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Journal

Global Change Biology, 28(23)

ISSN

1354-1013

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Publication Date

2022-12-01

DOI

10.1111/gcb.16415


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RESEARCH ARTICLE

Distribution and predicted climatic refugia for a reef-building cold-water coral on the southeast US margin

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Funding information

Bureau of Ocean Energy Management, Grant/Award Number: M17PC00009

Abstract

Climate change is reorganizing the planet's biodiversity, necessitating proactive management of species and habitats based on spatiotemporal predictions of distributions across climate scenarios. In marine settings, climatic changes will predominantly manifest via warming, ocean acidification, deoxygenation, and changes in hydrodynamics. *Lophelia pertusa*, the main reef-forming coral present throughout the deep Atlantic Ocean (>200m), is particularly sensitive to such stressors with stark reductions in suitable habitat predicted to accrue by 2100 in a business-as-usual scenario. However, with new occurrence data for this species along with higher-resolution bathymetry and climate data, it may be possible to locate further climatic refugia. Here, we synthesize new and published biogeographic, geomorphological, and climatic data to build ensemble, multi-scale habitat suitability models for *L. pertusa* on the continental margin of the southeast United States (SEUS). We then project these models in two timepoints (2050, 2100) and four climate change scenarios to characterize the occurrence probability of this critical cold-water coral (CWC) habitat now and in the future. Our models reveal the extent of reef habitat in the SEUS and corroborate it as the largest currently known essentially continuous CWC reef province on earth, and also predict abundance of *L. pertusa* to identify key areas, including those outside areas currently protected from bottom-contact fishing. Drastic reductions in *L. pertusa* climatic suitability index emerged primarily after 2050 and were concentrated at the shallower end (<~550m) of the regional distribution under the Gulf Stream main axis. Our results thus suggest a depth-driven climate refuge effect where deeper, cooler reef sites experience lesser declines. The strength of this effect increases with climate scenario severity. Taken together, our study has implications for the regional and global management of this species, portending changes in the biodiversity reliant on CWC habitats and the critical ecosystem services they provide.

KEYWORDS

climate change, cold-water coral, coral reef, deep-sea, habitat suitability model, *Lophelia pertusa*, species distribution model

1 | INTRODUCTION

Climate change is affecting global biodiversity by reorganizing species distributions. Spatial refugia (*sensu* Keppel & Wardell-Johnson, 2012) from climate change can dictate complex distributional legacies, which leave behind evidence of faunal origins and climate-induced fluctuations by selecting for resilience or by creating faunal patchworks through extirpation (Carpenter et al., 2001; Fernandez et al., 2021; Horne, 1999; McClain & Hardy, 2010). Therefore, locating and protecting refugia from additional human pressures is imperative to climate-smart management that is proactive against future changes in biodiversity (Arafah-Dalmau et al., 2021; Queirós et al., 2021).

In the marine realm, climate change manifests primarily through warming, acidification, deoxygenation, and alterations in hydrodynamics affecting food supply (Doney et al., 2012; Levin & Bris, 2015). In surface waters, models predict large expanses with either novel or disappearing climates by 2100 (Dixon et al., 2022; Lotterhos et al., 2021), yet little is known about no-analogue climates in the deep ocean (>200m depth) where most of the planet's habitable area exists. However, *in situ* trends (Desbruyères et al., 2016; Johnson et al., 2014; Meinen et al., 2020), and climate models (Morato et al., 2020; Sweetman et al., 2017) suggest rapid ocean change will accumulate at the seafloor this century. Many deep-sea ecosystems may soon experience oceanographic conditions with only distant spatial or temporal analogues. This can cause mobile species' distributions to move deeper toward cooler waters (Chaikin et al., 2021; Pinsky et al., 2013) and reorganization and compression of ecological communities (Chu & Tunnicliffe, 2015; Gasbarro et al., 2019; Mora et al., 2013; Sato et al., 2017). The temporal scales of ocean change make it less likely that slow-growing sessile species will be able to track their climatic niche via larval dispersal.

Amongst the most at-risk taxa are cold-water corals (CWCs), which form the basis for Vulnerable Marine Ecosystems including coral reefs and gardens (FAO, 2009). *Lophelia pertusa* (proposed revision to *Desmophyllum pertusum*; Addamo et al., 2016) is the most well-known reef-building coral in the deep ocean. It is found in every major ocean basin and as an autogenic habitat engineer creates coral reefs and carbonate mounds of varying sizes that are formed over thousands of years by generations of coral growth/death leading to mound build-up by coral skeleton and baffled sediment (Raddatz et al., 2014). This species has a long pelagic larval duration, and these planktotrophic larvae readily cross density gradients and may even spend time in the photic zone, suggesting an ability to disperse over great distances (Larsson et al., 2014; Strömberg & Larsson, 2017).

Notable *L. pertusa* reefs have been found in the South Atlantic on seamounts (Bridges et al., 2021), on the Brazilian (Cavalcanti et al., 2017), and west African margin (Hanz et al., 2019; Hebbeln et al., 2020); in the North Atlantic off of Florida (Reed et al., 2006) and Greenland (Kennington et al., 2017), Norway (Fossa et al., 2002), Canada (Buhl-Mortensen et al., 2017), the UK (Howell et al., 2011), and the Mediterranean (Carlier et al., 2009; Freiwald et al., 2009; Mastrototaro et al., 2010). These mounds can cluster

into large mound provinces covering up to thousands of square kilometers in areas where oceanographic conditions allow, including in the Gulf of Mexico (Hebbeln et al., 2014; Roberts & Kohl, 2018), Northeast Atlantic (Dullo et al., 2008; Flögel et al., 2014; Howell et al., 2011; Kenyon et al., 2003; Masson et al., 2003) and Northwest Atlantic (Reed et al., 2006). These CWC mounds and the living reefs that often top them are remarkable both in their spatial extent and their functioning as important hotspots of biodiversity (Henry & Roberts, 2017; Roberts et al., 2006) and nutrient recycling (Cathalot et al., 2015; van Oevelen et al., 2009). Thus, accurate predictions of their expanse are needed to improve our understanding of the function of ecosystem services of the global ocean.

The Blake Plateau is a large depositional feature on the Southeast US (SEUS) margin, shaped by the influence of the Gulf Stream and associated eddies. Vibrant CWC ecosystems flourish underneath the Gulf Stream due to elevated currents and pulses of fresh phytodetritus to the seafloor (Mienis et al., 2014). Since 2018, numerous research and exploratory expeditions to CWC habitats in this region have built upon historical baseline surveys (Reed et al., 2006; Stetson et al., 1962) with mapping efforts revealing the largest nearly continuous mound province on Earth with tens of thousands of apparent CWC mounds extending over approximately 700 km from offshore Florida to Virginia (Sowers, 2020), including a remarkable coral reef complex over 200 km in total length off of Charleston, South Carolina herein referred to as the "Richardson Reef Complex" (Figure 1). Coral rubble appears to be the dominant substrate on even the smallest mounds in the region, indicating CWC habitability at some point in the Holocene, if not currently. It is unknown how many of the mounds are topped with living coral and, if so, how much.

These sites face imminent climate threats, as climate change causes the Gulf Stream to deliver increasingly warm and acidic subtropical waters to their depth range (~400–900 m) (Saba et al., 2016) but potentially at lower velocities (Boers, 2021; Caesar et al., 2021), simultaneously lowering the rate of food delivery to less optimal levels. However, all CWC ecosystems of this region may not be affected equally by climatic changes, as many shallower sites near the shelf break sit directly underneath the Gulf Stream's velocity core while deeper sites on the eastern Blake Plateau are affected more intermittently by Gulf Stream meanders. Paleoecological reconstructions of past climates from a Cape Lookout coral mound indicate that CWCs in the SEUS proliferated most recently following hydrographic changes in the Gulf Stream system ~7 kya that changed the oceanographic conditions experienced by CWCs (Matos et al., 2015), suggesting that these ecosystems are sensitive to changes in climate.

Here, we present a novel biogeographic, geomorphological, and climatic data synthesis to build ensemble, multi-scale habitat suitability models for *Lophelia pertusa*. We project these models onto the present-day SEUS margin and two future timepoints (2050, 2100) under four climate change scenarios to characterize the extent of critical CWC ecosystems in the region and test several hypotheses regarding their future. First, our models test whether the smallest of the coral mounds mapped in the region

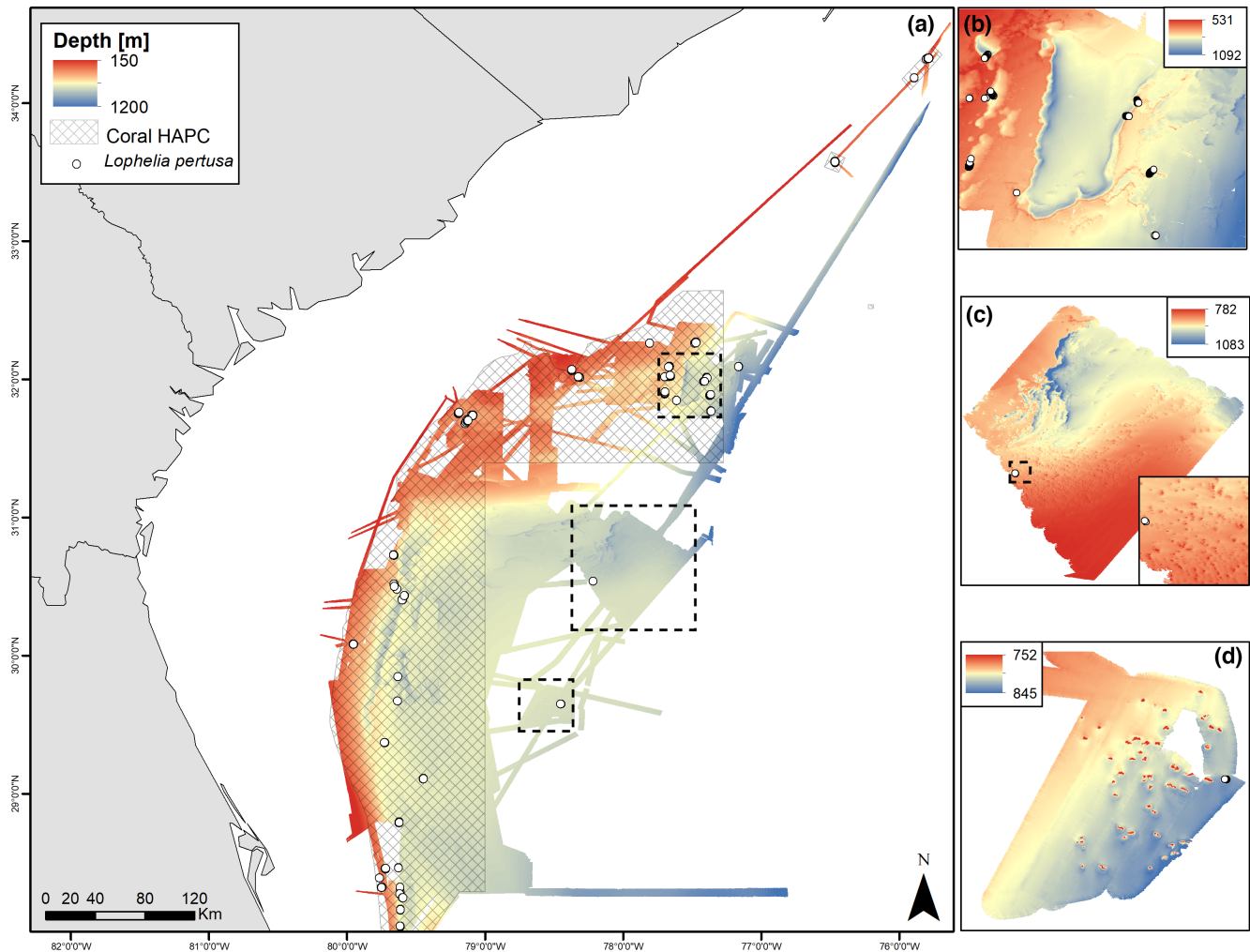


FIGURE 1 (a) *Lophelia pertusa* sites (white points) and coral Habitat Area of Particular Concern (hatched area) on the SEUS margin overlain on high-resolution bathymetry compilation of Sowers (2020). Notable seafloor features on the deep, eastern portion Blake Plateau are outlined (dashed boxes) and include the (b) Richardson Reef Complex (c) Central Plateau Mounds (with additional inset highlighting many small mounds) and (d) Blake Plateau Knolls sites. Note the different depth scales used for each inset to highlight local geomorphology (e.g., mounds) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

are likely to contain *L. pertusa*, and whether terrain with high habitat suitability index (HSI) scores will be concentrated on one or more landforms associated with these mounds (i.e., peaks, ridges, and slopes). We also test whether greater declines in climatic suitability index (CSI) scores occur in more severe emissions scenarios, and whether the time of emergence for notable declines in CSI will be before 2050. Finally, we test for regional disparities in climate change outcomes by depth, predicting that shallower populations will face greater CSI and abundance declines due to their proximity to the Gulf Stream, with deeper sites serving as spatial climate refugia with more modest changes. We also calculate climate change velocities to test this depth-disparity hypothesis, predicting higher velocities at shallower seafloor depths and isotherm trajectories will show a general trend toward deeper locations. Taken together, our results provide timely information required for both mitigation and adaptive spatial management of these ecosystems and the critical services they provide.

2 | MATERIALS AND METHODS

2.1 | Occurrence data

L. pertusa occurrence points were generated from submersible dive imagery from 11 dives completed in 2018–19 (Table S1.1). Dive video was annotated for *Lophelia* presence and georeferenced by timestamp. Additional presence points were downloaded from the NOAA Deep-sea Coral Research & Technology Program database (v102020; <https://deepseacoraldata.noaa.gov/>). Points with location error >1000m were removed, which generally excludes older, less reliable records (e.g., trawl records) that likely have lower fidelity to gridded environmental data. All points falling within a grid cell were merged to curtail pseudoreplications.

Abundance (= % cover) data were generated from one-minute video segments during the above dives. Video segments were chosen where the submersible was transecting the seafloor and image

quality was high (i.e. not obscured by the submersible or water column turbidity). Five random screenshots were taken for each segment by selecting random numbers between 1 and 60 (1 representing the first second of the 1-minute segment), and then 50 random points overlain on each screenshot in ImageJ software using a custom-written macro. Points falling on live *Lophelia* were counted, giving an estimate of percent cover for each screenshot and mean/standard deviations for each segment. In total, 516 segments were used to train abundance models (Table S1.1).

2.2 | Terrain and climate data

We used the bathymetric dataset covering much of the Blake Plateau generated by Sowers (2020) to create bathymetric terrain variables at the highest available resolution for this area ($3.5 \times 10^{-4}^\circ$ or ~ 35 m). Slope, aspect [both cosine (N-S) and sine (E-W)], three types of curvature, fine (100 m) and broad-scale (1000 m) bathymetric position indices (BPI) comprised the initial set of terrain variables (Table 1). BPI was calculated with an inner radius of one cell. All terrain variables were generated from the bathymetric data with Benthic Terrain Modeler v3.0 (Walbridge et al., 2018) in ESRI Arcmap version 10.8. In addition, we used a 'bathymorphon' (underwater landform) classification scheme (Sowers, 2020) of valley, flat, slope, ridge, and peak bathymorphons *post-hoc* to test whether *L. pertusa* occurrence probability was higher on particular bathymorphons. This classification was achieved using the Bathymetry- and Reflectivity-based Estimator for Seafloor Segmentation (Masetti et al., 2018) using an inner and outer radius of one and six cells, respectively, and a flatness parameter of 1.5° .

A number of variables were used to model climatic suitability for *L. pertusa* (Table S1.2). Global Atmosphere/Ocean General Circulation Model data were downloaded in four-dimensional (X, Y, depth, time) netCDF format from the Earth System Grid Federation as either monthly or annual means. All data come from Climate Model Intercomparison Project 6 (CMIP6; Eyring et al., 2016), which includes higher-resolution models than those used to build basin-scale models for *L. pertusa* based on CMIP5-era data (e.g., Morato et al., 2020). CMIP6 data included the variables pH, mean dissolved oxygen, and export carbon from the high-resolution implementation of the Max Planck Institute's MPI-ESM1-2 model (Müller et al., 2018). Bottom temperature data were available from several modeling groups and thus a multi-model ensemble was used (see Table S2 for climate metadata).

CMIP6 models used in this study were forced under Shared Socioeconomic Pathways (SSPs). These SSPs range from the SSP1-2.6 "Sustainable Future" to the SSP5-8.5 "Business As Usual" scenarios with two intermediate pathways (SSP2-4.5, SSP3-7.0). The SSPs incorporate revised emission and land use pathways than those in the Representative Concentration Pathways of CMIP5 (see O'Neill et al., 2016; Riahi et al., 2017). Data for each SSP were averaged into current (1995–2014), mid-century (2031–2050), and end-of-century (2081–2100) timepoints, giving a rough estimate of the time of emergence for suitability changes. Climate Data Operators (Schulzweida, 2019) was used to convert data from each model to annual means where necessary, re-grid from curvilinear to lat/long grids, and to extract bottom-most (= benthic) data at their native resolution (Table S1.2). These data were cropped and re-gridded at 0.007° (~ 700 m) for the SEUS using bilinear interpolation.

TABLE 1 Variables included in habitat suitability models

Variable	Short_name	Type	Nominal resolution	Units	Reference(s)
Depth	Depth	Terrain	35 m	m	Sowers (2020)
Bathymorphon	Bathymorph	Terrain	35 m	Landform	Sowers (2020)
Slope	Slope	Terrain	35 m	°	—
BPI_1000m	BPI_1000m	Terrain	35 m	—	—
BPI_100m	BPI_100m	Terrain	35 m	—	—
Aspect (sin)	Aspect_sin	Terrain	35 m	°	—
Aspect (cos)	Aspect_cos	Terrain	35 m	°	—
Curvature (general)	Curv_gen	Terrain	35 m	—	—
Curvature (plan)	Curv_plan	Terrain	35 m	—	—
Curvature (profile)	Curv_prof	Terrain	35 m	—	—
Temperature	Temp	Climate	7–50 km	°C	Müller et al. (2018); Gent (2020); Roberts (2017); Alexander et al. (2020)
pH	pH	Climate	50 km	pH	Müller et al. (2018)
Dissolved oxygen	DO	Climate	50 km	$\mu\text{mol L}^{-1}$	Müller et al. (2018)
Export carbon	Expc	Climate	50 km	$\text{mol m}^{-2} \text{ s}^{-1}$	Müller et al. (2018)

Note: All terrain variables were derived from [1]. Variables selected for final models are in bold.

CMIP6 bottom temperature data for the SEUS were compared to data from Alexander et al. (2020)'s dynamically downscaled model data that covered the study area with comparable data for the historical and 2100 business-as-usual scenarios at a higher native resolution (see Supplementary Materials 2). We chose to not include the Alexander et al., (2020) temperature data in the models due to the differences in methodology and native resolution between these and CMIP6 data, and thus used the Alexander et al., (2020) data to explore possible biases in the CMIP6 data for the region. We did, however, use these data to calculate distance-based climate change velocity, i.e. the distance to the geographically closest thermal analogue in the SEUS in the year 2100 using the R package 'VoCC' (Molinos et al., 2019) due to its higher native resolution. A climate tolerance of 0.25°C and margin-wide search radius was used to find analogous cells. Thermal trajectories were overlain on the velocity map to visualize isotherm movements.

2.3 | Habitat suitability and abundance modeling

Variables with Variance Inflation Factors >5 and/or highly correlated (Pearson's $R > 0.9$) variables were sequentially removed before the modeling process to minimize multicollinearity (Figure S3.1). The final variable set (Table 1) still included a few correlated variables (temperature, pH, O_2) that were included in the model for their ecological relevance to *L. pertusa* (Brooke et al., 2013; Georgian, DeLeo, et al., 2016; Hennige et al., 2014).

A multi-scale framework was used to model the distribution of *L. pertusa* to incorporate the variation in the species' ecological response to both terrain and climate at relevant scales. That is, we captured the fine-scale (~35 m) landscape morphology that is fundamental to predicting CWC distributions by proxying hydrodynamics (Rengstorf et al., 2013), while separately modeling climatic suitability at a downscaled resolution (~700 m). Suitability of both terrain and climate is a prerequisite for *L. pertusa* presence, and so decreasing the terrain resolution to match the climatic data would smooth over important information and decrease model precision (Miyamoto et al., 2017). The climatic niche of *L. pertusa* was first constructed for the whole of the North Atlantic on the native resolution grid, then projected onto each scenario climate grid for the SEUS ($n = 9$), as the entirety of their niche was not represented in the SEUS. For example, pH is relatively high in the region. Thus, SEUS data would not capture a lower limit for *L. pertusa* suitability and a model trained solely on current SEUS climatology would not predict an influence of pH declines in future scenarios, despite the known relevance of pH in this range to the species' distribution and survival (Davies et al., 2008; Georgian, DeLeo, et al., 2016; Hennige et al., 2020; Lunden et al., 2014; Morato et al., 2020). Thus, there may be regional variability in *L. pertusa* climate-stressor tolerance in the SEUS that was not captured in our models (e.g., Georgian, Dupont, et al., 2016).

Suitability scores were computed with one regression [Generalized Linear Models (GLM)] and two machine-learning algorithms [Random Forest (RF), Gradient Boosting Machines (GBM)]. For both the terrain

and climate models, three presence/background replicates were run with 10,000 pseudoabsences each selected from <1000 km from presence points. This distance was chosen to reflect this species' capability of long-distance dispersal (Strömberg & Larsson, 2017). Models were evaluated with repeat split-sample cross validation (70–30 testing/training splits). Five evaluation runs were computed for each pseudoabsence set and algorithm combination for a total of 45 models for each of terrain and climate. Response curves were generated according to Elith et al. (2005) and inspected for biologically plausible responses for each algorithm. Then, we calculated ensemble means and variances from model runs across algorithms to minimize individual model biases (Buisson et al., 2010). Individual and ensemble model discrimination accuracy was assessed with True Skill Statistic (TSS; Lawson et al., 2014) and area under the Receiver Operating Characteristic (ROC) metrics. Relative variable importance in the models was estimated by the variable randomization approach recommended by Guisan et al., (2017). In addition, the degree to which the models make predictions outside of the environmental envelope of present-day *L. pertusa* was assessed using the Extrapolation Detection Tool of Bouchet et al. (2020).

Projected scenario climatic suitability index scores were compared to scores from the present-day model and suitability scores at known *L. pertusa* sites were regressed against depth to test the hypothesis that the deepest, eastward sites containing *L. pertusa* may act as climate refugia. The combined terrain-climatic suitability scores were then used to model the areal percent cover for each scenario using the Random Forest regression as in Hill et al., (2017). All computations were performed in R version 4.0.5 (R Core Team, 2021) on Temple University's High-Performance Computing server cluster. The R packages 'biomod2' (v. 3.5.1; Thuiller et al., 2020) and 'randomForest' (Liaw & Wiener, 2002) were used for terrain/climatic suitability and abundance modeling, respectively.

3 | RESULTS

3.1 | Terrain suitability

GBM, GLM, and RF runs were incorporated into the ensemble terrain model, with TSS and ROC scores showing excellent discrimination capacity (both >0.9 on average) in recreating the *L. pertusa* distribution (Figure 2). Broad (1 km) BPI, slope, and depth were respectively the most important variables in the models, with high BPIs and slopes favored along with a depth range of ~200–900 m (Figure 3).

Broad expanses of habitat with high HSI were predicted by the model (Figure 4a), including the ~200 km length of the Richardson Reef Complex (Figure 4b), notable mound provinces with many mounds topped by live *L. pertusa* (Figure 4c, d), and ridge and terrace features along the southwestern portion of the mapped area (Figure 4a). A portion of this habitat fell outside of the South Atlantic Fisheries Management Council's 'Stetson Banks-Miami Terrace Habitat Area of Particular Concern' (HAPC) (Figure 4a). Flats and valleys typically had lower HSI scores, while peaks, ridges, and

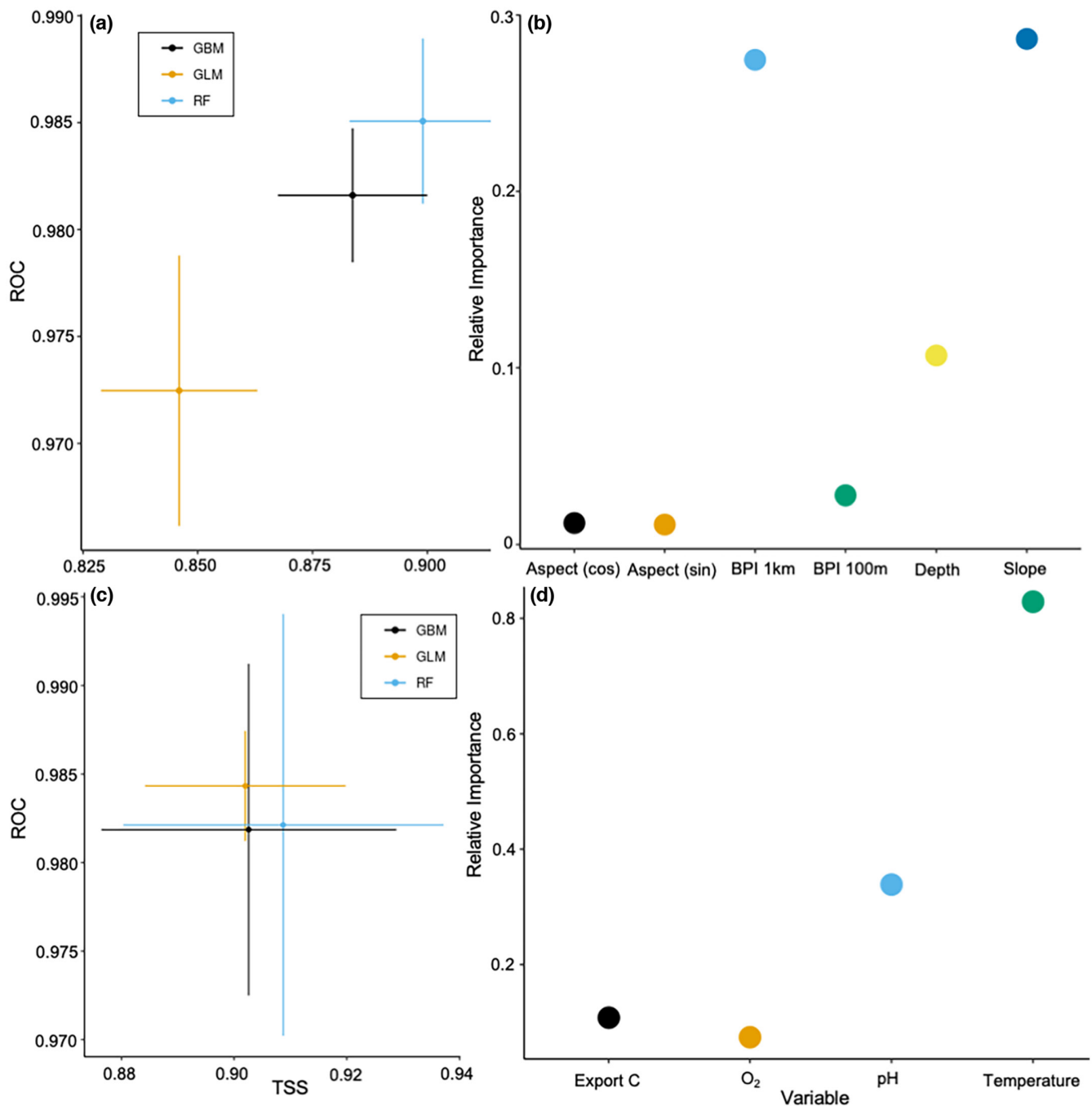


FIGURE 2 Receiver operating characteristic and TSS scores (a, c) and variable importance (b, d) for terrain-based suitability models (a, b) and climatic suitability models (c, d) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

slopes each contained a sizeable portion of the areas with HSI > 0.75 (Figure 5). Peaks, which included the tops of mounds of all size ranges shown in Figure 1, generally had the highest HSI.

3.2 | Climatic suitability

Notable changes in temperature and pH at *L. pertusa* sites were observed in the CMIP6 data by 2100, with more modest changes

in dissolved oxygen and export carbon (Figure 6). In each scenario besides SSP 1–2.6, all sites with current *L. pertusa* populations experienced pH levels below which there is an analogue in the present-day SEUS. These conditions are highly unfavorable for the species based on the climatic response curves for the N. Atlantic (Figure 7). Only RF and GBM runs algorithms were used in the ensemble model due to biologically implausible responses in the GLM runs (Figure S3.5). Despite this, TSS and ROC scores were > 0.9 (Figure 2c, d).

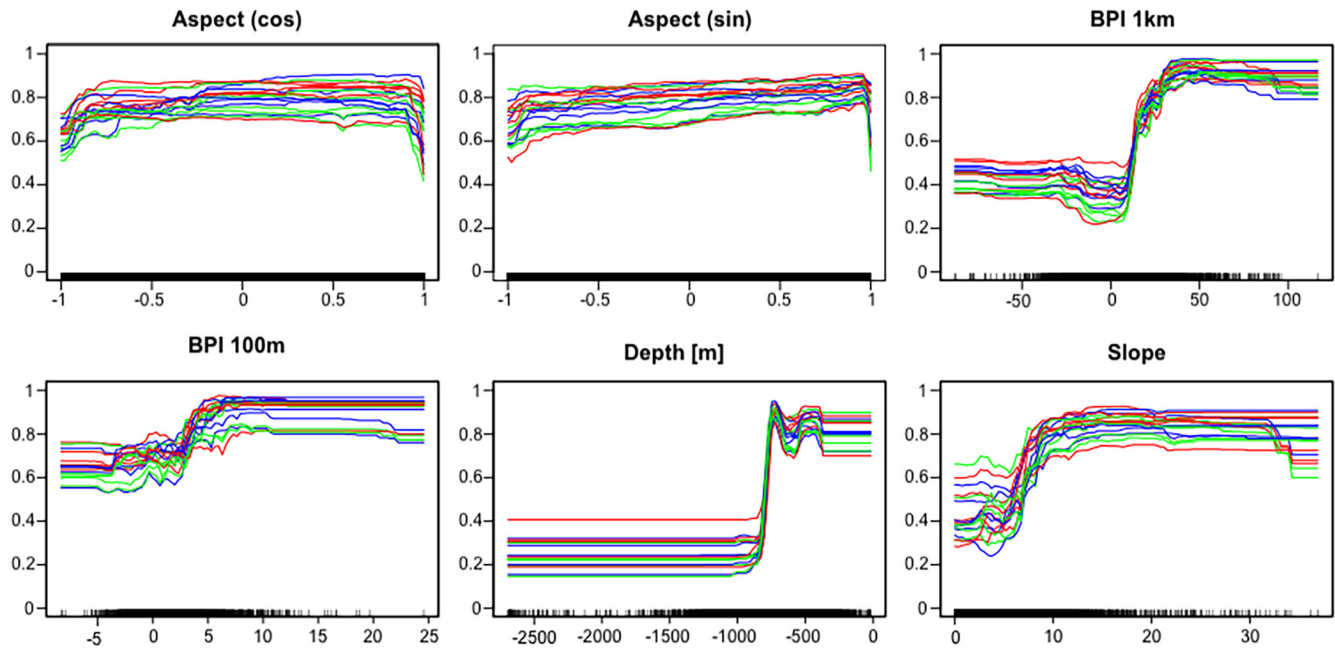


FIGURE 3 Terrain response curves of *Lophelia pertusa* from Random Forest model runs. Scores for each model run (lines) and plotted across the range of each variable, with higher scores indicating suitability [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

Ensemble projection onto the SEUS showed that almost all of the region from the shelf break to 1000m currently has high climatic suitability index (CSI) scores (Figure 8). This was not the case in the climate change scenarios, however, which displayed spatiotemporal patterns of CSI declines (Figure 9). In the 2050 timepoint, ~20% declines in CSI on the Blake Plateau were apparent near the shelf break and appeared regardless of SSP. Lesser CSI declines extended onto the Blake Plateau in a similar way in all scenarios, with the southernmost Blake Plateau a notable exception. At the 2100 timepoint, CSI declines were more severe and widespread. Near the shelf break, 80% declines were projected, and the extent of these declines increased with increasing emissions in the SSPs. In SSP1-2.6, however, the spatial extent and severity of these declines was notably lesser than the other three scenarios (Figure 9). A spatial pattern emerged with CSI declines significantly correlated with depth at both known *L. pertusa* sites (Linear Regression, $p < .05$; Figure 10a) and peak grid cells (Linear Regression, $p < .05$; Figure 10b). The slope and variance explained by this relationship increased in each successively higher emissions scenario. At known *Lophelia* sites the regression slopes (i.e., the change in $\Delta\text{CSI m}^{-1}$ depth) ranged from -2×10^{-4} in SSP 2-4.5 to -5.5×10^{-4} in SSP 5-8.5 while R^2 values in those were, respectively, 0.10 and 0.51; this corresponds to 2 and 5.5% worse respective declines in occurrence probability for every 100m in depth. At all 'peak' bathymorphon grid cells ($n = 262,822$), the regression slopes ranged from -2.8×10^{-4} in SSP 1-2.6 to -7.3×10^{-4} in SSP 5-8.5 while R^2 values in those respectively were 0.09 and 0.72; this corresponds to 2.8 and 7.3% worse respective declines in occurrence probability per 100m depth. A notable exception to this pattern occurred in SSP1-2.6 at known *Lophelia* sites where the relationship between depth and CSI declines were not significant ($p > .05$).

3.3 | Abundance of *Lophelia pertusa*

We found a wide range of coral cover in 1-minute video segments from sites on the SEUS margin, ranging from zero to 80.4% cover at Blake Plateau Knolls (see Figure 1d). Observed abundances were correlated with those predicted by terrain-climate suitability indices (RF Regression; $p < .01$, $R^2 = 0.51$, RMSE = 9.9; Figure 11a). Sites predicted to have $> \sim 20\%$ coral cover cease to exist in SSP5-8.5, but are still present in SSP1-2.6 (Figure 11b). The sites retaining relatively high cover were concentrated on the eastern Blake Plateau, with the Richardson Reef Complex maintaining the largest areal extent of high cover while more isolated individual mounds maintained lesser abundances (Figure S3.8).

3.4 | Climate velocity

Climate velocities varied throughout the region, with some of the highest velocities occurring near the shelf break where many of the shallower *L. pertusa* sites occur (Figure 12). Here, isotherms moved at approximately four kilometers per year (km year^{-1}) from 2015 to 2100, while isotherms at sites on the eastern Blake Plateau (e.g., Richardson Reef Complex, Central Plateau Mounds) moved $< 1 \text{ km year}^{-1}$. Velocities were also lower to the north, with sites off Cape Fear and Cape Lookout, Virginia experiencing similarly low velocities. While these sites are predicted to experience severe warming, they are closer to deep areas, lowering their velocities. Isotherm trajectories generally moved toward the eastern Blake Plateau, which is predicted to offer a more similar thermal environment to what currently occurs at the *Lophelia* sites $< 500\text{m}$.

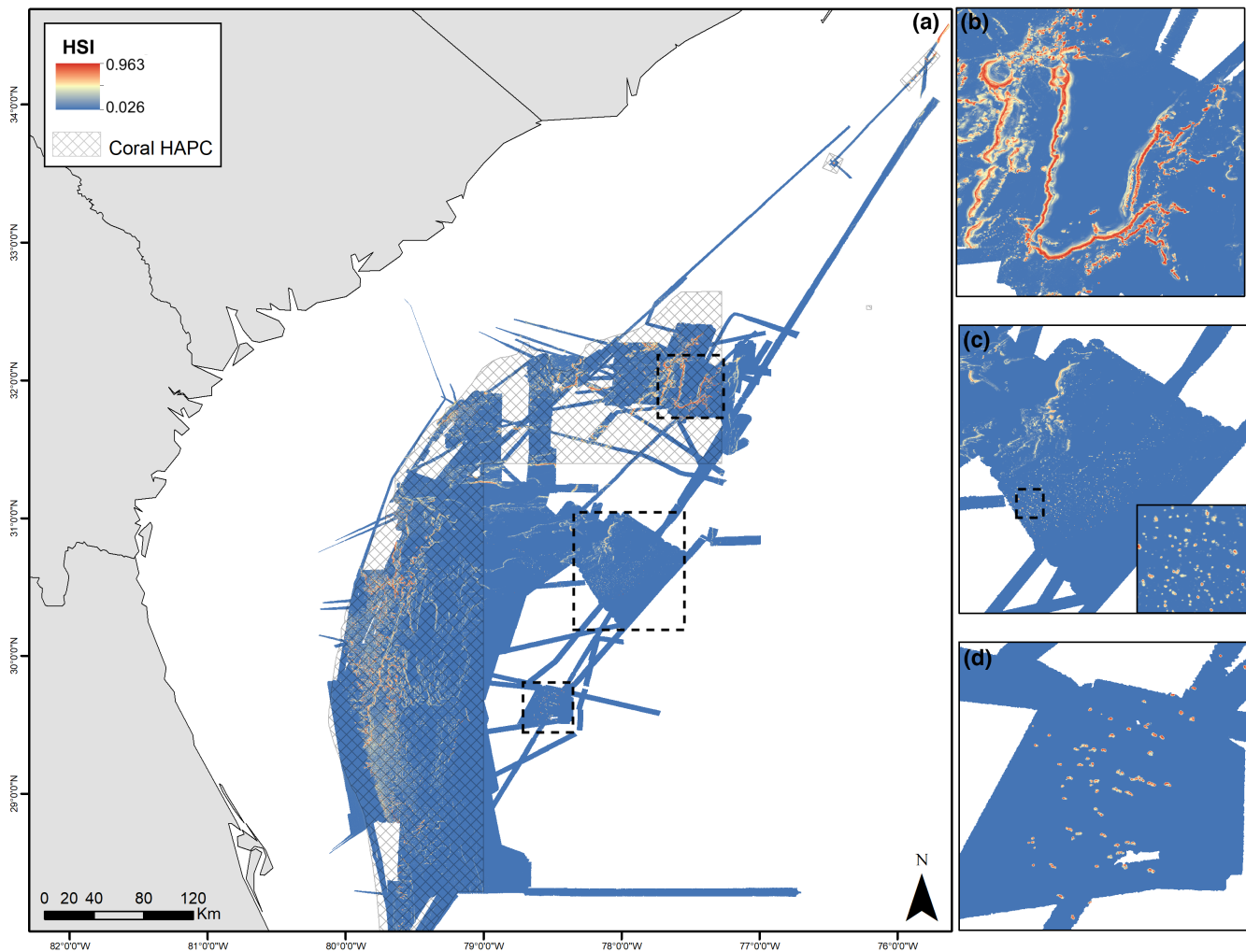


FIGURE 4 (a) Mean terrain-based habitat suitability index (HSI) of the SEUS margin and coral Habitat Area of Particular Concern (hatched area). Insets show key areas including (b) the Richardson Reef Complex, (c) the Central Plateau Mounds, and (d) the Blake Plateau Knolls [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

4 | DISCUSSION

4.1 | Habitat extent

Our models project a previously underappreciated extent of *L. pertusa* habitat in the SEUS, including outside of the boundaries of protected areas that are closed to bottom-contact fishing due to the presence of CWC habitat (coral HAPC; Figure 1). Although there are >50,000 apparent CWC mounds in the roughly 500km by 100km region of highest suitability index scores—with many predicted to be topped with live coral by our models (Figure 4)—the coral mounds are predominantly unvisited. Most of the areas highly likely to contain live *L. pertusa* fell on peak and ridge bathymorphons (Figure 5), highlighting the importance of these features for conservation and exploration. Future expeditions to the region will help ground-truth the models presented in this study. It should be noted that preliminary versions of these models were used to predict the presence of the mounds in Central Plateau Mounds and Blake Plateau Knolls

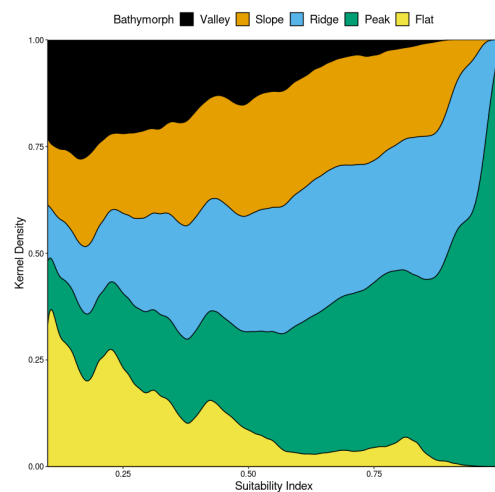


FIGURE 5 Kernel density estimates of terrain suitability scores across different bathymorphons in the SEUS [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

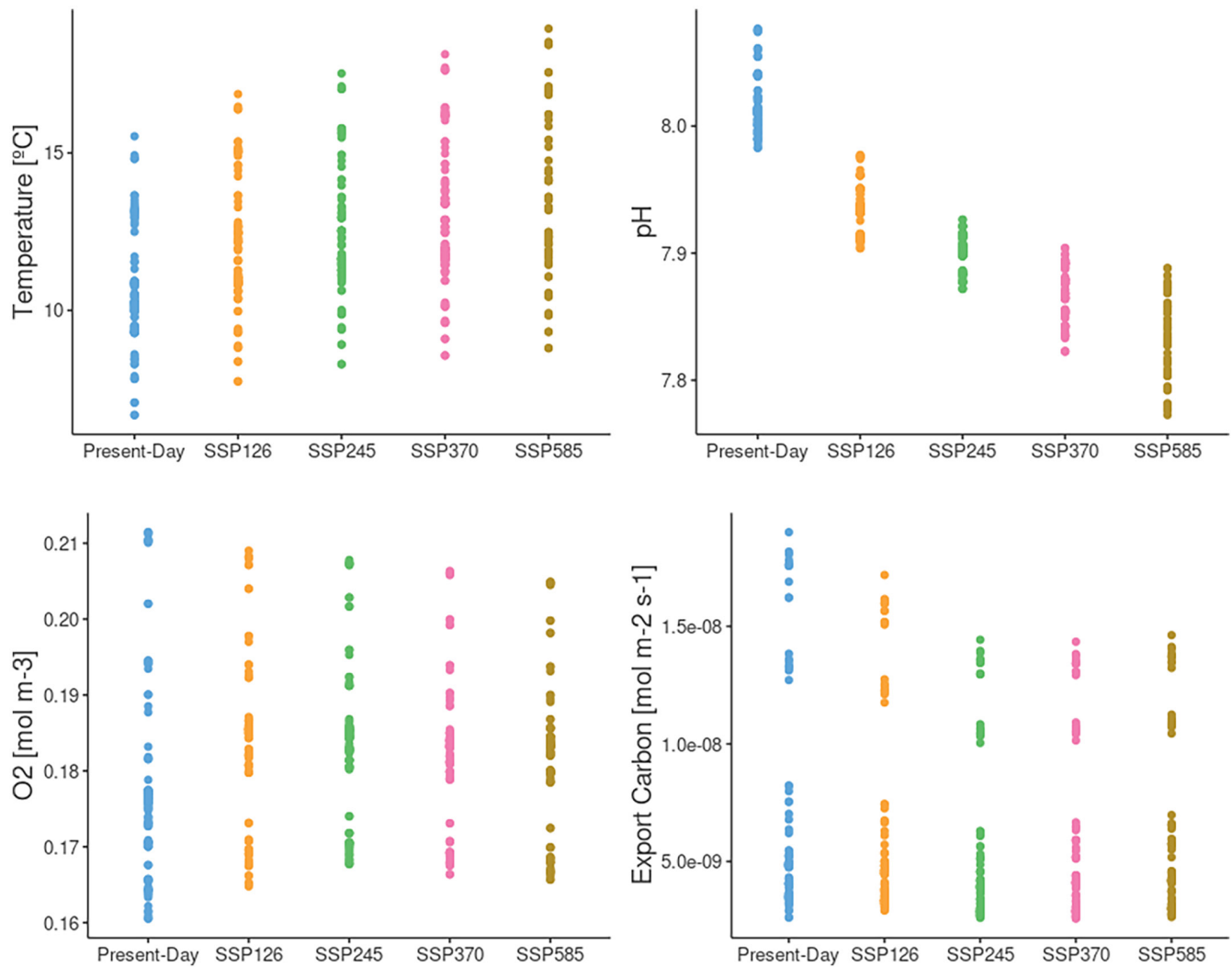


FIGURE 6 Change in climatic variables at *Lophelia pertusa* sites on the SEUS margin ($n = 97$ on ~ 700 m grid) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

areas following the discovery of the Richardson Reef Complex in 2018, and the predictions were later confirmed on expeditions by the NOAA Ship *Okeanos Explorer* (Table S1.1). The spatiotemporal predictions arising from our models, in conjunction with the differences observed between bathymorphon types (Figure 5), allow for most complete broad-scale characterization of *Lophelia* habitat in the SEUS to date.

4.2 | Climate-driven distribution changes

Currently, most of the SEUS is has high CSI scores for *L. pertusa* (Figure 8). However, the waters overlying most of the suitable terrain will become oceanographically unfavorable by 2100 (Figure 9) with conditions outside of the current climate domain of the species (Figure S1.2). Shallower sites near the shelf break will be the first to feel climate-induced stress and will experience the most acute long-term reductions in CSI. These shallow sites retain relatively high CSI scores at the 2050 timepoint, however, suggesting that they could

still be important transitory habitats as the spatiotemporal connectivity of the deep, eastern sites and the shallower sites diminishes. The relevance of such transitory habitats remains an open question but may prove important with increased temporal resolution in future HSM iterations (Huang et al., 2020).

Our results are consistent with the growing consensus on temperature as a major biodiversity driver in the ocean (Doi et al., 2020; Hunt et al., 2005; Yasuhara & Danovaro, 2016). The Northwestern Atlantic is a warming hotspot (Saba et al., 2016). Accordingly, our models that a warming-driven deepening of the *L. pertusa* distribution will occur this century, and that the eastern Blake Plateau sites could serve as critical climate refugia. Interestingly, at the 2050 timepoint some CSI declines emerged but notable differences between scenarios did not (Figures 8–9). By 2100, the depth-driven refugia effect increased with increasing emissions. In fact, SSP1-2.6 was the only scenario in which many of the Blake Plateau coral sites retained CSI scores >0.7 (Figure 8) and cover of $\sim 20\%$ (Figure 11). This suggests flourishing reef habitats typified by high live coral cover may face regional extirpation outside of this best-case scenario.

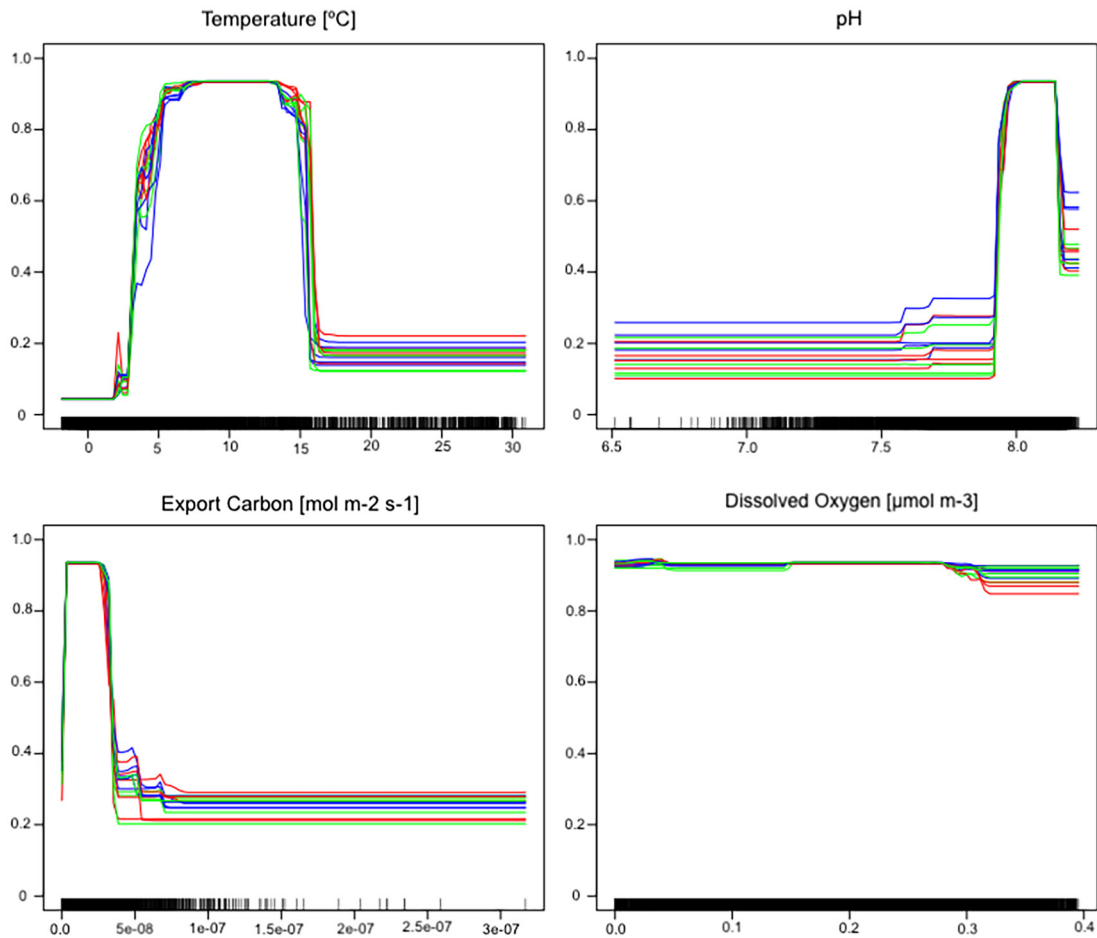


FIGURE 7 Climate response of *Lophelia pertusa* from Random Forest model runs. Scores for each model run (lines) and plotted across the range of each variable on the horizontal axis, with scores ranging from 0 (unsuitable) to 1 (suitable) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

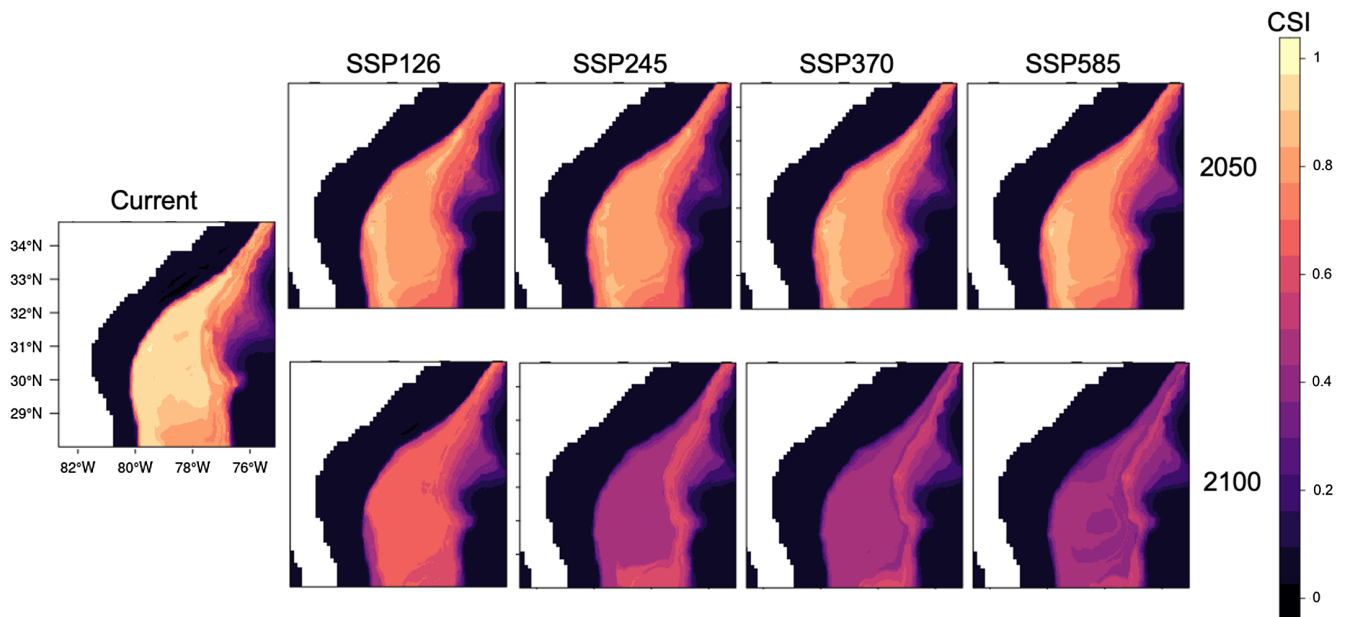


FIGURE 8 Projected climatic suitability index (CSI) of *Lophelia pertusa* habitat on the Southeast US margin in the present-day (left) and four Shared Socioeconomic Pathways (SSPs) in 2050 (top row) and 2100 (bottom row) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

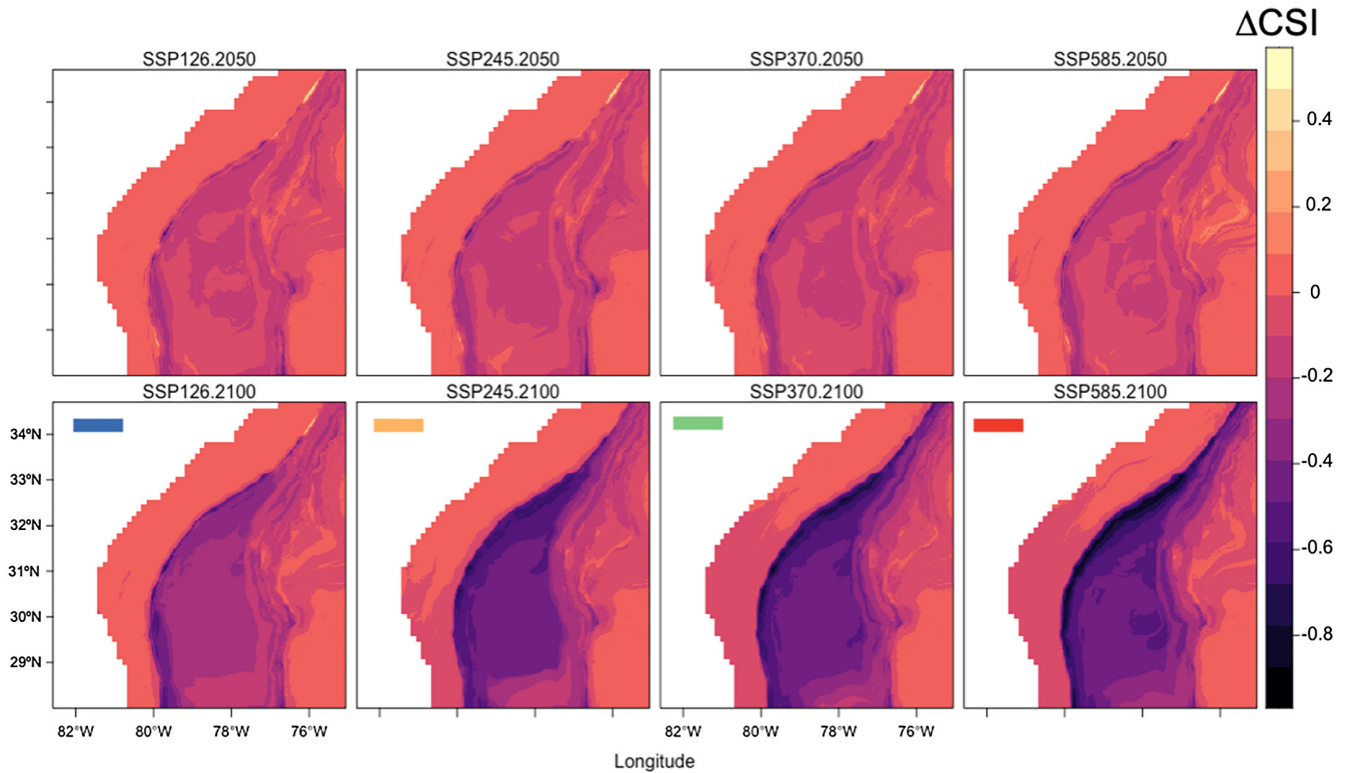


FIGURE 9 Change in climatic suitability index (Δ CSI) maps for the Southeast US margin in each SSP in 2050 (top row) and 2100 (bottom row) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

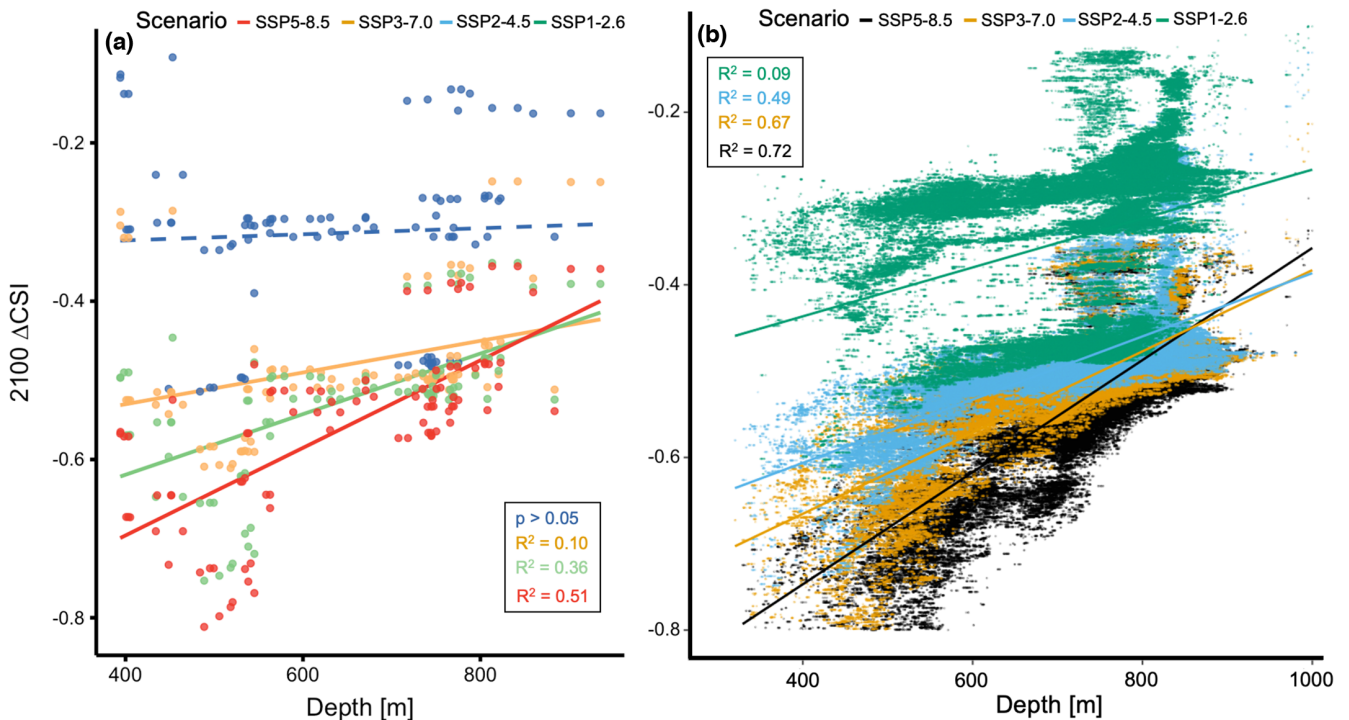


FIGURE 10 Change in climatic suitability index (Δ CSI) at (a) Southeast US (SEUS) margin *Lophelia pertusa* sites on 700m grid ($n = 97$) and (b) all grid cells classified as peaks on mapped SEUS region ($n = 262,822$) in each 2100 Shared Socioeconomic Pathway (SSP) scenario regressed against depth. Solid and dashed lines represent significant and insignificant linear trends, respectively. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

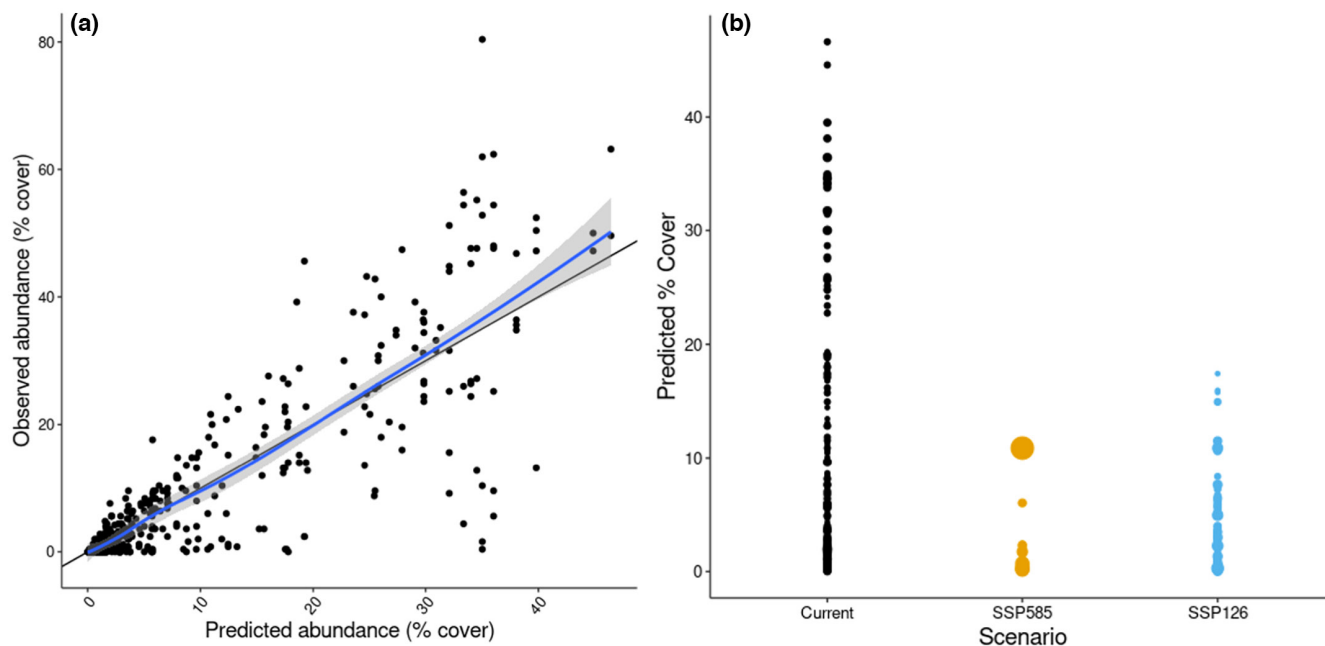


FIGURE 11 (a) Predicted versus Observed Results of Random Forest regression. 1:1 line is shown in black and LOESS smoother in blue. (b) The distribution of predicted abundances (= % cover) of *Lophelia pertusa* in the present-day, SSP5-8.5 and SSP1-2.6 scenarios at the 2100 timepoint. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

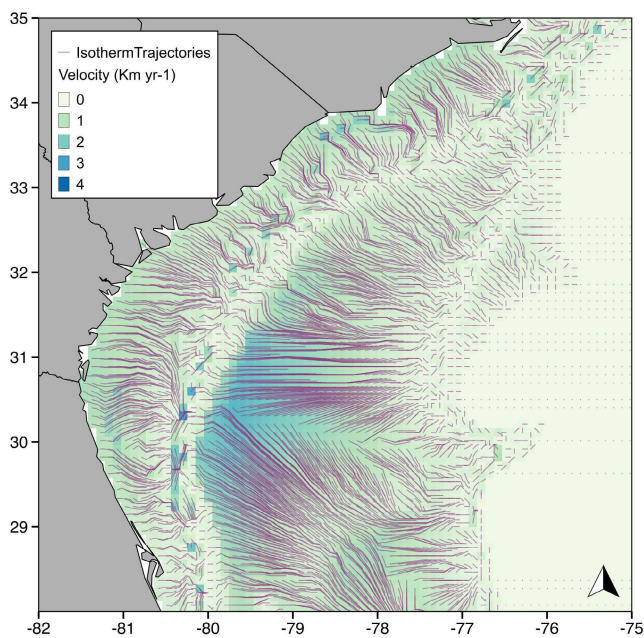


FIGURE 12 Climate velocity (distance to nearest thermal analogue cell in km year⁻¹ from 2015 to 2100) based off regional ocean model data (Alexander et al., 2020). Trajectory lines tracking isotherms from each grid cell are overlain and display the general eastward (depthward) trajectories that the distribution must follow to track suitable isotherms. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16415)]

In other regions, for example, the Mediterranean or Northeast Atlantic, losses of *L. pertusa* could be somewhat compensated by the proliferation of *Madrepora oculata*, which co-occurs at high densities with and is more thermally resilient than *L. pertusa* (Chapron

et al., 2021). However, in the SEUS, *M. oculata* occurrences are sparser and growth of this species is unlikely to keep pace with *L. pertusa* declines. Relaxation of spatial competition from *L. pertusa* may also positively impact hexactinellid sponges such as *Vazella pourtalesii*, which grows primarily on coral rubble in the SEUS and is predicted to expand its range with climate change (Beazley et al., 2021).

Coral mounds in the northern parts of the region, for example, known reefs off Cape Lookout and Cape Fear, Virginia are predicted to be amongst the sites with the fastest warming. These sites also currently experience frequent short-term (i.e., days-to-weeks) temperature spikes associated with Gulf Stream dynamics and/or downfluxes of surface-waters (Mienis et al., 2014). Although similar temperature spikes have been observed at the deeper reefs in the region, their lower mean temperatures give them a buffer against shorter-term spikes. In 7-day experimental exposures to a temperature increase from 8 to 14°C, corals from the Richardson Reef Complex exhibited increased respiration and excretion rates as well as higher rates of protein catabolism, indicating a distinct stress response, although all of the corals survived (Gómez et al., 2022). The incorporation of short-term variability in environmental data into models may reveal further vulnerable and/or refuge areas for CWCs but is currently beyond the purview of large-scale correlative models such as the ones we present here.

The deep, eastern Blake Plateau sites are especially notable because they may not only be climate refugia, but they currently contain thriving reef habitat with the highest coral cover and megafaunal biodiversity observed in the SEUS (Table S1.2; Gasbarro et al., unpubl.). This biodiversity may be impacted by our predicted declines, as it can correlate with the percent cover of live coral (Price et al., 2021; Rowden et al., 2020), although a mix of live and

dead standing coral framework can also foster high biodiversity (Cordes et al., 2008; Mortensen et al., 1995). The losses of living coral we project may also lead to positive feedbacks of declining geomorphological complexity, as dead skeleton is more susceptible to dissolution and colonization by bioeroding species (Freiwald & Wilson, 1998; Hennige et al., 2020), flattening the habitat and making it even less suitable for CWC growth. While there was a significant positive relationship between our abundance predictions and those observed, there is a notable amount of variance, particularly at high cover values. This may be caused by species interactions or finer-scale environmental dynamics not incorporated in the present study. Despite these caveats, our models of *L. pertusa* abundance could have further utility when combined with laboratory and/or *in situ* carbon and nitrogen flux measurements to refine first-order estimates of the contributions of these ecosystems to margin- and even basin-wide functioning (De Clippele et al., 2020, 2021), and to better quantify the ecosystem services lost with projected coral declines (Cordes et al., 2021).

Somewhat surprisingly, oxygen and export carbon flux were not significant environmental drivers in our models. CWCs may be more resilient to deoxygenation if other conditions such as food supply are well met (Hebbeln et al., 2020), or oxygen limitation may be a regional phenomenon where availability is lower than in the North Atlantic, for example, the North Pacific (Auscavitch et al., 2020; Chu et al., 2019). However, low oxygen concentrations have an effect on *L. pertusa* metabolic function (Dodds et al., 2007; Lunden et al., 2014) and the window for metabolically viable habitat will be narrowed by deoxygenation and warming in concert (Deutsch et al., 2015; Ern, 2019; Pörtner et al., 2017). Thus, more research is needed into the additive and/or synergistic effects of deoxygenation and warming. Our data suggests that the waters overlying the SEUS will remain normoxic until at least 2100, however.

Export carbon, on the other hand, will likely decline, particularly under the velocity core of the Gulf Stream (Figure 6; Figure S3.4). Despite energy availability's pervasive influence on seafloor biodiversity (Woolley et al., 2016), the degree to which CWC distributions are influenced by large-scale export carbon patterns is debated (Portilho-Ramos et al., 2022; Raddatz et al., 2014; Roberts & Kohl, 2018). In addition, projected declines in open ocean productivity may be somewhat alleviated by increasing terrigenous carbon inputs (Lacroix et al., 2021). pH did not have as strong an effect on CSI as temperature. Its importance may have been masked by the correlation between the two, however (Figure S1.1). In the Mediterranean, where temperatures are also high, pH does appear to be a critical driver *L. pertusa* reef persistence (Matos et al., 2021). Indeed, there is both *in situ* and laboratory evidence of ocean acidification affecting the physiology of *L. pertusa* (Dorey et al., 2020; Gómez et al., 2018; Hennige et al., 2014; Kurman et al., 2017) and eroding the dead skeleton that forms the basis for their mound habitat (Hennige et al., 2015, 2020).

Our models generalize the climate response of the species from the whole of North Atlantic to the SEUS. It is possible that because *L. pertusa* in this region—especially near the shelf break—are already

exposed to some of the warmest temperatures recorded for this species, there may be a degree of acclimatization or adaptation as hypothesized in the Gulf of Mexico for acidification (Georgian, Dupont, et al., 2016; Kurman et al., 2017) or for hypoxia on the west Angolan margin (Hebbeln et al., 2020). Although acclimatization for marine calcifiers does not appear to be a viable strategy in shallow waters (Comeau et al., 2019), it may be achieved deeper where climate change proceeds slower. CWCs at these sites are possibly compensated for increased metabolic demand in high temperatures by current-driven high food supply. Further slowing (Boers, 2021) or eastward movement (Matos et al., 2015) of the Gulf Stream may tip this delicate balance.

It is unknown whether climate corridors represented by the climate velocity trajectories will match dispersal corridors. That is, will larvae be able to track the lines in Figure 12b at sufficient speeds to allow recruitment to more accommodating habitat, or will the western-most populations face extirpation? Particle release models of the hexactinellid sponge *Vazella pourtalesii*, which commonly co-occurs with *L. pertusa*, suggest that larval exchange may be partially split among the eastern Blake Plateau and the shallower sites on the upper shelf (Wang et al., 2021). However, genetic evidence indicates that *L. pertusa* populations on the Blake Plateau are mixed (Morrison et al., 2011), suggesting connectivity whereas Northeast Atlantic populations appear to recruit locally with differentiation apparent between certain sub-populations (e.g., fjords vs. offshore banks; Le Goff-Vitry et al., 2004). Larval dispersal models incorporating realistic ontogenetic behaviors have shown the connection between *Lophelia* reefs and oil rigs in the North Sea (Henry et al., 2018), and may be of use in describing connections between CWC habitat in the SEUS. If there is indeed genetic exchange between populations and a spatial gradient in the magnitude of climate change, the eastern Blake Plateau reefs meet both assumptions of the “deep reef refuge hypothesis” that posits mesophotic coral ecosystems can be larval sources for shallow reefs (Bongaerts et al., 2010), suggesting the potential for an analogous process between CWC habitats separated by depth. Further studies of community similarity and identification of distinct faunal assemblages (e.g. Murillo et al., 2018) between reefs in the region could also provide further tests of our hypothesized deep reef refuges and the utility of this framework in the deep ocean.

Our notable findings of potential climate refugia on the eastern Blake Plateau warrant additional protections including the extension of the HAPC to unprotected mound features (Figure 1), to prevent damaging these valuable ecosystems with bottom-contact fishing gear. Our study also highlights the utility of regional models in refining habitat suitability projections from coarser models (e.g., Davies et al., 2008; Morato et al., 2020), and of using multiple climate scenarios rather than a single business-as-usual scenario that is unlikely to occur (Burgess et al., 2022; Meinshausen et al., 2022). Indeed, visual comparison of our model outputs with those from Morato et al. (2020) suggest that more of the eastern Blake Plateau is within the current climatic niche of *L. pertusa* (Figure S3.11), which may also be due in part to our inclusion of additional occurrence

locations. Our results corroborate their findings that a business-as-usual scenario (e.g., RCP 8.5 or SSP 5-8.5) would lead to precipitous declines in area on the Blake Plateau that *L. pertusa* is likely to occupy. We hope that this iterative refinement of model predictions continues as the spatiotemporal resolution of both climatic and mapping data increases, potentially revealing more localized refugia and aiding in conservation and exploration of the seafloor. Ultimately, this will lead to better accounting of the ecosystem services and vulnerable marine ecosystems both in US waters and other exclusive economic zones. Despite limited evidence that active restoration of CWC habitats is possible (Montseny et al., 2021), our results suggest that sharply curtailing greenhouse gas emissions is the only reasonable way in which the extent and health of these ecosystems will be maintained into the 22nd century.

ACKNOWLEDGMENTS

Thanks to the science parties, captains, and crews of the DEEP SEARCH expeditions AT41 and RB1903 aboard the R/V Atlantis and NOAA Ship Ronald H. Brown and for all of the NOAA Ship *Okeanos Explorer* expeditions completed on the Blake Plateau. We also thank Michael Alexander and Charles Stock for sharing ROMS data. Funding for DEEP SEARCH came from the Bureau of Ocean Energy Management (contract M17PC00009 to TDI Brooks International), the U.S. Geological Survey (to USGS scientists from the USGS Environments Program), and the NOAA Office of Ocean Exploration and Research (for ship time). Additional support comes from the NOAA Deep-Sea Coral Research and Technology Program. RG and AM were respectively supported by a Presidential Fellowship and a Diamond Research Scholars Award from Temple University. High-Performance Computing resources were supported by the NSF through major research instrumentation grant 1625061 and the US Army Research Laboratory (contract W911NF-16-2-0189).

CONFLICT OF INTEREST

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

All newly presented *Lophelia* occurrence locations presented in this study have been incorporated into NOAA's Deep Sea Coral database (<https://deepseacoraldata.noaa.gov/>). Raw climate data are available from the Earth System Grid Federation (esgf.llnl.gov). Bathymetric survey data are available from NOAA NCEI (<https://www.ncei.noaa.gov/>). Raw model outputs presented in this study are available on Dryad at the following link: <https://doi.org/10.5061/dryad.jh9w0vtfc>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Gasbarro, R., Sowers, D., Margolin, A., & Cordes, E. E. (2022). Distribution and predicted climatic refugia for a reef-building cold-water coral on the southeast US margin. *Global Change Biology*, 28, 7108–7125. <https://doi.org/10.1111/gcb.16415>