**Key Points:**

- Interannual acidification trends were detected in the mid-channel, offshore, and oceanic zones of Florida's Coral Reef
- At the inshore reefs, strong seasonal variability in carbonate chemistry and increasing TA mitigated or obscured acidification trends
- Higher pH and aragonite saturation states occur in the Upper and Middle Keys, which could favor reef habitat persistence in these regions

# Coral Reef Carbonate Chemistry Reveals Interannual, Seasonal, and Spatial Impacts on Ocean Acidification Off Florida

A. M. Palacio-Castro[1,2] , I. C. Enochs[1], N. Besemer[1] , A. Boyd[1,2], M. Jankulak[1,2] , G. Kolodziej[1,2], H. K. Hirsh[1,2] , A. E. Webb[1,2], E. K. Towle[3] , C. Kelble[1] , I. Smith[1,2], and D. P. Manzello[4]

[1]NOAA, Atlantic Oceanographic and Meteorological Laboratory, Ocean Chemistry and Ecosystem Division, Miami, FL, USA, [2]University of Miami, Cooperative Institute for Marine and Atmospheric Studies, Miami, FL, USA, [3]NOAA Coral Reef Conservation Program, Silver Spring, MD, USA, [4]Coral Reef Watch, Center for Satellite Applications and Research, Satellite Oceanography & Climatology Division, U.S. National Oceanic and Atmospheric Administration, College Park, MD, USA

**Abstract** Ocean acidification (OA) threatens coral reef persistence by decreasing calcification and accelerating the dissolution of reef frameworks. The carbonate chemistry of coastal areas where many reefs exist is strongly influenced by the metabolic activity of the underlying benthic community, contributing to high spatiotemporal variability. While characterizing this variability is difficult, it has important implications for the progression of OA and the persistence of the ecosystems. Here, we characterized the carbonate chemistry at 38 permanent stations located along 10 inshore-offshore transects spanning 250 km of the Florida Coral Reef (FCR), which encompass four major biogeographic regions (Biscayne Bay, Upper Keys, Middle Keys, and Lower Keys) and four shelf zones (inshore, mid-channel, offshore, and oceanic). Data have been collected since 2010, with approximately bi-monthly periodicity starting in 2015. Increasing OA, driven by increasing DIC, was detected in the mid-channel, offshore, and oceanic zones in every biogeographic region. In the inshore zone, however, increasing TA counteracted any measurable OA trend. Strong seasonal variability occurred at inshore sites and included periods of both exacerbated and mitigated OA. Seasonality was region-dependent, with greater variability in the Lower and Middle Keys. Elevated pH and aragonite saturation states ($\Omega_{Ar}$) were observed in the Upper and Middle Keys, which could favor reef habitat persistence in these regions. Offshore reefs in the FCR could be more susceptible to global OA by experiencing open-ocean-like water chemistry conditions. By contrast, higher seasonal variability at inshore reefs could offer a temporary OA refuge during periods of enhanced primary production.

**Plain Language Summary** Elevated carbon dioxide ($CO_2$) input into the atmosphere is causing the acidification of the oceans, hindering the ability of corals to grow their hard skeleton and thus affecting coral reef habitat persistence. However, shallow ecosystems such as coral reefs can experience strong temporal and spatial variability in carbonate chemistry (such as pH and $CO_2$), which may both mitigate or exacerbate exposure to ocean acidification (OA). From 2010 to 2021, we sampled seawater carbonate chemistry at 38 permanent stations along and across the Florida Coral Reef to assess its variability among seasons, years, and reef areas. OA was detected in most of the Florida Coral Reef, including the mid-channel and offshore reefs. However, there were no OA trends at inshore reefs, where seasonal variability in the carbonate parameters was the greatest. Among the regions, the Upper and Middle Keys had higher pH values compared with the Lower Keys, suggesting more favorable conditions for reef persistence in the first two regions. This temporal and spatial variability may have important implications for coral reef resilience to OA.

## 1. Introduction

The ocean is a major sink of anthropogenic carbon dioxide ($CO_2$), absorbing approximately 30% of the carbon added to the atmosphere (Caldeira & Wickett, 2003; Sabine et al., 2004). Rising anthropogenic $CO_2$ in seawater has reduced ocean pH by ~0.1 units since pre-industrial times (Bates et al., 2014; Haugan & Drange, 1996), a phenomenon referred to as ocean acidification (OA; Bolin, 1959). Without drastic intervention, global pH is expected to further decline by 0.3–0.5 units by the end of the century (Caldeira & Wickett, 2005). The reduction in pH has important implications for the physiology of numerous marine organisms and the health of the ecosystems they comprise (Chan & Connolly, 2013; Doney et al., 2009; Koch et al., 2013; Orr et al., 2005). This

is particularly relevant for coral reef ecosystems, where OA has been shown to impair coral calcification and accelerate carbonate dissolution and bioerosion, tipping the balance toward net erosion and habitat loss (Enochs et al., 2016; Morris, Enochs, Webb, et al., 2022).

The shallow-water coastal environments where many coral reefs are found experience higher spatiotemporal variability than open ocean environments, primarily due to the combination of biological modulation acting on smaller water volumes. As water moves over coral reefs, seagrass beds, and sand patches, the metabolic activity of the benthic communities transforms the overlying water chemistry (Anthony et al., 2011, 2013; Ricart et al., 2021). Changes in photosynthesis, respiration, calcification, and dissolution modify the dissolved inorganic carbon (DIC), total alkalinity (TA), and aragonite saturation state ($\Omega_{Ar}$) in the surrounding water, creating temporal (diel to seasonal; Middelboe & Hansen, 2007; Ricart et al., 2021) and spatial (cm to 100's km) differences in carbonate chemistry (Enochs et al., 2019; Hurd et al., 2011; Kleypas et al., 2011; Manzello et al., 2012). These changes could mitigate, exacerbate, and/or counteract global OA trends at the local level (Anthony et al., 2013; Ricart et al., 2021) and will ultimately determine ecosystem exposure to OA conditions (Duarte et al., 2013). As such, careful characterization of carbonate chemistry in OA-sensitive environments, such as coral reefs, is paramount to predicting the manifestation and subsequent impacts of expected global change.

The Florida Keys National Marine Sanctuary (FKNMS) encompasses a complex mosaic of benthic ecosystems including Florida's Coral Reef (FCR; previously referred to as the Florida Reef Tract), a bank-barrier coral reef system that stretches along the Florida Straits (Figure 1). Primary producers are abundant in the FKNMS, with more than 50% of the shallow benthos covered by seagrass (Anderson, 2011). Seagrass beds present a relatively continuous distribution in Biscayne Bay and the Upper Keys regions, becoming more discontinuous in the Middle and Lower Keys (Figure 1). Calcifiers in the region include corals, crustose coralline algae, calcifying macroalgae, and mollusks. Although average coral cover in the FCR has been reduced from 20% to 40% in the 1980s (Jaap et al., 1988; Porter et al., 2002) to <7% in the past decades (Grove et al., 2022; Soto et al., 2011), some reefs have exhibited higher resilience (Gintert et al., 2018; Manzello et al., 2019). Coral reefs in the FKNMS are critical to the local communities, providing ecological and economic services estimated at $8.5B. These services support over $1B annually in tourism and generate over 71,000 jobs (Palandro et al., 2008; Storlazzi et al., 2019; Towle et al., 2020). The persistence of these services relies on the growth and maintenance of the reef framework. However, the loss of coral cover due to disease outbreaks (Aronson & Precht, 2001; Walton et al., 2018), hurricane impacts (Gardner et al., 2005), coastal development and land-based sources of pollution (Patterson et al., 2002; Ward-Paige et al., 2005), as well as both warm and cold-water and mass bleaching events (Lirman et al., 2011; Ruzicka et al., 2013) are pushing the FCR into an erosional state (Enochs et al., 2016; Morris, Enochs, Besemer, et al., 2022).

Previous studies across the FCR have identified the spatial and seasonal variations in carbonate chemistry, despite sampling durations of less than 3 years (e.g., Enochs et al., 2019; Manzello et al., 2012; Muehllehner et al., 2016). For example, during 2009–2010, Muehllehner et al. (2016) estimated that most reefs in the FCR were experiencing seasonal dissolution during autumn/winter and the northernmost reefs were found to already be dissolving. During 2009–2011 Manzello et al. (2012) observed elevated $\Omega_{Ar}$ and pH at inshore Upper Keys sites, likely due to higher photosynthesis of seagrass beds during the spring. From 2014 to 2015, Enochs et al. (2019) observed localized acidification around navigational inlets. Longer time series (~8 years) from a moored autonomous $p$CO$_2$ (MapCO2) buoy have also been used to describe the seasonal variability and metabolic rates in the FCR, but these data are limited to a single inshore site in the Upper Keys (Meléndez et al., 2020, 2022). Together, these studies highlight the spatiotemporal complexity of the carbonate chemistry system in the FCR, though their relatively short duration or limited spatial scope has hampered their ability to examine these trends in the context of OA.

Here, we summarize a carbonate chemistry time series reflecting an unprecedented degree of spatiotemporal characterization of a large reef system spanning the FCR from Biscayne Bay to Key West. These data, from the combined efforts of NOAA's National Coral Reef Monitoring Program (NCRMP) and the South Florida Ecosystem Restoration Research (SFER) cruises, comprise discrete seawater samples collected at 38 permanent stations since 2010, with approximately bi-monthly periodicity starting in 2015 (totaling 47 sampling cruises and 1,538 samples). We used these data to assess (a) how OA trends are affecting the different areas of the FCR, (b) how seasonal fluctuations in carbonate chemistry could exacerbate or mitigate OA at the local level, and (c) how year-round community metabolism and average carbonate chemistry might result in areas that are more favorable for coral reef
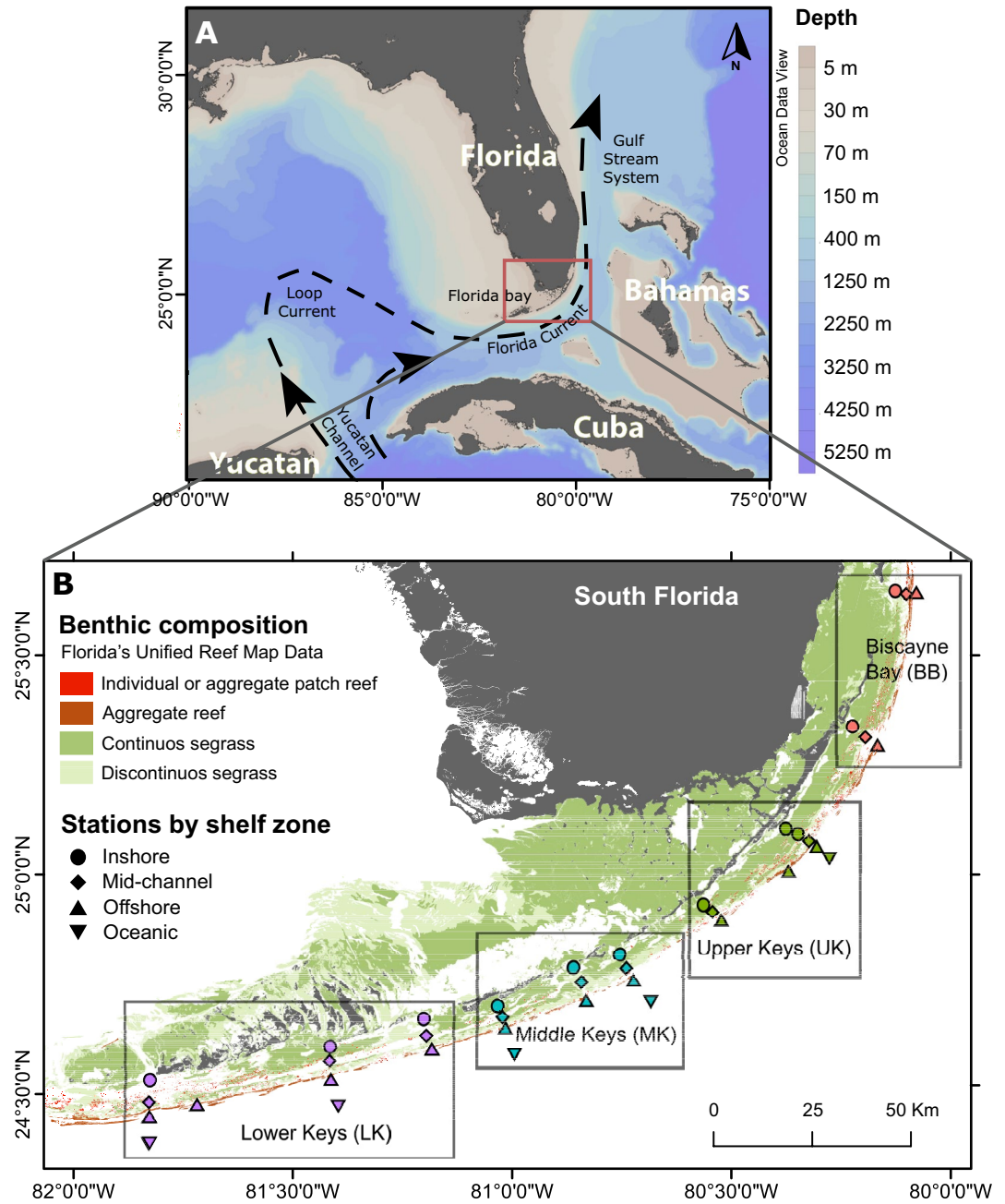
**Figure 1.** Location of the permanent sampling stations along the Florida Coral Reef. (a) Bathymetry (sourced from Ocean Data View) and major current systems near the Florida peninsula. (b) Permanent sampling stations and major benthic composition around them. The boxes and color of the station markers delimit the biogeographical regions. The shape of the station markers represents their position along the shelf (zone). Colored areas denote the composition of the benthos based on data sourced from Florida's Unified Reef Map (FWC).

calcification. Our data show significant OA trends in most of the FCR between 2015 and 2021. However, seasonal and spatial differences in carbonate chemistry along and across the FCR offer insights about potential hotspots for OA exposure and/or refugia that could inform management, restoration and research priorities.

## 2. Methods

### 2.1. Study Area

The study area spans ∼250 km along the Florida Keys, covering four major biogeographic regions: Biscayne Bay (BB), the Upper Keys (UK), the Middle Keys (MK), and the Lower Keys (LK, Figure 1). In each region, two to three transects were established perpendicular to the shore, with each transect consisting of three to five stations across four zones of the shelf (inshore, mid-channel, offshore and oceanic; Figure 1). Inshore reef stations were located <2 km from shore and had a mean depth of 5.8 m; mid-channel reef stations were 2–6 km from shore and had a mean depth of 9.8 m; offshore reefs were located 8–10 km from shore with a mean depth of 32.5 m; and oceanic stations were >10 km from shore, with a mean depth of 121 m (Table S1 in Supporting Information S1).

Due to its subtropical location, South Florida's seasonal changes in temperature are high relative to other coral reef systems, with seasonal climatological minima occurring in January, maxima occurring in August, and a seasonal range of 22–30°C on the offshore reefs (Manzello, 2008). Sea temperature seasonality becomes greater from the offshore to mid-channel reefs and is the greatest on the inshore reefs (Manzello et al., 2019). The Spring (April–June) and Summer (July–September) seasons roughly coincide with a period of higher rainfall that extends from May/June through October/November. Autumn (October–December) and Winter (January–March) seasons are characterized by drier conditions that extend from October/November through April/May.

The Gulf Stream is the main current system influencing the study area (Morey et al., 2017). A branch of the Gulf Stream enters the Gulf of Mexico from the Caribbean Sea forming the Loop Current, and then turns eastward and exits the Gulf through the Straits of Florida. This water flows northward along the east Florida coast as the Florida Current (Figure 1a). Tides in Southeast Florida are predominantly semi-diurnal. Water from Florida Bay has been known to pass through channels in the Middle Keys, influencing the distribution of reefs along the FCR (Porter et al., 1999). Although the region lacks a thorough characterization of water residence time around the sampling stations, previous data suggest that it is likely higher in the more enclosed inshore sites compared to the more open offshore sites (Muehllehner et al., 2016).

### 2.2. Sample Collection and Analyses

Discrete seawater samples were collected starting in March 2010 across the aforementioned regions and zones as part of NCRMP and SFERR cruises. From 2010 to 2014, 16–36 stations were sampled during nine cruises (two in 2010, five in 2011, and one in both 2012 and 2014; $n = 220$; Table S1 in Supporting Information S1). From April 2015 to December 2021, 35–38 stations were sampled approximately every 2 months ($n = 1,318$). All samples (500 mL) were collected from the ocean surface (∼1 m depth) and were preserved with 200 μL mercuric chloride to stop the biological activity. Temperature and salinity were measured at collection time using a CTD (SeaBird SBE 911 Plus). From 2015 to 2021, salinity was also measured using a densitometer (DMA 5000M, Anton Paar). TA was determined through automated titration using an AS-ALK2 (Apollo SciTech). DIC was analyzed using an AS-C3 (Apollo SciTech). TA and DIC samples were run in duplicate and corrected using certified reference materials following Dickson et al. (2007), with a precision of ±2 and ±3 μmol kg$^{-1}$ for DIC and TA, respectively.

### 2.3. Data Analysis

#### 2.3.1. Carbonate System Calculations and Normalization

Temperature, salinity, TA, and DIC were used to calculate $pCO_2$, pH, and aragonite saturation state ($\Omega_{Ar}$) using the Seacarb package (Gattuso et al., 2019) for R v3.6.3 (R Core Team, 2020) with the default dissociation constants [K1 and K2 from Lueker et al. (2000), Ks from Dickson (1990), b from Uppström (1974) and Kf from Perez and Fraga (1987)]. TA and DIC values were not normalized since normalization procedures to constant salinity (Millero et al., 1998) or to nonzero TA or DIC versus salinity $y$-intercept (Friis et al., 2003) resulted in stronger correlations with salinity (Figure S1 in Supporting Information S1). Statistical significance and patterns in the data analysis were the same with and without salinity normalization.

#### 2.3.2. Interannual OA Trends

Interannual trends of TA, DIC, $pCO_2$, pH, and $\Omega_{Ar}$ were evaluated with linear mixed models using the lme4 (v3.1) package (Bates et al., 2015) for R. For these models, only samples collected starting in 2015 ($n = 1,318$) were

used to avoid potential bias in the long-term trends related to less frequent sampling prior to 2015 (Table S1 in Supporting Information S1). The linear models were run individually for inshore, mid-channel, offshore, and oceanic zones. Initial models included biogeographical regions (BB, UK, MK, and LK) and years (2015–2020) as fixed interactive effects. Month of the year and station were included as random effects to remove seasonal variation and station-specific signs. The significance of the factors and their interactions was evaluated with the anova function in R. The factors region and station were dropped from the models in which they were non-significant using the function "step" (lmerTest v3.1). This resulted in simplified final models that describe TA, DIC, $pCO_2$, pH, and $\Omega_{Ar}$ trends in the different regions and zones of the FCR (Tables S2–S6 in Supporting Information S1). Model predictions were then obtained using the lme4 function "predict" and plotted using ggplot2 (Wickham, 2016). In models where the region was a significant factor, pairwise Tukey's HSD comparisons among regions were performed using the package emmeans v1.7.2 (Lenth, 2018) with an alpha value of 0.05 (Table S7 in Supporting Information S1).

### 2.3.3. Seasonal Variability

Variability in water temperature, salinity, and carbonate chemistry (TA, DIC, $pCO_2$, pH, and $\Omega_{ar}$) in the FCR was summarized using monthly and yearly descriptive statistics (Figure 3; Table S9 in Supporting Information S2). Monthly mean values ($\pm$sem) were computed from all the samples collected (2010–2020) during a given month of the year per region and shelf zone ($n = 1{,}538$). The maximum and minimum monthly mean values for each parameter were used to describe the range of the seasonal variation occurring at each location over the yearly cycle (peak-to-peak amplitude). Finally, yearly mean values ($\pm$sd) were computed using the monthly mean values by region and shelf zone to avoid bias associated with more frequent sampling during a given month/season (Table S8 in Supporting Information S1).

### 2.3.4. Reef-Ocean Gradients

To assess the net effects of benthic metabolism on the overlying seawater carbonate chemistry (e.g., calcification/dissolution, photosynthesis/respiration) reef-ocean gradients in carbonate chemistry were determined. Accordingly, the differences in TA, DIC, pH, and $\Omega_{Ar}$ in the reef zones versus oceanic sites ($\Delta$) were calculated by subtracting the individual inshore, mid-channel, and offshore values from the mean of all oceanic stations measured during a given cruise (Figure 1). Seasonal and yearly $\Delta$ values (mean $\pm$ sd) were computed from the monthly mean values by region and shelf zone. For the seasonal analyses, samples collected between January and March were classified as Winter, April and June as Spring, July and September as Summer, and October and December as Autumn. This classification allows comparison with prior studies that analyzed the data with a similar seasonal structure (Manzello et al., 2012; Muehllehner et al., 2016). Spatial and seasonal differences in $\Delta$TA, $\Delta$DIC, $\Delta$pH, and $\Delta\Omega_{Ar}$ were tested with linear mixed models using lme4 (Table S10 in Supporting Information S1). These models included season, biogeographical region, and shelf position as fixed interactive factors and station as a random effect. Pairwise post-hoc Tukey's HSD comparisons were performed for significant factors using the "emmeans" (Tables S11–S14 in Supporting Information S1). Model predictions were obtained using the lme4 function "predict" and plotted using ggplot2 (Figure 4).

TA versus DIC plots were used to visualize the relative magnitude of calcification, photosynthesis, and respiration processes creating inshore-ocean gradients in carbonate chemistry (Figure 5). TA versus DIC slopes were calculated using model II simple linear regressions with the ordinary least squares (OLS) method. Regressions were calculated per region and shelf position (Figure 5a; Table S15 in Supporting Information S1), as well as further parsing the samples by region, shelf position, and season, and transect (Figure 5b; Table S16 in Supporting Information S2).

### 2.3.5. Drivers of Interannual and Seasonal Changes in $\Omega_{Ar}$ and pH

To better understand the effects of TA, DIC, salinity, and temperature variability on interannual and seasonal carbonate chemistry patterns, we quantified the contribution of these variables on $\Omega_{Ar}$ and pH. First, the function "derivnum" in the R package Seacarb (Gattuso et al., 2019; Orr et al., 2018) was used to estimate the partial derivatives of $\Omega_{Ar}$ and pH with respect to TA, DIC, salinity (S), and temperature (T). Oceanic mean values for TA (2381.47 µmol kg$^{-1}$), DIC (2047.92 µmol kg$^{-1}$), temperature (27.37°C), and salinity (35.99) were used as the inputs for the function. Then, the contribution of each input variable was calculated by multiplying their derivatives by the anomalies of each input parameter relative to the oceanic means ($\Delta_{Oc}$) (Equations 1 and 2).

$$\Delta_{\underline{Oc}}\Omega_{Ar} \approx \left(\frac{\delta\Omega_{Ar}}{\delta TA}\right)\Delta_{\underline{Oc}}TA + \left(\frac{\delta\Omega_{Ar}}{\delta DIC}\right)\Delta_{\underline{Oc}}DIC + \left(\frac{\delta\Omega_{Ar}}{\delta T}\right)\Delta_{\underline{Oc}}T + \left(\frac{\delta\Omega_{Ar}}{\delta S}\right)\Delta_{\underline{Oc}}S \qquad (1)$$

$$\Delta_{\underline{Oc}}pH \approx \left(\frac{\delta pH}{\delta TA}\right)\Delta_{\underline{Oc}}TA + \left(\frac{\delta pH}{\delta DIC}\right)\Delta_{\underline{Oc}}DIC + \left(\frac{\delta pH}{\delta T}\right)\Delta_{\underline{Oc}}T + \left(\frac{\delta pH}{\delta S}\right)\Delta_{\underline{Oc}}S \qquad (2)$$

The quantitative contributions of TA, DIC, temperature and salinity were summarized to show the dominant drivers of the seasonal and interannual variability in $\Omega_{Ar}$ and pH in each zone (Figure 6).

The TA and DIC values used in this study were not normalized to a constant salinity (Millero et al., 1998) or to a nonzero TA or DIC versus salinity *y*-intercept (Friis et al., 2003). Thus, to assess the potential impact of seasonal variations in freshwater inputs on carbonate chemistry, the relationships of TA, DIC, and TA/DIC with salinity and temperature were determined for each region and zone (Figure 7). Model II simple linear regressions were computed using the OLS method (Tables S17–S19 in Supporting Information S1). Differences among the slopes were tested with pairwise post-hoc Tukey's HSD using the package emmeans and an alpha value of 0.05.

## 3. Results

### 3.1. Interannual OA Trends

OA was detectable in the mid-channel, offshore, and oceanic zones, with increasing $pCO_2$, decreasing pH, and decreasing $\Omega_{Ar}$ from 2015 to 2021 (year $p < 0.05$ in all models, Figure 2; Table 1). The rate of change for these parameters was greatest in the oceanic zone, followed by offshore and mid-channel (Figure 2). OA trends were not significant at the inshore reefs for $pCO_2$, pH, or $\Omega_{Ar}$ (year $p > 0.05$). Both TA and DIC showed increasing concentrations over the years (Figure 2). DIC trends were significant in all zones, but TA trends were not significant in the inshore and mid-channel reefs (year $p > 0.05$, Table 1). In 2019, three time points (July, September, and November) were characterized by high DIC, which resulted in low pH and $\Omega_{Ar}$ (Figure 2). These measurements fell under the range of variability observed in the inshore stations but were conspicuous in the mid-channel, offshore, and oceanic sites.

The biogeographical region was also a significant factor in carbonate chemistry variability of the inshore, mid-channel, and offshore zones (region $p < 0.05$) but not in the oceanic zone (Figure 2). Lower pH, $\Omega_{Ar}$, and TA occurred in the inshore, mid-channel, and offshore zones of the LK compared to the same zones in the UK and MK (Tukey's HSD $< 0.05$; Table S7 in Supporting Information S1). However, the interaction between year and region was non-significant in all models, suggesting that the rates of change in $pCO_2$, pH, $\Omega_{Ar}$, TA, and DIC are similar across biogeographical regions.

### 3.2. Seasonal Variability

All water sample parameters (temperature, salinity, TA, DIC, $pCO_2$, pH, and $\Omega_{Ar}$) exhibited the highest seasonal variability in the inshore zone, followed by mid-channel, offshore, and oceanic, regardless of the biogeographical region (Figure 3; Table S9 in Supporting Information S1). At inshore sites, the difference between the maximum and minimum monthly mean for TA and DIC often exceeded 200 µmol kg$^{-1}$, but TA and DIC seasonal variation was only ~20–50 µmol kg$^{-1}$ in the offshore and oceanic zones. There were also regional differences in TA and DIC seasonality, with higher seasonal amplitude occurring in the LK and MK compared to BB and UK (Figure 3). The region also affected the time of the year when the stations experienced the minimum TA and DIC values. This was especially pronounced in inshore reefs, where the minimum monthly mean TA occurred first in the UK (April), followed by BB (June), MK (July), and LK (August). Similarly, minimum DIC values inshore occurred first in the UK (April), followed by LK (May), and MK and BB (June; Figure 3).

Similar to TA and DIC, the amplitude of pH and $\Omega_{Ar}$ seasonal variation was higher inshore followed by mid-channel, offshore, and oceanic stations and included periods of exacerbated and mitigated OA (Figure 3). Seasonal variability in inshore and mid-channel reefs, however, was dependent on the region. Greater seasonal changes in pH and $\Omega_{Ar}$ occurred in the UK compared to other regions, driven by greater enhancement of pH and $\Omega_{Ar}$ during the Spring (Figure 3). Within each zone, the UK region always had the highest maximum monthly mean $\Omega_{Ar}$ values and the LK reefs had the lowest minimum monthly means (Figure 3).
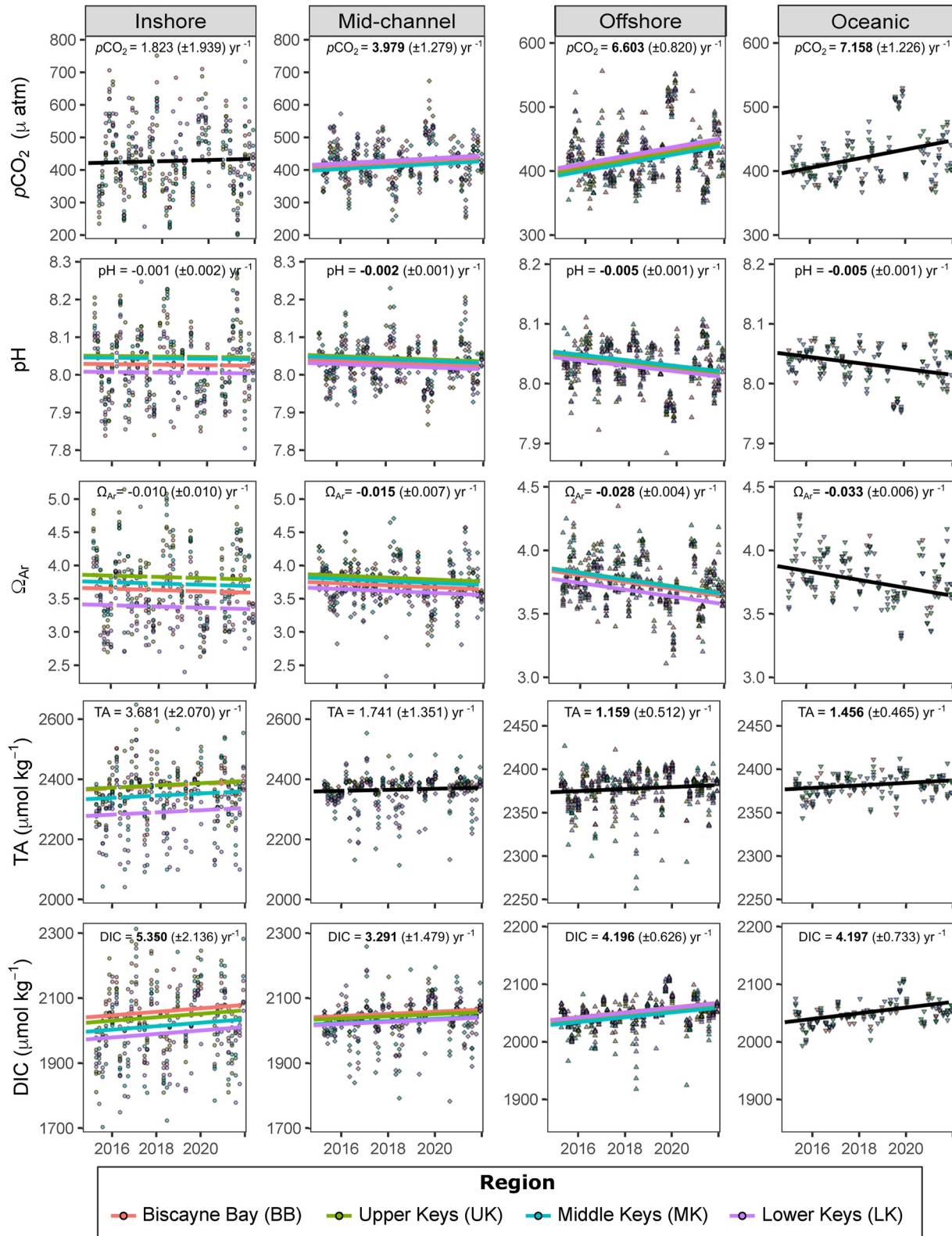
**Figure 2.**

**Table 1**
*Carbonate Chemistry Trends ± Standard Error for the Parameters Reported in Figure 2*

| Model | Inshore ($n = 375$) | Mid-channel ($n = 350$) | Offshore ($n = 427$) | Ocean ($n = 163$) |
|---|---|---|---|---|
| $p\text{CO}_2$ (µatm yr$^{-1}$) | 1.823 ± (1.939) | 3.979 ± (1.279) | 6.603 ± (0.820) | 7.158 ± (1.226) |
| slope $p$-value | 0.347 | 0.003 | <0.001 | <0.001 |
| $R^2$ conditional | 0.661 | 0.615 | 0.656 | 0.565 |
| pH (yr$^{-1}$) | −0.001 ± (0.002) | −0.002 ± (0.001) | −0.005 ± (0.001) | −0.005 ± (0.001) |
| slope $p$-value | 0.682 | 0.029 | <0.001 | <0.001 |
| R$^2$ conditional | 0.705 | 0.652 | 0.693 | 0.587 |
| $\Omega_{Ar}$ (yr$^{-1}$) | −0.010 ± (0.010) | −0.015 ± (0.007) | −0.028 ± (0.004) | −0.033 ± (0.006) |
| slope $p$-value | 0.321 | 0.04 | <0.001 | <0.001 |
| $R^2$ conditional | 0.619 | 0.459 | 0.435 | 0.517 |
| TA (µmol kg$^{-1}$ yr$^{-1}$) | 3.681 ± (2.070) | 1.741 ± (1.351) | 1.169 ± (0.515) | 1.456 ± (0.465) |
| slope $p$-value | 0.076 | 0.198 | 0.023 | 0.002 |
| $R^2$ conditional | 0.521 | 0.314 | 0.151 | 0.202 |
| DIC (µmol kg$^{-1}$ yr$^{-1}$) | 5.35 ± (2.136) | 3.291 ± (1.479) | 4.196 ± (0.626) | 4.917 ± (0.733) |
| slope $p$-value | 0.012 | 0.026 | <0.001 | <0.001 |
| $R^2$ conditional | 0.605 | 0.401 | 0.279 | 0.309 |

*Note*. The $p$-values represent the significance of the estimated trends. All models include month of the year (yr) as a random effect in order to deseasonalize the data. The $R^2$ conditional represents the variance explained by the fixed effects (year and region), and random effects (month of the year) describing the total fit of the model.

### 3.3. Reef-Ocean Gradients

The magnitude of the reef-ocean differences (Δ values) varied by shelf zone, season, and region, with the greatest differences from oceanic values occurring in the inshore zone (Figure 4). In general, mid-channel-ocean Δ values followed similar trends as inshore-ocean Δ values across regional and seasonal scales. The magnitudes of the mid-channel Δ values, however, were generally less than those inshore. Offshore-ocean Δ values were not significantly different from zero, regardless of the season and region considered (Figure 4).

The relative magnitudes of calcification, photosynthesis, and respiration processes in the different reef areas and seasons were assessed using ΔTA and ΔDIC. These two variables were significantly affected by shelf zone, season, region, and their interactions ($p < 0.01$; Table S10 in Supporting Information S1). At the inshore and mid-channel reefs, ΔTA and ΔDIC were characterized by negative values during the spring and summer (Figure 4). However, some regions were characterized by greater ocean-reef gradients. At inshore reefs, for example, negative ΔTA and ΔDIC were more extreme in the LK and MK compared to BB and the UK. The autumn and winter seasons were characterized by positive ΔTA and ΔDIC. However, inshore ΔTA and ΔDIC in the LK were significantly more negative compared to the other regions (Figure 4; Table S11 in Supporting Information S1). Net yearly ΔTA and ΔDIC also differed among regions in the inshore zone ($p < 0.05$; Table S12 in Supporting Information S1), with negative ΔTA and ΔDIC in the LK and MK, and values close to zero in BB and the UK (Figure 4).

Potential OA hotspots and/or refugia were assessed using ΔpH and Δ$\Omega_{Ar}$. These parameters were significantly affected by season, region, and their interactions ($p < 0.01$; Figure 4). The shelf zone had a significant effect on Δ$\Omega_{Ar}$ ($p < 0.001$) but not on ΔpH ($p = 0.33$; Table S10 in Supporting Information S1). At inshore and mid-channel reefs, ΔpH and Δ$\Omega_{Ar}$ were positive during the spring and negative during the summer and autumn.

**Figure 2.** Ocean acidification trends in the Florida Coral Reef. Time series and model outputs for $p\text{CO}_2$, pH, $\Omega_{Ar}$, TA, and DIC. The colors represent the biogeographical regions, and the panels separate the locations by shelf zone. The text on the top of each panel shows the coefficient of change in the parameter per year for significant slopes (± standard error). Solid lines represent models with significant trends (year $p < 0.05$). Multiple colored lines are depicted for models where the regions have different intercepts (region $p < 0.05$) and one black line for models with a single intercept (region $p > 0.05$). Dashed lines represent models with non-significant trends (year $p > 0.05$, intercept $p < 0.05$). The plotted data points are not deseasonalized, but trends are calculated on the basis of deseasonalized data with models that include the month of the year as a random effect. The significance ($p$-values) and fit of the models ($R^2$) are shown in Table 1.
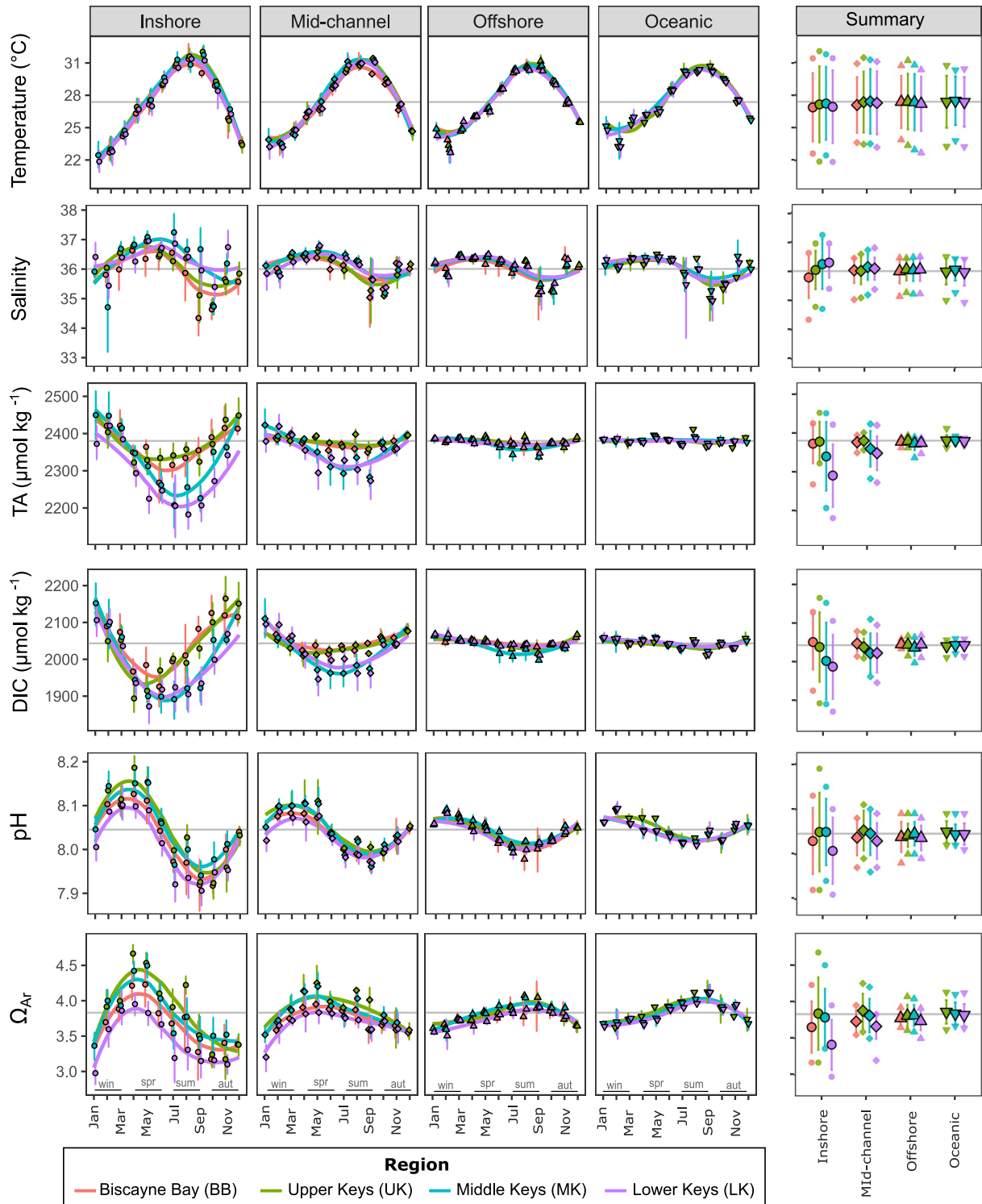
**Figure 3.** Seasonal variation in temperature, salinity, and carbonate chemistry in the different regions and shelf zones of the Florida Coral Reef. Left side panels: Monthly mean values (±95 CI) of temperature, salinity, TA, DIC, pH, and $\Omega_{Ar}$. The colors represent the biogeographical regions and the vertical panels separate the locations by shelf zone. The lines are the smoothed curves for the data (method = "loess," formula "y ~ x," span = 0.8). Right side panel: Yearly summary of seasonal variation in each region and zone. The larger (outlined) markers show the year mean values (±sd), and the small markers show the maximum and minimum monthly mean values for each location. Gray horizontal lines in all panels demarcate the mean values of the parameters at the oceanic stations.
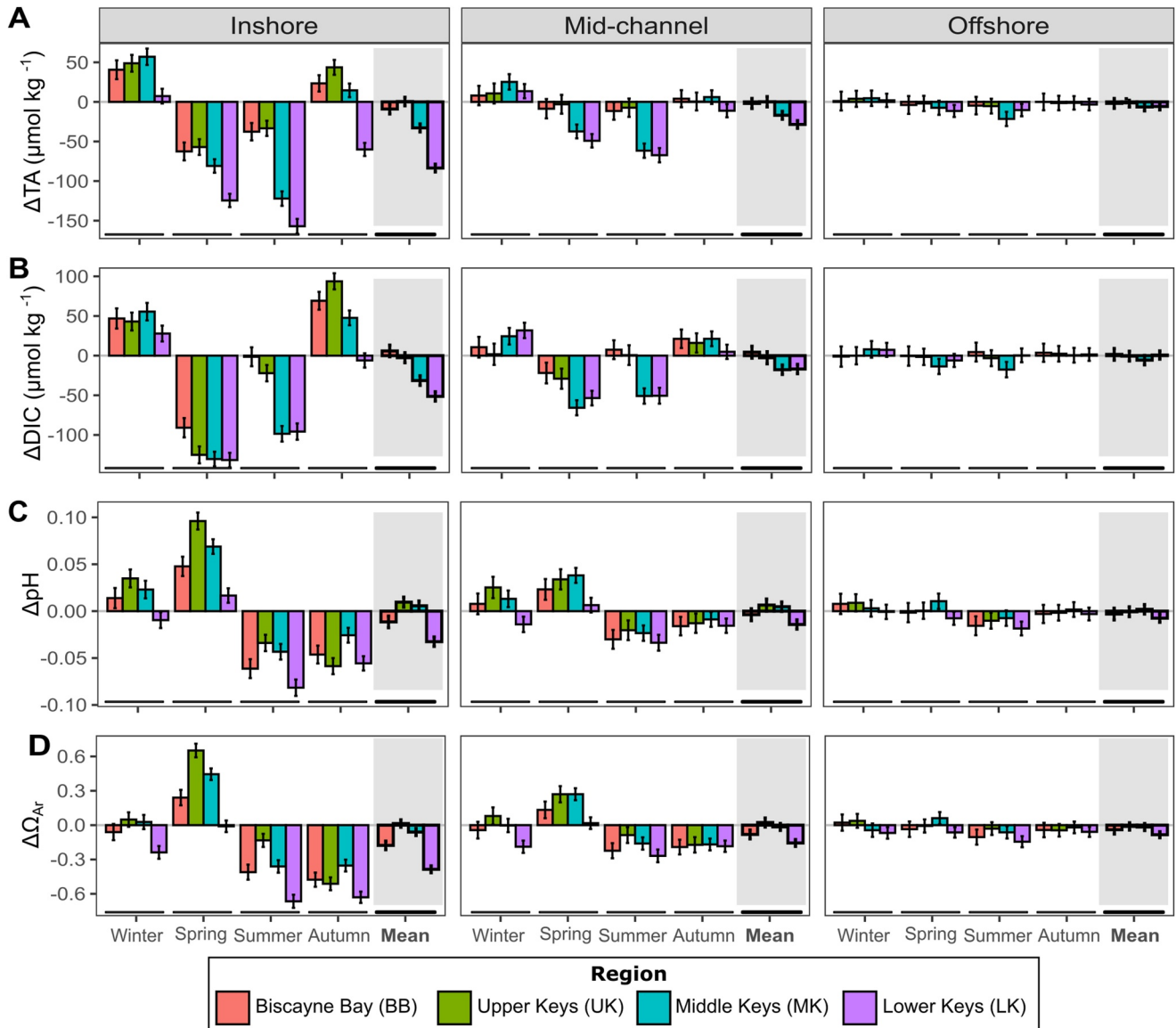
**Figure 4.** Reef-ocean seawater chemistry gradients (Δ*s*) in the Florida Coral Reef (a) TA, (b) DIC, (c) pH, and (d) $\Omega_{Ar}$. The bars represent the model-estimated mean Δ (reef-ocean) values (±SE). The colors represent the biogeographical regions, and the vertical panels separate the locations by shelf zone. The *x*-axis separates the Δ values by season (left) and overall year (right-shaded areas).

However, spring-time enhancement of these parameters was significantly greater at inshore reefs of the UK and MK compared to the LK. Similarly, summer-time reductions in these parameters were stronger in the LK and BB compared to the UK and MK (Figure 4; Table S13 in Supporting Information S1). Net yearly Δ values for pH and $\Omega_{Ar}$ revealed a significant reduction in the LK and BB but were close to zero in the UK and MK (Figure 4; Table S14 in Supporting Information S1).

The TA versus DIC plots were centered at the endmember (oceanic) mean values (TA = 2,381.47 μmol kg$^{-1}$ ± 12.51 sd, DIC = 2047.92 μmol kg$^{-1}$ ± 20.93 sd). The overall TA versus DIC slopes per region and zone ranged from a minimum of 0.32 in the mid-channel reefs of the UK to a maximum of 0.85 in the inshore reefs of the LK (Figure 5). In general, the inshore zone and the MK and LK regions were characterized by higher slopes compared to the mid-channel and offshore zones and the BB and UK regions (Figure 5a). When parsed by seasons, slopes in the MK and LK regions were higher during the spring and summer compared to winter and fall. Contrary, BB and UK slopes tended to be smaller during the spring and summer compared to winter and fall (Figure 5b, Table S16 in Supporting Information S1). Two known extreme weather events stood out in the TA versus DIC plots.
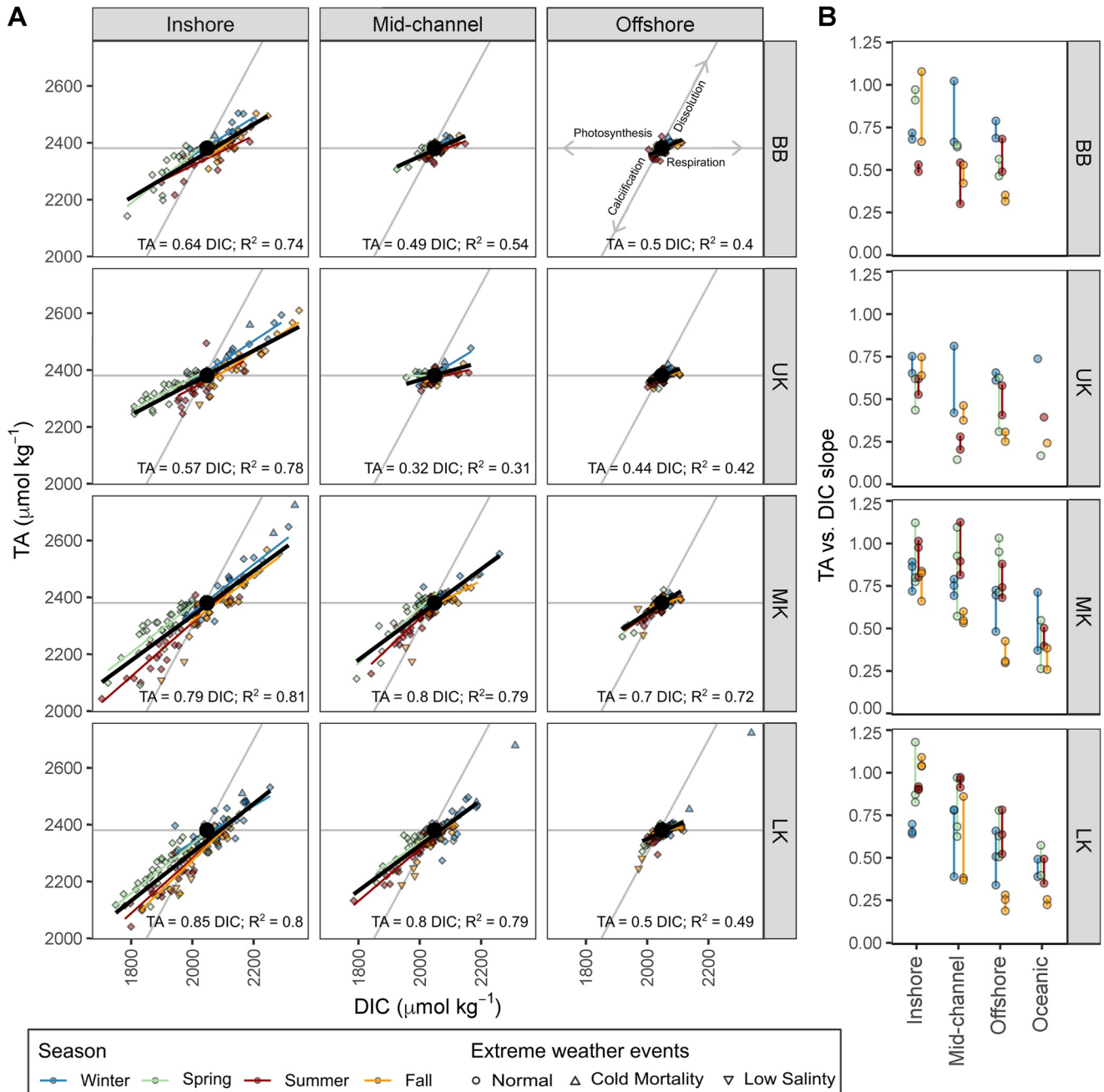
**Figure 5.** TA versus DIC slopes by region and shelf position. (a) Type II linear regressions for each region and shelf position including all seasons and transects. The colors differentiate the samples collected during each season, while the shapes highlight samples collected during extreme weather events (shown but not included in the linear regressions). The black solid circle in the center of each panel represents the endmember reference obtained from the mean values of oceanic samples. (b) TA versus DIC slope range of variation among individual regressions for each season and transect (Figure 1). Detailed statistics, including *p*-values and standard errors for the linear regression parameters, are summarized in Table S15 in Supporting Information S1 and Table S16 in Supporting Information S2.

A cold-water event of January 2010, which resulted in catastrophic coral mortality, is evidenced by higher than normal TA values in the MK and LK (Colella et al., 2012); and high rainfall in October 2011, which resulted in reduced salinity and changes in TA and DIC (Manzello et al., 2012). Values obtained during these two periods were plotted but excluded from the linear regressions (Figure 5).
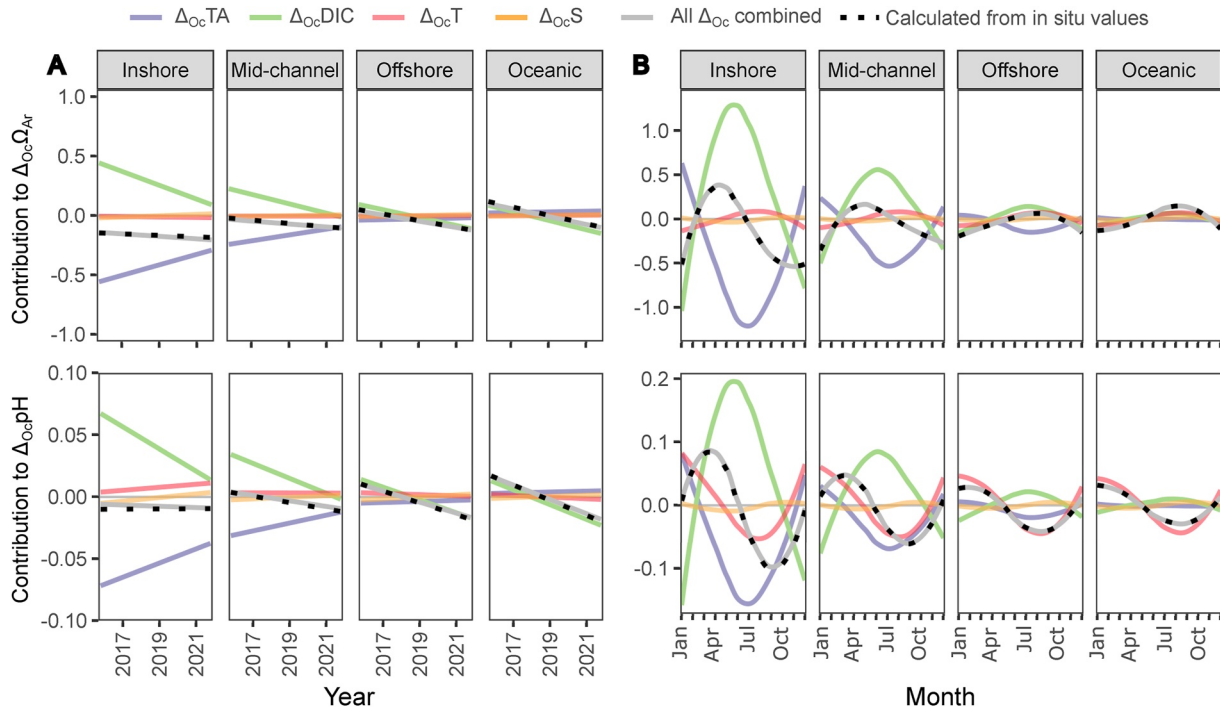
**Figure 6.** Drivers of interannual (a) and seasonal (b) variability in $\Omega_{Ar}$ and pH in the Florida Reef. The solid lines represent the contributions of changing TA, DIC, temperature, and salinity to $\Omega_{Ar}$ and pH variability. Delta values were calculated using the mean oceanic values as the reference ($\Delta_{Oc}$). Gray lines represent the combined effects estimated from TA, DIC, temperature, and salinity contributions. Black dashed lines represent the calculated $\Omega_{Ar}$ and pH from the in situ values.
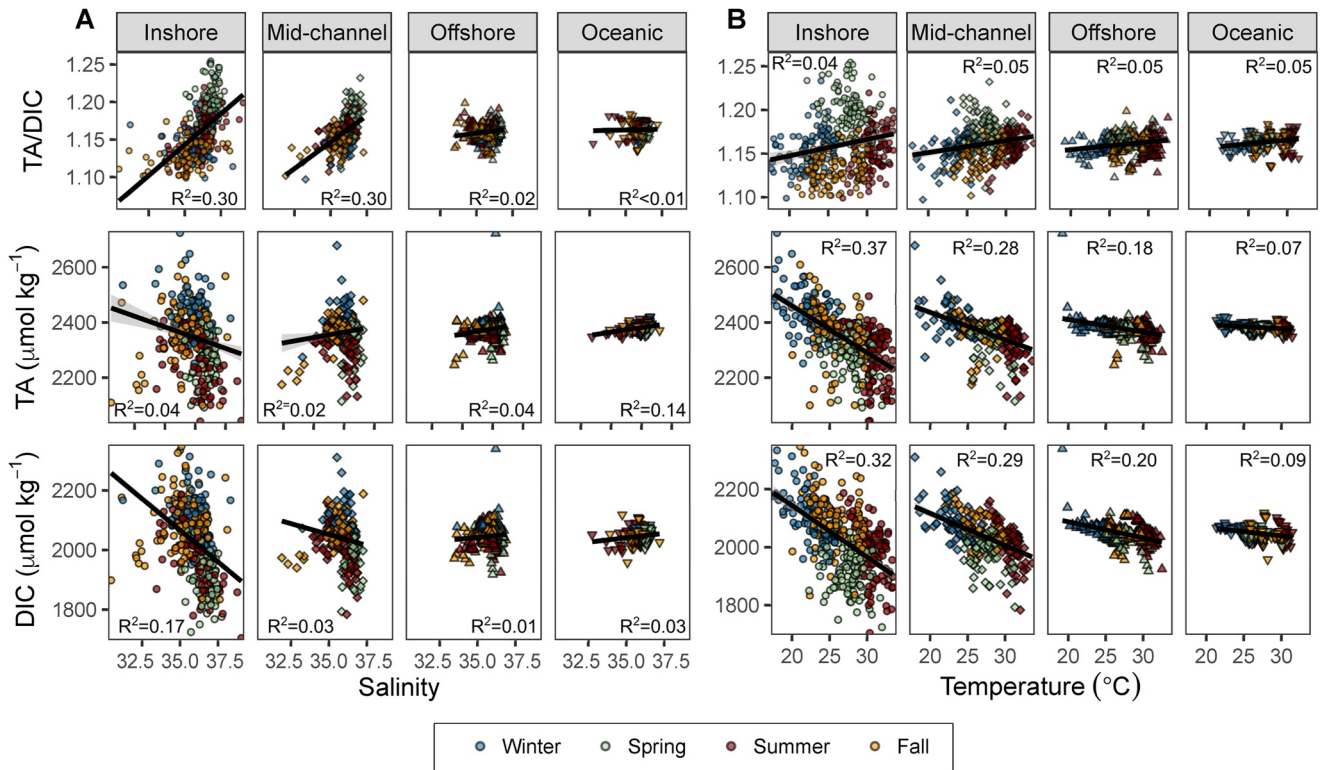


**Figure 7.** TA, DIC, and TA/DIC as a function of (a) salinity and (b) temperature. The vertical panels separate the locations by shelf zone. The black line and text on the top of each panel show type II linear regression for all regions combined inside each zone. Detailed statistics, including *p*-values and standard errors for the linear regression parameters, are summarized in Tables S18 and S19 in Supporting Information S1.

### 3.4. Drivers of Seasonal and Interannual Changes in $\Omega_{Ar}$ and pH

The effects of temperature, salinity, TA, and DIC variability on $\Omega_{Ar}$ and pH were dependent on the zone and time scale assessed (Figure 6). Increasing DIC over the years was the main driver in declining $\Omega_{Ar}$ and pH. However, increasing TA counteracted any OA trends in the inshore and mid-channel zones (Figure 6a).

TA and DIC were the dominant drivers of $\Omega_{Ar}$ and pH seasonal variation in the inshore and mid-channel reefs (Figure 6b). Seasonal changes in TA and DIC, however, acted in opposite directions, resulting in a smaller effective variation of $\Omega_{Ar}$ and pH. A time lag between the lowest DIC (spring) and the lowest TA (summer; Figure 3) results in net $\Omega_{Ar}$ and pH enhancement during the early summer and net depression during autumn. Seasonal changes in pH, and to a lesser degree $\Omega_{Ar}$, were also dependent on temperature. Higher temperatures during the summer reduced pH and increased $\Omega_{Ar}$ with the opposite pattern occurring during the winter. Since TA and DIC variations were minimal in the oceanic zone, seasonal fluctuations in $\Omega_{Ar}$ and pH were primarily due to changes in temperature, with the highest $\Omega_{Ar}$ and lowest pH occurring during the warmest months (Figures 2 and 6b). The effect of salinity on $\Omega_{Ar}$ and pH was negligible among all zones and time scales.

Inshore TA and DIC were both negatively correlated with salinity, with zero salinity intercepts of 3,044.3 $\mu$mol kg$^{-1}$ and 3,548.4 $\mu$mol kg$^{-1}$, respectively (Figure 7a). In the offshore and oceanic zones, however, TA and DIC slopes change direction, representing positive correlations with salinity and smaller zero salinity intercepts (Figure 7a). Although TA and DIC relationships to salinity were significant ($p < 0.05$), the linear models explained a small proportion of the TA and DIC variability ($R^2 < 0.2$). In general, TA/DIC ratios were positively correlated with salinity, but the slope magnitude declined when moving from the inshore toward the offshore zone (Figure 7a). In the inshore zone, TA/DIC versus salinity slopes differed by region, with greater slopes in UK and BB (0.027 and 0.023, respectively) compared to the MK and LK (0.013 and 0.012; TukeyHSD $p < 0.05$; Table S18 in Supporting Information S1). TA/DIC ratios versus salinity regressions were not significant in the oceanic zone. At inshore and mid-channel reefs, a higher proportion of TA and DIC variability was explained by temperature compared with salinity (Figure 7b; $p < 0.05$). In general, temperature had a negative correlation with TA and DIC, but the slope magnitude declined when moving from the inshore toward the offshore zone (Figure 7b).

## 4. Discussion

### 4.1. Ocean Acidification on the Florida Coral Reef

Using 7 years of bi-monthly monitoring data for carbonate chemistry along (regions) and across (zones) the FCR, we have detected significant OA trends in all zones, with the exception of the inshore reefs. These rates increased from the mid-channel to the oceanic zones, with offshore reefs experiencing trends comparable to those recorded at the oceanic stations (Figure 2). The rates calculated here are higher than the nearest comparable surface ocean $CO_2$ rates estimated as part of the Bermuda Atlantic Times-series Study (BATS) from 1982 to 2012 (DIC = 1.37 ± 0.07 $\mu$mol yr$^{-1}$, $p$CO$_2$ = 1.69 ± 0.11 $\mu$atm yr$^{-1}$, pH = −0.0017 ± 0.0001 years$^{-1}$, $\Omega_{Ar}$ = −0.0095 ± 0.0007 years$^{-1}$; Bates et al., 2014); as well as the trends estimated in surface waters of the Florida Straits from 2002 to 2018 (DIC = 0.96 ± 0.16 $\mu$mol yr$^{-1}$, pH = −0.0021 ± 0.0039 years$^{-1}$, $\Omega_{Ar}$ = −0.0061 ± 0.0017 years$^{-1}$; Xu et al., 2022). However, they are less pronounced than those estimated from the nearest surface coastal $CO_2$ time series data in the Florida Keys from 2012 to 2016 ($p$CO$_2$ = 11.44 ± 0.26 $\mu$atm yr$^{-1}$; Chen & Hu, 2019). Continuous monitoring at these reef stations will be instrumental in elucidating whether OA trends in the FCR indeed surpass those estimated in the open ocean or if interannual variability over the past decade has accentuated the OA signal in the FCR.

The occurrence of accelerated OA near coral reefs is not without precedent. A global analysis of coral reefs from 1992 to 2012 showed that $p$CO$_2$ in coral reefs has increased ~3.5 times faster (6.6 ± 1.4 $\mu$atm yr$^{-1}$) than in the open ocean likely due to changes in the metabolic balance of the reefs associated with increasing stressors such as higher nutrient and organic matter inputs (Cyronak et al., 2014). However, given its short duration, our dataset is sensitive to interannual variability and potentially to multi-year teleconnections that can influence the ocean carbon cycle (Bates et al., 2014; Feely et al., 2006; Levine et al., 2011). For example, three sampling cruises in 2019 (July, September, and November) were characterized by high DIC, which resulted in lower than normal pH and $\Omega_{Ar}$ (Figure 2). The exclusion of these cruises from the interannual analysis still resulted in significant OA trends but with slower rates (e.g., oceanic trends for DIC = 2.46 ± 0.57 $\mu$mol yr$^{-1}$, $p$CO$_2$ = 1.90 ± 0.89 $\mu$atm yr$^{-1}$,

pH = −0.001 ± 0.001 years$^{-1}$, $\Omega_{Ar}$ = −0.006 ± 0.001 years$^{-1}$). Further monitoring will help determine whether these 2019 values were exceptional or reflective of ongoing conditions in the region.

OA trends in the FCR were primarily due to increasing DIC across all regions and zones (Figure 6a). Although inshore DIC showed larger increases over the years than the oceanic sites, the slopes were not significantly different, suggesting that terrestrial DIC sources did not substantially influence nearshore trends. At inshore and mid-channel reefs, however, the effects of increasing DIC were attenuated by a concurrent rise in TA. This led to non-significant trends in OA inshore and smaller trends in the mid-channel, compared to the offshore and oceanic zones (Figure 6a). TA in the surface open ocean is relatively stable, and its variability is mainly controlled by the addition or removal of freshwater (e.g., precipitation and evaporation; Millero et al., 1998). To verify if TA trends were explained by changes in precipitation over the years, the same interannual models used for TA were run with values that were normalized to a constant salinity (n36TA, salinity = 36), as well as values normalized to a nonzero endmember obtained from the TA versus salinity regression of data from the oceanic region (nTA). Significant and positive TA trends were obtained from the two normalized data sets, providing compelling evidence of rising TA in the study sites (e.g., nTA$_{inshore}$ = +3.7 μmol yr$^{-1}$, nTA$_{offshore}$ = +1.9 μmol yr$^{-1}$, n36TA$_{inshore}$ = +9.6 μmol yr$^{-1}$, nTA$_{offshore}$ = +6.4 μmol yr$^{-1}$).

Changes in nutrients and/or organic matter inputs (Kerr et al., 2021) as well as continental weathering driven by acidic rain (Müller et al., 2016) can modulate TA in coastal areas. Although there is currently no evidence of rising impacts of land pollution near the FCR over the duration of this study, changes in the Everglades runoff into Florida Bay might influence nutrient and organic matter inputs into the Florida Keys (Ward-Paige et al., 2005). However, it is more likely that increasing TA in the study area is related to a decline in the ratio of calcification to dissolution among the benthic communities of the study area. The FCR has been impacted by multiple stressors in the past decade, including back-to-back bleaching events in 2014 and 2015 (Gintert et al., 2018; Manzello et al., 2019), as well as the emergence of a new and deadly coral disease in 2014 (Stony coral tissue loss disease; Walton et al., 2018; Precht et al., 2016). These disturbances, resulting in declines in coral cover, may have reduced calcification that would have otherwise reduced TA. Similarly, higher abundances of bioeroders colonizing dead coral substrates or OA-accelerated dissolution (Enochs et al., 2015) may have contributed to elevated TA. Finally, it is worth noting that while the greatest interannual TA trends were observed at inshore and mid-channel reef sites, these trends were not statistically significant. Trend detection times are longer in data series with higher noise, such as in the inshore sites subjected to strong natural variability (Sutton et al., 2022). Continuation of this time series will help refine these trends and their significance.

### 4.2. Carbonate Chemistry Variability Across the Inshore-Offshore Gradient

Overall, the combination of carbonate chemistry interannual trends and seasonality resulted in contrasting scales of variability between inshore and offshore reefs, with intermediate patterns in the mid-channel. While offshore reefs experienced relatively small seasonality but greater interannual OA trends, interannual OA was not detected inshore where strong oscillations in pH and $\Omega_{Ar}$ occur throughout the year (Figures 2 and 3).

Sensitivity analyses indicated that inshore pH and $\Omega_{Ar}$ seasonality were predominantly controlled by changes in TA and DIC, with moderated impacts of temperature variability, and minimum impacts of salinity (Figure 6b). During the spring, the combined effects of TA and DIC led to net increases in pH and $\Omega_{Ar}$ at inshore reefs, given that the effects of DIC depletion outweighed the effects of TA depletion. During the summer, DIC and TA depletion effects on pH and $\Omega_{Ar}$ were balanced, resulting in inshore pH and $\Omega_{Ar}$ conditions similar to those in the oceanic zone. However, increasing DIC during the early autumn reduced pH and $\Omega_{Ar}$ at inshore reefs, despite rising TA during this season. Similar seasonal patterns in pH and $\Omega_{Ar}$ have been identified in previous studies in South Florida (Enochs et al., 2019; Manzello et al., 2012; Meléndez et al., 2020, 2022; Muehllehner et al., 2016) and other coral reefs of the world (Kleypas et al., 2011; Takeshita et al., 2018) emphasizing the key role of the metabolism of the benthic communities controlling local carbonate chemistry in shallow ecosystems.

These strong seasonal changes in DIC and TA inshore suggest that seasonal variability in carbonate chemistry in this zone is likely amplified by longer seawater residence times as well as shallow depths (Falter et al., 2013). Offshore seasonal variability, on the other hand, was mainly driven by changes in temperature. At offshore reefs, the highest $\Omega_{Ar}$ coincided with the lowest pH and was associated with the peak temperature conditions in late summer (Figures 3 and 6). These results can be explained by the deeper and more exposed location of the offshore

reefs, which facilitates water exchange with the open ocean and reduces the accumulated effect of the benthic metabolism on their seawater.

The limited correlation between TA and DIC with salinity, accompanied by varying correlations within different zones (Figure 7a), suggests that biological processes are the primary drivers of TA and DIC seasonality in the inshore and mid-channel zones. At offshore and oceanic stations, a weak yet positive correlation of TA and DIC with salinity likely arises from the effects of higher precipitation during the summer and autumn months, leading to the dilution of TA and DIC when compared to drier periods in the winter and spring. However, the inshore zone TA and DIC had negative correlations with salinity, implying that processes beyond freshwater dilution play a significant role in shaping the TA and DIC dynamics within this zone.

Stronger and positive TA and DIC correlations with temperature (Figure 7b) suggest that these parameters are mainly influenced by seasonal shifts in biological alterations of seawater carbonate chemistry by benthic communities. Temperature and daylight seasonality in the subtropical FRC are relatively high compared to tropical reefs. Both temperature and light are known to exert substantial effects on the metabolic processes of corals and primary producers, including calcification and photosynthesis rates (Fourqurean & Zieman, 1991; Gattuso et al., 1999; Mallon et al., 2022). In the FCR, months with colder temperatures generally coincide with shorter daylight hours, and vice versa. Consequently, the combination of elevated temperatures and increased light availability likely stimulates primary production and calcification during the spring and summer, resulting in lower DIC and TA levels along with higher TA/DIC ratios when compared to the autumn and winter (Figure 7b). This seasonality aligns with the patterns of productivity and abundance of seagrass and macroalgal species in the Florida Keys, with peaks occurring in June/July and lows in January (Collado-Vides et al., 2005; Fourqurean et al., 2001; Lirman & Biber, 2000; Manzello et al., 2012).

To unravel the underlying factors contributing to the variability in carbonate chemistry across the diverse zones and regions of the FCR, there is an urgent need for a more comprehensive understanding of benthic cover and seawater flow patterns. The FCR still lacks a comprehensive characterization of seawater flow and residence times, which obstructs the precise quantification of how specific benthic communities influence TA and DIC in the sampled seawater. We hypothesize that longer residence time at inshore reefs will continue to result in strong seasonality driven by biological activity. Similarly, faster water exchange between the reef and the open ocean endmember will likely continue to expose offshore sites to open ocean OA trends, with the benthic community metabolism exerting minimal impact on these conditions.

### 4.3. Regional Differences Along the FCR

In addition to the differences in seasonal amplitude among reef zones, there were region-specific seasonality patterns at inshore and mid-channel reefs. For example, although the magnitude of the seasonal ΔTA and ΔDIC were similar among the regions during winter and spring, summer DIC and TA depletion were up to three times greater in the MK and the LK regions compared to BB and the UK (Figure 4). Overall, yearly net calcification and photosynthesis were found only in the LK and the MK regions, while the northernmost reefs in BB and UK seem to be closer to their tipping point (average ΔTA and ΔDIC values close to zero). Similar regional patterns have been observed in earlier (2009–2011) carbonate chemistry surveys (Manzello et al., 2012; Muehllehner et al., 2016) and in carbonate budget studies (Enochs et al., 2015; Morris, Enochs, Besemer, et al., 2022), highlighting the higher risk of reef erosion in the northeast areas of the FCR compared to the southwest. Reefs in the BB and UK regions are in closer proximity to the city of Miami and thus could be exposed to more frequent anthropogenic disturbances. Similarly, their location at a higher latitude might expose them to stronger seasonal gradients in light and temperature that could be suboptimal for coral development (Muehllehner et al., 2016).

Further variation in carbonate chemistry among the regions was observed in the TA versus DIC plots (Figure 5). For instance, TA versus DIC slopes in the MK and LK tend to rise from winter to spring and summer, indicating a relative increase in calcification compared to photosynthesis during this period. In contrast, slopes in the UK, and to a lesser degree in BB, tend to decline from winter to spring and summer, indicating an increase in photosynthesis relative to calcification (Figures 4 and 5). These regional differences in the biological modification of water chemistry (the balance between photosynthesis/respiration and calcification/dissolution) contributed to differences in pH and $\Omega_{Ar}$, especially inshore, facilitating more favorable conditions for calcification in the UK (Figure 4). Because of their closer proximity to extensive seagrass beds (Figure 1b), UK reefs could be benefiting

from the high productivity of these ecosystems and could act as temporary OA refugia in the FCR (Manzello et al., 2012). Contrastingly, lower TA values in the LK resulted in persistent lower pH and $\Omega_{Ar}$ in this region. The underlying cause of this increased calcification in comparison to photosynthesis remains unclear. Irrespective of the causative factors, the already lower pH and $\Omega_{Ar}$ conditions make the LK a particularly susceptible region to further OA.

### 4.4. Implications for Coral Reefs' Resilience to OA

In this study, we describe high spatiotemporal variability in the carbonate chemistry of a large reef system. This includes differences in interannual OA trends and seasonality, which are defined by inshore-offshore gradients as well as regional location. These differences offer an opportunity to study potential hotspots for OA exposure and/or refugia as well as the effects of carbonate chemistry variability on long-term responses to OA. Evaluating how carbonate chemistry variability impacts the metabolic activity of reef organisms as well as their response to global OA trends is experimentally challenging. Ex-situ experiments of 1-year duration are unfeasible for most laboratories and in situ comparisons among sites with different seasonal variability introduce confounding effects associated with additional differences between the sites (e.g., temperature, light, water flow, nutrient levels).

Insights from the few studies that have assessed the effects of diel variability on calcification and bioerosion suggest that the effects might be species-specific (Cornwall et al., 2018) and will likely vary with the amplitude of the seasonal oscillations and the amount of time spent above and below a species' metabolic thresholds (Enochs et al., 2018). For example, some corals sustain higher calcification rates when exposed to variable pH compared to corals exposed to static pH (Chan & Eggins, 2017; Comeau et al., 2014; Dufault et al., 2012; Enochs et al., 2018). Similarly, sponge bioerosion rates have been found to increase under variable pH, but the effects depended on the species and mean pH values (Morris, Enochs, Webb, et al., 2022).

Carbonate chemistry variability may increase OA resilience by promoting adaptation and acclimation. Local environmental variability has been shown to increase corals' tolerance to stressors (Langlais et al., 2017; Safaie et al., 2018) through the selection of more tolerant coral genotypes or symbiotic communities (Barshis et al., 2018; Kelly et al., 2014), and through corals' acclimatization by epigenetic or gene expression changes induced during stress pulses (Kenkel & Matz, 2016; Putnam et al., 2016). Although these mechanisms have been extensively studied regarding corals' response to heat stress, little is known about how pH variability influences the responses of calcifiers and bioeroders to OA. Positive effects of pH variability history have often been found for calcifying organisms other than corals (e.g., echinoderms, mollusks, and crustaceans), mainly from temperate environments (Gaitán-Espitia et al., 2017; Kapsenberg & Cyronak, 2019; Vargas et al., 2017). However, to date, there is no compelling evidence that tropical corals originating from places with higher pH variability can maintain higher calcification rates under reduced pH compared with corals from more constant environments (Camp et al., 2016; Cornwall et al., 2018). Further work is needed to test if higher variability in carbonate chemistry might reduce OA vulnerability through adaptation or acclimation or if, conversely, it will exacerbate OA impacts by temporarily reducing pH beyond the global OA rates.

## 5. Implications for Conservation and Conclusions

Understanding and predicting how OA will impact different ecoregions and organisms is fundamental to developing and implementing efficient management actions to respond to climate change. Global OA predictions might not provide the granularity to manage reefs at the local level, since natural temporal and spatial variability in carbonate chemistry could result in areas and times of enhanced or reduced stress. Here, we documented significant differences in OA trends, seasonal variability, and year-round carbonate chemistry conditions that could be applied to the management of the FCR.

Significant OA trends were detected in the mid-channel, offshore, and oceanic zones from 2015 to 2021. However, these trends were not observed in the inshore reefs, where they seem to be ameliorated by rising TA. Additionally, within the inshore and mid-channel zones, the biogeographic region plays a pivotal role in shaping carbonate chemistry conditions with potential OA refugia in the UK and hotspots in the LK. These findings are important for policymakers and conservation practitioners to better understand and manage the impacts of OA on coral reef ecosystems. Higher pH and $\Omega_{Ar}$ in the UK and MK regions could favor calcification and coral growth in these regions, suggesting that if the coral cover is restored, these reefs could have a higher capacity to sustain

reef accretion. These carbonate chemistry patterns could be incorporated into the vast literature describing the impacts and hotspots of other stressors (e.g., warming and diseases) to design effective restoration practices needed to offset the coral cover reduction and reef degradation in South Florida reefs over the past decades (Grove et al., 2022; Ruzicka et al., 2013; Soto et al., 2011).

In contrast to multiple regions where global OA is being exacerbated by coastal acidification (Enochs et al., 2019; Hall et al., 2020; Uthicke et al., 2014; Wallace et al., 2014), we found that inshore reefs in the FCR, which co-exist with seagrass communities, may be exposed to reduced OA trends. The potential for OA refugia in inshore reefs through enhanced primary production highlights the relevance of seagrass ecosystems for the neighboring corals in the context of future climate scenarios (Bergstrom et al., 2019). Thus, coral reef conservation efforts should consider the possible interactions between the preservation of seagrass and reef resilience to OA. Research efforts should be directed to understand (a) the OA buffering capacity of the local seagrass species and how the local hydrodynamic regimes might enhance or limit the carbonate system changes resulting from seagrass metabolism, (b) the metabolic effects of pH variability for local calcifying and bioeroding species under current and future mean conditions, and (c) if differences in carbonate chemistry variability between the offshore and inshore zones have resulted in differential OA acclimatization or adaptation by the keystone species that could be incorporated into reef restoration.

## Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

## Data Availability Statement

Data used in the study are publicly available at NOAA's National Centers for Environmental Information (https://doi.org/10.25921/vfz0-dg77). The code to reproduce the data analyses is available in a GitHub repository (https://anampc.github.io/FLK_2021/) and permanently archived in Zenodo (Palacio-Castro, 2023).

## References

Anderson, M., Analytical Laboratories of Hawaii, Eastlake, R., & Photo Science Inc (2011). Benthic habitats of Florida keys derived from IKONOS satellite imagery. Retrieved from https://ocean.floridamarine.org/IntegratedReefMap/Docs/Metadata_Keys_NOAA.html

Anthony, K. R. N., Diaz-Pulido, G., Verlinden, N., Tilbrook, B., & Andersson, A. J. (2013). Benthic buffers and boosters of ocean acidification on coral reefs. *Biogeosciences Discussions*, *10*(2), 1831–1865. https://doi.org/10.5194/bg-10-4897-2013

Anthony, K. R. N., Kleypas, J. A., & Gattuso, J.-P. (2011). Coral reefs modify their seawater carbon chemistry—Implications for impacts of ocean acidification. *Global Change Biology*, *17*(12), 3655–3666. https://doi.org/10.1111/j.1365-2486.2011.02510.x

Aronson, R. B., & Precht, W. F. (2001). White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia*, *460*(1/3), 25–38. https://doi.org/10.1023/a:1013103928980

Barshis, D. J., Birkeland, C., Toonen, R. J., Gates, R. D., & Stillman, J. H. (2018). High-frequency temperature variability mirrors fixed differences in thermal limits of the massive coral Porites lobata. *Journal of Experimental Biology*, *221*.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 51. https://doi.org/10.18637/jss.v067.i01

Bates, N., Astor, Y., Church, M., Currie, K., Dore, J., Gonaález-Dávila, M., et al. (2014). A time-series view of changing ocean chemistry due to ocean uptake of anthropogenic $CO_2$ and ocean acidification. *Oceanography*, *27*(1), 126–141. https://doi.org/10.5670/oceanog.2014.16

Bergstrom, E., Silva, J., Martins, C., & Horta, P. (2019). Seagrass can mitigate negative ocean acidification effects on calcifying algae. *Scientific Reports*, *9*(1), 1932. https://doi.org/10.1038/s41598-018-35670-3

Bolin, E. (1959). Changes in the carbon dioxide content of the atmosphere and sea due to fossil fuel combustion. In E. Bolin (Ed.), *The atmosphere and sea in motion* (pp. 130–142). Rockefeller Inst. Press.

Caldeira, K., & Wickett, M. E. (2003). Oceanography: Anthropogenic carbon and ocean pH. *Nature*, *425*(6956), 365. https://doi.org/10.1038/425365a

Caldeira, K., & Wickett, M. E. (2005). Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *Journal of Geophysical Research*, *110*(C9), C09S04. https://doi.org/10.1029/2004jc002671

Camp, E. F., Smith, D. J., Evenhuis, C., Enochs, I., Manzello, D., Woodcock, S., & Suggett, D. J. (2016). Acclimatization to high-variance habitats does not enhance physiological tolerance of two key Caribbean corals to future temperature and pH. *Proceedings of the Royal Society B*, *283*(1831), 20160442. https://doi.org/10.1098/rspb.2016.0442

Chan, N. C. S., & Connolly, S. R. (2013). Sensitivity of coral calcification to ocean acidification: A meta-analysis. *Global Change Biology*, *19*(1), 282–290. https://doi.org/10.1111/gcb.12011

Chan, W. Y., & Eggins, S. M. (2017). Calcification responses to diurnal variation in seawater carbonate chemistry by the coral Acropora formosa. *Coral Reefs*, *36*(3), 763–772. https://doi.org/10.1007/s00338-017-1567-8

Chen, S., & Hu, C. (2019). Environmental controls of surface water $pCO_2$ in different coastal environments: Observations from marine buoys. *Continental Shelf Research*, *183*, 73–86. https://doi.org/10.1016/j.csr.2019.06.007

Colella, M. A., Ruzicka, R. R., Kidney, J. A., Morrison, J. M., & Brinkhuis, V. B. (2012). Cold-water event of January 2010 results in catastrophic benthic mortality on patch reefs in the Florida Keys. *Coral Reefs*, *31*(2), 621–632. https://doi.org/10.1007/s00338-012-0880-5

Collado-Vides, L., Rutten, L. M., & Fourqurean, J. W. (2005). Spatiotemporal variation of the abundance of calcareous green macroalgae in the Florida keys: A study of synchrony within a macroalgal functional-form group. *Journal of Phycology*, *41*(4), 742–752. https://doi.org/10.1111/j.1529-8817.2005.00099.x

Comeau, S., Edmunds, P. J., Spindel, N. B., & Carpenter, R. C. (2014). Diel $p$CO$_2$ oscillations modulate the response of the coral Acropora Hyacinthus to ocean acidification. *Marine Ecology Progress Series*, *501*, 99–111. https://doi.org/10.3354/meps10690

Cornwall, C. E., Comeau, S., DeCarlo, T. M., Moore, B., D'Alexis, Q., & McCulloch, M. T. (2018). Resistance of corals and coralline algae to ocean acidification: Physiological control of calcification under natural pH variability. *Proceedings of the Royal Society B*, *285*(1884), 20181168. https://doi.org/10.1098/rspb.2018.1168

Cyronak, T., Schulz, K. G., Santos, I. R., & Eyre, B. D. (2014). Enhanced acidification of global coral reefs driven by regional biogeochemical feedbacks. *Geophysical Research Letters*, *41*(15), 5538–5546. https://doi.org/10.1002/2014gl060849

Dickson, A. G. (1990). Standard potential of the reaction: AgCl(s) + 12H$_2$(g)=HCl(aq), and the standard acidity constant of the ion HSO$_4^-$ in synthetic sea water from 273.15 to 318.15 K. *The Journal of Chemical Thermodynamics*, *22*(2), 113–127. https://doi.org/10.1016/0021-9614(90)90074-z

Dickson, A. G., Sabine, C. L., & Christian, J. R. (2007). *Guide to best practices for ocean CO$_2$ measurements* (Vol. 3, p. 191). PICES Special Publication.

Doney, S. C., Fabry, V. J., Feely, R. A., & Kleypas, J. A. (2009). Ocean acidification: The other CO$_2$ problem. *Annual Review of Marine Science*, *1*, 169–192. https://doi.org/10.1146/annurev.marine.010908.163834

Duarte, C. M., Hendriks, I. E., Moore, T. S., Olsen, Y. S., Steckbauer, A., Ramajo, L., et al. (2013). Is ocean acidification an open-ocean syndrome? Understanding anthropogenic impacts on seawater pH. *Estuaries and Coasts*, *36*(2), 221–236. https://doi.org/10.1007/s12237-013-9594-3

Dufault, A. M., Cumbo, V. R., Fan, T.-Y., & Edmunds, P. J. (2012). Effects of diurnally oscillating $p$CO$_2$ on the calcification and survival of coral recruits. *Proceedings of the Royal Society B*, *279*(1740), 2951–2958. https://doi.org/10.1098/rspb.2011.2545

Enochs, I. C., Manzello, D. P., Carlton, R. D., Graham, D. M., Ruzicka, R., & Colella, M. A. (2015). Ocean acidification enhances the bioerosion of a common coral reef sponge: Implications for the persistence of the Florida reef tract. *Bulletin of Marine Science*, *91*(2), 271–290. https://doi.org/10.5343/bms.2014.1045

Enochs, I. C., Manzello, D. P., Jones, P. J., Aguilar, C., Cohen, K., Valentino, L., et al. (2018). The influence of diel carbonate chemistry fluctuations on the calcification rate of Acropora cervicornis under present day and future acidification conditions. *Journal of Experimental Marine Biology and Ecology*, *506*, 135–143. https://doi.org/10.1016/j.jembe.2018.06.007

Enochs, I. C., Manzello, D. P., Jones, P. R., Stamates, S. J., & Carsey, T. P. (2019). Seasonal carbonate chemistry dynamics on southeast Florida coral reefs: Localized acidification hotspots from navigational inlets. *Frontiers in Marine Science*, *6*. https://doi.org/10.3389/fmars.2019.00160

Enochs, I. C., Manzello, D. P., Kolodziej, G., Noonan, S. H. C., Valentino, L., & Fabricius, K. E. (2016). Enhanced macroboring and depressed calcification drive net dissolution at high-CO$_2$ coral reefs. *Proceedings of the Royal Society B*, *283*(1842), 20161742. https://doi.org/10.1098/rspb.2016.1742

Falter, J. L., Lowe, R. J., Zhang, Z., & McCulloch, M. (2013). Physical and biological controls on the carbonate chemistry of coral reef waters: Effects of metabolism, wave forcing, sea level, and geomorphology. *PLoS One*, *8*(1), e53303. https://doi.org/10.1371/journal.pone.0053303

Feely, R. A., Takahashi, T., Wanninkhof, R., McPhaden, M. J., Cosca, C. E., Sutherland, S. C., & Carr, M.-E. (2006). Decadal variability of the air-sea CO$_2$ fluxes in the equatorial Pacific Ocean. *Journal of Geophysical Research*, *111*(C8), C08S90. https://doi.org/10.1029/2005jc003129

Fourqurean, J. W., Willsie, A., Rose, C. D., & Rutten, L. M. (2001). Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology*, *138*(2), 341–354. https://doi.org/10.1007/s002270000448

Fourqurean, J. W., & Zieman, J. C. (1991). Photosynthesis, respiration and whole plant carbon budget of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series*, *69*(1/2), 161–170. https://doi.org/10.3354/meps069161

Friis, K., Körtzinger, A., & Wallace, D. W. R. (2003). The salinity normalization of marine inorganic carbon chemistry data. *Geophysical Research Letters*, *30*(2). https://doi.org/10.1029/2002gl015898

Gaitán-Espitia, J. D., Villanueva, P. A., Lopez, J., Torres, R., Navarro, J. M., & Bacigalupe, L. D. (2017). Spatio-temporal environmental variation mediates geographical differences in phenotypic responses to ocean acidification. *Biology Letters*, *13*(2), 20160865. https://doi.org/10.1098/rsbl.2016.0865

Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A., & Watkinson, A. R. (2005). Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. *Ecology*, *86*(1), 174–184. https://doi.org/10.1890/04-0141

Gattuso, J.-P., Allemand, D., & Frankignoulle, M. (1999). Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. *American Zoologist*, *39*(1), 160–183. https://doi.org/10.1093/icb/39.1.160

Gattuso, J.-P., Epitalon, J.-M., Lavigne, H., & Orr, J. (2019). Seacarb: Seawater carbonate chemistry. R package version 3.2. 12 (version 3.3.1). Retrieved from https://hal.u-pec.fr/UMS-829/hal-02345814v1

Gintert, B. E., Manzello, D. P., Enochs, I. C., Kolodziej, G., Carlton, R., Gleason, A. C. R., & Gracias, N. (2018). Marked annual coral bleaching resilience of an inshore patch reef in the Florida keys: A nugget of hope, aberrance, or last man standing? *Coral Reefs*, *37*(2), 533–547. https://doi.org/10.1007/s00338-018-1678-x

Grove, L. J. W., Blondeau, J., Cain, E., Davis, I. M., Edwards, K. F., Groves, S. H., et al. (2022). *National coral reef monitoring program biological monitoring summary Florida: 2020–2021. Coral reef conservation program*. National Centers for Coastal Ocean Scienc; Southeast Fisheries Science Center. https://doi.org/10.25923/9jns-v916

Hall, E. R., Wickes, L., Burnett, L. E., Scott, G. I., Hernandez, D., Yates, K. K., et al. (2020). Acidification in the U.S. Southeast: Causes, potential consequences and the role of the southeast ocean and coastal acidification network. *Frontiers in Marine Science*, *7*. https://doi.org/10.3389/fmars.2020.00548

Haugan, P. M., & Drange, H. (1996). Effects of CO$_2$ on the ocean environment. *Energy Conversion and Management*, *37*(6), 1019–1022. https://doi.org/10.1016/0196-8904(95)00292-8

Hurd, C. L., Cornwall, C. E., Currie, K., Hepburn, C. D., McGraw, C. M., Hunter, K. A., & Boyd, P. W. (2011). Metabolically induced pH fluctuations by some coastal calcifiers exceed projected 22nd century ocean acidification: A mechanism for differential susceptibility? *Global Change Biology*, *17*(10), 3254–3262. https://doi.org/10.1111/j.1365-2486.2011.02473.x

Jaap, W. C., Halas, J. C., & Muller, R. G. (1988). Community dynamics of stony corals (Milleporina and Scleractinia) at Key Largo National Marine Sanctuary, Florida during 1981–1986. *Proceedingsof the 6th International Coral Reef Symposium*, *2*, 237–243.

Kapsenberg, L., & Cyronak, T. (2019). Ocean acidification refugia in variable environments. *Global Change Biology*, *25*(10), 3201–3214. https://doi.org/10.1111/gcb.14730

Kelly, L. W., Williams, G. J., Barott, K. L., Carlson, C. A., Dinsdale, E. A., Edwards, R. A., et al. (2014). Local genomic adaptation of coral reef-associated microbiomes to gradients of natural variability and anthropogenic stressors. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(28), 10227–10232. https://doi.org/10.1073/pnas.1403319111

Kenkel, C. D., & Matz, M. V. (2016). Gene expression plasticity as a mechanism of coral adaptation to a variable environment. *Nature Ecology & Evolution*, *1*(1), 14. https://doi.org/10.1038/s41559-016-0014

Kerr, D. E., Brown, P. J., Grey, A., & Kelleher, B. P. (2021). The influence of organic alkalinity on the carbonate system in coastal waters. *Marine Chemistry*, *237*, 104050. https://doi.org/10.1016/j.marchem.2021.104050

Kleypas, J. A., Anthony, K. R. N., & Gattuso, J.-P. (2011). Coral reefs modify their seawater carbon chemistry - Case study from a barrier reef (Moorea, French Polynesia). *Global Change Biology*, *17*(12), 3667–3678. https://doi.org/10.1111/j.1365-2486.2011.02530.x

Koch, M., Bowes, G., Ross, C., & Zhang, X. H. (2013). Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Global Change Biology*, *19*(1), 103–132. https://doi.org/10.1111/j.1365-2486.2012.02791.x

Langlais, C. E., Lenton, A., Heron, S. F., Evenhuis, C., Sen Gupta, A., Brown, J. N., & Kuchinke, M. (2017). Coral bleaching pathways under the control of regional temperature variability. *Nature Climate Change*, *7*(11), 839–844. https://doi.org/10.1038/nclimate3399

Lenth, R. (2018). Emmeans: Estimated marginal means, aka least-squares means (version 1.1.3). Retrieved from https://cran.r-project.org/package=emmeans

Levine, N. M., Doney, S. C., Lima, I., Wanninkhof, R., Bates, N. R., & Feely, R. A. (2011). The impact of interannual variability on the uptake and accumulation of anthropogenic $CO_2$ in the North Atlantic. *Global Biogeochemical Cycles*, *25*(3), GB3022. https://doi.org/10.1029/2010gb003892

Lirman, D., & Biber, P. (2000). Seasonal dynamics of macroalgal communities of the northern Florida reef tract. *Seasonal Dynamics of Macroalgal Communities of the Northern Florida Reef Tract*, *43*(4), 305–314. https://doi.org/10.1515/bot.2000.033

Lirman, D., Schopmeyer, S., Manzello, D. P., Gramer, L. J., Precht, W. F., Muller-Karger, F. E., et al. (2011). Severe 2010 cold-water event caused unprecedented mortality to corals of the Florida reef tract and reversed previous survivorship patterns. *PLoS One*, *6*(8), e23047. https://doi.org/10.1371/journal.pone.0023047

Lueker, T. J., Dickson, A. G., & Keeling, C. D. (2000). Ocean $p$CO$_2$ calculated from dissolved inorganic carbon, alkalinity, and equations for K1 and K2: Validation based on laboratory measurements of $CO_2$ in gas and seawater at equilibrium. *Marine Chemistry*, *70*(1), 105–119. https://doi.org/10.1016/s0304-4203(00)00022-0

Mallon, J., Cyronak, T., Hall, E. R., Banaszak, A. T., Exton, D. A., & Bass, A. M. (2022). Light-driven dynamics between calcification and production in functionally diverse coral reef calcifiers. *Limnology & Oceanography*, *67*(2), 434–449. https://doi.org/10.1002/lno.12002

Manzello, D. P. (2008). Short and long-term ramifications of climate change upon coral reef ecosystems: Case studies across two oceans. Ph.D. Thesis (p. 97). University of Miami.

Manzello, D. P., Enochs, I. C., Melo, N., Gledhill, D. K., & Johns, E. M. (2012). Ocean acidification refugia of the Florida reef tract. *PLoS One*, *7*(7), e41715. https://doi.org/10.1371/journal.pone.0041715

Manzello, D. P., Matz, M. V., Enochs, I. C., Valentino, L., Carlton, R. D., Kolodziej, G., et al. (2019). Role of host genetics and heat tolerant algal symbionts in sustaining populations of the endangered coral Orbicella faveolata in the Florida Keys with ocean warming. *Global Change Biology*, *25*(3), 1–16. https://doi.org/10.1111/gcb.14545

Meléndez, M., Salisbury, J., Gledhill, D., Langdon, C., Morell, J. M., Manzello, D., et al. (2020). Seasonal variations of carbonate chemistry at two western Atlantic coral reefs. *Journal of Geophysical Research: Oceans*, *125*(8). https://doi.org/10.1029/2020jc016108

Meléndez, M., Salisbury, J., Gledhill, D., Langdon, C., Morell, J. M., Manzello, D., & Sutton, A. (2022). Net ecosystem dissolution and respiration dominate metabolic rates at two western Atlantic reef sites. *Limnology & Oceanography*, *67*(3), 527–539. https://doi.org/10.1002/lno.12009

Middelboe, A. L., & Hansen, P. J. (2007). High pH in shallow-water macroalgal habitats. *Marine Ecology Progress Series*, *338*, 107–117. https://doi.org/10.3354/meps338107

Millero, F. J., Lee, K., & Roche, M. (1998). Distribution of alkalinity in the surface waters of the major oceans. *Marine Chemistry*, *60*(1), 111–130. https://doi.org/10.1016/s0304-4203(97)00084-4

Morey, S., Koch, M., Liu, Y., & Lee, S.-K. (2017). Florida's oceans and marine habitats in a changing climate. In E. P. Chassignet, J. W. Jones, V. Misra, & J. Obeysekera (Eds.), *Florida's climate: Changes, variations, & impacts*. Florida Climate Institute.

Morris, J., Enochs, I., Webb, A., de Bakker, D., Soderberg, N., Kolodziej, G., & Manzello, D. (2022). The influences of diurnal variability and ocean acidification on the bioerosion rates of two reef-dwelling Caribbean sponges. *Global Change Biology*, *28*(23), 7126–7138. https://doi.org/10.1111/gcb.16442

Morris, J. T., Enochs, I. C., Besemer, N., Viehman, T. S., Groves, S. H., Blondeau, J., et al. (2022). Low net carbonate accretion characterizes Florida's coral reef. *Scientific Reports*, *12*(1), 19582. https://doi.org/10.1038/s41598-022-23394-4

Muehllehner, N., Langdon, C., Venti, A., & Kadko, D. (2016). Dynamics of carbonate chemistry, production, and calcification of the Florida Reef Tract (2009–2010): Evidence for seasonal dissolution. *Global Biogeochemical Cycles*, *30*(5), 661–688. https://doi.org/10.1002/2015gb005327

Müller, J. D., Schneider, B., & Rehder, G. (2016). Long-term alkalinity trends in the Baltic Sea and their implications for $CO_2$-induced acidification. *Limnology & Oceanography*, *61*(6), 1984–2002. https://doi.org/10.1002/lno.10349

Orr, J. C., Epitalon, J.-M., Dickson, A. G., & Gattuso, J.-P. (2018). Routine uncertainty propagation for the marine carbon dioxide system. *Marine Chemistry*, *207*, 84–107. https://doi.org/10.1016/j.marchem.2018.10.006

Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., et al. (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, *437*(7059), 681–686. https://doi.org/10.1038/nature04095

Palacio-Castro, A. M. (2023). Pipeline for "Coral reef carbonate chemistry reveals interannual, seasonal, and spatial impacts on ocean acidification off Florida: Submitted to GBC (v2). *Zenodo*. https://doi.org/10.5281/zenodo.10052146

Palandro, D. A., Andréfouët, S., Hu, C., Hallock, P., Müller-Karger, F. E., Dustan, P., et al. (2008). Quantification of two decades of shallow-water coral reef habitat decline in the Florida Keys National Marine Sanctuary using Landsat data (1984–2002). *Remote Sensing of Environment*, *112*(8), 3388–3399. https://doi.org/10.1016/j.rse.2008.02.015

Patterson, K. L., Porter, J. W., Ritchie, K. B., Polson, S. W., Mueller, E., Peters, E. C., et al. (2002). The etiology of white pox, a lethal disease of the Caribbean Elkhorn coral, Acropora palmata. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(13), 8725–8730. https://doi.org/10.1073/pnas.092260099

Perez, F. F., & Fraga, F. (1987). Association constant of fluoride and hydrogen ions in seawater. *Marine Chemistry*, *21*(2), 161–168. https://doi.org/10.1016/0304-4203(87)90036-3

Porter, J. W., Kosmynin, V., Patterson, K. L., Porter, K. G., Jaap, W. C., Wheaton, J. L., et al. (2002). Detection of coral reef change by the Florida Keys coral reef monitoring project. In J. W. Porter & K. G. Porter (Eds.), *The everglades, Florida Bay, and coral reefs of the Florida keys* (pp. 749–769). CRC Press.

Porter, J. W., Lewis, S. K., & Porter, K. G. (1999). The effect of multiple stressors on the Florida keys coral reef ecosystem: A landscape hypothesis and a physiological test. *Limnology & Oceanography*, *44*(3part2), 941–949. https://doi.org/10.4319/lo.1999.44.3_part_2.0941

Precht, W. F., Gintert, B. E., Robbart, M. L., Fura, R., & van Woesik, R. (2016). Unprecedented disease-related coral mortality in southeastern Florida. *Scientific Reports*, *6*(1), 31374. https://doi.org/10.1038/srep31374

Putnam, H. M., Davidson, J. M., & Gates, R. D. (2016). Ocean acidification influences host DNA methylation and phenotypic plasticity in environmentally susceptible corals. *Evolutionary Applications*, *9*(9), 1165–1178. https://doi.org/10.1111/eva.12408

R Core Team. (2020). *R: A language and environment for statistical computing (version 3.6.3)*. R Foundation for Statistical Computing. Retrieved from https://www.r-project.org

Ricart, A. M., Ward, M., Hill, T. M., Sanford, E., Kroeker, K. J., Takeshita, Y., et al. (2021). Coast-wide evidence of low pH amelioration by seagrass ecosystems. *Global Change Biology*, *27*(11), 2580–2591. https://doi.org/10.1111/gcb.15594

Ruzicka, R. R., Colella, M. A., Porter, J. W., Morrison, J. M., Kidney, J. A., Brinkhuis, V., et al. (2013). Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. *Marine Ecology Progress Series*, *489*, 125–141. https://doi.org/10.3354/meps10427

Sabine, C. L., Feely, R. A., Gruber, N., Key, R. M., Lee, K., Bullister, J. L., et al. (2004). The oceanic sink for anthropogenic $CO_2$. *Science*, *305*(5682), 367–371. https://doi.org/10.1126/science.1097403

Safaie, A., Silbiger, N. J., Mcclanahan, T. R., Pawlak, G., Barshis, D. J., Hench, J. L., et al. (2018). High frequency temperature variability reduces the risk of coral bleaching. *Nature Communications*, *9*(1), 1671. https://doi.org/10.1038/s41467-018-04074-2

Soto, I. M., Muller Karger, F. E., Hallock, P., & Hu, C. (2011). Sea surface temperature variability in the Florida keys and its relationship to coral cover. *Journal of Marine Biology*, *2011*, 1–10. https://doi.org/10.1155/2011/981723

Storlazzi, C. D., Reguero, B. G., Cole, A. D., Lowe, E., Shope, J. B., Gibbs, A. E., et al. (2019). *Rigorously valuing the role of US coral reefs in coastal hazard risk reduction*. Open-File Report-US Geological Survey. Retrieved from https://www.cabdirect.org/cabdirect/abstract/20193359083

Sutton, A. J., Battisti, R., Carter, B., Evans, W., Newton, J., Alin, S., et al. (2022). Advancing best practices for assessing trends of ocean acidification time series. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.1045667

Takeshita, Y., Cyronak, T., Martz, T. R., Kindeberg, T., & Andersson, A. J. (2018). Coral reef carbonate chemistry variability at different functional scales. *Frontiers in Marine Science*, *5*. https://doi.org/10.3389/fmars.2018.00175

Towle, E., Geiger, E., & Grove, J. (2020). Coral reef condition: A status report for Florida's coral reef. Coral reef conservation program (U.S.). https://doi.org/10.25923/RXD1-D467

Uppström, L. R. (1974). The boron/chlorinity ratio of deep-sea water from the Pacific Ocean. *Deep-Sea Research and Oceanographic Abstracts*, *21*(2), 161–162. https://doi.org/10.1016/0011-7471(74)90074-6

Uthicke, S., Furnas, M., & Lønborg, C. (2014). Coral reefs on the edge? Carbon chemistry on inshore reefs of the Great Barrier Reef. *PLoS One*, *9*(10), e109092. https://doi.org/10.1371/journal.pone.0109092

Vargas, C. A., Lagos, N. A., Lardies, M. A., Duarte, C., Manríquez, P. H., Aguilera, V. M., et al. (2017). Species-specific responses to ocean acidification should account for local adaptation and adaptive plasticity. *Nature Ecology & Evolution*, *1*(4), 84. https://doi.org/10.1038/s41559-017-0084

Wallace, R. B., Baumann, H., Grear, J. S., Aller, R. C., & Gobler, C. J. (2014). Coastal ocean acidification: The other eutrophication problem. *Estuarine, Coastal and Shelf Science*, *148*, 1–13. https://doi.org/10.1016/j.ecss.2014.05.027

Walton, C., Hayes, N. K., & Gilliam, D. S. (2018). Impacts of a regional, multi-year, multi-species coral disease outbreak in Southeast Florida. *Frontiers in Marine Science*, *5*, 323. https://doi.org/10.3389/fmars.2018.00323

Ward-Paige, C. A., Risk, M. J., & Sherwood, O. A. (2005). Reconstruction of nitrogen sources on coral reefs: $\delta^{15}N$ and $\delta^{13}C$ in gorgonians from Florida reef tract. *Marine Ecology Progress Series*, *296*, 155–163. https://doi.org/10.3354/meps296155

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York.

Xu, Y.-Y., Wanninkhof, R., Osborne, E., Baringer, M., Barbero, L., Cai, W.-J., & Hooper, J. (2022). Inorganic carbon transport and dynamics in the Florida straits. *Journal of Geophysical Research: Oceans*, *127*(10). https://doi.org/10.1029/2022jc018405