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COMPARING HABITAT SUITABILITY FORECASTS FOR THE GULF OF MAINE AND SOUTHERN NEW ENGLAND AMERICAN LOBSTER STOCKS

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ABSTRACT The future of American lobster (*Homarus americanus*; H. Milne Edwards, 1837) habitat has been extensively studied in the Gulf of Maine and Georges Bank regions, but studies quantifying spatiotemporal changes to suitable habitat in Southern New England (SNE) regions remain sparse. The American lobster stock assessment for SNE is conducted separately from the northern stock because of negligible migration and recruitment sharing between them. This fact, coupled with the assumption of spatial nonstationarity between the two stocks when it comes to environmental preferences, suggests that analyses of suitable habitat must be conducted for each stock region independently. This study employs the use of a previously developed habitat suitability index model for American lobster to map historical and forecasted habitat in both the Gulf of Maine and SNE stock regions so that comparisons between long-term forecasts can be accurately made. The suitability indices generated in this study support the hypothesis of environmental nonstationarity between the stocks, with lobster in SNE preferring significantly different environments than their northern counterparts. In the coming decades, the Gulf of Maine lobster fishery may see changes in lobster migration timing as spring suitability decreases and fall suitability rises, whereas the SNE fishery will most likely see the continued use of northern waters by lobsters as more southern waters become less suitable. The rate of change in SNE remains smaller than in the Gulf of Maine owing to the lesser rate of warming observed.

KEY WORDS: bioclimate, American lobster, habitat forecasts, climate change, bottom temperature

INTRODUCTION

The American lobster (*Homarus americanus*) fishery in the Northwest Atlantic represents the most valuable single species fishery in the United States (NMFS 2020). In addition to a landing value of 730,596,022 US dollars in 2021 (Maine DMR 2022), the lobster fishery is composed of many individual owner–operator vessels rather than a vertically integrated corporate structure and provides an important source of revenue, food, and cultural identity for New England coastal communities (GMRI 2012). The successful management of this valuable fishery relies on a comprehensive understanding of the spatial distribution of the stock across life stages and the variations between stock distribution and total density encompassing multiple spatial scales.

American lobster is assessed and managed as two distinct stocks: the Gulf of Maine/Georges Bank (GOM/GBK) stock and the Southern New England (SNE) stock. These two stocks are considered separate because there is little migration and recruitment sharing between the regions (ASMFC 2015). As ectothermic benthic crustaceans, American lobster distribution and physiology are influenced by bottom habitat, most notably temperature and depth (Tanaka & Chen 2015).

Habitat suitability index (HSI) models (also known as bioclimate models) are a type of predictive spatial model that map the distribution of suitable habitat for a species given environmental and climatic conditions (Mbogga et al. 2010, Watling et al. 2013, Tanaka & Chen 2015, 2016, Tanaka et al. 2019,

Hodgdon et al. 2021). HSI models for American lobster have been previously used to infer the spatial distributions of lobsters in the GOM/GBK stock area (Tanaka & Chen 2016, Hodgdon et al. 2021) and areas within the SNE (Tanaka & Chen 2015). Changes in suitable habitat for American lobster are expected as the waters off the Mid-Atlantic and northeast United States warm (Stanley et al. 2018, Hodgdon et al. 2021).

Climate change has contributed to warming within both the GOM/GBK and SNE regions (Howell 2012, Pershing et al. 2015), with the GOM warming faster than most of the oceans. Historically, inshore fisheries have contributed the most to the harvest in both regions. In recent decades, landings in the SNE have significantly decreased, whereas landings in the GOM/GBK have increased, which is reflected by an overall northward shift in the distribution of lobsters in the northwest Atlantic (Steneck & Wahle 2013, ASMFC 2020). Both fisheries operate at shifting spatial scales within their respective regions, pursuing a lobster distribution that follows seasonal migrations as well as increasingly pronounced climate change-forced distribution shifts (Chen et al. 2005a, Tanaka & Chen 2015).

The GOM/GBK fishery exists as a year-round fishery with distinct seasonal behaviors that track lobster distribution patterns (Chen et al. 2005b) and a split between inshore and offshore vessels with a combined landings average of 60,450 mt since 2016 (NMFS 2020). The GOM/GBK fishery saw a dramatic increase in landings from the late 1990s to mid-2000s where it currently harvests record high levels. This “boom” of landings is often attributed to not only increases in temperature, but also decreases in predators and increases in conservation-focused management (Le Bris et al. 2018, Goode et al. 2019, ASMFC 2020). Operating on a seasonal basis largely as a supplemental fishery, the SNE fishery is much smaller and

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in decline with landings of 1,042 mt in 2020 (NMFS 2020). There seems to be a spatial shift in landings in recent years, with increasing proportions coming from offshore areas (Ellertson et al. 2022). Historically, the SNE fishery was much larger than it is today, but suffered massive declines in landings and recruitment during the late 1990s and early 2000s (ASMFC 2010, Howell 2012, Le Bris et al. 2018, ASMFC 2020). The mechanism behind this change is hypothesized to be environmental in nature; not because of fishing effort (Howell 2012, Le Bris et al. 2018, ASMFC 2020).

During the declining phase of the SNE fishery, stressful temperatures were becoming increasingly frequent in the region and the prevalence of epizootic shell disease was growing (Glenn & Pugh 2006, Howell 2012, ASMFC 2020), the latter of which may be a symptom of rising temperatures (Glenn & Pugh 2006, ASMFC 2010, Le Bris et al. 2018, ASMFC 2020). These symptoms of climate change and habitat degradation led to increased mortality and eventual recruitment failure (ASMFC 2010, Howell 2012, ASMFC 2020). Additionally, SNE fishers have had to travel farther offshore to find lobsters, now spending more time in deeper waters to avoid the warm shallows (Wahle et al. 2015, ASMFC 2020). Changes in regional water temperature between the GOM and SNE are driven by the interaction of the Gulf Stream and Labrador Current (Pershing et al. 2015). Whereas the GOM is seeing extreme warming, it remains overall cooler than the SNE and more suitable for lobster habitat (Tanaka & Chen 2016). It is currently unknown whether the GOM/GBK stock will experience similar symptoms in the coming decades as temperatures of the region approach those observed in SNE.

Knowledge about climate-forced habitat suitability changes in the GOM/GBK and SNE stock areas allows management to plan proactively for changes in lobster distribution, with potentially great effects on this valuable fishery. Management can consider these forecasted changes to HSI and implement proactive stock protective measures to prevent sudden drastic changes to fishery policy. This is critical, as the American lobster fishery has low social resilience to cope with drastic management changes (Henry & Johnson 2015). Past studies focus on how GOM/GBK habitat will change, with smaller concern for the SNE area. This study therefore uses a previously developed bioclimate model to map and forecast suitable habitat for American lobsters in both the GOM/GBK and SNE stock areas, with the intent of describing the futures of both stocks.

METHODS

Suitability Indices

An American lobster HSI model, hereafter referred to as the bioclimate model, was initially developed by Tanaka and Chen (2015, 2016) and expanded by Hodgdon et al. (2021). The bioclimate model is capable of determining relationships between adult (larger than 53 mm carapace length) American lobster abundance from fishery-independent surveys to environmental variables and using these relationships to predict suitable habitat over a given spatial extent.

Survey data of lobster catch were acquired from the Maine Department of Marine Resources and New Hampshire Fish and

Game Department Inshore Bottom Trawl Survey (MEDMR & NHFGD, respectively) for 2000 to 2006, the Massachusetts Division of Marine Fisheries' Inshore Bottom Trawl Survey for 1978 to 2016, NOAA Northeast Fisheries Science Center Bottom Trawl Survey for 1978 to 2016, the Rhode Island Department of Environmental Management Coastal Trawl Survey for 1981 to 2016, the New Jersey Department of Environmental Protection Trawl Survey for 1988 to 2016, and the Virginia Institute of Marine Science Northeast Area Monitoring and Assessment Program for 2007 to 2016. These seasonal bottom-trawl surveys cover the stock areas of GOM/GBK and SNE (Fig. 1) and are used to inform management of the species. To standardize these catch data, a comparable catch-per-unit-effort (*CPUE*) value was calculated for all trawl stations in all surveys. This value was calculated as:

$$CPUE = \frac{Count}{Width \times Length} \quad (1)$$

where *Count* is lobster abundance at a trawl station, *Width* is the width of the trawl in meters, and *Length* is the distance traveled by the trawl in meters.

These trawl surveys additionally record values of bottom temperature, bottom salinity, and depth at each station. These three variables have been proven to be influential for mapping and forecasting lobster habitat (Hodgdon et al. 2021) and were thus used as initial variables in this analysis in addition to the spatial variables latitude and longitude. First, to test whether all variables could be used together in this analysis, a variance inflation factor test (VIF) was conducted. Next, all survey data was broken up into spring (April–June) and fall (September–October) components. This was done because seasonal differences have been shown to be an important factor in bioclimate modeling for American lobster (Hodgdon et al. 2021). Following the methods of Hodgdon et al. (2021), variables were then delineated into 20 classes (*k*) using Fisher's natural break classification method. For each stock area and season, suitability Indices (*SI*s) for each *k* of environmental variable *i* were calculated as:

$$SI_{k,i} = \frac{CPUE_{k,i} - CPUE_{i,min}}{CPUE_{i,max} - CPUE_{i,min}} \quad (2)$$

where $CPUE_{k,i}$ is the average *CPUE* across all trawl stations within class *k* of habitat variable *i*, $CPUE_{i,min}$ is the minimum average *CPUE* value across all *k* of variable *i*, and $CPUE_{i,max}$ is the maximum average *CPUE* value across all *k* of variable *i*. Suitability curves are thus always from a scale of zero to one: zero representing the lowest suitability and 1 representing the highest. From these estimations, generalized additive models were used to smooth the relationships, effectively minimizing noise and enhancing biological realism. When this process was complete, *SI* curves were produced for each environmental and spatial variable in each season. Note that this process was completed twice: once for each stock area (Fig. 1). This was done because GOM/GBK and SNE lobster populations appear to have differential habitat preferences, indicating a spatial non-stationarity (Hodgdon et al. 2021), and using data across stocks to produce population-wide (instead of stock-wide) *SI*s could severely bias the estimates of suitability. Thus, *SI*s were created for each variable, season, and stock.

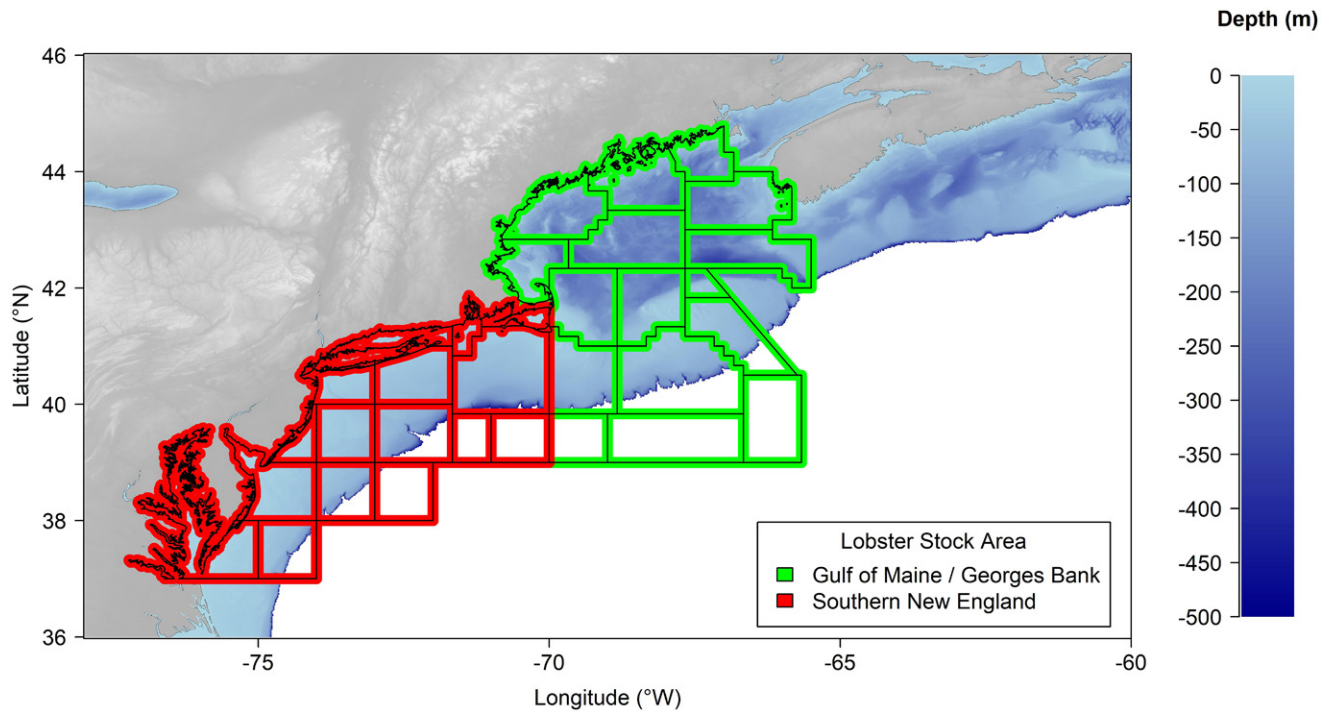


Figure 1. NOAA statistical areas outlined in black with statistical areas that comprise the Gulf of Maine/Georges Bank American lobster stock outlined in green, and statistical areas that comprise the Southern New England American lobster stock outlined in red. Blue-shaded regions indicate depth, where darker blue represents deeper waters. White areas represent areas deeper than 500 m.

Interpolation Data

Interpolation data used in this study was generated from a process described by Friedland et al. (2019, 2020) and used in Hodgdon et al. (2021). This dataset uses the observed environmental data from the aforementioned bottom-trawl surveys and climatological data to produce a fine resolution (0.1°N by 0.1°W) interpolation over the years 1992 to 2005 of bottom temperature and bottom salinity in spring and fall over the GOM/GBK and SNE stock areas.

HSI values are then estimated across these interpolation grids for each stock using the SI calculations in Eq. 2. HSI values, which represent an average of the individual SI values, were calculated using an arithmetic mean:

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

where n is the total number of environmental variables used in the analysis. Because they are an average of SIs, HSIs are also always on a scale of zero to one: one representing the lowest suitable habitat and one representing the highest.

Forecasting and Comparisons

Future fields of bottom temperature and bottom salinity can be obtained by applying climate anomalies to the kriged interpolations described in Historical and Forecasted Habitat section. Anomalies, which represent changes between a historical reference period (1992 to 2005) and a future period (2086 to 2099), were obtained from the ensemble projection framework known as the Coupled Model Intercomparison Project 5. This

framework, which is used in the Intergovernmental Panel on Climate Change Fifth Assessment (IPCC 2019), represents a conglomerate of climate forecasting model results used jointly to create global climate projections. Projections are determined under Representative Concentration Pathways (RCPs), which represent different levels of future carbon emissions. This study used data under RCP 8.5, which represents a “business-as-usual” future carbon emissions scenario. Anomaly data from this framework is publicly available through the NOAA Climate Change Web Portal (<https://psl.noaa.gov/ipcc/ocn/>).

The anomalies were delta-downscaled and interpolated using thin plate splines to coincide with the kriged grid described in Historical and Forecasted Habitat section. This statistical process is known to reduce bias in estimates and is commonly used in bioclimate modeling practices (Hare et al. 2012, Navarro-Racines et al. 2020, Tanaka et al. 2020, Hodgdon et al. 2021). Anomaly grids were added to the historical grids to produce future (2086 to 2099) spatial extents of bottom temperature and bottom salinity.

Using these forecasted grids and a temporally static grid for depth, latitude, and longitude, Eq. 3 can be used to estimate future habitat suitability estimates across the entire spatial domain of both stocks. Historical habitat estimations can be subtracted from future habitat estimations to generate maps indicative of change in suitable habitat from the historical period to the future period. Each of these grids was mapped using ordinary kriging methods. Lastly, average HSI values and estimates of percent HSI over 0.2, 0.5, and 0.8 are calculated for each stock area (GOM/GBK and SNE; Fig. 1). These values represent habitat that is “Fair,” “Good,” and “Excellent,” respectively (McMahon 1983, Tanaka et al. 2019, Hodgdon et al. 2021).

RESULTS

Suitability Indices

As a result of the VIF tests, salinity was removed from the analyses, and only temperature, depth, and the spatial variables latitude and longitude were used in all subsequent analyses. There were noticeable differences between seasons concerning temperature, but not concerning depth (Fig. 2).

Bottom temperature preferences for GOM/GBK lobsters are around 6°C–7°C in the spring and around 11°C–12°C in the fall (Fig. 2). SNE lobsters prefer temperatures around 7°C–8°C in the spring, with a wider dispersion than in the GOM/GBK. SNE lobsters in the fall prefer relatively cold temperatures, closer to 6°C–7°C. This could be attributable to SNE lobsters during this time seeking deeper waters. What is of note is the second peak of the SI curve in this region and time around 15°C. Almost all the data that comprise this peak at 15°C occur in very southern waters below 40°N, and almost all the data that comprise the peak around 6°C–7°C occur in waters north of 39°N, perhaps indicating a spatial nonstationarity that exists at a finer scale than the stock level.

Depth preferences for GOM/GBK lobsters do not shift much between seasons, with spring and fall preferred depths existing around 15–25 m (Fig. 2). SNE lobsters in general prefer greater depths than their GOM/GBK counterparts, preferring depths around 80–90 m in the spring and 90–100 m in the fall. SNE lobsters are also found over much wider depth ranges than their GOM/GBK counterparts, with depths out to 250 m often remaining good habitat in the spring and depths out to 300 m often remaining good habitat in the fall (Fig. 2).

Both GOM/GBK and SNE lobster prefer the far northern extents of their respective stock boundaries, supporting a general tendency of lobster of the northwest Atlantic moving northward over time in search of more suitable habitats. SNE lobsters prefer the eastward most extents of their stock, as this water is closest to the GOM/GBK stock area and has more ideal environmental ranges. In the GOM/GBK region, the most preferred longitudes exist at 68° W–69° W, coinciding with the Mid-Coast area of the Maine coast: an area historically known for their high lobster abundances.

Historical and Forecasted Habitat

Spatially in the GOM/GBK stock region, suitable habitats in the spring historically occur along the entire Maine coast and most of GBK, as well as many shallow areas surrounding both Wilkinson and Jordan Basins (Fig. 3), with the highest suitabilities occurring in the Mid-Coast Maine shallows and areas around the Great South Channel. These areas are recognized as both relatively shallow and relatively warm. This same general spatial trend is true for the fall (Fig. 4), but with overall lower suitabilities, comparatively (Table 1). Areas between the Maine coast and GBK as well as offshore past GBK are recognized as less suitable in both spring and fall (Figs. 3 and 4), with very low suitabilities in the fall season. Forecasts for this region show an overall decrease in the spatial extent of spring suitable habitat, except for the Mid-Coast Maine region, which shows increasing habitat suitability. In the fall, GOM/GBK seems to experience increases in habitat suitability, with many historically unsuitable areas between GBK and the Maine coast becoming suitable.

Spatially, in the SNE stock region, historical habitat is most suitable in the northernmost areas where lobsters have congregated in recent years to avoid the warm temperatures in the most southern waters. This trend is apparent in both spring and fall (Figs. 3 and 4). Forecasts for this region show overall decreases in habitat suitability in both spring and fall (Fig. 5, Table 1). Like the GOM/GBK stock area, there are still local hotspots of increasing habitat suitability over this time period, namely in waters closest to GOM/GBK (Fig. 4).

Seasonality is a strong component of stock-dependent forecasts. The magnitude of spring changes in the GOM/GBK stock area over the forecasting period is more extreme than in SNE (Table 1). GOM/GBK will see decreases in spring suitability of approximately 8% compared with a 3% decrease in SNE. In the fall, GOM/GBK will see increases in habitat suitability up to 16%, whereas SNE will see declines in suitability of up to 6%.

DISCUSSION

The GOM/GBK American lobster stock has the potential for massive change in the next 80 y. The results agree with Hodgdon et al. (2021) in that spring HSI will generally decrease, but fall HSI will generally increase. Owing to the strong seasonality of the changes, the decreasing HSI in the spring could have profound negative effects on the fishery. The lobster fishery experiences high seasonal variation in prices, influenced by seasonal patterns in landings volume (Mills et al. 2017), changes in HSI across seasonal scales could profoundly influence this relationship if landing patterns followed commensurately. Lobster migrational timing is heavily influenced by environmental cues (Crossin et al. 1998, Mills et al. 2017). As spring HSI decreases, these inshore migrations from their overwintering grounds in deeper waters may be pushed later into the year. The highest productive time for the GOM/GBK lobster fishery is in the summer and fall months when the lobsters are present in shallower waters (Boenish & Chen 2018) and the highest landings periods have been correlated with the temperature patterns of the region (Mills et al. 2017). These decreases in spring HSI and increases in fall HSI could disrupt or temporally shift this bulk, shifting the migrations and hence the timing of the fishery later into the year (Hodgdon et al. 2021).

This study had two major differences from the Hodgdon et al. (2021) analysis for the GOM/GBK region. Firstly, this study used a different environmental dataset for the calculation of HSIs. Interpolated data were chosen to be used in this study, rather than the traditionally used model-generated data because interpolated data may be more biologically realistic because of their ability to preserve the observational nature of the dataset. As a consequence of this decision, this study ignored the effects of salinity on HSI calculations because the VIF tests did not allow for the inclusion of this effect.

The future of the SNE American lobster stock region appears generally bleak, but comparatively less severe in the spring compared with the GOM/GBK region in terms of habitat degradation. The GOM/GBK region is one of the fastest warming areas on the planet, with rates higher than 99% of the rest of the oceans (Pershing et al. 2015). It is of little surprise then that spring forecasts for the SNE lobster stock are of a lesser magnitude. Temperatures in this region

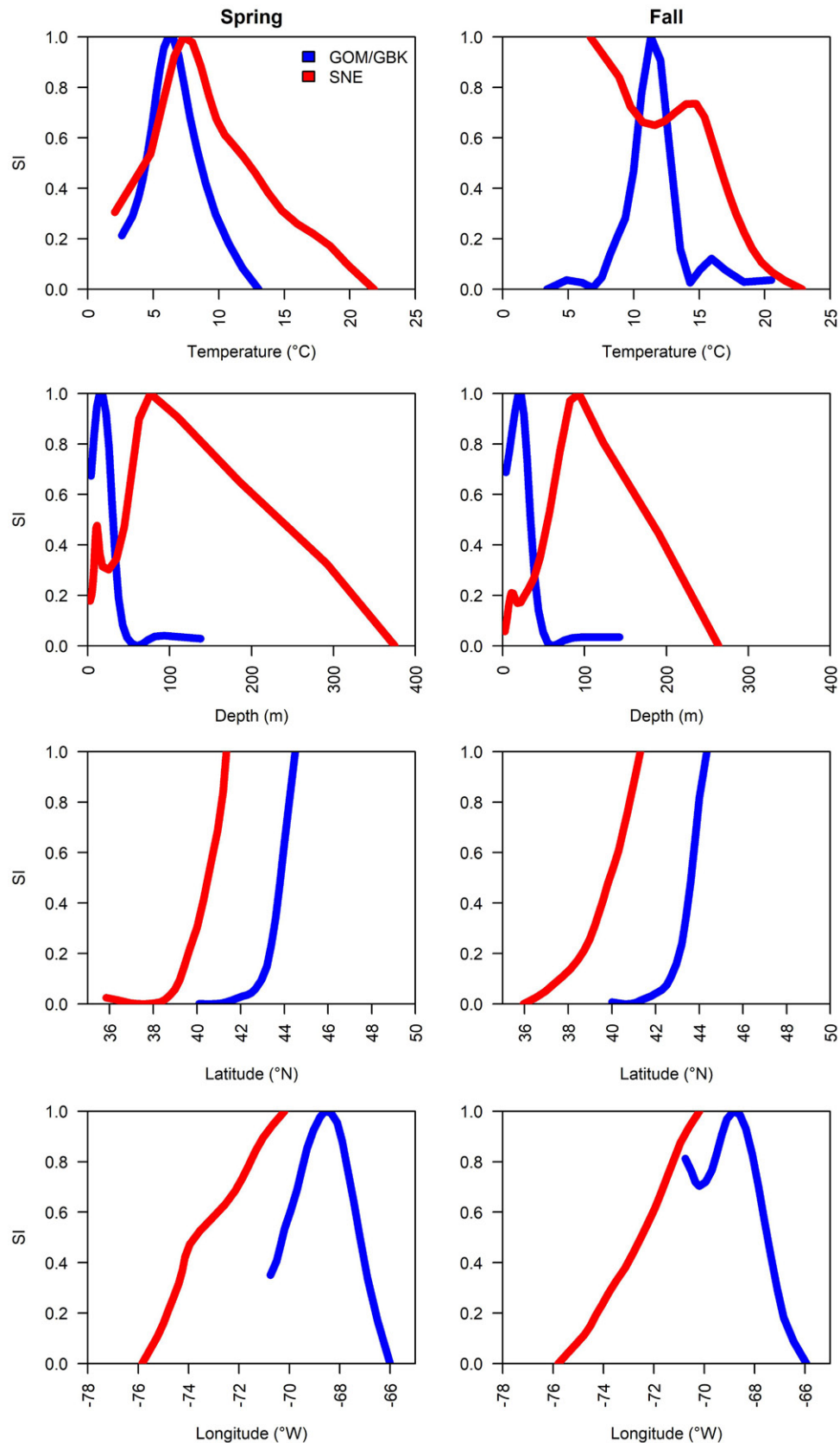


Figure 2. Suitability indices (SI) of bottom temperature in degrees Celsius (top), depth in meters (first from top), latitude (second from top), and longitude (bottom) for American lobster across the Gulf of Maine/Georges Bank (blue) and Southern New England (red) stock regions in both the spring (left) and fall (right). Fair, good, and excellent suitabilities are at values of 0.2, 0.5, and 0.8, respectively.

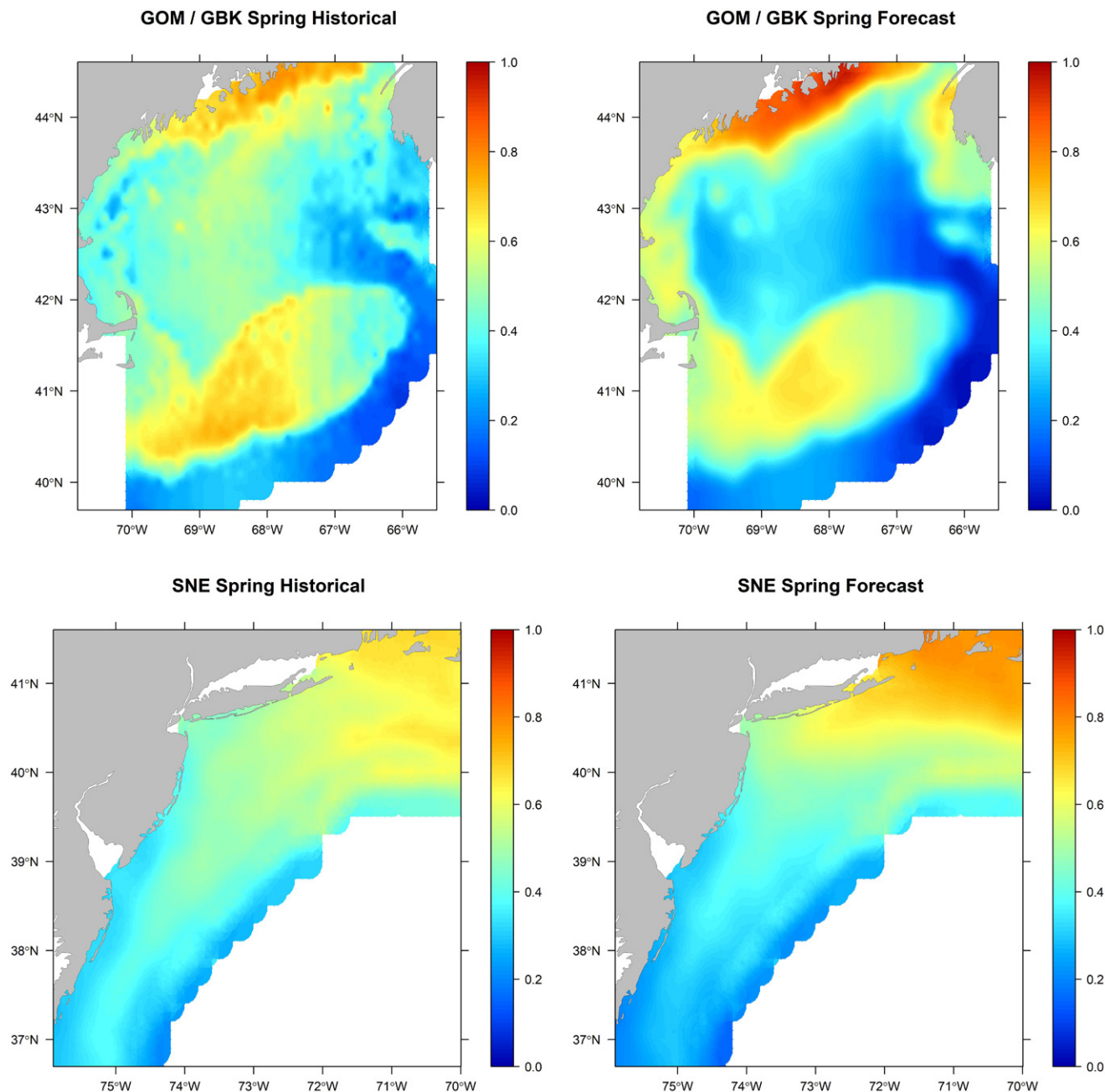


Figure 3. Spring habitat suitability from 0 (blue) to 1 (red) for American lobster in the Gulf of Maine/Georges Bank (top) and Southern New England (bottom) stock regions. Panels on the left are for the historical time period (1992 to 2005), and panels on the right are for the forecasted time period (2086 to 2099) under RCP 8.5.

of the oceans are increasing at a rate of $0.09^{\circ}\text{C}/\text{year}$ (Howell 2012) compared with $0.24^{\circ}\text{C}/\text{year}$ in the GOM/GBK region (Pershing et al. 2015). It is interesting to note this relationship of spring decreases in lobster habitat suitability being directly related to warming effects. This suggests that current stock-wide warming rates could be a reliable indicator of long-term changes to spring lobster habitat suitability, and future research should further explore this relationship. This relationship only appears in the spring, as SNE fall habitat will still see declines in suitability, where GOM/GBK waters will see large increases.

Lobsters in SNE have been spending more time in northern, cooler waters as southern waters warm. These northern areas of higher suitability off Long Island to Nantucket are already subject to anthropomorphic development and conservation efforts, with an overlap of critically endangered North Atlantic right whale habitat as well as offshore wind development (Quintana-Rizzo et al. 2021). These ongoing distribution shifts into more northern waters will likely impact fisher behavior. Distribution shifts into these waters mean that considerably more time and resources will be necessary to harvest lobster, as fishers will have to travel farther distances northward from port.

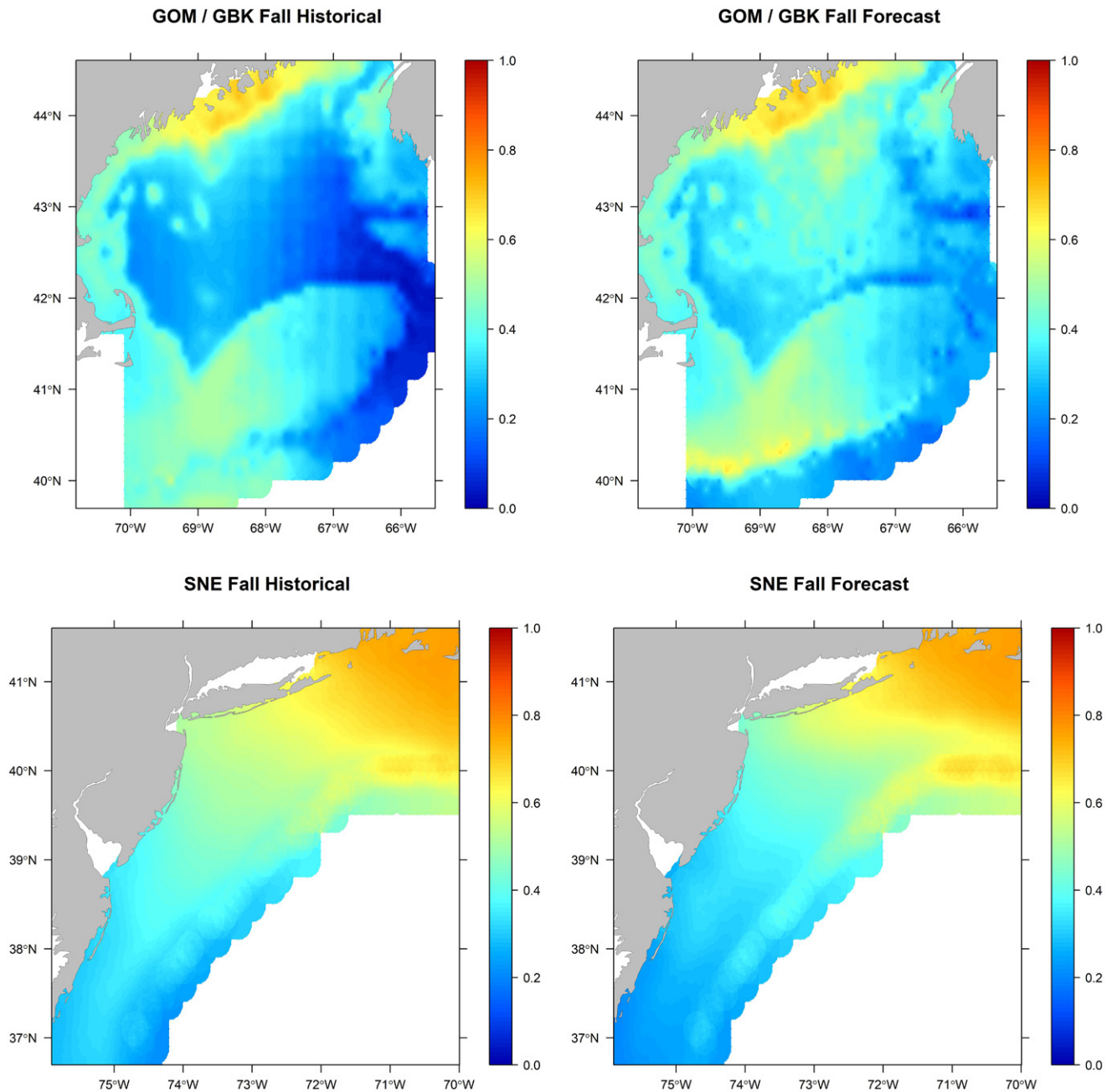


Figure 4. Fall habitat suitability from 0 (blue) to 1 (red) for American lobster in the Gulf of Maine/Georges Bank (top) and Southern New England (bottom) stock regions. Panels on the left are for the historical time period (1992 to 2005), and panels on the right are for the forecasted time period (2086 to 2099) under RCP 8.5.

More fuel, longer trips, and gear adjustments may be needed to target lobster in these waters. Adjustments in gear may need to conform to changes in regulation, such as may be necessary for addressing endangered North Atlantic right whale entanglements. Higher minimum trawl lengths common as an entanglement risk reduction measure could preclude smaller vessels from participating in the fishery entirely (Willse et al. 2022). Fishers will also need to contend with the fact that the SNE lobster stock abundance is already at historic lows. If the costs of participating in the fishery outweigh the benefits, socioeconomic impacts on local communities will likely ensue,

potentially requiring intervention. Managers should be cognizant of these future impacts as they implement assessment and management approaches for the SNE stock.

SNE and GOM/GBK stocks were done separately in this study because there appears to be spatial nonstationarity in environmental preferences between lobsters of the two regions (Hodgdon et al. 2021) and there is little migration and recruitment sharing between the stocks (ASMFC 2020). A large unknown in this analysis is the potential for increased connectivity between the stocks as waters warm and lobster continue on an increasingly northward trend (Steneck & Wahle 2013).

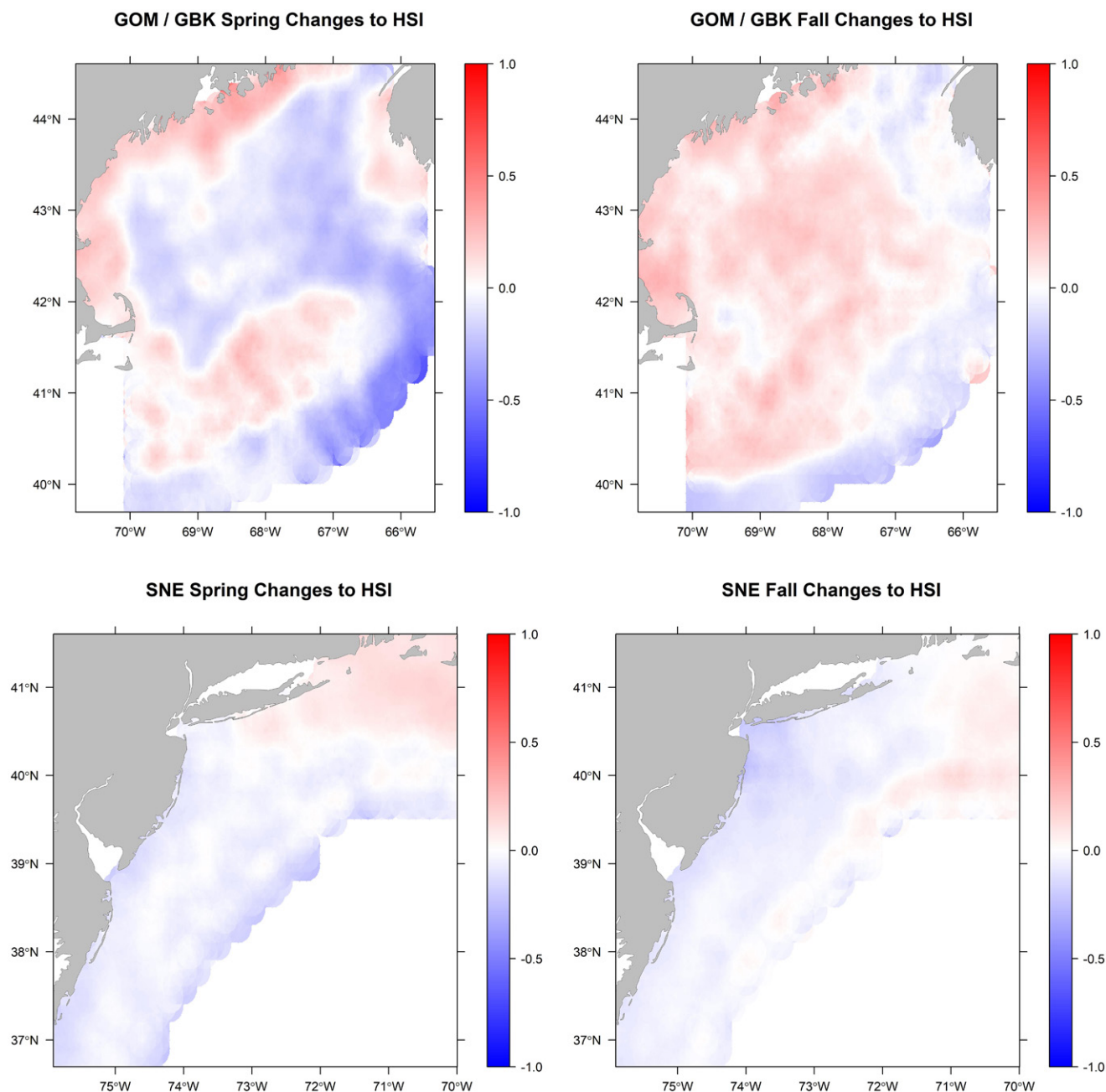


Figure 5. Changes to habitat suitability for American lobster between the historical time period (1992 to 2005) and the forecasted time period (2086 to 2099) under RCP 8.5. Changes to habitat suitability across the Gulf of Maine/Georges Bank (top) and Southern New England (bottom) stock regions for both the spring (left) and fall (right) range from -1 (blue) to 1 (red). Thus, blue represents areas where habitat suitability will decrease over this time period, and red represents areas where it will increase.

As spring and fall SNE suitability decreases in the future and coverage of suitable habitat is contracted, this may push more of the population into GOM/GBK waters. Owing to the strong seasonality of GOM/GBK lobster habitat suitability, it remains unclear what future levels of migration outside of this stock area into Canadian waters to the north might be.

There are myriad unknowns concerning the projections presented here. Lobster population dynamics can be inferred from changes to suitable habitat, but factors such as increased disease prevalence (Glen & Pugh 2006) or predation (Hanson

2009) may also significantly alter the future of American lobster stocks in both SNE and GOM/GBK. To truly understand the future of these animals and their fishery, comprehensive forecasts of these biological factors must also be considered. Future work should strive to simulate lobster populations and distributions about their suitable habitats under regimes of changing disease and predator prevalence. Pending impacts from these biological factors, both stock areas will continue to have the capacity to support lobster populations during the forecasted period as there will remain a high coverage of fair and good

TABLE 1.

Summary statistics of suitable habitat for the Gulf of Maine/Georges Bank (GOM/GBK) American lobster stock and the Southern New England (SNE) American lobster stock for the historical time period (1992 to 2005) and forecasted time period (2086 to 2099) under RCP 8.5 in both spring and fall.

Stock	Season	Period	Average	Fair	Good	Excellent
GOM/GBK	Spring	Historical	0.451	93.123	35.657	0.000
		Future	0.413	85.775	37.070	3.815
	Fall	Historical	0.331	83.090	9.279	0.000
		Future	0.384	96.609	14.743	0.000
SNE	Spring	Historical	0.468	99.929	39.576	0.000
		Future	0.455	98.445	36.749	0.283
	Fall	Historical	0.491	100.000	48.127	0.000
		Future	0.463	99.788	41.060	0.000

Statistics are HSI spatial averages (Average) and percent spatial coverages of HSI more than 0.20 (Fair), 0.50 (Good), and 0.80 (Excellent).

habitat. To determine when these environments would no longer support a population, these forecasts would have to be extended until these good habitats disappeared. Forecasts that far into the future, though, have increased bias and are generally less reliable.

In conclusion, there are juxtaposing futures for the SNE and GOM/GBK American lobster stocks. In general, the GOM/GBK area has a strong seasonality in habitat change and as a result, the timing of population migrations and the fishery may be severely impacted. The SNE region will see declines in

habitat across seasons and a continued use of northern waters by the SNE lobster stock.

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LITERATURE CITED

- Atlantic States Marine Fisheries Commission (ASMFC). 2020. American lobster benchmark stock assessment and peer review report. American Lobster Stock Assessment Review Panel. Woods Hole, MA. 558 pp.
- Atlantic States Marine Fisheries Commission (ASMFC) American Lobster Stock Assessment Review Panel. 2015. Atlantic states marine fisheries commission: American lobster stock assessment peer review report. Woods Hole, MA. 493 pp.
- Atlantic States Marine Fisheries Commission (ASMFC) American Lobster Technical Committee. 2010. Recruitment failure in the Southern New England lobster stock. New Bedford, MA. 58 pp.
- Boenish, R. & Y. Chen. 2018. Spatiotemporal dynamics of effective fishing effort in the American lobster (*Homarus americanus*) fishery along the coast of Maine, USA. *Fish. Res.* 199:231–241.
- Chen, Y., M. Kanaiwa & C. Wilson. 2005a. Developing and evaluating a size-structured stock assessment model for the American lobster, *Homarus americanus*, fishery. *N. Z. J. Mar. Freshw. Res.* 39:645–660.
- Chen, Y., C. Wilson, K. Scheirer, D. Couture & J. Wilson. 2005b. Spatial dynamics of the lobster fishery and oil spills in the Gulf of Maine: a risk analysis of oil spills on the lobster fishery. Orono: University of Maine, Maine Oil Spill Advisory Committee/Department of Environmental Protection/Sea Grant Report. Available at: <https://seagrant.umaine.edu/research/projects/mosac-02-01-spatial-dynamics-of-the-lobster-fishery-and-oil-spills-in-the-gulf-of-maine-a-risk-analysis-of-oil-spills-on-the-lobster-fishery>.
- Crossin, G., S. Al-Youb, S. Jury, W. Howell & W. Watson, III. 1998. Behavioural Thermoregulation in the American lobster *Homarus americanus*. *J. Exp. Biol.* 201:365–374.
- Ellertson, A. A., J. D. Waller, T. L. Pugh & N. D. Bethoney. 2022. Differences in the size at maturity of female American lobsters (*Homarus americanus*) from offshore Southern New England and eastern Georges Bank. USA. *Fish. Res.* 250:106276.
- Friedland, K., C. McManus, R. Morse & J. Link. 2019. Event scale and persistent drivers of fish and macroinvertebrate distributions on the northeast US Shelf. *ICES J. Mar. Sci.* 76:1316–1334.
- Friedland, K., R. Morse, J. Manning, D. Melrose, T. Miles, A. Goode, D. Brady, J. T. Kohut & E. N. Powell. 2020. Trends and change points in surface and bottom thermal environments of the US northeast continental Shelf ecosystem. *Fisheries oceanography*. 29:396–414.
- Glenn, R. & T. Pugh. 2006. Epizootic shell disease in American Lobster (*Homarus americanus*) in Massachusetts coastal waters: interactions of temperature, maturity, and intermolt duration. *J. Crustac. Biol.* 26:639–645.
- Goode, A. G., D. C. Brady, R. S. Steneck & R. A. Wahle. 2019. The brighter side of climate change: How local oceanography amplified a lobster boom in the Gulf of Maine. *Glob. Change Biol.* 25:3906–3917.
- Gulf of Maine Research Institute (GMRI). 2012. An independent evaluation of the Maine limited entry licensing system for lobster and crab. Technical Report. Available at: http://lldc.mainelegislature.org/Open/Rpts/kf1773_s45g47_2012.pdf.
- Hanson, J. M. 2009. Predator-prey interactions of American lobster (*Homarus americanus*) in the Southern Gulf of St. Lawrence, Canada. *N. Z. J. Mar. Freshw. Res.* 43:69–88.
- Hare, J. A., J. P. Manderson, J. A. Nye, M. A. Alexander, P. J. Auster, D. L. Borggaard, A. M. Capotondi, K. B. Damon-Randall, E. Heupel, I. Mateo, L. O'Brien, D. E. Richardson, C. A. Stock & S. T. Biegel. 2012. Cusk (*Brosme brosme*) and climate change: assessing the threat to a candidate marine fish species under the US Endangered Species Act. *ICES J. Mar. Sci.* 69:1753–1768.
- Henry, A. & T. Johnson. 2015. Understanding social resilience in the Maine lobster industry. *Mar. Coast. Fish.* 7:33–43.
- Hodgdon, C., M. Mazur, K. Friedland, N. Willse & Y. Chen. 2021. Consequences of model assumptions when projecting habitat

- suitability: a caution of forecasting under uncertainties. *ICES J. Mar. Sci.* 78:2092–2108.
- Howell, P. 2012. The status of the Southern New England lobster stock. *J. Shellfish Res.* 31:573–579.
- IPCC. 2019. Technical summary. In: Pörtner H.-O., D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegria, M. Nicolai, A. Okem, J. Petzold, B. Rama & N. M. Weyer, editors. IPCC special report on the ocean and cryosphere in a changing climate. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 39–69.
- Le Bris, A., K. E. Mills, R. A. Wahle, Y. Chen, M. A. Alexander, A. J. Allyn, J. G. Schuetz, J. D. Scott & A. J. Pershing. 2018. Climate vulnerability and resilience in the most valuable North American fishery. *Proc. Natl. Acad. Sci. USA* 115:1831–1836.
- Maine Department of Marine Resources (Maine DMR). 2022. Historical Maine fisheries landings data. Available at: <https://bit.ly/3OReXm7>.
- Maine Department of Marine Resources (MEDMR) and the New Hampshire Fish and Game Department (NHFGD). 2000–2016. *Inshore bottom trawl survey*. Raw data.
- Massachusetts Department of Marine Fisheries (MADMF). 1978–2016. *Bottom trawl survey*. Raw data.
- Mbogga, M., X. Wang & A. Hamann. 2010. Bioclimate envelope model predictions for natural resource management: dealing with uncertainty. *J. Appl. Ecol.* 47:731–740.
- McMahon, T. 1983. Habitat suitability index models: Coho Salmon. FWS/OBW-82/10.49. Ft. Collins: U.S. Fish and Wildlife Service. 40 pp.
- Mills, K. E., A. J. Pershing & C. M. Hernández. 2017. Forecasting the seasonal timing of Maine's lobster fishery. *Front. Mar. Sci.* 4:337.
- National Marine Fisheries Service (NMFS). 2020. Landings Report. U.S. Department of Commerce, NOAA Current Fishery Statistics. Accessed July 2022 Available at: <https://www.fisheries.noaa.gov/foss/f?p=215:200>.
- Navarro-Racines, C., J. Tarapues, P. Thornton, A. Jarvis & J. Ramirez-Villegas. 2020. High-resolution and bias-corrected CMIP5 projections for climate change impact assessments. *Sci. Data* 7:14.
- New Jersey Department of Environmental Protection (NJDEP). 1988–2016. *Trawl survey*. Raw Data.
- Northeast Fisheries Science Center (NEFSC). 1978–2016. *Bottom trawl survey*. Raw data.
- Pershing, A., M. Alexander, C. Hernandez, L. Kerr, A. Le Bris, K. Mills, J. Nye, N. R. Record, H. A. Scannell, J. D. Scott, G. D. Sherwood & A. C. Thomas. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350:809–812.
- Quintana-Rizzo, E., S. Leiter, T. V. N. Cole, M. Hagbloom, A. Knowlton, P. Nagelkirk, O. O'Brien, C. Khan, A. Henry, P. A. Duley, L. Crowe, C. Mayo & S. Kraus. 2021. Residency, demographics, and movement patterns of North Atlantic right whales *Eubalaena glacialis* in an offshore wind energy development area in southern New England, USA. *Endanger. Species Res.* 45:251–268.
- Rhode Island Department of Environmental Management (RIDEM). 1981–2016. *Coastal trawl survey*. Raw Data.
- Stanley, R. R. E., C. DiBacco, B. Lowen, R. G. Beiko, N. W. Jeffery, M. Van Wyngaarden, P. Bentzen, D. Brickman, L. Benestan, L. Bernatchez, C. Johnson, P. V. R. Snelgrove, Z. Wang, B. F. Wringe & I. R. Bradbury. 2018. A climate-associated multispecies cryptic cline in the northwest Atlantic. *Sci. Adv.* 4:3.
- Steneck, R. & R. Wahle. 2013. American lobster dynamics in a brave new ocean. *Can. J. Fish. Aquat. Sci.* 70:1612–1624.
- Tanaka, K., J. Cao, B. Shank, S. Truesdell, M. Mazur, L. Xu & Y. Chen. 2019. A model-based approach to incorporate environmental variability into assessment of a commercial fishery: a case study with the American lobster fishery in the Gulf of Maine and Georges Bank. *ICES J. Mar. Sci.* 76:884–896.
- Tanaka, K. & Y. Chen. 2015. Spatiotemporal variability of suitable habitat for American lobster (*Homarus americanus*) in Long Island Sound. *J. Shellfish Res.* 34:531–543.
- Tanaka, K. & Y. Chen. 2016. Modelling spatiotemporal variability of the bioclimate envelope of *Homarus americanus* in the coastal waters of Maine and New Hampshire. *Fish. Res.* 177:137–152.
- Tanaka, K., M. Torre, V. Saba, C. Stock & Y. Chen. 2020. An ensemble high-resolution projection of changes in the future habitat of American lobster and sea scallop in the Northeast US continental shelf. *Divers. Distrib.* 26:987–1001.
- Virginia Institute of Marine Science (VIMS). 2007–2016. *Northeast area monitoring and assessment program*. Raw Data.
- Wahle, R., L. Dellinger, S. Olszewski & P. Jekielek. 2015. American lobster nurseries of southern New England receding in the face of climate change. *ICES J. Mar. Sci.* 72:i69–i78.
- Watling, J., L. Brandt, F. Mazzotti & S. Romanach. 2013. Use and interpretation of climate envelope models: a practical guide. Gainesville, FL: University of Florida. 43 pp.
- Willse, N., R. Summers & Y. Chen. 2022. Vertical line requirements and North Atlantic right whale entanglement risk reduction for the Gulf of Maine American lobster fishery. *Mar. Coast. Fish.* 14:e10203.

APPENDIX

The results presented here (Table A1, Figs. A1–A3) are derived from a bioclimate model run structured nearly identical to the one in the main text, but with the exclusion of latitude and longitude when hindcasting and projecting habitat suitability. This was done because habitat forecasts have the potential to be biased if the variables these spatial coordinates are proxy for are actually spatiotemporal in nature (and thus may change in the forecasted period). If the factors latitude and longitude are proxy for are spatiotemporal in nature and not strictly

spatial, then the results presented here have the potential to be more accurate in the context of changes in suitability over time (Fig. A3). Historical maps concerning this model run appear unreliable and do not match well with what is observed by the surveys or fishery. This is because they should not be interpreted the same way as the maps in the main text. The maps presented here represent spatial suitability for lobster only in the context of parameters bottom temperature and depth, and therefore do not match well with spatial lobster density, which is in fact influenced by other factors that latitude and longitude account for.

TABLE A1.

Summary statistics of suitable habitat for the Gulf of Maine/Georges Bank (GOM/GBK) American lobster stock and the Southern New England (SNE) American lobster stock for the historical time period (1992 to 2005) and forecasted time period (2086 to 2099) under RCP 8.5 in both spring and fall.

Stock	Season	Period	Average	Fair	Good	Excellent
GOM/GBK	Spring	Historical	0.400	91.427	21.102	0.330
		Future	0.248	48.045	0.754	0.000
	Fall	Historical	0.400	58.408	41.404	16.392
		Future	0.455	94.866	36.364	3.109
SNE	Spring	Historical	0.388	90.601	9.965	1.343
		Future	0.306	80.777	5.512	0.000
	Fall	Historical	0.400	89.541	8.975	0.212
		Future	0.331	72.226	9.258	0.000

Statistics are HSI spatial averages (Average) and percent spatial coverages of HSI more than 0.20 (Fair), 0.50 (Good), and 0.80 (Excellent). Results are from a bioclimate model run without the inclusion of spatial parameters latitude and longitude.

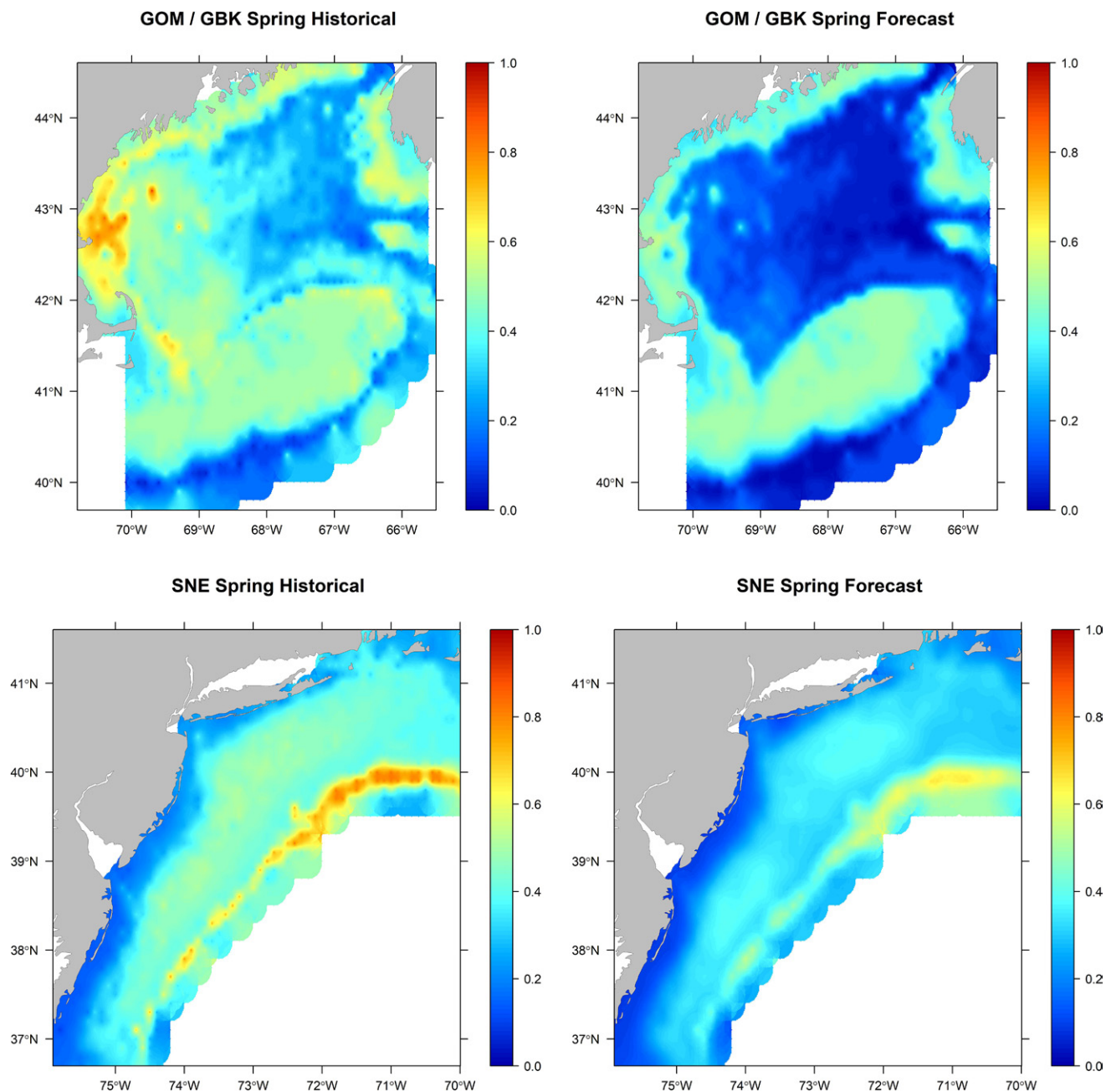


Figure A1. Spring habitat suitability from 0 (blue) to 1 (red) for American lobster in the Gulf of Maine/Georges Bank (top) and Southern New England (bottom) stock regions. Panels on the left are for the historical time period (1992 to 2005) and panels on the right are for the forecasted time period (2086 to 2099) under RCP 8.5. Results are from a bioclimate model run without the inclusion of spatial parameters latitude and longitude.

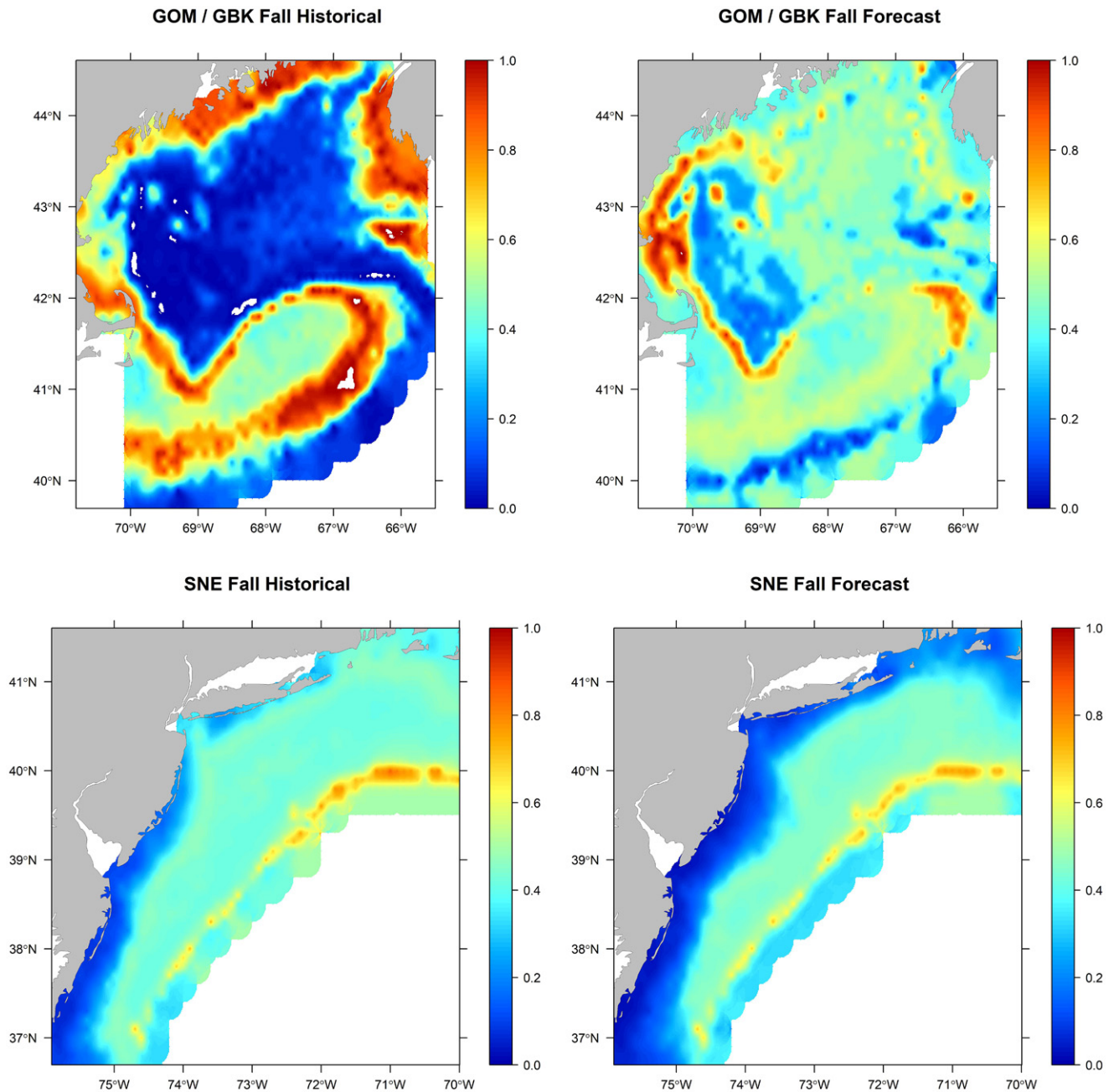


Figure A2. Fall habitat suitability from 0 (blue) to 1 (red) for American lobster in the Gulf of Maine/Georges Bank (top) and Southern New England (bottom) stock regions. Panels on the left are for the historical time period (1992 to 2005) and panels on the right are for the forecasted time period (2086 to 2099) under RCP 8.5. Results are from a bioclimate model run without the inclusion of spatial parameters latitude and longitude.

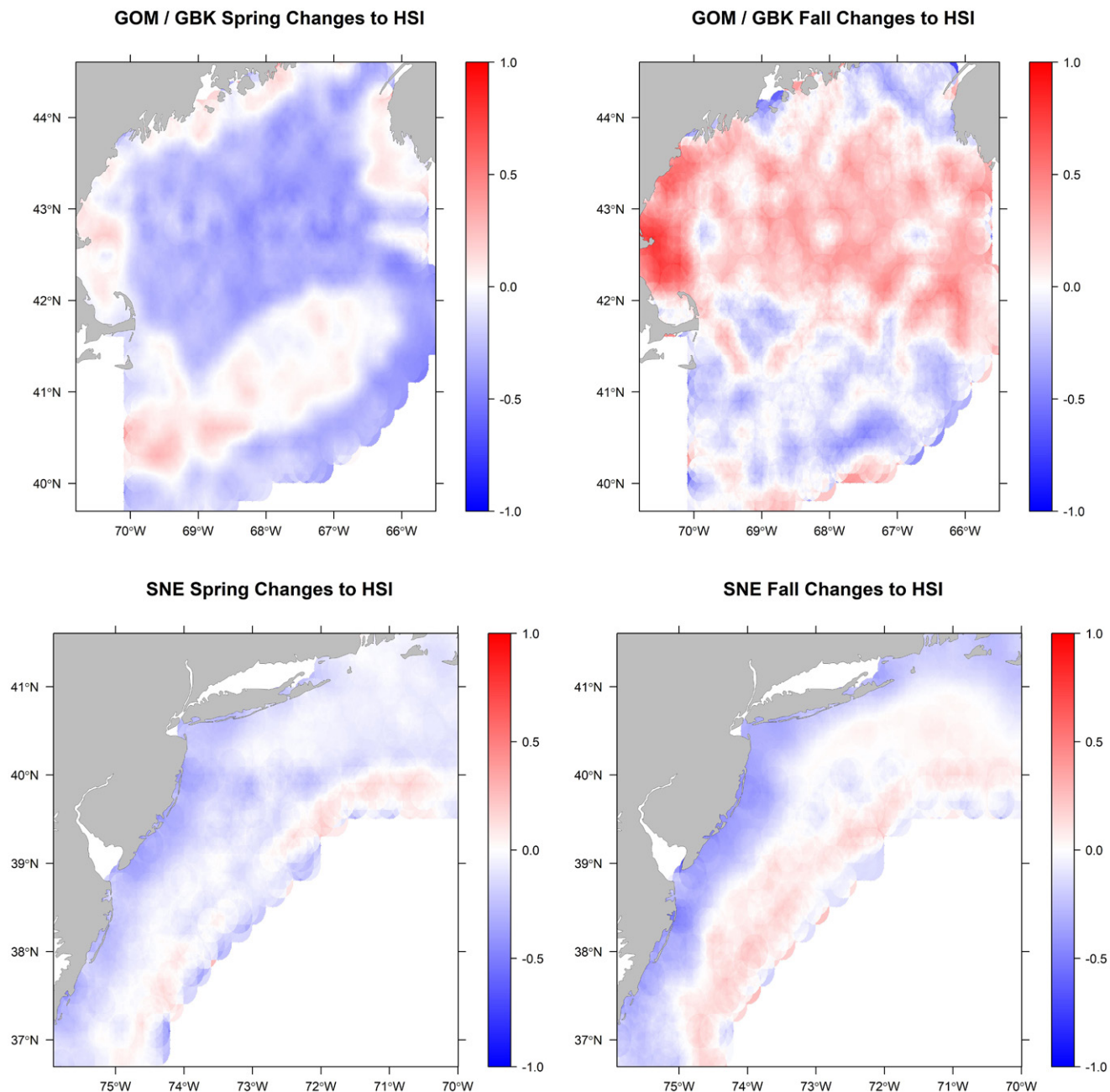


Figure A3. Changes to habitat suitability for American lobster between the historical time period (1992 to 2005) and the forecasted time period (2086 to 2099) under RCP 8.5. Changes to habitat suitability across the Gulf of Maine/Georges Bank (top) and Southern New England (bottom) stock regions for both the spring (left) and fall (right) range from -1 (blue) to 1 (red). Thus, blue represents areas where habitat suitability will decrease over this time period, and red represents areas where it will increase. Results are from a bioclimate model run without the inclusion of spatial parameters latitude and longitude.