Climate Change and Atlantic Multidecadal Oscillation as Drivers of Recent Declines in Coral Growth Rates in the Southwestern Caribbean

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Historical records of growth rates of the key Caribbean reef framework-building coral *Orbicella faveolata* can be fundamental not only to understand how these organisms respond to environmental changes but also to infer future responses of reef ecosystems in a changing world. While coral growth rates have been widely documented throughout the Caribbean, the drivers of coral growth variability remain poorly understood. Here, we provide a record spanning 53 years (1963–2015) of the coral growth parameters for five *O. faveolata* core samples collected at Serrana Atoll, inside the Seaflower Biosphere Reserve, Colombian Caribbean. Coral cores were extracted from reefs isolated from direct anthropogenic impacts, and growth estimations (skeletal density, linear extension, and calcification rates) were derived using computerized tomography. Master records of coral growth parameters were evaluated to identify long-term trends and to relate growth responses with sea surface temperature (SST), the Atlantic Multi-decadal Oscillation (AMO), North Atlantic Oscillation (NAO) and Southern Oscillation indexes, aragonite saturation state (Ω_{arag}), and degree heating months (DHM). We found significant negative relationships between density and mean SST, maximum SST, AMO, and DHM. Moreover, density showed significant positive correlations with NAO and Ω_{arag}. Extension rate did not show significant correlations with any environmental variable. However, there were significant negative correlations between calcification and maximum SST, AMO, and DHM. Trends of coral growth indicated a significant reduction in density and calcification over time, which were best explained by changes in Ω_{arag}. Inter-annual declines in calcification and density up to 25% (relative to historical mean) were associated to the impacts of previously recorded mass bleaching events (1998, 2005, and 2010). Our study provides further evidence that AMO and Ω_{arag} are important drivers affecting coral growth rates in the Southwestern Caribbean. Therefore, we suggest upcoming variations of AMO and future trajectories of Ω_{arag} in the Anthropocene could have a substantial influence on future disturbances, ecological process and responses of the Caribbean reefs.

Keywords: coral growth parameters, Atlantic Multi-decadal Oscillation, ocean acidification, coral reefs, *Orbicella faveolata*, Serrana Atoll

INTRODUCTION

Interpreting coral growth records is critical to identifying responses of coral reefs to environmental conditions over time and to predict future trajectories of these ecosystems (Pandolfi, 2011). For instance, the annual density banding of massive coral skeletons allows retrospective analysis of different coral growth parameters such as skeletal density, linear extension and calcification rates (Lough and Barnes, 1992). Because coral growth responses are determined by changes in environmental conditions (Lough and Cooper, 2011), it is possible to associate the variability in annual growth with previously known environmental and climatic conditions and disturbances (Bessat and Buigues, 2001; Lough, 2008; Carilli et al., 2010). While coral growth is controlled by several environmental factors such as seawater temperature, light, carbonate saturation state, wave energy and turbidity (Lough and Barnes, 2000; Cruz-Piñón et al., 2003; Fabricius, 2005; Marubini et al., 2008; Tanzil et al., 2009; Yan et al., 2011), drivers of recent observed declines in coral growth parameters require further investigation (Lough and Cantin, 2014). Reductions in coral growth rates of massive corals have been linked to bleaching events (Carilli et al., 2009a,b), SST increase (Cantin et al., 2010; Tanzil et al., 2013), attributed to ocean acidification (Crook et al., 2013; D'Olivo et al., 2013), and to the combination of warming and ocean acidification (Cooper et al., 2008; De'ath et al., 2009). Results are, however, inconsistent across broad spatial scales.

Several studies in the Caribbean have documented a wide variability among species and reef habitats in the response of coral growth rates to environmental conditions, thus complicating accurate region-wide predictions of future climatic impacts on coral reefs. Guzman et al. (2008) linked declines in growth rates of the coral *Siderastrea siderea* to runoff and sedimentation derived from the construction of the Panama Canal. Reefs subject to chronic anthropogenic stressors in the Mesoamerican Reef (MR) displayed suppressed growth rates of massive *Orbicella faveolata* for several years after the 1998 mass bleaching event (Carilli et al., 2009a). In contrast, for inshore *O. faveolata* colonies from the Florida Keys, growth rates recovered quickly (~within 1 year) after thermal stress (Manzello et al., 2015). Also MR coral reefs experiencing thermal variability appear to enhance the tolerance of corals to thermal stress, as skeletal rates of *Siderastrea siderea* were not affected in back reef and nearshore colonies compared to colonies within more thermally stable fore reef environments, in which a significant decline in skeletal extension was found (Castillo et al., 2011, 2012). Evaluating calcification rates and SST trends from MR, Carricart-Ganivet et al. (2012) found *Porites astreoides* to be more sensitive to increasing temperature than *O. faveolata* and *O. franksi*. Furthermore, Crook et al. (2013) documented a significant decrease in calcification rates of *P. astreoides* concomitant with a natural gradient in pH and aragonite saturation (Ω_{arag}) on the MR. Considering that declines in coral growth parameters seem to be primarily temperature-related rather than attributable to ocean acidification (Lough and Cantin, 2014), negative impacts on coral growth rates are excepted under future ocean warming. Yet, responses of growth parameters under the combined effects of ocean warming and acidification are not well understood for the Caribbean.

The modulating effect of climatic cycles such as the Atlantic Multi-decadal Oscillation (AMO) on coral records has also been identified as an important driver of coral growth rates in the Caribbean (Hetzinger et al., 2008). However, the identification of primary drivers of coral growth that are modulated by decadal climate variability requires more attention (Lough and Cantin, 2014). Evidence of multidecadal variability in annual coral growth rates has been documented for *S. siderea* in Belize and the Bahamas (Saenger et al., 2009), and Mexico (Vásquez-Bedoya et al., 2012); and for *O. faveolata* in Florida (Helmle et al., 2011). Furthermore, reanalyzing previously published coral growth records from Belize (*O. faveolata*) and Panama (*S. siderea*), Kwiatkowski et al. (2013) found that variations in growth rates between 1880 and 2000 displayed a decadal variability which was linked to regional climatic drivers (i.e., volcanic and anthropogenic aerosol emissions) rather than global drivers (i.e., climate change or ocean acidification). Thus, coral records from remote reefs, isolated from direct anthropogenic influence (e.g., coastal development and contamination, eutrophication, particulate organic matter, tourism) can be useful to clarify sources of decadal climate variability and support understanding of past and future climatic impacts on the Caribbean coral reefs.

Here, we provide the first decadal-scale record (1963–2015) of coral growth parameters from *O. faveolata* colonies that grew on patch reefs isolated from direct anthropogenic impacts at Serrana Atoll, Southwestern Caribbean. Growth parameters such as skeletal density, linear extension and calcification rates were evaluated to identify long-term trends and to relate growth responses with SST, AMO, The North Atlantic Oscillation (NAO) and Southern Oscillation (SOI) indexes, aragonite saturation states (Ω_{arag}), and degree heating months (DHM). This analysis provides insight into how corals from an isolated Caribbean reef responded to environmental and climatic conditions over the last 50 years, and how they are likely to respond to a changing ocean.

MATERIALS AND METHODS

Coral Collection

Five cores from the massive coral *Orbicella faveolata* were collected on SCUBA at 4–9 m depth in lagoonal patch reefs of Serrana Atoll, inside the Seaflower Biosphere Reserve, Colombian Caribbean (**Figure 1**), during August 2016. Each coral core was extracted using an underwater pneumatic hand drill supplied with compressed air. Coral colonies were drilled along the maximum vertical growth axis (Helmle and Dodge, 2011). Cores were 6 cm in diameter and 0.6–0.9 m long (**Table 1**). A polystyrene ball was inserted and fixed with epoxy resin into the core hole to avoid colonization by boring organisms, diseases on exposed surfaces and promote coral tissue recovery.

Growth Rates

The cores were rinsed with freshwater and then oven dried for 24 h at 50–60°C. A GE LightSpeed VCT 64 (General Electric Company) computerized tomography (CT) scanner was
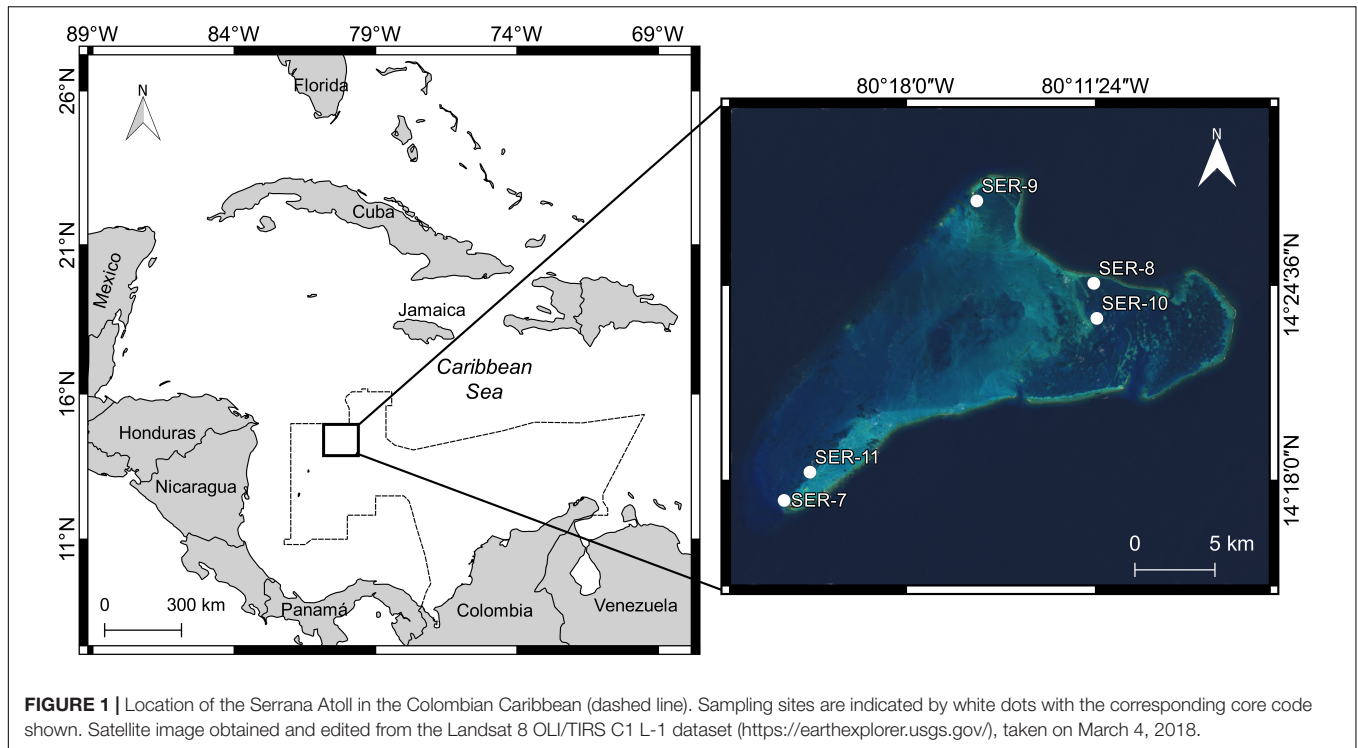
FIGURE 1 | Location of the Serrana Atoll in the Colombian Caribbean (dashed line). Sampling sites are indicated by white dots with the corresponding core code shown. Satellite image obtained and edited from the Landsat 8 OLI/TIRS C1 L-1 dataset (https://earthexplorer.usgs.gov/), taken on March 4, 2018.

TABLE 1 | Location and details of *O. faveolata* colonies used in this study.

Core ID	Latitude	Longitude	Depth (m)	Timespan	Density (g cm^{-3})	Extension (cm year^{-1})	Calcification (g cm^{-2} year^{-1})
SER-7	14°17'20.2''N	80°22'14.0''W	6	1974–2015	1.12 ± 0.13	0.87 ± 0.19	0.97 ± 0.22
SER-8	14°24'39.1''N	80°11'28.4''W	9	1969–2015	1.01 ± 0.18	1.03 ± 0.19	1.02 ± 0.23
SER-9	14°27'25.6''N	80°15'32.3''W	4	1963–2015	1.35 ± 0.21	1.00 ± 0.21	1.33 ± 0.27
SER-10	14°23'28.3''N	80°11'22.1''W	5	1971–2015	0.93 ± 0.16	1.12 ± 0.28	1.04 ± 0.33
SER-11	14°18'17.3''N	80°21'20.2''W	6	1963–2015	0.93 ± 0.09	0.79 ± 0.16	0.72 ± 0.13

Growth parameters are means ± SD of the respective timespans.

used to image the coral cores along with an aragonite step-wedge standard obtained from the shell of the giant clam *Tridacna maxima* (see **Supplementary Information**). The solid aragonite standard with known density was used to estimate coral density. The software RadiAnt DICOM Viewer 4.0 was used to view the DICOM files obtained from the CT scan and generate multi-planar reconstructions of all coral cores. Coronal and sagittal planes were examined to choose one image for each core, respectively. By using this method, the alternate pattern of horizontal density bands (high and low density) in the coral skeleton were visualized from different angles and slices. A density banding pattern is important to follow the vertical growth of massive corals and construct the coral chronology (see **Supplementary Information**). Skeletal density was calculated following the method by Carricart-Ganivet and Barnes (2007) for X-ray images, adapted to CT scan images (see **Supplementary Information**). Linear extension was measured between contiguous years or high-to-high density bands. Each coral year is formed by a pair of bands, corresponding to high and low density bands. Calcification rates were estimated as the

product of skeletal density and linear extension rate. These three growth characteristics are sensitive to environmental changes and their variations are recorded in the coral skeleton (Barnes and Lough, 1996).

Annual growth values (i.e., density, extension and calcification) of each coral core were derived from the averaged measurements made in one transect, of both the coronal and sagittal planes, along the vertical growth axis of the coral colony. Master chronologies of skeletal density, linear extension and calcification were constructed averaging the annual values of the five cores, therefore the number of cores contributing to a specific year varied through the maser chronology (**Table 1**). To detect trends in growth parameters over time, linear regressions were applied to the master chronologies. Coefficients of variation (CV) were calculated for each growth parameter to demonstrate the inter-annual variability irrespective of differences in the means (Helmle et al., 2011). Annual density, extension and calcification rates were correlated to examine the relationship between coral growth parameters. Significance level for correlations was $\alpha = 0.05$. In addition, master chronologies of the standardized

anomalies (STDA) were obtained for each growth parameter. STDA consisted of the annual values minus the mean (over the period 1963–2015), divided by the standard deviation (Helmle et al., 2011). The five standardized chronologies were then averaged to create a single standardized record. As a result, the inherent variability of each core was accounted for, and a regional signal was detected (Jones et al., 2009; Grove et al., 2013).

Drivers of Growth Variability and Environmental Records

To explore potential drivers of growth variability, annual means, minimum, and maximum of sea surface temperature (SST), DHM, Ω_{arag}, AMO, Southern Oscillation Index (SOI) and NAO, were correlated with annual values of skeletal density, linear extension and calcification rates (Pearson's correlations). Additionally, growth responses to thermal stress were assessed by plotting growth master chronologies and annual changes of growth parameters against DHM. Annual changes in growth parameters were calculated as the percentage of change relative to the 1963–2015 mean values. Finally, master chronologies of STDA were plotted against SST and AMO to comparatively evaluate long-term trends. A 13-year smoothing was applied to STDA and SST data to reduce inter-annual variability and facilitate the comparison of both time series.

SST was obtained from the 1° × 1° gridded HadISST1 dataset (Rayner et al., 2003) centered on 13.5°–14.5°N and 79.5°–80.5°W. The AMO was calculated from the Kaplan SST dataset (Enfield et al., 2001), which is an index of North Atlantic temperatures. The NAO and SOI indexes were constructed from normalized sea level pressure differences between the Azores–Iceland (Jones et al., 1997) and Darwin–Tahiti (Ropelewski and Jones, 1987), respectively. These indices are typically associated with climatic changes at large scales both in the Pacific and Atlantic oceans (i.e., ENSO events).

Aragonite saturation state (Ω_{arag}) data were extracted from the NOAA Coral Reef Watch (CRW) Experimental Ocean Acidification Product Suite (OAPS) for the period 1988–2011 centered on 15°–16°N and 79°–81°W (Gledhill et al., 2008). The Ω_{arag} data used here was 1°N adjacent to the area where Serrana Atoll is located.

DHM were calculated using the SST monthly data from HadISST on the same grid, in a similar manner to the degree heating weeks (DHW) used by NOAA Coral Reef Watch to predict coral bleaching. Thermal stress is considered to occur when temperatures surpass the bleaching threshold, which is established as 1°C above the mean of the climatological month with the highest temperature (Liu et al., 2006). However, for the HadISST dataset DHM were calculated as the annual sum of the difference between average monthly SSTs that exceeded the long-term maximum monthly mean (Carilli et al., 2010).

To further explore potential drivers of growth variability, a distance-based linear model (DISTLM) using a resemblance matrix of master chronologies values of density, calcification and extension (based on Euclidean distance), and forward selection, was adopted (Legendre and Anderson, 1999; Anderson et al., 2008). Forward selection adds one variable at a time to the model,

selecting the variable that produces the greatest improvement in the value of adjusted r^2 at each step. We used adjusted r^2 as the selection criterion instead of r^2 as we aimed to include only variables that significantly explained variation in the model. This method was applied to the time period 1988–2011, including as explanatory variables DHM, AMO, Ω_{arag}, and NAO (data sets available for this period). DISTLM results provide a marginal test, fitting each variable individually (ignoring all other variables), and a sequential test, fitting each variable one at a time, restricted to the variables that were already included in the model (Anderson, 2003; Anderson et al., 2008). In addition, for the period 1963–2015, we applied the DISTML only to evaluate the individual contribution of each variable (marginal test) as our set of explanatory variables for this period were temperature-based (redundant variables). DISTLM analysis were performed in PERMANOVA+ package for PRIMER v6.

RESULTS

Coral Growth

Over the period 1963–2015, the coral *Orbicella faveolata* of Serrana Atoll presented an overall mean ± SD skeletal density of 1.08 ± 0.08 g cm^{-3}, linear extension rate of 0.96 ± 0.11 cm year^{-1} and calcification rate of 1.02 ± 0.12 g cm^{-2} year^{-1}. Mean values for individual cores are shown in **Table 1**. The CV was 7% for density, 12% for extension rate and 12% for calcification rate. Extension rate was positively related to calcification rate ($r = 0.82$, $p < 0.001$, $n = 53$), calcification rate was positively related to density rate ($r = 0.29$, $p = 0.04$, $n = 53$) and density rate was negatively related to extension rate ($r = -0.28$, $p = 0.04$, $n = 53$). Skeletal density and calcification rate increased significantly over time (**Figure 2A**, $r^2 = 0.16$, $p = 0.004$, $n = 53$; $r^2 = 0.10$, $p = 0.021$, $n = 53$, respectively), whereas no significant change was observed in linear extension rate ($r^2 = 0.003$, $p = 0.698$, $n = 53$).

Drivers of Growth Variability

Mean ± SD of environmental conditions in Serrana Atoll were SST of 28.04 ± 0.31°C for the period 1963–2015, and Ω_{arag} of 4.06 ± 0.09 for the period 1988–2011.

Skeletal density was negatively related to the mean SST, maximum SST, AMO, and DHM, based on coral growth master chronologies and environmental records (**Table 2**). In contrast, density was positively related to the NAO and Ω_{arag}. Extension rate was not related to any of the environmental variables. However, there were significant negative correlations between calcification and maximum SST, AMO, and DHM. The 13-year smoothed anomalies of coral growth master chronologies tended to show opposite variation patterns to SST and AMO (**Figure 3**).

Thermal stress in recent decades has been recurrent and intense (**Figure 2B**). Peaks of DHM in 1998, 2005, 2010 and 2015, coincident with El Niño events, had a negative effect on coral growth parameters. Reductions up to 25% (2005), 13% (2010), and 15% (2005) in calcification, extension and density, respectively, were detected (**Figure 4**). However, high DHM values observed before 1997, as in 1969, showed no negative effects on coral growth. During the period 1963–1997, thermal
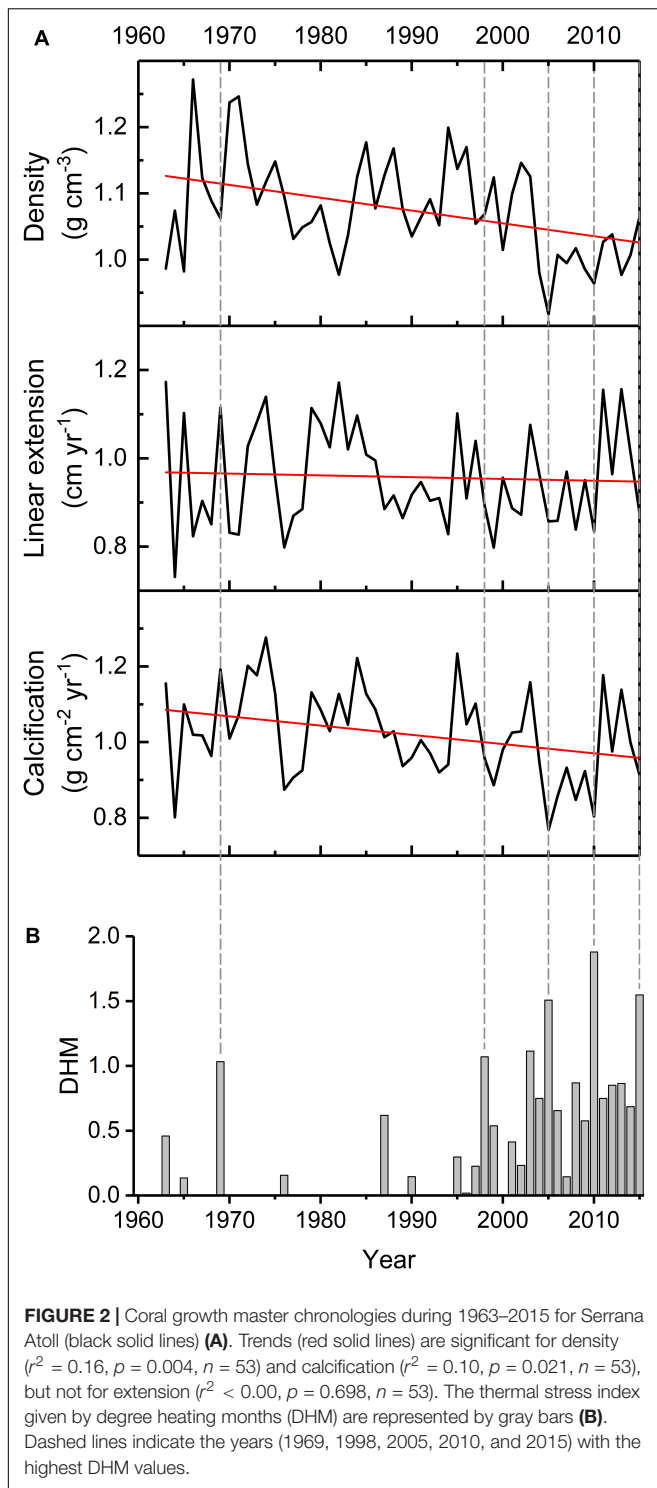
FIGURE 2 | Coral growth master chronologies during 1963–2015 for Serrana Atoll (black solid lines) **(A)**. Trends (red solid lines) are significant for density ($r^2 = 0.16$, $p = 0.004$, $n = 53$) and calcification ($r^2 = 0.10$, $p = 0.021$, $n = 53$), but not for extension ($r^2 < 0.00$, $p = 0.698$, $n = 53$). The thermal stress index given by degree heating months (DHM) are represented by gray bars **(B)**. Dashed lines indicate the years (1969, 1998, 2005, 2010, and 2015) with the highest DHM values.

TABLE 2 | Pearson correlations of coral growth parameters with environmental variables during 1963–2015 ($n = 53$), and 1988–2011 for Ω_{arag} ($n = 24$).

	Density	Extension	Calcification
SST mean	**$r = -0.43$, $p = 0.001$**	$r = 0.07$, $p = 0.599$	$r = -0.21$, $p = 0.125$
SST max	**$r = -0.37$, $p = 0.007$**	$r = -0.03$, $p = 0.843$	**$r = -0.27$, $p = 0.050$**
SST min	$r = -0.23$, $p = 0.097$	$r = 0.07$, $p = 0.607$	$r = -0.11$, $p = 0.415$
AMO	**$r = -0.41$, $p = 0.003$**	$r = -0.09$, $p = 0.514$	**$r = -0.36$, $p = 0.009$**
DHM	**$r = -0.44$, $p = 0.001$**	$r = -0.05$, $p = 0.728$	**$r = -0.30$, $p = 0.029$**
NAO	**$r = 0.28$, $p = 0.045$**	$r = 0.09$, $p = 0.541$	$r = 0.22$, $p = 0.116$
SOI	$r = 0.13$, $p = 0.341$	$r = -0.08$, $p = 0.556$	$r = 0.04$, $p = 0.795$
Ω_{arag}	**$r = 0.61$, $p = 0.002$**	$r = -0.11$, $p = 0.621$	$r = 0.24$, $p = 0.265$

Bold values are significant at $p < 0.05$.

by Ω_{arag}, which accounted for 37% of the total variation (see marginal and sequential tests, **Tables 4**, **5**).

DISCUSSION

Located far away from direct anthropogenic disturbances, corals from Serrana Atoll allow a clear identification of environmental and climatic signatures on growth rates. Here we present a 53-year record of coral growth parameters for *O. faveolata* for remote Southwestern Caribbean reefs. To the best of our knowledge, this is the first record of its kind for this region of the Caribbean, complementing the geographic coverage of previous studies and providing new insights into the understanding of coral growth responses in a period characterized by human-induced environmental and climatic changes (1963–2015).

Overall, coral growth records from Serrana Atoll indicate that calcification processes for *O. faveolata* have suffered disparate changes over the last 50 years, mainly associated to thermal stress, and occurring more frequently during recent decades. While the values of growth parameters of *O. faveolata* are within the ranges found for other Caribbean reefs (Dodge and Brass, 1984; van Veghel and Bosscher, 1995; Gischler and Oschmann, 2005; Helmle et al., 2011; Manzello et al., 2015), the CVs (7–12%) observed suggest important inter-annual variations in growth responses to environmental conditions. Indeed, between 1963 and 1990 growth parameters were characterized by positive anomalies. However, in the last 20 years negative anomalies have dominated the variability of growth parameters (**Figure 3**). Although values of CV were low in comparison to those reported by Helmle et al. (2011) for *O. faveolata* in Florida, probably reflecting latitudinal differences as well as lesser variability in environmental conditions in Serrana Atoll during the last decades, it is highly likely that thermal stress caused significant inter-annual variations over the studied period.

Degree heating months showed a negative effect on calcification rates during 1998, 2005 and 2010, coinciding with severe coral bleaching events in the region (Hughes et al., 2017). Signatures of bleaching on coral growth parameters include an increase in skeletal density and a marked reduction in extension and calcification rates (Carilli et al., 2009a). Corals growing in clear and oligotrophic waters are highly vulnerable to changes in temperature and thermal stress, which can result
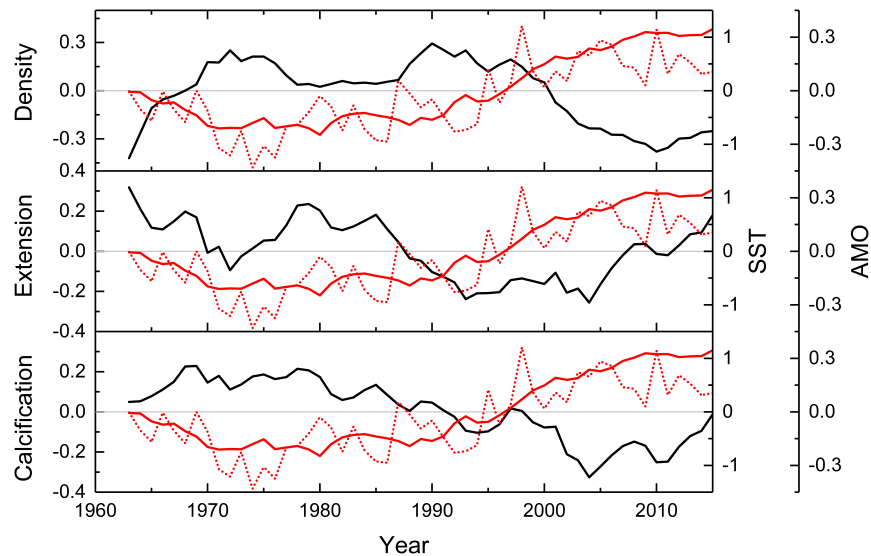
stress events were sporadic, and did not explained important reductions in growth parameters (e.g., 1964, 1976 and 1977).

DISTLM analysis for the period 1963–2015 did not identify a predominant predictor explaining most of the variation in the master chronologies (see marginal test, **Table 3**). For the period 1988–2011, the variation in coral density was mainly explain
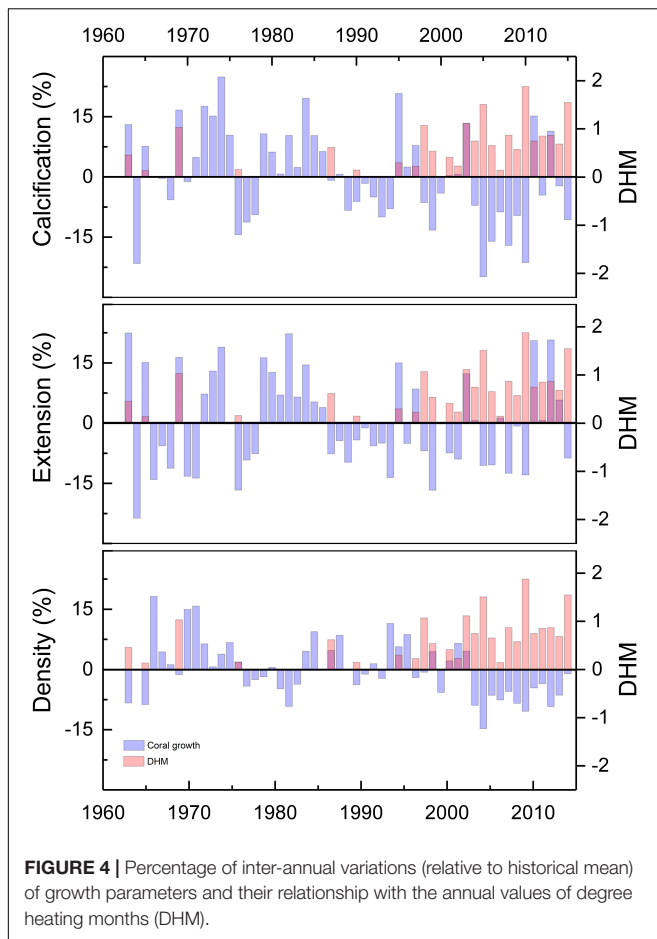
FIGURE 3 | Coral growth, SST and AMO correlations. Values of coral growth parameters (black solid lines) and SST (red solid lines) are presented as 13-year smoothed standardized anomalies (STDA). AMO is represented by red dotted lines. Density and calcification are negatively correlated with cyclical temperature trends.

in mass coral bleaching (Hughes et al., 2017), and significant decreases in their growth parameters (Carilli et al., 2009a,b). Whilst we cannot relate every single decline in growth parameters to thermal stress, we highlight that bleaching-induced impacts on growth parameters were unprecedented before 1997, and more frequent in recent years, corresponding with bleaching events linked to global warming (Hughes et al., 2018). Nevertheless, the magnitude of declines in Serrana Atoll were relatively small when compared to those in Belize during the 1998 bleaching, where *O. faveolata* corals showed pronounced decreases in extension and calcification rates (over four standard deviations outside the mean more chronology) and even interruption of growth (Carilli et al., 2009a). This outcome suggests that *O. faveolata* corals at Serrana Atoll, isolated from direct chronic human impacts (e.g., pollution, costal development, tourism), seem to have responded better to recent bleaching events than Belizean counterparts. This observation supports the hypothesis that corals with higher local anthropogenic stressors present reduced coral resistance to bleaching or thermal tolerance (Carilli et al., 2009a, 2010).

The significant relationships between growth parameters provide insights into historical growth strategies of *O. faveolata* at Serrana Atoll. We found a strong positive relationship between extension and calcification, and weaker relationships between extension and density (negative), and density and calcification (positive). These correlations are usually used to infer how corals invest increased availability of resources for calcification in extension or density (Carricart-Ganivet, 2007). While previous studies report that skeletal density tends to be the primary driver of variations in calcification for *O. faveolata* (Carricart-Ganivet, 2004), here extension was the key driver. This indicates that the growth strategy of the corals is favoring extension rather than the skeletal density at Serrana Atoll, as the extension did not showed a declining trend, but instead was strong related with the skeletal calcification rate. We argue that corals at Serrana

Atoll are investing their calcification resources into maintaining extension as a response to a reduction of Ω_{arag}, attributed to ocean acidification in recent years (see below for details), and long-term increases in SST. This growth response seems to correspond to the "stretching" modulation phenomenon (in a temporal context) postulated by Carricart-Ganivet and Merino (2001), in which corals respond to environmental stress by extending their skeletons and maintaining calcification. This was clearly observed during the last decade (**Figure 3**), where despite the decline in density, both extension and calcification did not decline and remained relatively unchanged.

The most significant responses detected in growth parameters were the long-term decreases in skeletal density and calcification rates, and the absence of a temporal trend in extension rates. The downward trend in density was mainly linked to a decline in Ω_{arag} (**Table 2** and **Figure 5**) and, to a lesser extent, to warmer conditions in recent decades, which in turn could affect calcification responses. For the studied period (1963–2015) moderate to weak relationships were observed between density and the environmental variables considered (mainly SST related). The DISTML analysis indicated that temperature-based explanatory variables explained a modest part of the observed variability in density ($<19\%$), suggesting that there are additional factors implicated in the declining trend. For the period 1998–2011, the DISTLM analysis identified that Ω_{arag} explained most of the variability observed in density. Thus, it is reasonable to suppose that long-term declining trends in density and calcification were modulated by a decrease in Ω_{arag}, the latter attributed to ocean acidification (Gledhill et al., 2008). Other studies have found that ocean acidification has a direct effect on skeletal density but not on linear extension rates (Tambutté et al., 2015; Mollica et al., 2018) as observed in our coral cores. Similarly to Kleypas (1999) and Helmle et al. (2011), we argue that Ω_{arag} has not yet reached a critical threshold needed to negatively

FIGURE 4 | Percentage of inter-annual variations (relative to historical mean) of growth parameters and their relationship with the annual values of degree heating months (DHM).

TABLE 3 | DISTLM marginal test for the period 1963–2015.

Variable	SS (trace)	Pseudo-F	*p*-value	Proportion
		Density		
DHM	0.06	12.31	0.002	**0.19**
SST (°C)	0.05	11.35	0.003	**0.18**
AMO	0.05	10.01	0.003	**0.16**
NAO	0.02	4.21	0.045	**0.08**
SOI	0.01	0.92	0.356	0.02
		Extension		
DHM	0.00	0.10	0.734	0.00
SST (°C)	0.00	0.28	0.561	0.01
AMO	0.01	0.43	0.494	0.01
NAO	0.01	0.38	0.527	0.01
SOI	0.00	0.35	0.574	0.01
		Calcification		
DHM	0.07	5.00	0.027	0.09
SST (°C)	0.03	2.43	0.129	0.05
AMO	0.09	7.45	0.013	**0.13**
NAO	0.04	2.56	0.118	0.05
SOI	0.00	0.07	0.798	0.00

Significant proportions of explained variation (p < 0.05) are given in bold.

TABLE 4 | Results of the marginal test for the period 1988–2011 performed by DISTLM forward analysis.

Variable	SS (trace)	Pseudo-F	*p*-values	Proportion
		Density		
DHM	0.03	8.74	0.009	**0.28**
Ω_{arag}	0.04	12.69	0.003	**0.37**
AMO	0.02	5.51	0.030	**0.20**
NAO	0.04	9.59	0.007	**0.30**
		Extension		
DHM	0.00	0.11	0.748	0.01
Ω_{arag}	0.00	0.25	0.623	0.01
AMO	0.00	0.03	0.861	0.00
NAO	0.00	0.00	0.974	0.00
		Calcification		
DHM	0.03	2.98	0.100	0.12
Ω_{arag}	0.02	1.30	0.268	0.06
AMO	0.01	0.67	0.409	0.03
NAO	0.03	2.22	0.185	0.09

Significant proportions of explained variation (p < 0.05) are given in bold.

impact linear extension. Nevertheless, ocean acidification is an increasing threat for corals as ongoing reduction in carbonate ion concentration will lead to less dense and more fragile coral skeletons (Fantazzini et al., 2015; Tambutté et al., 2015; Mollica et al., 2018), compromising reef ecosystem function within decades (Kleypas and Yates, 2009; Albright et al., 2018). Some models predict an average 12.4% decline in skeletal density for *Porites* corals globally by the end of the century due to ocean acidification (Mollica et al., 2018). In light of the decreasing trends documented here and global predictions of decreasing coral density, we speculate that ocean acidification will play a major role in coral calcification at Serrana Atoll (and elsewhere within the coralline complexes from the Seaflower Reserve) in the near future.

Our study provides further evidence concerning the multi-decadal variability in coral growth rates in the Caribbean (Hetzinger et al., 2008; Helmle et al., 2011). Particularly we found a significant negative correlation of the skeletal density and calcification with AMO, and no relationship between extension and AMO. The majority of studies only report the relationship between AMO and extension, identifying a positive correlation for locations such as Belize and Panama (Kwiatkowski et al., 2013), and negative correlations in Mexico (Vásquez-Bedoya et al., 2012), Bahamas and Belize (Saenger et al., 2009), and

Florida (Helmle et al., 2011). In Florida, Helmle et al. (2011) found a positive relationship between density and AMO, and no relationship with calcification, contrary to our finding. These varying outcomes do not diminish the importance of multi-decadal variability in coral growth rates in the Caribbean but underline the need to improve our understanding of the significant role of the AMO in influencing coral growth rates in the region. As previous AMO analyses were based on coral records up to only 2000 (Helmle et al., 2011; Kwiatkowski et al., 2013), just after the AMO shifted from a cold to a warm phase (Zhang and Delworth, 2006), our master chronologies add crucial data to infer coral growth responses in such warm AMO phases.

TABLE 5 | Results of sequential test for the period 1988–2011 performed by DISTLM forward analysis.

Variable	Adjusted r^2	SS (trace)	Pseudo-F	p-Value	Proportion	Cumul.
			Density			
Ω_{arag}	0.336880	4.45E-02	12.685	0.001	**0.37**	0.37
			Extension			
Ω_{arag}	−0.033651	2.10E-03	0.25123	0.616	0.01	0.01
			Calcification			
DHM	0.079387	3.50E-02	2.9834	0.106	0.12	0.12
AMO	0.084099	1.30E-02	1.1132	0.339	0.04	0.16
NAO	0.106950	1.75E-02	1.5372	0.226	0.06	0.22
Ω_{arag}	0.185130	3.03E-02	2.919	0.111	0.10	0.33

Significant proportions of explained variation (p < 0.05) are given in bold. Cumul, cumulative proportion of explained variation.

In our study area, long-term trends of skeletal density and calcification varied inversely to AMO, with positive anomalies during the cold phase of the AMO (1965–1995), and negative anomalies during the last warm phase after 1995 (Zhang and Delworth, 2006).

The master chronologies analyzed provide key details regarding the latest trends of coral growth parameters that can support predictions of future trajectories of coral growth and calcification processes for the Southwestern Caribbean. Since 2010, calcification and extension rates have shown baseline averages, but density values remain below the long-term average (negative anomalies). We attribute this to ocean acidification given that Ω_{arag} apparently contributed to the declining trend observed for density. Thus, although long-term calcification processes at Serrana Atoll have been modulated by SST oscillations at decadal scales (AMO), it appears that in the most recent phase of the AMO decreasing Ω_{arag} dominated the effect of SST. The ocean acidification and temperature oscillations controlled by AMO are therefore important to understand how coral growth parameters may respond to those oscillations in the coming decades. Climatic predictions indicate the oceans will continue to acidify, negatively affecting coral reefs by reducing carbonate ion concentrations which result in corals with more fragile skeletons and more susceptible to bioerosion (Kleypas, 1999; van Woesik et al., 2013; Mollica et al., 2018). Temperature is another key variable that is expected to continue increasing and threatening corals (Meissner et al., 2012). However, temperature stress on Caribbean reefs might be less in coming decades than in recent years (1990–2015). According to historical ocean temperature oscillations it has been suggested that in the following decades these oscillations will shift from a warm phase (the present) to a cold phase (Klöwer et al., 2014; McCarthy et al., 2015; Frajka-Williams et al., 2017; Page, 2017). In spite of this, models indicate that most coral reefs will suffer marked deterioration over the next few decades, even reducing global warming to 2°C and under the optimistic assumption of corals undergoing thermal adaptation (Frieler et al., 2012). Calcification might be oscillating in response to the AMO, however, the decline in Ω_{arag} will be critical for coral growth. Consequently, the prediction of future responses of Caribbean reefs has to consider the combined role of warming, AMO variability and ocean acidification on coral growth and calcification processes.
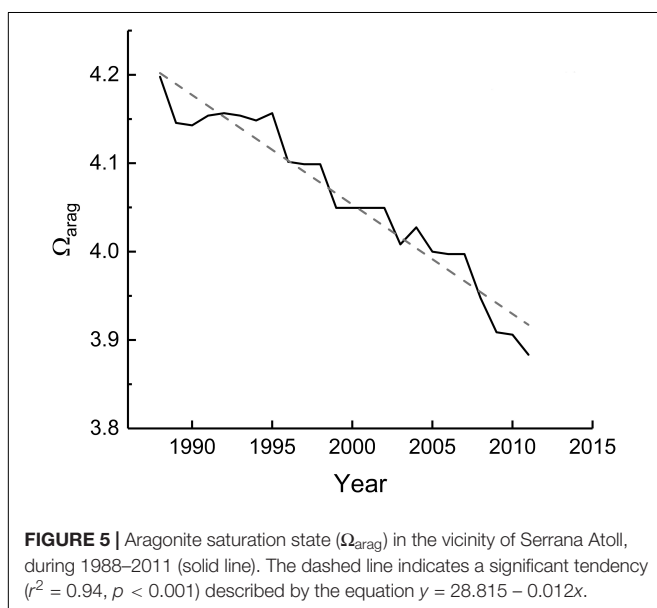
AUTHOR CONTRIBUTIONS

LL-S processed and analyzed the cores, performed statistical analyses, and contributed to manuscript writing. ÁM-G contributed to core processing and analysis. ML-V collected the samples, processed and analyzed the cores, and contributed to manuscript writing. AR-R analyzed the cores, performed statistical analyses, contributed to manuscript writing, and directed the work. All authors participated in study conception and design.

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FIGURE 5 | Aragonite saturation state (Ω_{arag}) in the vicinity of Serrana Atoll, during 1988–2011 (solid line). The dashed line indicates a significant tendency ($r^2 = 0.94$, $p < 0.001$) described by the equation $y = 28.815 − 0.012x$.

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SUPPLEMENTARY MATERIAL

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