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# Regional coral growth responses to seawater warming in the South China Sea

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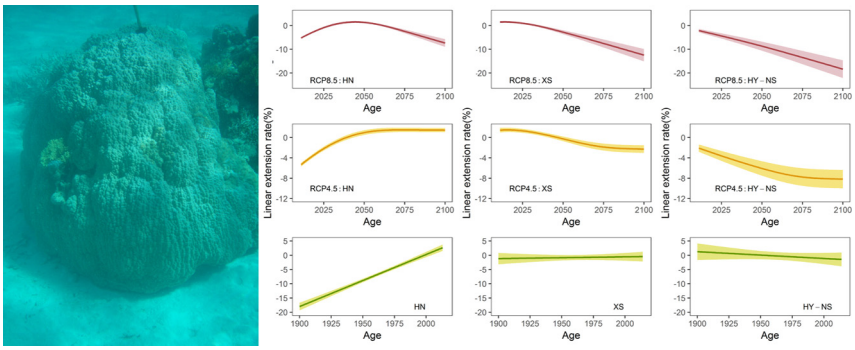
## HIGHLIGHTS

- It's of concern how coral growth in South China Sea responses to global warming.
- Multiple series of linear extension rate were used to reveal coral growth history.
- Coral growth and SST show regional long-term trends and interdecadal variations.
- Nonlinear response relationship exists between coral growth and SST.
- Coral growth will decline overall in South China Sea by the end of this century.

## GRAPHICAL ABSTRACT

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## ABSTRACT

Seawater temperature is one of the main environmental factors controlling coral skeleton growth. Sustained seawater warming is regarded as a major threat to coral growth and reef development. Coral reefs are widespread in the South China Sea (SCS), where the history and future of coral growth are of great concern. We integrated 99 linear extension rate series of the coral *Porites* from 12 locations at three regions in SCS, which include the Hainan Island (HN), the Xisha Islands (XS), and the Huangyan Island–Nansha Islands (HY-NS), and explored the regional responses of coral growth to sustained seawater warming. The sea surface temperature (SST) rose linearly by 0.47 °C, 0.71 °C, and 0.76 °C at HN, XS, and HY-HN, respectively, between 1900 and 2014. During this period, coral growth increased linearly by ~21.0% and ~0.7% at HN and XS, while HY-NS saw a decline of ~2.8% in coral growth. Moreover, interdecadal variations were found for both SST and coral growth. A nonlinear response relationship was revealed between coral growth and SST, with a thermal optimum of ~27.5 °C for *Porites*, which is responsible for the regional difference in the long-term trend in coral growth in SCS. In recent decades, reductions in coral growth have occurred in SCS, especially at HN, with the largest fall of ~15.1% over the past century, which is attributed mainly to intensifying human impacts instead of seawater warming. A preliminary estimate presents regional-different coral growths in SCS by the end of 21st century, with declines of ~8.9–16.3% under the atmospheric $CO_2$ emission scenario (RCP 8.5), implying that the overall downturn of coral growth will be inevitable under the future sustained seawater warming in SCS. The mitigation of global warming is essential to maintain coral growth and coral reef ecosystems in SCS.


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## 1. Introduction

Coral growth is important for maintaining coral reef ecosystems and reef development. Coral growth is influenced by various environmental factors (Buddemeier and Kinzie, 1976; Kleypas et al., 1999a; Lough and Cooper, 2011; Nie et al., 1997a), where seawater warming and ocean acidification are its two global threats (Hoegh-Guldberg et al., 2007; Hughes et al., 2003; Lough and Cooper, 2011). Skeletal growth parameters are used to reveal the history of coral growth and its response to climate and environment (Lough and Cooper, 2011; Lough and Cantin, 2014), and are important for understanding coral growth and reef development under global warming and ocean acidification in the future.

Research has been carried out on the coral growth history in major coral reefs around the world. The most concerning finding is the dramatic decline in coral growth at many reefs in recent decades, including the Great Barrier Reef (GBR) off eastern Australia (Carricart-Ganivet et al., 2012; Cooper et al., 2008; De'ath et al., 2009), the Thai–Malay peninsula in Southeast Asia (Tanzil et al., 2009; Tanzil et al., 2013), the Central Red Sea (Cantin et al., 2010), Panama in eastern Pacific (Manzello, 2010), and the Caribbean Sea (Carricart-Ganivet et al., 2012; Bak et al., 2009). The main reasons for these declines were related to or at least did not preclude global seawater warming and/or ocean acidification. Seawater warming causes coral bleaching by loss of its symbiotic algae (Hoegh-Guldberg, 1999) or restricts coral growth by exceeding the thermal optimum (Cantin et al., 2010; Carricart-Ganivet et al., 2012; Tanzil et al., 2009; Tanzil et al., 2013); ocean acidification causes a decrease in seawater carbonate saturation (Caldeira and Wickett, 2003; Feely et al., 2004; Kleypas et al., 1999b), limiting calcification of coral skeletons (Doney et al., 2009; Gattuso et al., 1998; Kleypas et al., 1999b). Based on the above findings, coral growth and reef development have been predicted to stagnate in the future, with coral reef ecosystems being severely degraded or even rendered extinct (Hoegh-Guldberg et al., 2007). However, coral growth history has not shown a declining trend; instead, most of the long-term trends are significantly increasing and are correlated positively with the long-term trend in SST (Bessat and Buigues, 2001; Lough and Barnes, 1997; Nie et al., 1997b; Nie et al., 1999; Cooper et al., 2012). From view of the long-term trend, coral growth has been influenced mainly by the seawater warming rather than acidification, and rising seawater temperature can promote coral growth. These studies have identified temporal differences in coral growth and its response to seawater warming. Of note, coral growth exhibits different regional long-term trends at the reefs off western Australia (Cooper et al., 2012). These regional and temporal differences could cause biases in inferring the relationship between coral growth and environment variables and in predicting the future coral growth.

Coral reefs are distributed widely in the South China Sea (SCS), and coral growth and the effects of seawater temperature in SCS have been studied in recent decades (Chen et al., 2011; Chen et al., 2013; Jiang et al., 2016; Nie et al., 1997b, 1999; Shi et al., 2002; Shi et al., 2012; Su et al., 2012; Su et al., 2016; Zhang et al., 2014). However, most of these studies have been based on individual or several samples from one or a few locations and lack a holistic knowledge of coral growth history and its response to the environment. The integration of multiple locations and coral cores is becoming common in international research on coral growth (Carilli et al., 2010; Cooper et al., 2012; De'ath et al., 2009; Lough and Barnes, 1997; Lough and Cantin, 2014; Tanzil et al., 2013). Multiple coral cores help to overcome the effect of individual and local differences and can more reliably reveal coral growth history throughout a region and its response to regional environmental and even global climate change. In this study, we combined multiple series of coral growth and records of seawater temperature from different reefs in SCS. We analyzed the history of coral growth and SST over the past century to reveal the regional responses of coral growth to seawater temperature and their relationship and to predict the future trends of regional coral growth under sustained seawater warming.

## 2. Materials and methods

### 2.1. Study region and location

SCS is one of the largest marginal seas in the world, with an area of about 3.5 million km$^2$, and spans more than 20° of latitude (about 3°N–24°N). Coral reefs are widespread in SCS, with a complete reef covering approximately 30,000 km$^2$ representing ~5% of total coral reef area globally (Zhang et al., 2005). The coral community flourishes in SCS, with scleractinian coral consisting of 14 families, 54 genera, and 174 species, with the species number accounting for about 1/3rd of all the Indo-Pacific coral fauna (Zou, 2001). *Porites* is the dominant coral genus and species in the Indo-Pacific coral fauna (Cooper et al., 2008) and in SCS (Zou, 2001) as well, and is widely used in studies on coral growth and environmental response and in paleoclimatic reconstruction. In this study, all coral growth data were extracted from coral samples, most of which belong to *Porites lutea* and a few of which are *Porites lobata*.

Coral growth data in this study came from 12 locations in SCS (Fig. 1), 8 of which were reported in previous literature, including Qionghai (QH) and Sanya Bay (SY) at the Hainan Island in the northern SCS; Yongxing Island (YX) and Yongle Atoll (YL) at the Xisha Islands in the middle SCS; and Zhongye Island (ZY), Jiuzhang Atoll (JZ), Chigua Reef (CG), and Meiji Atoll (MJ) at the Nansha Islands in the southern SCS (Table S1). At 5 locations including Wenchang (WC) at the Hainan Island in the northern SCS; YL, Langhua Atoll (LH), and Panshiyu Atoll (PS) at the Xisha Islands; and Huangyan Island (HY) at the Zhongsha Islands in the middle SCS (Table S1), coral colonies were sampled and analyzed in this study. All samples were collected from a water depth above 10 m, which is within the suitable depth range for optimal growth in massive coral species (Lough and Cantin, 2014) where coral growth is not affected by light and depth.

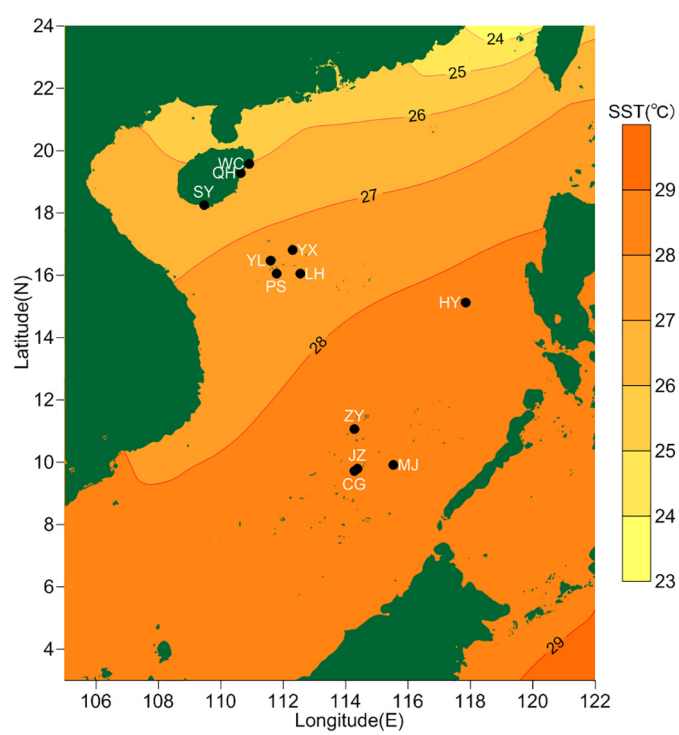


**Fig. 1.** Distribution of multi-annual SST (1980–2014) and sample locations of the coral *Porites* in SCS. Abbreviations of locations are shown in the text, Section 2.1.

### 2.2. Coral linear extension rate

Coral growth refers to the growth of coral skeletons and is reflected by annual growth variables extracted from massive corals that contain annual density banding patterns. Coral annual growth variables include the linear extension rate, skeletal density, and calcification rate (Lough and Barnes, 1997, 2000). Calcification rate is the product of the linear extension rate and skeletal density, representing the mass of calcium carbonate skeleton deposited per unit of time, so the calcification rate is always used as a synthetic coral growth proxy. Different coral species have different growth strategies, which determine the contribution of the linear extension rate and skeletal density to the calcification rate. The growth strategy of *Porites* is that the coral enhances its calcification rate to promote skeletal growth by increasing the linear extension rate rather than skeletal density (Carricart-Ganivet, 2007). This means that the calcification rate is mainly determined by the linear extension rate and is positively correlated with the linear extension rate instead of skeletal density in *Porites* (Cooper et al., 2008; De'ath et al., 2009; Lough and Barnes, 2000; Shi et al., 2012; Tanzil et al., 2013). As a result, the linear extension rate can be substituted for the calcification rate to represent the growth of the coral *Porites*. Notably, a new research has found sustained linear extension rate and calcification rates, but a long-term reduction in skeletal density in the subtropical zone (Rippe et al., 2018). Ideally, coral growth should be described by all three annual growth variables. Because of the lack of skeletal density data, we analyzed and discussed the growth of *Porites* using only the linear extension rate in this study.

The linear extension rate (cm/a) represents the width of the annual density band in the coral skeleton. X-ray photos (Knutson et al., 1972) show a series of clear annual bands composed of alternating high- and low-density sub-bands in the *Porites* skeleton, with the width of the annual density band along the main growth axis being regarded as the linear annual extension rate of the skeleton. The linear extension rate can, therefore, be obtained by measuring the width of the annual band directly on a skeletal X-ray photo (Nie et al., 1997a), or is calculated from an X-ray photo by using software such as CoralXDS (Helmle et al., 2002) and MATLAB (Shi et al., 2012) and from other sources such as Computerized Tomography images (CT) (Bessat and Buigues, 2001; Cantin et al., 2010; Carilli et al., 2012), luminescent images (D'Olivo et al., 2013; Tanzil et al., 2013), or gamma densitometry (Chalker and Barnes, 1990). The software can divide annual density bands and calculate linear extension rates based on image gray variation between high- and low-density sub-bands along the main growth axis on an X-ray photo.

There were four data sources used for linear extension rate in this study (Table S1). The first was original data of linear extension rate from literatures and authors; the second was retrieval of linear extension rate curves from previous researches; the third was calculated from X-ray photos of skeletal samples presented by authors to extract linear extension rate series using MATLAB; and the fourth was sample analyses by ourselves. Core samples were drilled from *Porites lutea* colonies at WC in 2013 and 2014; YL in 2013; and LH, PS, and HY in 2015 using an underwater hydraulic pressure driller (Tech2000), and were sliced and X-ray photographed to extract linear extension rate series using MATLAB. We finally obtained 99 linear extension rate series of *Porites* from 12 locations at different reefs in SCS. All linear extension rate series showed different age ranges, and the study period ranged from 1900 to 2014, a total of 115 years (Fig. S1). The basic data of linear extension rates are shown for locations in Table S2.

### 2.3. Seawater temperature

Since there is a lack of long-term observed SST data at the reefs in SCS, this study used the global SST dataset HadiSST provided by the UK Hadley Center (https://www.metoffice.gov.uk/hadobs/hadisst/), which is composed of 1° × 1° grid SST data (Rayner et al., 2003). Considering that recent decades saw large declines in coral growth attributed possibly to rising SST, the multi-annual SST was averaged between 1980 and 2014 through the SST data of the entire SCS extracted from HadiSST, showing a spatial distribution of multi-annual SST in SCS (Fig. 1). According to the spatial gradient of the SST in SCS, the studied locations can be divided into three regions (Fig. 1): HN, including three locations at Hainan Island with average SST below 27 °C; XS, including four locations at the Xisha Islands with average SST between 27 and 28 °C; and HY-NS, including five locations at Huangyan Island and Nansha Islands with average SST above 28 °C. In addition, the long series of annual SST were calculated for the locations and regions between 1900 and 2014 using monthly SST of the closest grids to the sampling locations. Fig. 2a shows the annual SST series at three regions over the past century.

### 2.4. Data analyses

To reduce the influence of individual differences in coral growth, the linear extension rate was converted to the percentage of linear extension rate anomalies (Cooper et al., 2012), calculated as the percent difference of the annual linear extension rate relative to the multi-annual averaged linear extension rate for the period (1980–2014) common to most of the series. The new data represents the percentage of relative variation in linear extension rate. Fig. 2b shows the series of average linear extension rates of *Porites* at three regions. We analyzed the linear trends and the nonlinear variations with interdecadal cycles in series of both SST and linear extension rate as the long-term trends and the interdecadal variations in SST and coral growth. Considering the age biases of linear extension rate caused by disorders in annual density bands due to differences in the skeletal microstructure (Lough and Barnes, 1997) and/or caused by errors in annual density band division, and a lack of sample cross-dating for integrated multi-series, it is difficult to avoid possible age error. So, we did not explore interannual variation in coral growth in this study.

Linear and nonlinear regression models are widely used in studies on trends in coral growth at multiple locations and in multiple series and their relationships with the environment (Cooper et al., 2012; De'ath et al., 2009; Shi et al., 2012; Tanzil et al., 2013). In this study, a Generalized Linear Model (GLM) of R language (https://cran.r-project.org/) was used to carry out the following analyses (Table S3): (1) Linear regression analysis on the long-term trends in the linear extension rate and SST series at three regions; (2) nonlinear regression analysis on interdecadal variations in the linear extension rate and SST series with the linear trends removed at three regions; (3) nonlinear regression analysis on the relationship between the linear extension rate and SST in the long-term trends; and (4) nonlinear regression analysis on the relationship between the linear extension rate and SST in interdecadal variations. The best fitted models were selected according to the statistical results in all regression analyses (Tables S6, S8, and S10). Moreover, univariate ANOVA was used to test the significance of regional differences of average linear extension rate and SST (Tables S4, S5) and the significance of long-term trends in both linear extension rate and SST (Table S7); correlation analysis was used to evaluate regional correlations in the interdecadal linear extension rate and interdecadal SST (Table S9).

## 3. Results

### 3.1. Regional SST

SST shows a spatial gradient owing to the effect of the land–sea distribution (Fig. 1). The average SSTs (1980–2014) were 26.17 °C, 27.03 °C, and 28.11 °C at HN, XS, and HY-NS respectively, with significant regional difference (Table S5). Over the past hundred years between 1900 and 2014, SST exhibited significant long-term trends in SCS (Fig. 3a, Table S6) with significant regional differences (Table S7). The linear rising

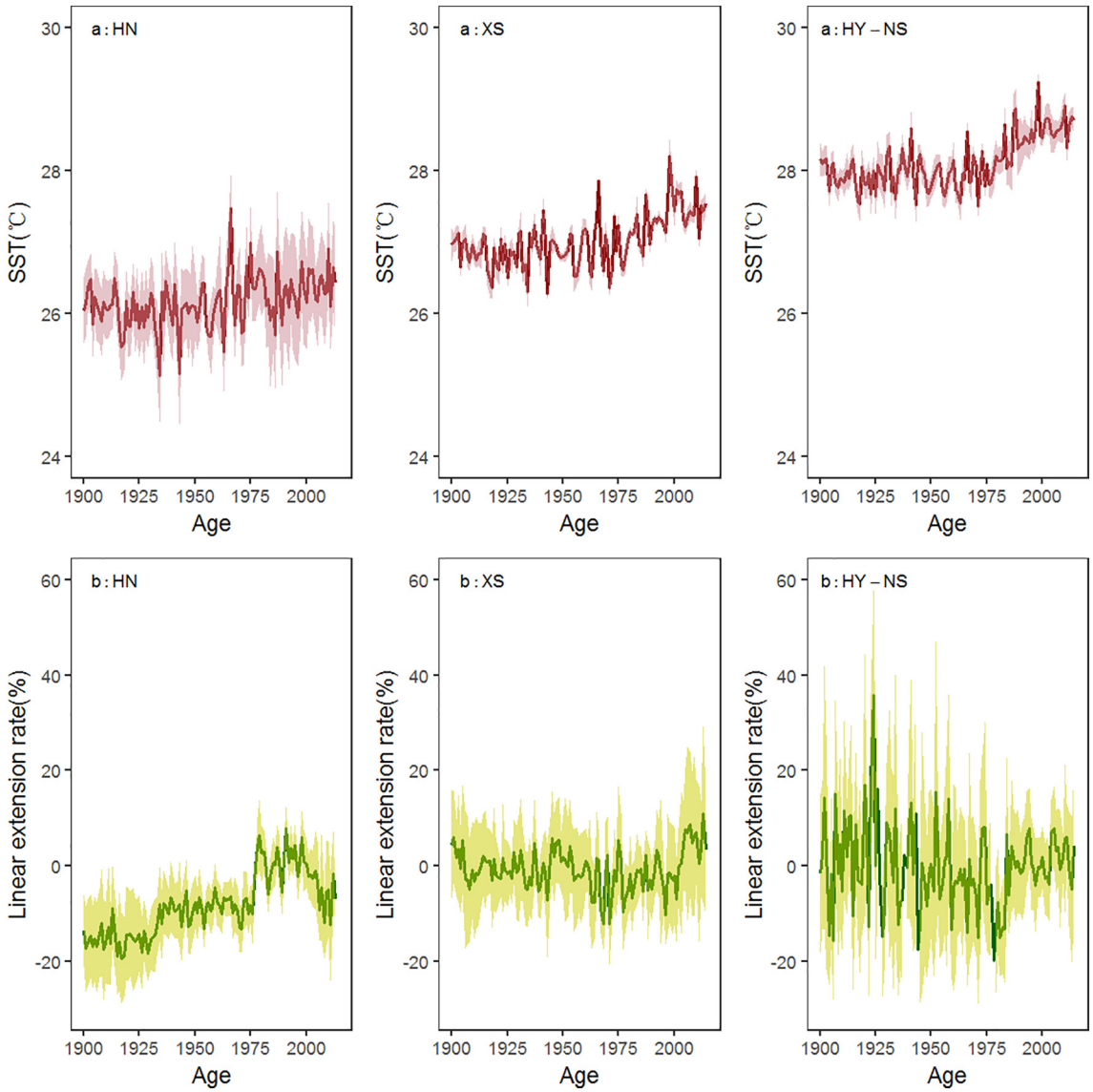


**Fig. 2.** Time series of annual SST (a) and linear extension rate of the coral *Porites* (b) at three regions in SCS. Abbreviations of regions are shown in the text, Section 2.1. The light-colored areas of the curves indicate 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

rate in regional SST is ~0.0 67 °C /10a, ~0.061 °C/10a, and ~0.041 °C/10a at HY-NS, XS and HN, respectively. In addition, SST had significant interdecadal variations over the past century (Fig. 4a, Table S8). The interdecadal variations in SST were consistent at XS and HY-NS with a significantly positive correlation coefficient (Table S9), while HN saw a different interdecadal variation in SST with insignificant correlation to HY-NS and a significantly positive correlation to XS (Table S9).

### 3.2. Regional linear extension rate

The average linear extension rate of *Porites* is quite different among the locations in SCS (Fig. S1) and varies between 0.76 ± 0.37 and 1.27 ± 0.37 cm/a (Table S2) with significant local difference (Table S4). The average linear extension rates are 0.91 ± 0.29 cm/a, 1.10 ± 0.22 cm/a, and 1.25 ± 0.37 cm/a at HY-NS, XS, and HN, respectively, with significant regional difference (Table S4). The linear extension rate shows different long-term trends in SCS over the past century (Fig. 3b, Table S6), with significant regional difference (Table S7). The linear extension rate increased significantly by ~21.0% at HN and increased insignificantly by ~0.69% at XS, respectively, while the linear extension rate decreased insignificantly by ~2.76% at HY-HN. Moreover, the linear extension rate also exhibits significant interdecadal variations over the past century (Fig. 4b, Table S8). XS and HY-NS had comparable interdecadal variations in the linear extension rate with a significantly positive correlation coefficient (Table S9), while the interdecadal variation in the linear extension rate was different at HN from those at HY-NS and XS with a significantly negative correlation (Table S9).

### 3.3. Relationship between linear extension rate and SST

GLM analysis found nonlinear relationships between the linear extension rate and SST in the long-term trend and the interdecadal variation in SCS (Table S10), respectively. In the relationship of the long-term trend, the linear extension rate transforms from an increase into a decline along with the constant rise in SST (Fig. 5a), and the turning point corresponds to a SST threshold of ~27.5 °C, representing the thermal optimum for *Porites* growth in SCS. And the relationship between the interdecadal SST and linear extension rate is characteristic of regional differences. The nonlinear fitting is similar between XS and HY-NS, showing the transition of the interdecadal linear extension rate from an increase to a decline with rising interdecadal SST (Fig. 5b), whereas HN saw the opposite nonlinear relationship (Fig. 5c).

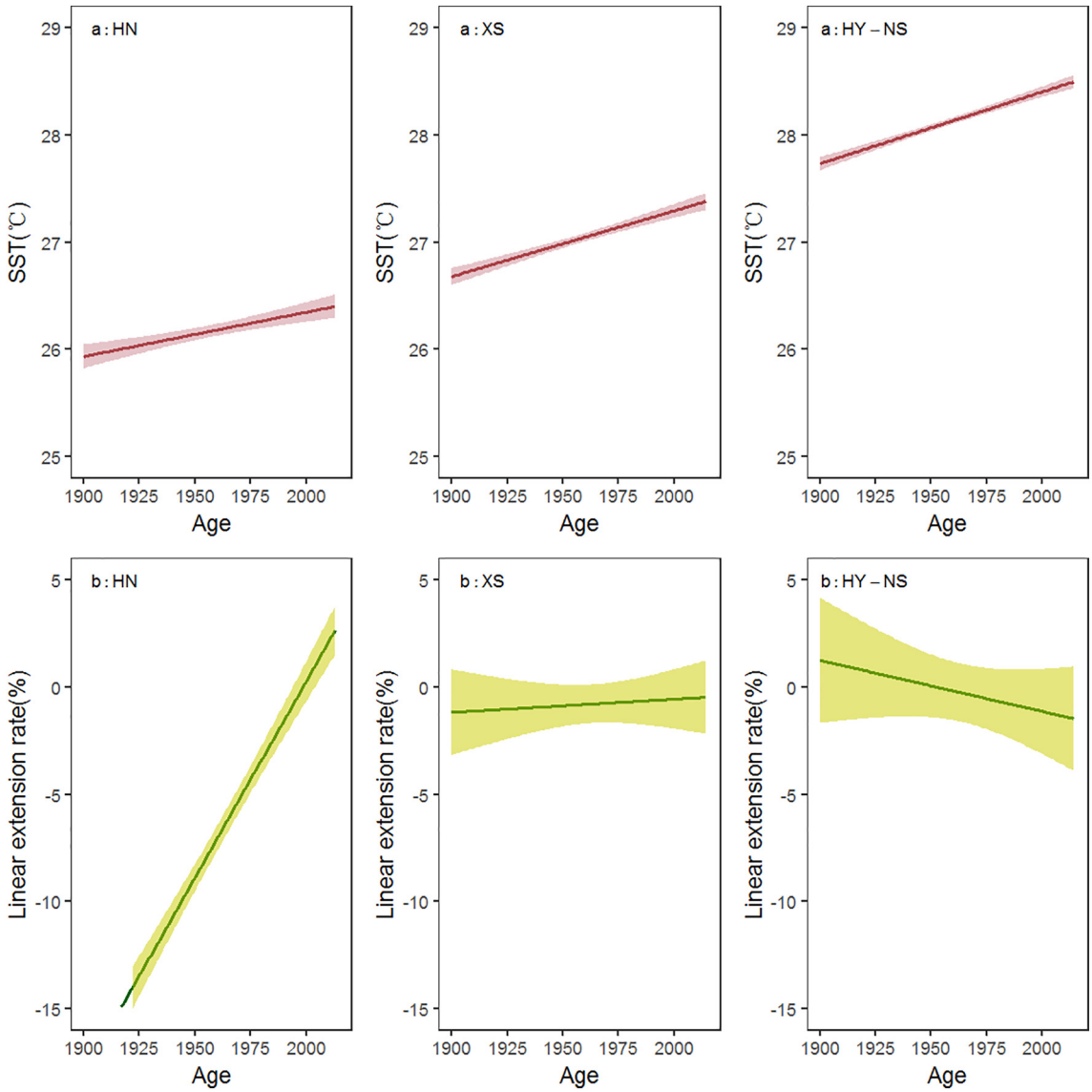


**Fig. 3.** Long-term trends in SST (a) and linear extension rate of the coral *Porites* (b) at three regions in SCS. Abbreviations of regions are shown in the text, Section 2.1. The light-colored areas of the curves indicate 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

### *3.4. Estimate of future linear extension rate*

The Intergovernmental Panel on Climate Change (IPCC) reported that the global climate will continue to warm with increasing greenhouse gas concentrations (IPCC, 2007, 2014). The Fifth Assessment Report of the IPCC predicted a variety of scenarios for future global warming based on the CMIP5 models (IPCC, 2014), showing a possible rise in global average temperatures by ~1.0–3.7 °C by the end of the 21st century. A study predicted future SST in the marginal seas of China under two $CO_2$ emission scenarios (RCP 4.5 and RCP 8.5) using the CMIP5 models, and found that SST will continue to rise by ~1 °C under the RCP 4.5 scenario and by ~3 °C under the RCP 8.5 scenario in SCS (Tan et al., 2016).

Based on the predicted future SST in SCS under the two emission scenarios (Fig. S2) (Tan et al., 2016) and combined with the nonlinear relationship of the long-term trend between SST and the linear extension rate over the past century (Fig. 5a), we produced a preliminary estimate for the future trends of the linear extension rate in SCS by the end of the 21st century. The result shows the regional differences in the future linear extension rate (Fig. 6). Under the RCP 4.5 scenario, the linear extension rate will decrease in a sustained fashion by ~6.1% at HY-NS by 2100, while an obvious decline will occur in the 2020s and then the linear extension will reduce by ~3.8% at XS by 2100. At HN, in contrast, the linear extension rate will maintain a rising trend into the 2050s with an increase of ~6.8%, which will be followed by a relatively constant linear extension. Under the RCP 8.5 scenario, the linear extension rate will decline heavily by ~16.3% at HY-NS and ~14.0% at XS by 2100, respectively, while the linear extension rate will decrease by ~8.9% at HN by 2100 after an increase of ~6.7% until the 2050s.

## 4. Discussion

### *4.1. Long-term trends in SST and coral growth*

The average multi-annual SST is distributed in SCS with the spatial gradient increasing from nearshore (HN) to open sea (XS and HY-NS). SST shows regional long-term trends between ~0.04 °C–0.07 °C/10a in SCS over the past hundred years (Fig. 3a), comparable with the linear rising rate of ~0.05 °C/10a in the global tropical ocean (30°N–30°S) between 1901 and 2012 (Lough and Cantin, 2014). There is a spatial pattern of regional long-term trends that is enhanced with the increase of regional SST; namely, the relatively high warming rate at HY-NS with

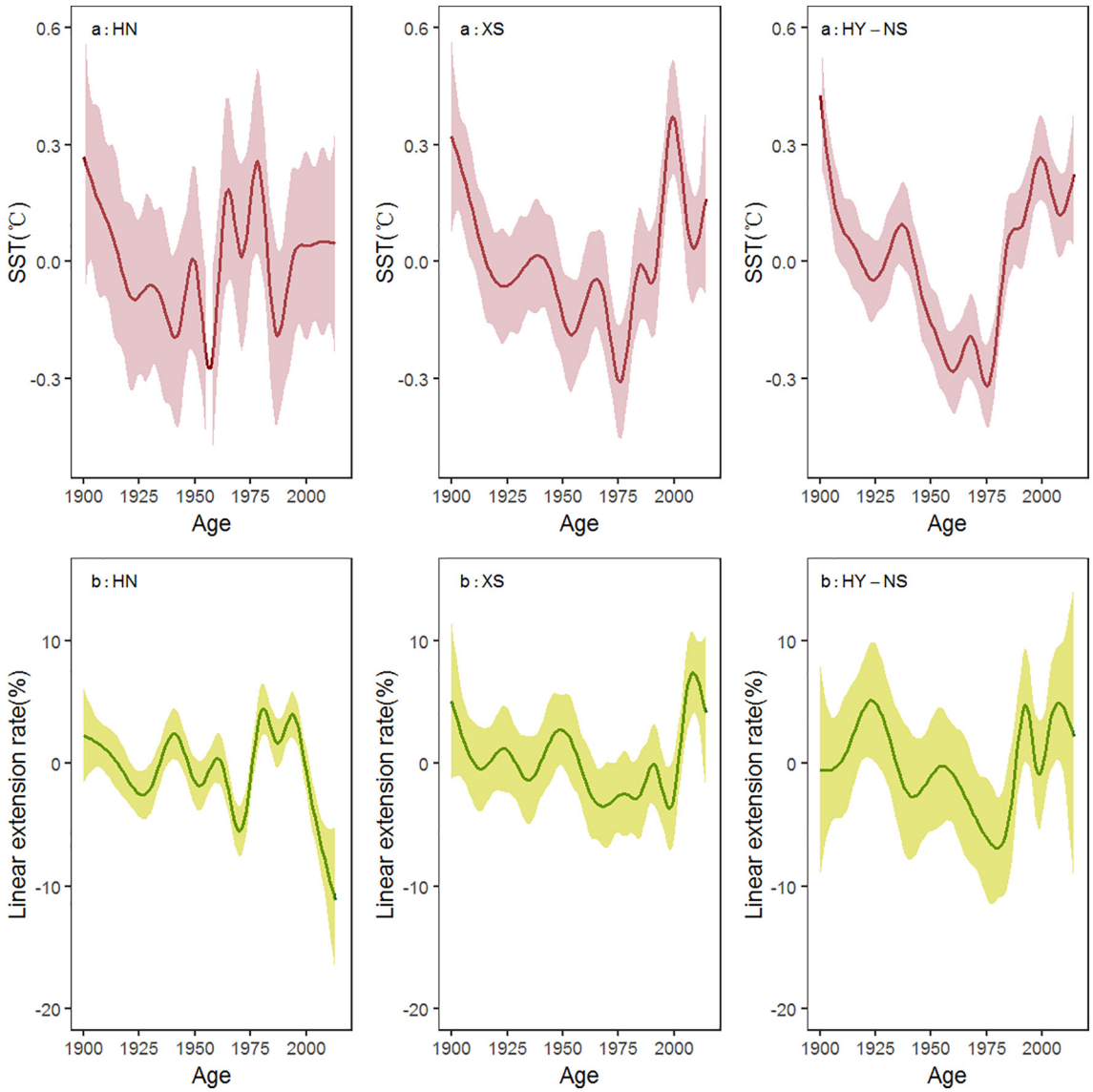


**Fig. 4.** Interdecadal variations in SST (a) and linear extension rate of the coral *Porites* (b) at three regions in SCS. Abbreviations of the regions are shown in the text, Section 2.1. The light-colored areas of the curves indicate 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the relatively high-SST, and the relatively low warming rate at HN with the relatively low-SST. At the reefs off western Australia, the linear rising rate of SST increased from 0.02 °C/10a at the relatively low-latitude, high-SST region (17°S, ~SST 27.6 °C) to 0.10 °C/10a at the relatively high-latitude, low-SST region (28°S, ~21.5 °C) between 1900 and 2010 (Cooper et al., 2012). A similar latitude gradient can be found in the long-term trends of regional SST in GBR off eastern Australia (De'ath et al., 2009). Obviously, the spatial pattern of the long-term trends in regional SST in SCS is opposite to that in the regions off western and eastern Australia. In addition to the influence of land–sea distribution, the pattern in SCS possibly correlates to the upwelling system in the continental shelf of northern SCS (Jing et al., 2009). The upwelling in northern SCS, especially the Qiongdong Upwelling off eastern Hainan Island, directly affects the coast of Hainan Island (Xie et al., 2012), causing an evidently low SST in summer. Therefore, the rise in SST is slower at HN than at XS and HY-NS.

The linear extension rate of *Porites* is generally within the range of 1.0–1.5 cm/a at reefs in the Indo-Pacific Ocean, where the lowest rate is only 0.4 cm/a and the highest reaches 2.5–3.0 cm/a (Lough and Cantin, 2014). The linear extension rate of *Porites* in SCS is within this common range. The regional average extension rates show a spatial gradient decreasing from HN to XS and HY-NS, opposite to the spatial distribution of SST. This phenomenon that coral grows fast in the relatively low-SST region (~26 °C) and grows slowly in the relatively high-SST region (~28 °C) in SCS is different from what is found in the Indo-Pacific Ocean (23–30 °C), where coral grows faster in the relatively high-SST region than in the relatively low-SST region (Lough and Barnes, 2000; Lough, 2008; Lough and Cantin, 2014). There is also a spatial pattern of the regional long-term trends in the linear extension rate, which changes with regional SST (Fig. 3b); namely, a significantly rising rate of ~21.0% in linear extension occurred at HN with the relatively low SST, and an insignificant rising rate was found at XS with a medium SST, while an insignificant declining rate existed at HY-NS with a relatively high SST. A similar spatial pattern of coral growth also occurs at the reefs off western Australia, where coral growth had an increasing long-term trend at the relatively low-SST reefs with the largest increase of ~23.7%, comparable to that at HN, while the long-term trend was not significant in coral growth at the relatively high-SST reefs (Cooper et al., 2012).

Although the regional pattern of long-term trends in SST were opposite between SCS and regions off western Australia, the regional pattern of long-term trends in coral growth were comparable. It is noteworthy

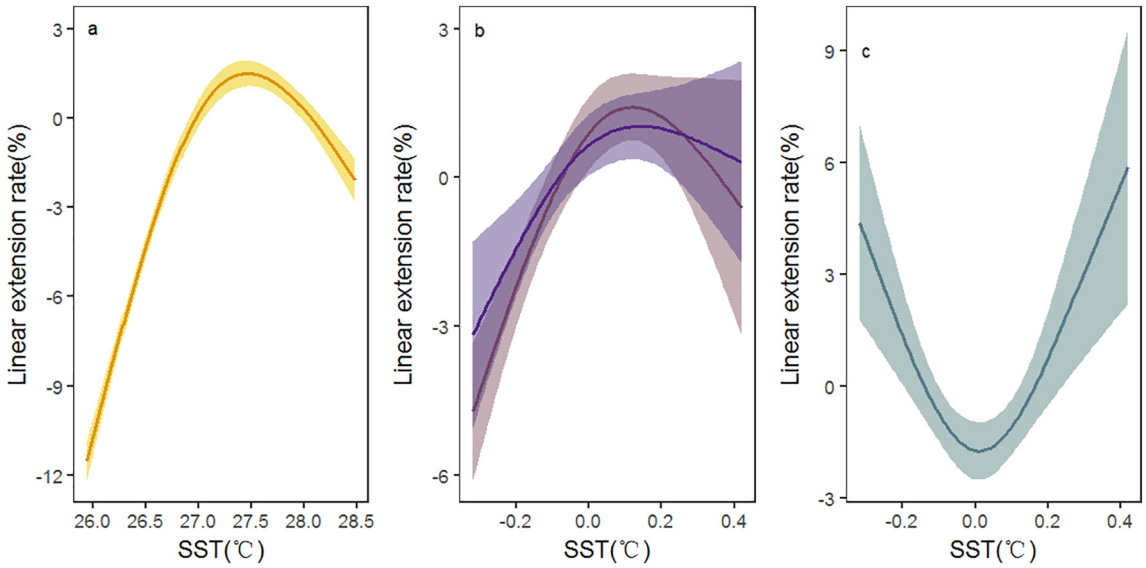


**Fig. 5.** Nonlinear relationships between SST and linear extension rate of the coral *Porites* in the long-term trend (a) and interdecadal variations (b; purple curve: XS; brown curve: HY-NS; c: HN) in SCS. The light-colored areas of the curves indicate 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

that HN in the northern SCS shows a relatively low rising rate in SST, but a relatively high increasing rate in coral growth. As mentioned above, SST and its long-term trend at HN are weakened by the Qiongdong Upwelling in SCS, but the aquatic environment has been changed by the upwelling in this region as well. The Qiongdong Upwelling influences the region off eastern Hainan Island remarkably, where the bottom water supply forms relatively low-temperature, high-salt, and high-nutrient surface water (Xie et al., 2012), promoting organism growth and the flourishing of coral communities at reefs at Hainan Island and the adjacent Leizhou Peninsula (Zhao et al., 2008). At coastal reefs in eastern Pacific, studies have found that the upwelling enhances the productivity of corals and reef organisms (Stuhldreier et al., 2015), and nutrients recharged by the upwelling are responsible for the high coral growth rate (Jimenez and Cortes, 2003). Therefore, the Qiongdong Upwelling has provided good water conditions for coral growth at HN over the past century. For similar relatively low-SST regions, coral growth was promoted mainly by the high rising SST at the region off western Australia, but also by the more appropriate aquatic environment caused by upwelling at regions in SCS.

### *4.2. Causes for the recent declines in coral growth in SCS: seawater warming or human impact*

In addition to the long-term trend, coral growth shows significant regional interdecadal variations in SCS (Table S8). Interdecadal variations have also been found in coral growth at Moorea Island in South Pacific over a hundred years (Bessat and Buigues, 2001) and in GBR over the past several centuries (Lough and Barnes, 1997). The interdecadal variations in coral growth had been supposed to recover to a normal level (Lough and Barnes, 1997). In recent decades, however, remarkable declines in coral growth have been found in many reefs around the world, most of which are unprecedented in the history.

At GBR, coral growth had a decline of ~21% in the northern reefs between 1988 and 2003 (Cooper et al., 2008), ~20% in the middle reefs between 1989 and 2002 (Carricart-Ganivet et al., 2012), and ~14.2% over the entire reefs between 1990 and 2005, which is the largest reduction in the last 400 years (De'ath et al., 2009). In the Caribbean, coral growth decreased by ~20–30% in the Mesoamerican Barrier Reef between 1985 and 2009 (Carricart-Ganivet et al., 2012), and ~7.2–10.7% at Curacao Island between 2002 and 2004 and 1971–1973 (Bak et al., 2009). In the Red Sea, the decline reached ~30% between 1998 and 2008 (Cantin et al., 2010), and one-third of coral growth was lost along the Panama coast in eastern Pacific between 1974 and 2006 (Manzello, 2010). In Southeast Asia, coral growth declined by ~23.5% in Phuket Island between 2003 and 2005 when compared with the period between 1984 and 1986 (Tanzil et al., 2009), and decreased by ~18.6% on the coasts around the Thai–Malay peninsula along both the Pacific and the Indian Oceans between 1980 and 2010 (Tanzil et al., 2013). The large declines in coral growth in recent decades have been attributed partly to SST exceeding the optimum threshold (Cantin et al., 2010; Carricart-Ganivet et al., 2012; Tanzil et al., 2009, 2013) or have been possibly related to ocean acidification (Bak et al., 2009; Manzello, 2010; D'Olivo et al., 2013); however, some authors have been unsure whether the cause is seawater warming, ocean acidification, or their combined effects (Cooper et al., 2008; De'ath et al., 2009). Moreover, the effects of various regional environmental changes are not ruled out (D'Olivo et al., 2013; Tanzil et al., 2013).

The interdecadal variation shows declines in coral growth in SCS in recent decades, but the duration and magnitude of the decline are different at the three regions. The recent decline was ~2.7% at HY-NS since 2007 and ~3.3% at XS since 2008 (Fig. 4b), corresponding to the small rises in interdecadal SST of ~0.10 °C at HY-NS and ~0.12 °C at XS, respectively (Fig. 4a). At HN, coral growth decreased evidently by ~15.1% since 1994, the largest decline over the past century (Fig. 4b), corresponding to a relatively constant interdecadal SST at HN in this period (Fig. 4a). It looks like the recent rise of SST in SCS was just beginning of an interdecadal warming phase, and coral growth could not respond fast enough as shown at HY-NS and XS. Although the recent decline in coral growth at HN is comparable to the declines at other major world reefs in recent decades, it cannot be imputed exclusively to seawater warming.

Investigations have found that coral communities have experienced widespread and severe degradation around Hainan Island in recent decades. Organism population and biodiversity of the coral community have decreased at Sanya Bay in southern Hainan Island since the 1960s, where the live coral coverage has been reduced by nearly 60–70% and has remained at only ~10% in recent years (Zhang et al., 2006; Zhao et al., 2012). A decrease in coral population has also occurred at the reefs near eastern Hainan Island, including Wenchang, Qionghai, Wanning, and Lingshui, where live coral coverage has been less than ~20% and dead coral coverage up to 20–60% (Wu et al., 2011a). Consequently, the large decline in coral growth is correlated

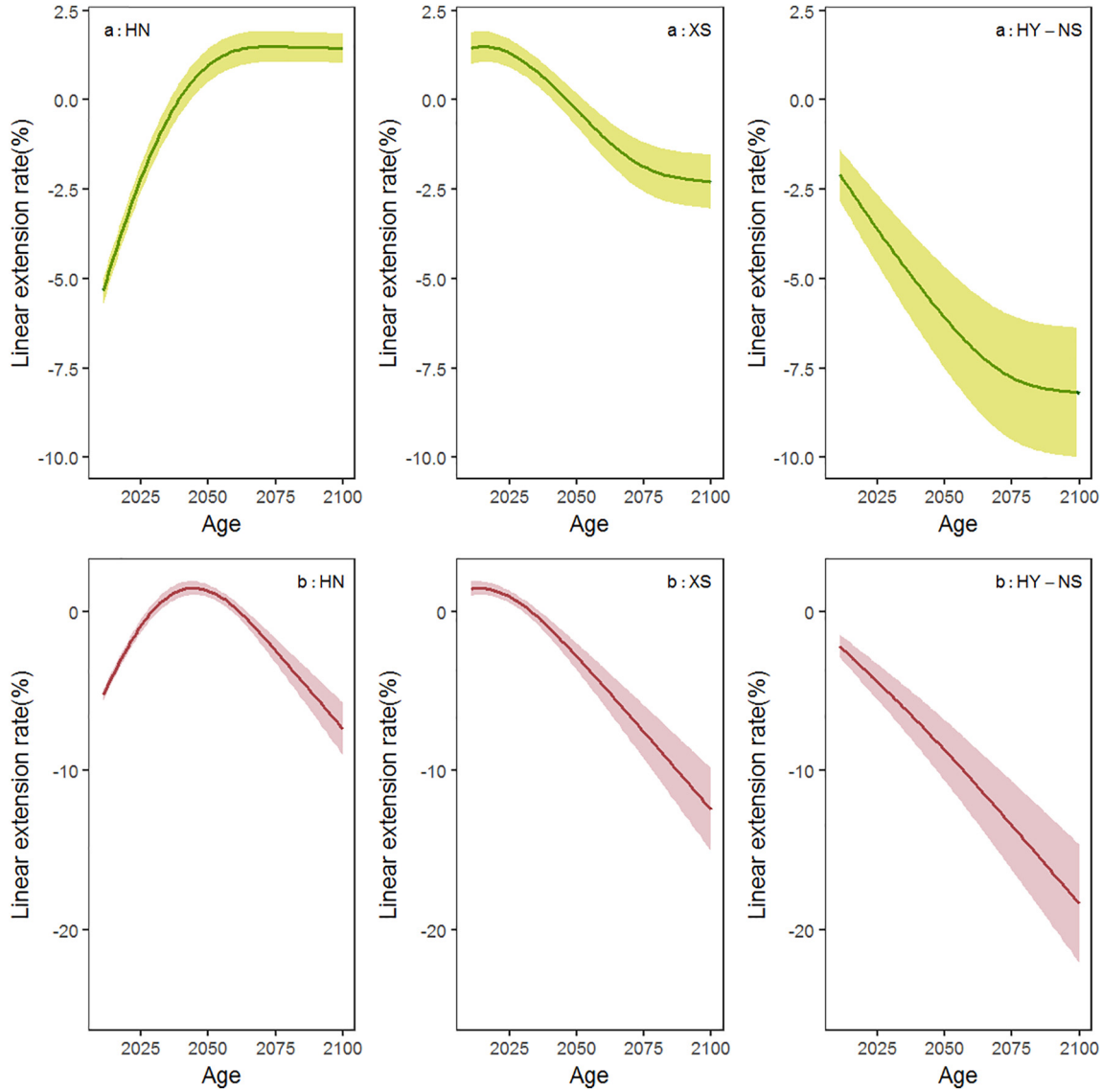


**Fig. 6.** Estimation of linear extension rate of the coral *Porites* under two $CO_2$ emission scenarios (a: RCP 4.5; b: RCP 8.5) in SCS in the 21st century. Abbreviations of the regions are shown in the text, Section 2.1. The light-colored areas of the curves indicate 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

closely with the severe degradation of the coral ecosystem at HN in recent decades.

The coral ecosystem degradation has been attributed mainly to the intensifying human impacts at Hainan Island, with rapid social and economic development since the 1970s and 1980s. The major human activities including destructive fishing by explosion and poison, reef excavation, engineering construction, aquiculture, and sewage (Shi et al., 2007; Wu et al., 2011a; Zhang et al., 2006; Zhao et al., 2012), all of which have caused severe deterioration of the ambient environment around the reefs, such as water pollution, suspended sediment, reef breakage, and algal blooms, which have widely damaged and killed individual corals, resulting in the reduction of coral coverage, biodiversity, and coral growth. Moreover, human impacts have also inevitably occurred at some locations of XS and HY-NS, such as overfishing and engineering construction (Huang et al., 2011; Shi et al., 2011; Wu et al., 2011b; Zhao et al., 2013, 2016), but the impacts have been less than those at HN due to their far distance from the mainland, which possibly correlates to the recent small declines in coral growth at HY-NS and XS. Similarly, at some reefs in Florida (Hudson et al., 1994), the central GBR (D'Olivo et al., 2013), Barbados (Tomascik, 1990), and Panama (Guzman et al., 2008), coral growth has suffered a large decline or remained at a consistently low level, mainly due to local human impacts such as oil spills, sewage discharge, construction, water deterioration, and increased land input. In SCS, therefore, human impacts instead of seawater warming are responsible possibly for the recent decline in coral growth, especially at HN.

### 4.3. Relationship between coral growth and SST

Earlier studies found a linear positive correlation between coral growth and SST series at reefs such as GBR (Lough and Barnes, 1997), Moorea Island (Bessat and Buigues, 2001), and the Xisha Islands and Hainan Island in SCS (Nie et al., 1997b, 1999) in the period of several hundred years before the 1980s and 1990s. A subsequent study reported that coral growth retained a positive correlation with rising SST at the reefs off western Australia over the past 100 years until to 2010 (Cooper et al., 2012). These findings manifest a positive relationship of coral growth with SST in the past long-term trend. A linear positive relationship has been found between the average coral growth and average SST at many reefs around the world as well (Lough and Barnes, 2000; Lough and Cantin, 2014). So, it's believed that rising SST promoted

coral growth, at least in the early stage (Cooper et al., 2012; Lough and Barnes, 2000; Lough, 2008; Lough and Cantin, 2014).

Differently from the linear positive relationship mentioned above, GLM analysis found that a nonlinear fitting better describes the relationship between coral growth and SST in the long-term trend in SCS (Fig. 5a). This nonlinear relationship produces a thermal optimum of ~27.5 °C for *Porites* growth. A nonlinear modal effect of SST on coral growth (Cooper et al., 2008) has also been reported in previous studies. Experimental results have indicated a thermal optimum of ~25–27 °C for several coral species (Jokiel and Coles, 1977; Highsmith, 1979; Marshall and Clode, 2004). The nonlinear relationship between coral growth and SST has revealed the thermal optimum at several reefs; for example, ~26.7 °C for *Porites* at GBR (Cooper et al., 2008), ~28.8 °C for *Montastraea* at Mexico near the Caribbean (Worum et al., 2007), ~29.4 °C for *Porites* at the Thai–Malay peninsula (Tanzil et al., 2013), and ~30.5 °C for *Diploastrea* in the Red Sea (Cantin et al., 2010). It can be considered that a nonlinear model more holistically reflects the true relationship between coral growth and SST than a linear model, and the thermal optimum for coral growth is different in different species and is related to regional SST.

Since having reached the thermal optimum, coral growth has responded differently to the regional SST in SCS. At HN and XS, SST was still under and close to the thermal threshold, respectively. However, SST exceeded the threshold at HY-HS. Correspondingly, coral growth maintained an increasing trend at HN and XS, while coral growth showed a declining trend at HY-NS, although the decline was not significant. It's reasonable to believe that sustained seawater warming has been detrimental to coral growth at high SST region in SCS over the past century. For similar relatively high-SST regions, coral growth was weakened mainly by the low rising SST at regions off western Australia, otherwise mainly by the high rising SST over the thermal threshold in SCS.

Coral growth shows a nonlinear relationship with SST in the interdecadal variations in SCS as well. A comparable nonlinear relationship was fitted at both XS and HY-NS (Fig. 5b), implying that the continuous rising interdecadal SST also impaired the interdecadal coral growth. In contrast, HN shows an opposite nonlinear relationship (Fig. 5c), contrary to common sense about the actual relationship between coral growth and SST. Correlation analysis reflects the regional differences in the interdecadal coral growth and interdecadal SST respectively (Table S9). A significantly positive correlation existed between HY-NS and XS in both interdecadal extension rate and interdecadal SST, whereas the two regions correlated negatively with HN in interdecadal growth and correlated weakly and insignificantly with HN in interdecadal SST. Thus, the response of coral growth to SST in the interdecadal variation only occurred at the southern-eastern and middle regions instead of the northern nearshore region in SCS, which may be related to the impacts of the Qiongdong Upwelling and human activities.

### 4.4. Future coral growth in SCS

Coral growth history and its relationship to the environment can help predict coral growth under future global climate change. In an early estimation based on the positive correlation between coral growth and SST and the future trend of rising SST, coral growth should increase by ~35% in the 21st century (McNeil et al., 2004). But with a new understanding of the relationship between coral growth and climate change, the prediction for future coral growth is not so optimistic. Considering the relationship between rising SST and declining coral growth in recent decades and the future warming trends, studies have predicted that the growth of *Porites* will stop around the Thai–Malay peninsula in the next 150 years (Tanzil et al., 2013) and is about to cease in both the GBR and the Caribbean in the next 100 years (Carricart-Ganivet et al., 2012). *Diploastrea* will stop growing in the Red Sea around 2070 (Cantin et al., 2010). Since we are only considering the recent decline in coral growth and rising SST, these projections could overestimate the decline of coral growth in the next hundred years. The relationship between coral growth and SST in the long-term trend over the past century will be better for estimating the future coral growth.

Based on the nonlinear coral growth-SST relationship over the past century and the projected future SST in SCS, regional coral growth was estimated under two $CO_2$ emission scenarios by the end of 21st century (Fig. 6). Coral growth will show an increased declining trend at HY-NS and will convert into a downtrend in the ~2020s at XS, respectively, while coral growth will experience an increase until the ~2050s and then keep steady (RCP 4.5) or turn into a decline (RCP 8.5) at HN. By the end of the 21st century, under the relatively low $CO_2$ emission scenario, the southern-eastern and middle regions (HY-NS and XS) in SCS will see significant declines in coral growth, and the northern nearshore region (HN) in SCS will not increase again; under the high $CO_2$ emission scenario, the all regions of SCS will face declines in coral growth to different extents. The largest estimated declines are ~8.9%–16.3% at the three regions under RCP 8.5, less than the projected declines at other world reefs. From the perspective of the long-term trend, coral growth should not experience such a striking decline by the end of 21st century; however, the downtrend will be significant and widespread in SCS.

The fate of coral under the future sustained warming depends on its adaptation to thermal stress. Coral adaptation is an important mechanism to react to climatic and environmental changes (Hughes et al., 2003). Studies have found that the corals that had experienced long-term high SST or short-term hot bleaching events had greater adaptation to thermal stress and avoided obvious declines in coral growth (Castillo and Helmuth, 2005; Castillo et al., 2012; Guest et al., 2012), implying that coral can improve its resistance and resilience under thermal stress. In addition, studies have reported that coral shows both short-term acclimation and long-term adaptation to heat stress (Palumbi et al., 2014), and coral responds to warming through rapid evolution of coral proteins (Voolstra et al., 2011). However, a new survey has revealed that an unprecedented coral bleaching event in GBR in 2016 was not lessened after the two bleaching events in 1998 and 2002, and found no evidence for acclimation or adaptation to the past extreme heat events (Hughes et al., 2017).

Although the pattern and mechanism of coral adaptation are debatable and unknowable, the thermal adaptation of coral can be revealed through the coral growth history and its relationship with SST in SCS. Over the past century, seawater warming has exceeded the thermal threshold and coral growth has entered a downtrend under the long-term heat stress at HY-NS. Coral growth did not exhibit adaptation to the long-term thermal stress at the high-SST region in SCS. In a new study, the concept of “ecological memory” was presented to describe the impact of the former on the latter within the back-to-back mass coral bleachings in GBR (Hughes et al., 2018), meaning that coral adaptation could be difficult because of the cumulative thermal stress of long-term warming. We have reasons to believe that long-term seawater warming has not promoted the thermal adaptation of coral in SCS, and coral growth will be less suitable for a hotter environment in the future. Moreover, regional environmental stress (increasing terrestrial sediments, water quality deterioration, etc.) caused by long-term human activities may have led to a weakening of coral thermal adaptation, reducing its resistance and resilience (Carilli et al., 2010; Wooldridge, 2009). Coral adaptation to thermal stress has and will be lessened inevitably by the intensifying human impacts in SCS, especially at nearshore regions, exacerbating the decline in coral growth in the future.

Some researchers believe that seawater warming will be more suitable for coral growth at relatively high-latitude, low-temperature regions, which may possibly create a refuge for coral in the future (Riegl and Piller, 2003; Halfar et al., 2005; Chen et al., 2009). Although there are regional differences within the projected trends in coral growth under future seawater warming, it is expected that the overall coral growth will unavoidably confront a crisis of decline in SCS in less than

100 years, and the decline would increase with additional seawater warming. Therefore, it is currently difficult to conclude that the relatively high-latitude region will become a coral refuge in SCS in the future. The key to maintaining future coral growth and reef stability is mitigation of global warming. Therefore, it is imperative to carry out IPCC's initiatives and measures to control greenhouse gas emissions and to alleviate the risk of climate change.

## 5. Conclusions

This study integrated and analyzed SST and the linear extension rate of the coral *Porites* from three regions, including twelve locations, and revealed the temporal and spatial patterns of coral growth and SST in SCS over the past century. The findings reveal different regional responses of coral growth to sustained seawater warming in SCS. Both the long-term trend and interdecadal variation show a nonlinear relationship between coral growth and SST. Since exceeding the thermal optimum, the increasing trend in coral growth has been reduced from HN to XS and lost in HY-NS over the past century following rising regional SST. In recent decades, human impacts instead of seawater warming were mainly responsible for the decline in coral growth in SCS, especially at nearshore regions like HN. Coral growth has not shown adaptation to thermal stress over the past hundred years, and will inevitably decline in SCS by the middle to the end of this century under sustained seawater warming and intensifying thermal stress. Therefore, mitigating global warming is the key to alleviating the crisis of declining coral growth in the SCS.

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## Appendix A. Supplementary data

Supplementary Figure (S1–S2), Table (S1–S10) associated with this article can be found in the supplementary materials file. Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.03.135.

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