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# The Future of Reef Ecosystems in the Gulf of Mexico: Insights From Coupled Climate Model Simulations and Ancient Hot-House Reefs

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# The Future of Reef Ecosystems in the Gulf of Mexico: Insights From Coupled Climate Model Simulations and Ancient Hot-House Reefs

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Shallow water coral reefs and deep sea coral communities are sensitive to current and future environmental stresses, such as changes in sea surface temperatures (SST), salinity, carbonate chemistry, and acidity. Over the last half-century, some reef communities have been disappearing at an alarming pace. This study focuses on the Gulf of Mexico, where the majority of shallow coral reefs are reported to be in poor or fair condition. We analyze the RCP8.5 ensemble of the Community Earth System Model v1.2 to identify monthly-to-decadal trends in Gulf of Mexico SST. Secondly, we examine projected changes in ocean pH, carbonate saturation state, and salinity in the same coupled model simulations. We find that the joint impacts of predicted higher temperatures and changes in ocean acidification will severely degrade Gulf of Mexico reef systems by the end of the twenty-first century. SSTs are likely to warm by 2.5–3°C; while corals do show signs of an ability to adapt toward higher temperatures, current coral species and reef systems are likely to suffer major bleaching events in coming years. We contextualize future changes with ancient reefs from paleoclimate analogs, periods of Earth's past that were also exceptionally warm, specifically rapid "hyperthermal" events. Ancient analog events are often associated with extinctions, reef collapse, and significant ecological changes, yet reef communities managed to survive these events on evolutionary timescales. Finally, we review research which discusses the adaptive potential of the Gulf of Mexico's coral reefs, meccas of biodiversity and oceanic health. We assert that the only guaranteed solution for long-term conservation and recovery is substantial, rapid reduction of anthropogenic greenhouse gas emissions.

**Keywords: climate change, coral reefs, coral bleaching, hot-house paleoclimates, adaptation, ocean acidification**

## 1. INTRODUCTION

Coral Reefs constitute some of the most biodiverse ecosystems in Earth's oceans. They are critical to the socioeconomic health of 500 million people globally, providing billions of dollars in tourism and food sources for island and coastal communities (Frieler et al., 2013). Coral reefs support 25% of all of Earth's marine species during various stages of their life cycle (NOAA Ocean Service Education, 2017) and throughout geological time reefs have produced high diversity in Earth's

oceans (Kiessling et al., 2010). Anthropogenic climate change is threatening reefs globally via multiple stressors including higher water temperatures, changes in water acidity, and fluctuating salinity. Today, there are no coral reefs left on the planet in pristine condition (Jackson et al., 2001; Hughes et al., 2003). Long-term surface temperature observations show a rate of global warming of 0.13°C per decade since 1979 (Trenberth et al., 2007), with an increase to 0.27°C per decade measured from 1985 to 2009 (Chollett et al., 2012).

Anthropogenic climate change affects coral biology via multiple compounding pathways (Rodolfo-Metalpa et al., 2011; Prada et al., 2017); multiple pressures (e.g., warming and acidification) combine to be significantly more damaging than either stressor alone. The majority of shallow-water, reef building corals are a holobiont consisting of an animal host (the coral) and zooxanthellae (photosynthetic endosymbiotic dinoflagellates of the family Symbiodiniaceae; LaJeunesse et al., 2018); this holobiont produces a skeleton made of calcium carbonate (aragonite). Scleractinian corals (or stony corals) are stenohaline and typically prefer a narrow range of water temperatures and carbonate saturation states. While they do have the ability to modify the saturation state ($\Omega_{aragonite}$) of the fluid from which they calcify their skeleton (e.g., Cohen and Holcomb, 2009; Ries et al., 2010; Anthony et al., 2011; Comeau et al., 2017a,b), changes in seawater pH and seawater carbonate chemistry can significantly reduce coral biomineralization, diversity, recruitment, and abundance (Fabricius et al., 2011). During times of extreme stress, in particular elevated sea surface temperatures (SST) or acidification, coral will expel their zooxanthellae, resulting in coral bleaching (Anthony et al., 2008; Baird et al., 2009; Frieler et al., 2013); in some cases on a global, sustained scale (Eakin et al., 2019; Skirving et al., 2019).

While much attention has been cast toward the sharp decline of coral reef systems in the Australia's Great Barrier Reef and across the tropical Pacific since the early 1980s (Frieler et al., 2013), considerably less work has been devoted to examining climate projections focused on corals and reef organisms from the Gulf of Mexico (GoM hereafter). The GoM is home to many coral reefs growing along coastal Texas, Louisiana, Florida, and Mexico in the upper ~1,500 m, and houses a wide array of deep sea coral species (as well as other reef builders, such as sponges) found along the continental shelf and slope (**Figure 1**, **Figures S1, S2**). Most of these reefs are within managed areas including Dry Tortugas National Park and Veracruzano Coral Reef System National Park, Flower Garden Banks and Florida Keys National Marine Sanctuaries, and Florida State Park John Pennekamp. Other coral reefs include Campeche Bank, Tuxpan, Tuxtlas, Yucatan Shelf, Florida Middle Grounds, and Pulley Ridge, the deepest stony coral reef in the US (Waddell and Clarke, 2008; Wilkinson and Souter, 2008; Ortiz-Lozano et al., 2013).

GoM reef systems are subject to myriad anthropogenic stressors including rising SSTs, over-fishing, bleaching, chemical pollution and increasing terrestrial runoff, coral mining, and unrestricted tourism (Jordán-Dahlgren and Rodríguez-Martínez, 2003), as well as disease and sedimentation (Tunnell et al., 2007; Carricart-Ganivet et al., 2011; Horta-Puga et al., 2015). The once structurally complex coral reefs in the GoM and Caribbean have declined since the 1970s, and very few reefs still exhibit a mean live coral coverage >10% (Waddell and Clarke, 2008; Wilkinson and Souter, 2008). The majority of GoM coral reefs are reported to be in poor or fair condition with the exception of Flower Garden Banks (a protected National Marine Sanctuary) in the northern Gulf and Dry Tortugas National Park in the westernmost Florida Keys (Waddell and Clarke, 2008; Wilkinson and Souter, 2008; Johnston et al., 2017). The largest changes, documented since the 1970s, indicate that the most prevalent branching corals, the Acroporid corals, have experienced population declines >90% (Acropora Biological Review Team, 2005). Two of these corals, *Acropora palmata* and *Acropora cervicornis*, are listed as threatened species under the Endangered Species Act of 2006 (Hogarth, 2006). In 2010, the National Marine Fisheries Service found significant evidence to list 82 coral species as threatened species, including eight Caribbean species (NOAA, 2010).

At present, there is strong evidence that GoM reefs have experienced thermal stress since 1878 (Kuffner et al., 2015) with recent bleaching events in 2016/2017 (Johnston et al., 2019a). *In situ* SST records show a 0.8°C increase over the last century in the Florida Keys, where corals have declined especially in the later part of the twentieth century. Observed rates of SST warming are spatially and temporally variable throughout the Gulf, but the highest warming rates tend to occur in summer months (June, July, and August); most recently, the highest heating rates have been observed in the central GoM in the Loop Current region (Chollett et al., 2012; del Monte-Luna et al., 2015; Allard et al., 2016). Multiple studies suggest higher probabilities of coral bleaching in mid-latitude reefs (15–20° of latitude) despite similar levels of thermal stress compared to equatorial reefs (Sully et al., 2019). Coral accretion rates must keep up with the current rate of sea level rise for these ecosystems to survive (Toth et al., 2015); today, sea level rise threatens Florida Keys reefs and other GoM reefs, which cannot keep pace (Shinn, 1976).

Many of the climatic changes affecting the future of coral reefs have been examined in climate model projections. Given a business as usual (RCP8.5) greenhouse gas forcing scenario, simulations from the Climate Model Inter-Comparison Project (CMIP5) indicate that by 2090–2100, temperatures will increase, pH will decrease, oxygen content in the oceans will drop, and there will be a decrease in primary productivity (Bopp et al., 2013; Freeman, 2015). Tropical oceans are warming the fastest of any region globally in most of the CMIP5 projections, but with lower acidification rates. GoM SSTs are projected to rise by 0.37°C per decade. This substantial rise in SST would severely stress GoM coral reefs. Indeed, research shows that Gulf corals are stressed when SSTs approach 31°C; today, summertime temperatures frequently reach 30°C in the Florida Keys and Veracruz. These simulations suggest that more than 50% of coral reefs globally will undergo frequent and severe thermal stress by the year 2080 (Donner et al., 2005).

For this special issue on GoM coral reef systems, we zero in on climate change in the GoM and future threats to the region's reef ecosystems. Recent catastrophic environmental events, such as hurricanes Harvey and Irma (Hickerson et al., 2008; Viehman, 2017), have cast justified attention to GoM

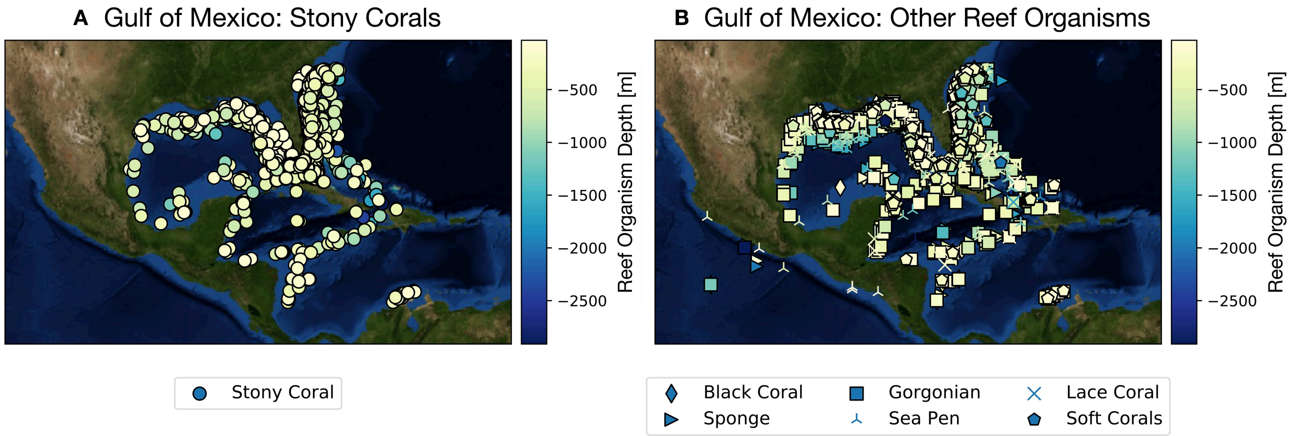


**FIGURE 1 |** Gulf of Mexico shallow and deep sea coral and sponge sites as reported in the deep sea coral database (NOAA, **Figures S1, S2**). Color scale along y-axis indicates depth of reef organism and symbols denote organism type (e.g., scleractinian coral vs. sponge). **(A)** Scleractinian corals (stony corals), **(B)** all other species reef locations. See also **Figures S1, S2**. From https://deepseacoraldata.noaa.gov/website/AGSViewers/DeepSeaCorals/mapSites.htm.

climate and ocean dynamics, including the well-being of Gulf species and ecosystems (Zavala-Hidalgo et al., 2014). This motivates careful examination of future climate predictions of all relevant variables to accurately capture spatial heterogeneity in reef response. In this work, we address the question: *what changes in climate and ocean chemistry will influence the corals and reef systems in the Gulf of Mexico?* We hypothesize that new model simulations confirm that the GoM will warm and acidify such that substantial coral bleaching will occur. A general circulation model (GCM) with a fully coupled ocean model is employed to test for changes in multiple environmental stressors that impact coral reefs in the GoM through 2100. The individual impacts of changes in temperature, salinity, and ocean acidification are partitioned to drive a more targeted reef impact mitigation plan. We contextualize future impacts to GoM reefs through the lens of geological time, exploring how present-day corals' predecessor species were able to adapt to analogous climate change events in the past. Finally, we discuss the future of GoM reefs in the Anthropocene, and provide a preview of the threats these ecosystems will soon face in this particular region.

## 2. METHODS

### 2.1. GCM Simulations

To build a Gulf of Mexico-centric forecast of the various conditions that interfere with coral reef health over the next several decades, we evaluated simulations from the Community Earth System Model version 1.2 (CESM) (Kay et al., 2015). CESM is a state-of-the-art, Intergovernmental Panel on Climate Change (IPCC)-class general circulation model (GCM) developed at the National Center for Atmospheric Research. We compared two periods from a high-$CO_2$ forcing IPCC representative concentration pathway (RCP) scenario (RCP8.5, which corresponds to 8.5 $W/m^2$ of radiative imbalance due to anthropogenic greenhouse gas emissions). RCP8.5 assumes a "business as usual" radiative forcing consistent with minimal mitigation; we chose to employ this high-forcing model ensemble in light of the fact that emissions trends over the past few decades track slightly above RCP8.5 (Peters et al., 2012). CESM 1.2 simulations include a large ensemble ($n$ = 33) of simulations spanning the period 2006–2100, from which we extracted four decades (2006–2026 and 2080–2100) for a modern vs. future comparison. From the early twenty-first century control period and the high-$CO_2$ RCP8.5 scenario, the model ensemble mean was computed for the following variables: SST, salinity (SALT), alkalinity (ALK), dissolved inorganic carbon (DIC), and pH for the upper-most ocean layer of POP2, the ocean model component of CESM. We additionally analyzed the RCP4.5 medium ensemble of CESM1.2 to contextualize the changes in RCP8.5 with those likely under a lower emissions scenario. Note that all of the scripts used in the extraction and analysis of climate model output are documented in section S2, and provided directly in the **Supplementary Material**.

While the CESM model keeps track of the saturation state of seawater with respect to the carbonate minerals calcite and aragonite, these values are not directly included as part of the standard model output. Thus, we recomputed saturation states (Ω) using the MATLAB implementation of the CO2SYS software (https://www.nodc.noaa.gov/ocads/oceans/CO2SYS/co2rprt.html) (Lewis and Wallace, 1998). The CESM model outputs of Alkalinity, DIC, salinity, water depth (pressure), and temperature were used alongside assumptions of phosphate and silicate concentrations of 0 $\mu$M, and the dissociation constants of carbonic acid, bicarbonate, and sulfuric acid from Mehrbach et al. (1973); Dickson and Riley (1979); Dickson and Millero (1987), and Dickson (1990). This "offline" approach to evaluating carbonate mineral saturation states also allows us to apportion the predicted changes between each of the input variables by sequentially holding each variable constant at its 2006–2026 mean values and allowing the remaining variables to change.

To evaluate the accuracy of the model predictions for the modern period, the model output was compared to field data from multiple sites within the GoM. The field data were all taken from the Global Ocean Data Analysis Project Version 2 (GLODAPv2) and include sites off of the coasts of Texas, Louisiana, and Florida that range in depth from the surface to 500 m water depth. Using the same CO2SYS approach, the field measurements of alkalinity, DIC, salinity, and temperature were used to calculate $\Omega_{aragonite}$.

## 2.2. Defining Coral Reef Stress Factors

Based on CESM's available output history files, we define the following stressors on GoM reefs, and examine changes in these stressors from 2006–2026 to 2080–2100. It should be noted that many of these factors are synergistic (e.g., Rodolfo-Metalpa et al., 2011; Prada et al., 2017).

- Degree Heating Months (DHM), a standard predictor for coral bleaching (Gleeson and Strong, 1995; Liu et al., 2003). DHM = 1 refers to heating in excess of or equal to 1°C above the long-term monthly climatology of the warmest month in a given region (Sully et al., 2019). DHM gives a measure of thermal stress applied to corals, which leads to bleaching. DHM is easier to compute given that coupled GCMs usually archived at monthly time steps; however, degree heating weeks (DHW) is considered the more accurate predictor of bleaching (Liu et al., 2003; Kayanne, 2017; Sully et al., 2019).
- SST Variance: Sully et al. (2019) show in a global survey of coral bleaching from 1998 to 2017 that higher SST variance zones over reefs are less susceptible to bleaching.
- Mean annual SST: an upper temperature limit for coral bleaching in the Pacific has been reported as 28.1°C, but more recent work shows an increasing bleaching threshold of 28.7°C (Sully et al., 2019). In the GoM, reported bleaching thresholds are higher, approaching 30–31°C. Wilkinson and Souter (2008) found corals bleached in the Caribbean when SST reached 31°C and were sustained; Florida Keys and Flower Garden Banks reefs bleach when SST reached 30–31°C (Johnston et al., 2019b) or 29.5°C if temperatures were sustained for 50 days (Johnston et al., 2019a). We consider mean annual SSTs approaching 30°C as high risk for coral bleaching in the GoM.
- Salinity: in laboratory experiments, some species of *Acropora* corals are sensitive to low salinity values, exhibiting threshold behavior below ∼22 g/kg (Berkelmans et al., 2012).
- Carbonate Chemistry: The saturation state of seawater with respect to aragonite ($\Omega_{aragonite}$) is an important control on coral growth as modern scleratinian (stony) corals biomineralize an aragonite skeleton. The saturation state of seawater is also a factor in coral growth and reef stabilization. The modern distribution of coral reefs is largely limited to regions of the ocean where $\Omega_{aragonite}$ exceeds 3 (modern distribution threshold; Kleypas et al., 1999; Fine and Tchernov, 2007; Hoegh-Guldberg et al., 2007; Guinotte and Fabry, 2008) and experimental studies suggest that the calcification rate of corals drops to zero when $\Omega_{aragonite}$ reaches 2 (experimental calcification threshold; Langdon et al., 2000; Albright et al., 2008). Nevertheless, there are some examples of corals and low diversity reefs growing in more acidified waters in both natural systems (Fabricius et al., 2011; Shamberger et al., 2014) and in controlled experiments (Cohen and Holcomb, 2009; Ries et al., 2010; Anthony et al., 2011). Finally, $\Omega_{aragonite}$ = 1 is a strong thermodynamic limit as, below this value, it is more likely for aragonite to dissolve in seawater than to precipitate.

# 3. THE FUTURE OF GULF OF MEXICO REEFS IN 21$^{ST}$ CENTURY PROJECTIONS

## 3.1. SST Changes

Corals demonstrate species-specific variable responses to increasing surface ocean temperatures (Sully et al., 2019) as well as changing carbonate chemistry (Bahr et al., 2018); this response can also vary regionally and within micro-climates. In the GoM, the CESM RCP8.5 ensemble mean SSTs rise to 28.5°C in the northernmost sector of the Gulf, and 29–30°C in the central and southeastern regions (**Figure 2**) for the end of the twenty-first century. There is some indication that global mean thermal bleaching thresholds may be shifting toward warmer temperatures as global SSTs rise (Sully et al., 2019). Nevertheless, the projected annual mean warming for the GoM exceeds the most recent thermal threshold estimates of 30°C (Johnston et al., 2019b) in several locations in the southern and central GoM, especially in the Caribbean.

The difference in 2080–2100 and 2006–2026 average SST is given in **Figure 3**. In most areas of the Gulf of Mexico, temperatures rise by ∼3°C; in the central GoM and the Caribbean, the SST changes are closer to ∼2.2–2.7°C. At 100 m depth, ocean temperatures increase more modestly by 1–1.5°C (**Figure S3**). The corals lining the Texas, Louisiana, and Florida coastlines are likely to experience the greatest temperature stress in the coming decades. Previous analyses of coupled climate model simulations (CMIP3) indicate that SST increases of just 1–1.5°C relative to the pre-industrial era places most reefs at a high risk for long-term degradation; an increase of 2°C will increase the risk of degradation or bleaching to 100% (Frieler et al., 2013). In all zones of the GoM, the change in surface ocean temperatures exceeds 2°C. Thus, the RCP8.5 changes in SST suggest wide-spread bleaching is likely by 2100 if a more aggressive mitigation strategy is not adopted in the coming decades.

To explore the potential influence of increased climate mitigation, we performed the same analysis of SST changes in the CESM RCP4.5 medium ensemble, corresponding to a lower greenhouse gas emissions scenario (**Figure S4**). GoM temperatures rise more modestly by 2060–2080 with lower forcing. While this ensemble only extends to 2080 (precluding a direct comparison of the RCP8.5 2080–2100 conditions), SST changes range from 0.92°C to 1.3°C by 2080. Despite the reduction in warming, this still constitutes changes leading to high risk of long-term degradation as defined by Frieler et al. (2013).

### 3.1.1. Degree Heating Months

We computed the cumulative number of months above the mean of maximum monthly SST climatology in each GoM

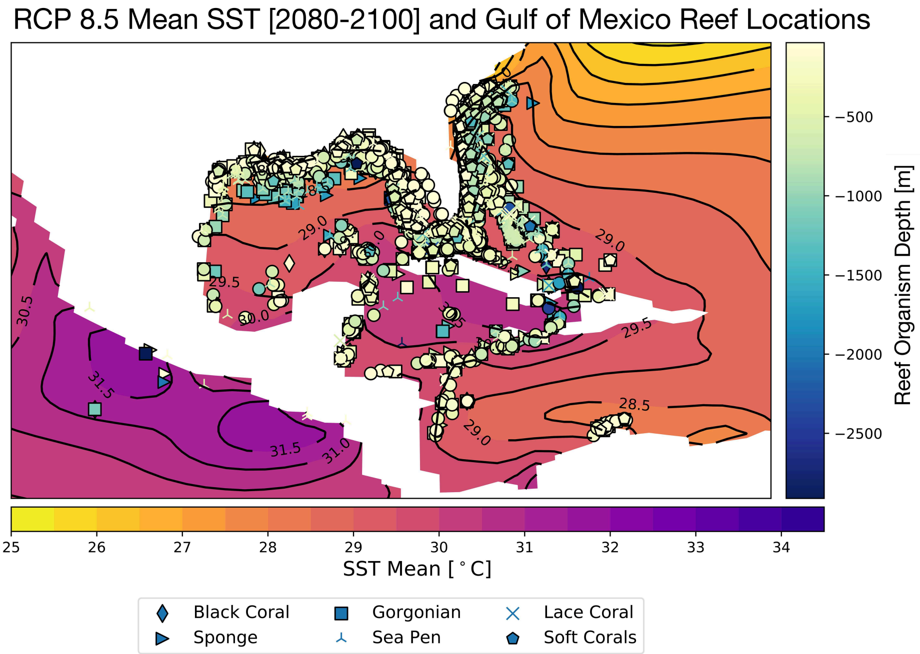


**FIGURE 2 |** Projected mean Gulf of Mexico SST for 2080–2100, RCP8.5 Large Ensemble, CESM1.2, with all reported Gulf of Mexico reef organism locations overlain. Colors of coral sites indicates reef organism depth [meters] and symbols denote type of reef builder, as in **Figure 1**. Continental regions are shown in white.

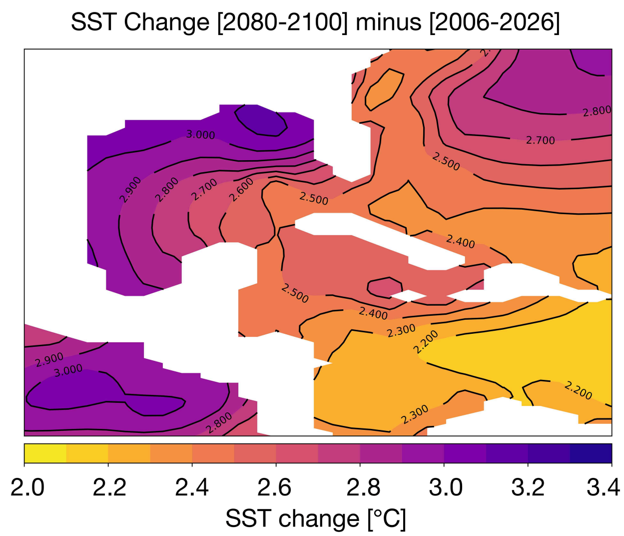


**FIGURE 3 |** Simulated changes in Gulf of Mexico SST [°C] in the RCP8.5 Large Ensemble, CESM1.2. (2080–2100 mean minus 2006–2026 mean). Continental regions are shown in white.

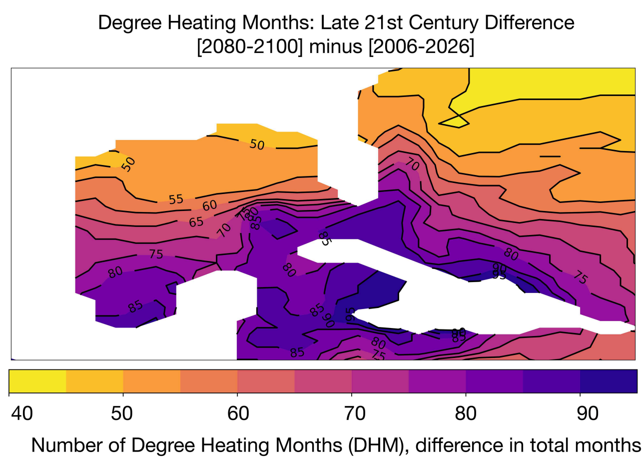


**FIGURE 4 |** Simulated changes in Degree Heating Months (DHM) in GoM SST [°C] in the RCP8.5 Large Ensemble. DHM climatology is based on the period 2006–2080. DHM are defined as months that exceed 1°C of the hottest month in the grid cell climatology. Continental regions are shown in white.

grid cell (following our definition of DHM, see section 2.2) (following Liu et al., 2003; Donner et al., 2005; Frieler et al., 2013). Multiple studies (Glynn and D'Croz, 1990; Hoegh-Guldberg, 1999; Sheppard, 2003; Donner et al., 2005) show that a SST exceedance threshold of 1°C in a given month will lead to bleaching; Donner et al. (2005) consider a higher temperature threshold to be anything exceeding 2°C above monthly climatologies, corresponding to a degree heating week (DHW) exceeding 8 weeks of high heating. **Figure 4** shows the difference in DHM between the beginning (2006–2026) and end of the twenty-first century. The number of DHM increases for the lower threshold of 1°C throughout the GoM, with the largest increases in DHM in the southern GoM and Caribbean (an increase of 75–90 DHM across the 20 year period). Along the Texas, Louisiana, and Florida coasts, DHM increases by 50–55 months total compared to the 2006–2026 base period. Put

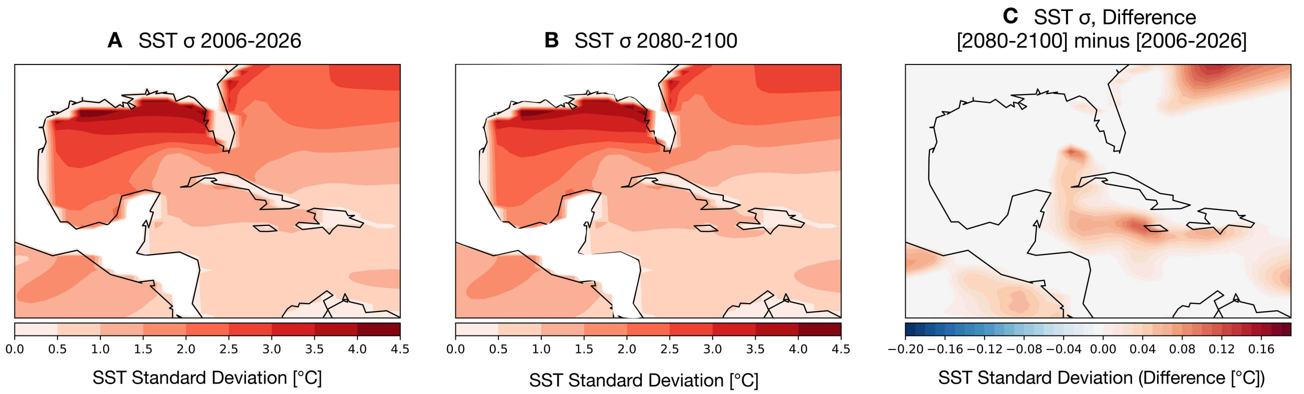


**FIGURE 5 |** Simulated changes in the standard deviation (1-$\sigma$) of GoM SST [°C] in the RCP8.5 Large Ensemble, CESM1.2. **(A)** 2006–2026 SST $\sigma$. **(B)** 2080–2100 SST $\sigma$. **(C)** (2080–2100 mean $\sigma$ minus 2006–2026 mean $\sigma$). Continental regions are outlined in black contours.

another way, GoM corals are likely to experience thermal stress for approximately 2–4 more months of the year by 2080–2100.

#### 3.1.2. SST Variance

Coral bleaching is less frequently observed in zones that experience high variance in SST anomalies (see Sully et al., 2019, for a review). To assess the potential for changes in SST variance to either dampen or amplify thermal stressors on GoM reefs, we computed the change in variance in the earlier part of the twenty-first century (**Figure 5A**) compared to the last 20 years (2080–2100) (**Figure 5B**). The overall spatial variance of SSTs remains largely unchanged throughout the twenty-first century: higher latitude GoM SSTs are highly variable, with more muted changes in the southern Gulf and Caribbean. The change in variance (**Figure 5C**) between the two time periods is close to zero degrees across much of the GoM with the exception of a few zones surrounding the Caribbean islands, which show an increase in overall variance. We note that these areas of higher SST variance correspond to main ocean currents driving GoM circulation, the Loop and Caribbean currents.

Given that increased variance is likely to help prevent bleaching, there is no modeling evidence that reductions in SST variance in the GoM will contribute to exacerbated coral bleaching.

### 3.2. Changes in Salinity and Carbonate Chemistry

While warming SSTs are expected to exert a primary influence on coral reefs over the coming decades, other hydrological and chemical changes in the ocean can also impact reef survival. Like SSTs, changes in variables such as salinity and pH exhibit spatial heterogeneity in simulations spanning the twenty-first century.

#### 3.2.1. Salinity

GoM salinity is projected to increase; **Figure 6** shows the average salinity for 2080–2100 (a) and the change from 2006 to 2026 (b). Salinity in the GoM and Caribbean is quite high, 36–37 g/kg, and the CESM RCP8.5 ensemble exhibits a trend toward saltier water characterizing the twenty-first century. Salinity falling below 22 psu is thus unlikely to stress GoM coral reefs. High salinities can also be a stress on coral reef communities, but the maximum salinities predicted for the GoM in the 2080–2100 simulation are well within the range of naturally observed salinities near reefs, and far lower than some regions (e.g., the Red Sea) (Coles and Jokiel, 1992). That said, changes in community structure among reef dwellers are possible with projected salinity shifts.

#### 3.2.2. Ocean Carbonate Chemistry

To measure the potential for ocean acidification to obstruct aragonite calcification and degrade coral skeleton growth, we examined changes in both pH and $\Omega_{aragonite}$ (see section 2). For the modern period, the model predictions under-predict $\Omega_{aragonite}$ relative to field observations (**Figure 7**). For the surface ocean (0–50 m), the offset between the model and data is relatively small with the exception of the highest latitude sites (**Figure 7**). At 100 m water depth, the model-observation offset is greater (due to higher model-predicted DIC at depth), but a general trend of decreasing $\Omega_{aragonite}$ with depth is present in both the field data and the model predictions. We note that the field data were collected in 2007 while the model predictions for the "modern" period span from 2006 to 2026. As a result, it is possible that the model-data discrepancy is due to the impacts of atmospheric $CO_2$ on carbonate chemistry that occurred after the field data were collected. Alternatively, the model predictions for deep-water reefs may be inaccurate in their absolute value.

**Figure 8** shows the CESM results for changes in pH across the GoM for the end of twenty-first century. The surface ocean in the entire GoM regions is predicted to acidify by approximately −0.265 pH points on average, with the largest drop in pH along the northern Gulf coast (**Figure 8**). To assess the direct impacts of this change in ocean chemistry on coral growth, we computed $\Omega_{aragonite}$ in CESM's ensemble mean for the 2080–2100 period (**Figure 9**). Given potential model biases at depth (see above), we focus on the surface (0–50 m), though model predictions for 100 m depth are shown in **Figure S5**; additionally, the model prediction for alkalinity changes at the surface is given in **Figure S6**.

As shown in **Figure 9**, our results suggest that the surface ocean of the entire GoM region will drop below $\Omega_{aragonite}$ = 3. This is notable as the modern scleractinian corals are largely

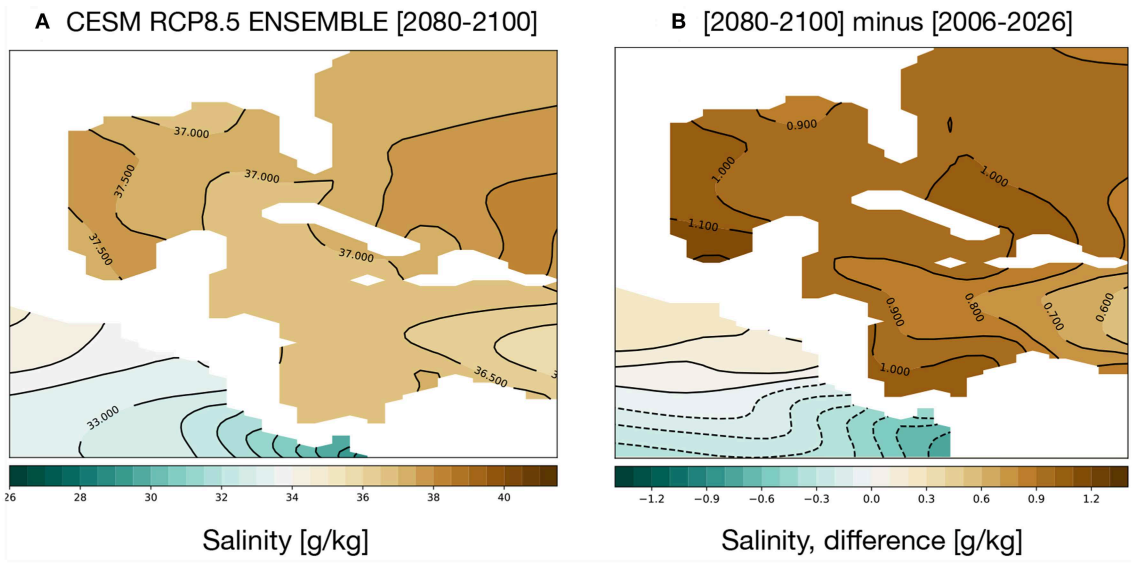


**FIGURE 6 |** Simulated changes in GoM salinity in the RCP8.5 Large Ensemble, CESM1.2. **(A)** 2080–2100 mean. **(B)** (2080–2100) mean minus (2006–2026) mean. Continental regions are shown in white.

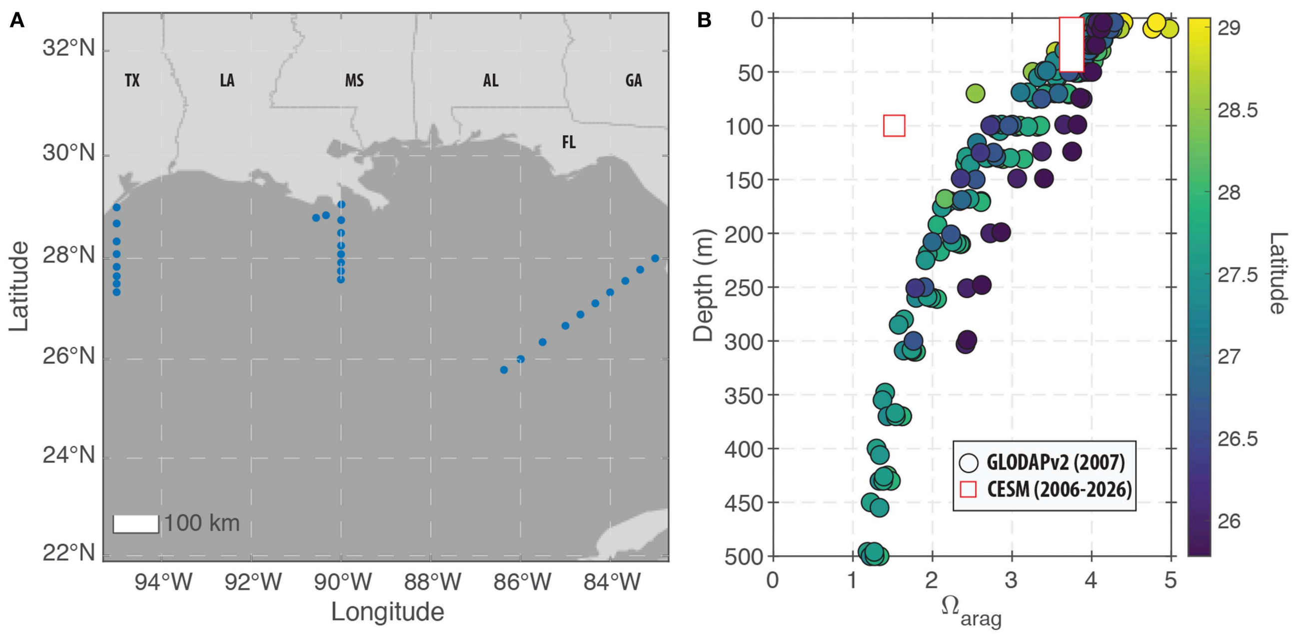


**FIGURE 7 |** Modern observations of carbonate chemistry in the GoM. **(A)** Map showing the locations of the GLODAPv2 stations within the GoM that are used for comparison to the CESM predictions. The displayed region (83°W to 95°W and 22°N to 33°N) defines the GoM region used for displaying the model predictions in **(B)** as well as **Figure 10**. **(B)** Field measurements (circles) and model predictions (squares) of changes in $\Omega_{aragonite}$ with depth in the GoM. For the surface ocean (0–50 m), the model reproduces most of the data with the exception of the highest latitude sites. However, at 100 m water depth, the model under-predicts $\Omega_{aragonite}$ relative to all of the field observations.

restricted to areas of the ocean where $\Omega_{aragonite}$ exceeds this value (Kleypas et al., 1999). No surface regions of the Gulf of Mexico are predicted go below the experimental calcification threshold of $\Omega_{aragonite}$ = 2 (Langdon et al., 2000; Albright et al., 2008) or to reach the thermodynamic limit for aragonite precipitation ($\Omega_{aragonite}$ = 1; **Figure 10**).

Compared to reefs in the upper 50 m of the water column, deeper water reefs would experience lower saturation states because aragonite has retrograde solubility (i.e., $\Omega_{aragonite}$ decreases with depth due decreased temperature and increased pressure). Modern field observations show that $\Omega_{aragonite}$ values at 100 m depth in the GoM are approximately 1 unit lower than

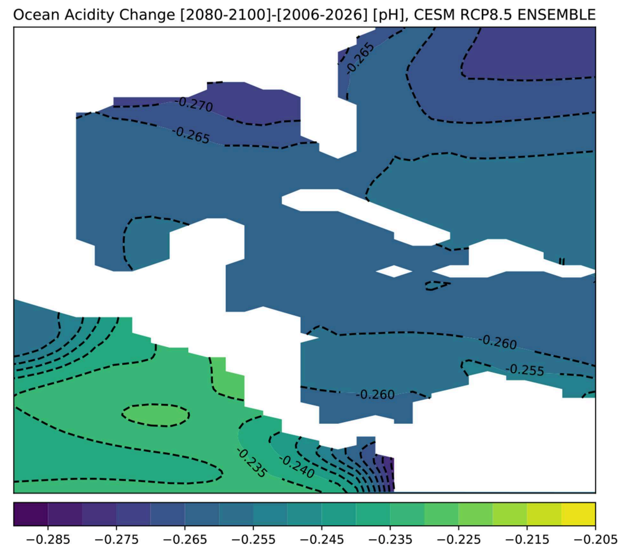


**FIGURE 8 |** Simulated changes in GoM pH in the RCP8.5 Large Ensemble, CESM1.2. (2080–2100 mean minus 2006–2026 mean). Continental regions are shown in white.

surface waters (**Figure 7**; Wanninkhof et al., 2015; Feely et al., 2018). This means that some of the deeper, mesophotic reefs (even those as shallow as 100 m) may already be experiencing stress due to low $\Omega_{aragonite}$ values. Alternatively, deeper-water reef builders (e.g., glass sponges, gorgonian corals, and sea pens) are likely adapted for those conditions.

The model predicted change in $\Omega_{aragonite}$ at 100 m depth is much less severe than at the surface; the CESM model estimates only a 0.3 unit change in $\Omega_{aragonite}$ at 100 m between the beginning and end of the century, with almost no change at the 500 m horizon (not shown). As mentioned above, the model predicted value for $\Omega_{aragonite}$ at 100 m water depth over the modern (2006–2026) period does not match existing field measurements (**Figure 7**) due to model-predicted DIC concentrations that are too high. While the model is inaccurate in terms of the absolute value for $\Omega_{aragonite}$ at depth, this does not necessarily mean that the magnitude of the change predicted by the model for 100 m water depth is also inaccurate. For example, the model prediction that changes in carbonate chemistry are greater in the surface ocean is consistent with the underlying driver being the addition of $CO_2$ to atmosphere, which exchanges more rapidly with the surface ocean relative to below the mixed layer.

The small change in $\Omega_{aragonite}$ predicted at depth may stress coral communities. That said, it is also possible that the predicted changes would not be as damaging as the changes predicted for shallow water reefs in that the deeper communities are already adapted/acclimatized to lower $\Omega_{aragonite}$ values (Farfan et al., 2018).

Due to the retrograde solubility of aragonite, the predicted increase in temperature acts to slightly increase $\Omega_{aragonite}$ (**Figure 10**); however, the effect of increasing atmospheric $CO_2$ and associated ocean acidification greatly exceeds the effect of temperature and leads to an overall decline in $\Omega_{aragonite}$ for the whole region (**Figure 10**). Similarly, the effect of increasing salinity on $\Omega_{aragonite}$ is negligible compared to the predicted pH changes. More importantly, the combination of heat and acidity stresses can often act synergistically (e.g., Rodolfo-Metalpa et al., 2011; Prada et al., 2017), meaning that even moderate heating and $\Omega_{aragonite}$ decreases can amplify each other leading to intolerable conditions for coral reefs. Furthermore, with surface oceans getting warmer and more acidic (low $\Omega$) waters at depth, it is possible that surface-adapted reef communities in the GoM will have no suitable refuge by the end of the century (e.g., Pereira et al., 2018; Rocha et al., 2018).

## 4. CONTEXTUALIZING ANTHROPOGENIC CHANGES WITH HOT-HOUSE CLIMATES OF THE PAST

Scleractinian coral reefs have a long history extending back to the Middle Triassic (242–247 million years ago) (Martindale et al., 2019). Specifically, there are numerous records of reefs in the paleo-GoM, including microbial reefs from the Upper Jurassic (164–153 Ma) (Mancini and Parcell, 2001), coral and rudist bivalve reefs from the Cretaceous (145–90 Ma) (e.g., Enos, 1974; Scott, 1984; Höfling and Scott, 2002; Hattori et al., 2019), sponge and coral reefs from the Paleocene (66 to 59 Ma) (Bryan, 1991), as well as the drowned and living reef banks that initiated during the last deglacial period (∼14,500 years ago) (Khanna et al., 2017).

Ancient coral reefs that grew during (or were killed off by) hyperthermal (sudden, extreme heating) events can be seen as analog case studies for changes in reef communities today. When looking at the entire Phanerozoic (the last 541 million years), many of the worst reef collapses are coincident with evidence of thermal stress and ocean acidification (Kiessling and Simpson, 2011). When scleractinian reef systems are considered (the last 250 million years), this trend is even more concerning. Heat stress and acidification occur coincident with the last 3 greatest metazoan reef collapses: the Triassic/Jurassic mass extinction at 201 Ma (a 99.4% loss of reef volume), Pliensbachian/Toarcian extinction and Toarcian Oceanic Anoxic Event at ∼183 Ma (a 98.3% loss of reef volume), as well as the early Cenozoic Hyperthermal Events [e.g., Paleocene-Eocene Thermal Maximum at 56 Ma (a 99.6% loss of reef volume) and Early Eocene Climate Optimum (54 Ma)] [reef loss calculated from metazoan reef volumes reported in Kiessling and Simpson, 2011]. It should be noted that since acidification events are so geologically short-lived, it is often difficult to attribute this stress to long-term community change (Hönisch et al., 2012). Ancient reefs are imperfect analogs; modern fast growing coral species, such as *A. cervicornis*, generally evolved in the last half million years (Hoegh-Guldberg et al., 2007) and thus the reef communities are not identical. Nevertheless, many coral genera (from the Cenozoic in particular) are extant (not extinct), so reasonable comparisons can be made between groups (Weiss and Martindale, 2019). Further, many important reef forming corals were present in the GoM as far back as the early Eocene, including

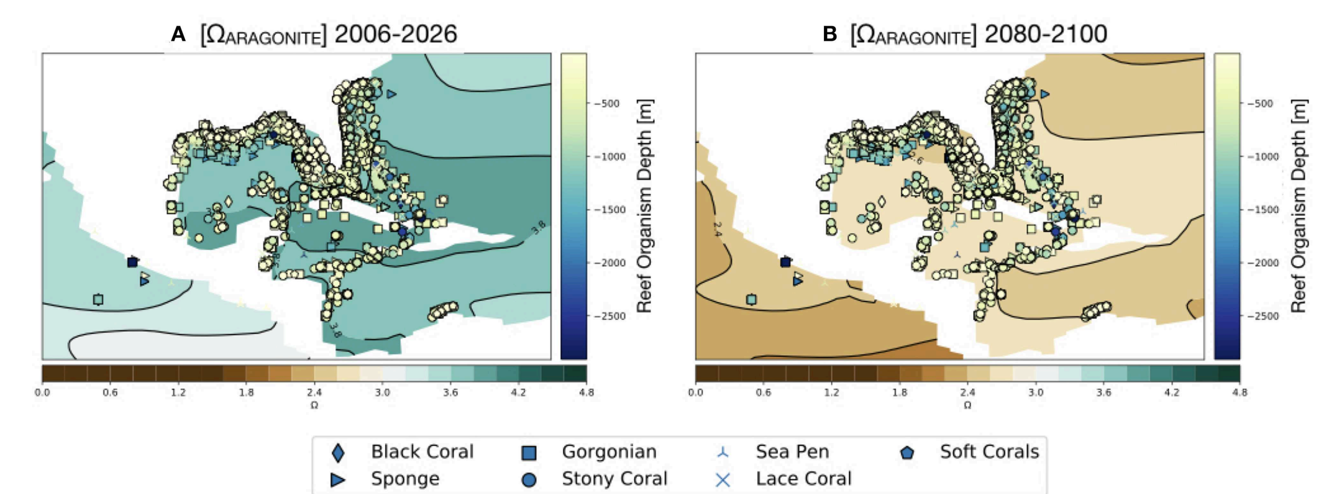


**FIGURE 9 |** Simulated values of $\Omega_{aragonite}$ for the GoMand northern Caribbean region in the RCP8.5 Large Ensemble (CESM1.2) in the surface ocean (0–50 m). Reef organisms and depth at which they occur [m] overlain (see **Figure 1**). **(A)** 2006–2026 mean, **(B)** 2080–2100 mean. Continental regions are shown in white.

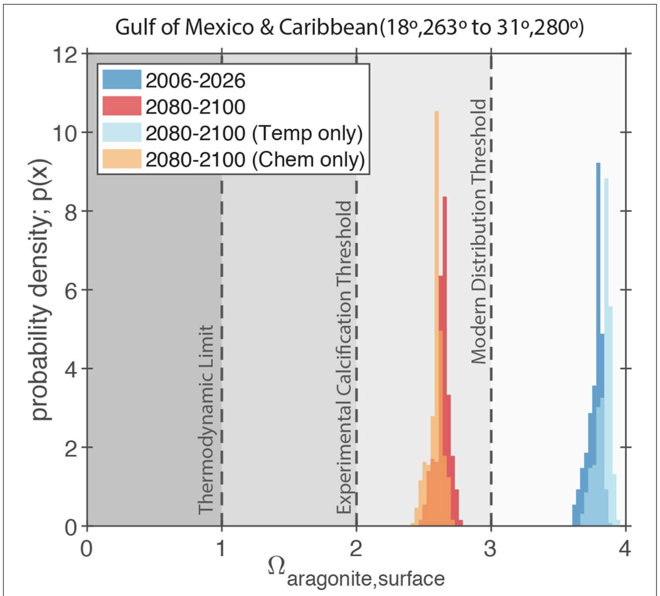


**FIGURE 10 |** Simulated values of $\Omega_{aragonite}$ for the GoM and northern Caribbean Region (i.e., the region shown in **Figure 7A**) in the RCP8.5 Large Ensemble, CESM1.2. The dark blue and dark red probability density functions (PDFs) show the model predictions for the 2006–2026 and 2080–2100 periods, respectively. The light blue and orange PDFs show the model predictions for the 2080–2100 period where either ocean chemistry or water temperature is held constant at the 2006–2026 values. The gray shading and dashed lines indicate the typical limits for the presence of scleractinian corals in the modern ocean ($\Omega > 3$; Kleypas et al., 1999), the experimentally measured limits for calcification by coral reef communities ($\Omega > 2$; Langdon et al., 2000; Albright et al., 2008), and the thermodynamic limit for aragonite precipitation ($\Omega = 1$).

*Astrocoenia*, *Favia*, *Goniopora*, *Montastraea*, *Siderastrea*, and *Stylophora* (Budd, 2000).

The Paleocene-Eocene Thermal Maximum in particular has been noted as one of the better analogs for modern climate change due to the similarities in the cause (i.e., greenhouse gas emissions) and its consequences (e.g., ocean acidification, increases in temperature) (Hönisch et al., 2012). In the Tethys Ocean, Paleocene coral reefs underwent a protracted, three-step collapse, from coral-dominated to foraminiferal or microbial reefs, before the complete demise of reef ecosystems near the Paleocene/Eocene boundary (Scheibner and Speijer, 2008; Zamagni et al., 2012). Nevertheless, these reef ecosystems were able to maintain a relatively high diversity (Zamagni et al., 2012). The main driver of the reef turnover is thought to be elevated temperature, but ocean acidification (Kiessling and Simpson, 2011), excessive sedimentation, and nutrification (Zamagni et al., 2012) are also implicated. In the GoM region, temperature, increased sedimentation, and nutrient input due to tectonism (Galloway et al., 2000) led to the development of sponge and coralline algae dominated reefs. Some zooxanthellate and apozooxanthellate massive and platy corals were also present (Bryan, 1991). Weiss and Martindale (2019) show that corals with particular traits, such as flexible photosymbiosis and feeding strategies and those that lived in siliciclastic environments, were better able to withstand change during the Cenozoic hyperthermal events. Because the GoM is largely siliciclastic, it is possible that GoM corals may prove more resilient than those in carbonate environments. Importantly, the rates of climate change in the modern are faster than during the Paleocene (Zeebe et al., 2016), barring direct comparison between the two time periods.

Finally, the Last Interglacial (LIG, ~129–116 ka) was the last time the Earth was as warm as today with 11% warmer temperatures in the northern hemisphere, a greater loss of Arctic sea ice, and a partial loss of the Greenland ice sheet (Kukla et al., 2002; CAPE-Last Interglacial Project Members, 2006); these conditions are all possible in the near future under realistic carbon emissions scenarios. The Florida Keys in the southeastern GoM had extensive coral reef coverage during the LIG. These reefs contained many of the coral species we find in the Florida Keys today with branching *Acropora* and *Porites*,

and boulder-shaped *Montastraea, Diploria,* and *Siderastrea* corals with ooid banks to the west and east of the reef (Stanley, 1966). Reconstructions from Tropical Atlantic locations find temperature and seasonality variability similar to present (Felis et al., 2015; Brocas et al., 2016, 2018). However, sea level was up to 6 m higher than today during the LIG, and likely exerted a dominant control on coral reef distributions. Evidence from Florida Keys, Bahamas, and Cayman Islands for the LIG found corals grew to about 3 m above current sea level, but not the peak 6 m (Blanchon, 2011). Evidence from the northern Yucatan peninsula suggest that a rapid depth change from 3 to 6 m induced a higher-energy wave environment that remobilized lagoonal sediments and buried or eroded adjacent reef framework resulting in marine sand bodies that prevented the submerged reefs from recovering (Blanchon et al., 2009). While the LIG is not a perfect analog for the current climate change, it provides some insights into coral response to quick pulses in sea level rise due to collapsing ice sheets and shifts in oceanic-atmospheric conditions. Coral reefs did exist and flourish in many locations during the LIG, but rapid changes in sea level given, for example, a partial collapse of the Greenland ice sheet could severely inhibit future growth.

These ancient events provide useful information regarding sensitivities, survival, and recovery during extreme stress events, as well as natural reef ecosystem responses to climate change in the absence of human-induced changes or interventions.

## 5. DISCUSSION: GULF CORALS IN THE ANTHROPOCENE

This study examines future projections for oceanic conditions in the GoM and the potential impacts of multiple stressors on coral reef ecosystems. Using CESM 1.2, a state-of-the-art coupled GCM, we compared two key 20-year periods: 2006–2026 (a base control) and 2080–2100 (end of twenty-first century). We find that GoM SSTs are likely to warm by 2.5–3°C, elevating mean temperatures to a range of 28–30.5°C in a high-$CO_2$ forcing scenario. While corals do show signs of an ability to evolve toward higher temperatures (e.g., Howells et al., 2012; Palumbi et al., 2014; Dixon et al., 2018), there are annual mean SST thresholds (e.g., 30°C, Wilkinson and Souter, 2008; Johnston et al., 2019b) beyond which corals simply bleach and die. By the end of the twenty-first century, the ensemble mean SST fields are spatially heterogeneous, but a great number of reefs, particularly off the coast of Belize, Florida, and Cuba, may experience mean annual temperatures closer to 30°C by 2100; further, these estimates potentially contain a cold bias (Liu L. et al., 2012), and in reality, GoM temperature observations are already hotter (Johnston et al., 2019b). Taken together, these results suggest that Gulf reef systems will experience frequent and severe thermal stresses by the end of the twenty-first century. Preventing such widespread and severe bleaching to the Earth's coral reef systems likely requires limiting global warming to 1.5°C, which is, at present, a lofty target (Frieler et al., 2013). To avoid widespread degradation of Gulf corals and reef communities, atmospheric $CO_2$ levels would likely need to be stabilized below measured 2005 levels (Donner et al., 2005).

The CESM1.2 RCP8.5 large ensemble provides no evidence that changes in GoM SST variance or salinity will adversely impact coral reef ecosystems. That said, an evaluation of relevant carbonate chemistry variables (i.e., pH and carbonate saturation state), suggest that a threshold may be crossed by the end of the century. Scleractinian coral reefs that are currently growing in supersaturated waters of $\Omega_{aragonite}$ greater than 3.4 (**Figures 9**, **10**) will experience significant pH and carbonate saturation state drops (**Figures 8**, **9**). These changes in carbonate chemistry will negatively impact GoM reef biomineralization. Today, scleractinian coral reefs that are found in low pH or $\Omega_{aragonite}$ waters have lower biodiversities and abundance of reef builders or dwellers than reefs in higher $\Omega_{aragonite}$ waters (Fabricius et al., 2011). Reefs in low $\Omega_{aragonite}$ regions are typically poorly cemented, have higher bioerosion, and have fewer structurally complex framework builders, which together result in lower structural integrity of the reef (Fabricius et al., 2011; DeCarlo et al., 2015). If the GoM becomes more acidic (lower $\Omega_{aragonite}$) we should expect the reef ecosystems to become less diverse and structurally weakened with a higher likelihood of significant coral bleaching. These issues are important on their own, but also lead to secondary issues; for example, lessened structural integrity can lead to more significant storm damage during hurricanes (Cheal et al., 2017), which will also increase in intensity and severity with rising temperatures (Molina et al., 2016; Murakami et al., 2018); reef species may also become more susceptible to disease or see a decline in fecundity.

The combination of thermal and chemical stress will make these environmental changes even more damaging (e.g., Donner et al., 2007, 2018; Rodolfo-Metalpa et al., 2011; Prada et al., 2017; Bahr et al., 2018). Deeper water, mesophotic reefs have distinct communities and ecosystems when compared to shallow water reefs (e.g., Bongaerts et al., 2010; Pereira et al., 2018; Rocha et al., 2018) but are, nevertheless, likely to experience severe thermal stress (Schramek et al., 2018). Given the issues of accuracy and resolution in predicting $\Omega_{aragonite}$ values at 100 m depth shown in this work, it is hard to make confident conclusions about the fate of mesophotic reefs. On the one hand, the predicted amount of $\Omega_{aragonite}$ change at 100 m depth is minimal (especially when compared to the surface), but on the other hand, these values are already below an important calcification threshold for scleractinian corals. If deep Mesophotic reefs are primarily inhabited by organisms that are well adapted to these lower $\Omega_{aragonite}$ conditions, the communities may not experience a catastrophic change. Future research should focus on the physiological limits of deep mesophotic reef communities as there is still very little known about these ecosystems (Bongaerts et al., 2010; Kahng et al., 2010).

We acknowledge several important caveats of this work. Coupled atmosphere-ocean GCMs contain significant cold temperature biases in the GoM and Caribbean (Liu L. et al., 2012; Martin and Schumacher, 2012; Ryu and Hayhoe, 2015; Exarchou et al., 2018; McGregor et al., 2018). Analysis of the Coupled Model Intercomparison Project (CMIP3) revealed that SST variability in the Intra-Americas Sea is less than observed in

historical simulations (Liu L. et al., 2012); many GCMs produce large cold biases across the Intra-Americas Sea when assessed with gridded SST data products. This is crucially important for coral bleaching thresholds, likely leading to underestimated temperature maxima in the GCM predictions. In Key West, for example, summer water temperatures during 2019 were frequently observed above 32°C (National Data Buoy Center, NOAA). Coral bleaching may thus be underestimated in CESM 1.2 as well, and anthropogenic bleaching events may occur with greater severity than projected in this study.

Recent event-based evidence demonstrates that increases in upwelling from stronger winds, frequent during tropical storms, can lead to cold water events and anoxic conditions, promoting coral death and disease (Lirman et al., 2011). An anomalous cold event in 2010 killed numerous near-shore corals in the Florida Keys (Colella et al., 2012) and in the winter of 1969–1970 (Hudson et al., 1976). Cold coral bleaching events might also be altered by climate change, but the evaluation of changes in frequency in such events requires analysis of daily wind patterns, which is beyond the scope of this work.

Finally, the spatial resolution of CESM is $1 \times 1°$; reefs typically occupy spatial scales at tens to hundreds of meters (Donner et al., 2005). This discrepancy in scale creates uncertainties related to downscaling and microclimate affects. While GCM simulations afford important future mean state projections, an inability to resolve details at the reef scale and examine local circulation changes may inhibit our ability to make robust predictions about the future of GoM reef bleaching. Advances in regional ocean modeling and downscaling climate model outputs may facilitate the simulation of local upwelling and upper-ocean heating processes; such advances would refine projections of reef impacts (Donner et al., 2005, 2007, 2018). Further, recent work shows $1 \times 1°$ IPCC-class GCMs contain biases in the simulation of the Loop Current, which largely moderates GoM temperatures (Liu Y. et al., 2012). The Loop Current carries warm waters into the central GoM; if this current slows, it could reduce the warming in the central GoM, mitigating the impacts of global warming. Adding embedded, online ecological models that explicitly simulate reef response to temperature and acidity changes would enhance the accuracy of the results presented here. These advances in model development are forthcoming (Bopp et al., 2013; Jones et al., 2019).

# 6. THE FUTURE OF THE GULF OF MEXICO'S CORAL REEFS

## 6.1. Climate Change and Biodiversity Loss

Coral reefs are critical ecosystem focal points in marine environments, supporting the world's fisheries, protecting coastlines, and promoting tourism. Through all of these structures, coral reefs generate hundreds of billions of dollars to the global economy each year (Mora et al., 2011; NOAA Ocean Service Education, 2017; Reef Relief, 2019). In the GoM alone, reef-related expenditures generate more than \$4.4 billion annually in southeast Florida and reef recreation supports more than 70,000 jobs (Carnes, 2010). The many threats posed by climate change to coral reefs, including bleaching and acidification, motivates a pointed look toward reef systems lining GoM coastlines. The reefs that protect the coastline of the GoM are subject to unique regional ocean changes, warranting this geographically-focused study.

Multiple secondary impacts are likely to accompany rising temperatures and climate change in the GoM. Warm SSTs drive stronger tropical storms (Molina et al., 2016; Murakami et al., 2018). In recent decades, major hurricanes (e.g., Mitch, which decimated reefs in Belize) have wiped out coral reefs. During the 2005 hurricane season, coral reefs in the GoM (Flower Garden Banks, the Dry Tortugas, and the Florida Keys) experienced extensive damage; however, these reefs were spared from widespread bleaching event that occurred that year because the passing hurricanes reduced water temperatures (Stone et al., 2005; Gierach and Subrahmanyam, 2008; Wilkinson and Souter, 2008). Recovery timescales are on the order of multiple years to decades in a relatively healthy reef. In reefs that are already degraded or experience repeated storm events, recovery from physical disturbance can take even longer (Dollar and Tribble, 1993; Edmunds and Gray, 2014). Given consistent projections showing increases in the frequency and severity of tropical storms and Gulf hurricanes (Balaguru et al., 2018; Klotzbach et al., 2018; Trenberth et al., 2018; Ting et al., 2019), it is likely that high storm surge and wave impacts could further degrade GoM reefs, especially if they are less robust due to weakened cementation. This could initiate a positive feedback loop: coral reefs in the GoM protect local shorelines and infrastructure through wave energy dissipation, prevention of shoreline erosion, import of sediments, and via stabilizing mangrove and seagrass populations (NOAA Ocean Service Education, 2017; Reef Relief, 2019). Storm-driven losses of coral reefs may further reduce the resilience of the built environment along Gulf coastlines. Indeed, the economic damages imparted by hurricane activity in Texas and Florida in 2017 alone surpassed a staggering 125 billion dollars (Klotzbach et al., 2018). Some of these storms also cause unpredictable damages such as low salinity runoff or pollution (Rice University, 2019).

Additional anthropogenic stressors will interact to further degrade coral reefs in the GoM. These include increased sedimentation, fresh-water run-off and pollution due to development (Yeats et al., 1978; Nelsen et al., 1994; Osterman et al., 2008; Liu et al., 2013; Ren et al., 2015), and nutrification, particularly due to agricultural sources such as fertilizers (Nelsen et al., 1994; Osterman et al., 2008) and hydrocarbon extraction (Guzman and Jarvis, 1996). A combination of the above can lead to hypoxia (Justić et al., 2003; Osterman et al., 2008; Rabalais et al., 2010). Many of these effects favor the growth of coral competitors, such as macroalgae, that can further hamper reef development and growth (Gorgula and Connell, 2004; Vermeij et al., 2010). In a healthy ecosystem, herbivorous fishes and invertebrates can help to balance the overgrowth of algae (Williams and Poulnin, 2001; Bellwood et al., 2006; Smith et al., 2010); however, the physiology and reproductive capabilities of these organisms are also compromised by climate change and ocean acidification (Munday et al., 2008; Pankhurst and Munday, 2011). Further, because fish depend on the structural complexity

of reefs (Graham and Nash, 2013), losing coral reefs can lead to a feedback where loss of fish leads to algae overgrowth, which then dampens reef development, leading to even fewer fish (Graham et al., 2007; Wilson et al., 2010; Nyström et al., 2012).

## 6.2. Adaptation and Mitigation

The ability of GoM reefs to adapt to the stressors outlined in section 3 is an open question. Corals may be able to survive in warmer temperatures through adaptation, epigenetic modification, or the utilization of thermal-tolerant symbionts (Howells et al., 2012; Palumbi et al., 2014; Dixon et al., 2018; Sully et al., 2019); however, acclimatization to acidification has not yet been demonstrated (Comeau et al., 2019). The adaptability of coral symbionts will likely play a key role in determining thermal resistance of GoM reefs. Reef structures may acclimate rather than completely dying off if symbiont species more tolerant to high temperatures and bleaching re-occupy coral tissues over time (Hughes et al., 2003) or if corals can acquire thermal tolerant symbionts (Howells et al., 2012). Coral reef generation times are on the order of several years and depend on favorable environmental conditions (Hughes et al., 2003), so if existing corals in a given community are stressed, they will not spawn. Bleaching onset research indicates adaptation via re-population of thermally tolerant symbionts occurs within 0–0.5° warming; given that most GoM SSTs warm by more than 2° in the CESM RCP8.5 ensemble mean, we must not discount the fact that zooxanthellate Gulf corals may disappear completely by 2100. Future reefs may shift toward populations typical of the late Cretaceous and early Cenozoic, when reefs were dominated by non-corals (i.e., rudists, sponges and red algae) and azooxanthellate coral types (Bryan, 1991; Kiessling and Baron-Szabo, 2004).

Coral communities could also migrate toward more favorable environments and regrow. The rate and direction of climatic shifts will likely drive coral species shifts across the GoM, and these changes in climate velocity (Pinsky et al., 2013) are crucial to robust predictions of reef survival (**Figure S7**). Projected climate velocities for the GoM in terms of SST changes indicate rapid shifts of up to 10 km/yr throughout the forthcoming twenty-first century (**Figure S7**). While some marine species can migrate rapidly, coral reefs are largely stationary and migrate over generations of new reefs established in new regions. The establishment process requires many factors to encourage reef growth, including the presence of crustose coralline algae (Morse et al., 1994, 1996; Heyward and Negri, 1996), low sediment input (Gilmour, 1999), lithified substrate (Jackson, 1977; Purkis et al., 2011), and precise water quality conditions (Negri and Hoogenboom, 2011). On evolutionary timescales, reefs often shift poleward to avoid thermal stress (e.g., Kiessling, 2001) and this has already been documented in geologically-recent and modern reefs (e.g., Greenstein and Pandolfi, 2008; Yamano et al., 2011; Pandolfi and Kiessling, 2014). Poleward migration may not be a feasible option since GoM corals are limited latitudinally and are already positioned at their northern limit (e.g., Kiessling, 2001; Jones et al., 2019).

It is also hypothesized that reefs may find refuge from thermal stress in the surface waters by migrating to deeper habitats where temperatures are lower (Riegl and Piller, 2003; Bongaerts et al., 2010; Bridge et al., 2013; Padilla-Gamiño et al., 2019); this has occurred to some extent in Pulley Ridge, though recent surveys have found that these deep water hermatypic corals are not surviving (Slattery et al., 2018). Deeper water, mesophotic reefs have distinct communities and ecosystems when compared to shallow water reefs (e.g., Bongaerts et al., 2010; Pereira et al., 2018; Rocha et al., 2018); thus these deeper habitats likely would make poor refuges for shallow-water reef species. Vertical migration in the water column is harder for the reef builders, which require clear water and sunlight for photosynthesis. With sea level rise, many deeper reefs that have narrow depth ranges will not be able to keep pace with increasing water depth. Furthermore, mesophotic reefs inhabit waters with lower $\Omega_{aragonite}$ values, leading to the possibility that GoM reef communities would experience an environmental pincer movement: thermal stress from above as well as acidification stress from below (which would also make pole-ward migration problematic). In general, there are myriad conditions that would prevent this from being a feasible adaptation for coral survival on a large scale (Smith et al., 2016; Bongaerts et al., 2017).

Even if corals adapt or acclimatize to some environmental stresses (e.g., temperature or salinity), they may not be able to adapt or acclimate to all of them (e.g., ocean acidification) (Okazaki et al., 2013; Comeau et al., 2019). A controversial solution involves geoengineering via reef-shading, covering large portions of reefs to reduce direct heating via solar radiation (Coelho et al., 2017). This is an expensive and precarious solution which cannot bolster coral resistance to thermal stress. Increasing coral tolerance through assisted evolution, such as selective breeding, assisted gene flow, transplanting of juveniles, epigenetic programming or conditioning, and coral microbiome manipulation may be viable within the next decade (Horoszowski-Fridman et al., 2011; van Oppen et al., 2015; Van Oppen et al., 2017), and would directly bolster reef resiliency to ecosystem collapse.

## 6.3. Looking Ahead

The marine organisms occupying the GoM evolved in the last 420,000 years; now, atmospheric $\rho CO_2$ levels dramatically exceed ice core measurements of greenhouse gas concentrations spanning their entire evolutionary history (Hoegh-Guldberg et al., 2007). In an even broader geologic context, the rate of greenhouse gas emissions, and therefore the rate of climate change, during the Paleocene-Eocene Thermal Maximum was orders of magnitude slower than the modern warming trend, meaning modern climate change is unprecedented in geological history (Zeebe et al., 2016). Given the innumerable benefits that coral reefs in the GoM provide to coastal societies, it is our hope that this work sheds light on future risks specific to this highly vulnerable ecosystem. While reef systems can recover from bleaching events, reefs generally require decades to return to their pre-bleached state (Frieler et al., 2013). It is likely that the accelerating rate of global climate change will exceed the speed at which corals reefs and their symbionts can adapt (multiple decades), a defining feature of abrupt climate change (Hughes et al., 2003; Frieler et al., 2013).

Widespread degradation of GoM reefs is especially likely under the RCP8.5 "business-as-usual" scenario considered in this work. To avoid consequential environmental, social, and economic damages (e.g. Chen et al., 2015) and promote long-term conservation and recovery of GoM coral reefs, substantial, rapid reductions of anthropogenic greenhouse gas emissions are past-due.

## DATA AVAILABILITY STATEMENT

The datasets analyzed for this study are housed in the Earth System Grid, a publicly available climate model output repository (https://www.earthsystemgrid.org/). Additional data information and our analysis code is available in the **Supplementary Material**.

## AUTHOR CONTRIBUTIONS

SD, RM, and KD designed the study and formulated scientific questions. SD extracted, post-processed and analyzed climate model data, and formulated coral stressor conditions with assistance from RM and KD. MT modeled the ocean carbon changes and assisted in estimating drivers of acidification as a coral stressor with help from RM. RM, KD, and AW contextualized future GoM change with information surrounding coral communities in past climates. All authors contributed to the writing of the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00691/full#supplementary-material

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