Progress in Oceanography 153 (2017) 24–36

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Marine species distribution shifts on the U.S. Northeast Continental Shelf under continued ocean warming

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ARTICLE INFO

Article history:
Received 14 September 2016
Received in revised form 21 March 2017
Accepted 4 April 2017
Available online 5 April 2017

Keywords:
Climate change
Thermal habitat
Global climate model
Northwest Atlantic
Temperature shifts

ABSTRACT

The U.S. Northeast Continental Shelf marine ecosystem has warmed much faster than the global ocean and it is expected that this enhanced warming will continue through this century. Complex bathymetry and ocean circulation in this region have contributed to biases in global climate model simulations of the Shelf waters. Increasing the resolution of these models results in reductions in the bias of future climate change projections and indicates greater warming than suggested by coarse resolution climate projections. Here, we used a high-resolution global climate model and historical observations of species distributions from a trawl survey to examine changes in the future distribution of suitable thermal habitat for various demersal and pelagic species on the Shelf. Along the southern portion of the shelf (Mid-Atlantic Bight and Georges Bank), a projected 4.1 °C (surface) to 5.0 °C (bottom) warming of ocean temperature from current conditions results in a northward shift of the thermal habitat for the majority of species. While some southern species like butterfish and black sea bass are projected to have moderate losses in suitable thermal habitat, there are potentially significant increases for many species including summer flounder, striped bass, and Atlantic croaker. In the north, in the Gulf of Maine, a projected 3.7 °C (surface) to 3.9 °C (bottom) warming from current conditions results in substantial reductions in suitable thermal habitat such that species currently inhabiting this region may not remain in these waters under continued warming. We project a loss in suitable thermal habitat for key northern species including Acadian redfish, American plaice, Atlantic cod, haddock, and thorney skate, but potential gains for some species including spiny dogfish and American lobster. We illustrate how changes in suitable thermal habitat of important commercially fished species may impact local fishing communities and potentially impact major fishing ports along the U.S. Northeast Shelf. Given the complications of multiple drivers including species interactions and fishing pressure, it is difficult to predict exactly how species will shift. However, observations of species distribution shifts in the historical record under ocean warming suggest that temperature will play a primary role in influencing how species fare. Our results provide critical information on the potential for suitable thermal habitat on the U.S. Northeast Shelf for demersal species in the region, and may contribute to the development of ecosystem-based fisheries management strategies in response to climate change.

1. Introduction

At a range of spatial scales, marine species worldwide are already experiencing the effects of global climate change due to increasing temperatures, altered weather patterns, changes in sea level, circulation patterns, nutrient loads, and the acidity of the oceans (Stock et al., 2011; Walther et al., 2002). Some species may respond to climate change by shifting their distributions to regions with more favorable conditions or by changes in productivity in response to the new conditions in a given region.

Within the Northwest Atlantic Ocean, the U.S. Northeast Continental Shelf (U.S. NES, Fig. 1) is a region where ocean warming has been identified as a major driver of changes in the distribution of marine species (Hare et al., 2010, 2016; Lynch et al., 2015; Nye et al., 2009; Pinsky and Fogarty, 2012; Pinsky et al., 2013;

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http://dx.doi.org/10.1016/j.pocean.2017.04.001
0079-6611/© 2017 Published by Elsevier Ltd.

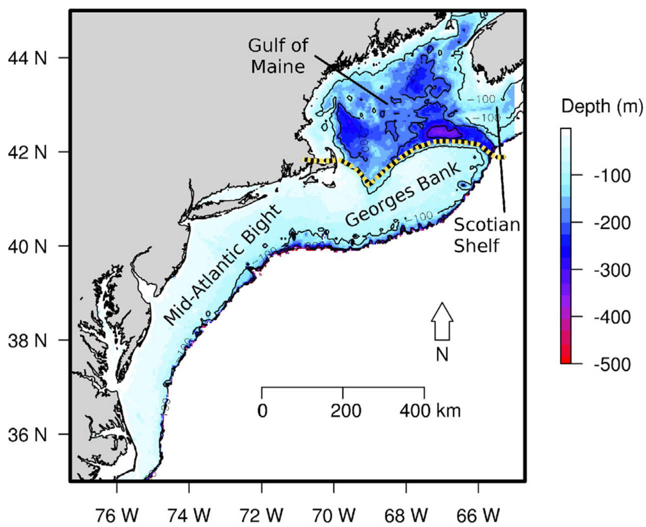

Fig. 1. The Northeast U.S. Shelf illustrating the southern region: the Mid-Atlantic Bight and Georges Bank, and northern region: the Gulf of Maine with shaded bathymetry (meters depth). Dashed line indicates the split between the northern and southern regions.

Rijnsdorp et al., 2009). Observations of sea surface temperature (SST), particularly within the Gulf of Maine, show a warming rate faster than 99% of the global ocean over the past decade (Pershing et al., 2015). Climate change projections from a high-resolution global climate model also suggest a U.S. NES warming rate that will be two to three times faster than the global average (Saba et al., 2016). Ocean temperature in the Northwest Atlantic has been linked to the relationship between the Atlantic Meridional Overturning Circulation (AMOC) and the position of the Gulf Stream (Zhang, 2008). The AMOC is a major component of the Earth's climate system and can be characterized by a northward flow of warm, salty water in the upper layers of the Atlantic Ocean, and a southward flow of colder water in the deep Atlantic Ocean. A weaker AMOC correlates with a more northerly position of the Gulf Stream, which is associated with warmer ocean temperatures (Zhang, 2008) and more Gulf Stream-associated slope water entering the Gulf of Maine (Saba et al., 2016). The enhanced warming of the U.S. NES in both observations and modeled climate change projections are thought to be due to the combined effects of global warming, a weakening AMOC, and changes in regional ocean circulation (Saba et al., 2016).

The U.S. NES is a highly productive, temperate system that is influenced by tides, wind-driven mixing, a strong seasonal cycle, and two major oceanic current systems: the Labrador Current (colder and fresher water from the north) and the Gulf Stream (warmer and saltier water from the south). The high primary productivity in the region combined with its location between warm and cold temperate regions results in a diverse array of fish and invertebrates, many of which are commercially important. With complex biotic, environmental, and anthropogenic forces at play, it is critical to gain a better understanding of the interactions between species, the effects of fishing pressure, and to understand the role of climate change in shifting species and community distributions.

There is consensus among researchers that climate change is going to affect marine taxa, but it is not clear that all species will be negatively impacted. There has recently been a focus on climate change 'winners and losers' (Glantz, 1995) and the idea that the abundance and distribution of some species or species groups may remain stable or expand with changes in climate whereas others may decline in abundance and distribution (Hare et al., 2016; Hoelzel, 2010). While it is appreciated that some species may do better while others worse under climate change, the complex interplay of changing species interactions and fishing patterns make understanding the intricacies of these changes difficult. Despite this complexity, understanding changes in thermal habitat availability will help clarify general patterns of change in species distributions. Using bottom trawl survey data collected within the U.S. NES, we estimated realized bathy-thermal niches for 58 demersal and pelagic species. A high-resolution global climate model developed by the NOAA Geophysical Fluid Dynamics Laboratory (GFDL) was used to generate future projections of bottom and surface ocean temperature across the U.S. NES region. We then used these future temperatures to project the distributions of marine species on the Shelf and explore the hypothesis that some species will be more impacted than others by changes in ocean temperature.

Kleisner et al. (2016) illustrated historical differences in regional oceanographic and environmental characteristics and bathymetry along the U.S. NES responsible for variability in the response of individual species and species assemblages to warming ocean temperatures over the past four decades. In particular, the Gulf of Maine is a semi-enclosed continental shelf sea with deep and variable topography that is strongly influenced by the mixing of water masses from the North and South, while Georges Bank and the Mid-Atlantic Bight have comparatively more uniformly shallow bathymetry and less mixing. Between the northern and southern U.S. NES, there were differential shifts in species and assemblage distributions over the 1968–2013 time period. In general, species on Georges Bank and the Mid-Atlantic Bight exhibited stronger pole-ward shifts, while species in the Gulf of Maine exhibited stronger shifts in depth rather than latitude. We expect that these strong regional patterns on the U.S. NES will carry forward under future climate change scenarios. Therefore, we hypothesize that species that are currently distributed in the southern U.S. NES will continue to have adequate levels of suitable thermal habitat within the survey region in the future because they can potentially shift northward following the movement of temperature isotherms. Conversely, species that are currently concentrated on the northern U.S. NES will ultimately experience a decline in suitable thermal habitat within the survey region. Here we present an analysis of historical and potential future species distribution change on the U.S. NES.

2. Materials and methods

2.1. Global climate model projection

The most recent Intergovernmental Panel on Climate Change (IPCC) assessment of projected global and regional ocean temperature change is based on global climate models that have relatively coarse (~100 km) ocean resolutions (IPCC, 2013). At this coarse resolution, the Gulf Stream position is misrepresented in the models, separating from the U.S. coast too far to the north, and therefore resulting in a warm bias in sea surface temperature (Saba et al., 2016).

Recently, a high-resolution global climate model was developed by NOAA GFDL, which has a 0.1° (10-km global) resolution ocean component and a 0.5° (50-km global) resolution atmosphere component (CM2.6). This model has been shown to resolve regional ocean circulation and bathymetry within the U.S. NES, including the position of the Gulf Stream, Georges Bank, and the Gulf of Maine's Northeast Channel, much more accurately than lower resolution models assessed by the IPCC (Saba et al., 2016). Consequently, CM2.6 has the lowest bias in SST and bottom temperature in the U.S. NES relative to coarser models (Saba et al., 2016). Under global atmospheric CO_2 doubling, the model's upper-ocean temperature in the Northwest Atlantic warms at a rate nearly twice as fast as the coarser model averages and nearly three times faster than the global average. The enhanced warming of the U.S. NES in CM2.6 is due to a synergy of global warming, a northern shift in the Gulf Stream, a retreat of the Labrador Current, and a higher proportion of Atlantic Temperate Slope Water entering the Gulf of Maine. Confidence in the climate change projection from CM2.6 for the U.S. NES is driven by the model's ability to resolve the Shelf's regional circulation and complex bathymetry.

The CM2.6 simulation consists of (1) a 1860 pre-industrial control, which brings the climate system into near-equilibrium with 1860 greenhouse gas concentrations, and (2) a transient climate response (2xCO2) simulation where atmospheric CO2 is increased by 1% per year, which results in a doubling of CO2 after 70 years. The climate change response from CM2.6 was based on the difference between these two experimental runs. Refer to Saba et al. (2016) for further details.

The CM2.6 80-year projections can be roughly assigned to a time period by using the IPCC Representative Concentration Pathways (RCPs), which describe four different 21st century pathways of anthropogenic greenhouse gas emissions, air pollutant emissions, and land use (IPCC, 2014). There are four RCPs, ranging from a stringent mitigation scenario (RCP2.6), two intermediate scenarios (RCP4.5 and RCP6.0), and one scenario with very high greenhouse gas emissions (RCP8.5). For RCP8.5, the global average temperature at the surface warms by 2 °C by approximately 2060–2070 relative to the 1986–2005 climatology (see Figure SPM.6a in IPCC, 2013). For CM2.6, the global average temperature warms by 2 °C by approximately years 60–80 (see Fig. 1 in Winton et al., 2014). Therefore, the last 20 years of the transient climate response simulation roughly corresponds to 2060–2080 of the RCP8.5 scenario.

Here, the monthly differences in surface and bottom temperatures ('deltas') for spring (February–April) and fall (September–November) are added to an average annual temperature climatology for spring and fall, respectively, derived from observed surface and bottom temperatures to produce an 80-year time series of future bottom and surface temperatures in both seasons. The observed temperatures come from the NEFSC spring and fall bottom trawl surveys conducted from 1968 to 2013 and represent approximately 30,000 observations over the time series.

2.2. Modeling changes in suitable thermal habitat

The National Oceanographic and Atmospheric Administration (NOAA) Northeast Fisheries Science Center (NEFSC) U.S. NES bottom trawl survey, which has been conducted for almost 50 years in the spring and fall, provides a rich source of data on historical and current marine species distribution, abundance, and habitat, as well as oceanographic conditions (Azarovitz, 1981). The survey was implemented to meet several objectives: (1) monitor trends in abundance, biomass, and recruitment, (2) monitor the geographic distribution of species, (3) monitor ecosystem changes, (4) monitor changes in life history traits (e.g., trends in growth, longevity, mortality, and maturation, and food habits), and (5) collect baseline oceanographic and environmental data. These data can be leveraged for exploring future changes in the patterns of abundance and distribution of species in the region. Here we explore species distribution shifts for 58 demersal species (see Tables S1–S3) for which there was sufficient temporal coverage (i.e., observed annually) in the trawl survey data.

While historical shifts can be modeled based on actual observations of biomass, temperature, and other variables, potential future distribution changes can only be estimated based on niche models that use forecasted temperature estimates from global climate models and variables that we assume static over time (i.e., depth and rugosity). In essence, we are not able to predict actual changes in biomass or to evaluate whether species maintain assemblages in the future, but we can say something about the probability of the presence of suitable thermal habitat availability for individual species. Therefore, here we use a similar Generalized Additive Model (GAM; Hastie and Tibshirani, 1986) structure to that described in Kleisner et al. (2016). However, we model individual species thermal habitat across the whole U.S. NES and not by sub-region because we did not want to assume that species would necessarily maintain these assemblages in the future. Indeed, the goal here is to determine future patterns of thermal habitat availability for species on the U.S. NES in more broad terms. We fit one GAM based on both spring and fall data (i.e., an annual model as opposed to separate spring and fall models) and use it to project potential changes in distribution and magnitude of biomass separately for each season for each species. By creating a single annual model based on temperature data from both spring and fall, we ensure that the full thermal envelope of each species is represented. For example, if a species with a wide thermal tolerance has historically been found in cooler waters in the spring, and in warmer waters in the fall, an annual model will ensure that if there are warmer waters in the spring in the future, that species will have the potential to inhabit those areas. Additionally, because the trawl survey data are subject to many zero observations, we use delta-lognormal GAMs (Wood, 2011), which model presence-absence separately from logged positive observations. The response variables in each of the GAMs are presence/absence and logged positive biomass of each assemblage or individual species, respectively. A binomial link function is used in the presence/absence models and a Gaussian link function is used in the models with logged positive biomass.

The predictor variables are surface and bottom temperature and depth (all measured by the survey at each station), fit with penalized regression splines, and survey stratum, which accounts for differences in regional habitat quality across the survey region. Stratum may be considered to account for additional information not explicitly measured by the survey (e.g., bottom rugosity). Predictions of species abundance are calculated as the product of the predictions from the presence-absence model, the exponentiated predictions from the logged positive biomass model, and a correction factor to account for the retransformation bias associated with the log transformation (Duan, 1983; and see Pinsky et al., 2013).

We calculate the suitable thermal habitat both in terms of changes in 'suitable thermal abundance', defined as the species density possible given appropriate temperature, depth and bathymetric conditions, and changes in 'suitable thermal area', defined as the size of the physical area potentially occupied by a species given appropriate temperature, depth and bathymetric conditions. Suitable thermal abundance is determined from the predictions from the GAMs (i.e., a prediction of biomass). However, this quantity should not be interpreted directly as a change in future abundance or biomass, but instead as the potential abundance of a species in the future given changes in temperature and holding all else (e.g., fishing effort, species interactions, productivity, etc.) constant. Suitable thermal area is determined as a change in the suitable area that a species distribution occupies in the future and is derived from the area of the kernel density of the distribution. To ensure that the estimates are conservative, we select all points with values greater than one standard deviation above the mean. We then compute the area of these kernels using the *gArea* function from the 'rgeos' package in R (R Core Team, 2016).

2.3. Measuring prediction skill

The presence-absence GAMs exhibit relatively high in-sample adjusted R^2 relative to the log of biomass GAMs many species

(Table S1). Regardless, a high R^2 value does not necessarily identify a model that exhibits high out-of-sample prediction skill. Indeed, long-term predictions will always be challenging. However, we can, at the least, test whether the annual model can provide skillful short-term seasonal predictions. To do so, we split the survey data set into a training set (1968–2002) and test set (2003–2012). The 'full' GAM (i.e., including year, stratum, depth, and bottom and surface temperature) was fit to the training set and used to predict seasonally. Prediction error was measured on the test set and put into context by comparing the full GAM to a simplified 'null' model, i.e., a random walk model with drift. A random walk model predicts the current state as the future state (i.e., it provides a constant forecast). A random walk with drift adds the long-term trend to the current state as the prediction. For each species, we fit a random walk with drift to the historical annual mean biomass observed in each stratum, and then made seasonal one-year-ahead stratum-specific predictions on the test set. Although simple, the random walk with drift model often outperforms more complicated models (e.g., Makridakis and Hibon, 2000; Ward et al., 2014). Here, the full GAM is considered to be suitable for long-term projections only for species in which its mean prediction error was lower than that of the null model.

Mean prediction error was quantified as the mean absolute error (*MAE*):

$$MAE = \frac{1}{n}\sum_{i=1}^{n}|f_i - y_i| \tag{1}$$

where f_i is the prediction of biomass at survey station i, y_i is the observed biomass at station i, and n is the total number of stations in the test set. Since the test set contains the observed temperature at each station, the predictions assume that the correct temperature values are known (i.e., predictions of temperature from the global climate model were not used).

We report the full GAM prediction error relative to the null model prediction error:

$$MASE = \frac{MAE_{fullGAM}}{MAE_{rw}} \tag{2}$$

where $MAE_{fullGAM}$ is the prediction error of the full GAM, and MAE_{rw} is the prediction error of the null model. This ratio, known as Mean Absolute Scaled Error (*MASE*), is used in forecasting studies because it allows for the comparison of prediction errors across time series with different scales, and it is defined under a wide range of time series characteristics (Hyndman and Koehler, 2006). Typically, MAE_{rw} is calculated on the training set, however we calculate MAE_{rw} on the test set to give a direct comparison between the two forecasting methods and to remove any differences in forecast performance that might be driven by differences in the statistical properties of the training set and test set (i.e., non-stationarity). Therefore, a $MASE > 1$ indicates that the full GAM gives less accurate predictions than the null model on the test set, while a $MASE < 1$ indicates better predictions from the full GAM versus the null model. There are no strict guidelines on how to interpret the MASE statistic, e.g., whether a MASE of 0.99 is statistically better than a MASE above 1.0. However, the MASE is frequently used in assessing forecast predictions. Therefore, we complement the MASE with the Diebold-Mariano test statistic, which evaluates the loss differential (error) between two forecasts (Diebold and Mariano, 1995). We use the function 'dm.test' in R to test the method one forecast (i.e., the null model predicted seasonally) against the method two forecast (i.e., the full GAM predicted seasonally). We set the time-step (h) to 1, the power of the loss function to 1, and set the alternative hypothesis test to 'greater' where a significant p-value is indicative of a rejection of the null hypothesis and that the full GAM provides a better prediction than the null model. We use a MASE < 1 and a significant result from the Diebold-Mariano test to indicate a model that can be used for forecasting. This results in 36 species (out of 58) that are deemed suitable for forecasting (Tables S2 and S3). The findings presented are based on this subset of species.

2.4. Assessing potential impact on fishing communities

We explore the potential impact that shifting distributions might have for fishing communities by examining (1) the distance between the main fishing port in each state and the center of the distributions of spring suitable thermal area and (2) the percent change in suitable thermal abundance over time for the top landed species (by weight) in each state. Statistics from the National Ocean Economics Program at the Middlebury Institute of International Studies at Monterey (Center for Blue Economics; http://www.oceaneconomics.org/LMR/topPorts.asp) are used to determine the port with the highest landed weight over the past five years (Table 1). Centers of distribution for each species in six 20-year periods (i.e., two historical time periods and four future time periods) are calculated following an approach developed by colleagues (Nye et al., 2009), which re-grids latitude and longitude using along-shelf and cross-shelf positions to avoid centers of biomass outside the survey area. The re-gridded points were weighted by the predicted biomass at each point and averaged to determine the centers of distribution for each species in a region. The bearing and direction of straight-line distance between the port and the center of distribution in each period was calculated for each species using the *bearing* and *distHaversine* functions of the 'geosphere' package in R (Hijmans, 2014).

3. Results

3.1. Observed and projected ocean temperature changes

From 1968 to 2013, observed surface temperatures at the survey locations have increased across the U.S. NES by approximately 3 °C in the fall and 0.2 °C in the spring (Fig. 2a). The modeled bottom and surface temperatures from CM2.6 were found to have very low bias when compared to observed temperatures (see Fig. 2 in Saba et al., 2016). The warming signal is also stronger regionally in the fall. Fall surface temperature trends are significant, and have risen by about 2.4 °C in the northern U.S. NES and about 3.2 °C in the southern U.S. NES (Fig. 2b). Spring temperatures have risen as well in the northern U.S. NES, but to a lesser degree, about 1.2 °C, and have remained relatively stable (an increase of only 0.006 °C) in the southern U.S. NES (Fig. 2b). With the exception of the spring surface temperature for the Gulf of Maine, the spring trends are not significantly different from zero. Fall bottom temperatures have also increased significantly across the survey regions over the past 45 years by about 1.76 °C, but declined

Table 1
List of main port in terms of weight of landings by state with approximate latitude and longitude position.

Port	State	Lat	Lon
Wanchese-Stumpy Point	North Carolina (NC)	35.85	−75.62
Reedville	Virginia (VA)	37.83	−76.28
Ocean City	Maryland (MD)	38.32	−75.09
Indian River Inlet	Delaware (DE)	38.61	−75.02
Cape May-Wildwood	New Jersey (NJ)	38.95	−74.87
Montauk	New York (NY)	41.08	−71.94
New London	Connecticut (CT)	41.35	−72.10
Point Judith	Rhode Island (RI)	41.36	−71.49
New Bedford	Massachusetts (MA)	41.64	−70.92
Newington	New Hampshire (NH)	43.08	−70.76
Portland	Maine (ME)	43.65	−70.25

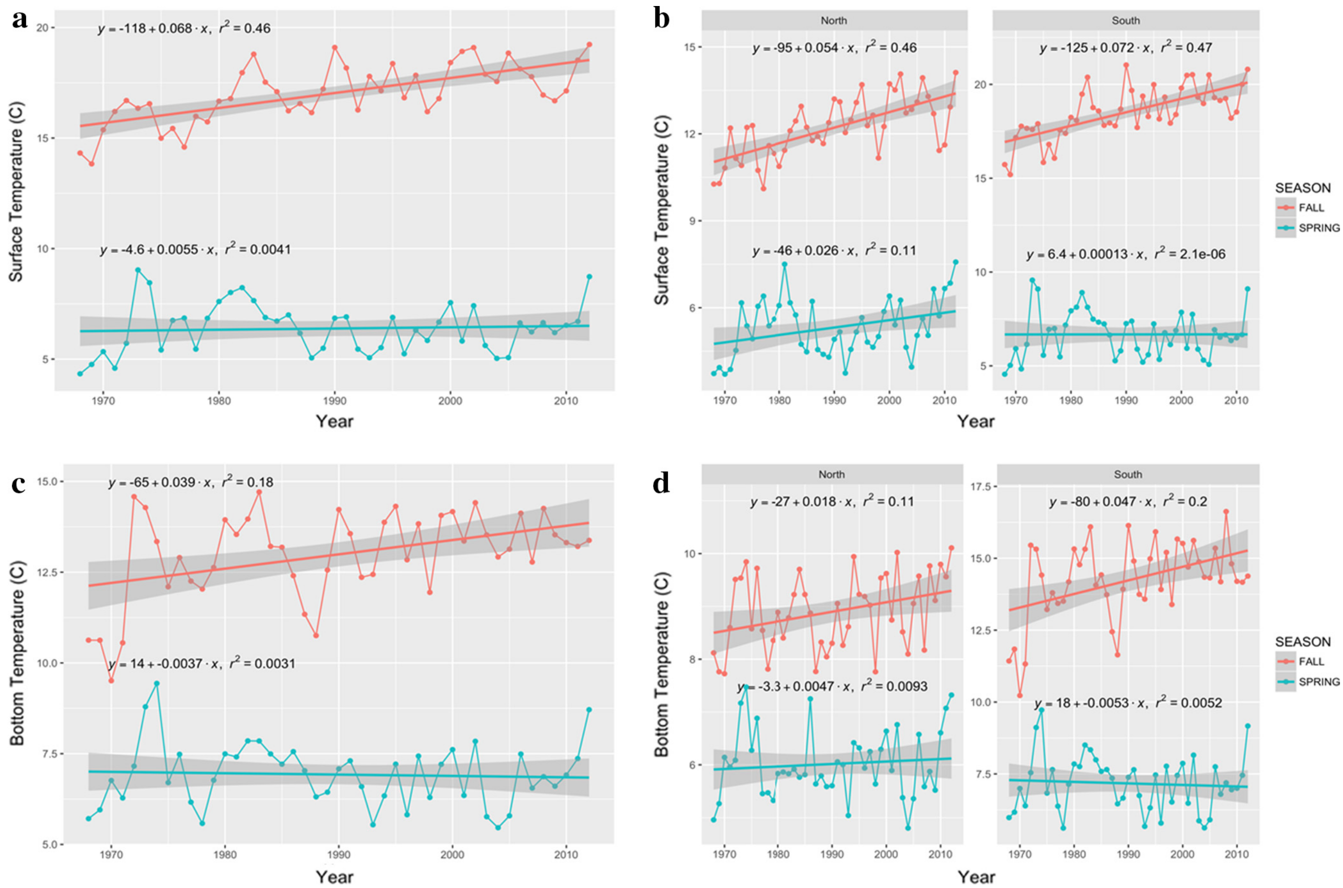

Fig. 2. Time series of average annual (a-b) surface and (c-d) bottom temperature over the observed time period (1968–2013) by season for the whole U.S. NES (a and c) and for the north (Gulf of Maine) and south (Mid-Atlantic Bight/Georges Bank) regions of the U.S. NES (b and d). The straight lines represent linear model fits with corresponding equations for each fit. All fall linear model fits were significant (p-value < 0.5) and none of the spring trends were significant, with the exception of the spring north surface temperature trend.

slightly in the spring by about 0.2 °C (Fig. 2c). Fall bottom temperatures have risen by about 0.8 °C in the northern U.S. NES and about 2.1 °C in the southern U.S. NES (Fig. 2d). The rate of warming over the past 45 years in the spring bottom temperatures has been about 0.2 °C in the southern NES and has actually shown a slight decline of about −0.2 °C in the southern U.S. NES (Fig. 2d). Neither trend is significant. In the Gulf of Maine, Pershing et al. (2015) found that temperatures since 1982 have risen at a rate of 0.03 °C per year, three times the global rate. Since 2004, the rate has increased to 0.23 °C per year (Pershing et al., 2015). Additionally, Friedland and Hare (2007) have noted that mean annual SST ranges have increased on the U.S. NES to the highest levels in 150 years, possibly suggesting a shift into a new phase of SST variability.

The temperature deltas from CM2.6 result in an average 3.9 °C increase in surface temperatures (Fig. 3a) and an average 4.3 °C increase in bottom temperatures (Fig. 3c) across the U.S. NES over the 80-year future time period. Along the Mid-Atlantic Bight and on Georges Bank, a projected 4.1 °C (surface) to 5.0 °C (bottom) warming of ocean temperature from current conditions over the 80-year future time period results in a northward shift of the thermal habitat for the majority of species inhabiting these two regions (Fig. 3b and d). In the Gulf of Maine, a projected 3.7 °C (surface) to 3.9 °C (bottom) warming from current conditions 80-year future time period results in substantial reductions in suitable thermal habitat such that existing species may not remain in these waters under continued warming (Fig. 3b and d).

In the forecasting comparison, the full GAMs outperformed the null models (MASE < 1) for most species, with the exception of alewife, American shad, Atlantic herring, Atlantic mackerel, barndoor skate, blueback herring, cunner, cusk, ocean pout, pin fish, pollock, sand lance, sea raven, sharpnose shark, spot, spotted hake, tautog, windowpane founder, winter flounder, winter skate, wolffish, and yellowtail flounder. Therefore, suitable thermal habitat for these 22 species is not projected in either season (Table S2).

In general, species that currently have a more southerly distribution had stable or increasing suitable thermal area (Figs. 4a and 5a) and in many cases increasing suitable thermal abundance (Figs. 4b and 5b) within the survey region. This likely reflects the fact that they are able to shift northward or deeper to maintain preferred temperatures. Conversely, species that currently have a more northerly distribution had decreases in suitable thermal habitat (Figs. 4a and 5a) and suitable thermal abundance (Figs. 4b and 5b) over the survey region. This may be indicative of the fact that temperatures in the Gulf of Maine will become too warm and inhospitable for these species. The increases in suitable thermal area and suitable thermal abundance were greater in the spring for species with a more southern distribution (Fig. 4).

It is important to note that species with distributions in U.S. waters that are currently at their southern limits (e.g., Atlantic cod), may find suitable thermal habitat in more northern waters or off the shelf. Therefore, this study can only determine whether areas within the U.S. NES region are likely to hold potential as suitable thermal habitat. These changes in suitable thermal habitat can

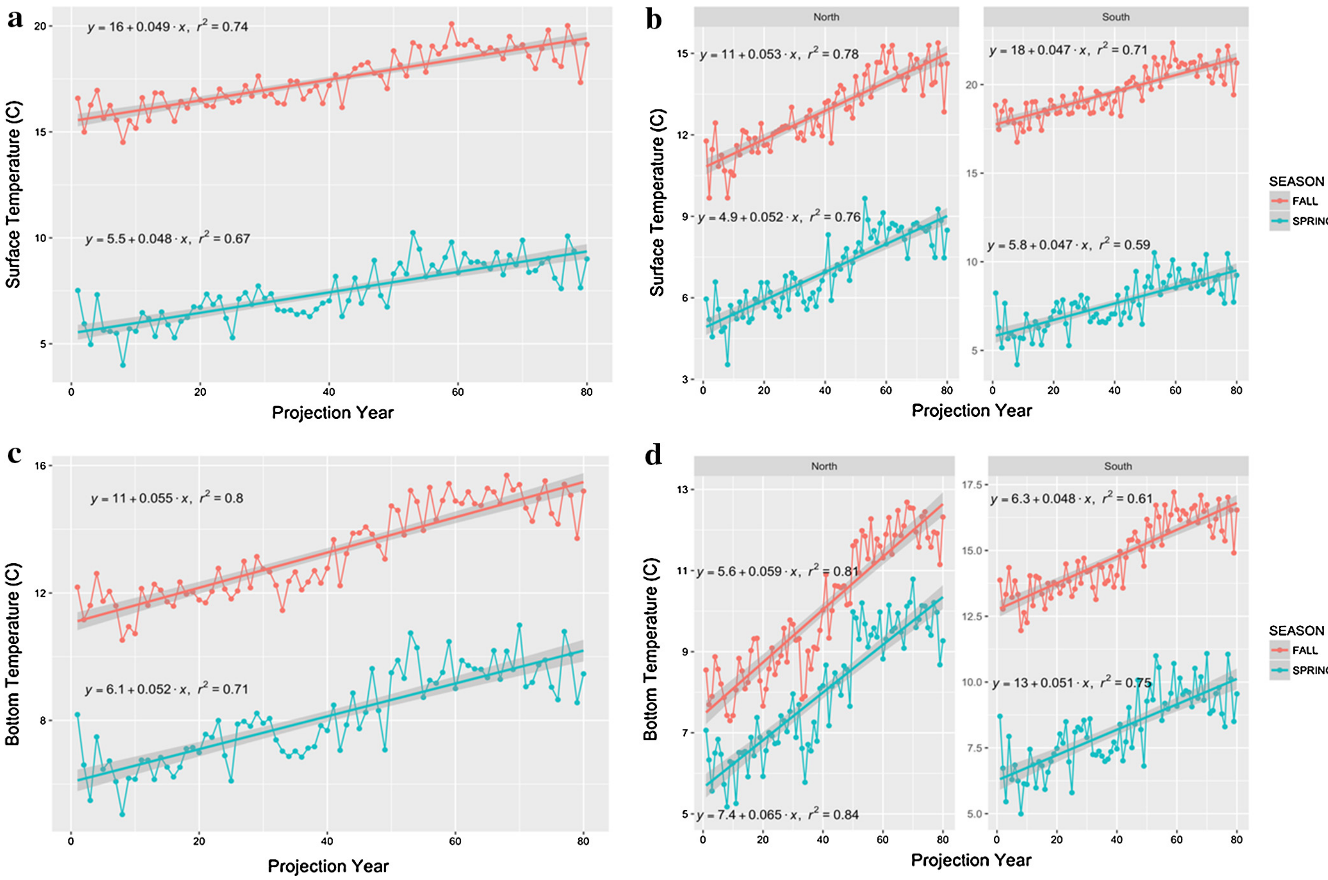

Fig. 3. Time series of average annual (a-b) surface and (c-d) bottom temperature over the projected 80-year time period by season for the whole U.S. NES (a and c) and for the north (Gulf of Maine) and south (Mid-Atlantic Bight/Georges Bank) regions of the U.S. NES (b and d). The straight lines represent linear model fits with corresponding equations for each fit.

be shown on a map for current and future time periods. We provide an example for two species that currently have a more southerly distribution (e.g., Atlantic croaker and smooth dogfish) and two species with a more northerly distribution (e.g., Atlantic cod and red hake) to illustrate regional differences (Figs. 6 and 7). Movies of future distribution shifts for all modeled species can be found at: (http://www.nefsc.noaa.gov/ecosys/climate-change/).

3.2. Changes in projected suitable thermal habitat relative to major ports

There were some distinct differences in distance of the centers of distribution of the top species landed from the main ports in each state (Table 1) and the change in suitable thermal abundance over time (Fig. 8). In states north of Cape Cod, the general trend in distance from the main port either decreases (Maine and New Hampshire) or remains relatively stable in the future (Massachusetts). In all three of these states, American lobster suitable thermal abundance is also projected to increase by more than 25%. This is an indication that the projected increases in warming waters in the Gulf of Maine may create beneficial conditions for American lobster populations and that they will continue to be accessible to fishing ports in this region. In contrast, species like monkfish, Atlantic cod, white hake, silver hake, witch flounder, and sea scallops, whose centers of suitable thermal abundance may remain accessible to major local fishing ports, could experience strong declines in suitable thermal habitat related to warming waters.

For the northern states in the Mid-Atlantic, e.g., Rhode Island, Connecticut, and New York, distance from ports to the centers of distribution and suitable thermal abundance are projected to remain relatively stable for most of the current top landed species. For states south of New York, there are more distinct increases in the distance of the centers of distribution for some species from the main ports. There are also some increases in suitable thermal abundance for certain species like striped bass and Atlantic croaker. Conversely, there are many decreases in suitable thermal abundance. For example, in New Jersey, the distance from port increases by about 25% for longfin squid and there is a slight decrease in suitable thermal habitat for this species. In Delaware, the distance from port increases by about 25% for black sea bass and bluefish, and only striped bass shows a clear increase in suitable thermal abundance. In Maryland, the distance from port increases for black sea bass, sea scallops, striped bass, and summer flounder, and, with the exception of striped bass, these species show relatively low and stable suitable thermal abundance. There are increases in suitable thermal abundance and decreases in distance from port for Atlantic croaker. In Virginia, there is a strong increase in distance from port for summer flounder, the third highest landed species currently. Among the top six species landed in Virginia, only Atlantic croaker (top landed species) and striped bass (4th highest landings) show increases in suitable thermal abundance of about 25%. North Carolina has increases in distance from ports to the centers of distributions for all six of the top landed species. Atlantic croaker, the top landed species in North Carolina, and smooth dogfish, also show strong increases in suitable thermal abundance.

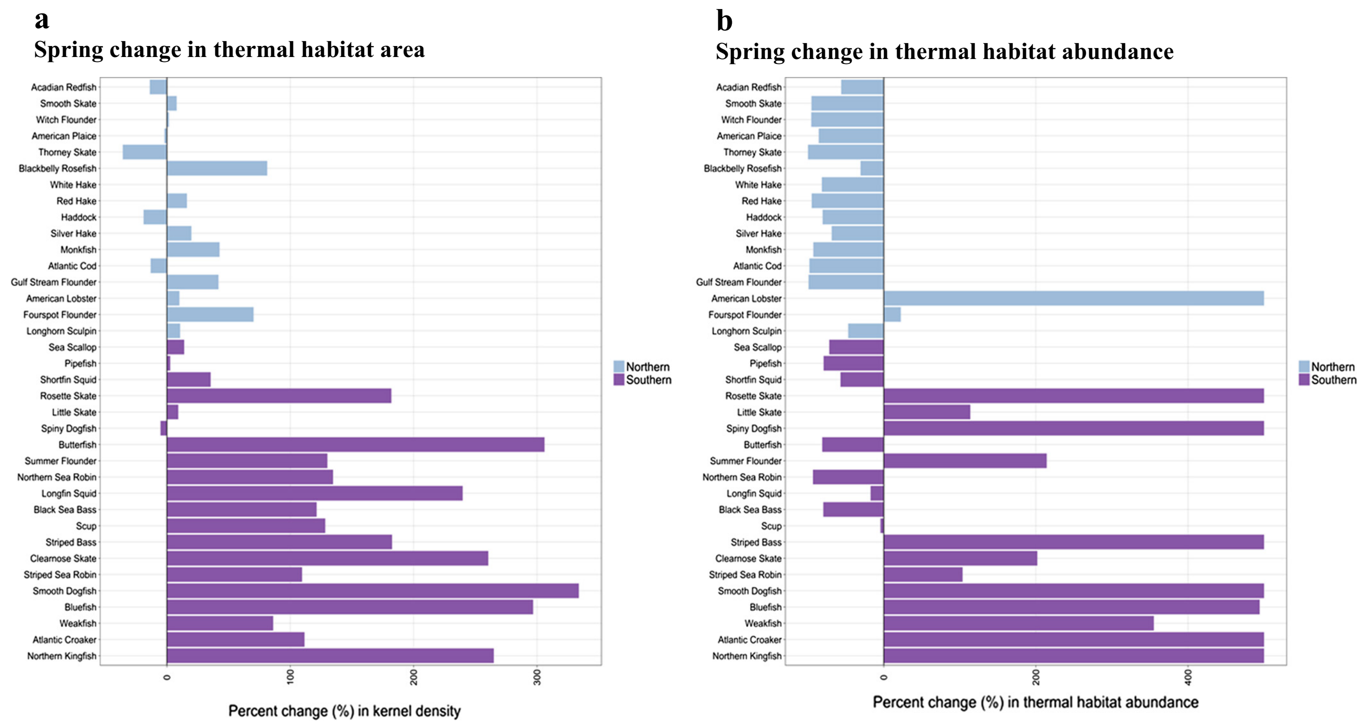

Fig. 4. Percent change (positive: increase; negative: decrease) in (a) sitable thermal area (based on the percent change in area of the kernels) and (b) suitable thermal abundance from the modeled 1991–2013 period to the future 60–80 year projected period for spring. Colors indicate species whose distribution is currently centered in the Gulf of Maine (light blue) or along the Mid-Atlantic Bight and Georges Bank (purple). Note that the x-axis in both panels is truncated at +500% change. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

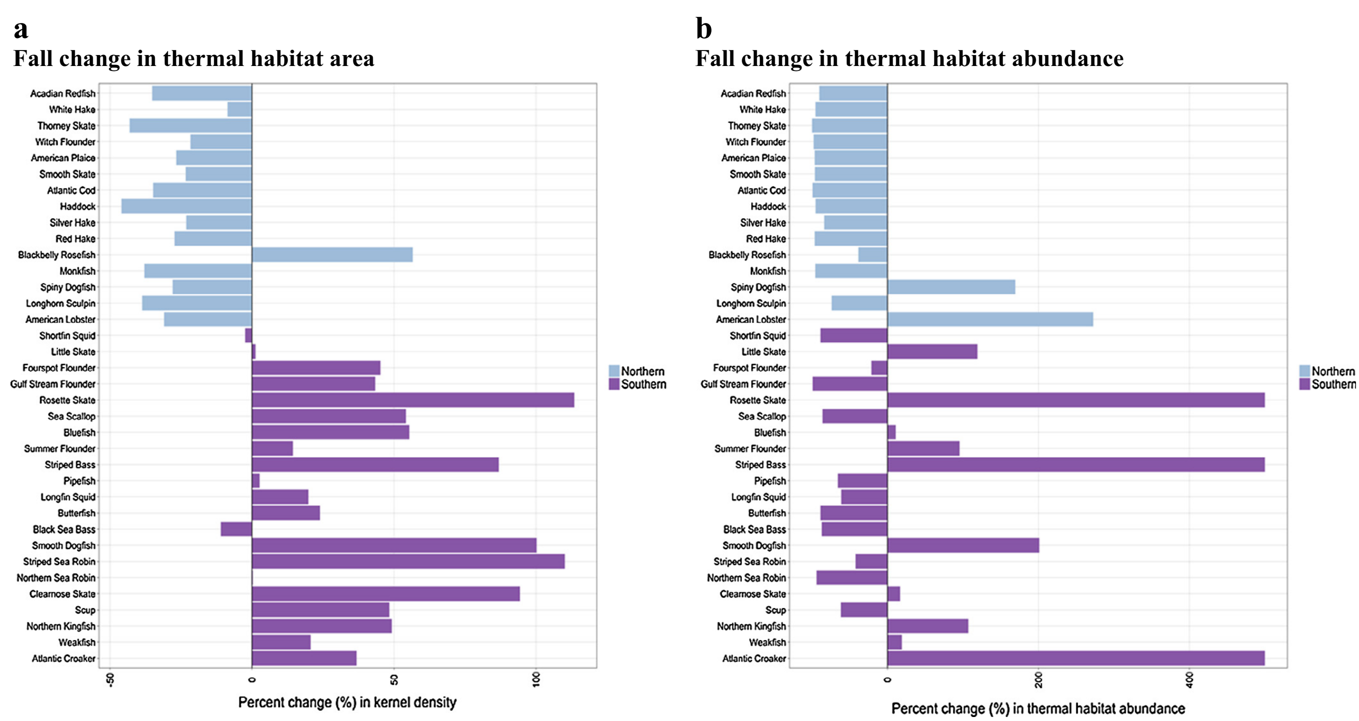

Fig. 5. Percent change (positive: increase; negative: decrease) in (a) suitable thermal area (based on the percent change in area of the kernels) and (b) suitable thermal abundance from the modeled 1991–2013 period to the future 60–80 year projected period for fall. Colors indicate species whose distribution is currently centered in the Gulf of Maine (light blue) or along the Mid-Atlantic Bight and Georges Bank (purple). Note that the x-axis in both panels is truncated at +500% change. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

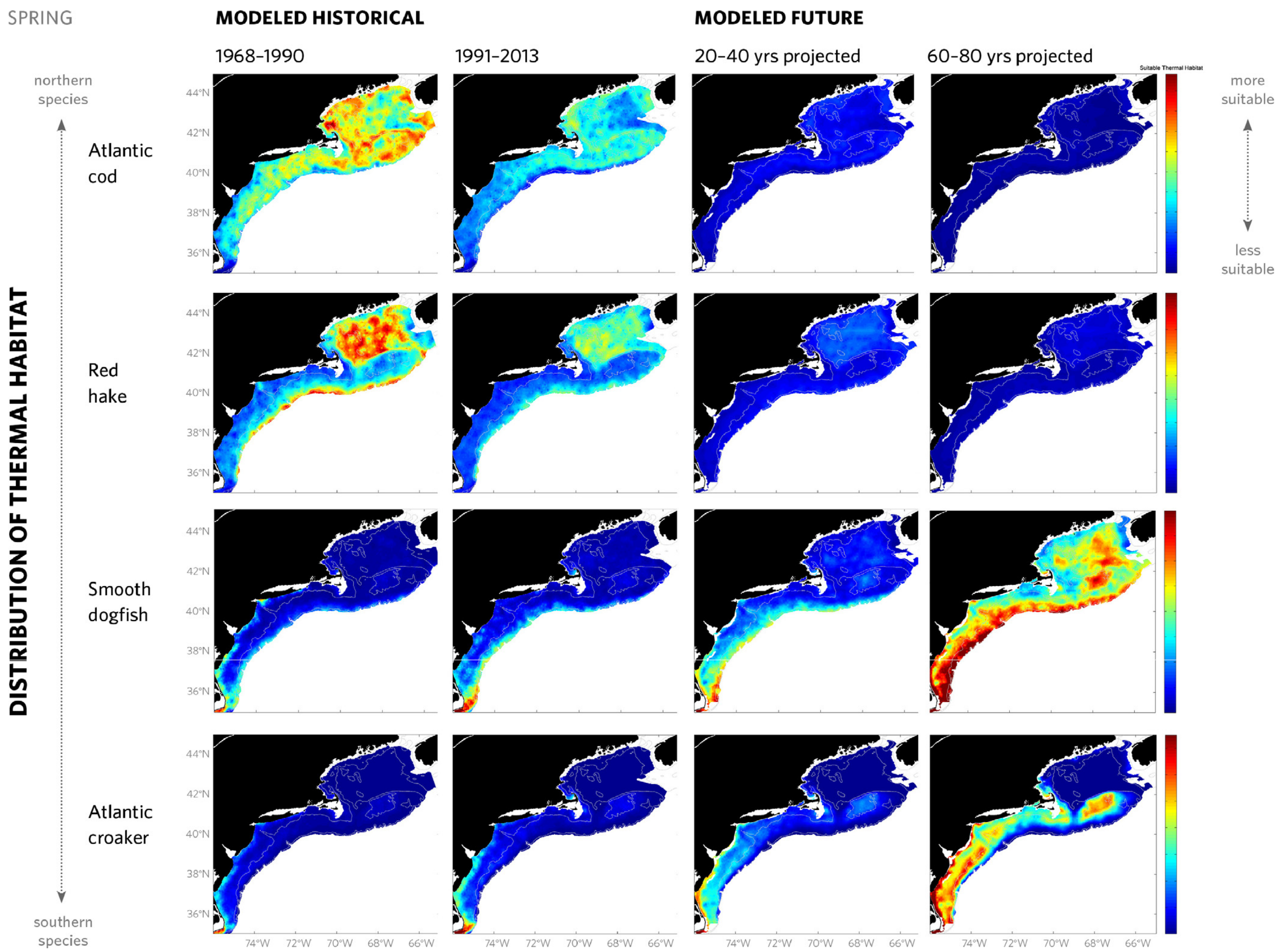

Fig. 6. Comparison of spring modeled historical and future distribution of suitable thermal habitat (red: more suitable, blue: less suitable) for species with more northern distributions (Atlantic cod and red hake) versus more southern distributions (Atlantic croaker and smooth dogfish). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Historical and projected shifts in suitable thermal habitat

Despite the modeling limitations associated with global climate model output and predicting species distributions, future projections of ocean temperature, coupled with models that consider environmental conditions for individual species based on historical information, can be useful for illustrating general trends and possible future states. While the models presented here cannot tell us what will happen in terms of increases in biomass or abundance or the exact locations of species distributions, they can provide us with some indications of the magnitude and scale of changes that may result as temperatures across the region increase. To ensure a more robust estimate of future thermal habitat, we made several choices in our modeling structure. For example, our decision to use annual models to forecast seasonally was deliberate. By modeling thermal habitat changes with annual models and using these models to project seasonally, we try to ensure that the full thermal envelope of a species is better represented and avoid limiting the future predictions of thermal habitat under future warming scenarios. For example, if a species has historically been found in cooler temperatures in the spring, but in much warmer temperatures in the fall, the use of a seasonal model would preclude a species from inhabiting an area in the spring that has much warmer temperatures than those observed in the historical spring temperature profile.

Changes in temperature over the historical period have been noted, and these changes have been linked to shifts in the distribution of species in the U.S. NES region by many previous studies (Bell et al., 2015; e.g., Kleisner et al., 2016; Nye et al., 2014; Pinsky et al., 2013). Here we have also shown that future rates of warming are likely to be strong and this will result in continued shifts in species distributions and changes in the abundance of species in the future. Species that are currently distributed along the Mid-Atlantic Bight and associated with warmer waters may fair better as they can shift into more northern waters on the U.S. NES. They may also replace or displace species in the northern U. S. NES that could see reductions in suitable thermal habitat.

4.2. Comparison of suitable thermal area with distribution effect from the NEVA

Recent studies have reported that marine species within the U. S. NES are likely to be significantly affected, and that some species may be more resilient to future climate change than others. The change in suitable thermal area estimated in this study and the results of a recent fisheries climate vulnerability assessment

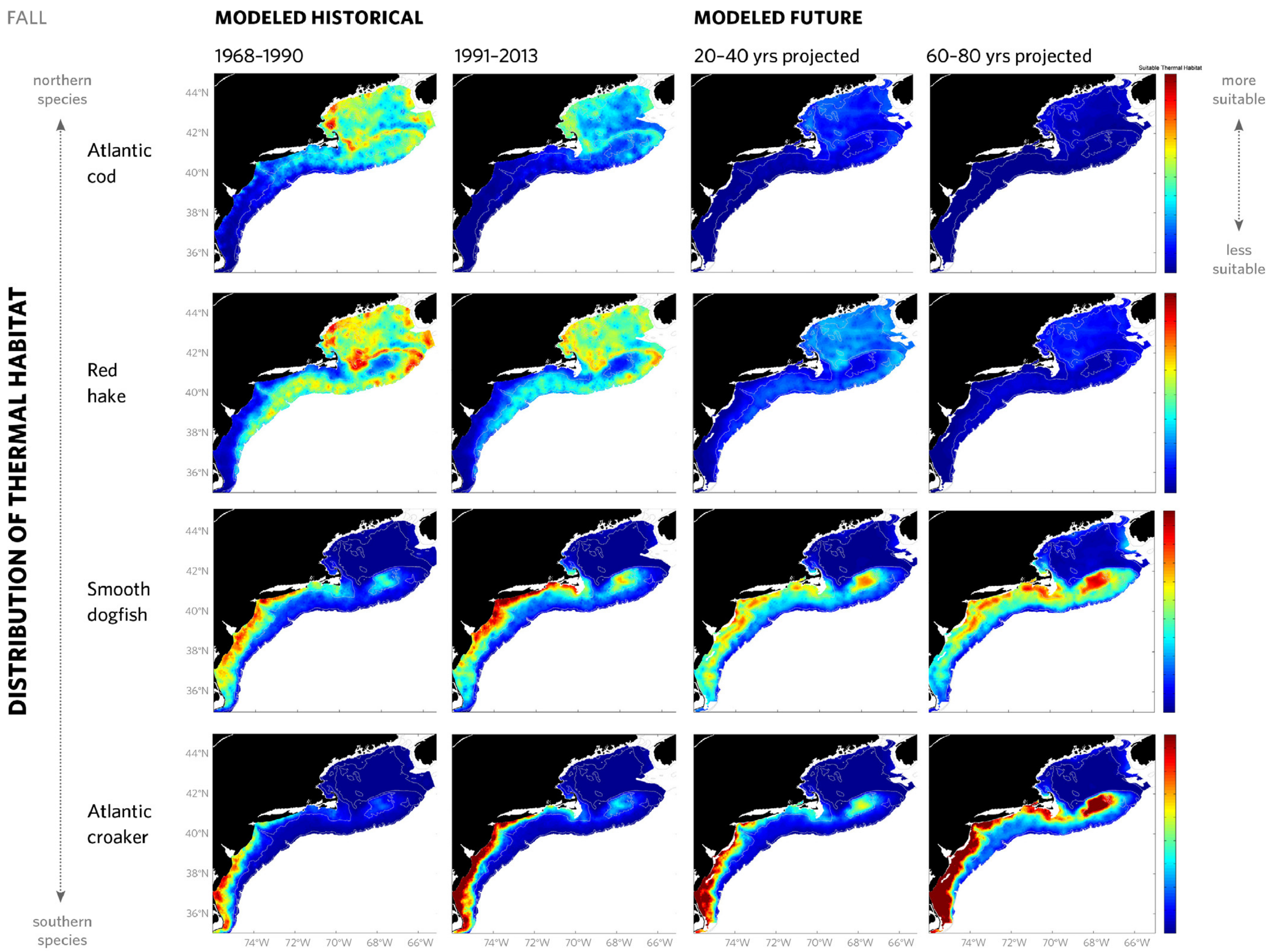

Fig. 7. Comparison of fall modeled historical and future distribution of suitable thermal habitat (red: more suitable, blue: less suitable) for species with more northern distributions (Atlantic cod and red hake) versus more southern distributions (Atlantic croaker and smooth dogfish). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Northeast Vulnerability Analysis, NEVA; Hare et al., 2016) are broadly consistent (Fig. 9, Table S4). While the NEVA study did not measure shifts in species distributions temporally and spatially, they were able to incorporate finer scale life history information to identify specific attributes that influence the resilience of different species to a warming ocean and characterize the risk posed to individual species. They noted that many species are likely to shift their spatial distributions as a result of climate change and that these shifts may be widespread and likely to continue for the foreseeable future.

For species that were assessed as likely to be positively affected by climate change by the NEVA, there was generally a larger increase in suitable thermal area predicted in our study (Fig. 9). This pattern was particularly evident during spring; prior studies have suggested that thermal habitat may be more limiting in spring for a host of species on the Northeast U.S. shelf (Bell et al., 2015). In particular, Hurst (2007) notes that during winter, colder temperatures are a major constraint on survival. We speculate here that warming future temperatures reduces this limitation, thereby expanding the suitable thermal habitat more during traditionally cooler months. In fact many of the discrepancies between estimated changes in thermal habitat and assessed effects of climate change seem to be associated with seasonal differences. The results differ for some warm water species in the fall (e.g., black sea bass, butterfish, scup) and cold water species in the spring (e.g., yellowtail flounder, witch flounder, white hake). These differences may be due in part to biases in the sampling by the trawl survey, which may miss critical habitat, especially nearshore regions or areas with a great deal of three-dimensional structure (Manderson et al., 2011).

Understanding the seasonal dynamics of habitat limitation is likely key in this ecosystem owing to the very large seasonal range in temperature. It is important to note that there may be other species-specific discrepancies between the estimated change in suitable thermal area and the assessed effects of climate change from the vulnerability assessment (Table S4). For example, for anadromous species (e.g., striped bass), the estimate of suitable thermal area considers only the marine adult stage, while the NEVA considered the entire life cycle. The NEVA also evaluated climate change factors in addition to temperature, which may explain some of the discrepancies for benthic invertebrates, species likely to be negatively impacted by ocean acidification. The comparison of suitable thermal area and the vulnerability assessment results for rosette skake, an elasmobranch, also seemed at odds. Prior studies have found southward shifts in elasmobranch distributions, while most other species are shifting northward (e.g., Kleisner et al., 2016; Nye et al., 2009). These results suggest a

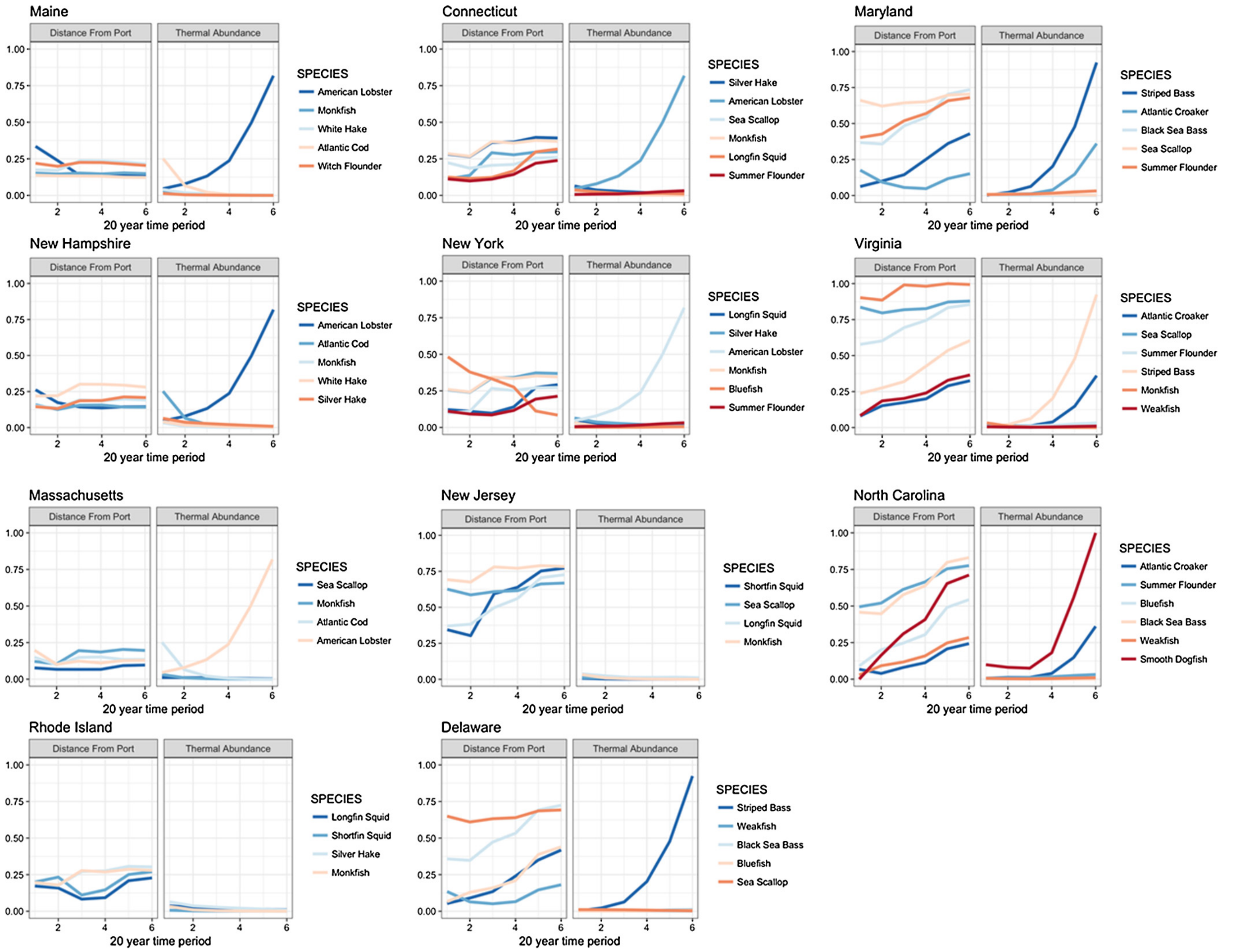

Fig. 8. Normalized (i.e., scaled between 0 and 1) values of change in distance from port to the center of the distributions (left panels) and change in suitable thermal abundance (right panels) over time for the top species (by landed weight) in each state. Periods 1 and 2 pertain to the historical time period (1968–2013) and periods 3–6 pertain to future projections. Species are ordered from highest (dark blue) to lowest average landings (dark red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

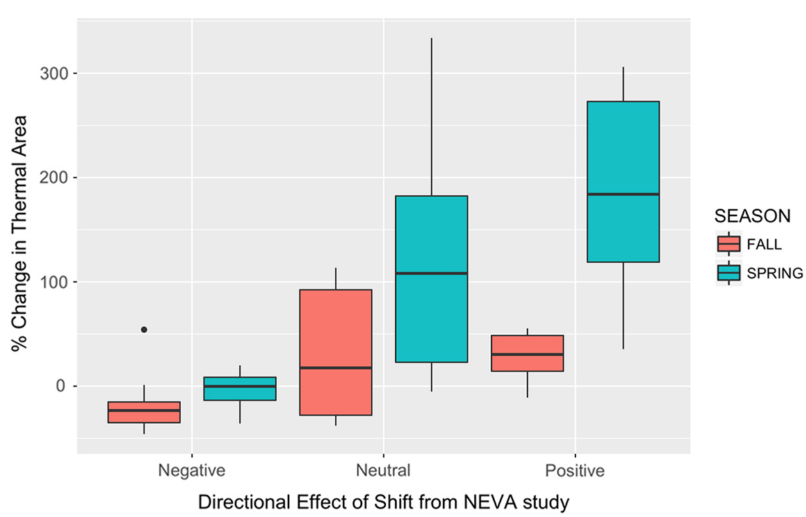

Fig. 9. Comparison of the "directional effect of shift" rating from the Northeast Vulnerability Analysis (NEVA) and the percent change in suitable thermal area calculated in this study by season. The bottom and top of the box are the 25th and 75th percentiles, and black line inside the box is the median.

greater focus is needed on elasmobranch biology and ecology in the region.

In general, we noted that the strong shifts of species in the southern U.S. NES illustrated by Hare et al. (2016) are likely to continue into the future. For some species that are currently abundant in southern U.S. NES waters, such as smooth dogfish, Atlantic croaker, and striped bass, warming waters may have a positive effect. This finding is exhibited by increases in suitable thermal habitat in terms of area and abundance for these species within the U.S. NES region. However, these same species are also shifting northwards, and in southern states, distance from ports may increase, suggesting that the distance needed to travel to reach the most abundant regions for these species will likely increase. A benefit of the spatial approach taken here is that it is possible to get a sense of the pace and magnitude of species distribution shifts on a sub-regional scale, and to evaluate the potential impacts on fishing communities.

4.3. Changes in projected suitable thermal habitat relative to major ports

With respect to the species considered in this study, changes in the amount and location of suitable thermal habitat could place an economic strain on southern fishing communities if they try to maintain historic catch rates for these species. However, it may also mean different opportunities for fishermen across the region as new species move into their local waters. These changes may be realized as species shifting into the Gulf of Maine from the southern U.S. NES, or as new species entering the Mid-Atlantic Bight region from outside the survey region. Overall, species' responses to climate change across the U.S. NES will be variable and it will be a complex issue for fisheries managers to determine how to manage quotas and assess stocks as species shift into and out of fishery management jurisdictions. We can illustrate some of this variability with a simple three species example (Fig. 10) that highlights how the center of the distribution of some species like Atlantic croaker and summer flounder may shift away from ports where they have traditionally been caught. In contrast, American lobster provides an example of a species that is not shifting its distribution as much, and is showing increases in suitable thermal habitat in the future that may mean that lobster remains an important fishery in northern U.S. NES waters. It is important to note, however that this illustration does not account for the shift of the edges of species distributions, only the center of the distribution.

In general, in the Gulf of Maine there were fewer large increases in thermal habitat for species currently distributed there. Additionally, there were generally decreasing or stable trends in distance from ports. This result is due in large part to the fact that the survey region is constrained. Indeed, the ability to evaluate the potential for shifts in species distributions outside of the U.S. NES region and into international or Canadian waters would likely illustrate increases in the distances between the centers of suitable thermal habitat and major fishing ports in the Gulf of Maine region. Nevertheless, it is also important to emphasize the fact that other factors such as fishing pressure and species interactions could act in unpredictable ways to mitigate the beneficial or detrimental effects felt by such shifts.

4.4. Conclusions

Our results highlight some important trends. First, there will potentially be some major changes in the complex of species occupying different regions of the U.S. Northeast Shelf. Along the Mid-Atlantic Bight, shifting distributions of traditionally harvested species will alter patterns of availability to local fishing communities. This may impose economic impacts as a result of lost access to stocks managed with species-specific quotas, and rising fuel and travel costs. In some cases, fishermen will need to adapt to altered ecosystems with new subtropical-temperate species. In contrast, the Gulf of Maine is likely to see new species that currently dominate more southerly waters along the Mid-Atlantic Bight or Georges Bank. In some cases, species that currently occupy the Gulf of Maine may be concentrated within deeper pockets as temperatures change, resulting in potentially increased vulnerability to fishing activity or possibly reduced catchability if the gear cannot access these areas. Alternatively, these species may be pushed out of the region altogether. Furthermore, species may shift from one management jurisdiction to another, or occur in multiple jurisdictions, including the potential to span state and federal jurisdictions. When these changes straddle fishery management boundaries, increased collaboration will be needed among governing bodies with respect to management measures including setting quotas and establishing allocations.

Projecting future species distributions is associated with high uncertainty due to unaccounted for variability from effects such as species interactions, complex ecosystem effects, and uncertainty in climate change scenarios. The GAMs here are only capturing potential changes in species' suitable thermal habitat, and are not predictions of abundance or future species distribution. By providing this caution, we are attempting to follow the advice of Dickey-Collas et al. (2014) who caution against "projecting into unknown space without generalism, or fitting empirical models and inferring causality". In particular, the future suitable thermal habitat estimates presented here are capturing a projection of the realized niche under contemporary ecological conditions. The true realized niche for a given species is likely to be smaller than our projection of the realized niche due to species and habitat interactions not captured in this analysis, as well as changes in spatial patterns of fishing effort. If this is the case, our projection of the realized niche, and the fact that it is not as limited, may be providing a more conservative estimate of the changes in distribution or abundance than what may actually occur. Fisheries management may also influence species abundance and affect the patterns observed in this study. Historical studies of distribution shifts typically try to account for the effects of fisheries management on population size explicitly (e.g., Kleisner et al., 2016; Pinsky et al., 2013), but it is difficult to estimate the effects of management in the future. We note that over a historical time period, Thorson et al. (2016) examined the relationship between species abundance and area occupied and found a very weak relationship on the NE Shelf. Ultimately, we believe that projections of species distributions based on an understanding of suitable thermal habitat can still be useful as scenarios for informing potential adaptation policies and management decisions.

Distribution shifts of marine taxa may have substantial effects on local fishing communities. If fishermen want to maintain catches of historically fished species that are shifting outside of regions where they are currently distributed, they will incur rising fuel and travel costs. Additionally, if fishermen cannot continue to fish these species, they will acquire costs associated with forgone harvest or possibly the need to buy new permits, vessels, and gear to harvest different species. Moreover, there will be management costs incurred under the current system of single-species stock assessments and static management jurisdictions as stock boundaries change and species shift in and out of management regions.

Overall, the changes that occur will depend both on the pace of climate change and on the ability of the species to adapt or shift to maintain a preferred habitat. Given the historical changes observed on the U.S. NES over nearly the past five decades, and the confidence in predictions of continued ocean warming in this region, it is likely that there will be major transformations within this

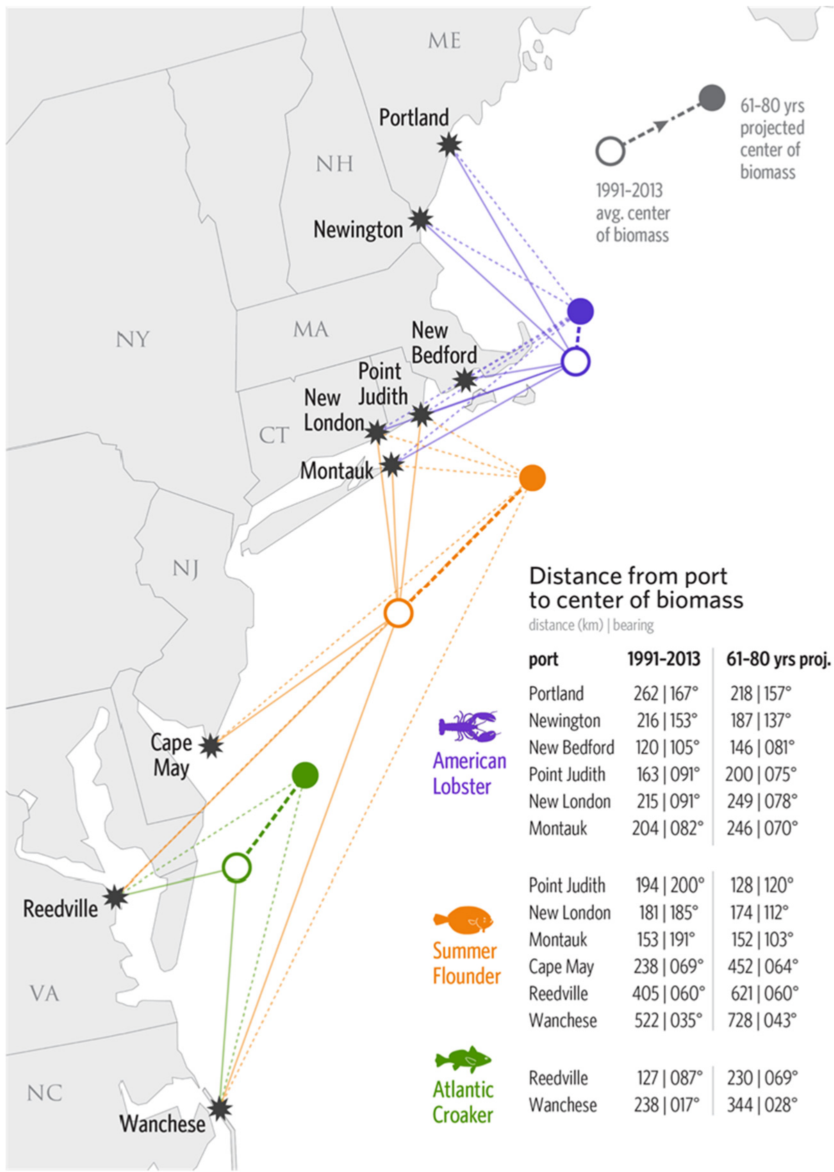

Fig. 10. Illustrative example of the spatial variability in the center of distributions of species from main ports that may be likely given shifts in species distributions under future climate change.

marine ecosystem. Collectively, these changes will result in important ecological, economic, social and natural resource management challenges throughout the region. This study represents one approach for understanding how these changes will unfold in order to plan for and potentially mitigate adverse effects.

Acknowledgements

Funding for this joint partnership project between the National Oceanic and Atmospheric Administration's Northeast Fisheries Science Center and The Nature Conservancy comes from a grant from the Gordon and Betty Moore Foundation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2017.04.001.

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