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# A 3,000-year lag between the geological and ecological shutdown of Florida's coral reefs

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## Abstract

The global-scale degradation of coral reefs has reached a critical threshold wherein further declines threaten both ecological functionality and the persistence of reef structure. Geological records can provide valuable insights into the long-term controls on reef development that may be key to solving the modern coral-reef crisis. Our analyses of new and existing coral-reef cores from throughout the Florida Keys reef tract (FKRT) revealed significant spatial and temporal variability in reef development during the Holocene. Whereas maximum Holocene reef thickness in the Dry Tortugas was comparable to elsewhere in the western Atlantic, most of Florida's reefs had relatively thin accumulations of Holocene reef framework. During periods of active reef development, average reef accretion rates were similar throughout the FKRT at ~3 m/ky. The spatial variability in reef thickness was instead driven by differences in the duration of reef development. Reef accretion declined significantly from ~6,000 years ago to present, and by ~3,000 years ago, the majority of the FKRT was geologically senescent. Although sea level influenced the development of Florida's reefs, it was not the ultimate driver of reef demise. Instead, we demonstrate that the timing of reef senescence was modulated by subregional hydrographic variability, and hypothesize that climatic cooling was the ultimate cause of reef shutdown. The senescence of the FKRT left the ecosystem balanced at a delicate tipping point at which a veneer of living coral was the only barrier to reef erosion. Modern climate change and other anthropogenic disturbances have now pushed many reefs past that critical threshold and into a novel ecosystem state, in which reef structures built over millennia could soon be lost. The dominant role of climate in the development of the FKRT over timescales of decades to millennia highlights the potential vulnerability of both geological and ecological reef processes to anthropogenic climate change.

## KEYWORDS

bioerosion, climate change, coral reefs, ecological tipping points, Holocene, reef accretion, sea level, western Atlantic

## 1 | INTRODUCTION

Climate change and other anthropogenic disturbances have reshaped the ecological and geological dynamics of coral-reef ecosystems

(Hughes et al., 2017; Kuffner & Toth, 2016; Perry et al., 2014). In just the past few decades, coral populations have declined by ~50% globally (Bruno & Selig, 2007; Jackson, Donovan, Cramer, & Lam,

2014), putting more than a third of coral species at risk of extinction (Carpenter et al., 2008), and leaving behind a landscape of degradation that would have been unrecognizable to coral-reef scientists just fifty years ago (Hughes et al., 2017; Jackson et al., 2014). Although acclimatization, adaptation, and human intervention may still have potential to slow or even reverse these declines (Hughes et al., 2017; van Oppen et al., 2017), the scale and magnitude of recent reef degradation has now reached a critical threshold wherein further disturbances threaten not only the ecological functionality of reef ecosystems, but also their persistence as geological structures (Kennedy et al., 2013; Kuffner & Toth, 2016).

Continuing loss of living coral (Bruno & Selig, 2007; Jackson et al., 2014) shifts to non-framework-building taxa (Kuffner & Toth, 2016; Perry et al., 2015; Toth et al., 2014), and decreasing rates of coral calcification (Cantin, Cohen, Karnauskas, Tarrant, & McCorkle, 2010; De'ath, Lough, & Fabricius, 2009) reduce carbonate production and flatten reef structure (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009; Perry et al., 2013, 2014, 2015, 2018). Coupled with the threat of further declines in calcification and enhanced bioerosion due to ocean acidification (Enochs et al., 2015; Hughes et al., 2017), ongoing disturbances are pushing reefs toward a tipping point beyond which reef erosion, rather than reef growth, will dominate (Kennedy et al., 2013; Perry et al., 2013, 2014, 2015, 2018; Yates, Zawada, Smiley, & Tilling-Range, 2017). Given that measurable declines in reef elevation (Yates et al., 2017) and structural complexity (Alvarez-Filip et al., 2009) have already been observed in some locations, there is a critical need to better understand how reef-framework production and erosion respond to environmental perturbations over decadal to millennial timescales (Kuffner & Toth, 2016; Perry et al., 2014).

In many locations, the modern collapse of coral-reef ecosystems is without precedent in recent millennia (e.g., Aronson, Macintyre, Precht, Murdoch, & Wapnick, 2002; Aronson, Macintyre, Wapnick, & O'Neill, 2004; Montaggioni, 2005); however, locations that have experienced pre-anthropogenic shutdowns in reef development can provide valuable insights into the modern coral-reef crisis (Budde-meier & Hopley, 1988; Hubbard, 1988, 2013; Perry & Smithers, 2011; Toth et al., 2012; Toth, Aronson, et al., 2015; Toth, Kuffner, Cheng, & Edwards, 2015). The subtropical setting of the FKRT is near several critical environmental thresholds for reef development (Kleypas, McManus, & Meñez, 1999; Precht & Aronson, 2004; Precht & Miller, 2007), suggesting that Florida's reefs may be especially sensitive to any perturbations to the ecosystem state. Furthermore, although most of Florida's coral reefs have degraded significantly over the last several decades, there is also high spatial variability in coral cover (Guest et al., 2018; Murdoch & Aronson, 1999; Ruzicka et al., 2013), rates of coral calcification (Kuffner, Hickey, & Morrison, 2013), and reef erosion (Yates et al., 2017) across the FKRT, which indicates that natural gradients in environmental conditions may modulate reef development.

Here, we present the first comprehensive reconstruction of Holocene coral-reef accretion across the ~350 km extent of the Florida Keys reef tract (FKRT). Our reconstruction of reef

development is based on analysis of 46 reef cores collected throughout the region and 147 radiometric ages from those cores. By evaluating the spatial and temporal variability in reef thickness, rates of accretion, and the timing of geological senescence on the FKRT, we examine the long-term controls on reef development and the likely drivers of a decline in reef accretion that predated modern coral-reef degradation by thousands of years.

## 2 | MATERIALS AND METHODS

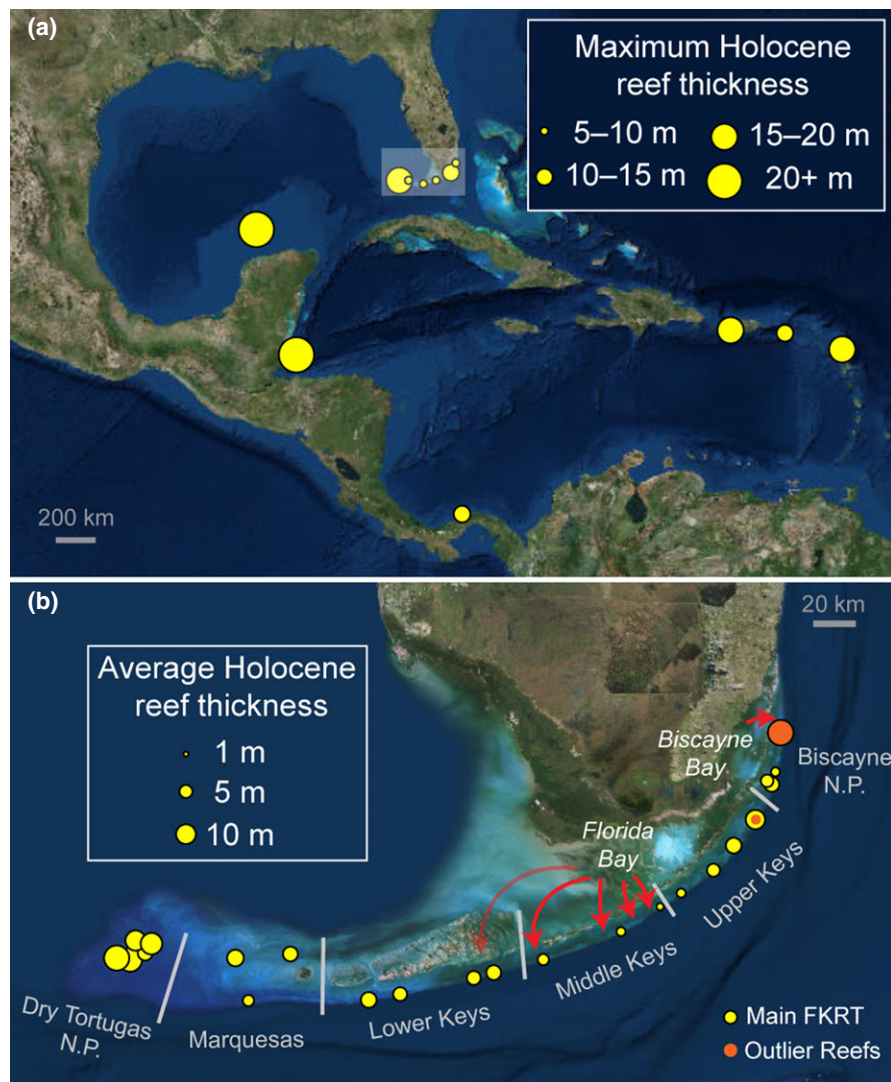
### 2.1 | Regional setting

The FKRT extends ~350 km along Florida's shelf edge, ~5–7 km seaward of the islands of the Florida Keys, from Biscayne National Park (N.P.) in the northeast to the Dry Tortugas N.P. in the southwest (Figure 1; Lidz, Reich, & Shinn, 2007, 2003). Although the FKRT is often considered to be the third largest reef system in the world, the shelf-edge reef tract is not continuous. Instead, Holocene reefs have grown preferentially on topographic highs of the Pleistocene bedrock (Lidz et al., 2003; Shinn, Hudson, Halley, & Lidz, 1977). Off-shore of the main FKRT in some locations are a series of "outlier reefs" that grew on elevated Pleistocene terraces during the early Holocene (Lidz et al., 2003; Lidz, Hine, Shinn, & Kindinger, 1991). Small patch reefs are also abundant inshore of the FKRT, but the geologic history of these reefs is largely unknown (Lidz et al., 2007). See Lidz et al. (2003) and Shinn and Lidz (2018) for a comprehensive review of the geological setting of the FKRT.

The FKRT can be divided into six subregions based on unique physical settings of the contemporary environments (c.f. Murdoch & Aronson, 1999): Dry Tortugas N.P., the Marquesas, the Lower, Middle, and Upper Florida Keys, and Biscayne N.P. (Figure 1b). Conditions are most stable in the open-ocean environments of Dry Tortugas N.P. and the Marquesas (see Toth, Cheng, Edwards, Ashe, & Richey, 2017a). In the Keys subregions and Biscayne N.P., outflows from Florida Bay and Biscayne Bay, respectively, can transport water masses with highly variable temperature, salinity, nutrients, and turbidity onto the reefs: conditions that are generally unfavorable or "inimical" to coral-reef development (sensu Ginsburg & Shinn, 1994).

### 2.2 | Collection and description of Holocene reef cores

The U.S. Geological Survey (USGS) Core Archive (<https://doi.org/10.5066/F7319TR3>) housed at the USGS Coastal and Marine Science Center in St. Petersburg, Florida, contains an extensive collection of reef cores from throughout the FKRT (Reich et al., 2012). This archive, which includes 44 Holocene reef cores collected from 1976 to 2009 and 14 new cores collected from 2014 to 2017 for this study, represents the legacy of more than half a century of geological research programs in the region (Reich et al., 2012; Shinn & Lidz, 2018; Toth, Stathakopoulos, & Kuffner, 2018). Data from all 58 cores are summarized in Table S2.



**FIGURE 1** Holocene reef thickness throughout the western Atlantic and within the Florida Keys Reef Tract (FKRT). (a) Comparison of maximum thickness (yellow circles) for each subregion of the FKRT to other reefs in the western Atlantic: Alacran reef, Mexico (Macintyre, Burke, & Stuckenrath, 1977), the Belize Barrier Reef (Gischler & Hudson, 2004), Galeta Point, Panama (Macintyre & Glynn, 1976), La Parguera, Puerto Rico (Hubbard, 2013), St. Croix, U.S. Virgin Islands (Hubbard, 2013), and Nonesuch Bay, Antigua (Macintyre et al., 1985). The shaded area in (a) is expanded in (b), which provides a map of core locations (circles) within the six subregions of the FKRT. The size of the circles is proportional to the average Holocene reef thickness at a given reef. Colors of the circles distinguish outlier reefs (orange) from the main FKRT (yellow). At Carysfort Reef in the Upper Keys, these reefs are only separated by ~200 m. Locations of outflows from Florida and Biscayne Bays onto the FKRT are indicated by red arrows. Impacts are somewhat diffused in the Lower Keys, as indicated by the faded arrow. Imagery provided by ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, AeroGRID, IGN, and the GIS User Community

The majority of the cores were collected using the USGS hydraulic wireline drilling system (Shinn et al., 1977). During collection, SCUBA divers position the hydraulic drill over the reef by suspending it from a cable attached to an aluminum tripod. Core barrels and a water hose are then attached to the drill, and a water pump is used to force seawater down the borehole to facilitate coring. Cores are collected using a double-barrel system, in which successive 5-ft (~1.5 m) sections of reef framework are cored and then recovered by removing the inner barrel, while the outer barrel remains in the reef. Three of the cores (LK-SK-6, UK-CF-1, and UK-CF-4; Table S1) were collected using the SCARID hydraulic drilling system developed by D.K. Hubbard

(Hubbard, 2013). The general concept of the SCARID system is the same as the USGS system, but instead of being suspended by a cable from a tripod, the drill is fixed to a rigid frame (Hubbard, 2013).

The cores were generally collected from reef-slope environments, between 0 and –10 m depth relative to mean sea level (MSL; Table S1; Fig. S1), which are characteristic of the shallow-water, offshore reef habitats of the FKRT (Lidz et al., 2007). To ensure that all the cores included in our study were from a similar environmental setting, we used the most recent reconstruction of Holocene sea-level variability in south Florida (Khan et al., 2017) to estimate the paleodepths of all dated intervals in the cores (sensu Hubbard, 2009; Fig. S2 and

Table S2). We excluded three cores (DT-GB-5, DT-TB-1, and DT-TB-2; Table S1) that contained intervals deposited in depths significantly deeper than 10 m below MSL (i.e., the full 95% confidence intervals [CIs] of the estimated paleodepths were deeper than 10 m; Table S2). More than 90% of the remaining intervals were from paleodepths less than 6 m (Fig. S2). We note that because of uncertainties in both the model of relative sea level and the estimates of depths in the cores, the paleodepth estimates for 28 intervals are slightly above MSL; however, the paleodepths were only significantly higher than MSL (i.e., the 95% CI did not overlap with zero) in nine cases.

Although we include data on reef thickness from the outlier reefs at Fowey Rocks in Biscayne N.P. and Carysfort Reef in the Upper Keys in Figure 1b, they were not included in our reconstruction of reef development because these reefs represent a separate reef system offshore of the main FKRT (Lidz et al., 1991, 2003). We also did not include data from the Marquesas in our reconstruction because the sample size from this subregion was too low (i.e., only three cores, six intervals). Finally, we excluded records from two cores (DT-LB-2 and LK-WS-1) that were taken from non-reef-building habitats (e.g., on loose sediment in reef grooves). The reasons for excluding particular cores are summarized in Table S2.

Our reconstruction of reef development was based on analysis of 46 cores collected from the five main subregions of the FKRT: 13 from Dry Tortugas N.P., eight from the Lower Keys, 10 from the Middle Keys, seven from the Upper Keys, and eight from Biscayne N.P. Although data from some of the cores have been published previously, existing core-based reconstructions of reef development on the FKRT were generally site-specific (Table S1; Shinn & Lidz, 2018). Shinn et al.'s (1977) compilation of 17 radiocarbon ages from seven reefs was the only other study to evaluate trends in Holocene reef development across the FKRT. Our study builds upon the foundation of previous studies to develop a comprehensive and quantitative reconstruction of the history of Holocene reef accretion throughout the FKRT.

We estimated percent recovery in the cores using core photographs (Toth et al., 2018) by dividing the projected surface area of core constituents in an interval by the theoretical projected surface area of the interval based on core penetration (as in Toth, Kuffner, et al., 2015). Recovery of intervals in the cores was highly variable (Toth et al., 2018; ranging from 25.6% to 55.0% among subregions) and averaged  $\sim 42.3\%$  ( $\pm 1.7$  standard error [SE]) for intervals included in our analysis. This degree of recovery is typical for western Atlantic reef frameworks, which are often dominated by unconsolidated sediments and void spaces (Hubbard, 2009). Although allochthonous deposits are common on many reefs in the western Atlantic (Blanchon et al., 2017; Hubbard, 2009), there were no statistically significant age reversals in any of our cores, suggesting that the cores used in this study were primarily composed of autochthonous reef framework. Detailed core logs are provided in Toth et al. (2018).

### 2.3 | Radiometric dating of Holocene reef cores

All corals dated in this study were carefully examined prior to analysis and were determined to be in excellent taphonomic condition

(i.e., less than  $\sim 20\%$  bioerosion and/or infilling; c.f. Toth et al., 2012). Some corals were also screened with X-ray diffraction or scanning electron microscopy, which confirmed that diagenesis was minimal (summarized in Toth, Cheng, Edwards, Ashe, & Richey, 2017b). The majority of the radiocarbon ages were determined using accelerator mass spectrometry (AMS) at either the Lawrence Livermore National Laboratory (processed at the USGS Radiocarbon Laboratory in Reston, VA) or the National Ocean Sciences AMS (NOSAMS) facility at Woods Hole Oceanographic Institution. Seventeen samples analyzed in previous studies (see Toth et al., 2018) were dated using standard radiometric dating at the University of Miami Radiocarbon Laboratory, Beta Analytic, Inc., or Geochron Laboratories. We report conventional  $^{14}\text{C}$  ages, corrected for fractionation of  $^{13}\text{C}$ . The  $\delta^{13}\text{C}$  of the samples was either measured by University of California, Davis Stable Isotope Laboratory or NOSAMS or, if not measured, was assumed to be  $0 \pm 3\%$  (Törnqvist, Rosenheim, Hu, & Fernandez, 2015). The conventional radiocarbon ages were calibrated in Calib 7.0.2 (<https://calib.org/calib/>; Reimer & Reimer, 2001) using time-varying estimates of the local reservoir age,  $\Delta R$ , for the near-shore and open-ocean environments of the FKRT (Toth et al., 2017a, 2017b). The full radiocarbon dataset is available in Toth et al. (2018). Two additional ages included in our study were determined by U-series analysis using multicollector inductively coupled plasma mass spectrometry at Xi'an Jiaotong University in China. The U-series data were screened according to the procedures outlined in Toth et al. (2017b), where the complete U-series data can be found.

Accretion rates can be artificially inflated when sequential dates within a core are similar enough that the entire layer could have been deposited simultaneously (Toth et al., 2012). To avoid this potential complication, we determined whether the differences between any pair of sequential dates that had conventional  $^{14}\text{C}$  ages or calibrated U-series ages within 500 years of one another were significant using the standard error of the difference ( $SE_{\text{diff}}$ ) to calculate 95% CIs of the two ages. In the 46 instances in which the 95% CI of two sequential dates in a core overlapped (i.e., were not significantly different), we omitted the age with a  $1\sigma$  uncertainty  $> 50$  years or the age that allowed for the most even spread of ages within the core. Ultimately, we retained 145 radiocarbon and 2 U-series ages ranging from 8,637 years before present (BP; with "present" being 1950) to present (Fig. S3; Toth et al., 2018).

### 2.4 | Quantifying reef thickness

We quantified the thickness of the Holocene reef framework using the core records that reached the Pleistocene bedrock. We only included records where we were able to confidently identify the Holocene–Pleistocene boundary on the basis of at least one of the following three criteria: (a) ages from samples on either side of the boundary, (b) the presence of a soilstone ("caliche") crust characteristic of the Holocene–Pleistocene boundary in south Florida, or (c) a clear distinction between the Holocene and Pleistocene based on diagenetic alteration to calcite or a shift from coral framework to carbonate grainstones or boundstones. In the 37 cores that met



these criteria, the estimated depth of core penetration to the base of the Holocene reef framework was used to quantify reef thickness. Core penetration was measured in the field based on the total length of the core barrel that had been drilled into the reef. In eight of the cores, there was a sand layer between the Holocene and Pleistocene facies, which was not included in the reef thickness estimates because it could not be definitively assigned to the Holocene epoch (Table S1). We compared our estimates of maximum Holocene reef thickness from each subregion on the FKRT with published data on maximum Holocene reef thickness elsewhere in the western Atlantic.

## 2.5 | Evaluating trends in reef accretion

We determined the timing of the initiation of reef accretion based on ages in the cores that were within 1 m of the Holocene–Pleistocene boundary (Table S1). Cores that did not reach the Pleistocene, did not have a clear Pleistocene boundary, or did not have an age within 1 m of the Holocene–Pleistocene transition, were not included in this dataset. To evaluate the impact of antecedent topography on the timing of reef initiation, we also calculated the total depth to the Pleistocene bedrock (relative to MSL) by adding the water depth where the core was collected to the total Holocene reef thickness (Table S1).

Rates of vertical reef accretion, in meters per thousand years (m/ky), were calculated by dividing the thickness of a section of reef by the time span over which it was deposited, based on median probabilities of the radiometric age calibrations. We calculated the average rates of reef accretion over the lifespan of the reefs (i.e., for each core) by dividing the length of the interval between the deepest coral dated in the core and the shallowest coral dated in the core by the difference in the ages of those corals (Table S1). Similarly, we calculated accretion rates for each dated interval in the cores by dividing the length of the interval by its time span. Temporal variability in reef accretion during the Holocene was evaluated by averaging reef accretion rates from all cores ( $\pm$ SE) within 500-yr bins from 8,500 BP to present for the entire FKRT and from 7,000 BP to present for each subregion (Table S3). We did not distinguish between sections of reef framework composed of *Acropora palmata* or massive coral framework when evaluating reef accretion, as Hubbard (2009) recently demonstrated that there was no significant difference in accretion rates between these facies.

The geological collapse of a coral reef occurs when reef accretion slows to the point that it is no longer keeping pace with the rate of sea-level rise (i.e., “drowned” or “relict” reefs [Schlager, 1981; Neumann & Macintyre, 1985] and reef “turn offs” [Budde-meier & Hopley, 1988]). Here, we refer to reefs that have experienced this sort of shutdown in reef accretion as “geologically senescent” (after Lidz & Shinn, 1991). To evaluate the timing of reef senescence across the FKRT, we compared the rates of sea-level rise from Khan et al.’s (2017) reconstruction of Holocene sea-level change in south Florida to the rates of reef accretion of intervals in our cores. We considered a reef to be senescent when the rate of

reef accretion was more than 1 m/ky (i.e., the average  $2\sigma$  uncertainty of the RSL rate reconstruction) below the contemporaneous rate of RSL rise. We used the age delimiting this transition to quantify the timing of reef senescence. The approximate ages of the reef surface (i.e., core-top ages) were used to estimate the timing of reef senescence in cases where the measured rates of reef accretion in the core never dropped significantly below the rate of RSL rise. These ages were always from samples in the first barrel (upper 1.5 m [5 ft]) of the core and were generally within 0.5 m below the reef surface. Four cores (LK-MG-1, LK-WS-1, MK-AR-2, and MK-TN-1; Table S1) were not included in the analysis of reef senescence because their accretion rates were always more than 1 m lower than the rate of RSL rise.

Records from four other cores (UK-GR-3, UK-GR-5, BP-AR-1, and BP-LR-1; Table S1) suggested that those reefs only began to keep pace with the rate of RSL rise during the late Holocene. Because these cores have no record of significant reef accretion during the middle Holocene when the rest of the FKRT was actively accreting (three of four initiated during the late Holocene), we suggest that they represent a separate, more recent period of reef development, and they were excluded from our analysis of the timing of reef senescence. Core UK-GR-3, which had a bottom age of 1,117 BP, accreted on pace with sea level until at least 1978, when it was collected. Including the other three “late Holocene” cores, which did record reef senescence, did not have a substantial impact on our results: we still found a significant difference in the timing of senescence among subregions (linear mixed-effects model [LME]:  $F_{4,15} = 4.73$ ,  $p = 0.01$ ), with significantly earlier termination of reefs in the Middle Keys relative to the Dry Tortugas (Tukey-like test:  $p = 0.02$ ), and timing of senescence was still a significant predictor of reef thickness (linear regression [LR]:  $F_{1,30} = 5.69$ ,  $p = 0.03$ ,  $r^2 = 0.13$ ).

## 2.6 | Statistical analyses

We compared the thickness of the Holocene reefs, the timing of reef initiation, the depth to the Pleistocene bedrock, the average rates of reef accretion, and the timing of reef senescence among subregions using the linear mixed-effects models in the R package “nlme,” with site treated as a random factor. Pairwise comparisons among subregions were conducted using the “lsmeans” package, which provides an approximation of the Tukey post-hoc test. The residuals of the models met the assumption of normality with untransformed data on reef thickness, depth to the Pleistocene, and reef initiation (Shapiro–Wilk tests:  $W = 0.98$ ,  $p = 0.68$ ,  $W = 0.98$ ,  $p = 0.73$ , &  $W = 0.93$ ,  $p = 0.07$ , respectively), log-transformed data on overall reef accretion ( $W = 0.97$ ,  $p = 0.35$ ), and rank-transformed data on the timing of reef senescence ( $W = 0.97$ ,  $p = 0.41$ ). We used linear regression analysis to test the following hypotheses: (a) the timing of reef initiation was related to the depth of antecedent topography (depth to the Pleistocene bedrock); (b) the rate of sea-level rise or paleodepth were significant predictors of the rate of reef accretion; and (c) subregional differences in the average rate of

reef accretion or the timing of senescence were responsible for the spatial variability in reef thickness. The residuals of the model of timing of reef senescence vs. thickness met the assumption of normality using the raw data (Shapiro–Wilk test:  $W = 0.98$ ,  $p = 0.92$ ). The residuals of the model of paleodepth vs. reef accretion met the normality assumption after log transformation (Shapiro–Wilk test:  $W = 0.99$ ,  $p = 0.55$ ). For the models of average reef accretion vs. reef thickness, reef initiation vs. depth to Pleistocene, and the rate of sea-level rise vs. reef accretion, the residuals of the model were not normally distributed even after log and square-root transformation so the data were rank-transformed. Subregional differences in the overall trends in reef accretion were evaluated by comparing accretion trajectories among subregions using a chi-squared test and through pairwise comparisons using a Kolmogorov–Smirnov test. All statistical analyses were performed in RStudio.

### 3 | RESULTS

The degree of reef development, as estimated by the thickness of Holocene reef framework in the cores, varied significantly among the five main subregions of the FKRT (Figure 1b; Table S1; LME:  $F_{4,15} = 10.07$ ,  $p < 0.001$ ), because reefs in Dry Tortugas N.P. were significantly thicker than elsewhere in the region (Shinn et al., 1977; Tukey-like test:  $p < 0.02$ ). Indeed, with the exception of Dry Tortugas N.P., the Holocene reefs of the FKRT are poorly developed compared with reefs elsewhere in the western Atlantic (Figure 1a; e.g., Hubbard, 2013). Elevated rates of contemporary coral calcification (Kuffner et al., 2013) and lower rates of bioerosion (Enochs et al., 2015; Kuffner et al., 2013) on some reefs in Dry Tortugas N.P. suggest that the reefs in the Dry Tortugas may simply accrete more rapidly than elsewhere on the FKRT; however, we found no significant differences among subregions in the average rates of reef accretion over the lifespan of the reefs (Fig. S4; LME:  $F_{4,15} = 0.21$ ,  $p = 0.93$ ) and no relationship between average rates of reef accretion and Holocene reef thickness (LR:  $F_{1,35} = 0.11$ ,  $p = 0.74$ ,  $r^2 = -0.03$ ). The millennial-scale trends in reef accretion during the Holocene (Figure 2) suggest that differences in the *duration* of reef growth, rather than the overall rate of reef accretion, may explain the spatial variability in reef development across the FKRT.

Reef development initiated on the FKRT between ~8,000 and 6,500 BP (Fig. S5; Table S1). Reefs began accreting earliest in Dry Tortugas N.P. and significantly later in the Middle Keys, Upper Keys, and Biscayne N.P. (LME:  $F_{4,6} = 7.28$ ,  $p = 0.02$ ; Tukey-like test:  $p = 0.03$ ). Differences in antecedent topography likely explain the relatively early initiation of reef development in the Dry Tortugas N.P. (Shinn et al., 1977), as the depth to the Pleistocene bedrock was significantly deeper in that subregion (Table S1; LME:  $F_{4,16} = 3.24$ ,  $p = 0.04$ ; Tukey-like test: Dry Tortugas vs. Middle Keys,  $p = 0.04$ ). Indeed, we found that the depth to the Pleistocene bedrock was a strong predictor of the timing of reef initiation (Fig. S6; LR:  $F_{1,22} = 13.82$ ,  $p = 0.001$ ,  $r^2 = 0.36$ ).

Rates of reef accretion were highest across all subregions during the middle Holocene and peaked during the earliest phase of reef

development at ~7,000 BP (Figure 2a). Average accretion rates throughout the FKRT were ~3.0 m/ky ( $\pm 1.4$  SE) at that time, which is similar to the average rates of Holocene reef accretion elsewhere in the western Atlantic (Aronson et al., 2002, 2004; Gischler & Hudson, 2004; Hubbard, 2009, 2013). The average rate of reef accretion declined significantly through the middle Holocene (based on the 95% CIs of accretion rates; Figure 2a), and by the late Holocene (~4,000 BP), the average rate of reef accretion was negligible at < 1 m/ky. By ~3,000 BP, 32% of the reefs in our study showed no net vertical accretion (i.e., the age of the reef surface was older than ~3,000 BP), and only ~22% were growing at a rate within 1 m/ky of the rate of sea-level rise (Khan et al., 2017; Table S2). This suggests that by the late Holocene, the FKRT had become geologically senescent (Kuffner & Toth, 2016; Lidz & Shinn, 1991).

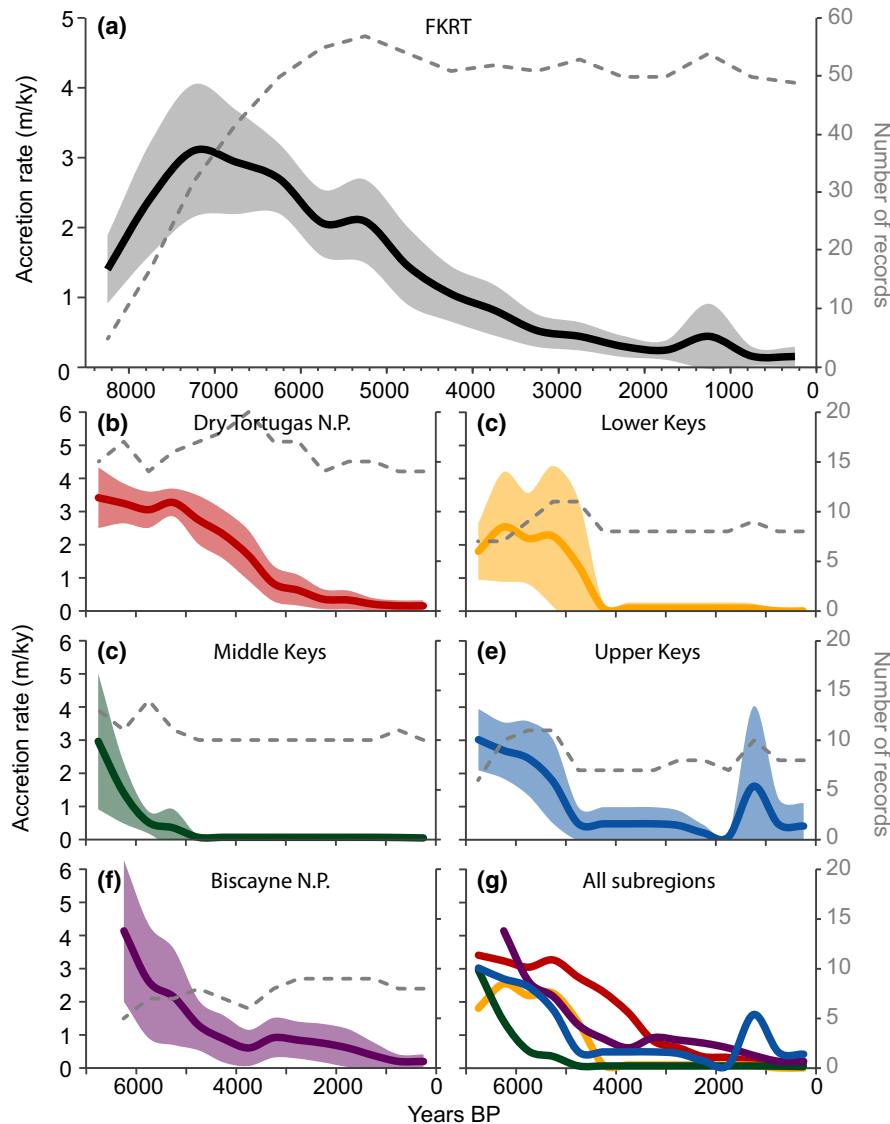
The trends in Holocene reef accretion varied significantly among subregions (Figure 2b–g; chi-squared test:  $\chi^2_{204} = 280$ ,  $p < 0.001$ ), however, as a result of the significantly earlier decline in the rate of reef accretion in the Middle Keys compared with the Dry Tortugas N.P., the Upper Keys, and Biscayne N.P. (Kolmogorov–Smirnov tests:  $p < 0.005$ , Bonferroni-corrected). Comparison of the timing of reef senescence among subregions confirmed that the decline in reef accretion was not synchronous across the FKRT (Figure 3; LME:  $F_{4,15} = 7.53$ ,  $p = 0.002$ ). Instead, reef accretion terminated significantly earlier in the Middle Keys compared with Dry Tortugas and Biscayne N.P. (Tukey-like test  $p = 0.02$ ). The timing of reef senescence was a significant predictor of reef thickness (LR:  $F_{1,28} = 10.57$ ,  $p = 0.003$ ,  $r^2 = 0.25$ ), supporting the conclusion that the duration, rather than the average rate of reef accretion drove the spatial variability in reef development on the FKRT. Records from four cores suggest that a secondary period of relatively rapid reef accretion may have initiated in a few locations during the late Holocene (Figure 2e,f; 16<sub>L</sub>, 19<sub>L</sub>, and 20<sub>L</sub> in Figure 3); however, reef accretion has been negligible across most of the FKRT for the last 3,000 years.

### 4 | DISCUSSION

The relatively poor development of the Holocene reefs on the FKRT (Figure 1) suggests that regional environmental variability may have modulated reef development in Florida over millennial timescales. Whereas most reefs elsewhere in the western Atlantic grew continuously from the early Holocene to recent decades (Aronson et al., 2002, 2004; Dullo, 2005; Gischler & Hudson, 2004; Hubbard, 1988, 2013), we show that the geological decline of Florida's reefs began ~6,000 years ago, and, by ~3,000 BP, the majority of the FKRT was geologically senescent (Figure 2). Below, we evaluate the Holocene history of Florida's reefs in relation to regional environmental variability to determine the primary controls on reef development and the likely causes of the geological shutdown of the FKRT.

#### 4.1 | Sea level and coral-reef development

Sea level is an important control on reef development over millennial timescales because the rate of vertical reef accretion is limited by

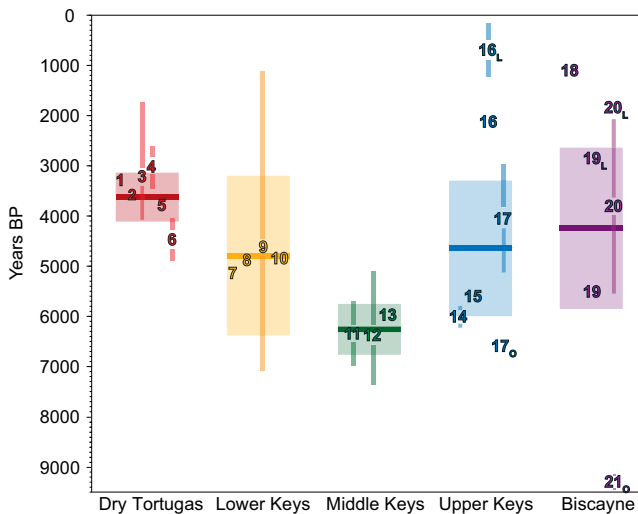


**FIGURE 2** Temporal trends in reef accretion on the Florida Keys Reef Tract (FKRT). (a) Average rates of vertical reef accretion (solid lines)  $\pm 95\%$  confidence intervals (shading) within 500-year age bins for the entire FKRT from 8,500 BP to present and (b–f) for each of the five main subregions of the FKRT from 7,000 BP to present. (g) Comparison of the average accretion rates among subregions. Dashed lines in each plot indicate the number of records used to calculate reef accretion rates within each bin. Values calculated within each age bin are plotted at the midpoint of that bin

the accommodation space provided as sea level rises (Buddemeier & Hopley, 1988; Dullo, 2005; Hubbard, 1988; Macintyre, 2007; Montaggioni, 2005; Neumann & Macintyre, 1985). Like many reefs throughout the western Atlantic, reef development initiated on the FKRT as sea level began to flood shallow-water shelf environments ~8,000–7,000 years ago (Macintyre, 2007; Neumann & Macintyre, 1985; Stathakopoulos & Riegl, 2015). The spatial variability in the depth to the Pleistocene bedrock in our records (Table S1) supports the results of regional seismic studies, which suggested that the topography of the south Florida platform slopes to the southwest (Lidz & Shinn, 1991; Lidz et al., 2003). As a result, reef habitats would have flooded earliest at the southwestern end of the FKRT (Lidz & Shinn, 1991), explaining the relatively early initiation of reef development in the Dry Tortugas (Fig. S5). As sea level rose, the

extent of the FKRT gradually expanded to the northeast, and by ~7,000 BP, there was sufficient accommodation space to allow rapid reef accretion throughout the region (Table S2; Figure 2; Fig. S5; Khan et al., 2017). The early history of Florida's Holocene reefs supports the conclusion of previous studies that the interaction between sea level and antecedent topography was a significant control on the timing of reef initiation (Hubbard, 1988; Lidz & Shinn, 1991; Lidz et al., 2003; Shinn et al., 1977). Similarly, accommodation space may have influenced the absolute rates of reef accretion of individual reefs, as we found a significant positive relationship between the rates of reef accretion and paleodepth on the FKRT (LR:  $F_{1,143} = 30.44$ ,  $p < 0.001$ ,  $r^2 = 0.17$ ; Fig. S7). There is less evidence, however, that sea level was a dominant driver of the demise of the FKRT ~3,000 years ago.





**FIGURE 3** Timing of reef senescence among subregions of the Florida Keys Reef Tract (FKRT). Average age of reef senescence is indicated by solid horizontal lines and vertical shading represents the 95% confidence intervals. Sites are numbered from southwest to northeast along the FKRT as follows: 1-Loggerhead Bank, 2-Fort Jefferson, 3-Southeast Reef, 4-Pulaski North Reef, 5-East Key Reef, 6-Pulaski Light Reef, 7-Sand Key Reef, 8-Western Sambo Reef, 9-Looe Key Reef, 10-Marker G Reef, 11-Sombrero Reef, 12-Tennessee Reef, 13-Alligator Reef, 14-Crocker Reef, 15-Key Largo Reef, 16-Grecian Rocks, 17-Carysfort Reef, 18-Pacific Reef, 19-Alina's Reef, 20-Long Reef, and 21-Fowey Rocks. The average timing of senescence for each site is indicated by the vertical position of the numbers, and vertical lines indicate the full range of estimates for that site when  $N > 1$ . Outlier reefs are indicated by an "O" subscript and records from reefs that initiated during late Holocene are indicated with an "L" subscript

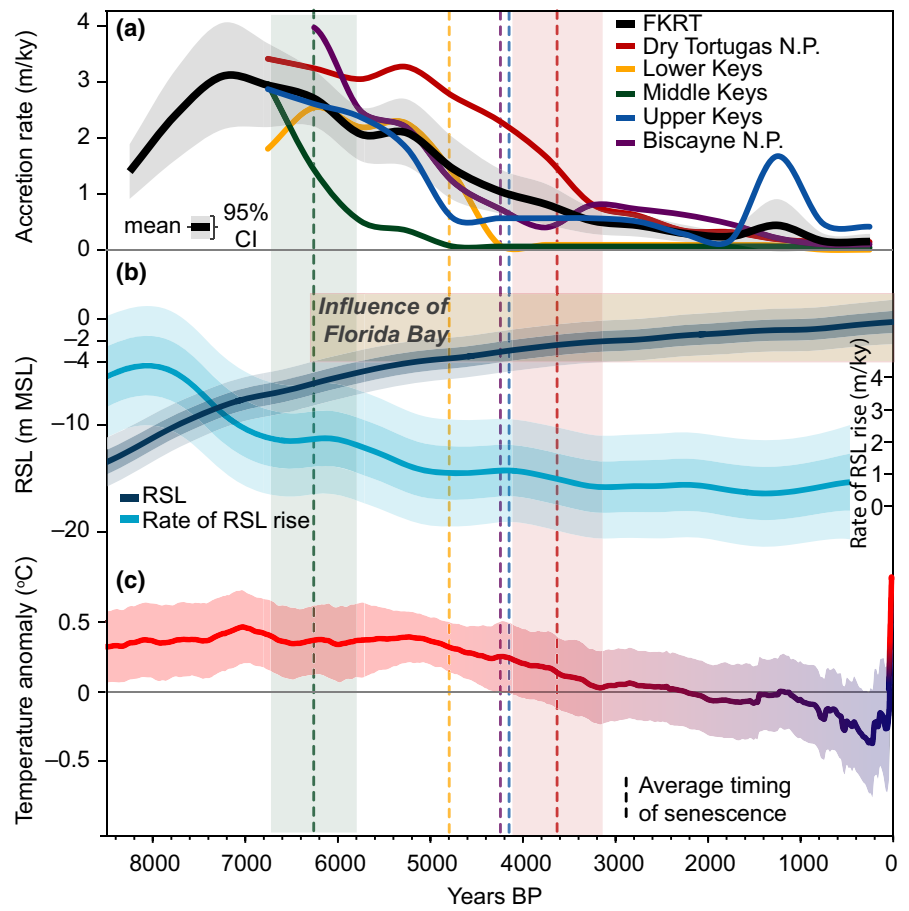
In the western Pacific, where sea level generally peaked during the middle Holocene and gradually fell during the late Holocene (Montaggioni, 2005), most reefs have been growing at or near sea level for millennia, and reef accretion has been strongly limited by accommodation space (Perry & Smithers, 2011). As a result, most Pacific reefs that initiated during the middle Holocene can no longer accrete vertically and have instead formed extensive, laterally accreting reef-flat habitats (Hubbard, 1988; Montaggioni, 2005). In contrast, sea level in the western Atlantic has been gradually rising to its present position during the Holocene (Khan et al., 2017; Figure 4b), and the extensive reef-flat habitats that are so ubiquitous in the western Pacific are not common (Dullo, 2005; Hubbard, 1988). Instead, most western Atlantic reefs continued to grow with rising sea level throughout the late Holocene (Dullo, 2005; Gischler & Hudson, 2004; Hubbard, 1988, 2013), suggesting that regional reef development was not significantly limited by accommodation space. Because the sea-level history of south Florida is very similar to that of the broader western Atlantic (Khan et al., 2017; Macintyre, 2007), lack of accommodation space was likely not the ultimate cause of reef senescence on the FKRT. Indeed, Florida's reefs were distributed across a broad range of paleodepths when they stopped keeping pace with sea level (Fig. S1; Table S2): fewer than half of

the reefs were growing within  $\sim 0.5$ – $1$  m of sea level and the paleodepth of  $\sim 30\%$  of the reefs was at least 2 m. Since  $\sim 3,000$  years ago, sea level in south Florida has risen an additional  $\sim 2$  m (Figure 4b; Khan et al., 2017) and the average water depth of the reef surfaces where the cores were collected is 4.8 m ( $\pm 0.4$  SE) at present (Fig. S1). Even if accretion on some parts of the FKRT had been limited by accommodation space at some point in its history, Florida's reefs should have resumed vertical accretion on pace with sea level as additional accommodation space was created.

The relationship between the rate of sea-level rise and the rate of reef accretion in our cores was statistically significant (Fig. S8; LR:  $F_{1,144} = 12.62$ ,  $p < 0.001$ ), but it explained only 7% of the variance in the rates of reef accretion ( $r^2 = 0.07$ ). The gradual decline in the rate of sea-level rise through the Holocene (Figure 4b; Khan et al., 2017) may have played some role in the decrease in the rates of reef accretion on the FKRT from the middle Holocene to present; however, if sea level was the primary control of reef accretion in Florida, the reefs should have continued to accrete toward sea level through the middle to late Holocene, like reefs elsewhere in the western Atlantic (Dullo, 2005; Gischler & Hudson, 2004; Hubbard, 2013), albeit at a slower rate. The fact that a third of Florida's reefs had no net accretion after 3,000 BP, and accretion rates of most the remaining reefs were significantly slower than the contemporaneous rates of sea-level rise, suggests that sea level was not the ultimate cause of reef senescence on the FKRT.

## 4.2 | The influence of inimical bank waters

Rising sea level may have contributed to the deterioration of conditions on some of Florida's reefs by establishing a connection between the FKRT and the shallow-water environments of Florida Bay when sea level reached  $\sim 4$  m below MSL (Lidz & Shinn, 1991; Lidz et al., 2003, 2007). Although Lidz and Shinn (1991) previously concluded that Florida Bay did not begin to influence the FKRT until  $\sim 2,000$  BP, the most recent sea-level reconstruction for south Florida (Khan et al., 2017) suggests that sea level could have reached  $-4$  m MSL by  $\sim 6,000$  BP (6,187–3,511 BP based on the 95% CI; Figure 4b). The shallow, restricted waters of Florida Bay experience dramatic changes in temperature, salinity, turbidity, and nutrients (Ginsburg & Shinn, 1994), conditions generally considered to be unfavorable, or "inimical," to reef development (Ginsburg & Shinn, 1994; Hallock & Schlager, 1986; Neumann & Macintyre, 1985; Precht & Miller, 2007; Schlager, 1981). Ginsburg and Shinn (1994) demonstrated that comparatively well-developed reefs on the FKRT are preferentially located adjacent to the islands of the Florida Keys, where they are putatively protected from the influence of inimical waters. In the Middle Keys, where tidal passes to Florida Bay are especially large (Figure 1b), only a few isolated reefs are present (Ginsburg & Shinn, 1994; Lidz et al., 2003). The shallow, nearshore environments between the FKRT and the islands of the Middle and Upper Keys could have been another source of inimical waters during the early phases of reef development, as they still are today (Colella, Ruzicka, Kidney, Morrison, & Brinkhuis, 2012). These



**FIGURE 4** Comparison of the trends in average reef accretion on the Florida Keys Reef Tract (FKRT) with regional environmental variability. Trends in average reef accretion (a) for the entire FKRT (black line) and within subregions (colored lines) are plotted against (b) relative sea level (dark blue line) and rates of sea-level change (light blue line) in south Florida (Khan et al., 2017) and (c) global temperature anomalies (Marcott et al., 2013). Uncertainties (shaded areas) represent 95% CIs. The period when Florida Bay would have been connected to the FKRT is shown in (b). Vertical dashed lines indicate the average timing of senescence for each subregion. Uncertainties ( $\pm 95\%$  CI) are shown for the earliest and latest subregions to become senescent: Middle Keys (green) and Dry Tortugas (red)

environments would have begun to flood during the early Holocene, when sea level reached  $-10$  m MSL (Lidz & Shinn, 1991; Lidz et al., 2003). It has been hypothesized that the periodic transport of inimical waters onto the reefs may have suppressed millennial-scale reef development on the FKRT (Lidz et al., 2003). The coincidence of reef senescence, the flooding of these shallow, nearshore environments, and the connection of Florida Bay to the reefs of the Middle Keys around 6,000 BP (Figure 4b), suggests that the negative influence of inimical waters did contribute to the poor reef development (Figure 1b) and relatively early termination of reef accretion in this sub-region of the FKRT (Figure 3). Elsewhere on the FKRT, the decline in reef development occurred significantly later (Figures 3 & 4), indicating that inimical waters were not the ultimate cause of reef shut-down throughout the FKRT.

### 4.3 | Climate and the geological senescence of Florida's reefs

Shifts in the regional climate of south Florida provide another potential explanation for the geological senescence of the FKRT during the late Holocene (Precht & Miller, 2007). Temperature is a central control on coral growth (Dullo, 2005), and, as a result, reef development is limited in areas where minimum temperatures frequently fall below  $\sim 18^{\circ}\text{C}$  (Kleypas et al., 1999). In the subtropical environments of south Florida, minimum monthly seawater temperatures typically

hover just above this threshold on modern reefs (Kuffner, 2018); however, occasional cold-water events have caused widespread mortality of important reef-building corals such as *Acropora* spp. and *Orbicella* spp. in south Florida (Lirman et al., 2011; Porter, Battley, & Smith, 1982; Precht & Aronson, 2004).

On a global scale, temperature was elevated during the early to middle Holocene (Marcott, Shakun, Clark, & Mix, 2013; Figure 4c), a period known as the Holocene thermal maximum (HTM; Haug, Hughen, Sigman, Peterson, & Röhl, 2001; Marsicek, Shuman, Bartlein, Shafer, & Brewer, 2018), relative to recent centuries. The trend of gradual cooling that has occurred since  $\sim 5,000$  BP (Marcott et al., 2013; Figure 4c) was primarily driven by declining sea-surface temperatures observed in marine records from the Northern Atlantic (Marcott et al., 2013; Marsicek et al., 2018). There are no continuous records of Holocene sea temperatures on the FKRT; however, coral-based climate reconstructions from Belize (Gischler & Storz, 2009) support the suggestion of cooling in the western Atlantic after  $\sim 5,000$  BP. Because environmental variability in the nearshore environments of south Florida is tightly linked with broader-scale changes in Atlantic climate (Flannery, Richey, Poore, & DeLong, 2016; Thirumalai et al., 2018), it is likely that the FKRT also experienced significant cooling at that time. A contemporaneous decline in the mean position of the intertropical convergence zone (ITCZ) over the Caribbean, which tracks regional temperature (Haug et al., 2001), provides further evidence for broad-scale changes in western

Atlantic climate during this period. With the exception of the recent southerly excursion of the ITCZ during the 16th century cool period known as the Little Ice Age (Thirumalai et al., 2018), the most significant equatorial migration of the ITCZ during the Holocene occurred at ~3,000 BP (Haug et al., 2001), coincident with the senescence of reefs throughout the FKRT.

We suggest that the relatively warm temperatures during the HTM (Figure 4c) provided an optimal climate for reef development in the subtropical environments of south Florida (c.f. Precht & Aronson, 2004). Indeed, the HTM was the only period when rates of Holocene reef accretion on the FKRT were on par with reefs in more tropical environments elsewhere in the western Atlantic (c.f. Gischler & Hudson, 2004; Hubbard, 2009, 2013). Reefs grew rapidly throughout the FKRT during the HTM (Figure 4a) and acroporid reefs, which are especially sensitive to temperature variability, expanded northward along the coast of southeast Florida (Precht & Aronson, 2004; Stathakopoulos & Riegl, 2015). As temperatures cooled after the HTM, reef accretion declined throughout the FKRT (Figure 4a & 4c), and the acroporid populations contracted to the south (Precht & Aronson, 2004; Stathakopoulos & Riegl, 2015). Climatic cooling was also implicated in a contemporaneous collapse of reefs in the analogous environmental setting of the northern Bahamas at ~3,000 BP (recalibrated from Macintyre, 2007). Whereas the degree of cooling after the HTM would likely have been too minimal to have significantly impacted reefs in more tropical regions of the western Atlantic, reefs in subtropical environments such as Florida and the Bahamas exist close to their lower thermal threshold (Kleypas et al., 1999; Precht & Miller, 2007). We hypothesize that the shift to a cooler climate by the late Holocene likely pushed Florida's reefs past a critical tipping point, wherein the frequency of cold-water coral mortality was sufficient to suppress reef accretion throughout the FKRT.

The impacts of regional climatic cooling may not have been synchronous across the FKRT, however. Indeed, the spatial variability in coral mortality during Florida's most recent cold-water event in 2010 mirrors the spatial trends in the timing of reef senescence (Figure 3), with the most extreme impacts near outflows from Florida Bay in the Middle Keys and shallow-water platforms in the Upper Keys (Colella et al., 2012; Lirman et al., 2011). The impact of regional cooling after the HTM was likely amplified in these shallow-water environments, which may explain the relatively early decline of reefs in the Middle Keys (Figure 2c; Figure 3), where the impacts of inimical waters are most extreme. Although early geological studies generally linked reef senescence with high turbidity and/or nutrients associated with the flooding of shallow carbonate platforms (Ginsburg & Shinn, 1994; Hallock & Schlager, 1986; Neumann & Macintyre, 1985; Schlager, 1981), recent studies have challenged this conclusion (Hubbard, 2013). In fact, although high turbidity may have been inimical to reef development in the past, it can benefit modern reefs by providing refugia from high-temperature stress (Cacciapaglia & van Woerik, 2015). The correlation of the timing of reef senescence with proximity to Florida Bay suggests that the thermal variability of shallow-water platforms may be more

important than turbidity in modulating reef development over millennial timescales (c.f. Macintyre, 2007; Precht & Miller, 2007).

We conclude that climatic cooling was likely the ultimate cause of the geological senescence of the FKRT, between ~6,000 and 3,000 BP, highlighting the central role of climate in the long-term development of coral reefs. In addition to the putative role of climatic cooling in the senescence of reefs in Florida (Precht & Aronson, 2004) and the northern Bahamas (Macintyre, 2007), colder sea temperatures were also hypothesized to have helped trigger the initiation of a prolonged hiatus in reef accretion in Pacific Panamá (Toth et al., 2012; Toth, Aronson, et al., 2015) and mass extinctions of reef assemblages during the Paleozoic (Stanley, 1988). The fact that cooling and not warming was the most likely cause of the geological senescence of Florida's reefs in the past does not mean that warming associated with anthropogenic climate change will not continue to be the major driver of reef declines now and in the future (Hughes et al., 2017). Instead, the history of reef development on the FKRT highlights the sensitivity of reefs to any perturbations that push them outside of their optimal climatic envelope, particularly in locations such as south Florida that already exist near the environmental limits for reef development (Kleypas et al., 1999; Precht & Miller, 2007).

#### 4.4 | The timeline of coral-reef shutdown

For most reefs around the world, declines in reef accretion have been synchronous with contemporary, ecological declines in coral populations (Kennedy et al., 2013; Perry et al., 2013, 2014, 2015, 2018); however, our study suggests that the beginning of the end for Florida's reefs occurred thousands of years before anthropogenic climate change and other human disturbances led to the modern coral-reef crisis. The geological decline of the FKRT began more than 6,000 years ago, when inimical waters from Florida Bay began to suppress reef accretion in the Middle Keys. Although reef development elsewhere on the FKRT continued for several millennia, by 3,000 BP, the relatively cooler climate of south Florida had driven the geologic senescence of reefs throughout the FKRT.

The historical observations of reefs with relatively high coral cover throughout the Florida Keys until the mid-1970s (Jackson et al., 2014; Porter & Meier, 1992; Shinn & Kuffner, 2017) indicate that although the reefs of the FKRT were no longer building reef framework, some ecosystem functions were maintained until coral bleaching and disease caused the decline of Florida's coral populations in recent decades (Ruzicka et al., 2013; Toth et al., 2014). Indeed, the carbonate budgets estimated for many of Florida's reefs during the pre-industrial period (Enochs et al., 2015) suggest that the FKRT apparently only recently reached an ecological threshold, in which reef erosion became a dominant process (Enochs et al., 2015; Yates et al., 2017). The cover of framework-building corals is the most significant determinant of when this tipping point is reached, and net erosional states generally occur when coral cover falls below ~10% (Kennedy et al., 2013; Perry et al., 2013, 2015). Coral cover is often the last ecological metric to respond to environmental

perturbations, and it has been shown to be insensitive to other symptoms of ecosystem degradation such as declines in fish biomass and changes in macroalgal abundance (McClanahan et al., 2011; Toth et al., 2014). We suggest that the veneer of living coral and other benthic biota that remained on the relict reefs of the FKRT was sufficient to keep Florida's reefs balanced at the tipping point between reef growth and erosion for several millennia (Kuffner & Toth, 2016). The recent decline in coral populations allowed that final ecological threshold to be crossed, triggering the onset of the structural degradation of Florida's reefs (Yates et al., 2017).

Our study demonstrates that reef accretion may be one of the most sensitive reef processes to environmental perturbations, and it may also be one of the most difficult to restore. The persistence of reefs, and the myriad of ecosystem services they provide, relies on maintenance of the three-dimensional structure built over millennia (Kuffner & Toth, 2016). In a business-as-usual scenario, anthropogenic climate change is on track to push most western Atlantic reefs past a geological and ecological tipping point wherein reef erosion will dominate within the next several decades (Kennedy et al., 2013). Aggressive management actions such as restoration of the reef-building corals *Acropora palmata* and *Orbicella* spp. (Kennedy et al., 2013; Kuffner & Toth, 2016), and the potential to breed resistant coral populations (van Oppen et al., 2017), may buy reefs some extra time; however, we must move past the hope that traditional solutions alone, such as protecting herbivorous fish populations, will have any meaningful impact on the long-term trajectories of reef development (Hughes et al., 2017; Kennedy et al., 2013; Kuffner & Toth, 2016; Toth et al., 2014). Whereas millennial-scale climatic cooling drove the geologic senescence of the FKRT, in just decades, modern climate change and other anthropogenic disturbances have diminished the remaining ecological functionality of Florida's reefs and have threatened the persistence of coral reefs on a global scale. The accelerating pace of coral-reef degradation suggests that only when these threats are lifted will we have the hope of a future in which both the ecological and geological functionality of the world's coral-reef ecosystems can be restored.

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## CONFLICT OF INTEREST

The authors declare no conflict of interests.

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## SUPPORTING INFORMATION

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

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