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Potential thermal habitat shifts of reef-associated species in response to projected bottom warming along the US Atlantic Coast

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ABSTRACT: Future ocean conditions will likely alter habitat suitability for many species, potentially resulting in range shifts. Climate models simulate environmental conditions under climate scenarios and serve as a valuable tool for projecting future changes in habitat suitability. Here, we use ocean bottom temperature patterns from a multi-model ensemble mean of 6 Coupled Model Intercomparison Project (CMIP6) models for 'low', 'medium', and 'high' emission socioeconomic climate scenarios (SSP2-4.5, SSP3-7.0, SSP5-8.5) to estimate changes in thermal habitat availability for 6 commercially important fish species along the US Atlantic coast from 2015 to 2100. Thermal preferences were derived from survey data, and modeled bottom temperatures were adjusted to better reflect observed habitat conditions. Projections indicated declines in suitable thermal habitat for all species, although rates varied, with poleward shifts in northern range edges evident by the end of the century. Projected changes in suitable thermal habitat are likely to contribute to shifts in species distributions, which may require fisheries management bodies to co-develop strategies that address the reorganization of marine ecosystems under climate change. Enhancing model resolution and accounting for regional factors should significantly improve these predictions, allowing for the use of robust species distribution models.

KEY WORDS: Thermal bottom habitat · Global climate models · Model validation · Model calibration · Habitat shifts · Species distribution

1. INTRODUCTION

Changes in the climate are altering the environmental conditions that define suitable habitat for marine species. Many ocean properties are being altered, including ocean temperature, water circulation, vertical mixing, salinity, and ocean chemistry, which are highly correlated with species distribution shifts (Pinsky et al. 2013). These shifts generally occur in a poleward direction when barriers to movement are absent and are often correlated with suitable thermal habitat to varying degrees (Pinsky et al. 2013, Morley et al. 2018, Gordó-Vilaseca et al. 2023). Shifts in species distributions are likely to cause a multitude

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of changes, including species assemblages, diet, habitat use, phenology, spawning dynamics, and productivity (Rice 1995, Doney et al. 2012, Pinsky et al. 2013, Sydeman et al. 2015, IPCC 2018, Morley et al. 2020, Ducklow et al. 2022, Quinlan et al. 2023). Distribution changes have already become evident in fishery landings and support a general poleward trend; however, variations in the rate of movement of fish species, timing of behaviors, regional differences, and compounding stressors highlight the need for region- and species-specific studies (Pinsky et al. 2013, Morley et al. 2018). The waters of the US East Coast have experienced surface and bottom warming, with recent years being some of the warmest on record (Craig et al. 2021). Distribution shifts poleward or into deeper waters have begun and are expected to continue (Morley et al. 2018, Lucey et al. 2023, Northeast Fisheries Science Center 2023, Cao et al. 2024). Thus, to understand and effectively prepare for distributional changes, it is necessary to first explore how suitable thermal habitat itself is projected to change.

Global climate models (GCMs) simulate physical and biogeochemical ocean patterns under projected climate scenarios, providing valuable inputs for determining thermal habitat. Subsequent outputs can support climate-informed fisheries objectives and determine research needs in anticipation of future changes (Holsman et al. 2019, Tebaldi et al. 2021). Distribution changes can occur via direct physiological responses to environmental conditions and indirect responses due to changes in prey, predators, and habitat. Variation in scenarios representing the anthropogenic influence on climate provides the range and magnitude of potential impacts, informing mitigation and management endeavors. Climate scenarios present plausible future changes under diverse emission scenarios but have many layers of uncertainty. Accordingly, planners should use scenarios to inform decision-making that encompasses a broad spectrum of potential outcomes rather than relying on a singular future projection (Bell et al. 2020). Comparing historical trends to those simulated in climate models aids in demonstrating unprecedented conditions that may occur and can parse out novel trends. Often, historical trends form the foundation of management objectives. However, as suitable habitat — and therefore, species — shift, more weight will need to be given to recent and projected trends in distribution and landings to reflect the current state of the stock more accurately. Climate scenarios have proven useful in estimating future trends of ocean conditions influencing multiple species distributions (Kleisner et al. 2017, Morley et al. 2018). Continued improvement and refinement will increase the ability to operationalize these tools to answer important questions relating to the marine ecosystem and fisheries management (Pinsky et al. 2013).

Awareness of when and where thermal habitat may be shifting and how that may influence harvested species is essential for making fisheries management climate-ready. Shifts in distribution may positively or negatively affect species as habitats may become more favorable and extensive, stay the same but shift, or become less favorable and decrease in size (Cheung et al. 2009, Johnstone et al. 2016, Troast et al. 2020). These responses are reflected in stock sizes as one zone may experience an increase in a particular stock while another experiences a decrease, irrespective of overall population size (Link et al. 2011, Karp et al. 2019). Fishery managers must respond appropriately to adapt to changing conditions, which may introduce new fishery resources to their region along with new challenges (Cheung et al. 2012, Madin et al. 2012, Quinlan et al. 2023). For example, lobster fishermen in New England began fishing the emerging blue crab *Callinectes sapidus* stock, resulting in increased bycatch of the diamondback terrapin *Malaclemys terrapin*, a threatened species (Miller 2018). Ongoing distribution shifts have caused allocation conflicts between management regions as managed species shift and catch limits must be altered (Bell et al. 2015, Pinsky et al. 2021, Vogel et al. 2023). Shifts in black sea bass *Centropristis striata* have caused discrepancies in state permitting and catch rates, where southern states have increased difficulty filling their quota, and northern states must discard fish after quickly filling their quota (Dubik et al. 2019). The catch of summer flounder *Paralichthys dentatus* is increasing in northern states; however, processing infrastructure is still located in southern states (Dubik et al. 2019). These examples show the impacts of changing species distributions and the need for robust climate data to support flexible and adaptive management strategies. Therefore, the future management of species affected by changes to suitable habitat will require increased communication between management regions to serve fishing communities best and protect marine resources. As demonstrated in 2016, the New England Fishery Management Council contacted the Mid-Atlantic Fishery Management Council, requesting joint jurisdiction over summer flounder, black sea bass, and scup *Stenotomus chrysops* as their presence in the region increased (Bell et al. 2020). Karp et al. (2019, p. 1307) laid out 6 steps of a climate-informed science-to-management system: '(1) detect and anticipate changes, (2) understand mechanisms of change, (3) evaluate risks and priorities, (4) conduct assessments and develop forecasts, (5) communicate advice to managers and stakeholders, and (6) manage fisheries under changing conditions'. These steps provide a framework for guiding management during uncertain changes and act as a call to action to implement these steps.

Here, we describe the initial steps for a climate-informed science-to-management system, exploring how climate models along the US East Coast compare to observed survey data and how they can be used to anticipate future changes in bottom temperature and, consequently, the bottom thermal habitat of 6 fishes managed under the South Atlantic Fishery Management Council's snapper–grouper fishery management plan (FMP). Bottom temperatures from the Coupled Model Intercomparison Project Phase 6 (CMIP6) were used for historical years (1950–2014) and future years (2015–2100) for 3 climate scenarios. We used derived species' thermal ranges to evaluate potential changes in the extent of suitable thermal habitat by the end of the century. To provide a temporal perspective on potential thermal habitat change, we calculated the yearly total area of estimated bottom temperature within each species' derived range under selected climate scenarios and compared mid-century to end-of-century rates of change. Lastly, we quantified the northern boundary of suitable thermal habitat to discern new areas a species may inhabit and how this relates to current regional management jurisdictions. Our study aims to investigate plausible changes in thermal bottom habitat under ocean warming, offering valuable insights for fisheries management and highlighting critical aspects for more comprehensive future analyses.

2. MATERIALS AND METHODS

2.1. Climate model

An ensemble of 6 models from CMIP6 provided historical estimates of climate variables from 1950 to 2014 and projected estimates from 2015 to 2100 for 3 climate scenarios (Table 1). The scenarios, referred to as shared socioeconomic pathways (SSPs), describe challenges to mitigation and adaptation to climate change and the radiative forcing in watts per square meter estimated by the end of the 21st century. We considered scenarios SSP2 (4.5 W m^{-2}), SSP3 (7.0 W m^{-2}), and SSP5 (8.5 W m^{-2}) from Scenario-MIP, described as 'middle of the road', 'regional rivalries', and 'fossil-fueled development' (O'Neill et al. 2017). This study examines bottom temperature to describe suitable thermal habitat due to its importance in the complex interactions between abiotic and biotic factors that ultimately determine a species' distribution. First, our species of interest are generally demersal or reef associated, and second, we were interested in comparing the modeled bottom temperature to observed temperatures from regional surveys. Third, temperature is critical to physiological processes such as metabolism, growth, and reproduction, and has been a skillful covariate for explaining latitudinal range shifts (Fry 1971, Dahms & Killen 2023). Bottom temperature can differ significantly from surface temperature; therefore, incorporating bottom temperature data for demersal and reef-associated species provides a more accurate representation than relying solely on surface variables (Duffy & Chown 2017).

CMIP6 models typically have a spatial resolution of about 50–100 km. Since the resolutions of the CMIP6 model are too coarse to properly resolve the ocean eddy and currents, which influence temperature and salinity in the model, the CMIP6 model has a systematic bias in simulating bottom temperature (Oey et al. 2005, Liu et al. 2012, Carolina Castillo-Trujillo et al. 2023). To reduce this bias, the bottom temperature from the CMIP6 models was corrected using the quarter-degree resolution temperature from the World Ocean Atlas (WOA; Boyer et al. 2018) for 1981–2010 as follows:

$$\text{Historical period: } TOB_{bc\_mod\_hist} = (TOB_{mod\_hist} - TOB_{mod\_hist\_avg}) + TOB_{WOA\_avg} \tag{1}$$

$$\text{Future period: } TOB_{bc\_mod\_future} = (TOB_{mod\_future} - TOB_{mod\_hist\_avg}) + TOB_{WOA\_avg} \tag{2}$$

where $TOB_{bc\_mod\_hist}$ is the bias-corrected bottom temperature from CMIP6 models in the historical period, TOB_{mod_hist} is the raw bottom temperature from the CMIP6 model in the historical period, $TOB_{mod\_hist\_avg}$ is the time-averaged raw bottom temperature from CMIP6 models in the historical period (1850–2014), TOB_{WOA_avg} is the time-averaged bottom temperature from WOA (1981–2010), $TOB_{bc\_mod\_future}$ is the bias-corrected bottom temperature from CMIP6 models in the future scenarios, and TOB_{mod_future} is the raw bottom temperature from the CMIP6 model in the future periods. All bottom temperatures from CMIP6 models were regridded to 0.25° × 0.25° resolution using a bilinear interpolation method to match the horizontal resolution of the WOA data. This simple bias correction method, which has been previously used in multiple studies (Liu et al. 2012, 2015, and others), ensures that the mean states of the CMIP6

Table 1. The six CMIP6 models and the resolutions of their ocean components used in this study

Model	Horizontal resolution (km)	Total vertical levels	Reference
ACCESS-CM2	~100	50	Bi et al. (2020)
ACCESS-ESM1-5	~100	50	Law et al. (2017)
BCC-CSM2-MR	~50	40	Wu et al. (2019)
CanESM5	~100	45	Swart et al. (2019)
CMCC-ESM2	~100	50	Lovato et al. (2022)
MRI-ESM2-0	~100	60	Yukimoto et al. (2019)

during the historical period (1981–2020) are comparable to those of the WOA.

2.2. Study area

The study area includes the US Atlantic Coast from Cape Canaveral, FL, to the Gulf of Maine, and spans 14 coastal states (Fig. 1). The area of analysis focused on the continental shelf (<200 m depth) and included some of its deeper areas within the boundary, shallower than 350 m. Limitations in the resolution of the CMIP6 model excluded nearshore shallow-water coastal areas, as displayed in Fig. 1. Three federal Fishery Management Councils encompass the region: the New England, the Mid-Atlantic, and the South Atlantic. Several biogeographic transition zones, areas that delineate boundaries between biota, have been described along the US East Coast, including south of Cape Canaveral, FL, near Cape Hatteras, NC, and near Cape Cod, MA, with evidence that the zone in Florida has shifted north as warming trends continue (Wilkinson et al. 2009, Pappalardo et al. 2015, Troast et al. 2020).

2.3. Selected species and survey data

Six fish species from the snapper-grouper FMP managed by the South Atlantic Fishery Management Council were selected based on the Southeast Reef Fish Survey (SERFS). These species are red grouper *Epinephelus morio*, red snapper *Lutjanus campechanus*, gag grouper *Mycteroperca microlepis*, red porgy *Pagrus pagrus*, vermilion snapper *Rhomboplites aurorubens*, and greater amberjack *Seriola dumerili*. These species were in the top 20 most abundant species in SERFS trap-video data that were bottom-associated, generally but not exclusively shallow-water reef species, and economically important. NOAA Fisheries' Status of Stocks report indicates that red snapper, red porgy, gag grouper, and red grouper are overfished, with red snapper and gag grouper experiencing overfishing in the South Atlantic (NOAA Fisheries 2024).

The SERFS is a combined trap-video survey consisting of the Marine Resources Monitoring, Assessment and Prediction (MARMAP) program, SEAMAP South Atlantic, and the NMFS-SEFSC Southeast Fishery-Independent Survey (SEFIS) program (Smart et al. 2016). The survey samples the continental shelf and shelf edge between Cape Hatteras, NC, and St. Lucie, FL, to assess the abundance and distribution of target reef species. The broader monitoring program includes several gear types, but this study exclusively uses abundance counts from videos attached to chevron trap sampling. Baited chevron traps with attached video cameras are deployed near live-bottom habitats and allowed to soak for 90 min. A conductivity, temperature, and depth (CTD) profile was also taken at each station location. Researchers analyze the videos in a laboratory using the MeanCount approach de-

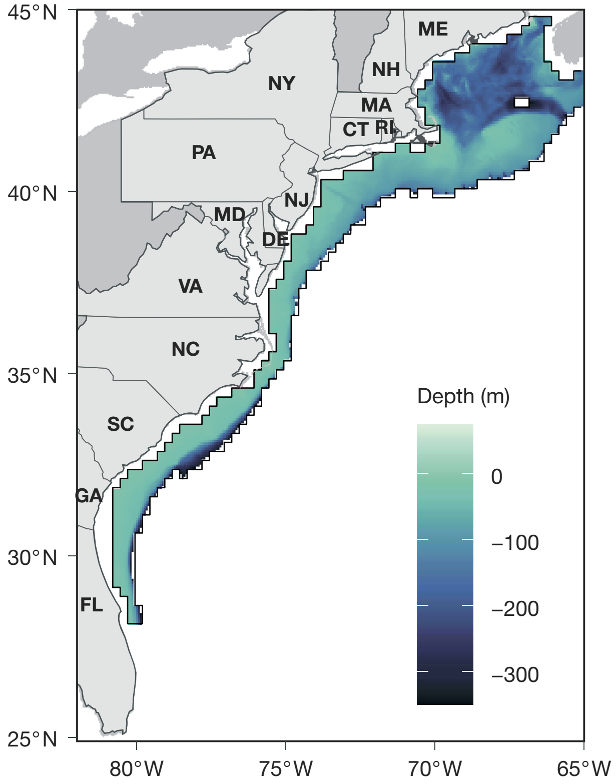

Fig. 1. US Atlantic Coast study area, from Cape Canaveral, FL, to the Gulf of Maine. Black outline: area of analysis based on 0.25° × 0.25° grid cells of depths to 350 m

tailed by Conn (2011) and Schobernd et al. (2014). This monitoring program generally captures the adult life stage of these species. Therefore, larval thermal ranges are not considered, which likely vary from adult thermal ranges. The species' presence in this data set demonstrates their demersal or reef affinity and, therefore, their likelihood of being influenced by changes in bottom temperature. Within the subset of SERFS survey years used in this study (2011–2014), the selected species were recorded in 2100 samples.

2.4. CMIP6 adjustments and thermal ranges

For this study, the thermal range for each species was determined by the 5th to 95th percentile range of observed bottom temperatures from when species were present in the survey data. This does not necessarily represent a species' thermal limits, since they are likely able to survive in more extreme temperatures. Instead, it represents common temperatures where the species occurs in this region and survey, while excluding extreme outliers. Bottom temperatures were used for these thermal ranges to inform the range of temperatures these reef-associated species were occupying.

Firstly, we evaluated how well CMIP6 bottom temperatures corresponded with observed CTD measurements from the SERFS survey to assess their suitability for estimating thermal habitat. Survey temperatures were paired with CMIP6 values at the corresponding grid cell, month, and year, revealing that CMIP6 estimates were consistently warmer (see Fig. 2A). Although previously calibrated with WOA data, further adjustment was needed, as CMIP6 bottom temperatures must correspond to adequate thermal habitat where it is currently observed; this ground-truthing step ensures that projections of future thermal habitat are based on realistic conditions.

To determine an appropriate adjustment, we assessed whether the observed temperature at sampling and the modeled bottom temperature at each corresponding observation point fell within the species' derived thermal range. This point-by-point comparison served to quantify the discrepancy between modeled and observed conditions and guide the calibration of CMIP6 temperatures. As the thermal ranges were derived from the survey data, they should closely align with observation temperatures. The proportion of points with temperatures that fell within a species' thermal range was calculated for 2011–2014, the years with available validation data (see Fig. 2B). As expected, approximately 90% of survey temperatures fell within the derived thermal ranges, reflecting the 5–95% quantile definition used to derive the ranges. By contrast, the warm bias of CMIP6 excluded many observed occurrences (i.e. many temperatures fell outside of the derived thermal ranges) and confirmed the need for calibration (see Fig. 2B,C). We corrected this bias by reducing CMIP6 bottom temperatures by 1°C. This adjustment brought the proportion of modeled temperatures within the derived thermal ranges in line with observed occurrences (approximately 90%). A paired Wilcoxon signed-rank test was performed to determine significant differences between the proportion of points that fell within the derived thermal ranges for observed, modeled, and adjusted temperatures. These calibrated temperatures (hereafter 'CMIPadj') were then used to project end-of-century shifts in thermal habitat.

2.5. Analysis

Mann-Kendall trend tests were conducted to determine if trends in mean bottom temperatures within climate scenarios occurred and to determine the percent change of estimated suitable thermal habitat by the end of the century (Mann 1945, Kendall 1975). Kendall's Tau (τ) statistic is reported, which determines the strength and direction of a trend if one occurs. This coefficient is on a scale of 1 to −1, determining a positive or negative trend, representing in this case a warming or cooling trend. Absolute values greater than 0.5 are generally considered strong trends, and absolute values less than 0.10 indicate little to no trend.

For analyses focusing primarily on spatial changes, historical estimates are based on 30 yr mean grid values from 1985 to 2014 and future estimates from 2071 to 2100 to evaluate end-of-century projections. First, we calculated the potential temperature degree difference by the end of the century compared to the historical temperature per grid cell, as spatial variability in warming is expected. To estimate patterns of potential suitable thermal habitat change for snapper–grouper FMP species, we mapped the grid cells with appropriate thermal habitat for each species, using the species' derived thermal range. To determine the overall change of potentially suitable habitat area on a finer time scale, we calculated the areal change (km^2) in suitable thermal habitat per year for each species under each climate scenario and compared that to the combined historical mean of suitable habitat from 1950 to 2014. Lastly, we determined a northern range edge for each species' suitable thermal habitat using the average latitude of the northernmost 5% grid cell centroids that fell within a species' derived thermal range. Grid cells consisted of the mean CMIPadj bottom temperature from the historical and projected time frames per scenario. The southern range edge was not estimated due to a lack of data in the South Florida region, and since it has been found that cold edges (northern range limit in the Northern Hemisphere) generally track changes in temperature better than warmer edges (southern range limits; Fredston-Hermann et al. 2020).

All analysis was performed in R v.4.3.1 (R Core Team 2023) using RStudio (Posit Team 2023). General data manipulation and visualization was completed using the 'tidyverse' package (Wickham et al. 2019), with additional customization using the packages 'patchwork', 'viridis', and 'wesanderson' (Garnier et al. 2023, Ram & Wickham 2023, Pedersen 2024). Spatial data was manipulated and analyzed using the packages 'ncdf4', 'terra', 'raster', and 'sf' (Hijmans 2023, 2024, Pebesma & Bivand 2023, Pierce 2024), with packages 'marmap' for bathymetry data and 'maps' for US polygons (Becker et al. 2023, Pante et al. 2023). The package 'trend' was used to conduct trend analysis (Pohlert 2023).

3. RESULTS

3.1. CMIP6 estimates and thermal ranges

CMIP6 bottom temperatures were consistently warmer than those observed in the trap-video data (Fig. 2A). The smallest mean monthly temperature difference was 0.4°C in October, and the largest difference was 5.5°C in June. The seasonality of the SERFS sampling scheme, for example, higher latitudes being sampled in July and lower latitudes being sampled in April, could result in typically cooler months recording warmer temperatures and typically warmer months recording cooler temperatures. To counteract this issue, the CMIP6 temperatures were paired with SERFS samples by time and location, ensuring their comparability and prompting adjustments to overcome the bias. Overall, the thermal envelopes for the individual species ranged from 15.65 to 27.51°C (Table 2). Observed bottom temperatures had on average (±SD) 89.74 ± 30.34% of points fall within a species' thermal range, while the CMIP6 temperatures only captured 68.54 ± 46.44%; however, after CMIP6 temperatures were reduced by 1°C, defined here as 'CMIPadj', 89.57 ± 30.57% of points fell within range (Fig. 2B). Before CMIPadj was applied, the proportion of CMIP6 temperatures that fell within the species thermal range significantly differed from trap-video temperatures for 4 out of 6 species, including gag grouper, greater amberjack, red snapper, and vermilion snapper, as well as when all species data were combined. No species exhibited a significant difference after CMIPadj was applied.

3.2. Temperature distribution

Historical temperatures (CMIPadj estimates) from 1950–2014 and forecasted temperatures from 2015–2100 all show a significant warming trend ($\tau > 0.82$, $p < 0.001$). The mean lower fifth percentile bottom temperature for the entire study area from the last 30 yr of the historical period (1985–2014) was 2.3°C and warmed to 5.1, 5.8, and 6.6°C under scenarios SSP2-4.5, SSP3-7.0, and SSP5-8.5 (2071–2100). The mean upper fifth percentile bottom temperature for the entire study area from the last 30 yr of the historical period (1985–2014) was 24.3°C and warmed to 26.8, 27.2, and 27.8°C under scenarios SSP2-4.5, SSP3-7.0, and SSP5-8.5 (2071–2100). This results in an average 3.5°C increase in minimum bottom temperatures and a 3.0°C increase in maximum bottom temperatures.

3.3. Spatial analysis

Spatial analysis shows the warmest bottom temperatures in the waters closest to shore in the South Atlantic region (Fig. 3). The greatest increases in the projected mean bottom temperature (2071–2100) compared to historical mean bottom temperatures (1985–2014) are 5.2°C for SSP2-4.5, 5.9°C for SSP3-7.0, and 7.0°C for SSP5-8.5 and occurred in the areas closest to the coast outside the Chesapeake Bay, around 38° N. The smallest changes in bottom warming occurred around North Carolina, with increases of 1.1°C in SSP2-4.5, 1.3°C in SSP3-7.0, and 1.5°C in SSP5-8.5. End-of-century projections estimate substantial thermal habitat loss off the coast of Florida, beginning offshore, for all species. Small increases in thermal habitat northward of historical habitat, between North Carolina and Delaware, are present for most species; however, they are smaller in magnitude than estimated losses in the south (Fig. 3).

The area of suitable habitat based on bottom temperature for all species under all future climate scenarios decreased compared to the historical mean (Fig. 4). Mann-Kendall tests determined that during the historical period, there was a moderate percent

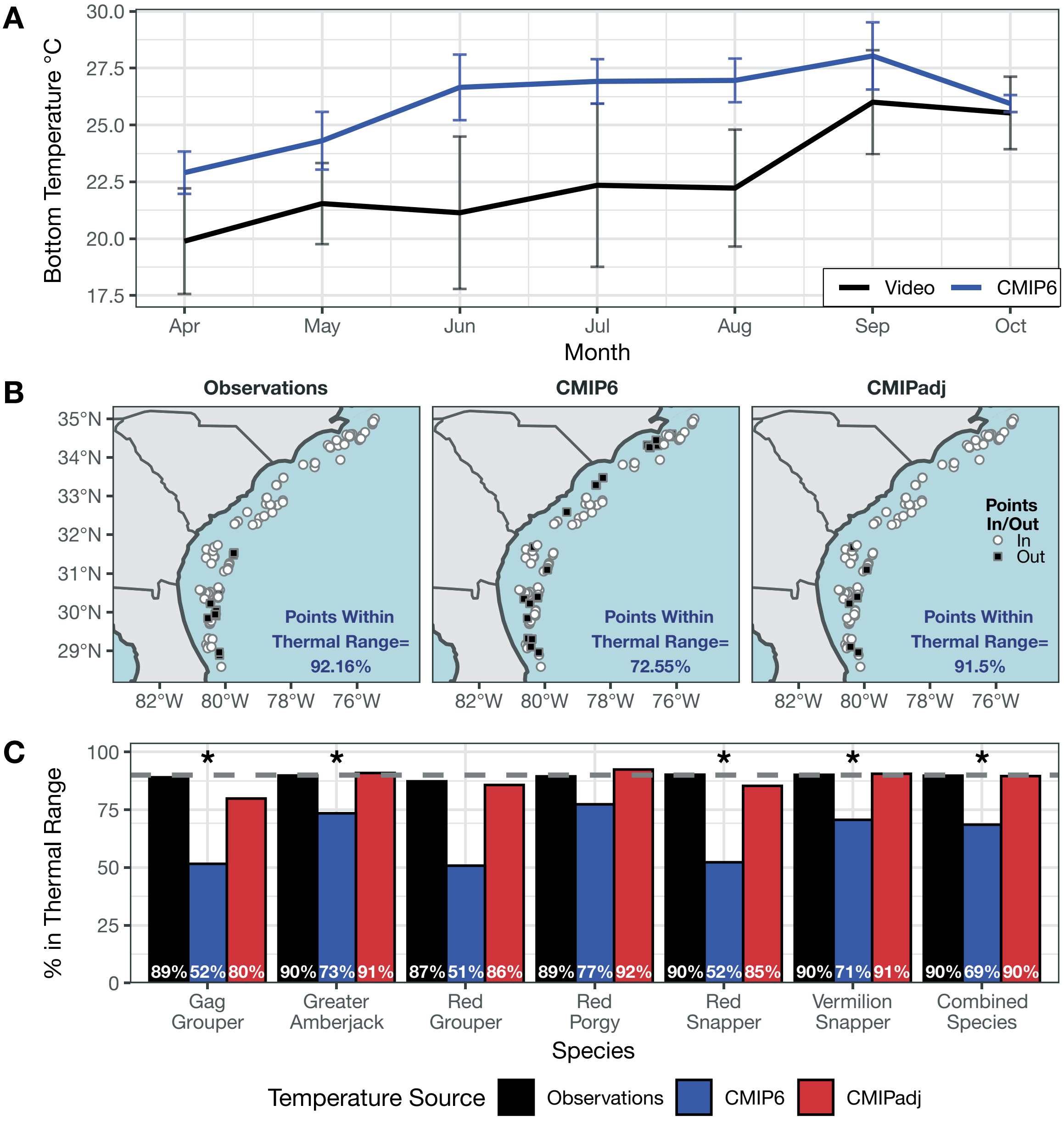

Fig. 2. (A) Comparison of mean (±1 SD) monthly bottom temperature observed by the trap-video survey data compared to CMIP6 bottom temperature for the same grid cells where the trap-video temperature was observed from 2011–2014. (B) Example depicting points where a species was observed in the SERFS survey. Left panel shows whether the observed temperature at that point was within the species thermal range (white dots), defined as the 5–95% of temperatures when the species was observed, or outside of the thermal range (black squares). Center panel shows the same for the modeled bottom temperature of the corresponding CMIP6 grid cell during the same month and year when the species was observed. Right panel shows the same for the adjusted CMIP6 (CMIPadj) temperature after a 1°C reduction to better match the observed bottom temperature. (C) Mean percent of survey points that fall within the associated species' derived thermal range. The derived thermal range is 90% of the observed thermal range to avoid outliers; therefore, 90% is the expected frequency of temperatures that fall within the derived thermal range (gray dashed line). Black bars: temperatures from the SERFS survey at time of observation; blue bars: temperature from the corresponding CMIP6 grid cell during the month and year of the observation; red bars: the same CMIP6 grid cell temperature after it was reduced by 1°C to better align with observed data. Asterisks: values that are significantly different from the observation data

increase in area ($\tau = 0.43$, $p < 0.001$). By contrast, all climate scenarios exhibited strong decreasing trends in percent area ($\tau < -0.54$, $p < 0.001$). As expected, the magnitude of change correlates with the intensity of the climate scenario. The average percent decrease in area at the year 2100 among selected species is 3.1%

Table 2. Derived thermal ranges of 6 snapper–grouper fishery management plan species. Thermal ranges are the 5–95% percentile range of bottom temperatures associated with SERFS trap-video survey samples within the study area

Common name	Scientific name	Derived thermal range (°C)
Red grouper	*Epinephelus morio*	16.39–26.62
Red snapper	*Lutjanus campechanus*	16.33–27.38
Gag grouper	*Mycteroperca microlepis*	16.68–26.81
Red porgy	*Pagrus pagrus*	15.65–27.07
Vermillion snapper	*Rhomboplites aurorubens*	16.68–27.51
Greater amberjack	*Seriola dumerili*	18.11–27.42

under SSP2-4.5, 12.3% under SSP3-7.0, and 25.2% under SSP5-8.5. Notably, all scenarios follow similar trajectories from 2015 to 2050. After 2050, SSP5-8.5 starts showing higher rates of decrease in area compared to the other 2 scenarios. SSP3-7.0 starts to differ from the most conservative scenario in 2065. Decadal rates of percent change in area at the mid-century (2050–2060) and end-of-century (2090–2100) compared to the historical baseline show that all scenarios are associated with decreases in thermal habitat area. The projected rate of decrease in thermal habitat area mid-century (1950–1960) is 0.3, 0.79, and 1.13 for scenarios SSP2-4.5, SSP3-7.0, and SSP5-8.5. The rate of decrease is much larger at the end-of-century projections (2090–2100) at 1.03, 2.45, and 8.29 for respective model scenarios. End-of-century rates of decreased thermal habitat grow in magnitude as the scenarios become more severe.

3.4. Range edge

All species in this study are estimated to have a poleward shift in the northern range edge of their suitable thermal habitat under all 3 climate scenarios (Fig. 5). The mean northern range edge for all species combined historically (1985–2014) is 35.60° ± 0.08° N, and is 36.60° ± 0.39°, 36.81° ± 0.43°, and 37.37° ± 0.77° N under climate scenarios SSP2-4.5, SSP3-7.0, and SSP5-8.5 (2071–2100), respectively. All species' mean historical northern range edges occurred within 35° N, while under projected climate scenarios, they ranged from 35.96–37.08°, 36.18–37.29°, and 36.45–38.41° N for scenarios SPP2-4.5, SSP3-7.0, and SSP5-8.5, respectively. Red porgy are estimated to have the most significant poleward shift in thermal habitat by the end of the century based on adjusted bottom temperature, with a potential 2.71° shift by 2100 from historical ranges under SSP5-8.5. These changes in the northern range edge also signify potential changes in management areas. All species show potential to enter new management zones under the most severe scenarios. Red porgy show potential to increase into the northernmost management zone. Many species' suitable habitat could enter new zones even at the most conservative climate scenarios, including red porgy, red snapper, gag grouper, and red grouper.

4. DISCUSSION

To help inform future species distribution analyses, we use climate models to estimate the availability of suitable thermal bottom habitat, which strongly influences where species can persist. Understanding the potential strengths and weaknesses of these models, and how they correlate to real-world observations, is essential as reliance on them for management decisions and navigating climate impacts increases. Substantial differences between survey-based and CMIP6 bottom temperatures would have undermined the utility of projections, as a model unable to capture current thermal habitat conditions offers little confidence in projecting future distributions (Fig. 2). After adjusting for the discrepancy by decreasing CMIP6 bottom temperatures to more closely match observed conditions and species' derived thermal habitat associations, the climate model captured historical occurrences very similarly to the survey data. This provided confidence that the adjustment produced more accurate projections of thermal habitat shifts than using the uncorrected modeled temperatures.

Biases are widely known to occur in climate models but improve with each new iteration (Saba et al. 2016, Zhang et al. 2023). Models were bias-corrected using WOA data to remove some of the bias; however, temperature discrepancies with survey data persisted. There are many reasons why temperatures may differ, and we realistically should not yet expect a perfect match between observed data and climate model estimates. Firstly, we compared monthly mean model estimates to sampling events, a snapshot of a temperature in time and space. However, data like these illustrate the reality of most standardized surveys. Also, model resolution likely contributed to temperature disparity in several ways. Here, we use climate models downscaled to a 0.25 × 0.25° resolution; a finer scale would likely improve the match with observed temperatures. Bathymetry is a key factor in bottom temperature dynamics, influencing oceanic circula-

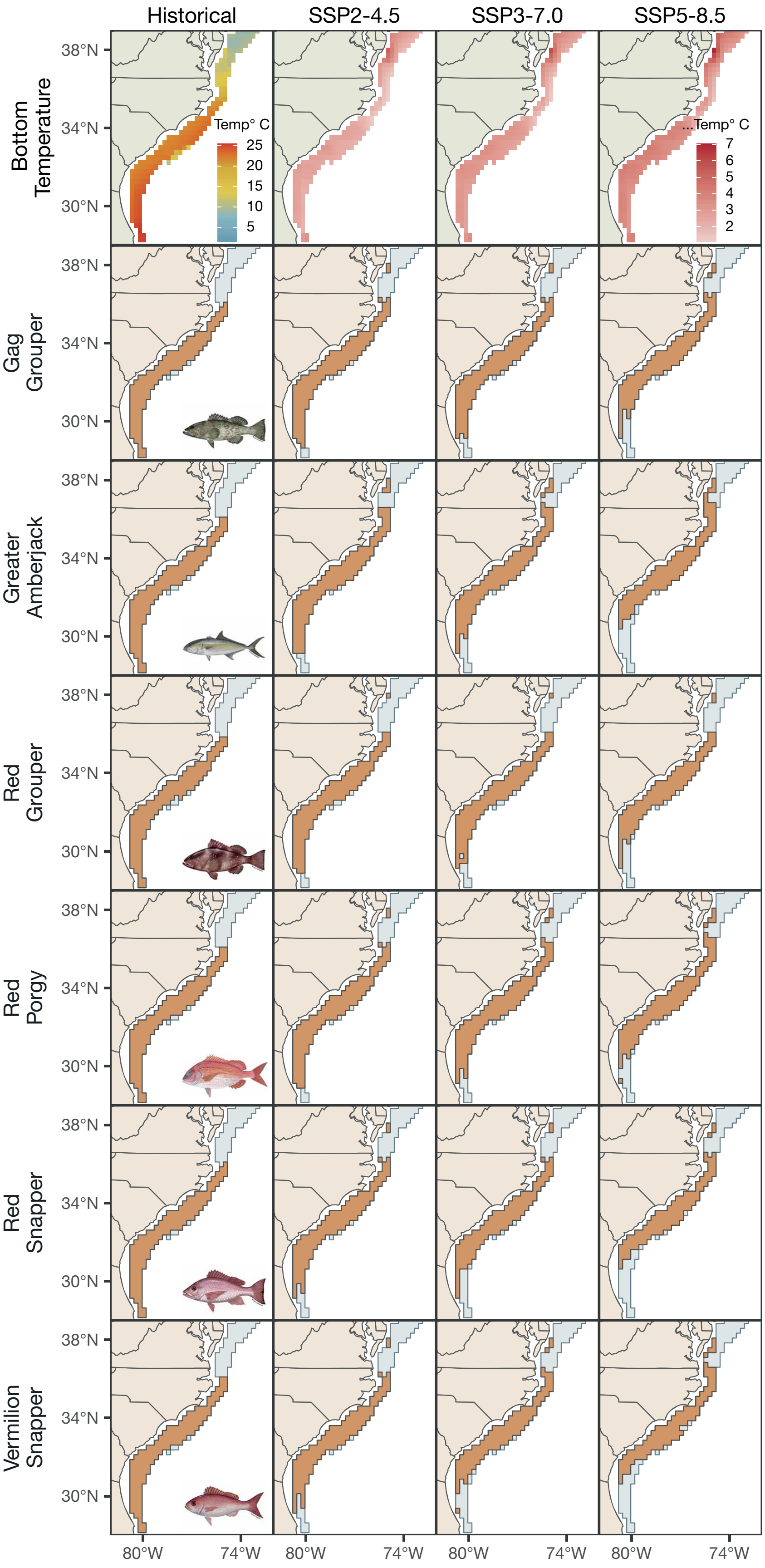

Fig. 3. Top row: historical bottom temperatures (1985−2014) from CMIPadj and the difference of degrees from historical for 3 climate scenarios (SSP2-4.5, SSP3-7.0, and SSP5-8.5) for end-of-century projections (2071−2100). All other rows show the grid cells (orange) with suitable bottom temperatures that fall within the species' derived thermal range for end-of-century projections (2071−2100)

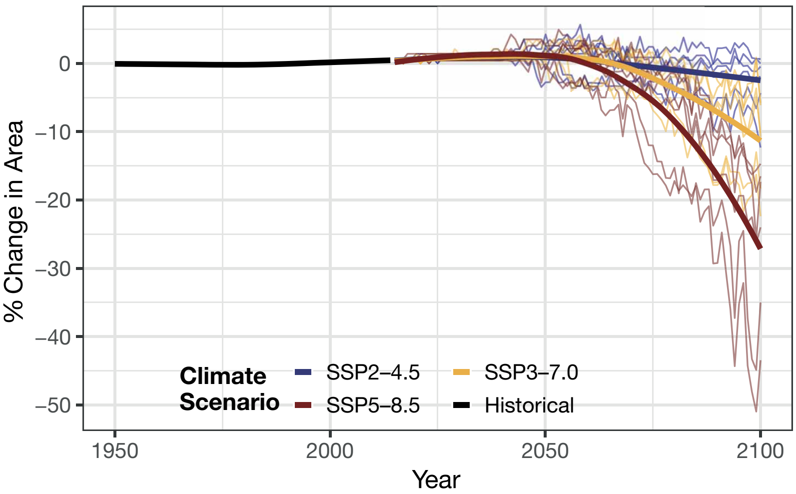

Fig. 4. Yearly percent change in the area (km^2) of suitable thermal habitat based on derived species thermal ranges for 3 climate scenarios compared to the historical mean from 1950—2014. Narrow lines: the 6 species in the study; bold lines: smoothed mean of all species

tion processes, including how waters vary in temperature and salinity mix. In the northeast, a persistent model bias has occurred because coarser climate models cannot resolve critical channels that carry cooler, fresher shelf waters into Gulf Stream waters; additional biases in the Gulf Stream location have made bottom temperature unreliable in the past. A finer-scale resolution that resolves key features of the bathymetric landscape provides more accurate estimates but is computationally expensive (Saba et al. 2016). Regional ocean models are one tool to increase the spatial resolution and address region-specific features, providing more realistic estimates of environmental conditions.

Many studies focus on comparing SST observations and CMIP6. These studies demonstrate that CMIP6 biases have significantly improved in replicating SST (Richter & Tokinaga 2020, Borchert et al. 2021, Yang & Huang 2023). Nonetheless, looking beyond SST and understanding the strengths and limitations is also necessary when exploring other variables essential to species distribution and life history to determine how well climate models estimate them. This study offers an early approximation for using the model to estimate a species' suitable thermal habitat. CMIPadj enabled the estimation of potential shifts in thermal habitat for several prominent snapper—grouper FMP species in the US South Atlantic. Several approaches to adjusting for the warm bias in the CMIP6 data could have been taken, such as decreasing the entire CMIP6 bottom temperature outputs by 1°C as undertaken in this study, increasing the thermal ranges of the species by 1°C, or extracting the bottom temperature from CMIP6 estimates at the respective time and location where species were observed in the survey data

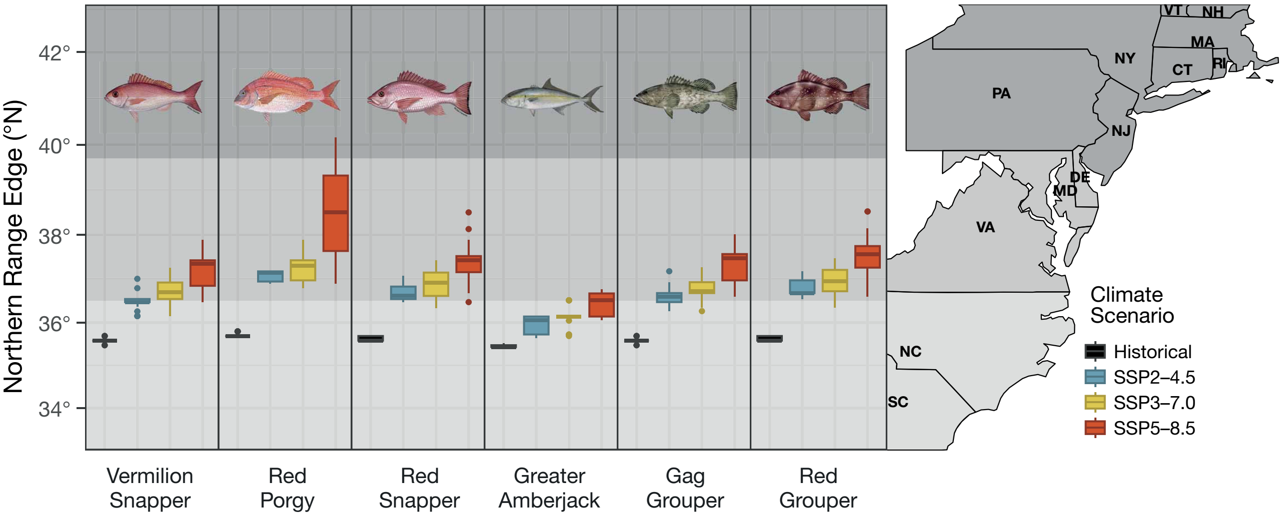

Fig. 5. Northern range edge of potential suitable thermal area calculated by the median latitude of the northern 5% of grid cells. Boxplots represent range edges historically (1985—2014) and under projected climate scenarios (2071—2100): bar: median; box: interquartile range (IQR); whiskers: max./ min. values within 1.5 × IQR above/ below box; dots: outliers. Shaded regions correspond with the states in the Southeast (light gray), Mid-Atlantic Bight (medium gray), and New England (dark gray) Fishery Management Councils

and deriving thermal ranges from those temperatures. Collecting temperatures at the time of sampling most realistically reflects the species' actual thermal range, which justifies the method used here; however, it required transforming the model data to coordinate with observed data. The problem arises as blanket transformations across large areas inevitably introduce errors and uncertainty, as temporal and spatial trends will likely have varying degrees of disparity. Here, the disparity was not uniform temporally, with warmer months having larger differences than cooler months, or spatially, with some areas having larger differences than others. Nevertheless, climate models are imperative to make predictions across the continuous spatial domain of the US East Coast. Many surveys along the East Coast are regional and exclusive to the northeast or southeast, with boundaries near Cape Hatteras, including the survey used in this paper to derive thermal ranges. Combining surveys, even those that follow similar sampling protocols, can be difficult without sampling overlap. Climate models provide continuous data for the entire study area and can be paired with additional data sets for more robust analyses. Problems still persist with acquiring robust biological data, but advanced modeling techniques paired with these climate models are helping to address the issue. Ultimately, this study helped illustrate areas for improvement in incorporating climate estimates with ecological data in this region.

Decreased thermal habitat will make it less likely that the numerous habitat requirements of a species will occur in the same space or time and could require species to settle for a less ideal habitat, potentially resulting in decreased abundance. As the climate changes, numerous factors can influence the ability of a species to use areas with temperatures within its thermal range. If the necessary bottom temperature no longer coincides with suitable physical bottom habitat, or if these temperatures occur in areas obstructed by barriers to movement, those thermal habitats may become inaccessible to the species. Additionally, specific required temperatures may no longer be associated with particular life history events, such as reproduction. For example, red grouper spawning is most abundant between temperatures of 19 and 21°C, indicating that temperatures may be a critical physiological trigger for essential biological events that may be affected by climate change (Moe 1969, Johnson et al. 1998). A higher magnitude of warming bottom temperatures occurs in higher latitudes, especially nearshore. However, potential thermal habitat loss occurs most often in the lower latitudes off the coast of Florida, as temperatures are projected to increase beyond these species' estimated thermal ranges. Movement farther north would make it more costly for southern fishermen to fish these species and could put them out of reach for many, especially recreational anglers. Moreover, not all habitats are created equal, so that equivalent gains in thermal habitat at northern latitudes may not necessary offset losses at southern latitudes in terms of species productivity. Habitat loss is a leading driver in decreased biodiversity in terrestrial, coastal, and marine ecosystems; however, it has been less of a focus in marine systems (Beatley 1991, Airoldi et al. 2008).

This study suggests that all species would have similar northward trajectories in their thermal habitat by the end of the century; however, the magnitude of those changes varied. As these species all belong to the snapper—grouper FMP, a similar trend is not surprising. However, a more diverse selection of species, including pelagic and estuarine species, may yield more varied results, significantly impacting overall species assemblage. Novel species assemblages can occur due to many processes influenced by temperature such as prey availability and competitive or predation interactions. A few broad patterns expected from novel species assemblages in an open system due to warming include decreased body sizes, dominance by generalist species, and shifts in species interaction strengths (Lurgi et al. 2012). Generalists will likely deal with novel changes more efficiently, while specialists will have more difficulty finding appropriate conditions. Changes in species assemblages could lead to conflicting trends in responses to environmental variables if a significant ecological impact occurs. For example, a release from a dominating predator shifting poleward may increase a prey's abundance in lower latitudes (Pinsky et al. 2013). Changes in predator responses may provoke a top-down cascade, and impacts on primary producers can activate bottom-up responses (Jones & Driscoll 2022). Explicitly incorporating species assemblage analysis and the associated indirect effects of climate change will produce a broader understanding of species distribution shifts.

Total thermal habitat is expected to increase minimally for these species until mid-century. Thereafter, warming trends and associated decreases in thermal habitat accelerate toward the end of the century, though at significantly different rates among scenarios. The ongoing rate of change remains relatively minor throughout the projection period under the mildest climate scenario. However, it increases several-fold between the mid- and end-of-century periods in the other scenarios. This suggests that ongoing climate mitigation efforts could reduce the severity of impacts and decelerate the rate of change, providing more time to implement or adjust management strategies. This trend is consistent with previous studies that note the increased rate of warming at Long-Term Ecological Research (LTER) sites as time goes on, with regions warming at least 2–3 times faster in 1980–2020 than in 1930–2020 (Jones & Driscoll 2022). Several studies show that all species may not move poleward or to deeper waters as expected under climate change (Parmesan & Yohe 2003, Perry et al. 2005, Pinsky et al. 2013, Cao et al. 2024). However, in this study, all species' northern range edges of suitable thermal habitat are estimated to shift poleward, if even by a marginal amount. Many species' thermal habitats could move into novel management areas, where suitable temperatures were previously absent.

Building upon this study, we hope to address many themes in marine responses to climate change for target species in US Atlantic waters. First, considering regional differences is essential to achieving region-specific responses. Region-specific characteristics can alter even general trends; for example, species cannot shift their distribution poleward in the Gulf of Mexico/Gulf of America due to physical barriers, limiting poleward movement trends (Jones & Driscoll 2022). Regional consideration may also be important in the climate models used. Regional ocean models that have a higher resolution, better resolve the nearshore coastal regions, and more accurately capture detailed bathymetry will support increasingly detailed analysis and allow for more precise management questions. Next, broadening the types of climate scenarios, including those incorporating mitigation efforts, could help identify thresholds that may be apparent in a species' response. Further, we focused here on yearly averages over a broad time scale, although seasonal temperature patterns, which were not considered, could also be important.

Overall warming and increased maximum temperatures indicate that most species in this study may be excluded from large sections of Florida; however, more realistically, they are likely to be able to occupy more of those waters in cooler months and less in warmer months than the yearly average provided here. Life history events like spawning further complicate the picture. Finally, climate models span varying time scales, including short-term seasonal and decadal models estimating periods from a few months to 10 yr and long-term models producing end-of-century projections. Here, we focused primarily on end-of-century projections; however, from a management perspective, short-term estimates are valuable for supporting near-term management decisions as well as informing long-term objectives (Holsman et al. 2019). Still, long-term estimates help us understand the range of possible changes, evaluate how current policies may perform under climate change, and help garner support for policy change before intervention is needed (Pinsky et al. 2013, Holsman et al. 2019). Combining results from both short-term and long-term models will enable the development of more robust management strategies that can accommodate a range of outcomes, thereby addressing and mitigating the inherent uncertainty present in models (Holsman et al. 2019, Karp et al. 2019).

A multitude of biological, physical, and ecological factors will influence the actual changes in species distributions across their various life stages, all encompassed in uncertainty. This study aimed to lay the foundation for more comprehensive and complex investigations in the future using regional ocean models by gaining insight into how available species sampling data and associated physical variables compare with climate model estimates and their accompanying results. Beyond temperature, integrating variables like salinity, pH, dissolved oxygen, and co-occurrence of prey and predators together with physical habitat characteristics would help to define potential habitat areas from those where species could realistically occur. Climate vulnerability analyses (CVA), like those in the US Northeast Continental Shelf, South Atlantic, and the Gulf of Mexico/Gulf of America, assess life histories to determine how vulnerable species are within a region and will be indispensable to inform future climate change response studies (Hare et al. 2016, Quinlan et al. 2023, Craig et al. 2025). Unfortunately, even with CVAs, it can still be challenging to determine ranges, limits, and critical information for a species, especially region-specific, to input into models to predict species distributions.

The Fishery Management Councils along the US East Coast acknowledge the importance of addressing climate change and stock distribution issues and therefore created the East Coast Climate Change Scenario Planning potential action menu to lay out the next steps of fishery management for the region (Mid-Atlantic Fishery Management Council 2023). This action menu covers several themes, including cross-jurisdictional governance, managing under increased uncertainty, and data sources and partnerships. Managing under increased uncertainty due to climate change highlights the need for analyses covering a range of possible outcomes. Future studies should prioritize improvements in these areas and carefully consider relevant factors to meet these challenges. Including ecosystem-based elements is essential to effectively manage species in a changing environment, as species inhabit a dynamic community influenced by more than just physical variables. However, as the focus shifts from physical to ecological factors, the certainty of our results may diminish (Ducklow et al. 2022). While this study highlights the strengths and limitations of climate models in projecting thermal habitat shifts, advances using robust regional ocean models will support more reliable forecasts of species distributions and ultimately provide critical insights for management.

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