



Meta-Analysis Reveals Reduced Coral Calcification Under Projected Ocean Warming but Not Under Acidification Across the Caribbean Sea

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Ocean acidification and warming are two of the many threats to coral reefs worldwide, and Caribbean reef-building corals are especially vulnerable. However, even within the Caribbean, experimental acidification and warming studies reveal a wide array of coral calcification responses across reef systems and among species, complicating efforts to predict how corals will respond to these global-scale stressors. We conducted a meta-analysis to investigate the calcification responses of Caribbean corals to experimentally induced seawater ocean acidification, ocean warming, and the combination of both stressors. Calcification rates were reduced for corals reared under warming alone, but acidification and the combination of both stressors did not clearly reduce calcification rates. Calcification responses of corals collected from the Florida Keys and Belize were compared for regional differences since a greater number of studies were performed on corals collected from these two regions. Notably, corals from the Florida Keys did not exhibit reduced calcification under acidification, warming, or the combination of both stressors, while corals from Belize exhibited reduced calcification under warming alone. Further investigation of these regional trends suggests that the warming and acidification treatments employed dictated calcification responses, rather than collection region. Results from this meta-analysis are constrained by the very few studies that have been conducted within the Caribbean to assess ocean acidification and warming and the large variation in experimental procedure among studies. This meta-analysis reveals existing gaps in our understanding of how corals will likely respond to projected acidification and warming and highlights ways to improve comparability among experimental studies conducted on corals within the same region to better predict coral calcification response under global change.

Keywords: meta-analysis, Caribbean corals, ocean acidification, ocean warming, calcification

INTRODUCTION

Reef-building corals provide the three-dimensional framework for tropical coral reef ecosystems across the globe, supporting many important ecological and economic goods and services (Costanza et al., 2014). However, coral reefs globally are experiencing declines in diversity and abundance (Pandolfi et al., 2003), raising concerns for the overall health of these essential ecosystems. Such changes in coral reef ecosystems are especially evident throughout the Caribbean Sea (Alvarez-Filip et al., 2009; Schutte et al., 2010). Declines in carbonate production rates (Perry et al., 2013) and reduced coral cover (Cote et al., 2005) on Caribbean reefs have shifted these ecosystems to less structurally complex reefs dominated by algae, sponges, and gorgonians (Norstrom et al., 2009). Over the past two decades, ocean warming and acidification have been identified as two of the primary stressors causing this shift and therefore there have been widespread efforts to better understand how coral reefs will likely respond to projected increases in these two human-induced global change stressors (Kleypas et al., 1999; Doney et al., 2009; Enochs et al., 2016; Stoltenberg et al., 2019).

The Intergovernmental Panel on Climate Change (IPCC) has projected that sea surface temperatures in the Caribbean region could rise between 0.6 and 3.0°C by the end of the twenty-first century (ocean warming), and atmospheric $p\text{CO}_2$ will surpass 600 μatm , causing surface ocean pH to decrease by 0.1–0.3 pH units (ocean acidification) (IPCC, 2014). These projections pose significant threats to reef-building corals throughout the Caribbean, causing mass mortality events, reducing recruitment, deteriorating key physiological processes, and lowering coral calcification rates (Jokiel and Coles, 1977; Grottoli et al., 2006; Davies et al., 2016; Okazaki et al., 2017). Despite the consensus that global change will negatively affect Caribbean reef-building corals, the extent of these impacts vary widely by species, region, or measured physiological response parameter (Harvey et al., 2013). A great example of such variation in coral responses to ocean acidification and warming is seen in Okazaki et al. (2017) where some species exhibited no response to ocean acidification or warming while other corals in the same experiment exhibited reduced calcification under one or both stressors. Furthermore, a study conducted by Kenkel et al. (2015) demonstrated a variety of physiological responses (i.e., calcification and Symbiodiniaceae physiology) of corals under ocean warming even within a single species. Understanding the variability in coral responses depicted in previous studies under projected ocean acidification and warming will improve our ability to predict how coral reef ecosystems will be impacted under global change stressors.

Meta-analyses are valuable tools for combining the findings from multiple studies to summarize results across the literature (Gurevitch and Hedges, 1999). Although the use of meta-analyses to better understand biological responses to ocean acidification and warming are common (Kroeker et al., 2010; Harvey et al., 2013; Kelley and Lunden, 2017), few have focused specifically on reef-building corals (Chan and Connolly, 2013). Further, those analyzing corals have not addressed

the combined effects of ocean acidification and warming (Harvey et al., 2013). Because these two stressors are not likely to act on reef-building corals independently from one another (Halpern et al., 2007), analyses that investigate the combined effects of acidification and warming provide a more realistic view of the future of tropical coral reefs. Caribbean coral reefs are experiencing region-wide declines more severely than reefs in the Red Sea and the Australian Great Barrier Reef (Pandolfi et al., 2003; Gattuso et al., 2014), highlighting the need to study coral reefs on more local scales. Because of projected further declines in Caribbean coral reefs, a better understanding of how these global stressors are impacting reef-building corals within this ocean basin is necessary for predicting the future success of these important marine ecosystems.

Here, we implement a meta-analysis approach of the peer-reviewed literature to investigate the impacts of experimentally induced ocean acidification, ocean warming, and the combination of acidification and warming on calcification responses of Caribbean corals under projected global change. This meta-analysis aims to address the following questions: (1) How do Caribbean corals respond to ocean acidification and ocean warming in isolation, and to the combined effects of acidification and warming? (2) How do coral calcification responses to these stressors vary by region within the Caribbean? In addressing these questions, this analysis will further the understanding of Caribbean-wide coral calcification responses under projected global change stressors, while providing future steps to improve this knowledge.

METHODS

Study Selection

Experimental studies conducted in the Caribbean Sea were identified using Google Scholar with the following search terms: “Caribbean coral,” “ocean acidification,” “ocean warming,” “experiment,” “manipulation,” “control,” and “calcification.” Studies derived from the search were examined, and those that presented all of the following information were included in the meta-analysis: coral species, location of specimen collection, control and experimental temperature, and/or control and experimental $p\text{CO}_2$ values, method of experimental manipulation, duration of exposure to treatment conditions, and calcification rate. Studies altering ocean acidification treatments with acid additions (i.e., hydrochloric acid) were excluded from this meta-analysis because these do not represent ecologically relevant changes in carbonate chemistry. Several other studies that met these criteria not present in the literature search were also included in the meta-analysis. Studies were collected for analysis until September 2018.

Data Extraction and Preparation

Detailed information on the location where coral colonies were collected and experimental design of each study was recorded (Table S1). Several studies included multiple species, collection sites, or experimental factors. In these cases, each species and/or collection site was considered as a separate experiment such

that multiple comparisons were made against the one control treatment. Although the inclusion of all species and collection sites could reduce independence of some data points, all possible combinations were included to expand the extent of species and location responses. Additionally, studies with other experimental parameters outside of acidification and warming were only utilized in this study when these external factors were considered to be under ambient conditions to prevent confounding results (Chan and Connolly, 2013). In studies that reported calcification over time, only the final growth rate was used in this analysis.

For consistency in treatment analysis, only $p\text{CO}_2$ concentrations were used as the measure of acidification manipulation because of the potentially large variation in pH scale based on measurement methods (Zeebe and Wolf-Gladrow, 2001). The wide variety of reported experimental $p\text{CO}_2$ values were categorized into one of the two categories: control or high. Below current-day or extreme $p\text{CO}_2$ treatments from selected studies were not included in this analysis. In experiments in which more than one elevated $p\text{CO}_2$ treatment was used to represent projected scenarios, the higher concentration treatment was selected for the meta-analysis. The $p\text{CO}_2$ treatment considered as current-day or ambient for each experiment was categorized in the 'control' group, despite variations in $p\text{CO}_2$ concentrations due to experimental design (380–513 μatm). Similarly, temperature treatments were categorized as either "control" when reported to represent current-day or ambient conditions (26–30.6°C), or as "elevated" in experiments testing warming scenarios (30–32°C). No study selected analyzed the impact of multiple warming levels.

Calcification rate was chosen as the response parameter in this meta-analysis due to its common use as a stress response in manipulations experiments on Caribbean corals. Mean calcification rate, standard error, and sample size of each experiment was extracted from all included studies for the desired treatments. When raw data were not reported, values were mined from the literature using Web Plot Digitizer for analysis (<https://apps.automeris.io/wpd/>). Two coral species exhibited net dissolution in the control treatments and therefore were excluded from this analysis because of potential bias from additional unknown stressors.

Calculation of Effect Size

Calcification rates in response to independent ocean acidification and warming treatments were measured for each experiment using standard mean differences (SMD), or Hedge's G, to establish the proportion of change between the treatment and control. SMDs were used in this analysis because of the presence of negative calcification rates in some treatments. Analyses were performed in the R (R Core Development Team, 2016) package *metafor* (version 2.0-0) (Viechtbauer, 2010) to calculate effect sizes (SMD) per experiment.

The interaction strength of ocean acidification and warming was determined using methods for factorial meta-analysis (Crain et al., 2008; Harvey et al., 2013). Only studies that reported outcomes for a fully factorial experiment including acidification (Y_{OA}), warming (Y_{OW}), the combination of the two (Y_{both}), and a control (Y_C) were used to calculate the interaction effect size.

The interaction strength was calculated as

$$\text{SMD}_{\text{both}} = \left[\frac{(Y_{\text{both}} - Y_{\text{OW}}) - (Y_{\text{OA}} - Y_C)}{2s} \right]$$

where Y is the mean calcification response for the denoted treatment, and s is the pooled standard deviation. Control values are denoted by subscript C, ocean acidification is denoted by subscript OA, warming is denoted by subscript OW, and the combination treatment is represented by subscript *both*. The sample variance of the effect size was calculated as

$$s_N^2(\text{SMD}_{\text{both}}) = \frac{1}{N_{\text{OA}}} + \frac{1}{N_{\text{OW}}} + \frac{1}{N_{\text{both}}} + \frac{1}{N_C} + \frac{\text{SMD}_{\text{both}}^2}{2(N_{\text{OA}} + N_{\text{OW}} + N_{\text{both}} + N_C)}$$

where N is the sample size of the indicated treatment.

Statistical Analyses

A random effects model was implemented using the *metafor* package (function *rma.mv*) to calculate the mean effect of each treatment on calcification to account for variation in responses due to species and study design. To assess the effects of study design parameters on resulting calcification rates in either acidification or warming studies, two fully additive random effects models (function *rma.mv*) were fit with magnitude change between control and treatment, irradiance ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$), and duration (days) as continuous predictors, and seawater (natural vs. artificial) and feeding (2 times a week, 3 times a week, or no data) were assessed as discrete predictors. An additional model was used to compare effect sizes of corals by region. For this model, only corals collected from the Florida Keys or Belize were considered because of the larger sample sizes from these regions. Random intercepts of study and species within treatment were included to account for potential correlation among results due to these factors. When the 95% confidence intervals of each estimated mean do not overlap zero, the effect size is considered clear statistical evidence. A test of moderators (Q_M) was used to determine differences between variables (temperature and/or region). Additionally, tests for residual heterogeneity (Q_E) were performed, with Q_E signifying that additional moderators not considered may be impacting the study results (Tables S2, S3).

To better understand the qualitative differences in calcification responses of corals from Florida and Belize to ocean acidification and warming, linear mixed effects models with observations weighted by sample size divided by standard error were fit using the *lme4* package (version 1.1-21) (Bates et al., 2015). Using all warming studies, we compared models with measured calcification rates as response variable and coral collection region, scaled temperature, and experiment duration as predictors with random slopes for study and species. We also fit a quadratic effect of temperature. Model selection using AICc was completed with random effects for species and study. A similar analysis was performed using reported aragonite saturation state (Ω_{Arag}) of each treatment to better assess ocean acidification on calcification rates.

RESULTS

In total, 11 studies met the standards of this meta-analysis, including the responses of 13 Caribbean coral species collected from five different countries across the Greater Caribbean Sea (Figure 1; Table S1). Of the studies selected, only four performed fully factorial ocean acidification and warming experiments, and one performed two independent acidification and warming experiments. The most studied coral species from the Caribbean region were *Porites astreoides* (5 studies), *Acropora cervicornis* (4 studies), and *Siderastrea siderea* (4 studies). Finally, the Florida Keys and Belize were the two most-studied regions within the wider Caribbean fitting the criteria of this meta-analysis.

Overall Calcification Response

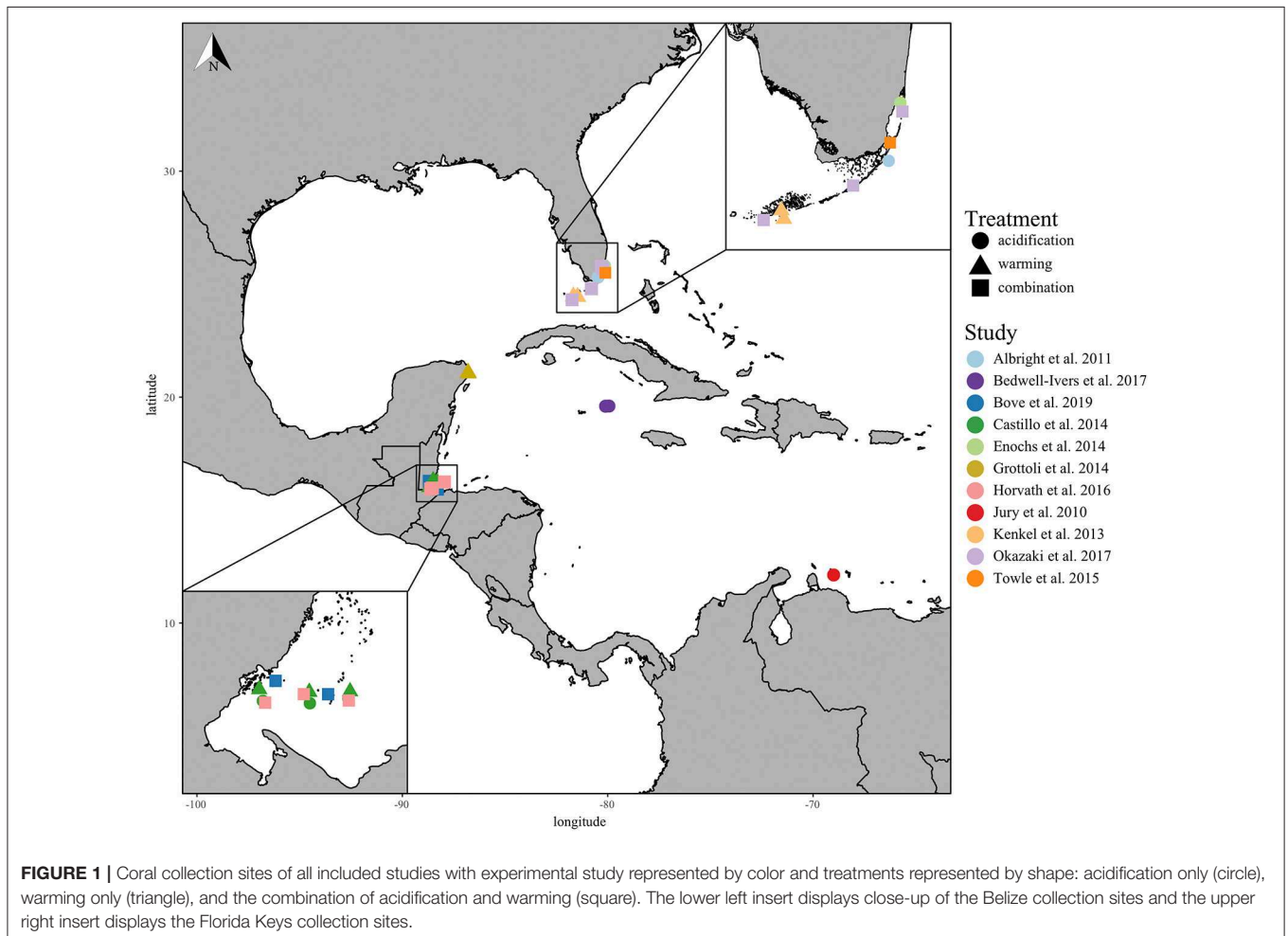
Meta-analysis of the dataset revealed that calcification rates of Caribbean corals were reduced by ocean warming but not ocean acidification (Figure 2; Figures S1–S4). However, the 95% confidence interval of the combination of ocean warming and acidification overlapped zero, indicating no statistically clear trend toward synergistic or antagonistic effects of these treatments (Figure 2; Figures S5, S6; Table S2).

Calcification Response of Florida Keys vs. Belize Corals

Corals from Belize only exhibited clearly reduced calcification rates under ocean warming (Figure 3A; Table S3), while acidification, warming, and the combination of both stressors did not clearly alter experimental calcification rates of corals from the Florida Keys (Figure 3B; Table S3). Further, the resulting Q_E suggests there is significant between-study variation (Table S3).

Temperature and Aragonite Saturation State Impacts on Calcification Rates Across Studies

Secondary analysis of mean calcification rates ($\text{mg cm}^{-2} \text{ day}^{-1}$) against treatment temperature across all Florida and Belize studies revealed a parabolic response to temperature (Figure 4; Tables S4, S5). Similarly, mean calcification rates across Ω_{Arag} resulted in a non-linear response to acidification (Figure 5; Tables S6, S7). Both non-linear trends in response to temperature and Ω_{Arag} were a result of treatment rather than region (Tables S6, S7), suggesting regional differences identified in the meta-analysis were due to experimental designs employed to represent current regional environmental differences.



Experimental Design Impacts on Coral Calcification Rate in Studies

Quantification of experimental design parameters within warming studies identified that magnitude of treatment, irradiance, seawater type used, and feeding frequency all clearly impacted calcification rates (Table 1). Specifically, studies that utilized natural seawater and those with a larger difference between the control and treatment temperatures within a study exhibited higher effect sizes, suggesting a less negative effect of treatment. Studies that employed higher irradiance levels in

their systems demonstrated more negative effects of treatment light level. Finally, studies that reported feeding their corals twice a week were less impacted by warming treatment than those feeding three times a week, however, studies with no data on feeding were the least affected by treatment. Duration of experiment was deemed redundant in the model and was thus dropped.

Within the acidification studies, irradiance, seawater type used, feeding frequency, duration, and the interaction of duration with treatment magnitude impacted effect sizes, while magnitude alone was not clearly different (Table 1). Studies using natural seawater, employing higher irradiance levels, and those with longer durations resulted in greater effect sizes, suggesting they

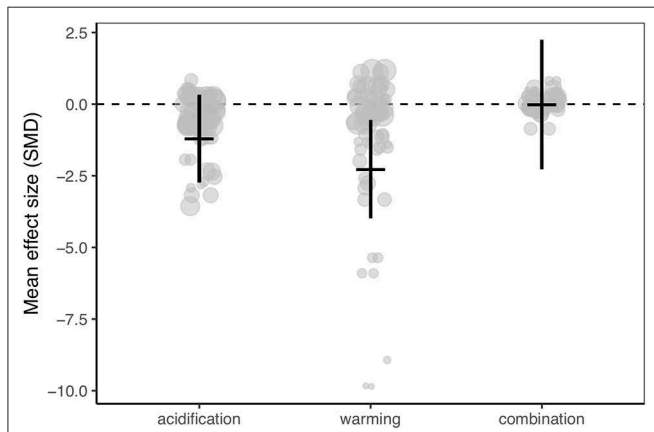


FIGURE 2 | Mean effect (standard mean difference) and 95% confidence interval of ocean acidification, warming, and the combination of acidification and warming on calcification rate for all studies in the meta-analysis. Gray circles indicate the effect size of each individual study and the size of each circle represents the weight of each study (1/SE). Clear statistical evidence of a treatment effect is identified when the 95% confidence interval does not overlap zero.

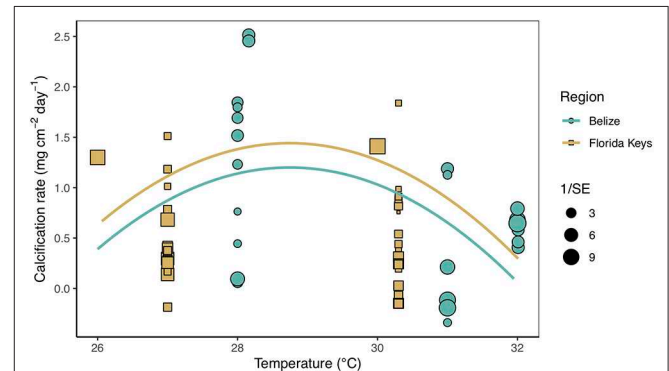


FIGURE 4 | Mean calcification rate ($\text{mg cm}^{-2} \text{ day}^{-1}$) of corals from each warming study by treatment temperature ($^{\circ}\text{C}$) with the linear mixed effects model quadratic fit by region and experimental duration (mean duration = 59.8 days). Shape and color of each point denotes study region (blue circle = Belize; brown square = Florida) and size of shape represents the weight (1/SE) of study.

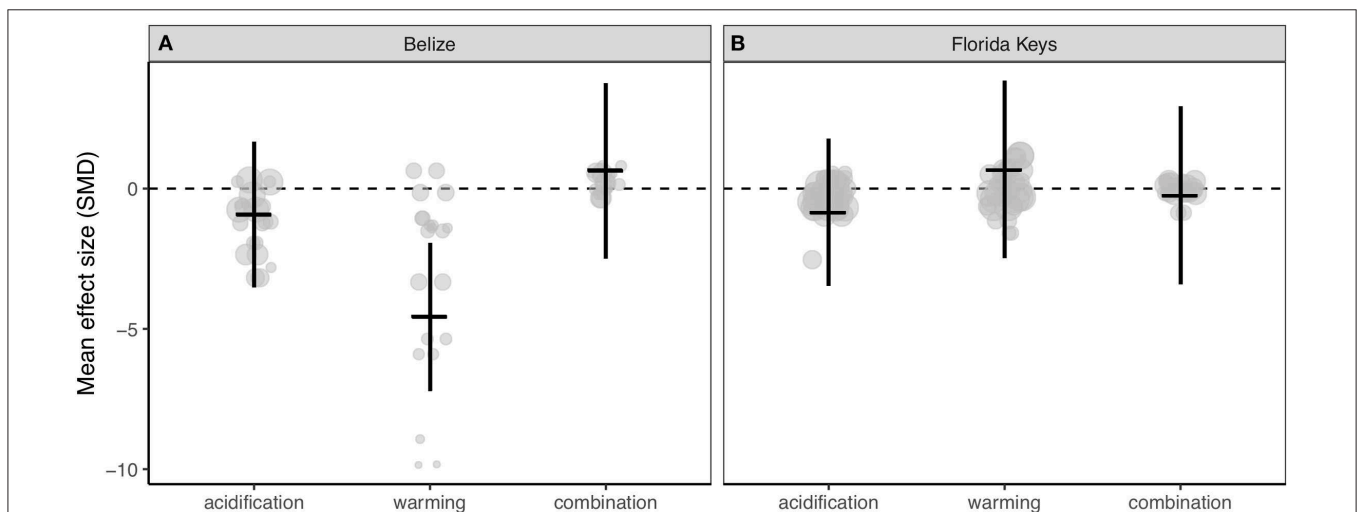


FIGURE 3 | Mean effect (standard mean difference) and 95% confidence interval of ocean acidification, warming, and the combination of acidification and warming on calcification rate for (A) Belize corals and (B) Florida Keys corals. Gray circles indicate the effect size of each individual study and the size of each circle represents the weight of each study (1/SE). Clear statistical evidence of a treatment effect is identified when the 95% confidence interval does not overlap zero.

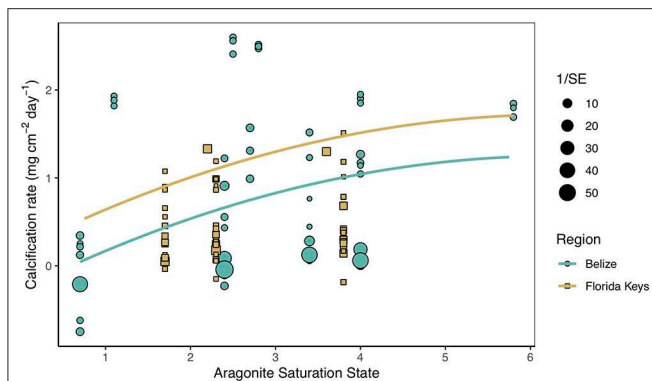


FIGURE 5 | Mean calcification rate ($\text{mg cm}^{-2} \text{day}^{-1}$) of corals from each acidification study by treatment aragonite saturation state (Ω_{Arag}) with the linear mixed effects model quadratic fit by region and experimental duration (mean duration = 66.5 days). Shape and color of each point denote study region (blue circle = Belize; brown square = Florida Keys) and size of shape represents the weight ($1/\text{SE}$) of study.

TABLE 1 | Effect size estimate and 95% confidence intervals of experimental design parameters calculated for all warming and acidification experiments.

	Estimate	Lower 95% CI	Upper 95% CI
Warming experiments			
Intercept	-29.39	-39.56	-19.22
Magnitude ($^{\circ}\text{C}$)*	10.34	5.58	15.1
Irradiance*	-0.24	-0.34	-0.14
Seawater (natural)*	29.77	19.72	39.82
Feeding (3x) *	-3.54	-4.97	-2.12
Feeding (N.D.) *	87.16	49.69	124.64
Acidification experiments			
Intercept	-2.03	-2.78	-1.28
Magnitude ($\mu\text{atm } p\text{CO}_2$)	0.000	-0.003	0.003
Irradiance*	0.009	0.004	0.014
Seawater (natural)*	2.39	1.14	3.64
Feeding (3x)*	-15.04	-22.61	-7.48
Feeding (N.D.)*	3.61	0.28	6.94
Duration*	0.21	0.09	0.32
Magnitude \times days*	-0.0005	-0.0007	-0.0003

Non-overlapping 95% confidence intervals of each design parameter were interpreted to indicate a significant influence on measured coral calcification response to treatment. Magnitude (difference between control and treatment condition), irradiance ($\mu\text{mol photons } \text{m}^{-2} \text{ s}^{-1}$), and duration (days) were evaluated as continuous predictors, while seawater (natural vs. artificial) and feeding (2 times a week, 3 times a week, or no data) were assessed as factors. Parameters denoted with an asterisk (*) were determined to clearly impact calcification response to treatment.

lessened the effects of acidification treatment on calcification responses. Similar to warming studies, acidification studies in which feeding corals was conducted twice a week exhibited less negative responses to treatment than those feeding three times a week, with studies reporting no feeding data exhibiting the least negative responses to treatment. Finally, coral calcification responses were less impacted by acidification in studies with longer duration of exposure and a greater $p\text{CO}_2$ change.

DISCUSSION

The current study utilized a meta-analytical approach to analyze the effects of ocean acidification, warming, and the combination of the two stressors on calcification rates of Caribbean corals. The two most-studied regions within the Greater Caribbean, the Florida Keys, and Belize, were further assessed for differences in calcification responses to ocean acidification, warming, and the combination of both stressors.

Ocean Warming, but Not Acidification, Independently Impairs Calcification of Caribbean Reef-Building Corals

Ocean warming alone induced an overall adverse effect on calcification rates of the Caribbean corals analyzed in this meta-analysis, contrasting a previous meta-analysis assessing coral calcification rates from multiple ocean basins (Harvey et al., 2013). However, increased bleaching, mortality, and declines in coral growth in response to warming is well-documented throughout the Caribbean Sea in field studies and reviews (Hughes et al., 2003; Hoegh-Guldberg et al., 2007; Carricart-Ganivet et al., 2012), supporting the overall reduced calcification rates to warming observed in the current meta-analysis. While there is evidence that suggests coral calcification rates, along with other physiological processes, increase along with warming seawater temperatures (Lough and Barnes, 2000), the physiological advantages of warmer waters diminish when a thermal maxima is reached (Bahr et al., 2018; Silbiger et al., 2019). Ocean warming has also been closely associated with coral bleaching (Brown, 1997) and since corals receive a significant proportion of their energetic need from their algal endosymbionts (Muscatine et al., 1981), it is likely that the loss of algal endosymbionts diminished energy reserves utilized in calcification. Thus, a significant number of corals in warming treatments from the included studies also likely exhibited signs of bleaching (i.e., reduced algal endosymbiont density) under elevated temperature, although bleaching was not assessed as a response variable in this meta-analysis due to low reporting and the diversity of bleaching metrics reported in the studies examined.

Ocean acidification did not clearly reduce calcification rates of Caribbean corals, contradictory to the findings of previous meta-analyses that have investigated the calcification response of tropical corals to ocean acidification from various other ocean basins (Kroeker et al., 2010, 2013; Chan and Connolly, 2013; Harvey et al., 2013). Coral calcification is influenced by the Ω_{Arag} of seawater, with higher Ω_{Arag} (lower $p\text{CO}_2$) often promoting faster calcification rates (Langdon and Atkinson, 2005). This aragonite-calcification relationship is most likely driven by corals' ability to control Ω_{Arag} at their calcification site by pumping Ca_2^+ into the calcifying fluid from the surrounding seawater, removing two protons (H^+) in the process, finally converting HCO_3^- to CO_3^{2-} (Cohen and McConnaughey, 2003; Allemand et al., 2010; Ries, 2011; Von Euw et al., 2017). Thus, even under low aragonite saturation (high $p\text{CO}_2$) corals that are able to elicit strong control over this process are likely to be more resilient against the

effects of ocean acidification, although it may be energetically costly (Davies et al., 2016) and may impair other physiological processes. It is therefore likely that corals included in this meta-analysis that did not exhibit reduced calcification rates in association with simulated ocean acidification may have stronger control of their calcifying fluid to maintain comparable growth rates. Overall, corals from the studies included in the current meta-analysis exhibited variable responses under experimental seawater acidification, highlighting the diversity of responses to stress on the individual and species levels (Comeau et al., 2014; Okazaki et al., 2017; Bove et al., 2019).

Although ocean warming caused reduced calcification of Caribbean corals in the included studies, the combination of acidification with warming was not clearly different from the two independent stressors (Crain et al., 2008). Because only four studies tested the combination of acidification and warming (Towle et al., 2015; Horvath et al., 2016; Okazaki et al., 2017; Bove et al., 2019), however, the sample size for the interaction term was very low. With this small samples size in conjunction with only about 17% of Caribbean reef-building coral species analyzed in the current study, the potential for synergistic or additive effects should not be ignored. Because synergistic relationships can be unpredictable, especially when additional stressors are introduced (Harvey et al., 2013), it is important that additional combined stressor experiments be conducted to better understand the response of Caribbean reef-building corals to these interrelated stressors.

Calcification Responses to Global Change Stressors Vary by Region Within the Caribbean

Coral calcification responses to ocean acidification, warming, and the combination of the two stressors varied between corals collected from the Florida Keys and those collected from Belize. Corals from the Florida Keys did not exhibit clearly reduced calcification rates under independent ocean acidification and warming, or the combination of ocean acidification and warming. However, corals from Belize reduced calcification rates from ocean warming treatments. This regional difference is likely due in part to adaptation of the corals in each region to their local environmental conditions (Oliver and Palumbi, 2011; Putnam et al., 2017). Corals found off the coast of Belize experience a much narrower range of annual sea surface temperatures (*ca* 24–32°C) than corals located off the southern coast of Florida (*ca* 18–31°C) (Castillo and Lima, 2010; Okazaki et al., 2017), resulting in a higher annual mean temperature in Belize than the Florida Keys. This difference in annual temperature variability has likely led to the adaptation of the corals in Florida to more extreme temperatures, resulting in different thermal susceptibilities than corals in Belize (Marshall and Baird, 2000; Guest et al., 2012) and may act as a potential pathway of adaptation or acclimatization to projected global change. Although statistically clear effect sizes may be due to variations in natal environments, differences in experimental treatment levels may also confound these results. Indeed, further analysis identified that treatment level predominately

drove resulting calcification rates, not specifically collection region. Further, the resulting model fit to the calcification rates across temperature exhibited a quadratic fit, similar to what would be expected for a thermal performance curve (Portner et al., 2006). Reef-building corals generally exhibit a threshold response to ocean warming when a particularly high temperature or prolonged exposure to warming water causes bleaching, reduced growth rates, and mortality (Glynn, 1996; Brown, 1997). However, the treatment temperatures used in the Florida and Belize experiments represent warming scenarios specific to the corresponding region, highlighting already-present warming patterns of these regions. Indeed, elevated temperatures employed in studies using Belize corals were 1–2°C higher than the elevated temperatures used in Florida experiments (31–32 vs. 30°C), reflecting differences in annual mean temperatures (Castillo and Lima, 2010; Okazaki et al., 2017). Additionally, the temperatures employed in the Florida Keys studies were representative of the bleaching threshold for the region (Manzello et al., 2007), while the Belize studies used end-of-century projections. Corals are known to live within a narrow thermal range (Kleypas et al., 1999) and the Florida studies tested the upper end of that threshold, while the Belize studies pushed beyond that limit. Consequently, the clear effect of temperature on Belize corals is due largely to the selected treatment temperature employed in each study, although this is likely indicative of differing warming patterns between these regions.

Overall coral calcification rates in response to region and treatment Ω_{Arag} across ocean acidification studies was also assessed, again resulting in a non-linear response to changing seawater chemistry. Because response of corals to ocean acidification is heavily dependent on extent of seawater chemistry change, duration, and individual colony susceptibility (Orr et al., 2005; Ries et al., 2010; Schoepf et al., 2017), it is not surprising that the non-linear response quantified in the present meta-analysis is not as dramatic as the temperature response. Although studies based their acidification treatments on projected end-of-century concentrations relevant for the environment from which the corals were collected, this resulted in a wide range of experimental $p\text{CO}_2$ concentrations (Belize 600–900 μatm vs. 750–1,340 μatm Florida Keys). While the exact relationship between calcification and $p\text{CO}_2$ (or Ω_{Arag}) varies, the general relationship suggests increased $p\text{CO}_2$ reduces coral calcification (Langdon and Atkinson, 2005; Chan and Connolly, 2013). Indeed, calcification rates of Caribbean corals exhibit a general decline in response to reduced Ω_{Arag} , similar to the 15% decline in calcification reported by Chan and Connolly (2013) for every unit decrease in Ω_{Arag} . Although this is a significant decline in skeletal growth in terms of maintaining reef production, this reduction is much less dramatic than that of the measured calcification decline associated in the included ocean warming studies. This difference in threshold responses suggests that while acidification is going to be a chronic stressor continually impacting carbonate production and maintenance on coral reefs, increasing warming events will pose a more immediate and dramatic threat on the future of tropical coral reefs.

Experimental Design Considerations and Recommendations for Future Research

With such variation in study implementation and lingering gaps in the literature, results from this meta-analysis may not capture all underlying causes of calcification responses to ocean acidification, warming, and the combination of stressors. Several gaps in simulated global change studies using corals were identified in this meta-analysis including coral collection sites, variety of species included, and experimental design differences. Although corals from the Florida Keys and Belize were heavily represented in the meta-analysis, only a single study collected corals from reefs south of Belize (Jury et al., 2010) and in the Eastern Caribbean (Bedwell-Ivers et al., 2017). This scattered sampling leaves much of the Caribbean understudied in regards to how coral reefs may respond to ocean acidification and warming as the two stressors continue to co-occur. Additionally, only about 17% of Caribbean coral diversity was represented, leaving out a significant percentage of coral species from the region, including several dominant reef-building species. Without having a better understanding of the calcification responses of other species within the Caribbean, meta-analyses like this will not be able to accurately predict potential reef-wide responses to global change. Future studies should consider what regions and species within the Caribbean have been extensively studied in similar ocean acidification and warming experiments and aim to expand outside of these regions and/or species in designing experiments.

In addition to ensuring that experimental treatments (temperature and $p\text{CO}_2$) represent ecologically relevant conditions, it is important to consider how experimental design dictates resulting coral calcification responses. For example, within all included studies in this meta-analysis experimental duration ranged from 2 h (Jury et al., 2010) up to 95 days (Castillo et al., 2014), with additional variation in seawater type used, irradiance, and how corals received nutrition throughout the experiments (see **Table 1**; **Table S1**). Upon further inspection of these design differences in both warming and acidification studies, the use of natural seawater was associated with higher effect sizes, suggesting less negative responses to treatment than when using artificial seawater, likely due to the different buffering capacity of natural seawater compared to many artificial seawater products (Atkinson and Bingman, 1997). By using natural seawater, especially taken from experimental corals' native reef environments, mesocosm studies may also be able to accommodate more difficult to rear species to expand the range of species used in such experiments. However, the benefits of using artificial seawater (i.e., potential for more consistent results between studies) should also be weighed in the planning of mesocosm experiments. Additionally, reported feeding across both acidification and warming studies played a significant role in resulting coral calcification rates, with studies feeding corals twice weekly exhibiting less negative effects of treatment than in studies feeding three times. Although increased heterotrophy may alleviate stress associated with increasing temperatures and decreasing Ω_{Arag} (Towle et al., 2015; Brown et al., 2018), the higher nutrient load on the experimental systems as a result of increased feeding may harm physiological processes

in the corals, reducing overall growth rates (D'Angelo and Wiedenmann, 2014). Of the studies that did not report feeding frequency, all utilized natural seawater in their experimental systems, thus it is likely that the authors relied on natural nutrients and plankton abundances that were more beneficial for the corals. Efforts should be made to establish and report reasonable feeding practices (i.e., quantity, frequency, type of food) based on coral species, collection depth, and collection location for each study to reduce the impacts of starvation or overeating on measured coral responses.

Interestingly, the present meta-analysis identified that higher irradiance levels in warming studies were associated with more negative effects of warming on calcification rates, while higher irradiance in acidification studies potentially acted as a rescue effect in response to treatment, contrary to Chan and Connolly (2013). These results suggest that the combination of high light levels with warming seawater temperatures may exacerbate bleaching-associated reduced growth rates (Brown, 1997), while higher light levels may alleviate the negative impacts of ocean acidification by stimulating photosynthesis of the coral algal endosymbionts (Suggett et al., 2013). In addition to different responses to irradiance between the two study types, experimental duration did not play a role in warming studies while longer acidification experiments exhibited slightly less negative responses to treatment, differing from the meta-analysis performed by Chan and Connolly (2013). However, longer acidification experiments with greater treatment magnitude exhibited more negative responses to treatment, likely indicative of ocean acidification being a chronic stressor while ocean warming is generally associated with acute stress events (Hoegh-Guldberg et al., 2007). As further experiments are designed, care should be taken to use ecologically-relevant experimental durations that appropriately address questions being addressed. In order to understand how corals respond under chronic acidification and acute warming stress, future experiments should consider conducting such research on the scale of months to years as possible. The recommendations put forth in this study should be considered when designing future Caribbean coral global change studies, even those outside acidification and warming treatments, along with other previously suggested (Widdicombe et al., 2010) to improve the overall understanding of Caribbean corals under projected global change.

CONCLUSIONS

Overall, results from this meta-analysis suggest the sensitivity of Caribbean corals to ocean warming, while also identifying several current knowledge gaps and potential opportunities for future research. Specifically, this analysis highlights the need for further studies including the combination of ocean acidification and warming, as well as expanding the research to additional Caribbean reef-building coral species and regions. Furthermore, although differences in calcification responses between the Florida Keys and Belize were detected in this meta-analysis, further analysis determined this difference was largely attributed to the treatments employed, highlighting the significance of experimental protocols in measured results. The

studies reviewed in the current analysis exhibit a wide range of experimental designs, including variations in duration, feeding, irradiance, treatment levels, and even seawater. These variations in experimental implementation play a major role in the results of the current meta-analysis and suggest that consideration of previous experimental designs should be made when designing new experiments to make the results more comparable. Additionally, future meta-analyses of Caribbean corals should include additional parameters outside of calcification, such as bleaching, metabolism, and survival. The inclusion of additional responses will improve the overall understanding of how corals within the wider Caribbean may respond under projected ocean acidification and warming. Because ecosystem level experiments are difficult to conduct, meta-analyses are important tools for understanding the responses of a wide variety of species to projected global change stressors. This analysis provides valuable insight into the calcification response of corals throughout the Caribbean; however, further experiments must be conducted to expand understanding beyond the small selection of species and regions included in this meta-analysis.

DATA AVAILABILITY STATEMENT

The datasets and code analyzed for this study can be found on GitHub (https://github.com/seabove7/Bove2020_MetaAnalysis_FrontMarSci).

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AUTHOR CONTRIBUTIONS

CB, JU, and KC conceived and designed the study. CB led and executed the meta-analysis. CB and JU completed all analyses. CB drafted the manuscript with contributions from co-authors. All authors gave final approval of this manuscript for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.00127/full#supplementary-material>

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- Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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