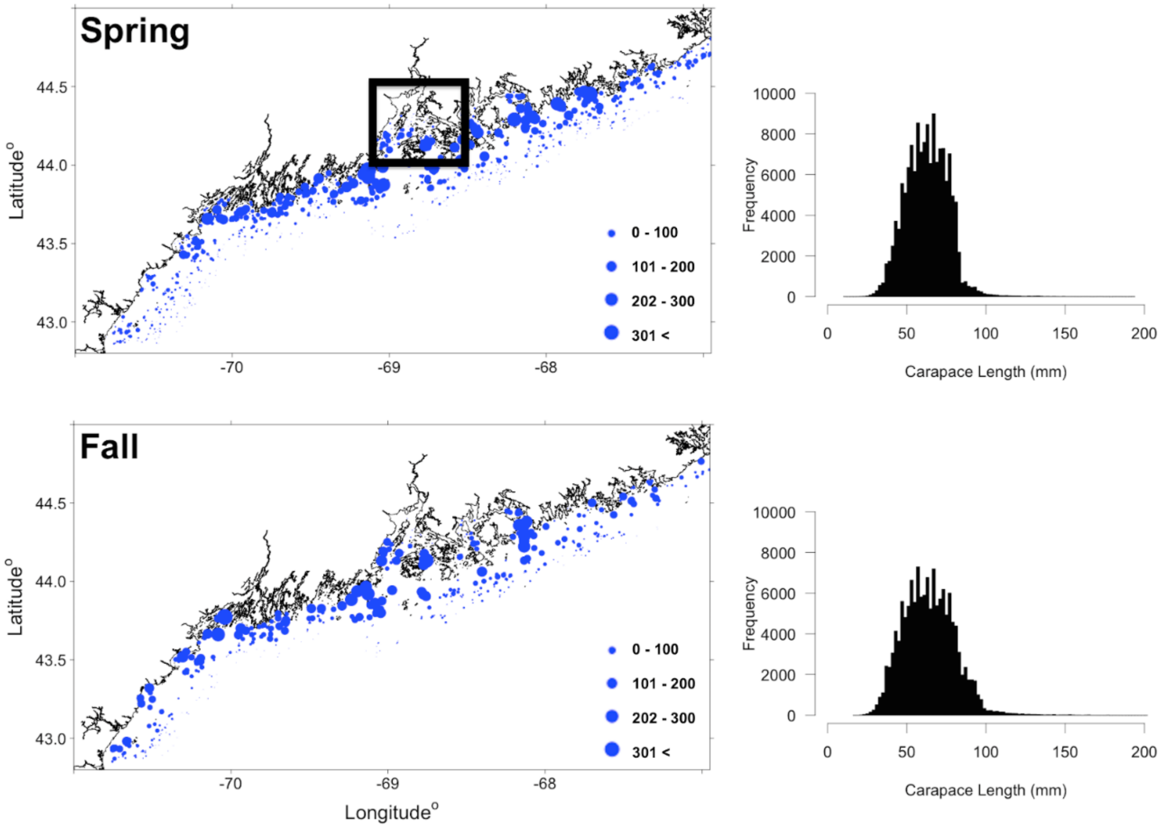

Figure 3-1: Spatial distribution of standardized *Homarus americanus* abundance and observed size frequency based on spring and fall surveys during 2000 - 2013. The box on the map indicates the location of Penobscot Bay.

3.3.2 Environmental data

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

3.3.3 Data analysis and model development

This study is an extension of an earlier modeling effort for *H. americanus* in Long Island Sound (Tanaka and Chen, 2015). The overall procedure for developing the HSI-based bioclimate envelope model (Fig. 3.2) was modified from Tanaka and Chen (2015). *H. americanus* exhibits season, size, and sex specific preferences to surrounding environment (Chang et al., 2010). For example, the species' response to change in temperature is determined by season or thermal history through acclimatization (Worden et al., 2006; Qadri et al., 2007; Jury and Watson, 2013). The survey data were consequently analyzed separately by season (spring and fall), sex and for two *H. americanus* stage classes (adult: > 60 mm carapace length, juvenile: ≤ 60 mm carapace length). The carapace length of 60 mm represents the minimum size at maturity defined by ASMFC (ASMFC, 2009).

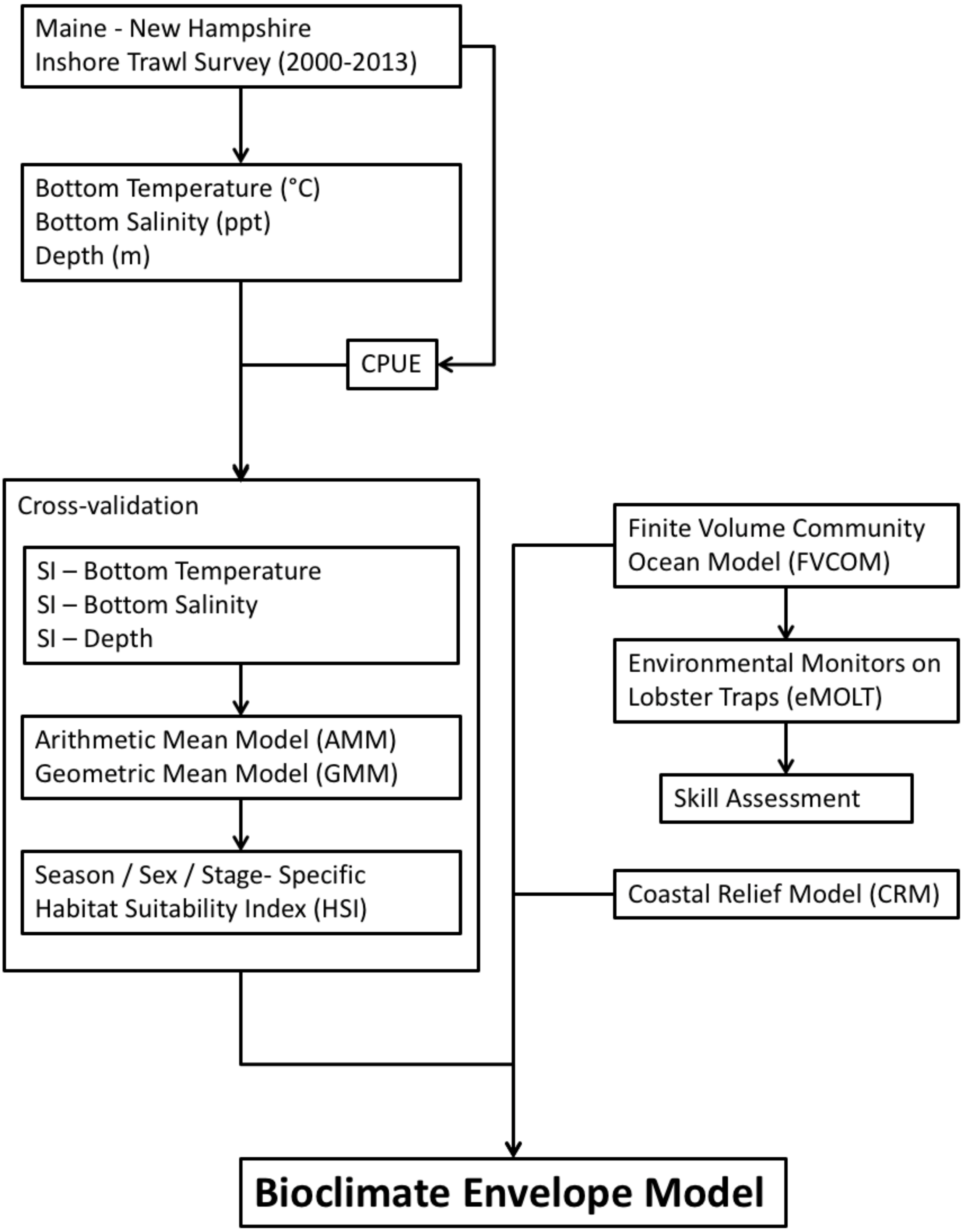

Figure 3-2: Schematic representation of the structure of the bioclimate envelope model developed in this study, implemented in R programming environment.

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

$$CPUE_{ijy} = \left(\frac{Count_{ijy}}{Tow\ Duration_{ijy}}\right) * 20 \qquad \textit{Eq. 3-1}$$

where Count represents the total quantity of either adult or juvenile *H. americanus* caught and Tow duration is measured in minutes. Continuous environmental variables (temperature, salinity and depth) were delineated into 10 classes using Fisher's natural breaks classification method (Bivand, 2013). The SI of class k for environment variable i, SIi,k, was calculated on a scale of 0.0 - 1.0 following (Chang et al., 2012; Tanaka and Chen, 2015):

$$SI_{i,k} = \frac{CPUE_{i,k} - CPUE_{i,min}}{CPUE_{i,max} - CPUE_{i,min}} \qquad \textit{Eq. 3-2}$$

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

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

Arithmetic Mean Model (AMM)

$$HSI = \frac{\sum_{i=1}^{n} SI_i}{n} \qquad \textit{Eq. 3-3}$$

Geometric Mean Model (GMM)

$$HSI = \left[\prod_{i=1}^{n} SI_i\right]^{1/n} \qquad \textit{Eq. 3-4}$$

where SIi represents a SI value associated with the ith environmental variable while n represents the number of environmental variables included in either AMM or GMM HSI.

3.3.4 HSI performance validation and FVCOM skill assessment

The predictive ability of HSIs was evaluated in a cross-validation study, which was conducted independently for each *H. americanus* group. A randomly selected subset representing 80% of all the data (training data set) was used for HSI development, while the remaining 20% (testing data set) was used for the evaluation of the HSI performance (Smith, 1994; Zuur et al., 2007; Tanaka and Chen, 2015). The predicted HSI values (based on the training data set) were compared against the observed HSI values (based on the testing data set), and linear regression analysis was performed to evaluate the predictive performance of the HSI. This cross-validation procedure was repeated 100 times using random selection in each step to obtain 100 sets of liner regression parameters (intercept, slope, R2, and Akaike Information Criterion AIC). The results for both AMM and GMM were compared to determine which model had better predictive ability, which was quantified by an intercept (α) closest to 0, a slope (β) closest to 1, higher R2 and lower AIC. The 95% conference intervals derived from the 100 runs of simulation were compared to evaluate the difference for each regression parameter between the AMM and GMM.

A collection of observed bottom temperatures provided by the Environmental Monitors On Lobster Traps (eMOLT) program was used to assess performance of FVCOM in the DMR bottom trawl survey area. The eMOLT provides a large collection of hourly bottom temperatures from lobster traps at more than 200 sites in the Gulf of Maine and Georges Banks, and is ideally suited for skill assessment of coastal ocean circulation and regional ocean models (Manning and Pelletier, 2009). In a preliminary analysis, observed bottom temperatures from 64 eMOLT sites in the DMR survey area were compared to modeled FVCOM bottom temperature at hourly temporal resolution from 2001 to 2013 (n = 969,249; Fig. 3.3). This univariate comparison of predicted (FVCOM) and observed (eMOLT) outputs were examined by six quantitative metrics; (1) correlation coefficient, (2) root mean squared error, (3) reliability index, (4) average error, (5) average absolute error, and (6) modeling efficiency (Stow et al., 2009). The results showed strong similarity between FVCOM and eMOLT outputs at an hourly resolution (correlation coefficient = 0.877, reliability index = 1.062, average error = 0.156, root mean squared error =1.704, average absolute error = 1.124, modeling efficiency = 0.759), demonstrating that modeled FVCOM bottom temperature can be used in this study.

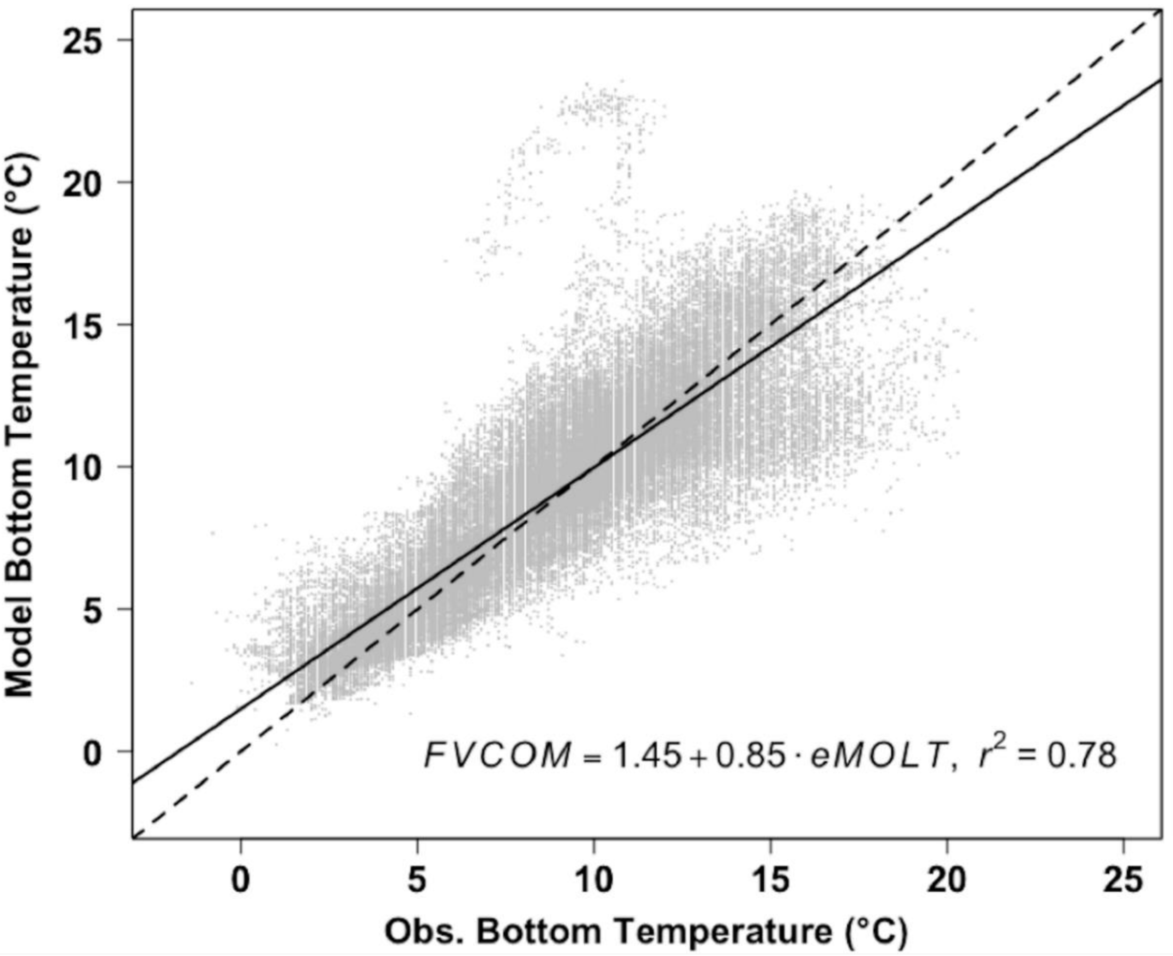

Figure 3-3: A linear regression plot of the modeled bottom temperature (FVCOM) compared to the observed bottom temperature (eMOLT). The linear regression for the model versus predicted value is plotted (solid line) relative to the 1:1 line (dashed line).

3.3.5 Spatial and temporal HSI-based bioclimate envelope analysis

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

A spatial interpolation technique using variogram modeling and ordinary kriging was implemented in the R programming environment to visualize the model outputs (Bailey and Gatrell, 1995; R Core Team, 2014). Semivariogram models were fitted with gaussian, exponential, and spherical variograms with non-linear least squares using R package “gstat”. The model with the lowest mean squared error was used for kriging (Pebesma, 2004).

Interpolated model outputs were mapped using “sp” R package (Pebesma and Bivand, 2005). The model outputs were first inspected visually. The interpolated surfaces for each modeled group were subtracted from one another to produce mean season, sex, and stage specific differences.

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

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

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

3.4 Results

3.4.1 Suitability index of each environmental variable

The highest SI for each environmental variable differed by sex, stage and season (Fig. 3.4; Table 3.1). Observed bottom temperature varied between 2.6-12.0 °C and 5.7-14.3 °C in spring and fall respectively. The suitable bottom temperature for adults varied from approximately 8.4-10.6 °C in spring and 11.6-14.3 °C in fall. Suitable temperature ranges for juveniles showed greater seasonal contrast, from approximately 6.6-10.1 °C in the spring, and shifted higher to 10.9-14.3 °C in fall. A broader suitable temperature range was observed for male juveniles compared to female juveniles.

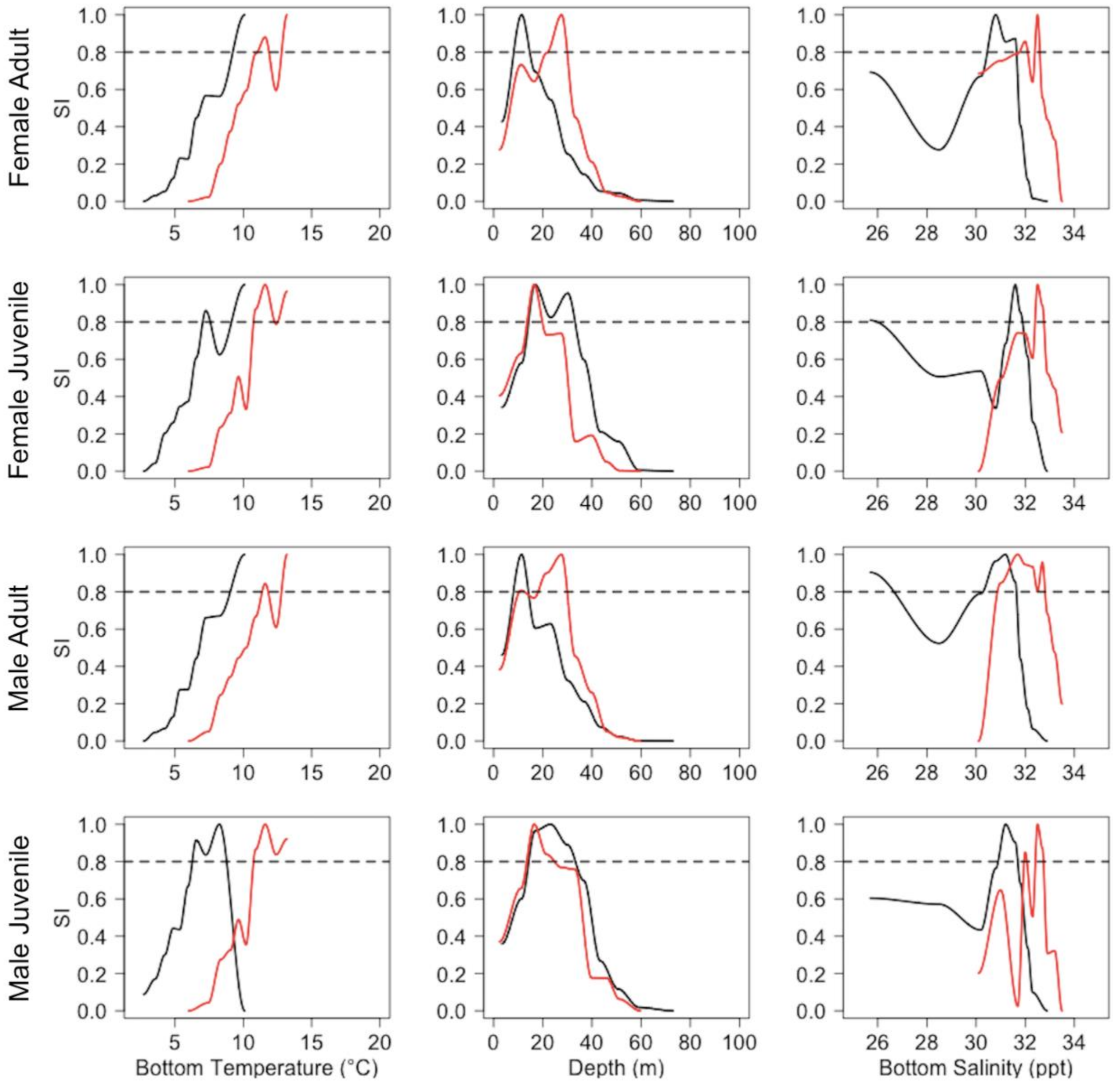

Figure 3-4: Suitability Index (SI) curves of bottom temperature, depth, and bottom salinity for four groups of *Homarus americanus* (2 sexes * 2 life stages). Both spring (black line; April - June), and fall (red line; September - November) SI curves are plotted.

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

Table 3-1: Summary of season, sex, and stage specific suitable range of each environmental variable.

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

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

3.4.2 Model validation

Table 3.2 shows a summary comparison of cross-validation results between AMM and GMM for eight modeling groups. AMM produced lower intercepts and higher slopes in 10 out of the 16 comparisons. AMM showed better predictive ability overall by showing smaller AIC values and higher R2 for all the 8 modeling groups. Therefore, AMM was determined to be more appropriate than GMM in this study. Among the eight modeling groups, spring-female-adult showed the best predictive performance with the highest R2 and the lowest AIC, while predictive performance for the fall-male-juvenile was the poorest with the lowest R2 and the highest AIC.

Table 3-2: Summary of linear regression results between the predicted and observed habitat suitability index (HSI) for Geometric Mean Model (GMM) and Arithmetic Mean Model (AMM) based on 100 rounds of cross-validations.

Season	Sex	Stage	Sample Size	Intercept				Slope			
				AMM mean	95 % CI	GMM mean	95 % CI	AMM mean	95 % CI	GMM mean	95 % CI
Spring	Female	Adult	38069	0.049	(0.040, 0.058)	0.023	(0.018, 0.028)	0.942	(0.923, 0.962)	0.959	(0.927, 0.991)
		Juvenile	31252	0.158	(0.146, 0.170)	0.101	(0.087, 0.114)	0.776	(0.755, 0.797)	0.848	(0.807, 0.888)
	Male	Adult	43822	0.053	(0.041, 0.064)	0.054	(0.042, 0.065)	0.909	(0.893, 0.926)	0.826	(0.782, 0.870)
		Juvenile	29825	0.191	(0.177, 0.204)	0.166	(0.150, 0.183)	0.764	(0.741, 0.787)	0.747	(0.711, 0.783)
Fall	Female	Adult	38069	0.235	(0.217, 0.254)	0.268	(0.241, 0.296)	0.690	(0.669, 0.712)	0.566	(0.539, 0.593)
		Juvenile	29686	0.261	(0.246, 0.275)	0.284	(0.262, 0.306)	0.636	(0.615, 0.658)	0.536	(0.511, 0.561)
	Male	Adult	41350	0.280	(0.256, 0.303)	0.301	(0.276, 0.324)	0.667	(0.642, 0.693)	0.539	(0.560, 0.568)
		Juvenile	30122	0.206	(0.193, 0.219)	0.176	(0.160, 0.193)	0.621	(0.595, 0.647)	0.505	(0.452, 0.558)

Season	Sex	Stage	Sample Size	R-squared				AIC			
				AMM mean	95 % CI	GMM mean	95 % CI	AMM mean	95 % CI	GMM mean	95 % CI
Spring	Female	Adult	38069	0.827	(0.813, 0.842)	0.817	(0.794, 0.840)	-557.18	(-577.60, -536.75)	-479.98	(-512.22, -477.74)
		Juvenile	31252	0.602	(0.580, 0.624)	0.544	(0.507, 0.580)	-287.93	(-297.56, -278.30)	-121.16	(-136.89, -105.44)
	Male	Adult	43822	0.815	(0.799, 0.831)	0.657	(0.609, 0.704)	-550.42	(-569.86, -530.97)	-349.45	(-378.45, -311.45)
		Juvenile	29825	0.623	(0.599, 0.646)	0.462	(0.432, 0.493)	-303.62	(-313.63, -293.60)	-101.49	(-114.40, -88.00)
Fall	Female	Adult	38069	0.569	(0.543, 0.595)	0.361	(0.333, 0.387)	-302.44	(-312.57, -292.31)	-124.22	(-135.76, -112.67)
		Juvenile	29686	0.522	(0.494, 0.551)	0.382	(0.358, 0.407)	-200.71	(-207.94, -193.45)	-110.15	(-117.12, -103.18)
	Male	Adult	41350	0.561	(0.534, 0.588)	0.362	(0.330, 0.389)	-290.29	(-299.78, -280.80)	-123.01	(-133.75, -122.26)
		Juvenile	30122	0.451	(0.422, 0.479)	0.249	(0.211, 0.288)	-159.38	(-165.75, -153.01)	-37.829	(-46.459, -29.198)

3.4.3 Model prediction

The season, stage, and sex specific bioclimate envelopes for *H. americanus* were generated based on predicted HSI at every FVCOM grid in the DMR bottom trawl survey area (Fig. 3.5). Overall, high habitat suitability in inshore waters appeared to occur together while offshore areas were of low habitat suitability. Visual inspection revealed a higher propensity for suitable habitat (i.e. HSI > 0.7) for both juveniles in spring, while a greater area of suitable habitat in the fall was observed for adults. Adult bioclimate envelopes were more extensive than juvenile bioclimate envelopes in both seasons and sexes. Finally, the model predicted higher habitat suitability for female juveniles in the Penobscot Bay in fall, compared to male juveniles (Fig. 3.5). Season, stage, and sex specific comparison of interpolated model predictions showed larger mean differences between seasons (0.2058), compared to the differences between stages (0.0926) and between sexes (0.0982).

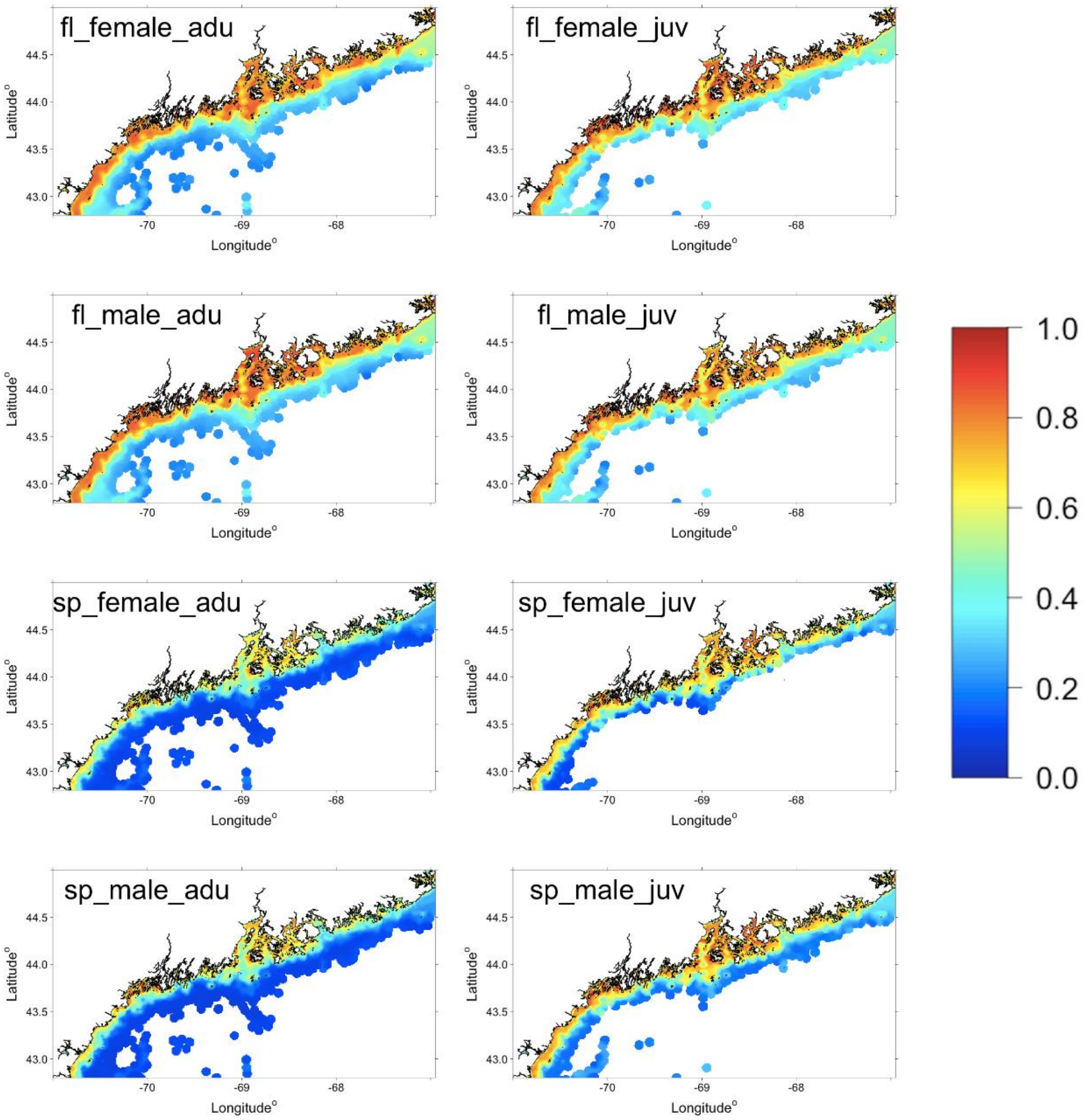

Figure 3-5: Season, sex, and stage specific maps illustrating the spatial distribution of the median habitat suitability index (HSI) over 1978 - 2013 in the coastal waters of Maine and New Hampshire for *Homarus americanus*. fl: Fall (September – November); sp: Spring (April – June); adu: Adult (> 60 mm carapace length); juv: Juvenile (<= 60 mm carapace length).

The changes in climate-driven habitat suitability during 1978 - 2013 are shown in Fig. 3.6. In the spring, there was greater change towards higher habitat suitability throughout coastal waters for both modeled stages and sexes. In the fall, the change was less significant in magnitude (fainter in color) for both sexes and stages. A declining trend in habitat suitability was observed in the upper Penobscot Bay in all eight modeled groups.

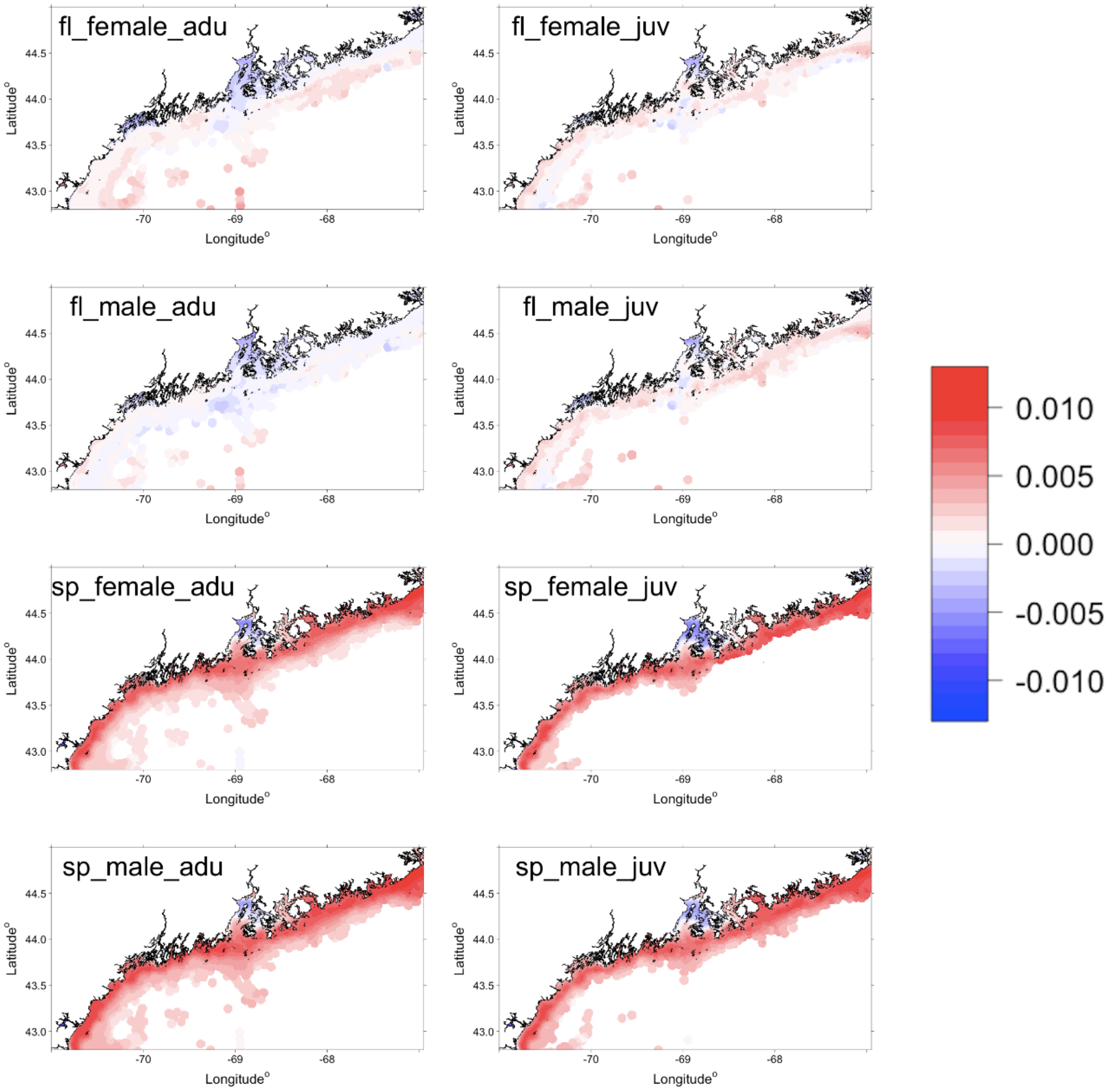

Figure 3-6: Season, sex, and stage specific heat maps illustrating change in habitat suitability index (HSI) over 1978 - 2013 in the coastal waters of Maine and New Hampshire for *Homarus americanus*. fl: Fall (September – November); sp: Spring (April – June); adu: Adult (> 60 mm carapace length); juv: Juvenile (<= 60 mm carapace length). Darker red indicates change towards higher habitat suitability at higher magnitude.

Temporal variation in climate driven-habitat suitability during 1978 - 2013 was observed for both seasons, stages and sexes of *H. americanus* (Fig. 3.7). A significant increasing trend in habitat suitability was observed in all groups, except in the fall ($\beta = -0.0001$, $p = 0.806$). The cross-correlation analysis revealed significant relationships between HSI and both temperature and salinity in the spring, while the correlations between the variables were less significant in the fall (Fig. 3.8).

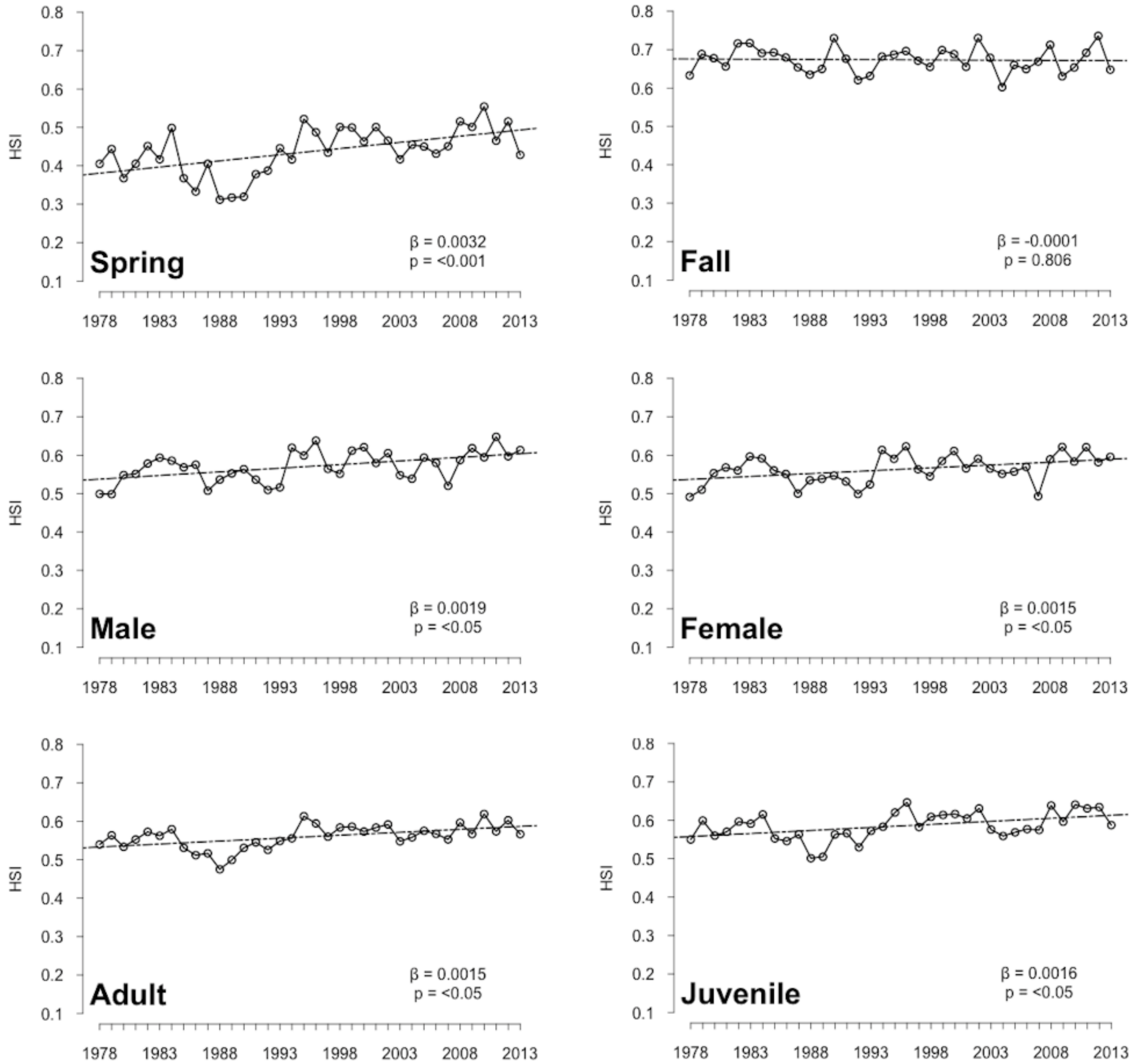

Figure 3-7: Median habitat suitability index (HSI) for each year from 1978 to 2013 (solid line). The trend in both seasons-sexes, and stages was shown by the fitted linear regression model (dashed line).

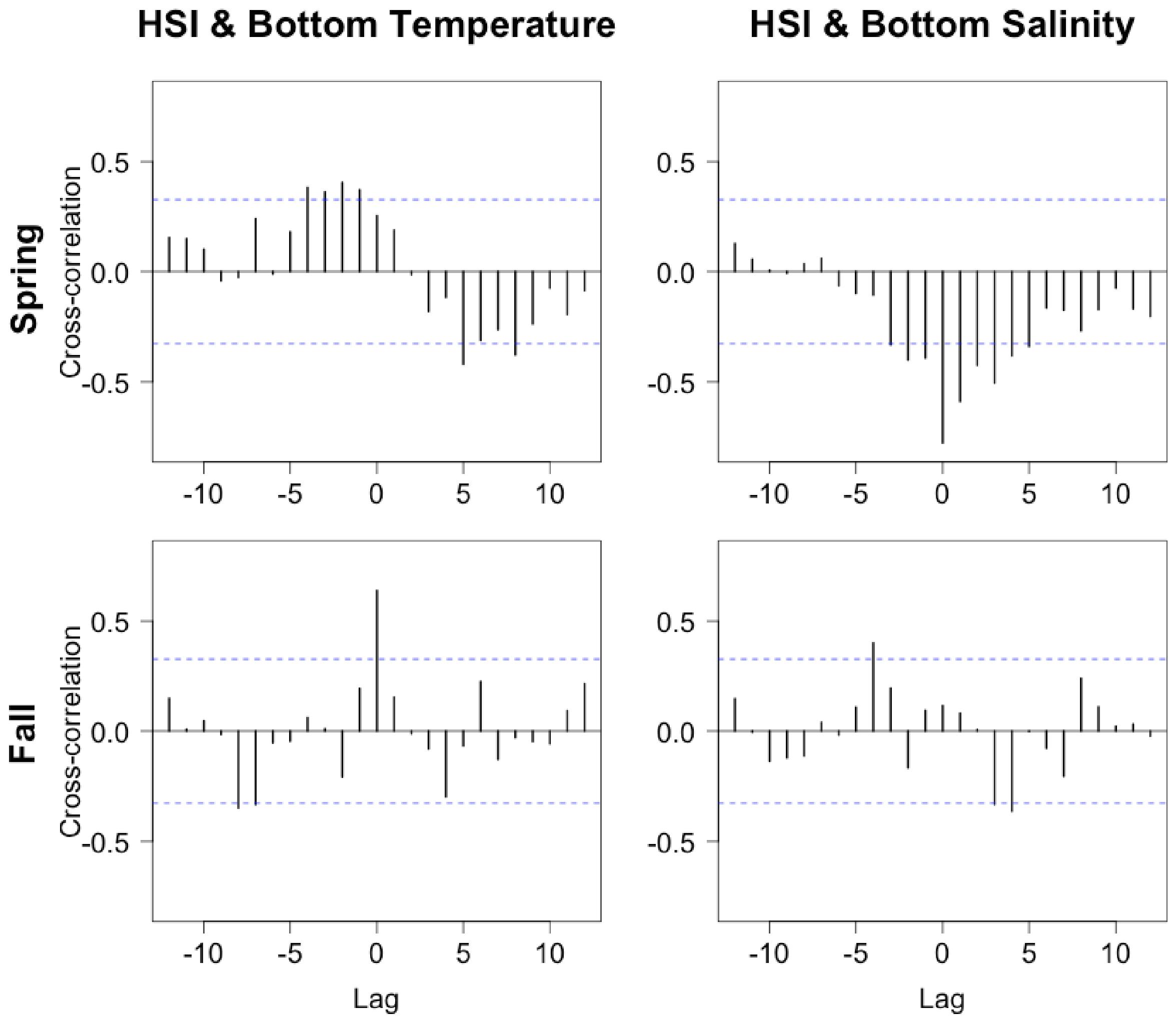

Figure 3-8: Cross-correlation functions measuring correlations between two time series at different lags (years). Every vertical line shows the correlation between the two time series at each lag indicated along the x-axis. A correlation extending above or below the dotted lines shows statistical significance.

The relative proportion of poor, fair, and good habitat conditions (HSI < 0.3, 0.3 <= HSI < 0.7, and 0.7 <= HSI) was identified for both modeled stages, sexes, and seasons (Fig. 3.9). Proportion of habitat condition showed a similar trend between adult - juveniles and male - females; however, a larger proportion of good habitat was observed during the fall while a pronounced proportion of poor habitat was observed during the spring (Fig. 3.9).

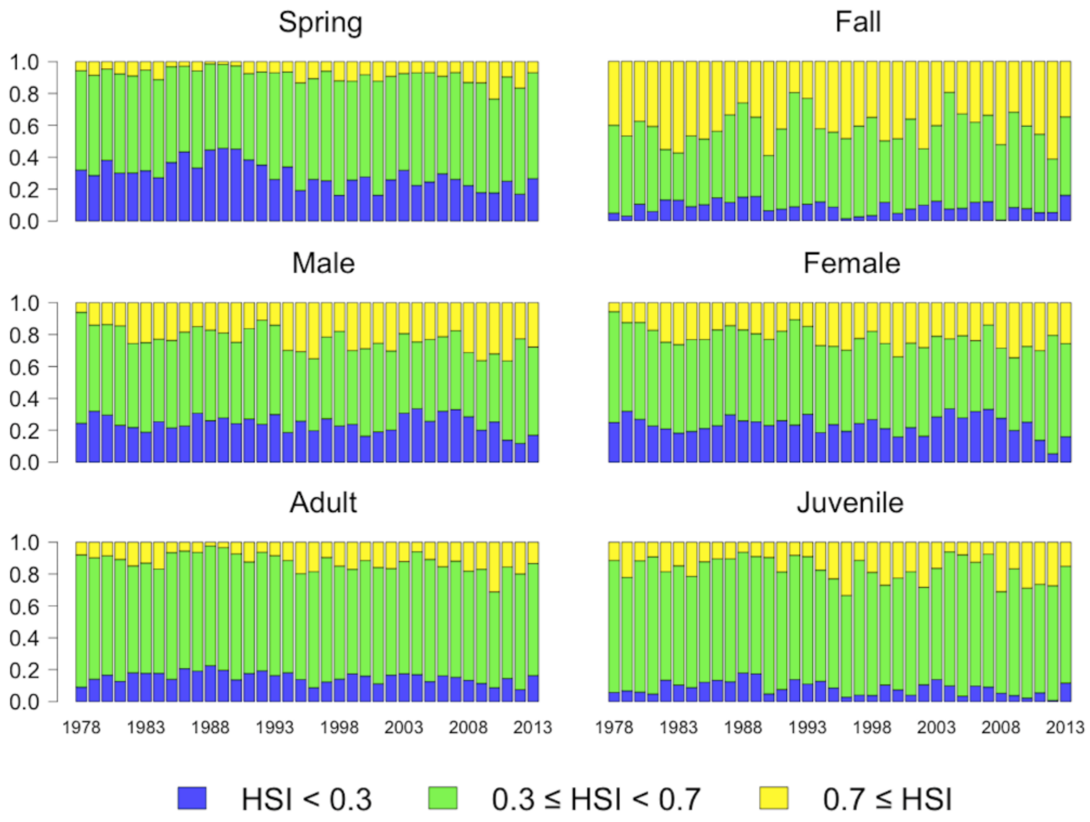

Figure 3-9: Relative proportion of good (yellow), fair (green), and poor (blue) habitat for *H. americanus* in the coastal waters of Maine and New Hampshire (1978 to 2013). Upper panel represents fall (September-November), while lower panel represents spring (April-June). y-axis represents percentage of the study area.

3.5 Discussion

3.5.1 Bioclimate envelopes and Suitability Index

The modeling results showed higher climate-driven habitat suitability during the fall, which was consistent with the field survey trends reporting higher lobster abundance during the fall survey (ASMFC, 2015b). The overall declining trend in habitat suitability in the upper Penobscot Bay suggests that contraction of *H. americanus* habitat is driven by the changes in bottom temperature and salinity. Empirical studies in the Great Bay Estuary, NH and Narragansett Bay, RI have shown the contraction of the species' suitable habitat in estuarine systems where temperature and salinity become sub-optimal (Howell et al., 1999; Jury and Watson, 2012). The greater propensity towards higher habitat suitability throughout coastal waters for both modeled stages and sexes during the spring indicates an increasing number of days that bottom temperature and salinity falls within the species' optimal range in this area. The modeling results show that the best predictive power was derived for adult females in spring (Table 3.2). This reflects adult females potentially exhibiting more significant behavioral thermoregulation compared to *H. americanus* of different stage, sex, and season (Campbell, 1986; Crossin et al., 1998). Hatching of eggs occurs in spring when bottom water temperature reaches approximately 15 ºC, and completes within a relatively short time span of 10 to 14 days (Hughes and Matthiessen, 1962). Although few studies have focused on relationships between behaviors of adult females and surrounding environment, it has been proposed that egg-bearing females seek to subject their eggs to a specific thermal regime during the spring to maximize degree-days required for egg development (Campbell, 1986; Ugarte, 1995; Goldstein and Watson III, 2015). This is plausible as *H. americanus* can detect very small changes in water temperature (Jury and Watson III, 2000), and the species' highly mobile and thermoregulated nature allow them to seek their preferred thermal regime (Crossin et al., 1998; Jury and Watson III, 2013; Reynolds and Casterlin, 1979). However, *H. americanus* also exhibits varying response and preference specific to changes in salinity, depth and other environmental factors depending on their physiological condition, sex, molt stage, and size (Mercaldo-Allen and Kuropat, 1994). Therefore, it is difficult to identify the extent to which environmental variables regulate the behavior of the species over others. in this regard, future bioclimate modeling efforts should actively incorporate mechanistic understanding of the species' metabolic response to each environmental variable.

The season- and stage-specific SIs for temperature, depth, and salinity were consistent with the existing literature of *H. americanus* habitat preferences. Seasonal shifts in SI curves likely reflect a composite result of interaction between different levels of temperature, light, oxygen concentration, salinity, food availability and predation dynamics exist at different water depths and seasons. The SI-temperature curves identified shifts in suitable thermal ranges between spring and fall for both adults and juveniles. Suitable temperature for *H. americanus* varied from 11.6 – 14.3 °C in the fall, and 8.4 – 10.6 °C in the spring. This was consistent with past findings reporting the species' avoidance of temperature below 5 °C and above 18 °C (Aiken and Waddy, 1986; Lawton and Lavalli, 1995; Crossin et al., 1998; Jury and Watwon III, 2013). The SI-temperature curves generally did not show unimodal shape, and with the reported thermal preference of the species of 15.9 °C (Crossin et al., 1998) and 16.5 °C (Reynolds and Casterlin, 1979) suggests even warmer bottom temperatures would be more suitable with no adverse effects. The significant shift in SI-depth curves for adults suggests a seasonal inshore/offshore migration, while a less significant shift in SI-depth curves for juveniles suggests a more localized migration along the coastal waters (Lawton and Lavalli, 1995). Adults exhibited a broader suitable salinity range in the fall, while juveniles showed a shift in suitable salinity ranges between spring and fall. The difference in suitable salinity ranges possibly reflected the juveniles actively moving to optimal salinity ranges due to their limited ability to osmoregulate (Charmantier and Aiken, 1987).

3.5.2 Model limitations and future improvements

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

3.5.2.1 Bottom Substrate

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

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

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

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

3.5.3 Assumptions and limitations inherent in bioclimatic envelope models

Calibration of bioclimate envelope model is often based on a restricted number of environmental variables, and forced to neglect food-web interactions, species dispersion, or ecosystem productivity because of the difficulty in obtaining reliable information (Pearson and Dawson., 2003; Cheung et al., 2008, 2009; Stock et al., 2011; Jian et al., 2013; Watling et al., 2013; Tanaka and Chen., 2015).

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

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

A mismatch between prediction and observation is inherent and ineviTable 3.in modeling of open environmental systems (Oreskes et al., 1994; Araújo and Peterson, 2012). When a bioclimate envelope model evaluates a specific environment for a given species, prediction error is often due to potential species presence in un-sampled areas or extrinsic factors not included in the modeling effort (Araújo and Peterson, 2012). Such commission error does not indicate model flaws, but simply indicates that the model needs further development (Oreskes et al., 1994).

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

The three environmental variables considered in this study were chosen based on perceived importance and data availability, but many other environmental variables can also greatly influence the species' habitat quality (Lawton and Lavalli, 1995). These variables may include more climate and ecological variables such as thermal fronts, latitude and longitude, coastal upwelling, regional climate forcing, change in pH level and dissolved oxygen concentration (Mercarldo-Allen and Kuropat., 1994; Boudreau et al., 2015). Alternatively, exclusion of certain habitat variables (e.g. depth) should be considered to allow greater change in the species' distribution as a result of changes in other variables in future projection (Hare et al., 2013). While this study focused on climatic impacts on the species' realized niche, a mechanistic niche modeling to understand how environmental conditions affect the species' growth, survival and reproduction should be considered for future projection of climate change impact (Kearney, 2006).

3.5.4 Management implications

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

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

As the rate of climate change is predicted to accelerate in the future, alongside the species' ongoing distributional shifts (Pinsky et al., 2013), there is a growing need to assess changes in *H. americanus* habitat condition. Under RCP 8.5 emissions scenario, average bottom temperature in Northeast U.S. Continental Shelf system is expected to increase more than 1 °C by 2050 (IPCC, 2014; NOAA, 2015). While the projected increase in bottom temperature in the Gulf of Maine is not expected to exceed the species' maximum temperature tolerance and may even considered favorable, management uncertainties at the southern range limits of the species can be addressed through scenario-based analysis (Hare et al., 2013; Shackell et al., 2014, ASFMC, 2015b). Bioclimate envelope models are valuable tools to; (1) evaluate climate impacts and aid implementation of ecosystem-based fishery management, and (2) generate hypotheses of large scale potential ecological changes in climate-driven marine environment (Cheung et al., 2009). Advancement in our understanding of climate-driven habitat suitability of *H. americanus* can play a critical role in the sustainability of the species' fishery.

3.6 Conclusion

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

CHAPTER 4 - A STATISTICAL MODEL FOR MONITRING SHELL DISEASE

4.1 Abstract

The expansion of shell disease is an emerging threat to the inshore lobster fisheries in the northeastern United States. The development of models to improve the efficiency and precision of existing monitoring programs is advocated as an important step in mitigating its harmful effects. The objective of this study is to construct a statistical model that could enhance the existing monitoring effort through (1) identification of potential disease-associated abiotic and biotic factors, and (2) estimation of spatial variation in disease prevalence in the lobster fishery. A delta-generalized additive modeling (GAM) approach was applied using bottom trawl survey data collected from 2001-2013 in Long Island Sound, a tidal estuary between New York and Connecticut states. Spatial distribution of shell disease prevalence was found to be strongly influenced by the interactive effects of latitude and longitude, possibly indicative of a geographic origin of shell disease. Bottom temperature, bottom salinity, and depth were also important factors affecting the spatial variability in shell disease prevalence. The delta-GAM projected high disease prevalence in non-surveyed locations. Additionally, a potential spatial discrepancy was found between modeled disease hotspots and survey-based gravity centers of disease prevalence. This study provides a modeling framework to enhance research, monitoring and management of emerging and continuing marine disease threats.

4.2 Introduction

The American lobster (*Homarus americanus*), which is of critical economic and ecological importance throughout northeastern USA and Atlantic Canada, is currently being threatened by the emergence of shell disease. The shell disease in *H. americanus* is manifested as necrosis and lesions on the dorsal carapace of infected individuals that can result in decreased survival (Shields 2013) and decreased reproductive success (Castro et al., 2006). Shell disease in *H. americanus* was first reported in the 1930s, and various forms of lobster shell disease have been observed (e.g., endemic shell disease, impoundment shell disease, and diet-induced shell disease) (Hess, 1937; Smolowitz et al., 1992; Tlusty et al., 2008). Notably, shell degradation associated with disease decreases the market value of infected individuals, resulting in economic and market loss in this lucrative fishery (ASMFC, 2009, 2015a).

Epizootic shell disease (ESD) is a recently observed degradation of the lobster cuticle by a suite of bacteria (e.g., *Aquimarina homaria*) (Shields 2013). Individual susceptibility to ESD has received increased research attention following the host susceptibility hypothesis proposed by Tlusty et al., (Tlusty et al., 2007). This hypothesis states that the internal condition of a lobster ultimately determines whether an infection becomes established, with physiological stress likely being the strongest indicator of susceptibility. This notion was generally supported by subsequent studies evaluating the influence of water temperature (Tlusty and Metzler, 2012), pollutants (Laufer et al. 2013; Shields 2013), and diet (Tlusty et al., 2008). Additional studies of shell disease etiology noted significant shifts in microbial communities between the shells of infected and uninfected lobsters, suggesting importance of a polymicrobial, rather than single species, pathogen (Meres et al. 2012). A major outbreak of ESD was first observed in Long Island Sound (LIS) in 1996, which was followed by the unprecedented rise and spread of ESD among Southern New England (SNE) lobster stocks. Prior to 1999, the lobster fishery in LIS was the third largest in the country, with landings valued at more than $35 million (NMFS, 2016). However, in 2013 the Atlantic States Marine Fisheries Commission (ASMFC) required the states surrounding LIS to take steps to reduce the total lobster harvest by 10 percent, resulting in the first-ever seasonal closure of the LIS lobster fishery (ASMFC, 2012). Concern over the stability of the lobster fishery has forced many fishermen to abandon their traditional livelihoods and pursue new careers outside of the lobster industry (Benson 2013; Lacurci 2014).

Tools are required that will allow the fishery to deal with possible future spread of lobster shell disease. The development of a modeling framework that can provide (1) ecological interpretation of factors associated with disease prevalence, and (2) more reliable, contemporary disease maps at policy-relevant spatial scales has been advocated as an important step in understanding the harmful effects of oceanic diseases (Harvell et al. 2004; Pullan et al. 2011). There are presently two broad types of modeling approaches available for predicting spatiotemporal disease prevalence: empirical-based statistical models that seek to quantify associations between disease prevalence and environmental factors (e.g., Pedersen et al., (2014)) and process-based mechanistic models that seek to simulate biological or ecological processes that drive disease prevalence (e.g., McCreesh et al., (2015)). It is generally acknowledged that both approaches can be used to facilitate proactive disease management.

The objectives of this study were to develop empirical-based statistical models to (1) quantify associations of lobster shell disease occupancy and abundance with environmental, spatial, and ecological factors, and (2) predict relative lobster shell disease prevalence in non-surveyed locations to provide a spatially-varying disease probability map across the entire study area to identify potential disease hotspots that remain undetected by the existing survey programs. We hypothesized that the spatial distribution of shell disease prevalence is associated with external factors such as salinity, water temperature, depth, distance offshore, sediment type, latitude and longitude, as well as host sex and life stages. To this end, a delta-generalized additive modeling (GAM) framework was developed to evaluate the relative contributions of a variety of environmental and biological factors to shell disease occupancy and abundance. GAMs have the advantage of reconciling highly non-linear and nonmonotonic relationships that are common in nature, and can serve as either descriptive or predictive statistical models (Guisan et al. 2002).

This study highlights the utility of pairing existing fishery-independent datasets with a non-parametric and parsimonious modeling approach to enhance the knowledge of how lobster shell disease associates with various abiotic and biotic factors. Ultimately, our findings will provide policy-relevant information for effective ecosystem-based marine disease surveillance programs, which could be of value for the U.S. lobster fishery.

4.3 Materials and methods

4.3.1 Case study area

The LIS is an estuary that is 182 km long and 33.8 km wide with an average depth of 22.6 m (Fig 4.1). The bathymetry of LIS is composed by four major basins with a maximum depth of 60.4 m. The LIS is weakly stratified as the salinity ranges from 23 ppt at the western end to 35 ppt at the eastern end (Gottschall 2013). Three major rivers (Thames, Housatonic, and Connecticut) account for the majority of freshwater input into LIS. Runoff and drainage along the coast of New York and Connecticut also deliver freshwater into the sound (Lee and Lwiza 2008).

4.3.2 Modeled data

The lobster shell disease data were collected by bi-annual bottom trawl survey conducted by the Connecticut Department of Energy and Environmental Protection (CTDEP) during 2001 and 2013 (Fig 4.2). The CTDEP survey employs a stratified random design based on 12 strata (4 depth strata * 3 substrate strata). Samples were collected using a 14-m otter trawl with a 51 mm codend. Date, location, bottom temperature, bottom salinity, depth, and biological information of each lobster (carapace length (CL), sex, and shell disease presence) were recorded at each tow (Table 4.1). The survey area is divided into 1.85*3.7 km sites assigned to the 12 strata (Gottschall and Pacileo 2013). Spring surveys were conducted during the months of April- June, and fall surveys were conducted from September through October. *In situ* data are collected once a month from 40 sites that are randomly selected from within each stratum, resulting in a total of 200 sites annually. The survey was conducted at 3.5 knots for a targeted duration of 30 minutes during daylight hours to reduce sampling bias related to diurnal variability in catchability (CTDEP, 2013; Sissenwine and Bowman, 1978). There were no changes associated with the size specification for the trawl equipment during the survey.

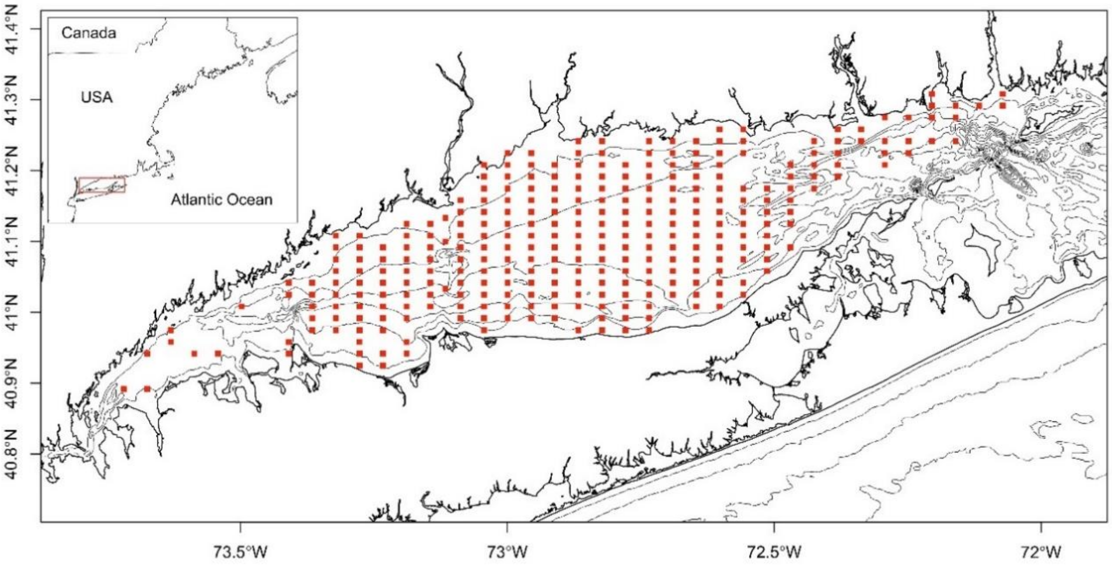

Figure 4-1: Sampling locations of the Long Island Sound bottom trawl survey used in this study (2001 to 2013). Each sampling site is 1.85*3.7 km.

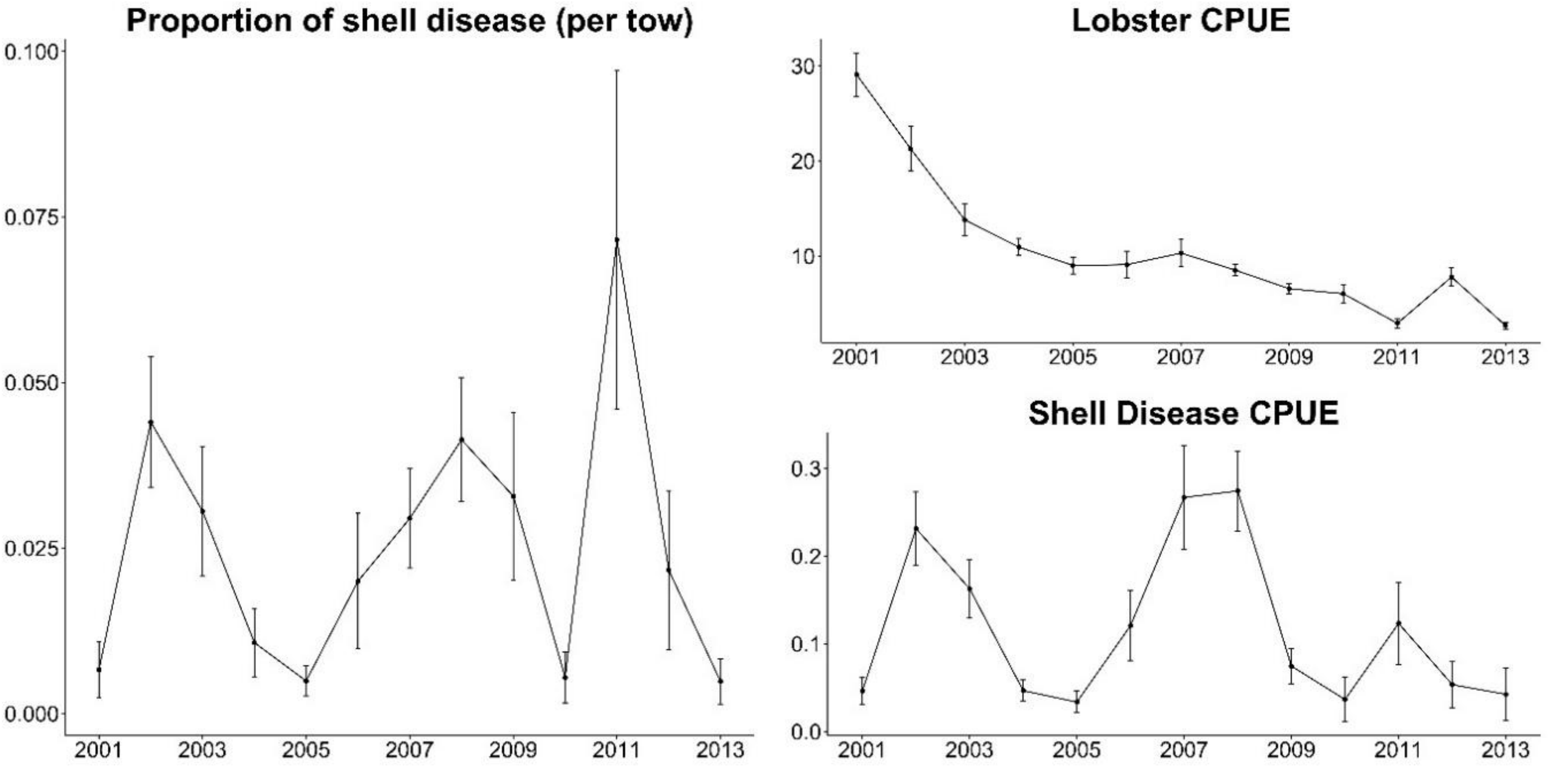

Figure 4-2: Abundance indices of American lobster (*Homarus americanus*) and shell disease per tow in Long Island Sound, USA. For calculation of American lobster CPUE see Tanaka and Chen (2015). CPUE: catch-per-unit-effort.

Table 4-1: A list of variables identified as candidate explanatory variables for delta generalized additive modeling approach with corresponding VIF value. All variables listed in this table were measured directly from the Long Island Sound bottom trawl survey (2001-2013).

Variables	Type	Description	VIF[b]
Season	Temporal	Season trawl was conducted: Spring = March-May, Fall = September-November	n/a
Year	Temporal	Year trawl was conducted	n/a
Latitude (Degree)	Spatial	Measurement of latitude trawl was conducted (mid trawl point)	2.2312
Longitude (Degree)	Spatial	Measurement of longitude trawl was conducted (mid trawl point)	1.9888
Distance Offshore (km)	Spatial	Measurement of distance between trawl location and coastline	1.5965
Depth (m)	Abiotic	Observed depth at trawl location	2.2378
Bottom Temperature (°C)	Abiotic	Observed bottom temperature at trawl location	1.4678
Bottom Salinity (ppt)	Abiotic	Observed bottom salinity at trawl location	1.7772
Stage	Biotic	Adult (CL[a] > 60 mm) and Juvenile (CL <= 60 mm)	n/a
Sex	Biotic	Female and Male (unspecified sex were omitted)	n/a

[a] CL: Carapace Length.

[b] VIF: Variance Inflation Factor.

The monitoring of lobster shell disease began in 2001, and a total of 1,246 tows that collected 18,322 lobsters were initially explored in this study. A tow was considered satisfactory for the analysis only when it recorded (1) number of shell disease-positive lobsters with relevant biological information (e.g. sex and carapace length), (2) geographical information (e.g. latitude and longitude), and (3) environmental information (e.g. bottom water temperature and salinity, depth). A total of 1,234 tows that collected 17,838 lobsters met these criteria were used for the analysis. The dataset showed an overdispersion of shell disease abundance due to the high number of tows that caught zero infected lobsters. A lobster was considered to be free of shell disease if the shell surface shows no signs of the disease (i.e. the default condition) or if the lobster had limited necrotic spots (e.g. pitting and "cigarette-like burn" mark on the shell surface) or lesions (e.g. damage that penetrates carapace to inner musculature). A visual inspection was conducted to identify shell disease on the claws, carapace, tail, and legs. A lobster was considered to be infected if more than 10% of shell surface shows signs of shell disease (e.g., pitting and lesions). Several types of lobster shell disease have been documented, which are not differentiated here. Despite our inability to distinguish among shell diseases, the condition we describe here is most likely ESD given its known prevalence throughout the study area (Castro and Somers, 2012; Cobb and Castro, 2006; Maynard et al., 2016; Shields, 2013).

The shell disease catch-per-unit-effort (CPUE) was considered to be a good indicator of lobster shell disease prevalence in the study area (Cao et al., 2009; Chen et al., 2008; Tanaka and Chen, 2015). Survey-CPUE is a commonly used indicator for monitoring changes in relative abundance of fish stocks (Maunder and Punt 2004). Studies have shown that CPUE is most reliable when the sampling units are homogeneous in their characteristics and operating procedure (Lehodey et al. 1997; Maunder and Punt 2004; Richards and Schnute 1986), and gravity centers of CPUE can be used to better understand the spatiotemporal dynamics of fish stocks (Lehodey et al. 1997; Tseng et al. 2011; Yasuda et al. 2014; Zhang et al. 2015). A nominal shell disease CPUE at station *i*, in season *j*, and year *y* was calculated as;

$$CPUE_{i,j,y} = \left(\frac{Count_{i,j,y}}{TowDuration_{i,j,y}}\right) * 20 \qquad \textit{Eq. 4-1}$$

where Count represents the total quantity of shell disease positive lobster caught. Tow duration varied between 20 to 30 minutes but was standardized to 20 minutes at each sampling station (Tanaka and Chen, 2015). To analyze the spatial distribution of lobster shell disease, the longitudinal and latitudinal gravitational centers of nominal disease CPUE in year *y* were calculated by;

$$Lon_y = \frac{\sum_{i=1}^{K}(Lon_i * CPUE_{y,i})}{\sum_{i=1}^{K} CPUE_{y,i}} \qquad \textit{Eq. 4-2}$$

$$Lat_y = \frac{\sum_{i=1}^{K}(Lat_i * CPUE_{y,i})}{\sum_{i=1}^{K} CPUE_{y,i}} \qquad \textit{Eq. 4-3}$$

where Lon_i represents the longitudinal point of the station *i* between -73.63 and -72.07 E; Lat_i represents the latitudinal point of the station *i* between 40.92 and 41.31 N; $CPUE_{y,i}$ denotes the nominal shell disease CPUE at station *i* in year *y*; *K* is the total number of stations.

4.3.3 Generalized additive model

4.3.3.1 Model development

A delta (also known as Hurdle or Two-stage) generalized additive modeling (GAM) approach was applied to account for zero-inflation and overdispersion (Jensen et al., 2005; Chang et al., 2010; Grüss et al., 2014). GAM is a semi parametric extension of the generalized linear model and commonly used in ecological studies (Zuur et al. 2007, 2009). GAMs assume that the response variables are independent, and use spline smooth function to define nonlinear relationships between the response and explanatory variables (Guisan et al.

2002). With the delta approach, occupancy and abundance observations are modeled separately to formulate the overall prediction of relative species abundance while it allows independent evaluation of predictor variables for both occurrence and abundance, which often differ (Potts and Elith 2006; Sagarese et al. 2014).s

Lobsters within each tow were grouped by stage (adult: >60 mm carapace length, juvenile: ≤60 mm carapace length) and sex (male and female), allowing every tow to have up to 4 groups of lobsters (2 stage * 2 sexes) (Chang et al., 2010; Tanaka and Chen 2015, 2016). This categorization technique developed by (Chang et al., 2010) can relate biological characteristics of a tow-subgroup to environmental information recorded by the corresponding tow. For each tow-subgroup, the delta-GAM separately modeled: (1) the “encounter rate probability” of shell disease (i.e. a proportion expressed as total number of shell disease positive lobsters divided by total number of lobsters), and (2) the “positive catch probability” of shell disease (i.e. number of shell disease positive lobsters conditional on presence). The general delta-GAM formulation can be written;

Encounter rate probability (y^1):

$$logit(y) = \alpha + \sum_{i=1}^{p} f(x_i) + \varepsilon \qquad \textit{Eq. 4-4}$$

Positive catch probability (y^2):

$$ln(y) = \alpha + \sum_{i=1}^{p} f(x_i) + \varepsilon \qquad \textit{Eq. 4-5}$$

Overall prevalence probability:

$$D = y^1 * y^2 \qquad \textit{Eq. 4-6}$$

where a denotes an intercept term, *f* denotes the non-parametric cubic spline smooth function; x_i denotes the i^{th} explanatory variable directly measured by the CTDEP survey; and ε is the residual error term. The first stage GAM modeled the proportion of shell disease per tow-subgroup (i.e. encounter rate probability) using a logit link function and a binomial error distribution. Here, the total number of lobsters in each response variable served as a prior weight on the contribution of the data to the first stage GAM fitting procedure to account for the difference in response variable size. The second stage GAM modeled the shell disease abundance per tow-subgroup conditional on presence (i.e. positive catch probability) using a log link function and a negative binomial error distribution. The overall prevalence probability (*D*) was derived by multiplying the products from both stages (Grüss et al. 2014; Sagarese et al. 2014).

Variance inflation factor (VIF) analysis with an acceptable value below 3.0 was conducted to minimize collinearity among candidate explanatory variables (Zuur et al. 2007). To avoid unnecessary model complexity and computation time, boosted regression tree (BRT) analysis was conducted for each GAM to incorporate candidate bivariate terms (Elith et al. 2008; Sagarese et al. 2014). To prevent model overfitting, the maximum degrees of freedom was set at 5 (k=5) for univariate terms and 30 (k=30) for bivariate terms (Rooper et al. 2014; Sagarese et al. 2014; Zuur et al. 2009). Furthermore, gamma = 1.4 was set for each GAM to place a heavier penalty on each term to prevent overfitting (Wood, 2012; Zuur et al., 2009).

All statistical analyses were conducted in the R programming environment (R Core Team 2016). GAMs were built and fitted using the *mccv* package (Wood, 2011) and *fmsb* [52] and *dismo* [53] were used to implement VIF and BRT analyses.

4.3.4 Model selection and validation

Chi-square statistical significance tests and Akaike information criteria (AIC) were used as the model selection criteria. A stepwise backward selection was applied to identify an optimal model in each stage (Truesdell 2013). First, a full model was built for each stage using all of the candidate univariate and bivariate terms identified through VIF and BRT analyses. Second, the least statistically significant variable was removed using the specified p-value significance threshold ($p < 0.05$) (Wood 2003; Truesdell 2013; Li et al., 2015; Chang et al., 2010). Variable removal was conducted one at a time and the reduced model was refit to the data. Candidate univariate and bivariate terms were kept in the model if they contributed to a lower AIC (Winton et al. 2014). The stepwise model selection procedure was repeated until an optimal model was identified according to the above criteria at each stage (i.e. a model with lowest AIC and included only significant variables). Finally, model diagnostic plots were examined to evaluate residual patterns and model assumptions.

A cross-validation study was conducted to evaluate the performance of the best-fitting delta-GAM (Zuur et al. 2007). A randomly selected subset representing 80% of the original data (training data) was used to develop and calibrate the delta-GAM, and the remaining 20% (testing data) was used to evaluate the model performance. The model predictions were compared to the observations and linear regression analysis was used to evaluate the model performance. The cross-validation process was repeated 100 times using a random partition in each step. The model performance was quantified by 100 sets of linear regression parameters: an intercept (α) closest to 0, a slope (β) closest to 1, and higher R^2.

4.3.5 Environmental data

Because a GAM does not generate coefficients that can be multiplied by conventional grid maps of the covariates, spatial predictions were made by constructing new environmental datasets of the study area (Franklin 2010). Bottom temperature and salinity estimates by depth, time, and location in the study area were modeled by the Finite-Volume Community Ocean Model (FVCOM) runs from 2001 to 2013. FVCOM is an ocean circulation model developed by University of Massachusetts Dartmouth and Woods Hole Oceanographic Institution (Chen et al., 2006). The FVCOM has been configured for the Northwest Atlantic Shelf region, with horizontal resolution ranging from 20 m in river mouths to as coarse as 10 km towards the open boundary off the shelf (Chen et al., 2006). Bathymetry layers were obtained from the U.S. Coastal Relief Model (NGDC, 1999). The surficial substrate layer in LIS was obtained from the U.S. Geological Survey (resolution: 0.00001 decimal degrees or 1.11 m; Poppe and Seekins, 2000). Substrate classifications in included; gravel (pebbles defined as 2.00–64.00 mm, cobbles defined as 64–256 mm, boulder defined as above 256 mm), gravel-sand (0.62–2.00 mm), sand-clay (0.001–0.004 mm), silt (0.004–0.062 mm)/sand, sand- clay/silt, sand-silt/clay, and sand/silt/clay (Poppe et al., 2000).

4.3.6 Predictions of spatiotemporal patterns in shell disease prevalence

The shell disease prevalence predictions derived by the best-fitting delta-GAM were assigned to every FVCOM grid in the study area and universal kriging interpolation technique was used to produce high-resolution maps for interpretation (Bivand et al., 2013; Pebesma, 2004; Zuur et al., 2007). This procedure was repeated for every year within the predictive capacity of the best-fitting delta-GAM (2001-2013). The spatial distribution of median GAM outputs was mapped to interpret the overall spatial variability in shell disease prevalence. The longitudinal and latitudinal gravitational centers of observed shell disease prevalence between 2001 and 2013 were compared to the modeled disease hotspots to evaluate magnitude of spatial discrepancy due to potential biases associated with the survey design and subsequent sample size.

4.4 Results

4.4.1 Significance of abiotic and biotic variables

A total of 2,008 tow-subgroups out of 1,234 tows were analyzed during the time period of 2001-2013 (n = 17,838 lobsters). Shell disease positive lobsters (n = 363) sampled in LIS ranged in size from 37.3 to 88.1 mm CL, with mean CL of 69.81 mm and median CL of 71 mm. The shell disease samples were collected at various depth ranges from 4.9-42.7 m and between 40.98:41.31 °N and 73.37:72.07 °W. The observed bottom temperature and salinity associated with shell disease positive lobster ranged from 3.9-22.1 °C and 24.8-31.5 ppt respectively.

The location variable identified as a bivariate interaction covariate by latitude and longitude was found to be the most important determinant in the probability of shell disease presence. The response surface of the location variable indicates that probability of shell disease presence increased toward the northeastern region of LIS (Fig 4.3). Neither longitude nor latitude was found to be significant in the best-fitting positive catch probability model.

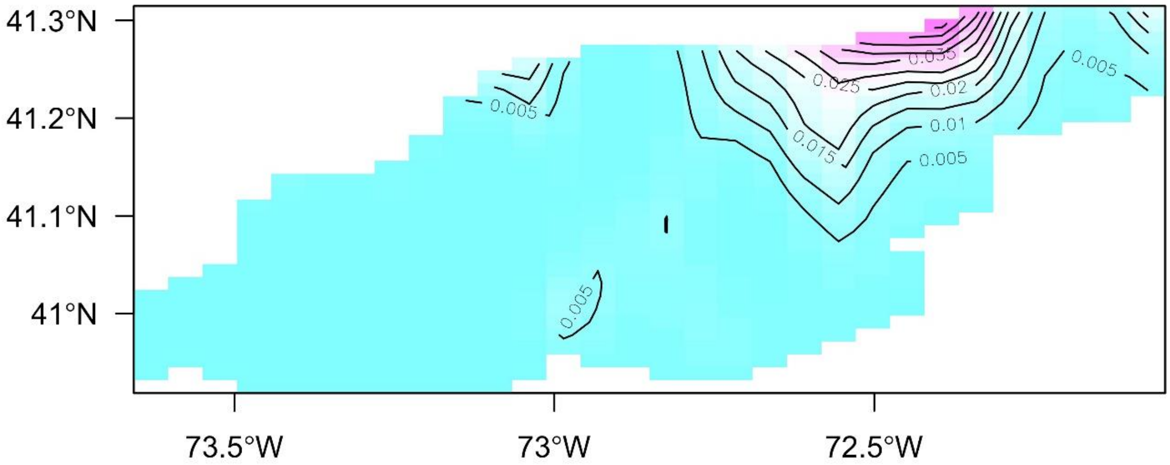

Figure 4-3: Partial generalized additive model (GAM) plot describing the significant interactive contribution of bivariate location variable in the best-fitting encounter rate probability model (1st stage).

Bottom temperature and bottom salinity were included in the best-fitting encounter rate probability model (Figs 4.4 and 4.5). Both abiotic variables had a significant non-linear effect on the probability of shell disease presence. The bottom temperature response curves from the best-fitting encounter rate probability model showed higher probability of shell disease presence at < 5 °C and between 10-15 °C, while the temperature response curve from the positive catch model showed that the relationship was dome-shaped with a peak probability of shell disease abundance between 10-15 °C. Bottom salinity also showed significant effect on both shell disease encounter rate and positive catch probability, where the probability of shell disease presence peaked at ~25 ppt, while the probability of shell disease positive catch increased at higher salinity ranges (Figs 4.4 and 4.5). Distance offshore was included in the best-fitting encounter rate probability model, while depth was included in the best-fitting positive catch model (Figs 4.4 and 4.5). The distance offshore response curve from the encounter rate probability model indicates that the probability of disease presence peaked between 5-10 km (Fig 4.4). The probability of conditional disease abundance was lowest at approximately 20 m depth (Fig 5).

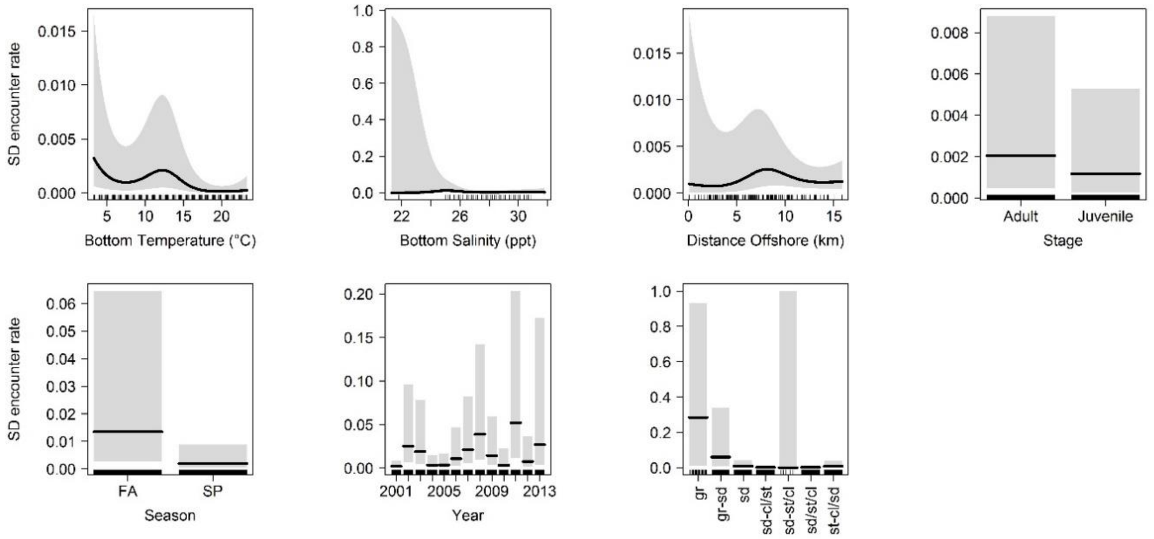

Figure 4-4: Fitted back-transformed smoothing curves for significant univariate explanatory variables in the best-fitting encounter rate probability model (1st stage). The tick marks on x-axis denote the relative density of observation. The grey envelopes represent the 95% confidence intervals. The boxes with "NS" represent univariate explanatory variables that were not significant in the model. The boxes with "INT" indicate that the variables were used as a bivariate interaction variable. Note that the range of y-axis differs among the panels for display purposes. SD: shell disease.

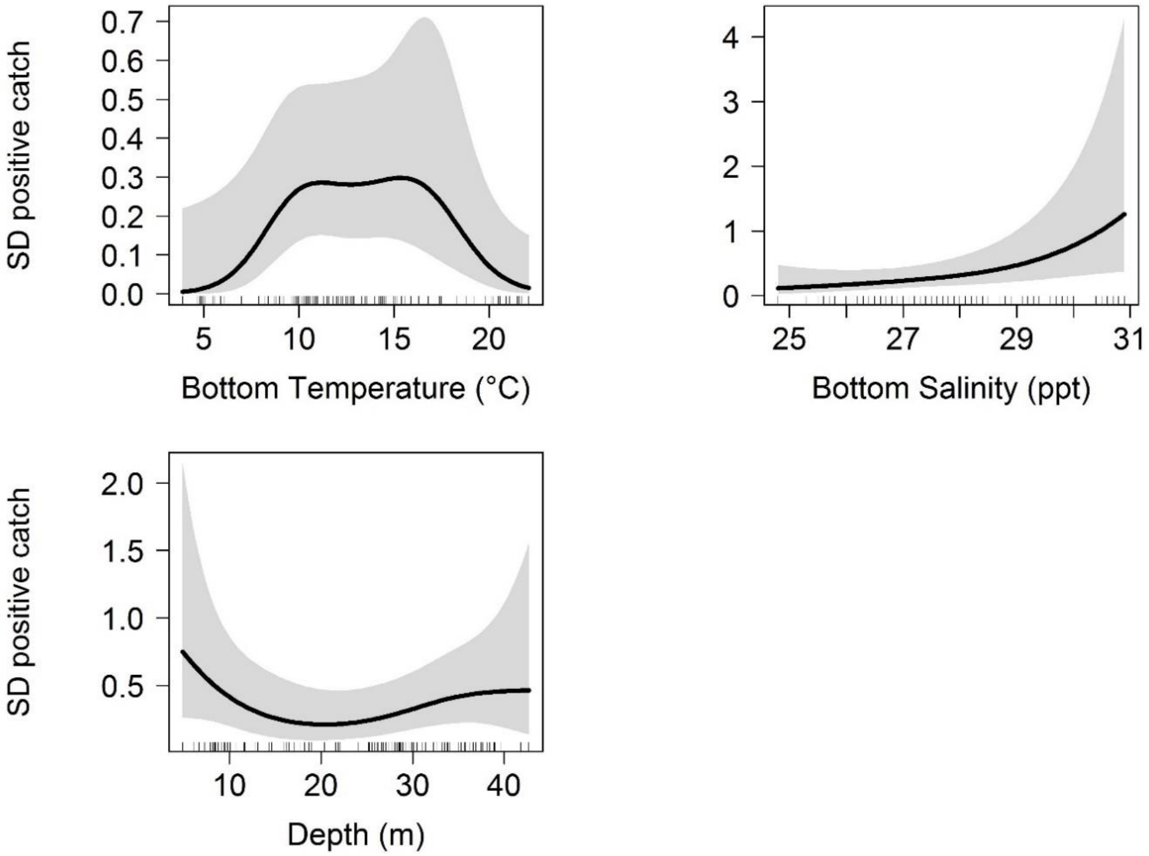

Figure 4-5: Fitted back-transformed smoothing curves for significant univariate explanatory variables in the best-fitting positive catch probability model (2nd stage). The tick marks on x-axis denote the relative density of observation. The grey envelopes represent the 95% confidence intervals. The boxes with "NS" represent univariate explanatory variables that were not significant in the model. Note that the range of y-axis differs among the panels for display purposes. SD: shell disease.

A year effect was included in the best-fitting encounter rate probability model as a significant temporal variable (Fig 4.4). The disease encounter rate probability per tow was the lowest in 2001, but peaked in 2011. Effects of bottom type, stage, and season were only significant for the encounter rate probability model. The highest disease encounter rate probability was associated with gravel, while the lowest encounter rate probability was associated with sand-silt/clay (Fig 4.4). The adult life stage and fall season (September-October) were also associated with higher probability of disease presence (Fig 4.4).

4.4.2 Model fitting and validation

All candidate explanatory variables were observed with VIF less than 3 (Table 4.1), therefore multicollinearity was determined to be negligible in the model development. The best-fitting binomial GAM (1st stage encounter rate probability model) explained 56.3% of the deviance, while the best-fitting negative-binomial GAM (2nd stage positive catch model) explained 31.3% of the deviance (Table 2). A comparison of the mean cross-validation results with an ideal model performance (e.g. a model without prediction bias; $\alpha = 0$, $\beta = 1$, and $R^2 = 1$) indicated that the delta-GAM predicted the overall shell disease prevalence well ($\alpha = 0.134$, $\beta = 0.809$, and $R^2 = 0.43$; Fig 4.6). A slight bias toward over-prediction at low prevalence was observed while the degree of over-prediction increased with higher prevalence. However, the model's predictive performance was considered to be sufficient for predicting an overall distribution of the true shell disease prevalence in this study.

Table 4-2: Comparison of full and best-fitting generalized additive model (GAM) results for the delta modeling approach.

1st stage "Encounter Rate Probability" GAM (n = 2008)

Model	**Formula**	**edf**[a]	**Deviance explained (%)**	**AIC**[b]
Full	Size + Sex + Season + Year + Sediment Type + s(Bottom Temperature) + s(Bottom Salinity) + s(Depth) + s(Distance Offshore) + s(Longitude) + s(Latitude)	3.98 3.89 3.62 3.50 3.06 1.00	50.10	1453.08
Best-fitting	Size + Season + Year + Sediment Type + s(Bottom Salinity) + s(Distance Offshore) + s(Bottom Temperature) + s(Longitude, Latitude)	3.86 3.67 3.95 26.72	56.30	1371.03

2nd stage "Positive Catch Probability" GAM (n = 142)

Model	**Model**	**edf**	**Deviance explained (%)**	**AIC**
Full	Size + Sex + Season + Year + Sediment Type + s(Bottom Temperature) + s(Bottom Salinity) + s(Depth) + s(Distance Offshore) + s(Longitude) + s(Latitude)	2.99 2.96 1.04 1.00 1.04 1.00	53.20	217.346
Best-fitting	s(Bottom Temperature) + s(Bottom Salinity) + s(Depth)	3.21 1.42 2.38	31.30	207.056

[a] edf: estimated degree of freedom

[b] AIC: Akaike information criterion

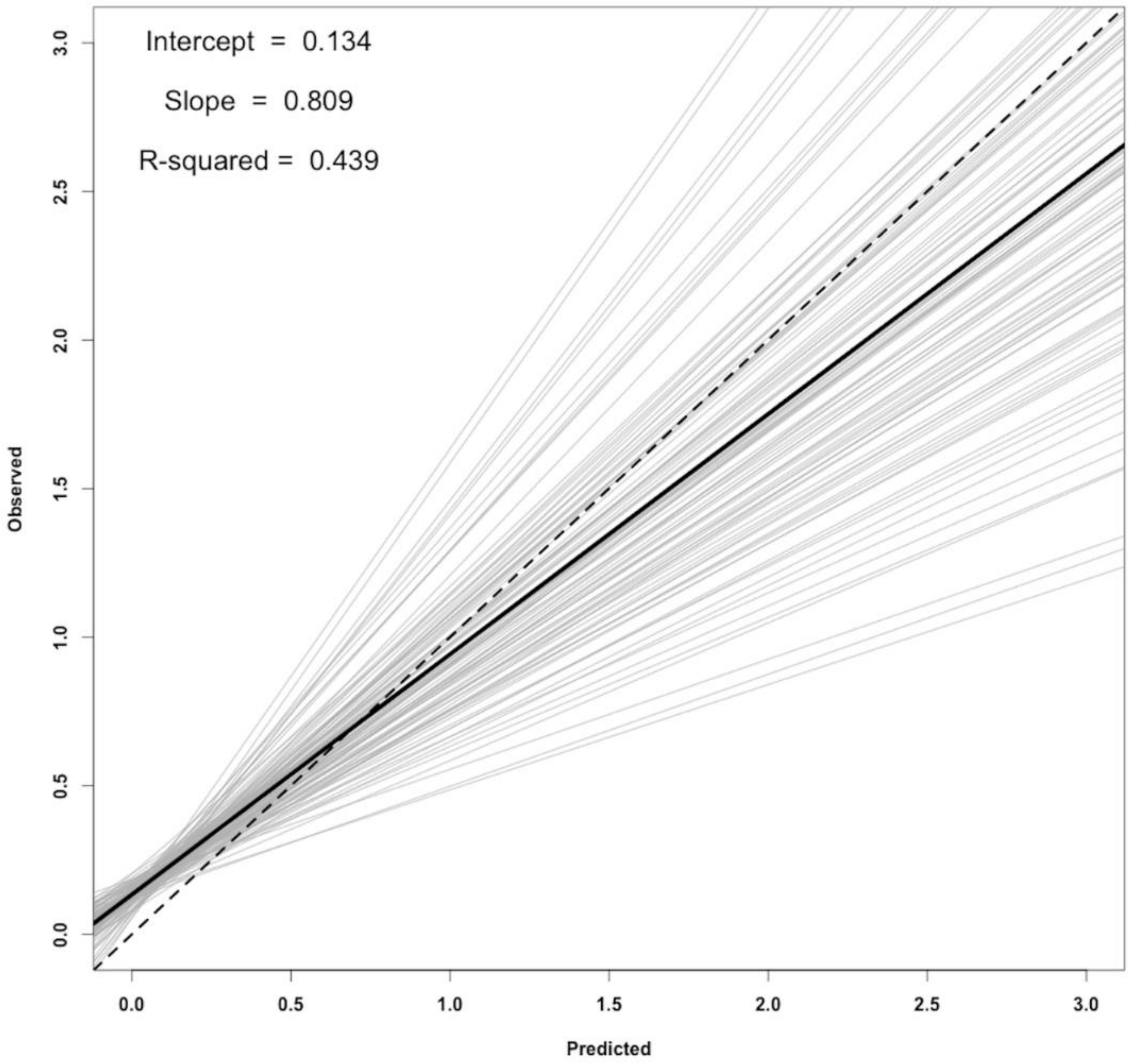

Figure 4-6: Bivariate observed versus predicted plot complemented by the graphical summary of regression analyses from 100 runs of cross-validations for the delta generalized additive modelling (GAM) effort. The light gray lines represent 100 linear regression lines. The black line represents the mean of 100 linear regression lines. The dashed line represents the 1:1 line and an ideal model performance.

4.4.3 Delta-GAM prediction and survey-based gravity centers of disease prevalence

The delta-GAM was used to generate zero inflation adjusted estimate of shell disease prevalence (per minute towing; 101 m^2). The predicted shell disease prevalence in LIS showed a ‘high-east: low-west’ spatial pattern (Fig 3.7a). The delta-GAM predicted high disease prevalence in the shallow waters on the southwestern and northeastern sides of Fishers Island in northeastern LIS. The survey-based gravity centers of shell disease shifted northeastward during 2001-2013 in the area between 72.8:72.3° W and 41.1:41.25 ° N (Fig 3.7b); however, the survey-based gravity centers did not coincide spatially with the predicted disease hotspots.

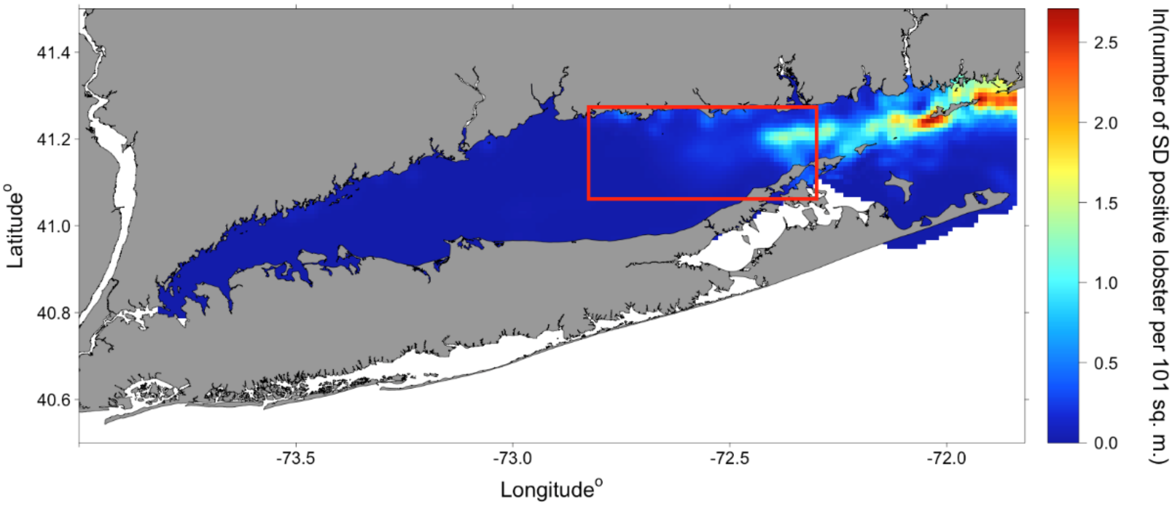

Figure 4-7: Mean spatial variation of predicted zero inflation adjusted shell disease (SD) prevalence, expressed as ln(number of SD positive lobster per 101 m^2), for 2001-2013. The red rectangle represents the spatial domain of Fig 7b.

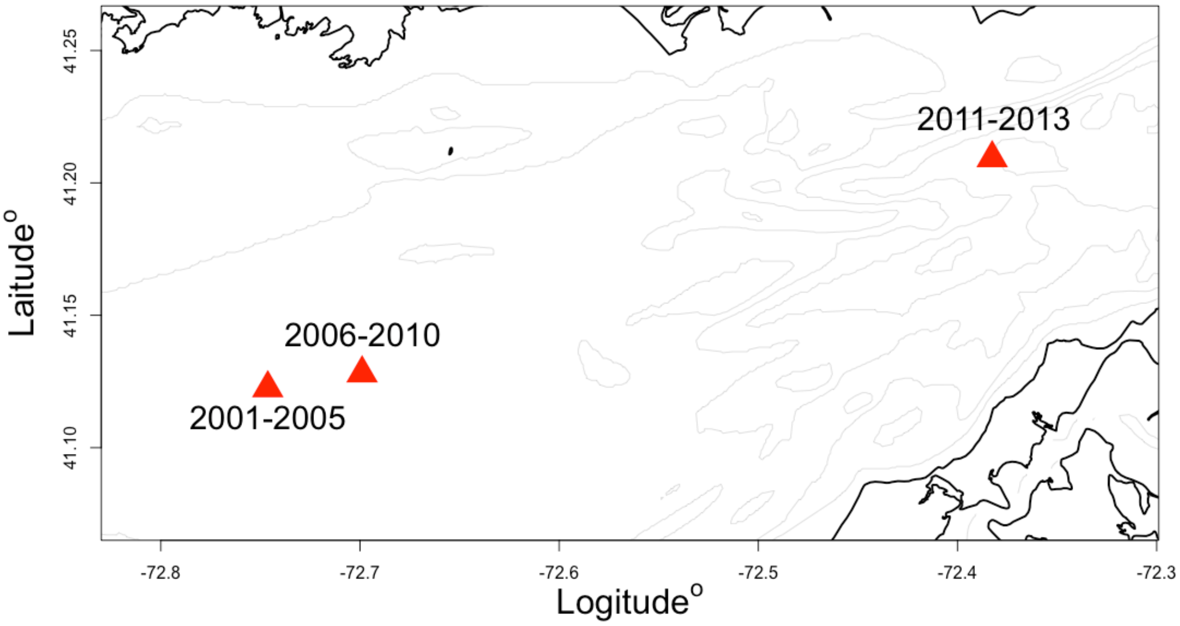

Figure 4-8: Observed inter-annual variability in shell disease gravity centers for 2001-2013.

4.5 Discussion

4.5.1 Ecological interpretation of model outputs

The delta-GAM developed in this study identified a high concentration of shell disease prevalence in northeastern LIS (Fig 3.7a). A similar pattern has been documented in other studies, although its drivers remain difficult to identify. However, bottom water temperature has been frequently cited as one major contributor to shell disease occurrence (Glenn and Pugh 2006; Shields 2013). Because eastern LIS has had higher rates of temperature increase and higher mean maximal monthly temperatures than western LIS (Maynard et al. 2016), this could be influencing the patterns we describe. Eastern LIS is also known to have higher levels of contaminants such as PCBs, pesticides, and metals than other regions of the Sound, which have also been noted as potential contributors to various lobster diseases (Harder et al. 1992; Shields 2013).

Other potential causes of shell disease seem to be distributed paradoxically to the east-high, west-low spatial prevalence patterns. For example, shell diseased symptoms occur when the loss of shell material exceeds its natural deposition (Tlusty et al., 2007), therefore it is expected that shell disease would coincide with areas with high concentrations of alkylphenols, which inhibit shell growth (Laufer et al. 2012). However, Jacobs et al., (Jacobs et al. 2012) found that levels of alkylphenol contamination was highest in lobsters from western LIS, where observed disease prevalence is generally lowest. Similarly, presumably stress-inducing hypoxia increases in severity from east to west, in opposition to the shell disease prevalence documented here (Robohm et al. 2005).

Potential insights into disease etiology in LIS can also be gained by evaluating univariate explanatory variables individually. For instance, the response curves from best-fitting binomial and negative-binomial GAMs were generally in agreement with existing literature related to habitat tolerance of American lobster with regard to bottom temperature, bottom salinity, depth and sediment type (Harding 1992; Jury et al., 1994; Mercaldo-Allen and Kuropat 1994; Crossin et al., 1998; Chang et al., 2010; ASMFC, 2015a; Tanaka and Chen 2015), indicating shell disease occurrence often coincides with optimal or near-optimal lobster habitat conditions. For instance, Tanaka and Chen (Tanaka and Chen, 2015) identified suitable salinity for lobster in LIS is between 21 and 30.4 ppt, which is also contained the salinity range where shell disease is found (Fig 4). These results are unexpected given past research (e.g., Tlusty et al., (2007) suggesting that environmentally-induced physiological stress is a precursor to shell disease incidence. However, this pattern could be explained by an increased propensity for infected individuals to move away from stressful conditions found in suboptimal environments, due to the costs they are incurring while subjected to stressful conditions.

Water temperature has been previously identified as a significant contributor to shell disease occurrence (Glenn and Pugh 2006; Shields 2013). The significant, nonlinear relationship between bottom water temperature and shell disease encounter rate probability we documented (Fig 3.4) is likely reflective of lobsters' varied molting rate at different temperatures and ability to molt out of a moderately infected shell (Stevens 2009). For instance, encounter rate probability peaks between 10-14°C, when disease progression may be outpaced by molting rates. Similarly, the reduction in prevalence toward 20 °C could be attributable to molting rate exceeding disease progression. The increasing presence of shell disease in fall as indicated by our model coincides with previous studies performed in eastern LIS where disease prevalence increased through the summer and into fall as waters warmed (Castro, 2005; Landers, 2005) as well as near Massachusetts where the highest concentration of shell disease in the study area correlated with cumulative periods of time where water temperatures exceeded 20°C (Glenn and Pugh 2006).

This model further reinforces the likely role of demographic characteristics to shell disease susceptibility. Because juveniles tend to molt more frequently, less time is allowed for shell disease to become established before a shell is molted. Therefore, the significance of age in our model are likely due to extended intermolt durations for large individuals (Stevens 2009). Ovigerous females have often been found to have a higher incidence of shell disease than either males or non-reproductive females due to delayed molting cycles (Castro and Somers, 2012; Howell, 2012); however, our model did not detect a significant effect of sex. We attribute this result to the concatenation of samples taken throughout the year, which may mask the effects of higher prevalence for females during egg-bearing times of the year when molting is postponed.

4.5.2 Model implications and limitations

For reasons of logistical rationality and simplicity, monitoring of marine species is conducted based on a spatiotemporal scale relevant to observers, not marine species (Horodysky et al. 2015). This bias, due to differences between the stratification strategies employed by the observer and marine species, results in disease presence, origins and spread often remaining undetected (Harvell et al. 2004). In this study, the delta-GAM predicted a significant hotspot of lobster shell disease in the non-surveyed area in the northeast of the LIS, which did not coincide with observed shell disease gravity centers. The model-based disease probability map can be used to generate hypotheses about exposure for further investigation by overlaying with maps of potential anthropogenic pollution sources and areas where lobsters are under prolonged environmental-stress. Association of the marine disease to surrounding abiotic and biotic factors in many cases is poorly understood. The delta-GAM approach developed in this study can enhance our understanding of continuing lobster shell disease threats and monitoring effort by (1) quantifying the significance and association of environment and host characteristics in lobster shell disease prevalence, and (2) developing a parsimonious statistical modeling framework to predict the spatial distribution of shell disease prevalence from zero-inflated observations.

Our approach has a number of potential limitations. While one of the objectives of this study was to develop a simple, parsimonious modeling framework to complement both descriptive and predictive research priorities, GAM is a data driven approach that is often limited by the data available for model calibration. For example, a p-value of 0.05 was used as cut off for statistically significant associations, but it is important to acknowledge that some key covariates (e.g. host sex) may be determined not statistically significant and excluded simply due to; (1) the relatively small number of diseased lobsters in the original data, and (2) significant associations exerted by abiotic (e.g. bottom temperature) and spatial variables (e.g. latitude *longitude interaction) “masking” the weaker associations of these biological variables. The location variables (i.e. latitude and longitude) were used to capture the localized effects (Rooper et al. 2016; Winton et al. 2014); however, provided that the data are available, incorporating key variables such as pollution, pH level, surface chlorophyll, hypoxia frequency, and population memory would likely allows us to further tune the delta-GAM to be a more comprehensive management tool (Grüss et al. 2014; Loots et al. 2010). Further improvements could be made by applying models that explicitly account for progression of disease prevalence over time, integrate both measured and unmeasured covariates, and include the consideration of spatial and temporal autocorrelation (Grüss et al. 2014; Shelton et al. 2014). However, while such an advanced model may yield better predictive performance, other aspects of model performance should also be considered (e.g. ecological realism as well as model usability to non-expert stakeholders)(Franklin 2010). It is also important to acknowledge that the best-fitting models identified in this study were developed for specificity over generality to allow interpolation in LIS (i.e. filling in the gaps in survey data and describing known disease distributions), and the model outcomes in the area outside of LIS should not be considered. A simpler model will be required to make more general but robust extrapolation through space or time (Franklin 2010; Hare et al. 2012).

Finally, distinction and trade-off between empirical-based statistical modeling approaches (e.g., GAM) and process-based mechanistic modeling approaches (e.g., agent-based model) should be addressed explicitly (Franklin 2010). In an epidemiological context, the strength of a statistical modeling approach lies in its ability to provide a mathematical basis for hypothesized associations between observed disease prevalence and environmental factors (Pedersen et al. 2014), while mechanistic modeling approaches can simulate underlying processes driving the disease prevalence (McCreesh et al. 2015). As for the trade-off, both approaches are subject to specific sources of uncertainty. For instance, where empirical-statistical models are unable to incorporate source-sink processes, process-mechanistic models are unlikely to capture the true complexity of ecosystems (Beale and Lennon 2012). The empirical-based statistical modeling framework presented in this study represents a first step toward comprehensive modeling efforts to better understand the complex epizootic disease dynamics. For example, GAM can be used to incorporate ecological information associated with the geographical distribution and habitat suitability of diseased lobsters for more mechanistic approaches (Keith et al. 2008), which can potentially predict the habitat-dependent environmental impact on shell disease dynamics more accurately.

4.5.3 Management Implications

Harvell et al., (Harvell et al. 2004) identified several key marine disease management priorities, which can enhance the research, monitoring and management of emerging and continuing marine disease threats. These include pinpointing the role of biotic and abiotic factors in disease spread, developing forecasting models for outbreaks that are sensitive to environmental and climatic factors, and implementing ecosystem-based surveillance programs for emerging marine diseases. The combination of empirical data and modeling presented here aims to address these management priorities and provide a valuable tool for the management of inshore and offshore lobster fisheries, which were the highest valued commercial fishery in 2014, worth in excess of half a billion dollars (NMFS, 2016). The approach can be used to guide decision-making in monitoring and management of lobster shell disease. Ultimately, our findings will provide policy-relevant information for effective ecosystem-based disease surveillance programs, which could be of value for the fisheries. The modeling approach described here also provides the framework from which similar models could be developed for other marine organisms and marine diseases in the U.S. and international fisheries. Groner et al., (Groner et al. 2016) call for *"data driven forecasting and predictive modeling"* to adaptively manage emerging marine diseases. The delta-GAM outputs presented in this study can potentially facilitate an effective ecosystem-based management of the commercially important fisheries that are under disease threat. If data are available, the model can also investigate the impact of anthropogenic agents and pathogens.

The success of these actions are dependent upon the major environmental risk factors for the disease being known and that the relevant environmental data are of the appropriate temporal and spatial resolution for the organism under investigation (Groner et al. 2016). As the origins and spread of most marine diseases are poorly known (Harvell et al. 2004), the modeling approach described in this study renders a novel first step towards identifying the potential biotic and abiotic conditions contributing to marine diseases (Groner et al. 2016). Furthermore, through establishment of a framework whereby environmental contributions to disease presence and prevalence may be identified, this modeling approach can potentially provide reliable information for future mechanistic models that may provide the basis for models more predictive in nature, a need highlighted in recent work on marine disease (Groner et al. 2016; Maynard et al. 2016).

Fisheries managers require flexible low-cost tools to help deal with the emerging threat of marine disease. This need is exacerbated by the increasing likelihood of abrupt, nonlinear environmental and climatic changes (Groner et al. 2016). Management strategies, such as closures to reduce fishing morality in order to help restore the stock at broad spatial scales can be costly to implement and to those whose livelihoods are dependent on the managed marine species. In addition, these ‘broad brush’ approaches may impact areas not impacted by disease, thus increasing their cost and impact unnecessarily. Reliable and up-to-date maps of marine diseases, like those provided by this modeling approach, can enhance the monitoring of emerging and continuing marine disease threats by improving the geographical targeting and cost-effectiveness of existing sampling programs which are often limited by logistical hurdles (e.g. cost, resources). Given the increasing uncertainty in the health of the marine resources upon which people rely driven by linear long-term climate trends and more abrupt climatic perturbations, the types of low-cost tools that leverage existing monitoring datasets (e.g. trawl surveys) like the model outlined here can provide essential information in managing wild harvest fisheries that are constantly under disease threats.

CHAPTER 5 - CLIMATIC IMPACTS ON THE LOBSTER DISTRIBUTION

5.1 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 climate 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.

5.2 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 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 system, 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 models 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).

5.3 Materials and Methods

5.3.1 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. 5.1). 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. 5.1) 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;).

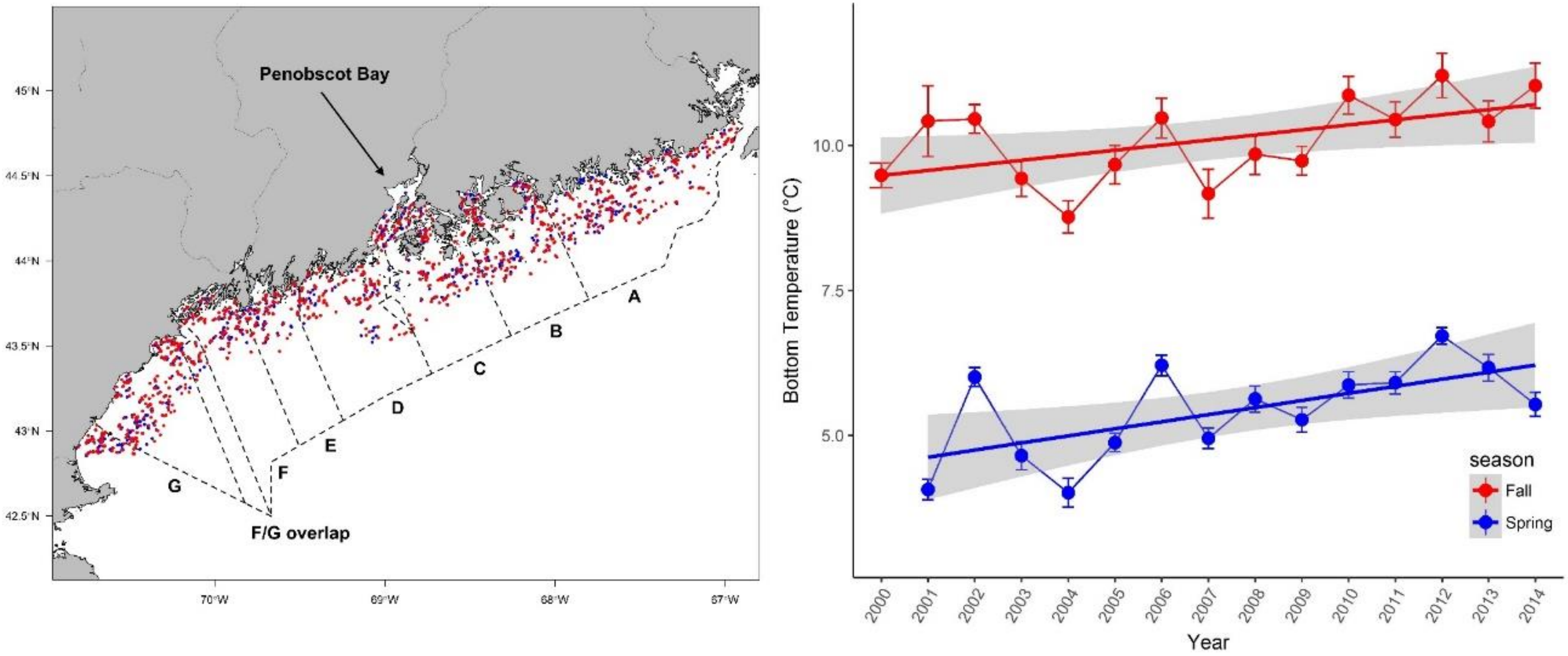

Figure 5-1: left: Study area in the inshore Gulf of Maine covered by Maine/New Hampshire (ME-NH) inshore bottom trawl surveys with station locations during spring (blue, n = 1312) and fall (red, n = 830). The polygons A-G are lobster management zones. right: Bottom temperature trends in the ME-NH bottom trawl survey for spring (0.12 °*C ye*ar^{-1}, R^{2} = 0.34, p <0.05) and fall (0.08 °*C ye*ar^{-1}, R^{2} = 0.24, p <0.05). The gray land lines represent major river systems.

5.3.2 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 and additional fixed 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 identify potential fixed stations, and stations that remained stationary within a 1 nm^2 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 m^{-2} min^{-1} of area swept (Chang et al., 2010: hereafter referred as lobster catch density). In this study, lobster catch density 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.

5.3.3 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 Sagarese 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 η can be expressed as;

$$g(\eta) = \alpha + \sum_{j=1}^{p} s_j\left(x_j\right) + \varepsilon \qquad \textit{Eq. 5-1}$$

where $g()$ represents the log link function between η and each additive predictor; α denotes the intercept term; $s_j()$ denotes a cubic spline function that might be linear or nonlinear; x_j is a single or pair of additive predictor; ε 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 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 (Nakazawa, 2015; Hijmans et al., 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. 5.2). 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 skewered 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).

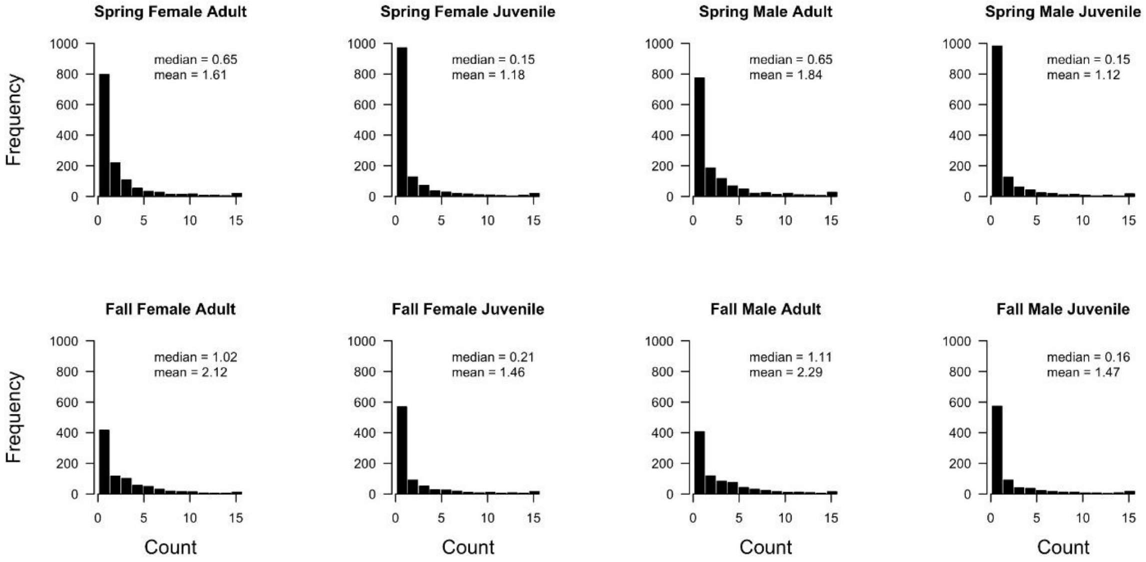

Figure 5-2: Frequency histograms of season, stage and sex specific standardized lobster catch (per 792 m^2) from Maine/New Hampshire bottom trawl survey (2000-2014). Lobster catch larger than 15 was truncated as a plus group to enhance readability.

5.3.4 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 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 (α), slopes (β), and adjusted R^2 to expectations for a precise and unbiased model with $\alpha = 0$, $\beta = 1$, and $R^2 = 1$.

5.3.5 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. For each assessed variable, a bivariate observation versus prediction plot and a set of linear regression coefficients such as the coefficient of determination (r^2), slope (α), and intercept (β) were used to evaluate agreement between observed and modeled data (Stow et al., 2009; Li et al., 2017).

5.3.6 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:

$$Lon_{s,y} = \frac{\sum_{i=1}^{K}(Lon_i * D_i)}{\sum_{i=1}^{K} D_i} \qquad \textit{Eq. 5-2}$$

$$Lat_{s,y} = \frac{\sum_{i=1}^{K}(Lat_i * D_i)}{\sum_{i=1}^{K} D_i} \qquad \textit{Eq. 5-3}$$

where Lon_i *and* 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 climatology (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. 5.3). 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).

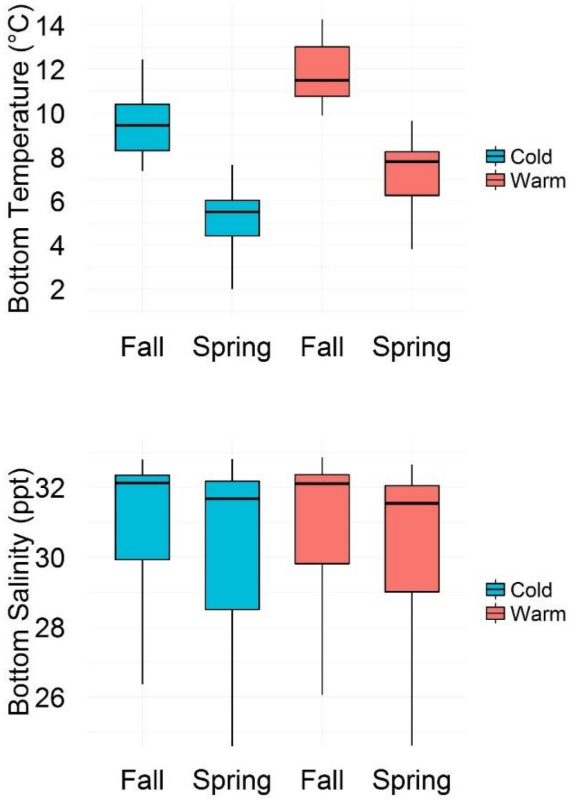

Figure 5-3: Bottom temperature and salinity distributions in the study area for hypothetical cold and warm climatology scenarios from Finite Volume Community Ocean Model. The scenarios were based on five coldest and warmest springs and falls during 1982-2013. Temperatures averaged 9.7 °C (median 9.5 °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.

5.4 Results

5.4.1 GAMs

Latitude (°) and depth (m) with VIF values > 3 were omitted before fitting all GAMs (Table 5.1). 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 5.2). Univariate salinity and longitude terms were included in fall models where statistically significant (Table 5.2). Percent deviance explained ranged from 47% to 56% and was somewhat higher for spring (Table 5.2). 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 5.3). However, variability in model accuracy increased at higher lobster catch density in every modeled group (Appendix A).

Table 5-1: 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. VIF: Variance Inflation Factors

Variables	Description	VIF - Spring	VIF - Fall
Latitude (°)	Mesurement of latitude trawl was conducted (mid trawl point)	15.5	13.2
Longitude (°)	Mesurement of longitude trawl was conducted (mid trawl point)	15.3	12.6
Distance Offshore (m)	Mesurement of distance between a trawl location and coastline	3.9	3.9
Depth (m)	Observed depth at a trawl location	4.4	4.5
Bottom Temperature (°C)	Observed bottom temperature at a trawl location	1.5	1.4
Bottom Salinity (ppt)	Observed bottom salinity at a trawl location	1.8	1.9

Table 5-2: 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.

Season	Sex	Stage	Model	edf	Dev.Exp	AIC
Spring	Female	Adult	s(Do) + s(Te) + s(S, Lo)	4.49, 4.21, 23.75	0.50	3370.33
		Juvenile	s(Do) + s(Te) + s(S, Lo)	4.68, 4.45, 24.88	0.56	3115.12
	Male	Adult	s(Do) + s(Te) + s(S, Lo)	4.21, 4.28, 24.08	0.53	3643.39
		Juvenile	s(Do) + s(Te) + s(S, Lo)	4.53, 4.14, 25.24	0.56	3017.63
Fall	Female	Adult	s(Do) + s(Te) + s(S, Lo)	4.92, 3.98, 19.87	0.47	2594.94
		Juvenile	s(Lo) + s(Do) + s(Te)	4.42, 4.33, 3.45	0.48	2334.61
	Male	Adult	s(Do) + s(Te) + s(S, Lo)	4.47, 3.24, 19.58	0.47	2800.67
		Juvenile	s(Lo) + s(S) + s(Do) + s(Te)	4.46, 3.87, 6.05, 3.51	0.50	2334.91

Spring: n = 1312, Fall: n = 830

Table 5-3: Summary of regression analyses from 100 runs of cross-validations for the season, stage and sex specific lobster generalized additive modelling (GAM) effort.

Season	Sex	Stage	Intercept		Slope		R-squared		GAM Adj. R-sq.
			Mean	95% CI	Mean	95% CI	Mean	95% CI	
Spring	Female	Adult	-0.10	(-0.42 , 0.15)	1.08	(0.85 , 1.38)	0.39	(0.32 , 0.46)	0.37
		Juvenile	0.04	(-0.16 , 0.26)	0.98	(0.70 , 1.20)	0.36	(0.23 , 0.51)	0.33
	Male	Adult	0.00	(-0.27 , 0.24)	1.00	(0.78 , 1.24)	0.39	(0.31 , 0.47)	0.38
		Juvenile	0.04	(-0.17 , 0.28)	0.96	(0.70 , 1.27)	0.35	(0.19 , 0.53)	0.32
Fall	Female	Adult	0.07	(-0.32 , 0.42)	0.96	(0.72 , 1.26)	0.31	(0.22 , 0.41)	0.28
		Juvenile	0.03	(-0.21 , 0.27)	0.98	(0.75 , 1.26)	0.32	(0.21 , 0.44)	0.30
	Male	Adult	0.07	(-0.32 , 0.42)	0.96	(0.72 , 1.26)	0.31	(0.22 , 0.41)	0.28
		Juvenile	0.03	(-0.21 , 0.27)	0.98	(0.75 , 1.26)	0.32	(0.21 , 0.44)	0.30

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. 5.4). 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 (Appendix B). Response curves for distance offshore were similar in all models (Fig. 5.4), 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 (Appendix A). 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. 5.4).

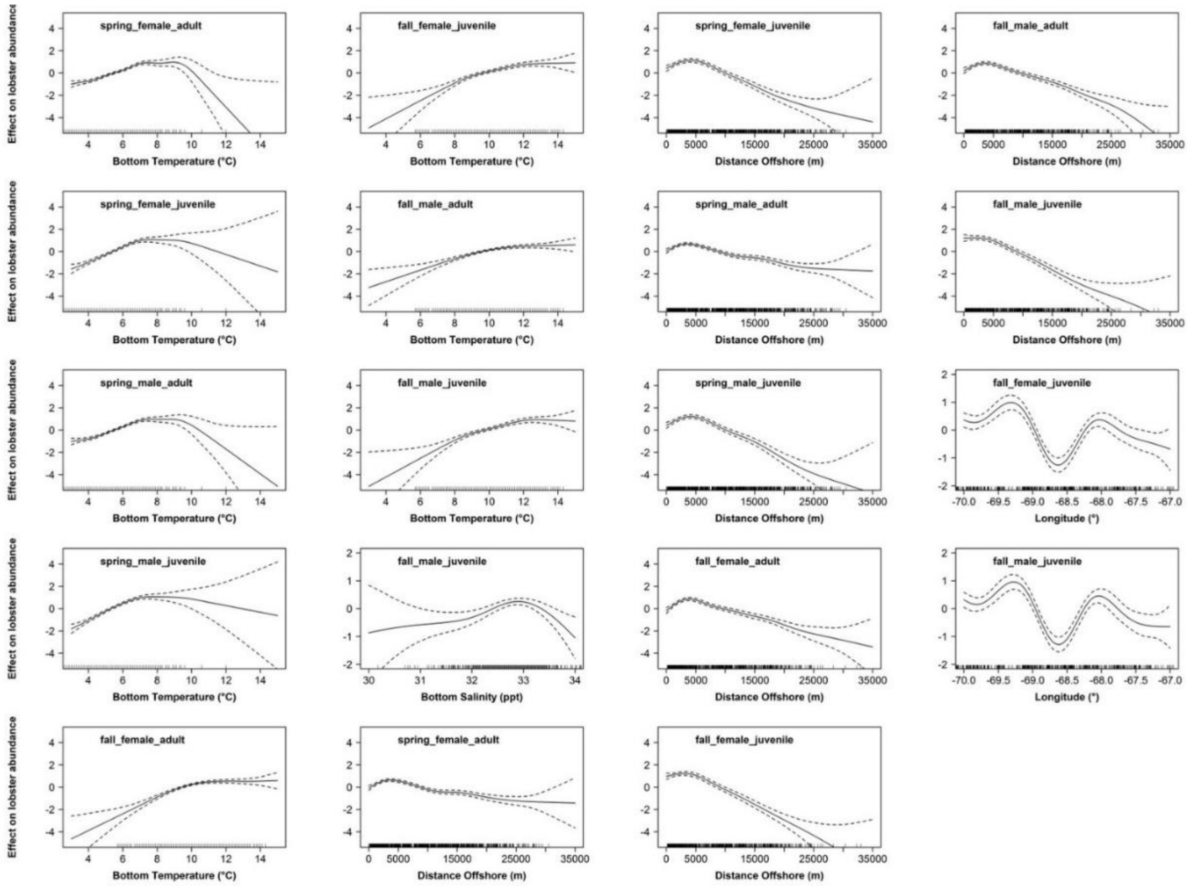

Figure 5-4: Plots describing the partial effect of significant univariate explanatory variables in the best-fitting generalized additive models for lobster catches in Maine/New Hampshire bottom trawl surveys with 95% confidence intervals for the fitted line. The y-axis represents the degree of smoothing with its range showing the relative importance of the explanatory variable. Tick marks on the x-axis denote observations.

5.4.2 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. 5.5). Regression coefficients showed that FVCOM and CRM predictions were almost unbiased for depth and bottom temperature, but biased for bottom salinity. 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.

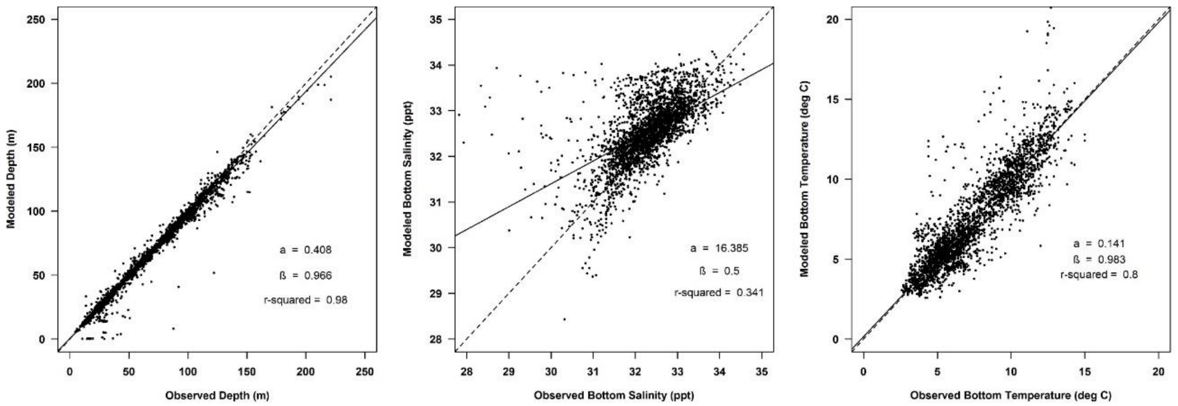

Figure 5-5: Bivariate observed versus predicted plots illustrating the similarity between modeled and observed environmental data. Total 2,982 modeled-observed match-ups were used to assess Coastal Relief Model (CRM) and Finite-Volume Community Ocean Model (*FVCOM*) skills in depth, bottom salinity, and bottom temperature.

5.4.3 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. 5.6). 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. 5.6).

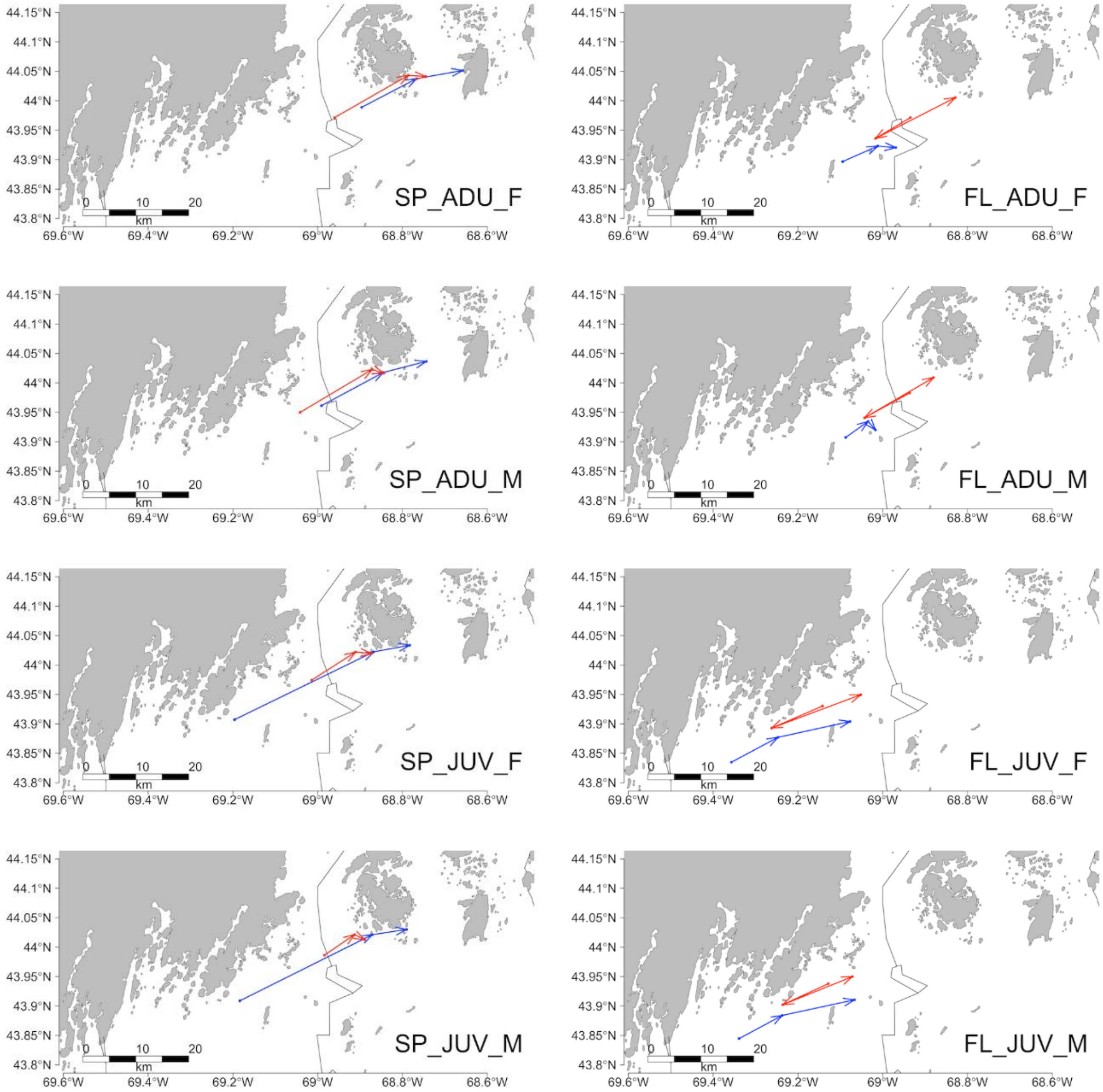

Figure 5-6: Changes in the centroids of predicted (red arrows) and observed (blue arrows) lobster catch densities in the Maine/New Hampshire bottom trawl survey (2000-2014). The observed and modeled shifts in centroids were aggregated to 3-time blocks for ease of visual interpretation (2000-2005, 2006-2010, 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

Median predicted lobster catch density in the study area ranged from 0.53 to 1.58 (Fig. 5.7). Predicted lobster catch density was higher in inshore, for adults, and during fall (Fig 5.7). Lobster catch density was projected to increase under the warm climatology scenario than in the cold climatology scenario across the study area in both seasons and for all size groups (Figs. 8-9). 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. 5.8). 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. 5.9). Lobster catch density was projected to increase across the Gulf of Maine under the warm climatology scenario than in the cold climatology scenario by 65.3% (fall adult male) to 119.8% (fall juvenile male) (Fig. 5.9).

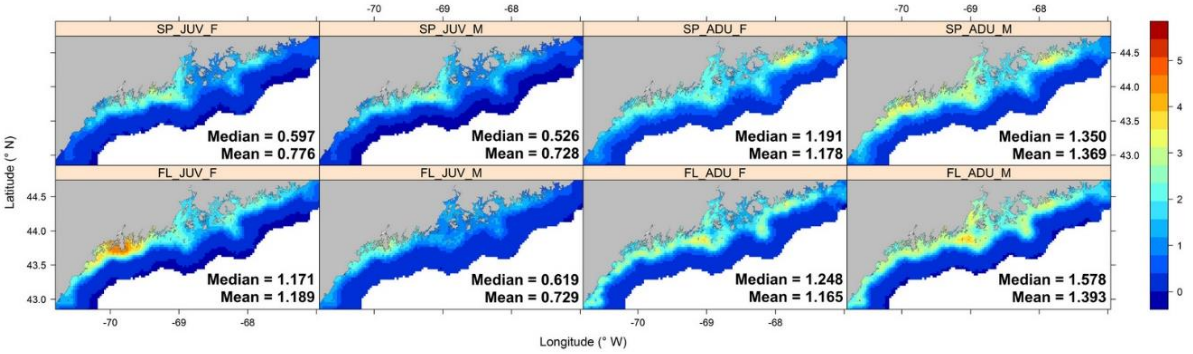

Figure 5-7: Average predicted season-, stage-, and sex- specific lobster catch densities in inshore Gulf of Maine during 1982-2013. The color key indicates predicted number of lobsters per 792 m^2. SP-Spring, FL-Fall, ADU-Adult, JUV-Juvenile, M-Male, F-Female.

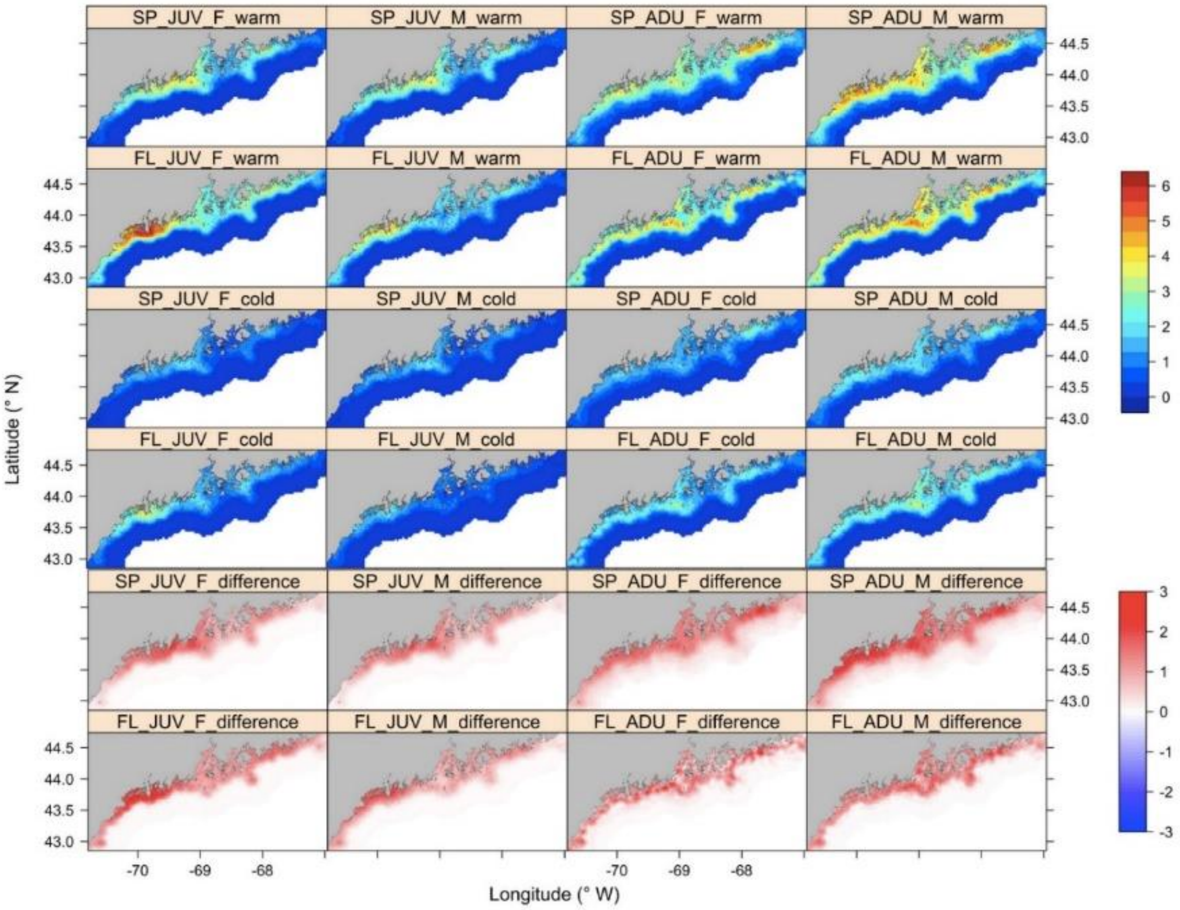

Figure 5-8: Predicted lobster catch densities under warm (1st & 2nd rows) and cold (3rd and 4th rows) climate scenarios. The 5th and 6th row shows difference in catch density between warm and cold climate scenarios derived through cell-by-cell map subtraction. The rainbow color key indicates predicted number of lobsters per 792 m^2, while the red-blue color key indicates changes in lobster catch per 792 m^2.

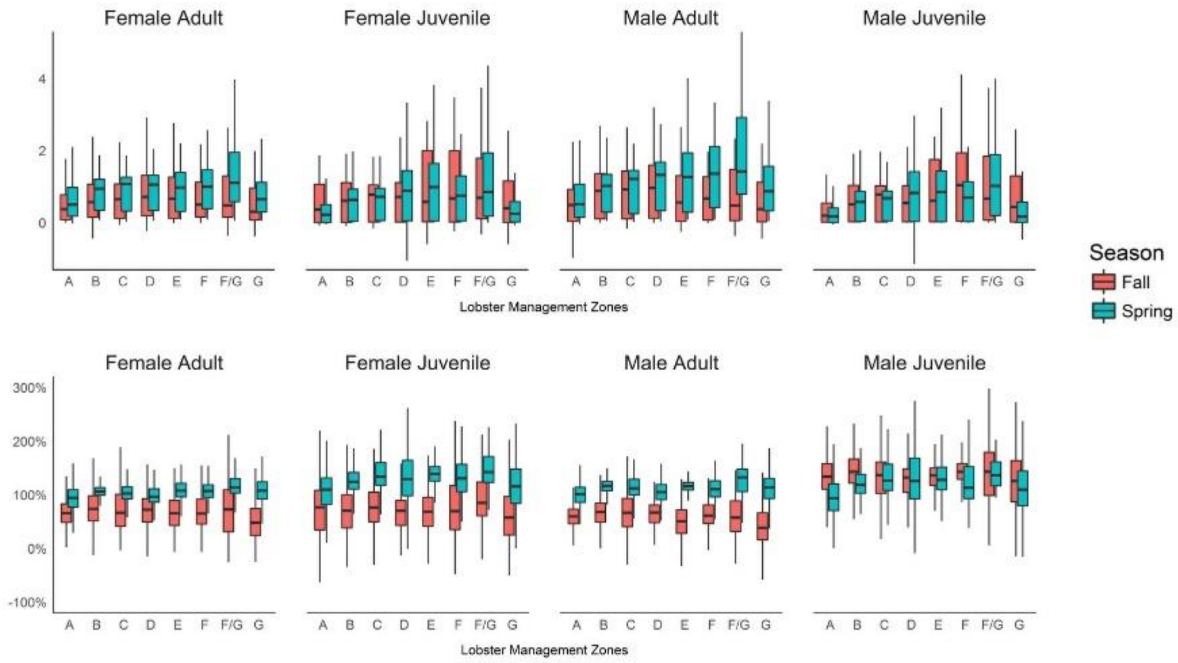

Figure 5-9: Difference (top row) and percentage difference (bottom row) in predicted season, stage, and sex specific lobster catch density per 792 m^2 between warm and cold climate scenarios in Maine Lobster Management Zones A–G.

5.5 Discussion

5.5.1 GAMs

The GAMs with Tweedie distributions for zero-inflated survey catch data were useful prediction tools based on cross-validation results (Table 3 & Appendix A), 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 6; 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 (Crossin et al., 1998; Ennis, 1984; 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 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 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 that low salinity is 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 (Fig. 5). 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 & Appendix B & C). 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 & Appendix C). This localized salinity-longitude effect is likely linked to the changes in bottom salinity in 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 ecological interactions and to 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 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 (Appendix C; McLeese, 1956; Mercaldo-Allen and Kuropat, 1994).

5.5.2 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 variabilities 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. 6). 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 Golf 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 likely opening 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 amount of bait subsidies increased faster in 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 number of traps enhancing lobster population growth in eastern portions of the Gulf of Maine through bait subsidies**.** 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). 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. 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.

5.5.3 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 would likely have a further positive influence on lobster abundance in this study area.

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 assist stakeholders to make an educated guess and prepare for the consequences of abrupt climate variability events and reduce potential management uncertainty as many living marine resource managements are also 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.

Finally, the ME-NH survey data were used as a proxy in this study for lobster distribution and abundance, which assumed that lobster catches (1) reflected the presence/absence and density of the species at a given location, and (2) are not influenced by bias associated with sampling procedure and environmental variability. This assumption was assumed to be reasonable for American lobster that have relatively stable and high survey catchability in the inshore Gulf of Maine (Runnebaum 2017). While there is little supporting empirical evidence around uncertainty for lobster catchability by active gears such as trawl, survey catchability changes due to the availability and behavioral pattern of lobsters that are further affected by factors such as water temperature and operating procedures. For example, water temperature is believed to be an important factor as colder water temperature is speculated to reduce lobster catchability (ASMFC, 2005); however, exact mechanisms are unknown as water temperature affects lobster behavior in many ways. Moreover, the inshore ME-NH survey area may have been relatively saturated any observed changes in lobster abundance may have been influenced by the changes in offshore lobster abundance (ASMFC, 2015). While it is outside the scope of this study, future studies should address need to standardize surveys to generate consistent indices.

5.5.4 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 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. 9). 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.

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 the lobster abundance and subject to future refinement. The future efforts towards advancing ensemble climate-niche modeling (Thuiller et al., 2016) or include 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.

CHAPTER 6 –INCORPORATING ENVIRONMEN INTO ASSESSMENT

6.1 Abstract

Changes in bottom-up forcing are fundamental drivers of the fish population dynamics. Recent literature has highlighted the need to incorporate the role of dynamic environmental conditions, particularly climate variability in the assessment of the fishery stocks as a key step toward the adaptive fishery management in a changing environment. Combining a bioclimate envelope model and a population dynamic model, we propose a model-based framework that can incorporate ecosystem products into single-species stock assessments. The proposed framework was applied to a commercially important American lobster stock in the Gulf of Maine - Georges Bank. The bioclimate envelope model was used to hindcast temporal variability in lobster recruitment habitat suitability index due solely to bottom temperature and salinity. The climate-driven habitat suitability index was used to inform the lobster recruitment dynamics within the size-structured population dynamics model. The performance of the assessment model with an environment-explicit recruitment function is evaluated by comparing relevant assessment outputs such as recruitment, annual fishing mortality, and magnitude of retrospective biases. The environmentally-informed lobster assessment model estimated (1) higher recruitment and lower fishing mortality in the late 2000s and early 2010s, and (2) showed reduced retrospective patterns and improved model fit. This analysis indicates that climate-driven changes in lobster habitat suitability contributed to increased lobster recruitment and present potential improvement to the species' assessment.

6.2 Introduction

The American lobster (*Homarus americanus*) is a commercially harvested benthic species in the Northwest Atlantic Ocean (ASMFC, 2015a). This species is an important fishery resource throughout its range and supports the most productive lobster fishery in the world (Wahle et al., 2013; ASMFC, 2015b). The 2016 ex-vessel value of the U.S. American lobster fishery exceeded USD 669 million and represented an historic high (ACCSP, 2017). The population is assessed as two distinct stock units based on geographic differences in life history parameters: Gulf of Maine/Georges Bank (GOMGBK) and Southern New England (SNE). Thus, for the purposes of assessment, these are considered unit stocks. The latest 2015 benchmark assessment found that the SNE stock is severely depleted while the GOMGBK stock is at record high abundance (ASMFC, 2015a). In 2016, the GOMGBK stock accounted for more than 95% of total American lobster landings, and approximately 85% of all commercial fish landings in the State of Maine (Maine DMR, 2016; ACCSP, 2017;). The dependence of New England's commercial fishing economy on a limited number of species increases the vulnerability of this coupled natural and human system to environmental changes (Steneck et al. 2011).

Climate-driven changes in the Northwest Atlantic ecosystem structure are a growing concern for the fishery because both mesoscale climate change and variability will (1) challenge equilibrium assumptions underlying the population dynamics and subsequent biological reference points of the lobster stocks (ASMFC, 2015b); and (2) introduce substantial uncertainty into management of the fishery (Caputi et al., 2013; Mills et al., 2013; Steneck and Wahle, 2013; ASMFC, 2015a; Le Bris et al., 2018). American lobsters are ectothermic and experience strong bottom-up control throughout their range and life stages (e.g., climate change; Caputi et al., 2013; ASMFC, 2015a; Boudreau et al., 2015). The Gulf of Maine sea surface temperature has increased 0.03 °C per year since 1982 (Pershing et al. 2015) and bottom temperature showed similar increasing trend (Kleisner et al. 2016). According to the latest Intergovernmental Panel on Climate Change - Representative Concentration Pathways 8.5 Emissions Scenario (IPCC-RCP 8.5), average bottom temperature in the Northeast U.S. continental shelf system is expected to increase more than

Climate-driven changes in the ecosystem are likely to influence lobsters as the species is known to track its realized niche in space (e.g. distribution shifts) and time (e.g. phenological shifts) (Caputi et al., 2013; Fogarty et al., 2007; Qadri et al., 2007). Tanaka and Chen (2016) reconstructed the spatiotemporal variability of American lobster bioclimate envelopes (i.e. lobster habitat quality and boundaries defined by physical and climatic variables) from 1978 to 2013 and found an increasing trend in climate-driven habitat suitability in the inshore Gulf of Maine. Mills et al., (2013) reported that record warm temperatures in the Gulf of Maine during the 2012 Northwest Atlantic Ocean heatwave resulted in unusually early and high landings of newly recruited lobsters to the fishery, which ultimately contributed to a decline in total value of the fishery.

Incorporating ecosystem variability into assessment of the US lobster stocks has been advocated as a key step towards implementing adaptive ecosystem-based fisheries management for this stock and potentially mitigating the negative effects of climate change (ASMFC, 2014). However, the current salient results of U.S. lobster stock assessments focus on harvest rates and spawning stock biomass (SSB) and do not explicitly incorporate the impact of environmental variability (ASMFC, 2015a). There remains a critical knowledge gap in evaluating the synergistic impacts of climate change on stock status as well as maximizing the efficiency and accuracy of the existing assessment program.

To this end, this study presents a model-based framework that can incorporate ecosystem products into single-species stock assessments. The framework consists of the following two modeling components: (1) an empirical bioclimate envelope model that quantifies the spatiotemporal variability of lobster habitat suitability due solely to bottom temperature and salinity; and (2) a size-structured population dynamic model that incorporates environmental effects to inform recruitment dynamics.

It was hypothesized that the GOMGBK lobster recruitment dynamics were driven by the climate-driven environmental variability, therefore incorporating environmental signals can potentially improve recruitment estimates. To test this hypothesis, changes in annual median lobster recruit habitat suitability index (HSI) during 1984-2013 were treated as an index of environmental variability, which was assumed to have influenced the stock recruitment dynamics during the period. The climate-driven habitat suitability index was used to inform the lobster recruitment dynamics within the size-structured population dynamics model. The performance of the assessment model with an environment-explicit recruitment function is evaluated by comparing relevant assessment outputs such as recruitment, annual fishing mortality, and magnitude of retrospective biases.

The framework was designed to improve assessment of the U.S. American lobster stocks but extendable to other fish populations that are impacted by environmental change. The proposed model-based framework can improve our understanding of environmental-driven marine ecological processes and ability to assess the status of exploited fishery resources, which can potentially enhance our adaptive management capacity in changing environment.

6.3 Materials and methods

6.3.1 Description of the GOMGBK lobster fishery

The fishery considered in this study encompasses portions of the Gulf of Maine and Georges Bank (Fig. 6.1). The commercial lobster fishery in the Gulf of Maine and Georges Bank started during the 19th century (Mateo et al., 2016). Total landings remained relatively low through the 1940s and began increasing during the 1970s. The fishery experienced increasing fishing effort throughout the region since 1984, and the total landing has increased by more than 600%. Commercial lobster landings in the Gulf of Maine were relatively stable through 1990 but increased substantially and reached a time series high of over 64,000 metric tons in 2013. In 2016, the fishery became the most valuable single-species fishery in the US (ACCSP, 2017). The fishery is regulated through a series of conservation measurements such as minimum and maximum size limitations and v-notching of egg bearing females (A v-notch is a cut on the tail flipper of a female lobster placed by commercial fishermen to identify and protect breeding individuals from harvest: ASMFC 2015a). The fishery is divided into several local co-management zones in state waters that regulate effort as well as a federally-managed offshore fishery. The GOMGBK stock is mainly harvested by boats homeported in the US states of Maine, New Hampshire and Massachusetts. More than 98% of the total lobster catch in the region was reported from the inshore fishery (< 3 nm from shore) which targets mainly lobsters newly molted to legal size. The dynamic of the fishery is modeled using a size-structured model that estimates numbers of lobster by size, sex, season, and year (Chen et al. 2005; ASMFC, 2015a).

While the largest American lobster population is found in the Gulf of Maine, lobsters in the Gulf of Maine and Georges Bank are considered a single biological stock unit for the purposes of population assessment (ASMFC, 2015a). Sex ratio in the GOMGBK lobster stock is skewed towards females (ASMFC, 2015a). This is potentially due to region-wide conservation efforts targeting egg-bearing and v-notched females. Lobsters are long-lived; they can reach 70+ years in the wild. Molt frequency varies with life history stage and size, and tagging studies show that molting lobsters generally increase in size by about 15% in length and weight (Factor, 1995). Lobsters normally require 20-30 molts from the early larval stage to reach the minimum legal size of 81 mm carapace length (CL). Molt frequency declines after sexual maturity is reached. American lobster is assumed to be a k-selected species and the GOMGBK stock experiences relatively low natural mortality ($M = 0.15\ y^{-1}$ assumed in the latest benchmark assessment; ASMFC 2015a).

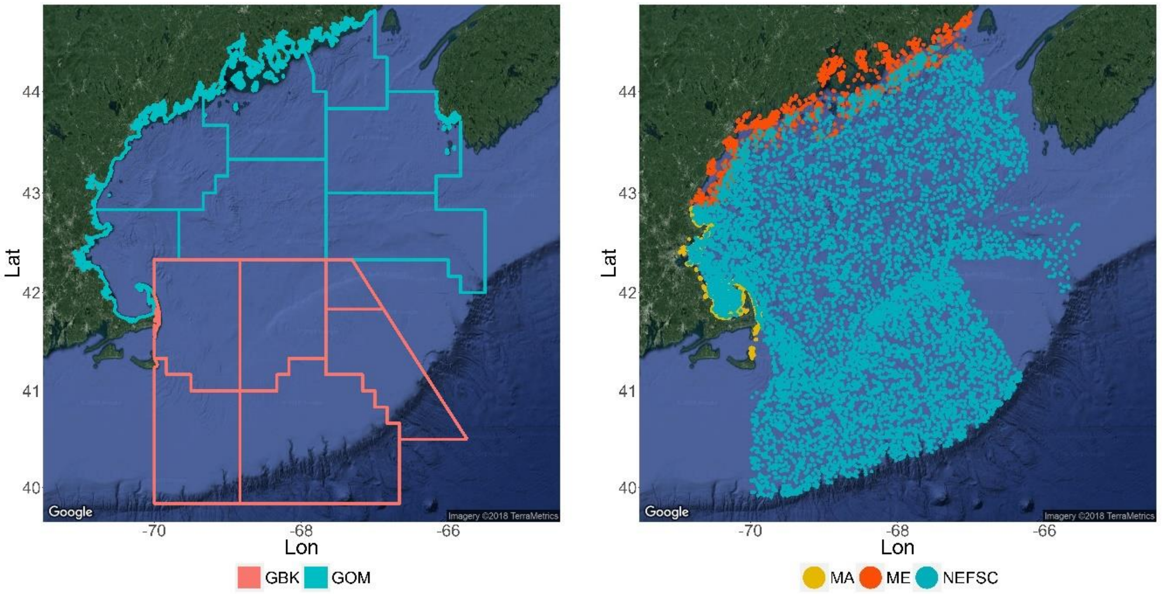

Figure 6-1: Left: Gulf of Maine/Georges Bank (GOM/GBK) lobster stock management areas based on the NOAA statistical reporting areas. Right: Sampling locations from bottom trawl surveys during 1984-2013 used in this study (MA-Massachusetts, ME-Maine New Hampshire, NEFSC-Northeast Fisheries Science Center).

6.3.2 Data

The data available for the bioclimate envelope model are 30 years of bottom trawl surveys and a selection of the associated biological (CL) and environmental (season, bottom temperature, bottom salinity and depth) variables (1984-2013: Fig. 6.1 & Appendix E). The data available for size-structured assessment model are 30 years of seasonal catch and effort, catch size compositions, and survey abundance indices and size-compositions (1984-2013: Appendix E). The following sections provide summaries of both fishery dependent and independent survey data used in this study.

6.3.2.1 Fishery independent data

The fishery-independent survey data used in this study were (1) bottom trawl survey data collected by the Northeast Fisheries Science Center (NEFSC: 1982-2013) that covers offshore continental shelf waters, and the Maine/New Hampshire (MENH: 2000-2013) and Massachusetts (MA: 1982-2013) state surveys that cover inshore waters; and (2) coast-wide ventless trap surveys (VT: 2006-2012) that cover untrawlable substrate (Smith and Tremblay 2003). All fishery-independent surveys employed a stratified random design. The inshore trawl surveys and the NEFSC offshore survey were conducted during the spring (Q2: April-June) and fall (Q4: October-December) of each year. The coast-wide ventless trap surveys were conducted during the summer (Q3: July-September). Information from the coast-wide ventless trap survey data (2006-2012) were used for the size-structured assessment model but not the bioclimate envelope model because the ventless data lacked necessary spatial (e.g. latitude and longitude) and environmental data (e.g. bottom temperature). More detailed information on survey area and timing, years surveyed, sampling design, gear, and methods for each survey can be found in ASMFC (2015a).

6.3.2.2 Fishery-dependent data

Seasonal commercial catch and effort data during the 1984-2013 fishing years were analyzed. These fishery-dependent data include a time series of landings and catch size composition by season and sex. The size structure of the landed catch reflects the fishery’s minimum (81 mm) and maximum (128 mm) legal sizes and was relatively stable over the time series. Commercial catch data for the different fisheries that fish the GOMGBK lobster stock were aggregated into a single fleet as lobsters are caught using lobster traps of a single gear type and the fishery prohibits the landing of lobsters caught by other mobile gear (ASMFC, 2015a).

6.3.3 Bioclimate envelope model

Using bottom trawl survey data (1984-2013 for NEFSC and MA, 2000-2013 for MENH) and the empirical bioclimate envelope model developed by Tanaka and Chen (2015 & 2016: Fig. 6.2), the impact of environmental variability on American lobster recruits during 1984-2013 was quantified as the climate-driven habitat suitability index (HSI) for the GOMGBK lobster recruits.

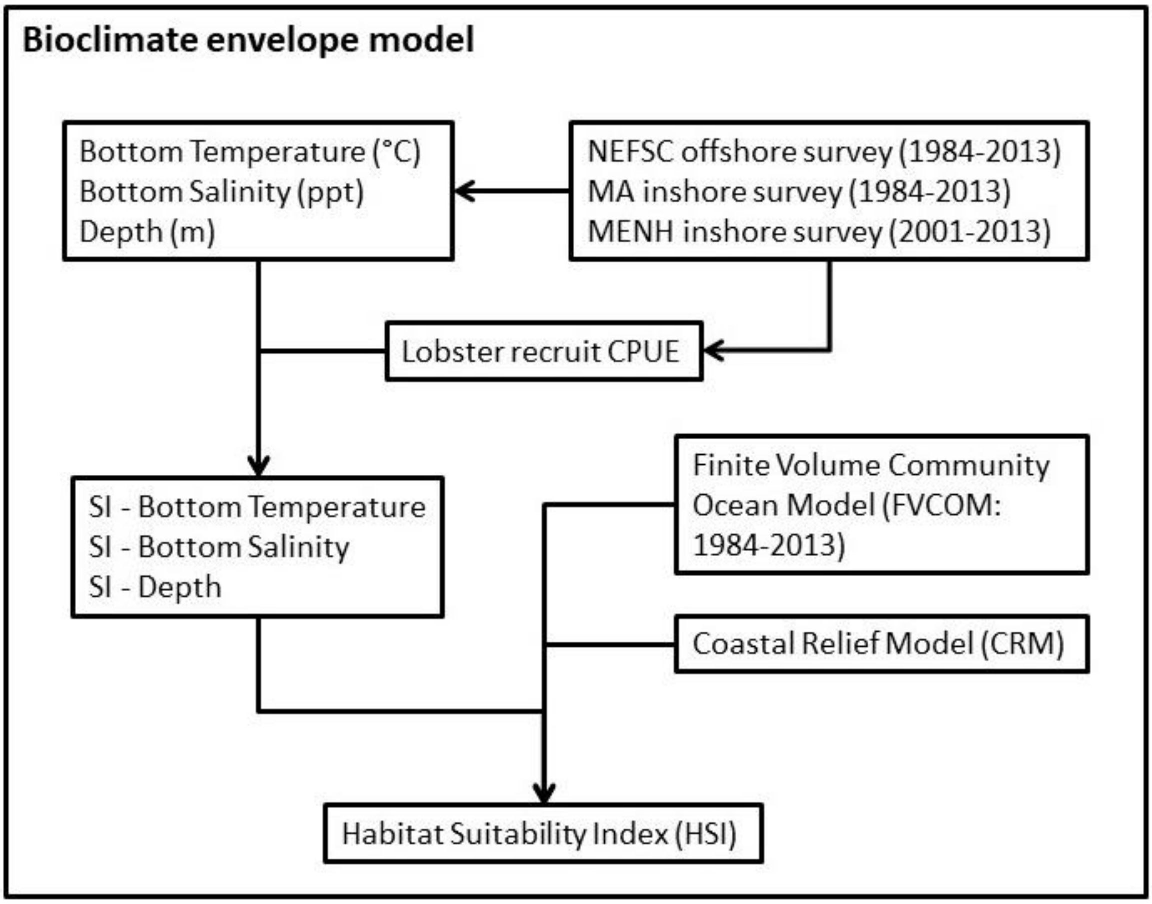

Figure 6-2: Schematic representation of the structure of the bioclimate envelope model developed in this study, implemented in R programming environment.

A bioclimate envelope model is a type of species distribution model commonly used to evaluate species' climate-driven habitat suitability based on quantitative associations between a set of physical/climatic variables and relative species abundance or occurrence (Cheung et al., 2008 & 2009; Tanaka and Chen 2015 & 2016). Lobster recruits were defined as lobster of 53–63 mm CL (ASMFC, 2015a). The nominal lobster recruit abundance index was calculated as a survey catch per unit of sampling effort (CPUE) at station *i*, in season *j*, and year *y* (Chang et al., 2012; Tanaka and Chen, 2015);

$$CPUE_{ijy} = \left(\frac{Count_{ijy}}{Area\ swept_{ijy}}\right) * 20 \qquad \textit{Eq. 6-1}$$

where *Count* represents the total quantity of individuals measuring 53-63 CL mm caught and *Tow duration* is measured in minutes. Continuous temperature, salinity and depth variables were delineated into 20 classes using Fisher's natural breaks classification algorithm (Bivand, 2013). The standardized lobster recruit index was used to develop suitability indices (SIs) for bottom temperature, salinity and depth that were treated as a key niche dimensions within the bioclimate envelope. The SI of class *k* for environment variable *i* was calculated as:

$$SI_{i,k} = \frac{CPUE_{i,k} - CPUE_{i,min}}{CPUE_{i,max} - CPUE_{i,min}} \qquad \textit{Eq. 6-2}$$

The SIs were combined to form composite habitat suitability index (HSI) also scaled from 0 to 1 following arithmetic mean equation.

$$HSI = \frac{\sum_{i=1}^{n} SI_i}{n} \qquad \textit{Eq. 6-3}$$

where SI_i is an SI value associated with the i^{th} environmental variable and n is the number of environmental variables (n=3) included in the HSI. The unstructured-grid Finite-Volume Community Ocean Model configured in the Northwest Atlantic Shelf region was used to provide monthly estimates of bottom temperature and salinity by location and time in the Gulf of Maine and Georges Bank from 1984 to 2013 (Chen et al. 2006; Li et al. 2017). Bathymetry data were obtained from the U.S. Coastal Relief Model (NGDC, 1999). A detailed description of the model calibration and validation procedures can be found in Tanaka and Chen (2015 & 2016).

Recruits were assumed to enter the population instantaneously at the end of the spring season; therefore, the bioclimate envelope model was applied to generate a climate-driven lobster recruit HSI for every spring between 1984 and 2013. Fall recruitment was not considered because this study focused on the primary molt which is assumed to occur at the end of spring (REF).

6.3.4 Size-structured American lobster assessment model

The stock assessment model used in this study is a modified version of a size-structured model that was originally developed by Cao et al., (2016). The model configurations in this study followed the base case for the 2015 ASMFC GOMGBK lobster stock benchmark assessment (Table 6.1: ASMFC, 2015a). The model uses multiple data sources and a prespecified number of size classes (5-mm size classes between 53 and 223 mm CL; Table 6.1). Inshore and offshore survey data that include abundance indices and size compositions for the time period (1984-2013) were used in the population model. Seasonal commercial catch and size composition data were available for the whole study period (Q1-4 & 1984-2013). The model was fitted over a 30-year period (1984-2013). The modelling time step is one season (Q1: January-March, Q2: April-June, Q3: July-September, and Q4: October-December) based on the management framework used in the GOMGBK lobster fishery. The model used the seasonal time step to account for strong seasonality in the GOMGBK lobster fishery dynamics (i.e. low fishing effort during the winter and spring, but extremely high fishing effort during summer). Pre-specified proportions of females-at-size at each time step was used to estimate male/female ratio at size/time. A detailed description and equations of this model can be found in Cao et al. (2016).

Table 6-1: Summary of data input and model configurations for the Gulf of Maine / Georges Bank lobster size-structured model.

Component	Description
Year	1984-2013
Season	4
Number of sexes	1
Size range	53-223 mm
Size bins	5 mm
Initial condition	First-year size composition assumed in the model
Recruitment size bins	53-63 mm
Spawner-recruit relationship	No functional relationship
Growth	Prespecified growth transition matrices (n=4)
Number of commercial fleet	1
Commercial fleet selectivity at size	Double logistic
Survey data	NEFSC spring (1984-2013) and fall (1984-2013) MA spring (1984-2013) and fall (1984-2013) MENH spring (2001-2013) and fall (2000-2013) Ventless Trap summer (2006-2012)
Survey selectivity at size	Double logistic
Fishing mortality rate	Instantaneous rates
Natural mortality rate	M = 0.15 y^{-1} for all size groups and seasons

Basic size-structured population dynamic model: The number of lobsters in size bin *k* at the beginning of year *t* and season *m*, $N_{k,t,m}$, is formulated as:

$$N_{k,t,m} = N_{k,t,m-1}V_{k,t,m-1}G_{k,m-1} + \hat{R}_{k,t,m} \qquad \textit{Eq. 6-4}$$

where $G_{k,m-1}$ is the growth transition matrix that describes the probabilities of a lobster growing from a size class in month m to another size class in month m+1 (no negative growth is allowed); $V_{k,t,m-1}$ is the survival rate from both fishing (*F*) and natural mortality (*M*) in the previous season of year *t*; and $\hat{R}_{k,t,m}$ is the recruitment in year *t* that recruits to season *m* and size class *k*.

Initial Conditions: the numbers-at size-at the beginning of the first year specifies the state of population when the model starts. The initial condition (i.e. numbers-at-size, N_k, at the first-time step, 1984 Q1) was calculated as:

$$N_k = Pia_k N \qquad \textit{Eq. 6-5}$$

where Pia_k are pre-specified proportions-at-size used to estimate the total numbers (*N; see appendix*) for the first year. The observed size composition values from the 1984 spring surveys were used as the initial size composition

Annual survival rate: Annual survival rate for lobsters in each size bin, season and year, $V_{k,t,m}$ is calculated as:

$$V_{k,t,m} = exp(-\left(\sum\left(F_{m,t,k}\right) + M\right) \qquad \textit{Eq. 6-6}$$

Natural mortality was assumed to be time/size-constant and fixed at M = 0.15. Fishing mortality was modeled as an instantaneous rate and the product of fully-selected fishing mortality (*Fmult*) and selectivity-at-size (S_k). The fishing mortality for year *t*, season *m,* and size bin *k* was calculated as:

$$F_{m,t,k} = Fmult_{m,t} S_k \qquad \textit{Eq. 6-7}$$

where *Fmult* is modeled as a random walk process and calculated in log space as;

$$log(Fmult_{m,t}) = log(Fmult_{m-1,t}) + log(FDev_{m,t}) \qquad \textit{Eq. 6-8}$$

$Fmult_{m,t}$ is determined by two sets of parameters, $Fmult_{m,1}$, the parameter for first year and each season, and, $FDev_{m,t}$, the deviation of the parameter from the value in the first year. The model estimates $Fmult_{,m,1}$ and a set of $FDev_{m,t}$ that is the error term of random walk that has mean of zero.

A double logistic function was applied to quantify the bottom trawl and fixed trap survey selectivities with each of the four parameters estimated during model-fitting. The selectivity vector was rescaled to maximum value of 1;

$$S_k = \frac{1}{1+exp\left(b(a-L_k)\right)}\left(1 - \frac{1}{1+exp\left(d(c-L_k)\right)}\right) \qquad \textit{Eq. 6-9}$$

$$S_k = \frac{s_k}{s_{max}} \qquad \textit{Eq. 6-10}$$

Growth: Lobster growth was assumed to vary by season and occur only in summer (Q3) and fall (Q4). Seasonal growth transition matrices were estimated externally and pre-specified as inputs (Appendix E). Seasonal growth transition matrices were held constant over the model time-period.

Recruitment: Lobster recruits were assumed to enter the first three size bins (53-63 mm CL) and recruit to the fishery at the beginning of summer. The proportion of the recruitment to the first three size bins was pre-specified (0.66, 0.33, 0.01). The proportion of recruitment in each season was also pre-specified (0, 0, 0.66 0.34). No functional relationship was assumed for the GOM-GBK lobster spawner-recruit relationship. Recruitment was modeled as the product of annual recruitment and the proportion of the annual recruitment (R_t) that recruits to each season (λ_m) and each size-class (λ_k):

$$R_{t,k,m} = R_t \lambda_k \lambda_m \qquad \textit{Eq. 6-11}$$

Annual recruits were estimated as:

$$R_t = \bar{R} e^{Rdev_t - \frac{\sigma_R^2}{2}} \qquad \textit{Eq. 6-12}$$

where $\bar{R}$ is expected recruitment (i.e. the mean estimated by the model); $Rdev_t$ is the recruitment deviation in year t and assumed to follow normal distribution; σ_R is the recruitment standard deviation in log space. $Rdev_t$ was a bounded vector with values that summed to zero ($\frac{\sigma_R^2}{2}$ is the lognormal bias correction so that the $Rdev_t$ is summed to zero).

The recruitment model assumed that the recruitment deviations follow trends in environmental variability (e.g. water temperature). The environmental index was essentially treated as a survey of annual recruitment deviations, i.e., $Rdev_t$ (Schirripa et al., 2009). The model then scales the environment-dependent recruitment variability using information from this source. The likelihood of the recruitment deviations, is added to the total likelihood and calculated as:

$$L_{Rdev} = \sum_t \left(\frac{Env_t - Rdev_t}{\sigma_t}\right)^2 \qquad \textit{Eq. 6-13}$$

where Env_t is the environmental index (i.e. lobster recruit HSI) in year *t*, and σ_t is the standard deviation of the observation error of the environmental time series. Recruitment in the base case model (without environmental index) was treated as parameters and estimated without assuming any functional relationship with SSB.

Weight & Maturity at size and Spawning Stock Biomass: Weight/maturity-at-size parameters were assumed known and used as inputs (Appendix E). While the model does not handle sex difference explicitly, a pre-specified proportion of females-at-size at each time step was used to estimate male/female ratio at size/time in calculating spawning stock biomass (Appendix). The spawning stock biomass as calculated using the population abundance at size (N_k), the weight-at-size (W_k), the pre-specified proportions mature-at-size (*Pm*), the pre-specified proportions of females-at-size (*Ps*), and the pre-specified proportion of total mortality during the year prior to spawning (p_{SSB}) as:

$$SSB_t = \sum_k N_{t,k}\, e^{-p_{SSB}{}^{Z_{t,k}}} W_{t,k} Pm_{t,k} Ps_{t,k} \qquad \textit{Eq. 6-14}$$

Model prediction: Predicted catch in weight for year *t*, season *m*, and size bin *k* was calculated using the Baranov catch equation and is based on corresponding population numbers, $N_{t,k,m}$, and fishing mortality, $F_{m,t,k}$:

$$C_{m,t,k}^{predicted,n} = \frac{F_{m,t,k}}{F_{m,t,k}+M}\left(1 - e^{\left(-(F_{m,t,k}+M)\right)}\right) N_{m,t,k} W_{t,k} \qquad \textit{Eq. 6-15}$$

Survey-specific catchability, q_i, is calculated internally as:

$$ln(q_i) = \frac{1}{n_b} \sum_b ln\left(\frac{Index_{i,t}^{observed}}{Biomass_{i,t}^{Survey}}\right) \qquad \textit{Eq. 6-16}$$

$$Biomass_{i,t}^{Survey} = \sum_k N_{i,t}^{survey} W_{t,k} \qquad \textit{Eq. 6-17}$$

$$N_{i,t}^{survey} = N_{i,t,k} S_{i,t,k} \qquad \textit{Eq. 6-18}$$

$$N_{i,t,k} = N_{t,k}(1 - exp\big(-(pSurvey)Z_{t,k}\big)) \qquad \textit{Eq. 6-19}$$

where $S_{i,t,k}$ is the selectivity of survey i, year t and size-class k, ; $pSurvey$ refers the proportion of year prior to the survey and allows model to adjust the timing of the survey and n_b is the number of time block (n_b =1). Predicted survey abundance index for survey i, in year t was calculated as

$$Index_{i,t}^{predicted} = q_i \sum_k N_{i,t,k}\, S_{i,t,k} \qquad \textit{Eq. 6-20}$$

Predicted catch size composition is calculated as

$$CS_{m,t,k}^{predicted} = \frac{C_{m,t,k}^{predicted}}{\sum_k C_{m,t,k}^{predicted}} \qquad \textit{Eq. 6-21}$$

where $CS_{m,t,k}^{predicted}{}_k$ is the proportion of predicted catch for year t, season m and size-class k.

The predicted survey size composition was calculated as:

$$SS_{i,t,k}^{predicted} = \frac{N_{i,t,k}^{Survey}}{\sum_k N_{i,t,k}^{Survey}} \qquad \textit{Eq. 6-22}$$

where $SS_{i,t,k}^{predicted}$ is the proportion of abundance at the survey time of survey i, year t, and size-class k.

Observational models and likelihood functions: Observational models are used to fit the population dynamics model to fishery independent and dependent data. Model fitting is conducted by maximizing the log-likelihood which is a function of several components (e.g., total commercial catches, total abundance indices from survey, and length composition of commercial and survey catches). The overall objective function is the sum of log likelihood functions linking observed and predicted values of various life history and fishery processes which were assumed that these are normally distributed on a log scale. A penalty function is included for estimated fishing mortality fishing mortality in the overall objective function to exclude biologically unrealistic estimate. The penalty is associated with any F greater than an input maximum value, calculated as 1000*(F-max F)^2 for F > max F, where max F should be a maximum fishing mortality level possible for the fishery and was defined as max F = 3.

Prespecified effective sample size (ESS) and coefficient of variations (CV) was used to account for assumed errors and variations associated with total catch, survey abundance indices (CV) and size composition (ESS). The CVs of the survey abundance indices and commercial catch were set to be 0.25 and 0.1 respectively. The following multinomial distribution likelihood function was assumed for catch and survey size compositions:

$$ln(L) = ln(ESS!) - \sum_k ln(x_k!) + ESS \sum_k p_k^{observed} \, ln(p_k^{predicted}) \qquad \textit{Eq. 6-23}$$

where *EES* is the input effective sample size and is used to create the number of lobster in each size bin, x_k; $p_k^{observed}$ is an observed proportion and $p_k^{predicted}$is the associated predicted proportion.

The following lognormal distribution likelihood function was assumed for catch, survey indices and recruitment deviation. Furthermore, an environmental index (i.e. HSI) was treated as an indirect observation for recruitment deviations.

$$ln(L) = -ln\left(\sqrt{2\pi\sigma_I^{observed}}\right) - ln(I^{observed}) - \frac{(ln(I^{observed} - I^{predicted}))^2}{2(\sigma_I^{observed})^2} \qquad \textit{Eq. 6-24}$$

Parameter estimations: All log likelihood functions were converted to negative log likelihoods for the minimization. Optimization was implemented using Automatic Differentiation Model Builder (ADMB; http://admb-foundation.org/), which was used to minimize the negative log-likelihood. The model outputs are predictions of relevant population and fishery parameters such as annual total catch, size composition for surveys and commercial catch, population abundance and biomass, and annual fishing mortality. The model generated estimates of abundance, spawning stock biomass, population size composition, recruitment, and annual fishing mortalities and exploitation rates.

6.3.5 Incorporating environmental variability into the lobster assessment model

This model has the capacity to use environmental effects to inform recruitment dynamics. Changes in annual median HSI over 30 years were treated as an index of environmental variability, which was assumed to have influenced the lobster recruitment dynamics during 1984-2013. While this study did not consider a “lag” between the environmental conditions that produce recruits in year (*t*) and when they actually ‘recruit’ to the assessment model, two different running averages (3 and 5-year average) of the HSI time series were both considered given the egg-to-recruit process likely takes more than one year. The bioclimate envelope model was used to derive a time series of median spring lobster recruit HSI as a function of changes in bottom temperature and salinity, and it was assumed that the GOMGBK lobster recruitment deviation during 1984-2013 was assumed to be positively related to the HSI. The temporal variability in the spring lobster recruit HSI was used as a composite environmental variability index for tuning the lobster recruitment deviations.

The performance of size-structured models with environmentally informed recruitment dynamics was evaluated by comparing relevant assessment outputs such as recruitment, annual fishing mortality, and magnitude of retrospective biases. The full assessment time series is compared with model runs of identical structure but with 1, 2, …, 7 years of data sequentially removed to quantify magnitude of retrospective bias using a revised Mohn’s rho statistic. The Mohn’s rho value is zero when the peeled assessments match exactly with full time series assessment; Hurtado-Ferro et al., 2014).

6.4 Results

6.4.1 Bioclimate envelope analysis of the GOMGBK lobster recruitment

Observed bottom temperature, salinity and depth varied between 1.2-14.0 ◦C, 25.7-35.6 ppt, and 0-449 m during springs of 1984-2013. The suitable spring bottom temperature range (SI > 0.8) for GOMGBK lobster recruits was found in 10.2 -14.0 ◦C. The suitable salinity range was observed at 31.2-32 ppt, and suitable depth range was observed at 28.3–68.5 m (Fig. 6.3).

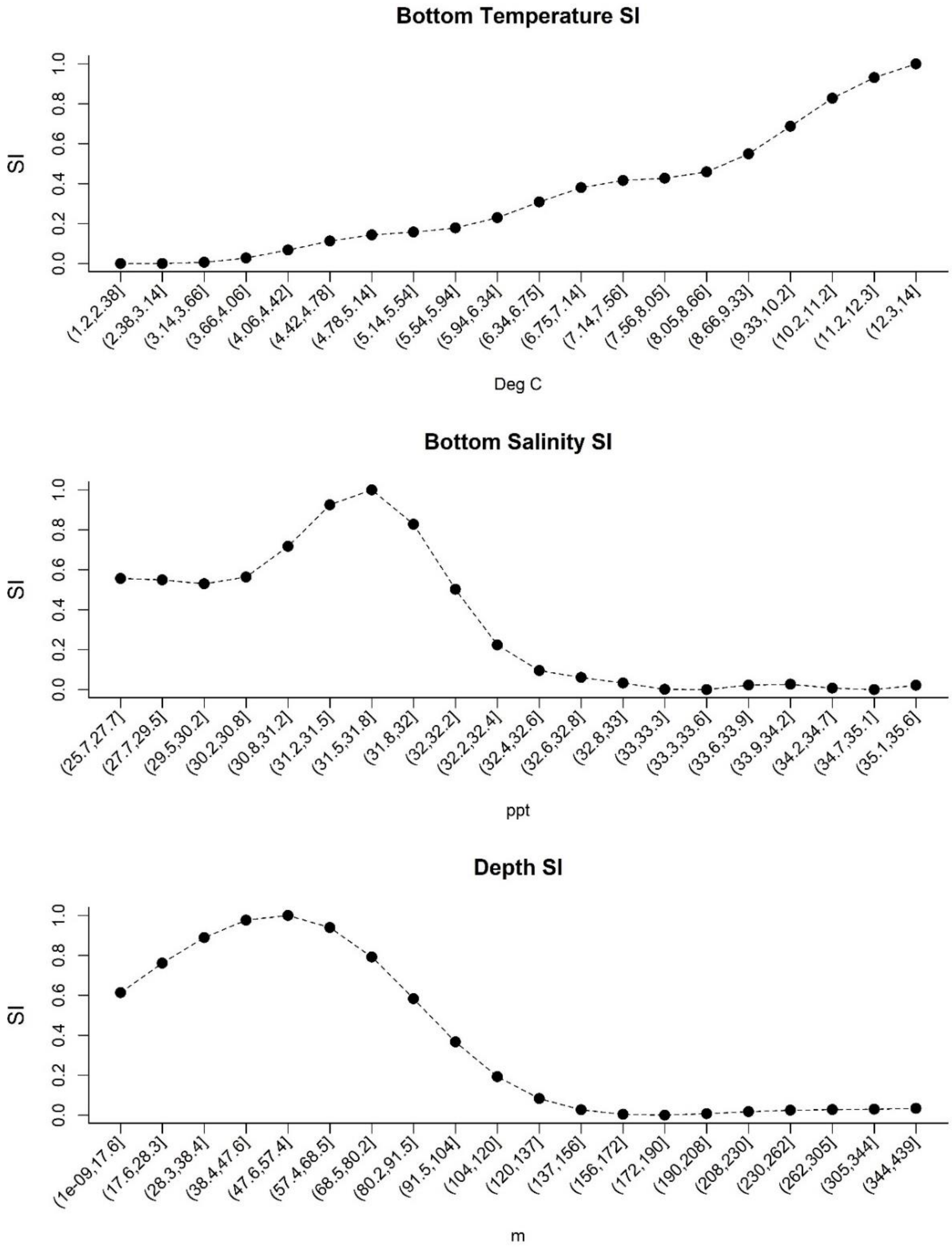

Figure 6-3: Suitability Index (SI) curves of bottom temperature, bottom salinity and depth for American lobster recruit size classes in spring (April–June).

Spatial variability of the bioclimate envelopes for American lobster recruits were visualized using the predicted HSI at every FVCOM grid in the GOMGBK statistical areas

(Fig. 6.4). Overall, the model predicted higher habitat suitability in inshore waters while offshore areas were charactarized by low habitat suitability during 1984-2013. The changes in climate-driven habitat suitability during 1978-2013 showed a ‘high-north: low-south’ spatial pattern (Fig. 6.4). In the spring, there was greater change toward higher habitat suitability in the southern Gulf of Maine/Georges Bank. Temporal variation in climate driven-habitat suitability during 1984-2013 showed an increasing trend in habitat suitability in 2007-2013 (Fig. 6.5).

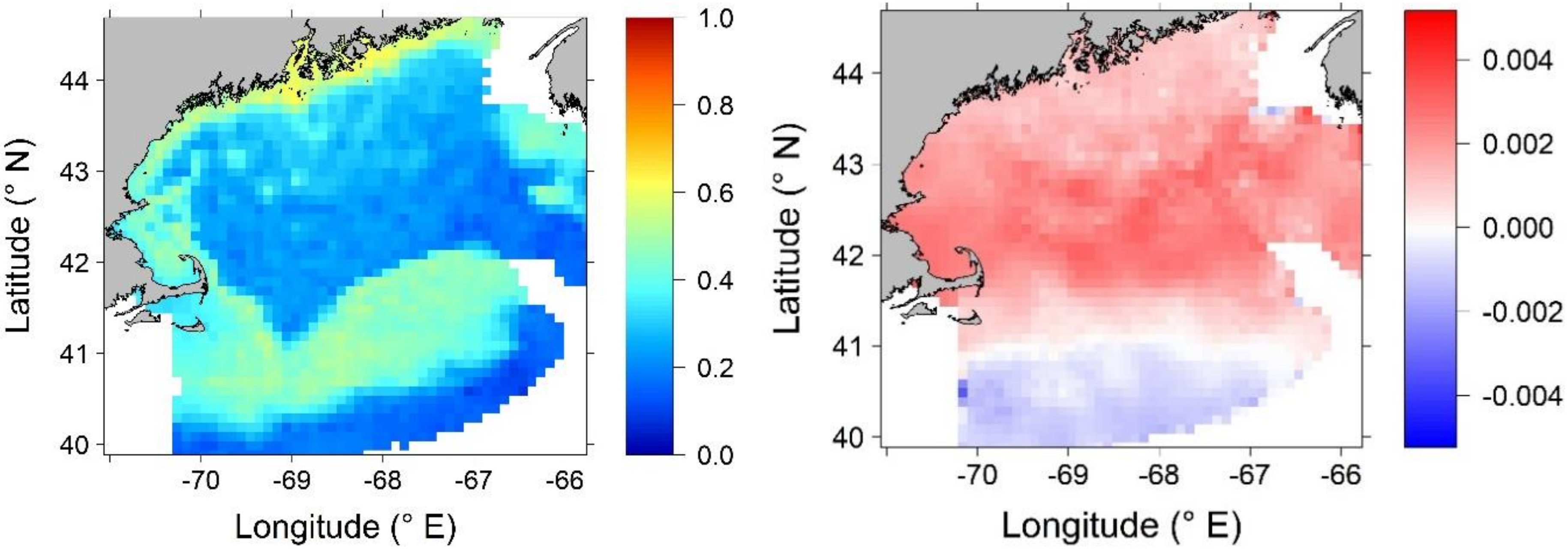

Figure 6-4: Left: spatial distribution of the median American lobster recruitment habitat suitability index (HSI) over 1984-2013. Right: change in HSI where darker red indicates change toward higher habitat suitability at higher magnitude. Bottom: temporal variability of HSI with the 3 and 5-year average.

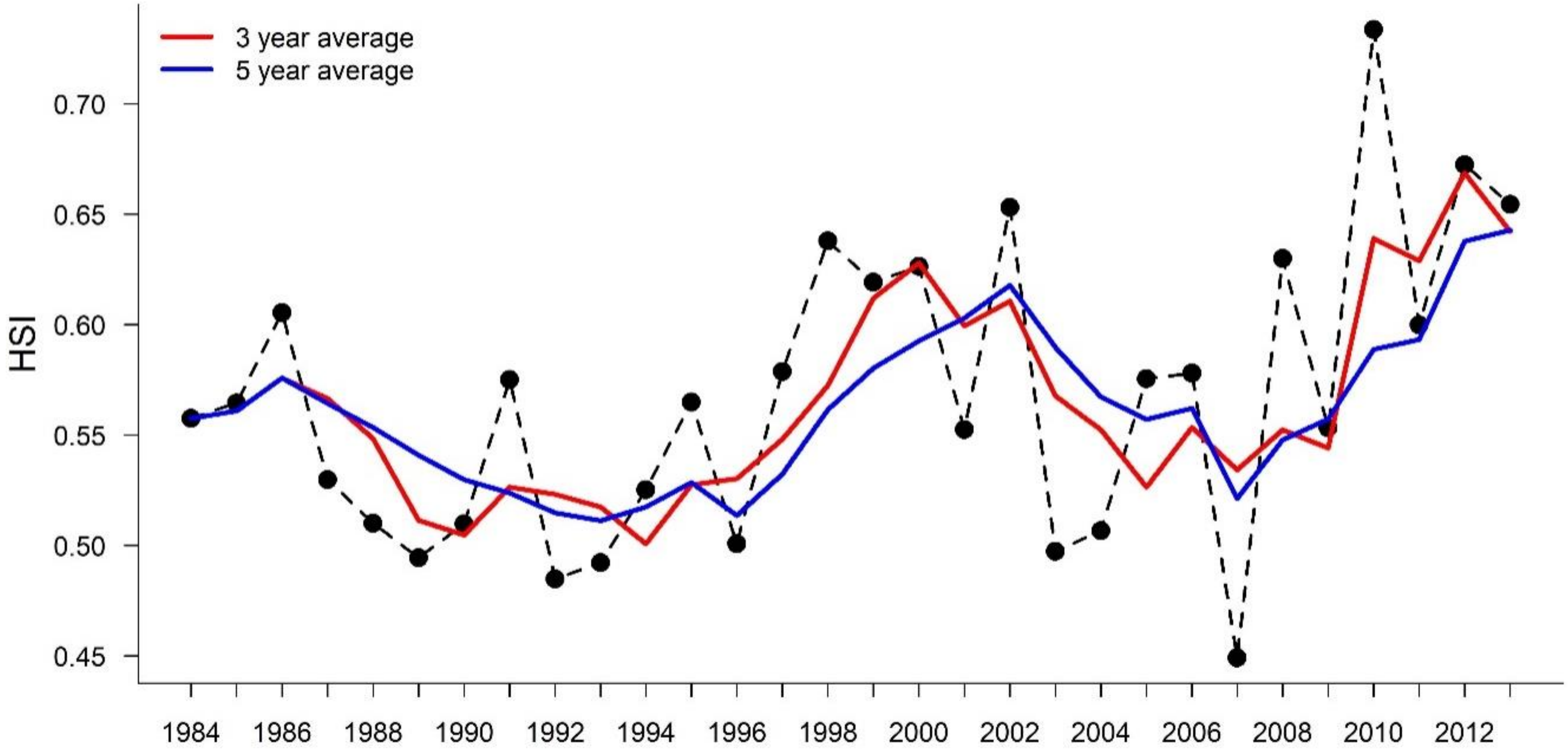

Figure 6-5: Temporal variability of American lobster recruit HSI with 3 and 5-year average

6.4.2 Fitting of observed data using size-structured lobster assessment model

Overall, the size-structured model captured the fishery-independent size compositions accurately, suggesting that satisfactory performances of the size-structured model and survey gear selectivities (Fig. 6.6). The model showed a tendency to estimate smaller size modes for some surveys (e.g. NEFSC Q2 & MA Q2). The model also captured the mode between minimum (81 mm) and maximum (128 mm) legal sizes in the fishery-dependent size composition data, which implied the satisfactory performance of the lobster trap selectivity model (Fig. 6.7).

The overall annual/seasonal trends in total landings were well estimated (Figs. 6.8). The predicted landings were closely aligned with the observed winter (Q1) and spring (Q2) landings, while the model slightly underestimated the summer (Q3) landings in 2005-2013. Temporal trends in the survey abundance indices were also well captured, but the model predicted the year effects in the surveys #4&5 (spring and fall MA surveys) with much smaller magnitudes (Fig. 6.9). Overall, larger discrepancies were observed in the survey abundance indices, which is likely due to the larger CV (0.25) associated with the abundance indices.

Predicted recruitment increased throughout the time series, and the highest recruitment was predicted in 2013 (Fig. 6.10). Predicted spawning stock biomass (SSB) increased overall except during 2004-2008, with the lowest and highest SSB occurring in 1984 and 2013 (Fig. 6.10). The stock–recruitment relationship was generally positive (Fig. 6.10), where the strong year classes were associated with years of high SSB.

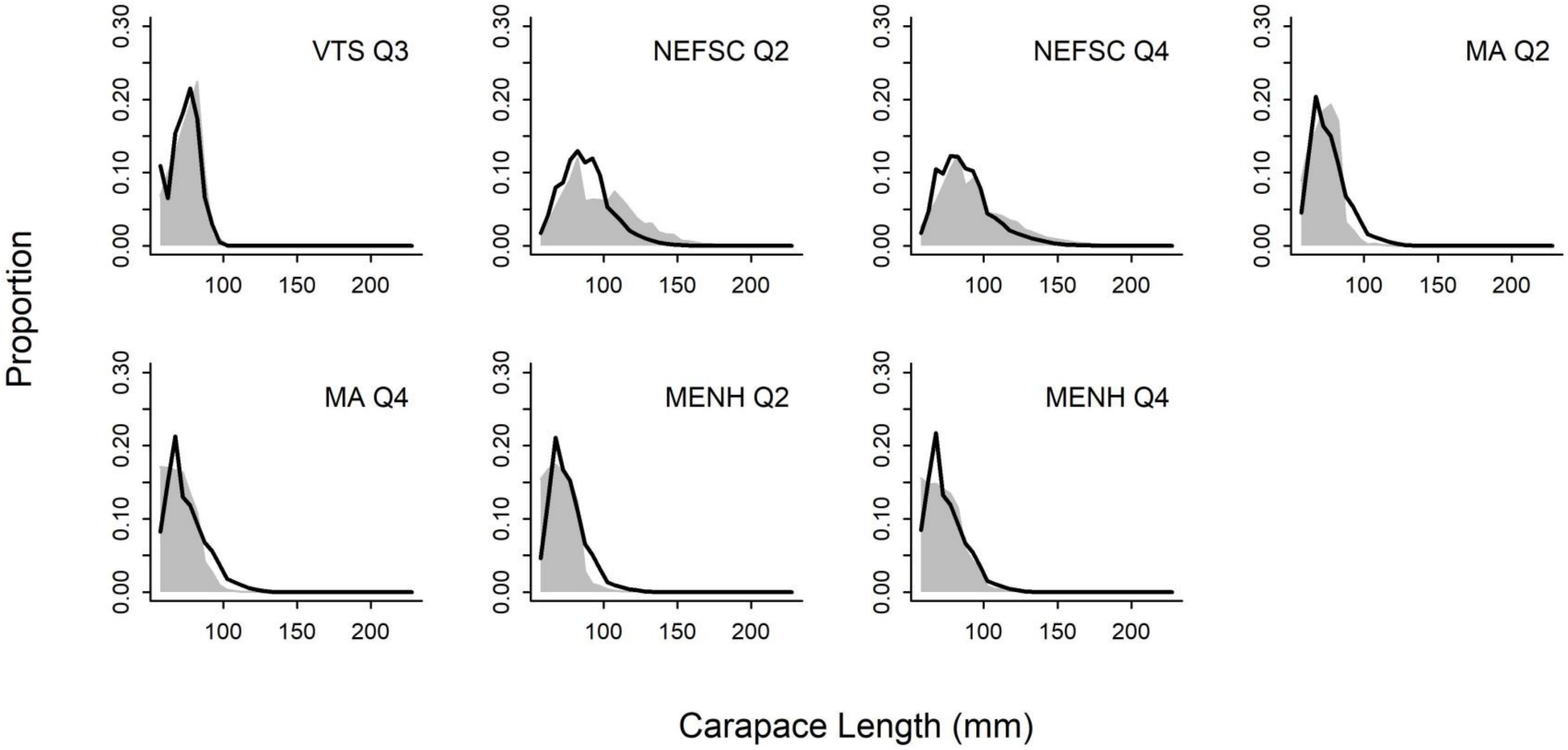

Figure 6-6: Observed (polygons) and estimated (solid lines) size compositions in fishery-independent surveys. Size compositions were aggregated across 1984-2013 by survey. Survey #1 - Ventless Trap (summer, 2006-2012); #2&3 - Northeast Fisheries Science Center (spring and fall, 1984-2013); #4&5 – Massachusetts (spring and fall, 1984-2013); #6&7 - Maine/New Hampshire (spring and fall, 2000-2013).

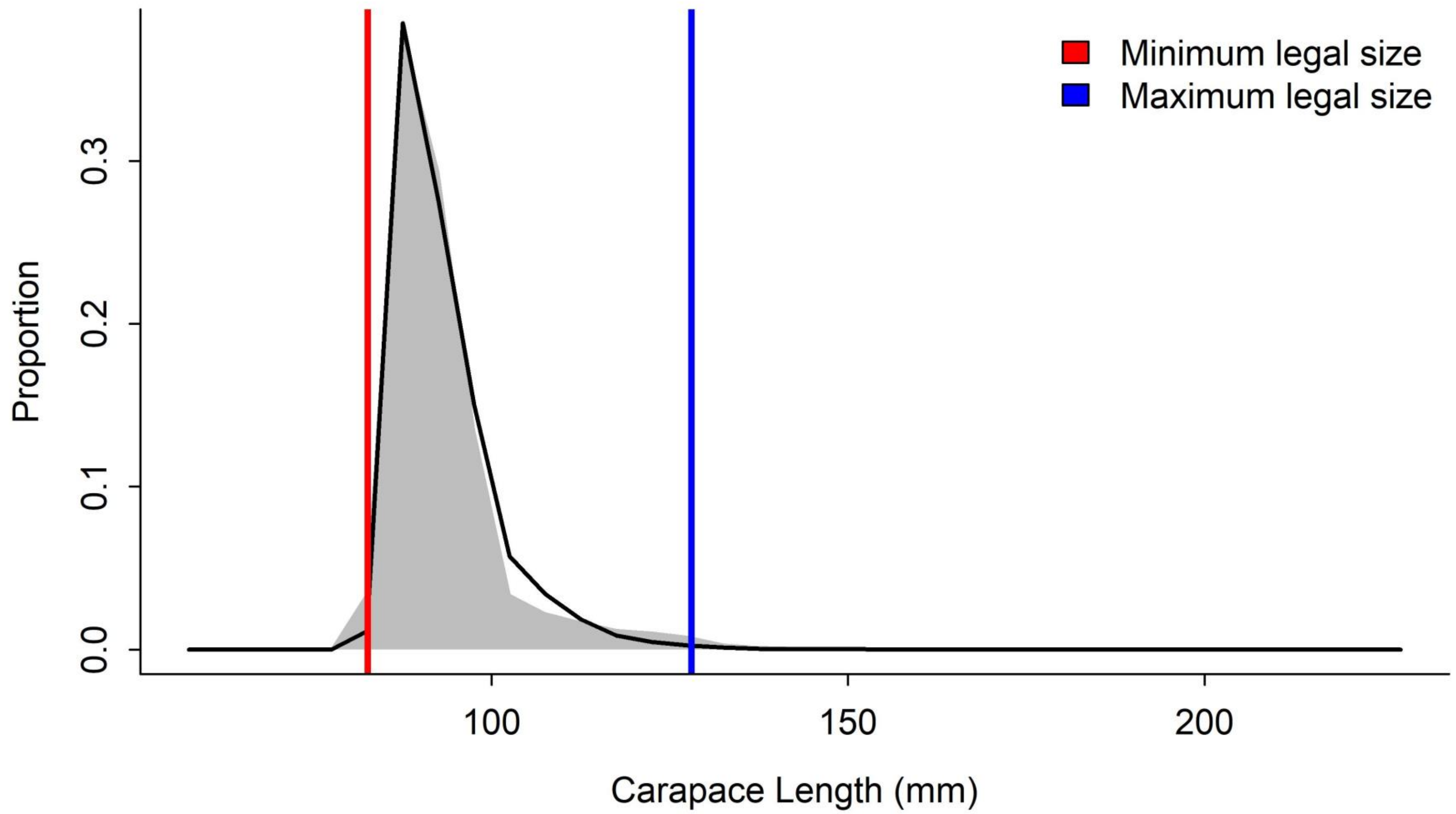

Figure 6-7: Observed (polygons) and predicted (solid lines) annual/seasonal size compositions of commercial catches for the Gulf of Maine/Georges Bank lobster trap fishery. Size compositions were aggregated across Q1-4 and 1984-2013.

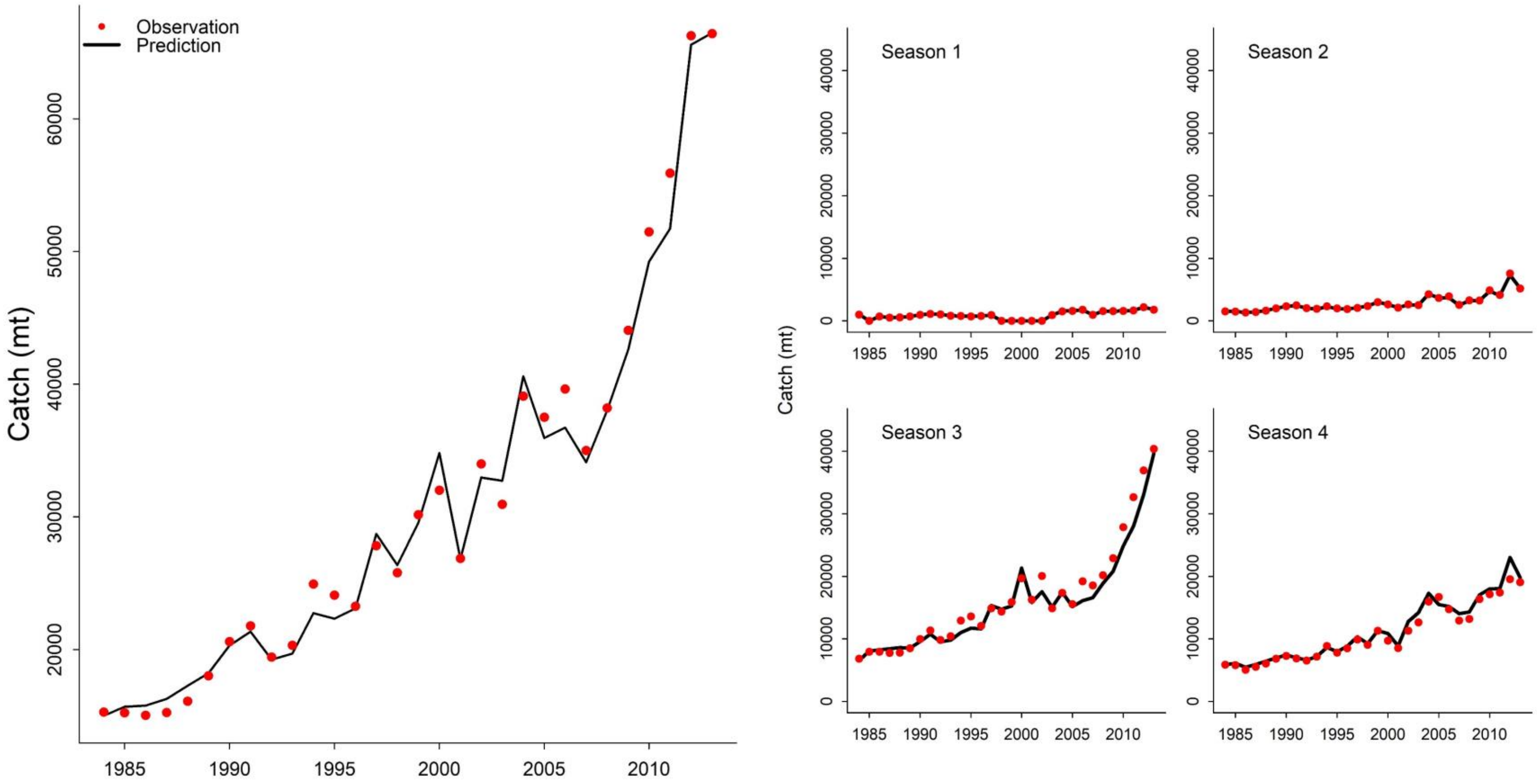

Figure 6-8: Observed (red dots) and predicted (solid lines) commercial catches from 1984 to 2013 for the Gulf of Maine/Georges Bank lobster trap fishery.

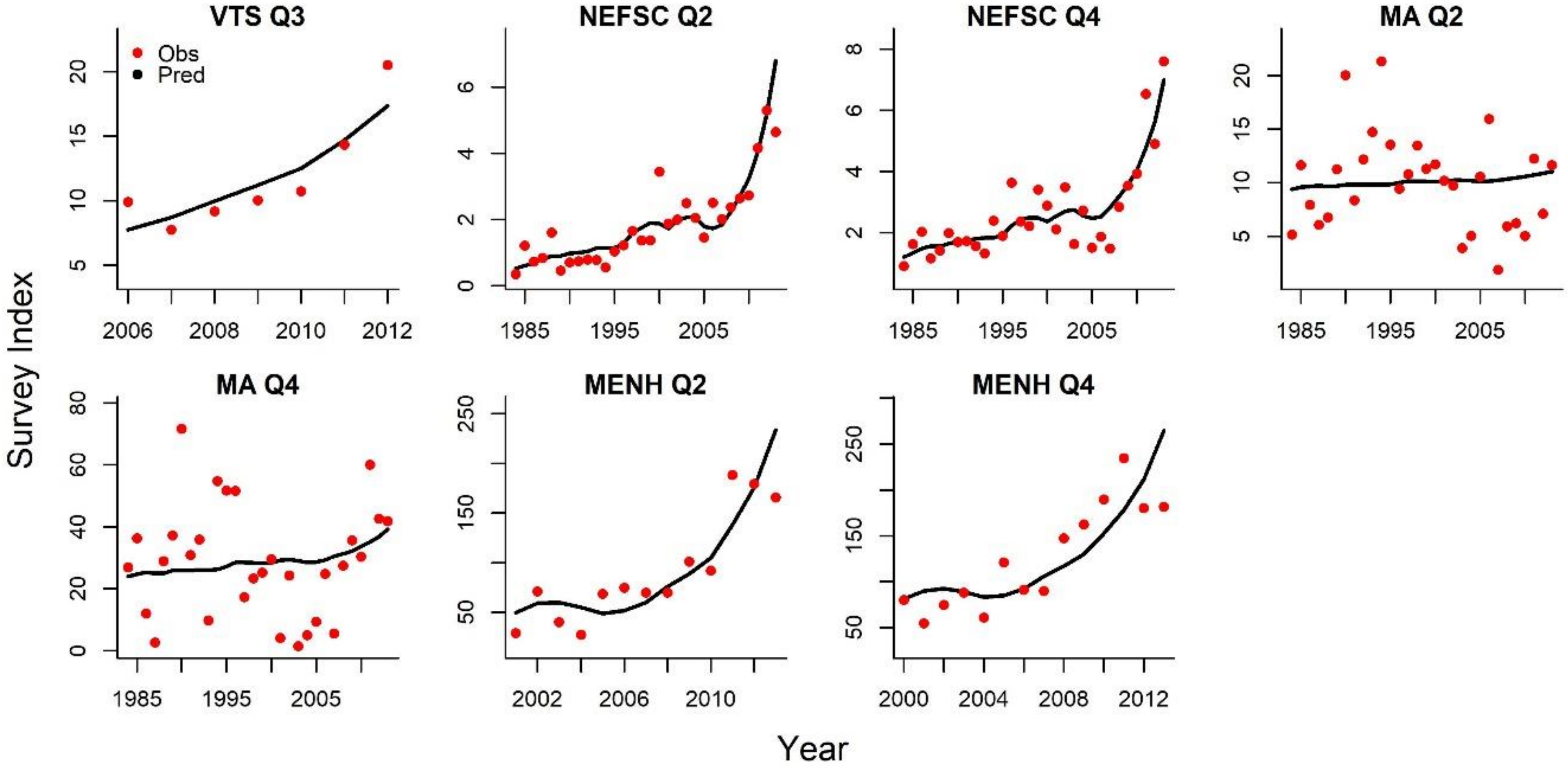

Figure 6-9: Observed (red dots) and predicted (solid lines) survey indices for the Gulf of Maine – Georges Bank lobster stock.

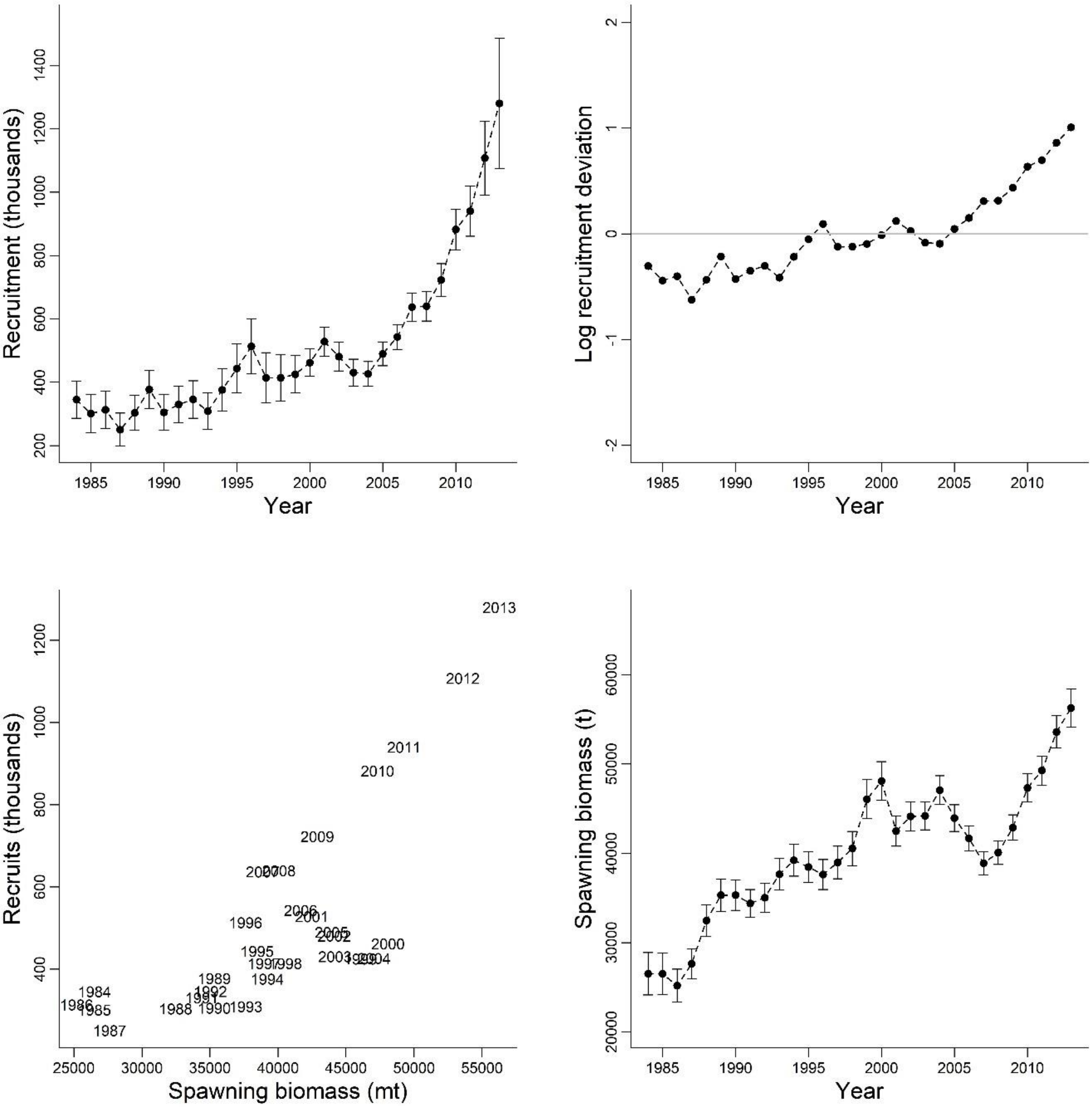

Figure 6-10: Estimated annual recruitment (top left). Estimated log recruitment deviations (top right). Estimated stock–recruitment relationship (bottom left). Estimated annual spawning stock biomass (bottom right).

The model estimated the highest fishing mortality during the summer (season 3; July-September), and the lowest fishing mortality during the winter (season 1: January-March) (Fig. 6.11). The difference in predicted seasonal fishing mortality reflects that the majority of fishing in the Gulf of Maine/Georges Bank occurs during the summer. The estimated fishing mortality increased over time during the summer. The model also estimated a higher fishing morality rate in the 2000s during the fall, peaking in the mid-2000s and declining in subsequent years.

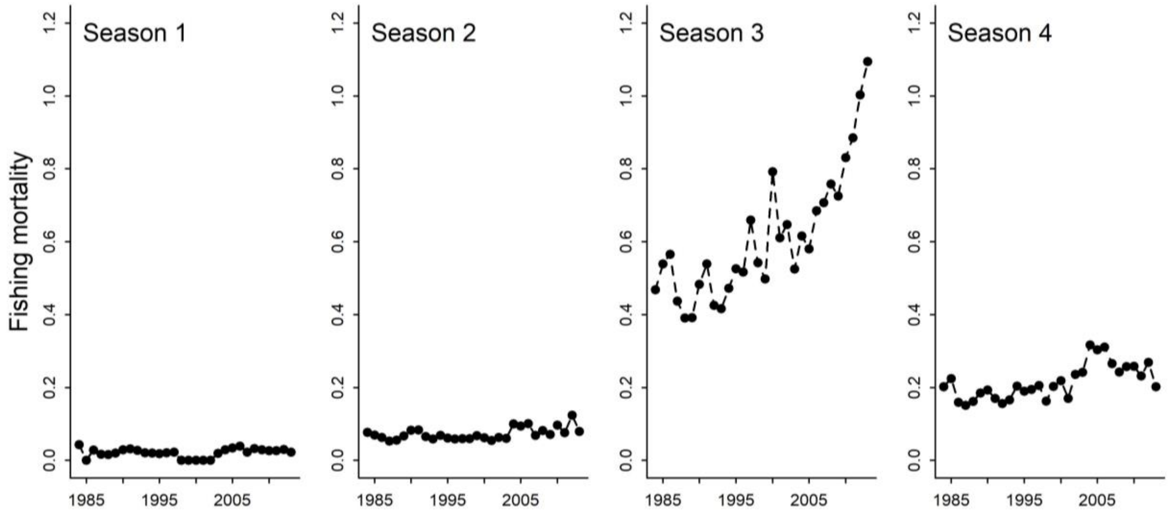

Figure 6-11: Estimated instantaneous fishing mortality from 1984 to 2013 for the Gulf of Maine/Georges Bank lobster trap fishery.

6.4.3 Incorporating environmental variability into the size-structured model

The impacts of incorporating bottom temperature- and salinity-driven HSI within the size-structured model were investigated. The trend in the recruitment deviations from the baseline model was positively and significantly correlated with the HIS time series (Fig. 6.12), indicating that the GOM-GBK lobster recruitments may have been driven in part by climatic environmental variability. The assessment model with an environmentally informed recruitment dynamics estimated higher recruitment and lower fishing mortality in the early 2000s and late 2010s (Fig 6.13).

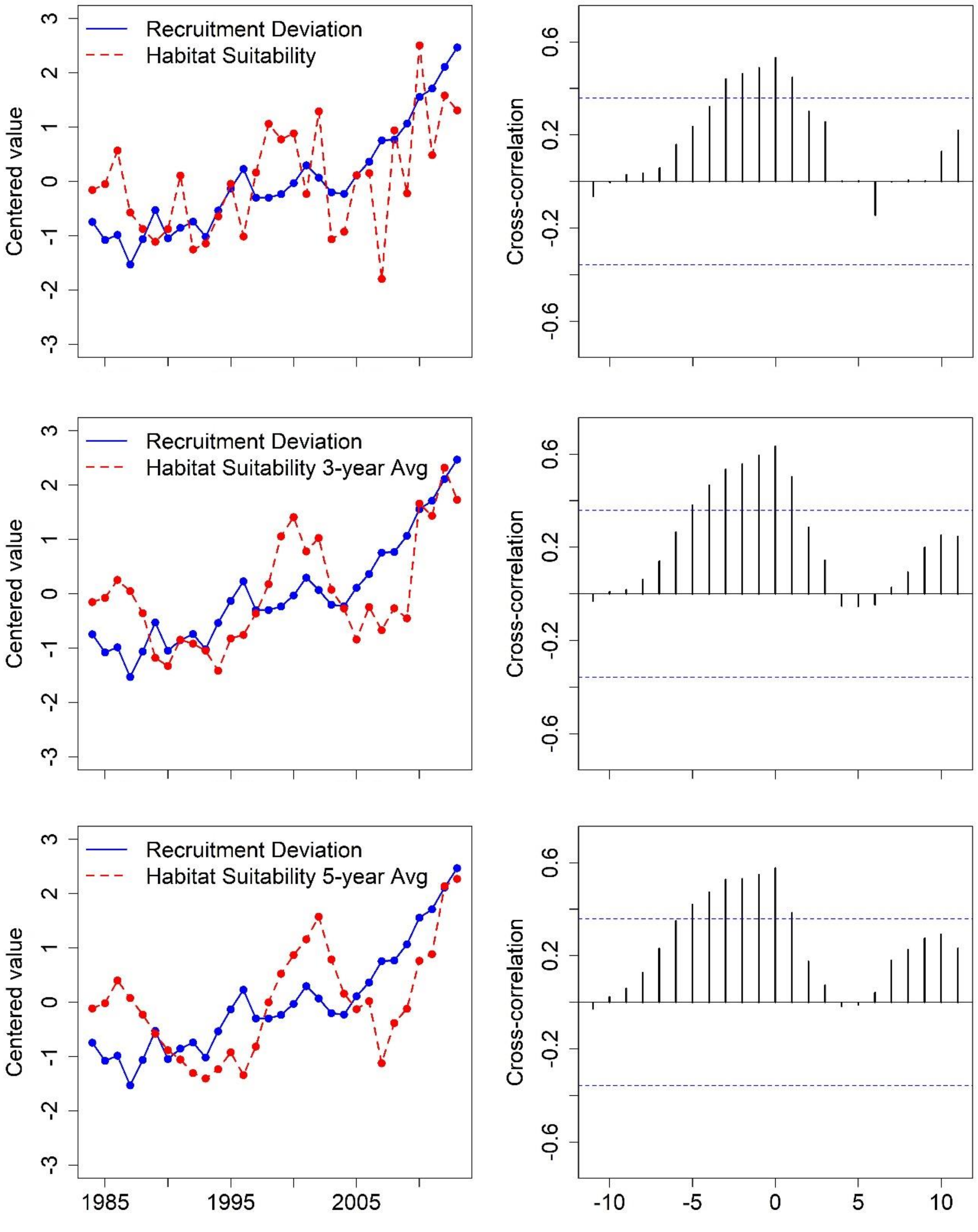

Figure 6-12: Left panels: estimated log recruitment deviations and habitat suitability index. Right panels: cross-correlation functions measuring correlations between the two-time series at different lags (years). Vertical lines indicate the magnitude of correlation and lines extending above or below the dotted lines shows statistical significance.

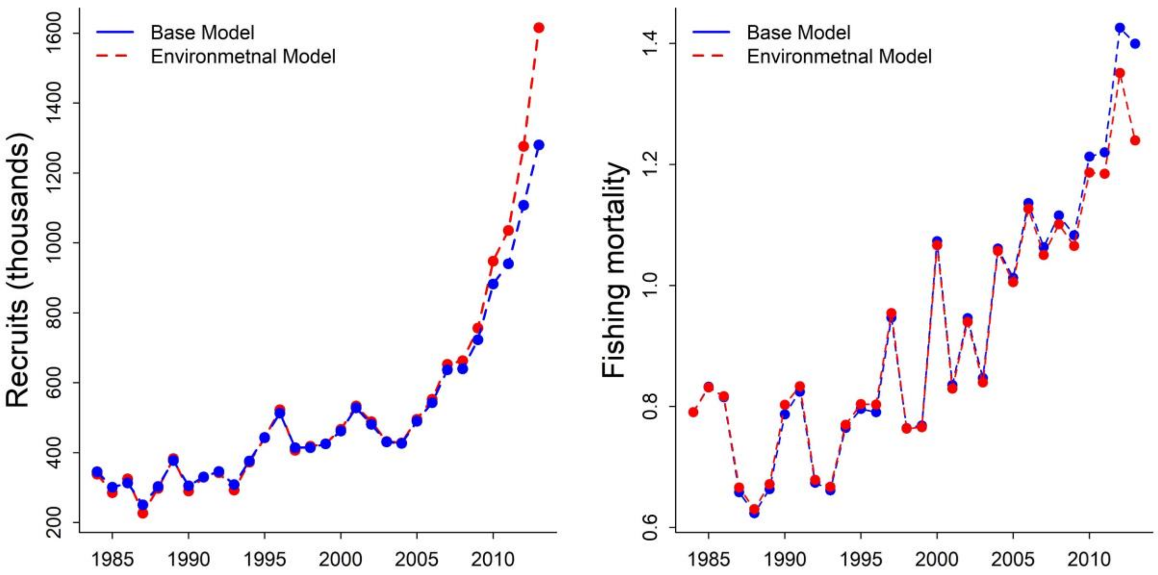

Figure 6-13: Comparison of estimated annual recruitment and fishing mortality with and without environmentally informed recruitment dynamics.

Incorporating environmental variability on recruitment dynamics led to less retrospective bias more consistent recruitment and fishing mortality estimates during the period over which retrospective error was assessed (Fig. 6.14 & Table 6.2). Retrospective patterns were reduced when environmentally informed recruitment dynamics were considered. The recruitment model tuned by HSI with the 5-year running average led to the largest reduction in the Moth’s Rho value, while the changes were less significant when the recruitment model was tuned by bottom temperature or salinity covariate alone (Table 2).

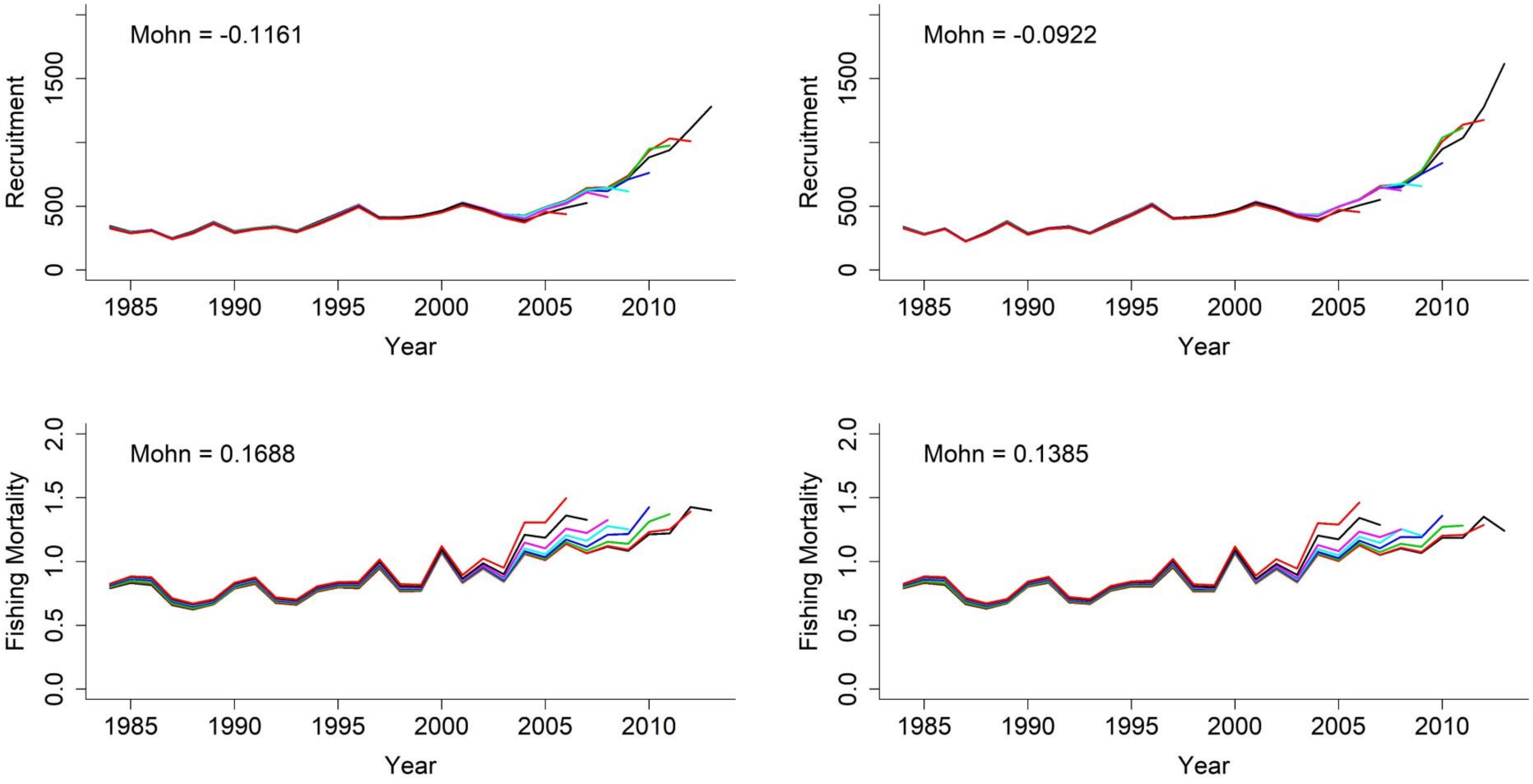

Figure 6-14: Retrospective analysis of recruitment and fishing mortality estimates based on the model without (left panels) and with (right panels) environmentally informed recruitment dynamics.

Table 6-2: Comparisons of Mohn's Rho values with different environmental covariates.

	Recruitment	Fishing Mortality
Base model	-0.116	0.169
HSI	-0.092	0.139
HSI 3-year average	-0.094	0.138
HSI 5-year average	-0.079	0.122
Bottom temperature	-0.102	0.155
Bottom salinity	-0.112	0.162

6.5 Discussion

Using the GOMGBK lobster stock as a case study, this study presented a modeling framework to incorporate environmental variability into stock assessment of commercial fisheries. The framework developed in this study integrated an empirical bioclimate envelope model, a regional circulation model, and a size-structured population model to demonstrate how inclusion of the climate-driven habitat suitability index can provide environmentally-tuned recruitment and fishing mortality estimates as well as reduced retrospective biases. The study results highlight some key benefits of incorporating environmental variability into a stock assessment and a potential improvement to management of commercial fisheries.

It has long been argued that incorporating environmental variability into a population dynamic model can reduce uncertainty in the stock assessment by improving parameter estimation and model predictions (Maunder and Watters 2003). While most studies have focused on linking recruitment to temperature and salinity (Myers 1998), incorporating modeled HSI values as an alternative recruitment covariate captures the composite effects of climate variability on the populations' recruitment dynamics. Inclusion of HSI helped explain the historic recruitment trend, especially by better capturing the steep increase in recruitment in the late 2000’s. This finding indicates that the base model potentially underestimated recruitment and overestimated fishing mortality later in the time series when the environmental variability was not considered. Decrease in the total and recruitment likelihoods as well as retrospective biases suggest the improvement in the model fits and performance.

These results indicate enhanced model plausibility and justify the increased model complexity. However, environmentally-explicit assessment also requires a theoretical justification and a careful evaluation of the relationship between environmental variables and population dynamics. For example, water temperature is often chosen as a candidate environmental variable as temperature regulates physiological and biological processes of most marine organisms (Fry 1971, Deutsch et al., 2015). Studies have shown that the assumption of an environmental variable (e.g. water temperature) as a main driver of recruitment fluctuations can also diminish over time. For example, the link between water temperature and marine organisms is often indirect, non-stationary and generally based on empirical statistical relationships. Water temperature may represent complex and compound effects of bottom-up or top-down changes such as thermal habitat availability, food web dynamics, larval retention: (Lluch-Belda et al. 1991; Rykaczewski and Checkley 2008; Nieto et al. 2014).

The use of HSI provides a flexible “optimal environmental window” framework that can integrate multiple ecologically-relevant environmental variables. While habitat suitability models can effectively combine multiple environmental indices to capture a species-environment relationship, users should exercise caution because this approach is prone to multiple hypothesis testing and potential Type I error (i.e. combining multiple indices until significant results are obtained). Using model outputs as ‘data’ also requires a cautionary approach (Brooks and Deroba 2015) because they are subject to the assumptions of the original model. Using a spurious environmental index without ecological and mechanistic support can lead to poor model predictions and hinders the incorporation of environmental variability into future stock assessments. A practitioner should develop criteria for inclusion of environmental variability that can address a balance between model performance and a plausible connection to population dynamics. For example, De Oliveira and Butterworth (2005) stated that an environmental index needs to explain at least ~50% of the variance in recruitment for it to be useful. Furthermore, this study showed that climate-driven HSI can improve estimation of the recruitment trend; however, the empirical environment–recruitment relationships used here will not be able to assess potential effects of future climate change. It is generally acknowledged that lobster behavior is strongly regulated by temperature and salinity, and that the relationships between lobster density and bottom temperature is dome shaped (Crossin et al., 1998). In this study, neither observed bottom temperature and salinity ranges in the Gulf of Maine / Georges Bank have fully captured the dome-shaped relationships. For example, ASMFC proposed that the optimum temperature range for lobster recruitment is from 12° to 18° C, the highest bottom temperature recorded by the bottom trawl surveys was 14° C. Most fishery data cannot fully capture the functional relationship between fish population and environment, especially when the population dynamics is already altered by fishing. To this end, the qualitative habitat suitability modeling approach presented in this study allows users to correct potential data-driven biases and provide a flexible platform to develop and test their optimal environmental window hypothesis with appropriate mechanistic evaluation for why a HSI can affect certain parameters.

The effect of climate change on American Lobster on the Northeast U.S. Shelf is estimated to be neutral, but with a moderate degree of uncertainty (Hare et al. 2016).For American lobster, the relationship between environmental variability and stage-specific survival rate has been thoroughly investigated (Factor 1995, Wahle et al., 2013, ASMC 2015). This study primarily focused on the lobster recruitment habitat suitability as a function of bottom temperature and salinity to better understand how climate-driven environmental variability can inform the historical recruitment trend. The bioclimate envelope model identified increasing trend in climate-driven habitat suitability for American lobster in recruitment size classes in recent years, which indicates an increasing number of days that bottom temperature and salinity falls within the species' optimal range in this area during the spring. The selection of these variables was assumed reasonable as studies have shown that temperature and salinity can be key bottom-up variables regulating ecology and population dynamics of American lobster especially during its recruitment stages. For example, due to its ectothermic nature, water temperature has a significant impact on lobster life history, especially when coupled with non-optimal salinity conditions (Mercaldo-Allen and Kuropat, 1994). Large fluctuation in these variables, whether in singularity or in combination, can create sublethal environment that is beyond the species' adaptive capacity. Water temperature is a key climatic variable that can exert a pervasive and direct influence on all aspects of the American lobster life history especially on growth, survival, and reproduction (Mercaldo-Allen and Kuropat, 1994). Temperature regulates the lobster phenology such as the timing and rate of molting cycle, which can have significant impact on the fishery recruitment. In the Gulf of Maine, approximately 90% of landings are comprised of lobsters molted into a legal-size class within a same year (ASMFC, 2015; Aiken, 1973; Aiken and Waddy, 1975; Kelly, 1993). Furthermore, changes in availability of thermal habitat (i.e. amount of time the temperature remains within the species' preferred range, rather than annual mean temperatures has been proposed as a better indicator for providing ecological context relative to overall recruitment trends (Taylor et al., 1956, Nye 2010, Kelly, 1993, Fogarty et al., 2007). Climate-driven temperature and salinity change will introduce significant uncertainty in recruitment and other population parameters as well as biological reference points derived under the traditional “fishery under equilibrium paradigm” assumptions.

Climate-driven changes in environment will introduce significant uncertainty in other population parameters such as growth, maturation, and natural mortality. Variations in growth rate and size at maturity has been related to the changes in water temperature. Growth rate of American lobster is slower in warmer water due to higher metabolic rate, molt frequency and subsequent smaller molt increment (Aiken, 1977, Aiken, 1980, Aiken & Waddy, 1986, Conan, 1985; Waddy et al., 1995; Aiken & Waddy, 1995). Studies also indicated smaller size at maturity for lobsters in warmer waters (Templeman, 1936, Estrella and McKiernan 1989). Parameters for the CL-W relationship ($\log(W)= -6.37+ 2.85*\log(L)$) and size at maturity (91 mm CL) were assumed to be known and held constant throughout the study period. Size at maturity for American lobster varies from approximately 70 mm CL in the warmer southern New England to 100 mm CL in the colder Bay of Fundy mature at 70-80 mm CL (Factor, 1995, Wahle & Fogarty. 2006). The CL-W relationship is a key biological parameter used in many aspects of the assessment (i.e. determining the overall weight of lobsters from trawl survey catch). Progression of the molt cycle is primarily regulated by water temperature and a proportional relationship between temperature and growth rate was observed throughout the species’ geographical range (Waddy etal.,1995). The prespecified seasonal growth transition matrices assumed that lobster growth takes place during the summer and fall, with majority of lobster’s molt during the summer and relatively small immature individuals molting again during the fall. Furthermore, natural mortality value of 0.15 was assumed for all size classes in all years following the base case model configuration in the 2015 benchmark assessment. The depletion of groundfish may continue to contribute to the low natural mortality for the GOMGBK lobster stock (Steneck and Wahle, 2013). However, given the increase in habitat suitability and changing predator fields driven by climactic shifts, alternative model runs to evaluate the impact of time/length-varying natural mortality for the GOMGBK stock should be explored. Thomas et al., (2017) summarized changes in SST phenology across the entire North American northeastern continental shelf using a 33-year (1982-2014) time series. The shift in SST phenology was characterized by significant trends towards earlier summer starts, longer summer duration, and later summer ends throughout the species' geographic range. Climate-driven changes (i.e. increasing summer duration) many have significant impacts on these base case model assumptions. Future applications of this integrated modeling framework should incorporate scenario-based approaches to investigate the effect of ignoring the effects of time-varying growth, maturity, and natural mortality, or incorrectly specifying the seasonal growth transition matrices.

Environmental variability can affect the stock recruitment and fishery productivity in many ways, but this information is rarely included in assessment models (Skern-Mauritzen et al. 2016). For the Gulf of Maine lobster fishery, the landings are closely related to the timing and magnitude of overlap between lobster thermal habitat and fishing efforts in inshore waters (i.e. lobsters reaching a legal size and moving into nearshore waters to encounter traps: Cooper and Uzmann, 1971; Aiken, 1973; Aiken and Waddy, 1975; Ennis, 1984; Crossin et al., 1998). The results show that incorporating environmental variability into population models has the potential to improve the GOMGBK lobster stock assessment by informing the historic recruitment trend with a climate-driven HSI hypothesized as drivers of recruitment.

With decades of declines in other fisheries, coastal communities around the Gulf of Maine became highly dependent on the lobster fishery, which accounted for 95% of total US landings in 2016. Climate-driven changes in the Gulf of Maine and Georges Bank ecosystems will have significant impacts on the life history and fishery of American lobster.

Studies have shown north-high/south-low recruitment trend in the fishery has been driven by climate-driven changes in environment and several other ecological effects (e.g. epizootic shell disease). The fishery is highly dependent on the lobster recruitment as approximately 85% of landings are lobsters joined the minimum legal-size class within the same year. While the fishery is highly dependent on environmentally driven recruitment, the management is still based on an equilibrium paradigm and assumes that changes in population parameters and productivity are centered around a stationary mean at a given harvest rate and that stock production may be controlled through regulating the harvest rate. The traditional management strategy under the equilibrium assumptions project the expected performance of the stock and the yield is predominantly based on stock abundance and create socioeconomic uncertainty in a climatically-altered marine ecosystems. An emerging consensus calls for more adaptive ecosystem approach to fisheries management to enhance responsiveness and precision relative to unexpected changes in recruitment and stock production. Fishery management in changing environmental conditions will require considerable effort to explore the implications of environmental variability on stock status as well as tools for new adaptive capacities.

Stock assessments are often challenged by limited data and rely on assumed empirical relationships to derive the complex population dynamic processes. Recruitment is a critical component to most of population dynamic model. However, its complex processes is not fully understood because direct observation of recruitment is rarely available and the relevant parameters of is generally derived by the best-fit estimates of recruitment and biomass with deviations due to many top-down and bottom-up factors. Our study will contribute to the management of this valuable resource in the changing ecosystem by showing that the GOMGBK lobster recruitment estimate can be more reliable if environmental factors are considered in the assessment (Jacobson and McClatchie, 2013; Hill et al., 2014; Pershing et al., 2015; Tommasi et al., 2017). make management of highly variable forage fish stocks more effective.

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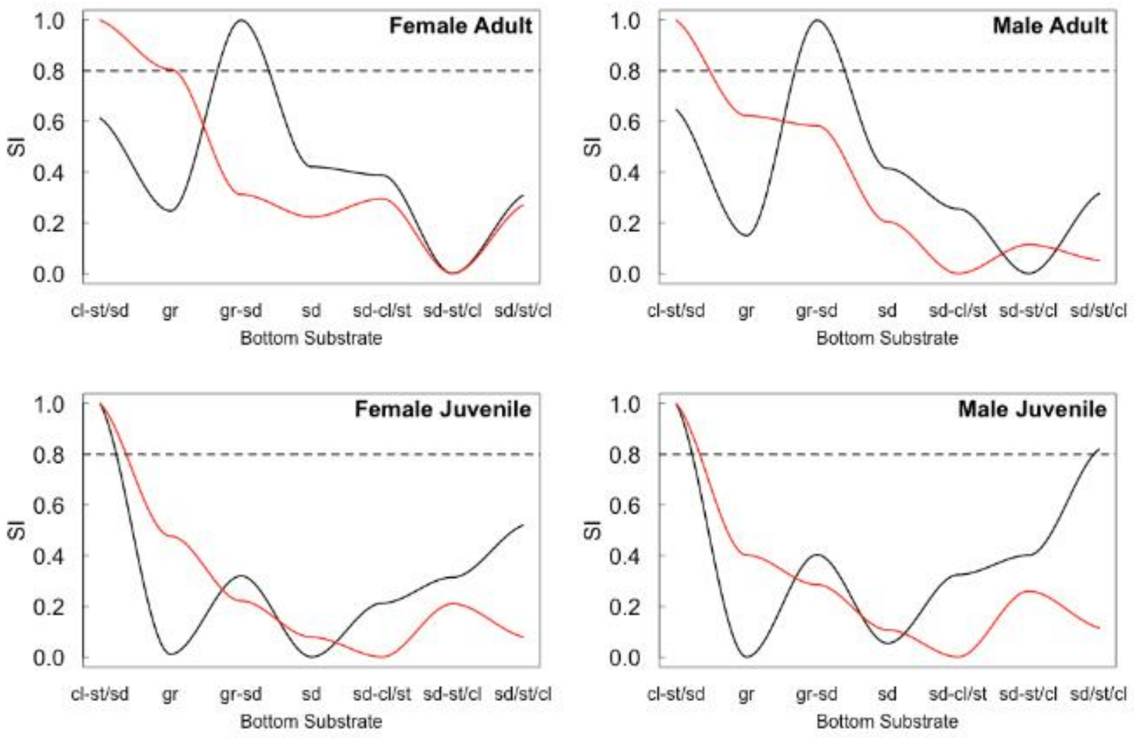
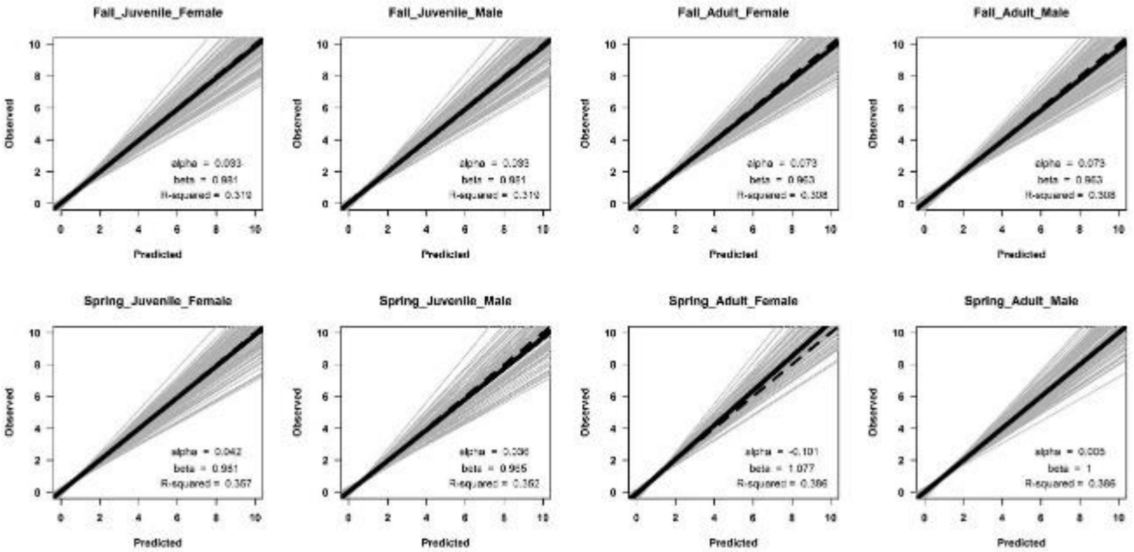
APPENDIX A: SUITABILITY INDEX CURVE OF BOTTOM SUBSTRATE TYPE

A1: Suitability Index (SI) curve of bottom substrate type for four groups of Homarus americanus (2 sexes * 2 life stages). Both spring (black line; April - June), and fall (red line; September - November) SI curves are plotted. cl = clay, st = silt, sd = sand, gr = gravel.



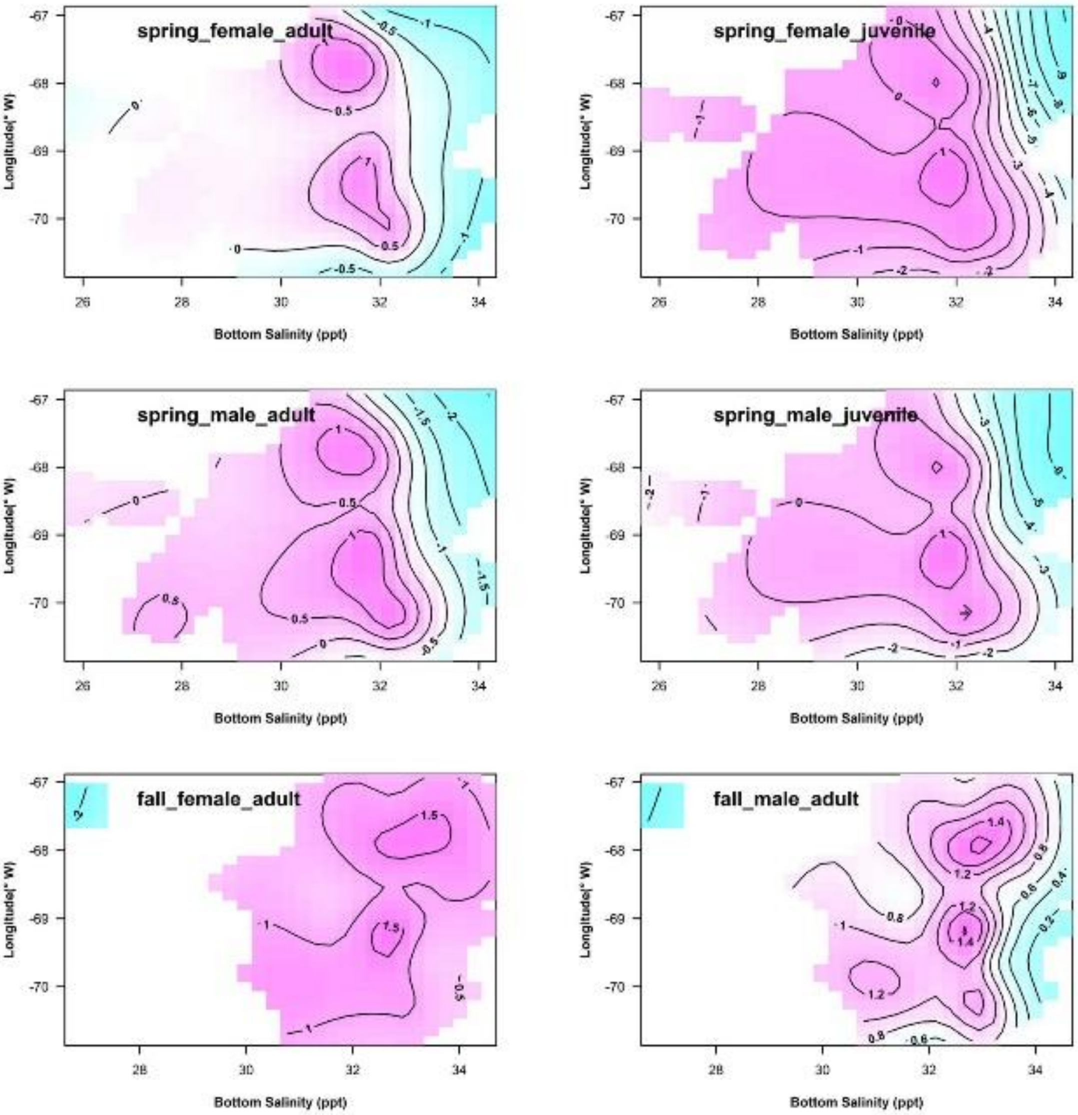
APPENDIX B: CROSS-VALIDATIONS FOR LOBSTER GAM

B1: 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.



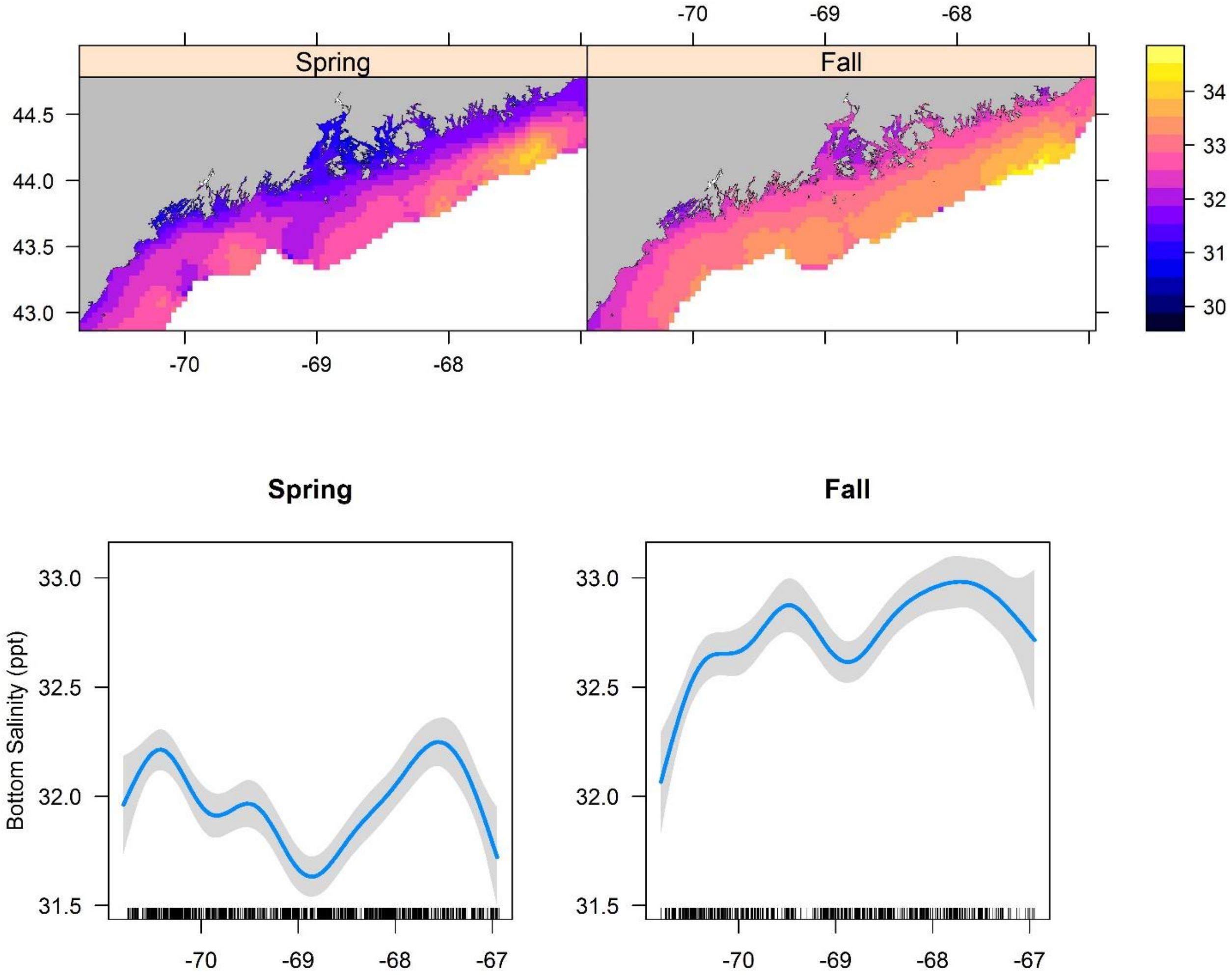
APPENDIX C: INTERACTIVE EFFECT OF SALINITY-LONGITUDE

C1: Partial generalized additive model (GAM) plots describing the significant interactive effect of bivariate bottom salinity-longitude variable in the best-fitting GAM.



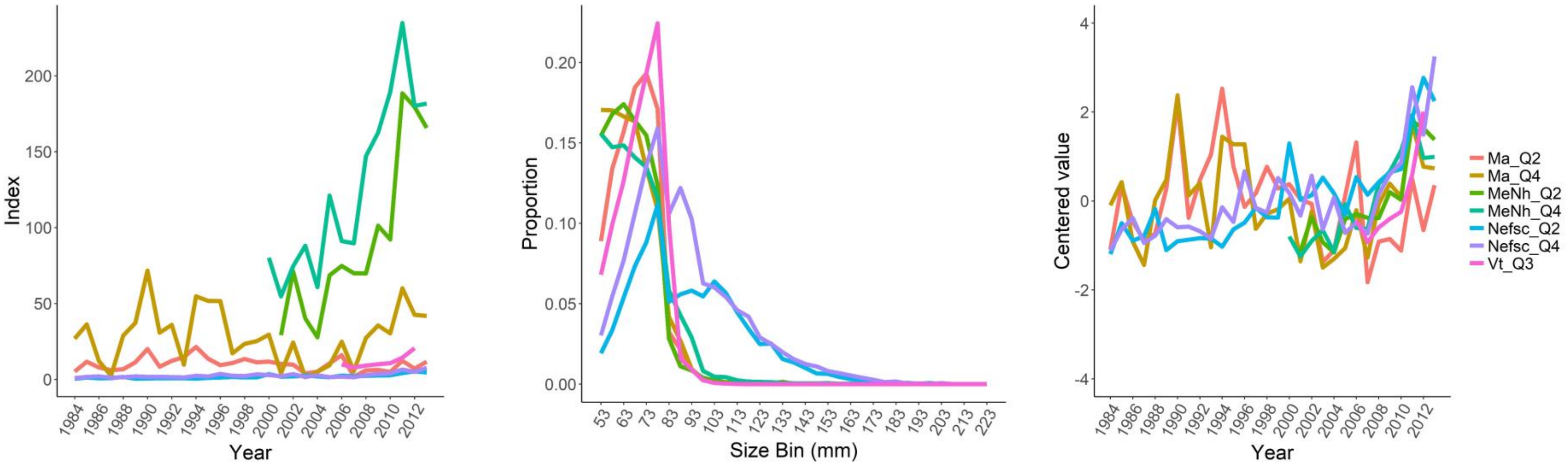
APPENDIX D: BOTTOM SALINITY TREND IN MENH TRAWL SURVEY

D1: Top: Seasonal spatial bottom salinity trend during 2000–2014 in Maine/New Hampshire (ME-NH) inshore bottom trawl survey. The color key represents salinity values in ppt. Bottom: Smooth trends of seasonal bottom salinity along the longitude values covered by the ME-NH bottom trawl survey.

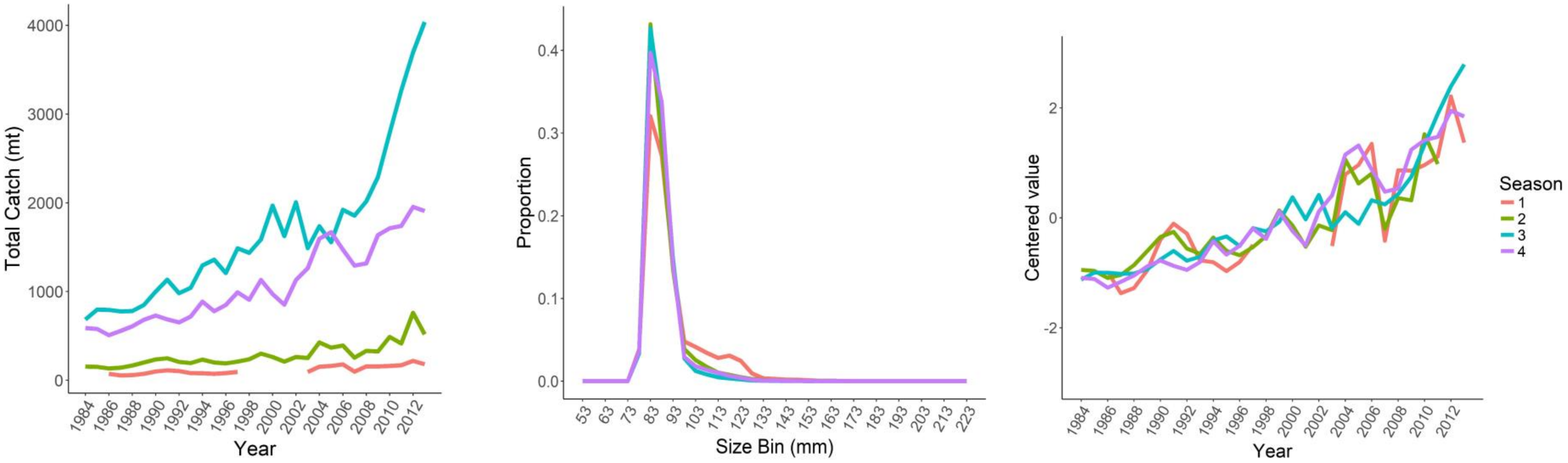


APPENDIX E: SUPPLEMENTAL FIGURES FOR SIZE-STRUCTURED MODEL

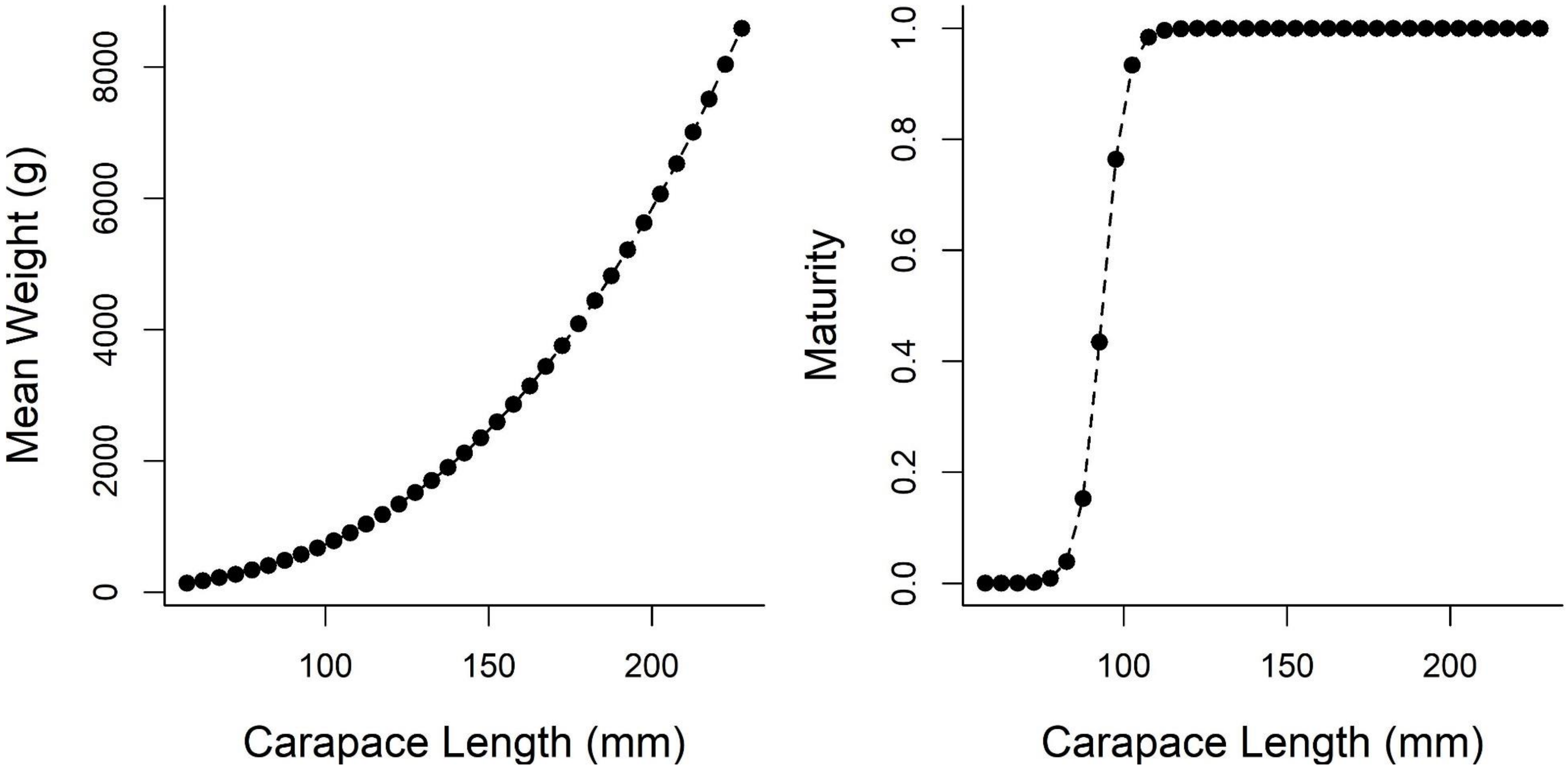
E1: Abundance indices (top left), centered abundance indices (bottom left), and size structures (right) based on bottom trawl surveys for Gulf of Maine / Georges Bank lobster stock. Ma – Massachusetts, MeNh – Maine/New Hampshire, Nefsc – Northeast Fisheries Science Center, VT – Ventless Trap. Q1: January-March, Q2: April-June, Q3: July-September, Q4: October-December. Carapace lengths were aggregated into 5 mm classes and ranged from 53 to 223 mm.



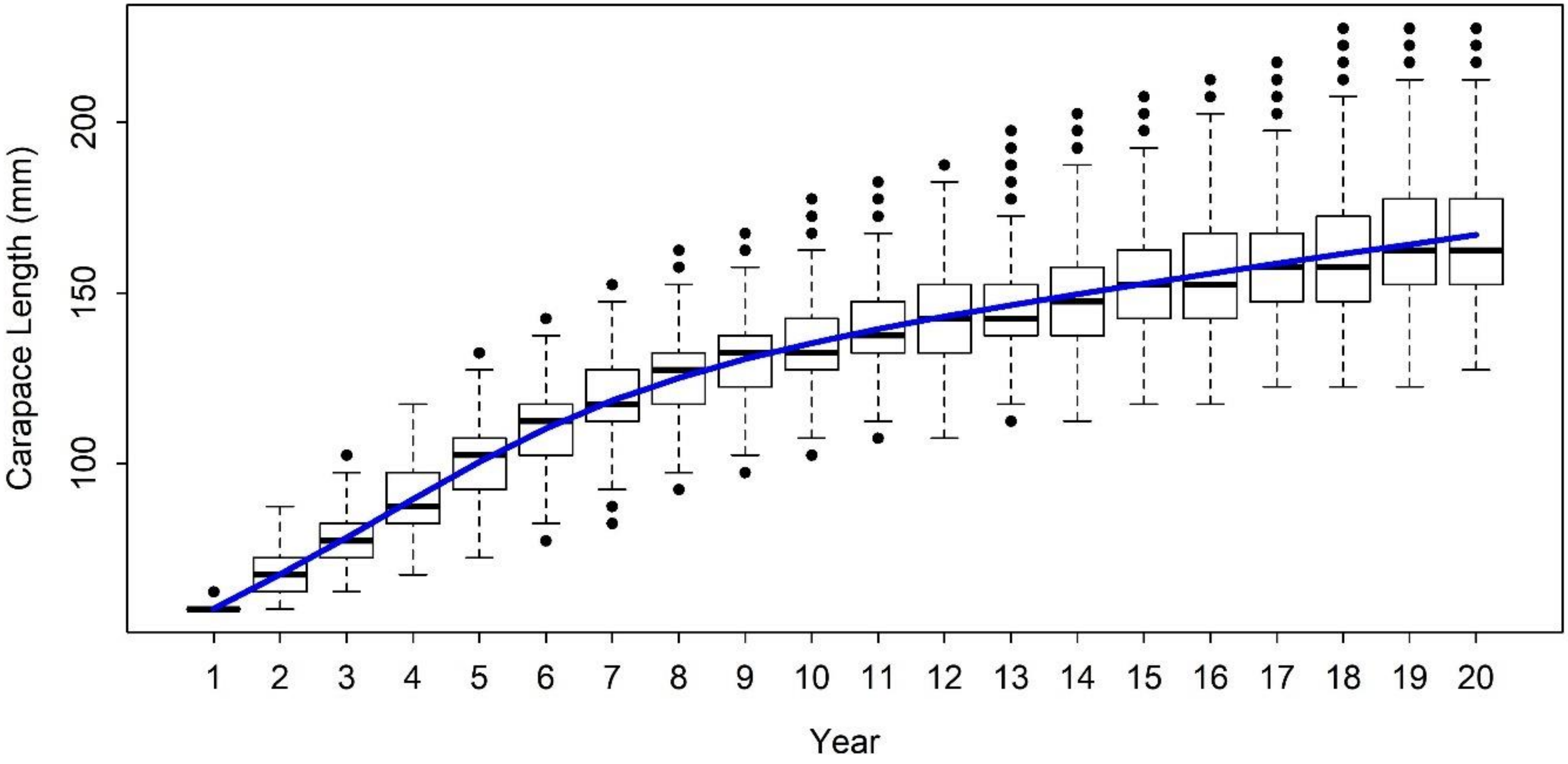
E2: Landings (top left), centered values (bottom left), and size compositions (right) of the Gulf of Maine / Georges Bank American lobster stock. Season 1: January-March 2: April-June 3: July-September 4: October-December. Carapace lengths were aggregated into 5 mm classes and ranged from 53 to 223 mm.



E3: Prespecified parameters of the population model. proportion mature by length and weight as a function of length.



E4: Growth of a cohort under no fishing mortality based on the prespecified growth transition matrices. Boxes represent the size distribution of the cohort in each year.



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