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Paleo-water depth variations since the Pliocene as recorded by coralline algae in the South China Sea

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ABSTRACT

Coralline algae are excellent archives for recording paleo-water depth, but to date few studies have used them for long-term paleo-water depth reconstruction. This study focuses on the Plio-Pleistocene section of Well CK2, which was drilled in the northern South China Sea. The section consists of 55.2 m of volcanic basement overlain by 873.55 m of carbonates. The chronological framework of Well CK2 has been well established using magnetostratigraphy and bulk sediment strontium isotope ratios. The Plio-Pleistocene section includes the uppermost 341 m (5.18 Ma). Based on observations of 201 petrologic thin sections, we identified nine coralline algae genera (nongeniculate: *Mesophyllum*, *Spongites*, *Lithothamnion*, *Lithoporella*, *Lithophyllum*, and *Hydrolithon*; articulated: *Amphiroa*, *Jania*, and *Corallina*), and five coralline algal assemblages (*Mesophyllum* assemblage, *Spongites* assemblage, *Lithothamnion* assemblage, *Mesophyllum-Lithophyllum* assemblage, and *Lithoporella-Lithophyllum* assemblage). The *Mesophyllum* assemblage dominates in the interval between 341 and 312 m (5.18–4.36 Ma; early Zanclean) and developed in a water depth between 15 and 25 m. The *Spongites* assemblage dominates in the interval between 312 and 309 m (4.36–4.28 Ma; middle Zanclean) and is characterized by subspherical rhodoliths (3 to 9 cm in diameter). This assemblage is probably related to the very shallow (0 to 5 m) water of the distal reef flat/reef crest. The *Lithothamnion* assemblage dominates in the interval between 309 and 200 m (4.28–2.20 Ma) and developed in a reef platform zone at a water depth of more than 25 m. The *Mesophyllum-Lithophyllum* assemblage dominates in the interval between 200 and 80 m (2.20–1.16 Ma) and developed in a water depth between 15 and 20 m. The *Lithoporella-Lithophyllum* assemblage dominates in the interval between 80 and 0 m (1.16–0 Ma) and develops in a water depth of 15 m or less. Our paleo-water depths are basically in agreement with global sea-level variations over time, indicating that paleo-water depths in the South China Sea were controlled mainly by eustatic variations. Based on the relationship between coral reef development and water depth, we further divided the Quaternary intervals into four long-term developmental stages. They consist of two catch-up stages: 1) from 5.18 to 4.28 Ma and 2) from 2.2 to 1.16 Ma; a give-up stage from 4.28 to 2.2 Ma; and a keep-up stage from 1.16 Ma to present. Our results confirm that the coralline algae in the coral reefs of the South China Sea can accurately record past water depth variations.

1. Introduction

Coralline red algae (Corallinales, Rhodophyta) are essential biogenic components in most Cenozoic shallow water carbonate successions from the Eocene to the Recent. They significantly contribute to carbonate production and reef development and are also an important constituent of Cenozoic marine carbonate sequences (Basso, 1998; Bassi, 2005; Bassi et al., 2009a; Braga and Aguirre, 2001; Braga and Aguirre, 2004; Braga and Martín, 1988; Checconi et al., 2007; Kundal, 2011; Liu et al., 2018; Sarkar et al., 2016; Braga et al., 2010; Ries, 2006). Since they are an excellent proxy of paleo-water depth (Braga et al., 2010; Pomar et al., 2017; Coletti et al., 2018), major reef builders, and maintain reef

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stability (Littler and Littler, 2011), coralline algae are extremely important for the geological record (Adey and Macintyre, 1973; Aguirre et al., 2000). They are commonly used to reconstruct the paleoenvironment and paleoclimate, and to analyze paleoecology and paleogeography (Adey and Macintyre, 1973; Aguirre et al., 2000; Bassi et al., 2009b; Bosence, 1991; Braga and Bassi, 2012; Wanamaker et al., 2011).

There are clear relationships between water depth, reef morphology and the role played by coralline algae in the construction of the reef (Adey and Macintyre, 1973; Adey, 1979; Adey, 1986; Perrin et al., 1995). Coralline algae grow on the edge of the outer reef, especially in the strong wave zone, building algal frameworks (Bosence, 1983a; Weiss and Martindale, 2017). When they develop in the shallowest water conditions (just below the reef crest), they can form algal ridges (Steneck et al., 1997) that provide information about sea-level changes in the cm-mm range (Adey, 1986). Coralline algae can also develop as algal cup reefs occurring on the shore and along the margins of the platform (also known locally as boilers or breakers), becoming as large as 30 m long and 12 m wide (Bosence, 1983b; Ginsburg and Schroeder, 2010). In addition, coralline algae can build "trottoirs" in the intertidal zone (Adey, 1986) or "coralligene de plateau" at depths below 20 m (Nalin et al., 2006). The geomorphological features formed by crustose coralline algae (CCA) have been used to reconstruct the paleo-water depth changes in Cenozoic fossil reefs (Braga and Aguirre, 2004).

Since coralline algae are extremely common in reef environments and different algal assemblages can be used to characterize different biozones within the reef, it is possible to use fossil algal assemblages for detailed paleoecological and paleo-water depth reconstructions within reef successions (Bassi et al., 2009a; Coletti et al., 2018; Iryu et al., 2009; Adey, 1986; Braga and Aguirre, 2004; Iryu et al., 2010; Roberts et al., 2010; Kundal et al., 2016). Using coralline algal assemblages identified from the deglacial carbonate sequences in Tiarei, Abbey et al. (2011) described variations in water depth environments from within 10 m to deeper than 20–30 m. Braga and Aguirre (2004) used coralline algal assemblages from the Great Barrier Reef as indicators of Pleistocene water depth and reef environments. In that study, the Corallinales dominated assemblages are associated with the shallowest water depths (within 10 m or even 6 m), while the Hapalidiales dominated assemblages are characteristic of platform zones below 15 m. Iryu et al. (2010) used coralline algal assemblages to reconstruct paleo-water depth in Tahiti reef; the authors recognized *Hydrolithon onkodes* dominated assemblages in shallow settings (less than 20 m), *Neogoniolithon myriocarpum* and *Lithophyllum insipidum* dominance at mid depth (20 to 35 m), and the presence of irregular rhodoliths in deep (more than 50 m) fore reef settings. In the Miocene shallow-water carbonates of the Eratosthenes Seamount, the paleo-water depth was reconstructed by Coletti and Basso (2020), indicating that shallow settings (0 to 20 m) are overwhelmingly dominated by Corallinales, and in slightly deeper settings (20 to 40 m) Hapalidiales are more abundant. In the Great Barrier Reef, coralline algal assemblages dominated by *Lithophyllum* can form algal nodules at depths of 10–12 m (Adey, 1986). Collectively, these various studies in the Indo-Pacific (Payri and Cabioch, 2003; Abbey et al., 2011; Iryu et al., 2010; Braga and Aguirre, 2004) and Mediterranean region (Coletti et al., 2019; Coletti and Basso, 2020) suggest that coralline algal depth distribution is rather constant and stable. Therefore, fossil coralline algae provide detailed characterizations for understanding the behavior and impacts of changes in sea level.

Coral reef evolution is controlled by the combined effects of tectonics, climate change, sea-level fluctuations, and oceanic circulation (Droxler and Jory, 2013; Braithwaite, 2016). Therefore, coral reefs can mark sea-level changes during their development (Bar et al., 2018). This is especially true in the Quaternary period, which is characterized by a succession of large sea-level oscillations caused by the succession of glacial and interglacial episodes (Montaggioni and Braithwaite, 2009; Miller et al., 2005). The evolution of the global environment from a warm and uniform climate state to an extreme climate state of typical glacial-interglacial cycles has greatly enhanced interest in the study of the Plio-Pleistocene as paleoceanography (Jiang et al., 2019, and references therein).

Very few sections are as long as Well CK2 (Fig. 1) from the South China Sea (SCS) and have as sturdy a chronological framework. Thus, Well CK2 is a perfect setting for studying coralline algal assemblages as depth indicators in reef environments. With new and extensive research on the paleoecology of coralline algae in Well CK2, this study aims at: 1) establishing the sequence of coralline algal assemblages throughout the core; 2) understanding the function and environmental significance of coralline algae during the development of the reef; and 3) reconstructing water depth and sedimentary evolution since the Pliocene. Finally, based on a comparison with global sea-level changes since the Pliocene, the development stages of coral reefs in the SCS are reconstructed.

2. Materials and methods

2.1. The study area

The Xisha Islands (Fig. 1), also known as Paracel Islands, are situated on the northern continental margin of the SCS. They are one of the four largest island groups in the SCS. They have a typically tropical marine climate with high precipitation of 1300–2000 mm/yr. The near-surface salinity ranges from ~33‰ to 34‰ (Shao et al., 2017a) and the annual mean temperature ranges from 26 °C to 27 °C (Wu et al., 2018). These conditions are suitable for the development of coral reefs.

The main tectonic element in the study area is the Xisha Uplift, which was subaerially exposed before the Mesozoic and began to subside from the late Oligocene to early Miocene (Wu et al., 2014). The tectonic activity in the study area nearly ceased around 5 Ma (the early Pliocene) (Wu et al., 2014). Existing studies indicate that the carbonate deposition in the Xisha Islands started during the early Miocene (Shao et al., 2017a; Shao et al., 2017b; Wu et al., 2014, Fan et al., 2020), with a relatively wide development during the middle Miocene (Ma et al., 2011), very weak development during the late Miocene, and moderate to active development during the Pliocene and Pleistocene (Shao et al., 2017b). Well CK2 (Fig. 1) was drilled in 2013 on Chenhang Island, Yongle Atolls, Xisha Islands. It has a total depth of 928.75 m from bottom to top and core recovery averages at ~70%. It can be divided into carbonate rock (0–873.55 m) and basaltic and volcaniclastic rocks (873.55–928.75 m). The chronostratigraphic framework used in this study is based on age constraints from Sr isotope stratigraphy and magnetostratigraphy reported in Fan et al. (2020). These sequences are regarded as in situ due to the lack of abnormal Sr dating. According to Fan et al. (2020), the investigated interval from 341 (5.18 Ma) to 237 m (2.6 Ma) is Pliocene and the interval from 237 to 16.7 m is Pleistocene (Fig. 2), which consists of the Yongle Formation, Yongxing Formation, Chenhang Formation, and Shidao Formation (Fig. 4) (Jiang et al., 2019). The sedimentation rate (m/Myr) in Well CK2 was calculated based on the thickness of the reef succession and the age model provided by Sr dating (Fan et al., 2020). The results showed that the sedimentation rate changed little and was relatively low in the Pliocene, while it was relatively high in the Pleistocene.

2.2. Sample description and methods

To study the development of the Xisha Islands reefs and the morphology/sedimentary dynamics of the resulting carbonate platforms, five wells, including Well Xiyong-1, Well Xiyong-2, Well Xishi-1, Well Xichen-1, and Well Xike-1 (Table 1), have been drilled over the last few decades. These wells have provided essential data on the paleontology, petrology, geochemistry, and other aspects of the reefs and carbonate platform. Although calcified algae are abundant in all drilling holes, existing studies on the coralline algae provide mostly qualitative descriptions. There is little further research, especially on paleoenvironmental indicators, due to the lack of materials or of continuous stratigraphic profiles and the rough chronological framework.

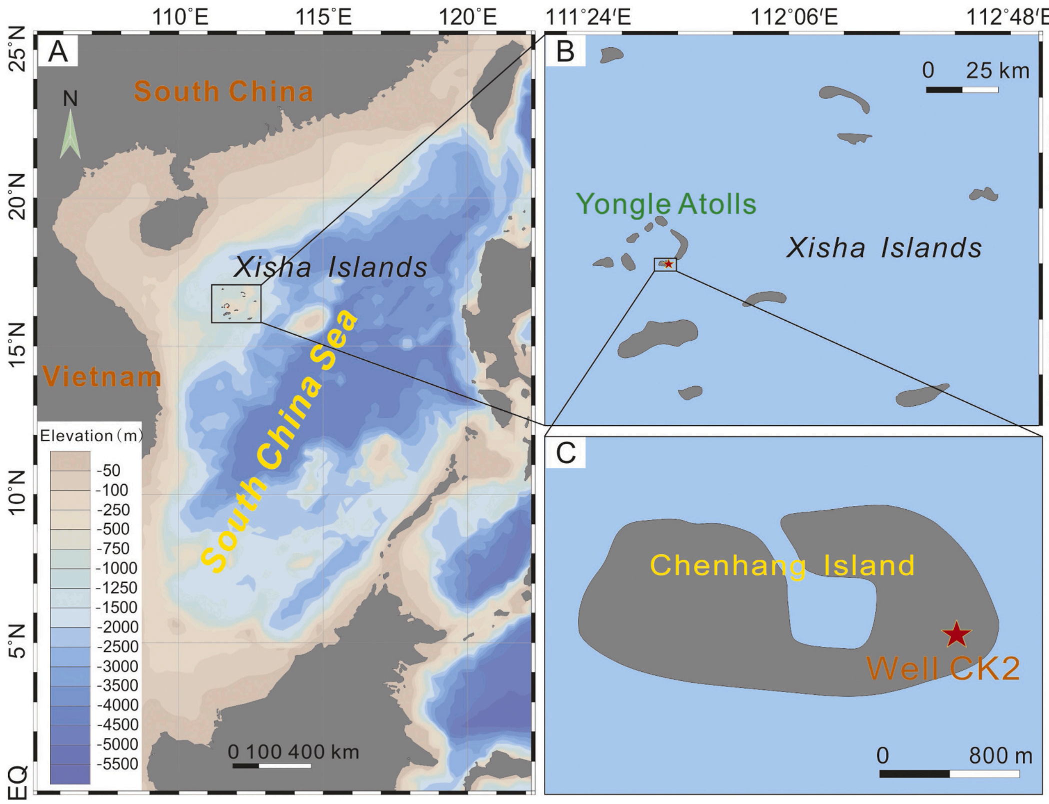

Fig. 1. Red dots indicate the location of the Well CK2 drilling core in the southeast of Chenhang Island, south Yongle Atoll. (A was downloaded from Ocean Data View (ODV)).

The upper 341 m of the core of Well CK2 were sampled every 3 m, resulting in 136 samples. Sixty-five additional samples were collected in coralline algal rich intervals. Two hundred and one standard thin sections (ca. 2 × 3 cm) were prepared with conventional methods from the 201 collected samples. All the thin sections are housed at the Guangxi Laboratory on the Study of Coral Reefs in the South China Sea, Coral Reef Research Center of China at Guangxi University.

Coralline algae were identified in thin sections under a polarizing microscope at the Coral Reef Research Center of China at Guangxi University. The vertical distribution of coralline algae from studied sections was noted and their abundance was quantified using point-counting. Groups were considered dominant when they had an abundance above 50%. Articulated coralline algae were found in only few sections, mostly as fragments. Coralline algal diversity was determined by identifying and counting the number of genera in each thin section. Coral abundance was calculated as the frequency of hand-specimen sized coral fragments found within the core. Among them, "abundant" means that there was one coral per meter; "present" means that there was one coral every two meters; and "rare/absent" means that there was one coral every ten meters, or no coral. The description and growth form terminology for coralline algae used in this study is from Woelkerling Irvine and Harvey (1993). "For-algaliths" is a special morphological fabric formed as a result of interaction between CCA and encrusting foraminifera (Prager and Ginsburg, 1989). The identification criteria of the Microbialites used in this study is from Braga et al. (2019). The classification terminology of carbonates used in this study is from Embry and Klovan (1971). The original data, including coralline algal percent and coral abundance, are shown in the supplementary materials.

2.3. Fossil identification

Traditionally, coralline algae are classified into geniculate (articulated) corallines and non-geniculate or CCA. Over the past few decades, the taxonomy of living and fossil coralline algae has changed significantly, leading to remarkable differences between the two coralline-algal taxonomic systems. However, using certain simple and clear morphological characteristics, it is still possible to recognize the most common genera (Aguirre et al., 2013; Bassi et al., 2009b; Harvey et al., 2003; Woelkerling et al., 1998; Basso et al., 1996; Braga and Aguirre, 1995; Braga et al., 1993; Gall et al., 2010; Harvey et al., 2003; Harvey et al., 2009; Iryu et al., 2009; Kato et al., 2011; Kundal, 2011; Littler and Johansen, 1981; Misra et al., 2009; Rösler et al., 2016; Coletti et al., 2018; Coletti et al., 2019). These characteristics include the size, shape and arrangement of cells, conceptacle diameter and height, conceptacle type, presence of secondary pits, and cell fusions. The position of the conceptacle and the characteristics of its roof and pore canal are also extremely important (Hrabovský et al., 2015). Using these diagnostic characteristics, coralline algae were identified in the 201 thin sections from Well CK2. Corals were identified in hand specimens at the genera level in this study following the taxonomic scheme used by Veron (2000) and Huang et al. (2016).

3. Results

3.1. Variations in biological assemblages

The investigated carbonate sequence of Well CK2 is composed of six distinctive stratigraphic intervals (Fig. 3), which are described in detail below from the top to 341 m based on variations in biological assemblages, coralline algal morphology, coralline algal diversity, coral abundance, and other relevant characteristics. Among them, the biological assemblages are dominated by coralline algae, corals, foraminifera, and other shallow-water carbonate-producing organisms (Fig. 2).

3.1.1. Interval a (0–30 m; 0–0.28 Ma)

This interval is composed mainly of coral gravel and numerous

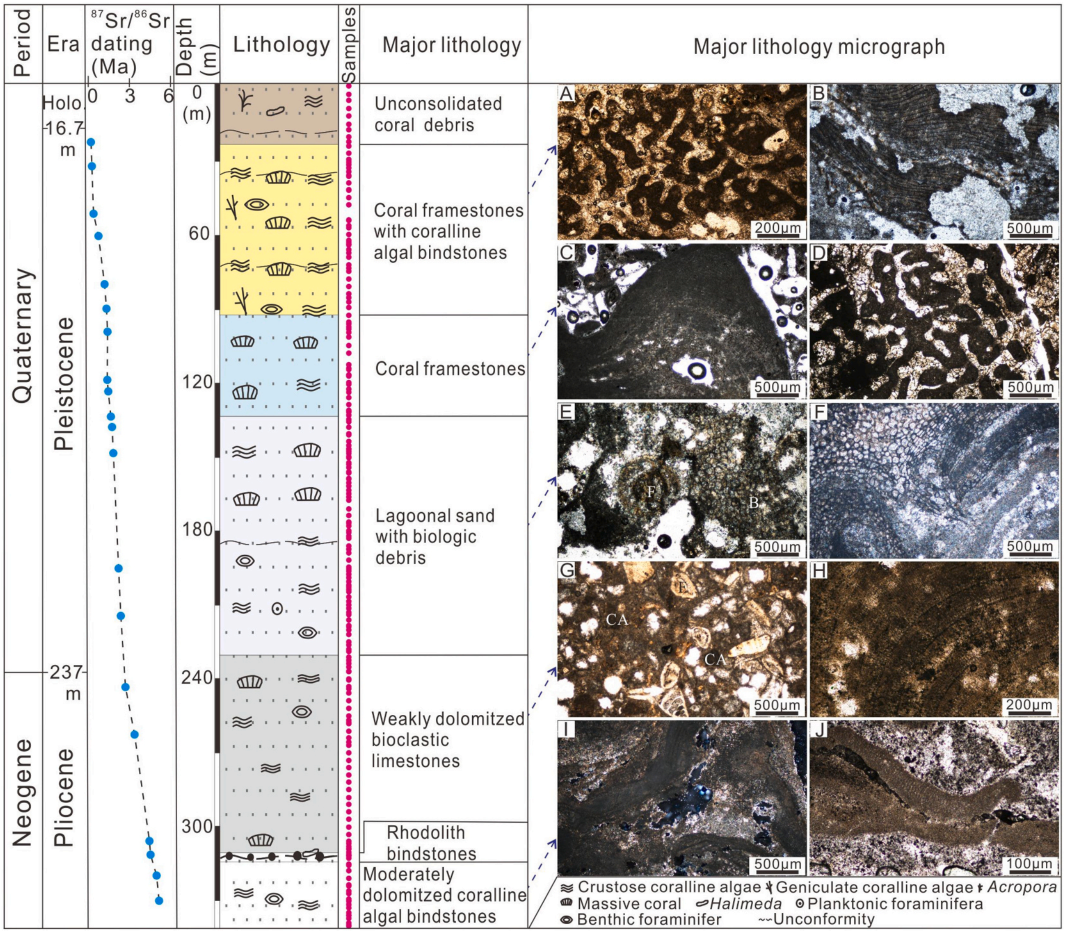

Fig. 2. Lithology and summary of representative micro-graphs of Well CK2. The Sr dating used in this study is from Fan et al. (2020). The red dots indicate the distribution of the samples studied. A Coral framework (Sample CK2-SY021, 64.90 m). B *Lithophyllum* sp. framestone eroded by organisms (Sample CK2-SY017, 54.50 m). C Coralline algae micrite and coralline algae skeleton micritization complete (Sample CK2-SY045, 177.96 m). D Coral framework (Sample CK2-SY041, 113.50 m). E Foraminifer (F) and bryozoa (B) and other flora debris (Sample CK2-SY066, 166.66 m). F Coralline algae and encrusting foraminifer framestones, for-algaliths (Sample CK2-SY070, 176.86 m). G Dolomitized coralline algae (CA), foraminifer and other bioclastic sparite limestone (Sample CK2-SY100, 257.50 m). H Dolomitized unidentified coralline algae limestone (Sample CK2-SY098, 243.50 m). I Micritization coralline algal framestones (Sample CK2-SY111, 323.94 m). J Dolomitized coralline algal framestones formed by *Mesophyllum* sp. (Sample CK2-SY110, 316.00 m), indicating deep water settings. (Each color corresponds to one major lithology).

Table 1
The depths and lat-longitude coordinates of wells in Xisha Islands.

Drilliing	Depth	Latitude	Longitude	References
Xiyong-1	1384.68 m	16°50′ N	112°20′ E	Zhao et al., 2010
Xiyong-2	600.02 m	16°51′ N	112°20′ E	Zhao et al., 2010
Xishi-1	200.63 m	16°50′45″ N	112°20′ E	Zhao et al., 2010
Xichen-1	802.17 m	16°25′24″ N	111°40′ E	Zhao et al., 2010
Xike-1	1268.02 m	16°50′41″ N	112°20′50″ E	Shao et al., 2017a
CK2	928.75 m	16°26′56″ N	111°00′54″ E	This study

branching *Acropora*, with minor amounts of *Halimeda* and coralline algae.

A total of 11 thin sections were made for this interval. Coralline algae (*Lithophyllum*) were observed only at 3.47 m (coralline algal percent 2.2%). The growth form of coralline algae is non-geniculate (Fig. 4), which cement the coral skeletons and other bioclasts. No further details are available because the coralline algal record is relatively scarce and incompletely sampled in this interval (Fig. 3). The algal diversity is the lowest of all the sampled intervals.

3.1.2. Interval b (30–80 m; 0.28–1.16 Ma; *Lithoporella-Lithophyllum* assemblage)

This interval is associated with coralline algal bindstone growing over coral colonies. Thin sections show that the biological assemblage in this section is dominated by corals and coralline algae. Benthic foraminifera are minor components.

The analysis of 28 thin sections displays that the coralline algal abundance ranges from 0% to 41.24% (average 5.54%). The main growth form of coralline algae is non-geniculate (Fig. 4), while articulated coralline algae are rare. The algal diversity is moderate. The common coralline algae genera are *Lithoporella* (Fig. 5E), *Lithophyllum* (Fig. 5A), *Hydrolithon* (Fig. 5C), and *Jania*. The coralline algae consist of the *Lithoporella-Lithophyllum* assemblage. The encrusting *Hydrolithon*, articulated *Jania* and unidentified genera occur sporadically. This interval is the acme zone of *Lithophyllum* (Fig. 2B), where this genus is relatively well-developed.

The corals present in this section (Fig. 3) include numerous massive corals such as *Turbinaria*, *Favites*, and *Platygyra*, some branching *Acropora*, a small number of free-living *Fungia*, and unidentified corals (Fig. 2A).

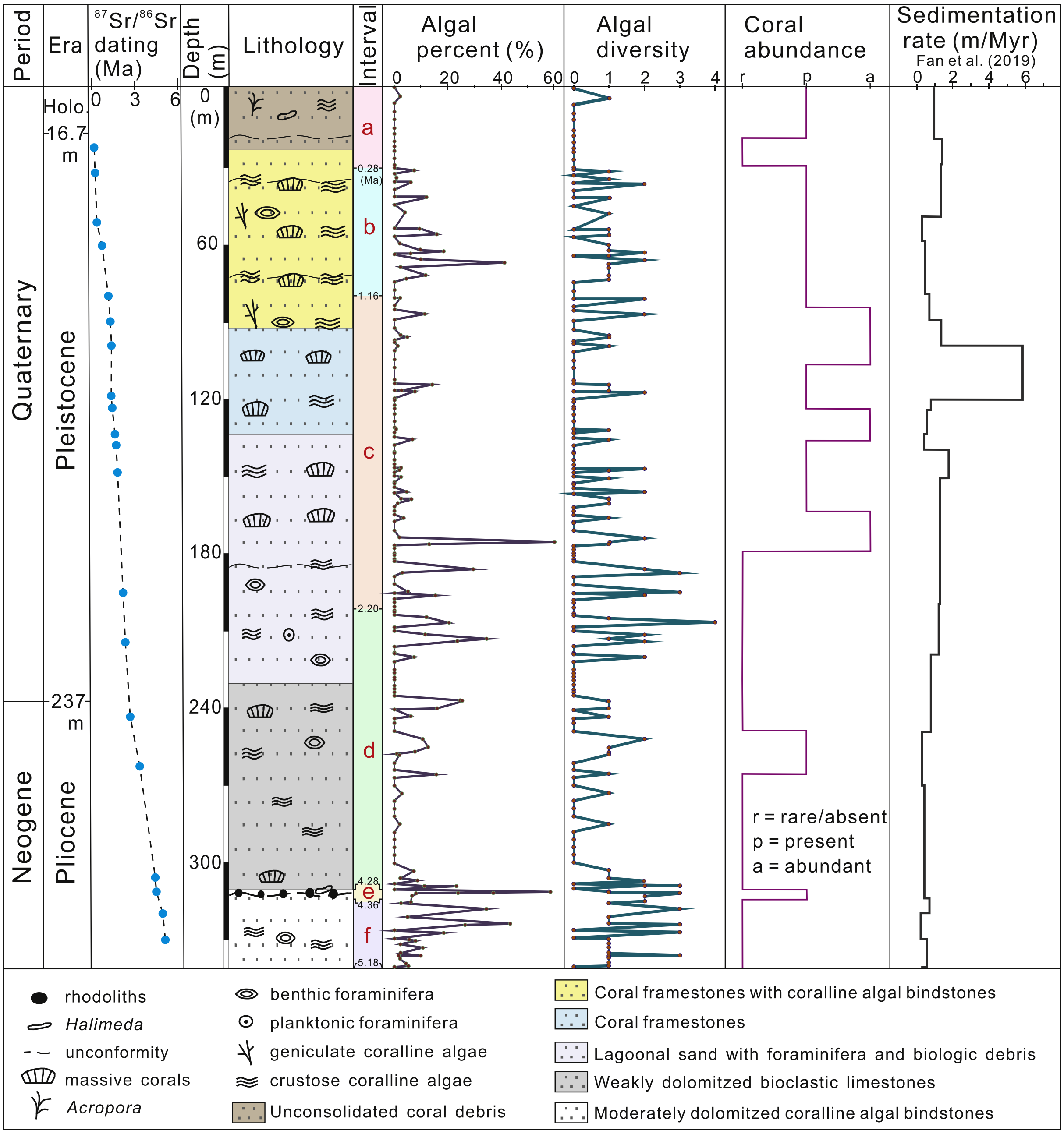

Fig. 3. Coralline algal percent, algal diversity, coral abundance, and sedimentation rate in Well CK2. Algal percent is the total area where coralline algae occupy in each thin section in this study. Algal diversity is the number of genera corresponding to each sample in Well CK2. Coral abundance is the frequency of coral at vertical depths of Well CK2. Sedimentation rate curves are from Fan et al. (2020). The investigated core has been divided into six intervals (Intervals a, b, c, d, e, and f). Every interval has been described including sedimentary structure, biological assemblage, coralline algal morphology, coralline algal assemblage, coral abundance, and other relevant factors.

3.1.3. Interval c (80–200 m; 1.16–2.20 Ma; Mesophyllum-Lithophyllum assemblage)

The coralline algae and corals dominate the biological assemblage. Benthic foraminifera are also important in this interval. In addition, planktonic foraminifera occur sporadically in the basal part of this interval.

The analysis of 77 thin sections reveals that the coralline algal abundance ranges from 0% to 60.33% (average 2.68%). The growth form of coralline algae is mainly non-geniculate, and for-algaliths are a minor component (Fig. 4, 2F). Non-geniculate coralline are distributed in the top and bottom of this interval. For-algalith bioconstructions mainly occur as bindstones and are especially concentrated in an interval between 165 m (1.94 Ma) and 180 m (2.05 Ma). The algal diversity is relatively high, especially in the bottom of this interval (Fig. 3). *Mesophyllum*, *Lithophyllum*, *Jania* and *Corallina* are common coralline algae genera. *Lithophyllum* first appears at 200 m (2.2 Ma) accompanied by *Mesophyllum*. *Mesophyllum* (Fig. 5F) and *Lithophyllum* dominate the algal assemblage. Coralline algal abundance decreases accordingly as corals grow into dominant communities and vice versa, resulting in a clear developmental waxing and waning tendency (Fig. 3).

Coral abundance ranges from present to abundant (Fig. 3), including massive (*Porites*, *Cyphastrea*, and *Galaxea*), branching (*Acropora*), and unidentified genera. *Heliopora* was first found in this unit at an interval of 169.7 m (1.97 Ma). At an interval of 121 m (ca. 1.42 Ma), the sedimentation rate is the highest among investigated intervals where corals are abundant and form relatively thick frameworks (Fig. 2D).

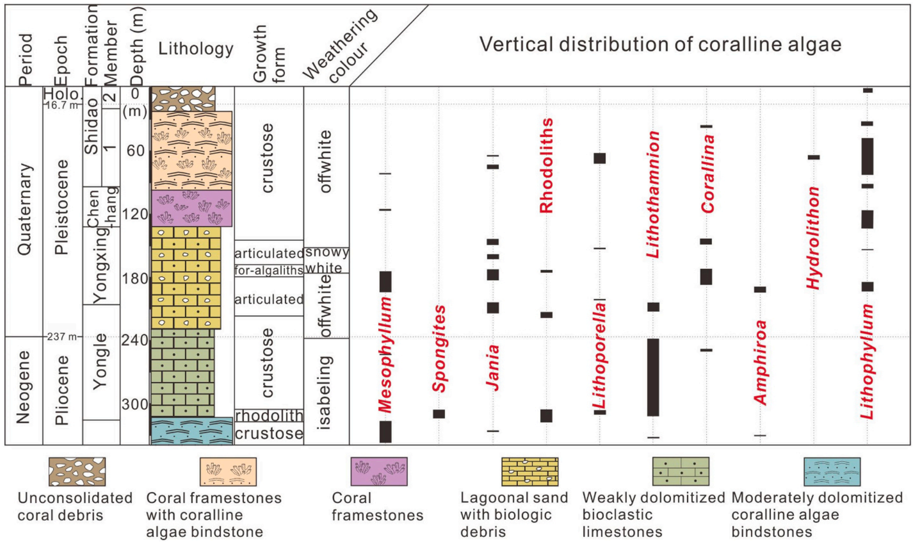

Fig. 4. Vertical distribution of coralline algae in Well CK2. Each bar graph from left to right indicates the order in which each coralline genus appears since the Pliocene. Among them, rhodoliths is a morphologic term and not associated with any specific composition. Undefined genera are not shown in the fig.

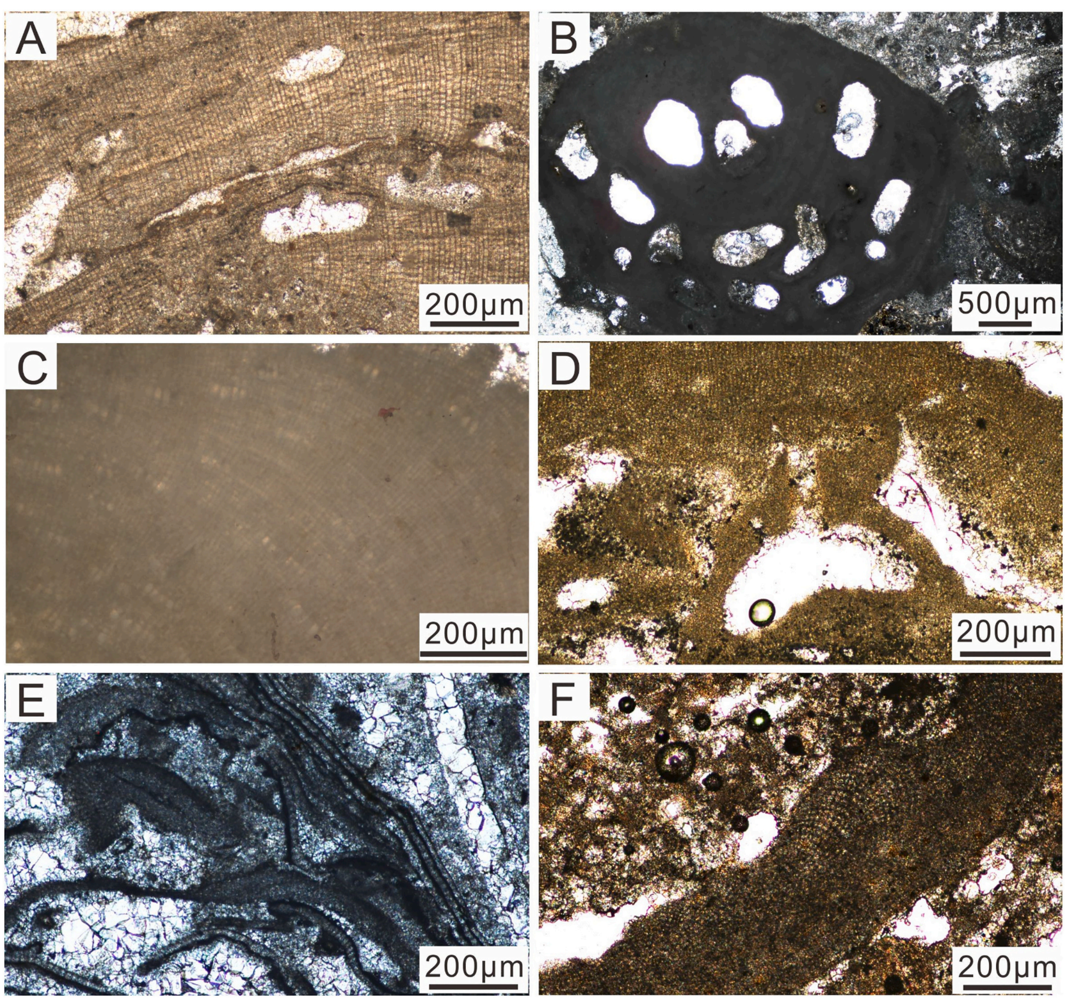

Fig. 5. Typical coralline algae indicating changes in paleobathymetry. A *Lithophyllum nitorum*Adey and Adey (1973) is a relatively common species found in shallow water environments (Sample CK2-P022, 68.00 m). B *Lithothamnium* sp. is found in relatively deeper water conditions (Sample CK2-S107, 324.50 m). C *Hydrolithon onkodes* (Heydrich) Penrose and Woelkerling (1992); Foslie (1909); Basso, 1998 is typical of megacells, indicating shallow water settings (Sample CK2-S022, 66.50 m). D *Spongites* sp. is a genus of the Corallinales, typical of shallow water (Sample CK2-SY108, 312.00 m). E *Lithoporella melobesioides* (Foslie) Foslie (1909) thallus displaying primigenous filaments (Sample CK2-SY008, 32.00 m). F *Mesophyllum* sp. thallus showing monomerous filaments (Sample CK2-SY032, 81.70 m).

3.1.4. Interval d (200–309 m; 2.20–4.28 Ma; Lithothamnion assemblage)

The biological assemblage is dominated by coralline algae. Corals and benthic foraminifera are a minor component. Planktonic foraminifera occur sporadically in the middle part of this interval.

The analysis of 58 thin sections shows that the coralline algal abundance is from 0% to 34.84% (average 4.54%). Most of the observed specimens are non-geniculated (Fig. 4). At 200–221 m, the algal diversity is relatively high, but decreases sharply from the middle (221–286 m) to the basal part (286–309 m) of this interval. The common genera are *Lithothamnion*, *Jania*, and *Lithoporella* (Fig. 4). *Lithothamnion* dominate the algae assemblage. At 222–237 m (2.38–2.6 Ma), benthic foraminifera, planktonic foraminifera, and corals are rare, while coralline algae become less abundant. Microbialites occur at 230 m (2.47 Ma).

Corals in this interval are rare/present (Fig. 3). The common genera are *Turbinaria*, *Porites* and *Fungia*.

3.1.5. Interval e (309–312 m; 4.28–4.36 Ma; Spongites assemblage)

The biological assemblage is dominated by coralline algae and rhodoliths, with important contributions from corals.

The analysis of 5 thin sections indicates that in this interval the coralline algal percentage ranges from 0% to 58.7% (average 23.47%). The coralline algal morphology is non-geniculate (Fig. 4). Relatively large autochthonous rhodoliths with a diameter of ~3–9 cm are well-preserved in the interval. The rhodoliths are mainly laminar (composed of thin layers) or warty. Other encrusting organisms can contribute to the rhodoliths and the nodules can accumulate locally, providing a suitable substrate for the development of algal bindstones. The coralline algae assemblage is dominated by *Spongites* (Fig. 4, 5D). The algal diversity is moderate in this interval.

Corals in this interval are present (Fig. 3), mostly as the massive coral genus *Turbinaria*. Undefined genera accounted for a small percent of fossils in this interval.

3.1.6. Interval f (312–341 m; 4.36–5.18 Ma; Mesophyllum assemblage)

Thin sections show that the biological assemblage is dominated by coralline algae, forming algal framestones (Fig. 2J) with sporadic benthic foraminifera.

The analysis of 22 thin sections indicates that in this interval the coralline algal percent ranges from 0% to 43.48% (average 10.42%). The most common coralline algal morphology in this interval is non-geniculate (Fig. 4). The common genera are *Mesophyllum*, *Spongites*, *Lithothamnion* (Fig. 5B), and *Jania*. *Mesophyllum* dominates the algal assemblage. The algal diversity is the highest of all sampled sections. Corals were not present in this interval (Fig. 3).

4. Discussion

4.1. Coralline algal assemblages in Well CK2 and their use as indicators of water depth changes since the Pliocene

Coralline algae, especially CCA, are common biological components of the studied sections of Well CK2. They grow mostly between corals, other crustose organisms, or other hard substrates. The distribution of coralline algae identified in Well CK2 varies between different intervals, as do the abundance and generic diversity of coralline algae. In Well CK2, the Hapalidiales dominate the coralline algal taxa at 2.03–5.18 Ma (177–341 m), while the Corallinales become the most important coralline algal taxa after 2.03 Ma (above 177 m) (Fig. 6). The changes in coralline algal taxa indicate that the paleo-water depth of Well CK2 has changed from deep to shallow over a long period. The following reef coralline algal assemblages were identified in the Well CK2 intervals: *Lithoporella-Lithophyllum* assemblage; *Mesophyllum-Lithophyllum* assemblage; *Lithothamnion* assemblage; *Spongites* assemblage; and *Mesophyllum* assemblage. By comparing our results with water depths associated with the distribution of modern coralline algal assemblages, we reconstructed paleo-water depth changes in the SCS since the

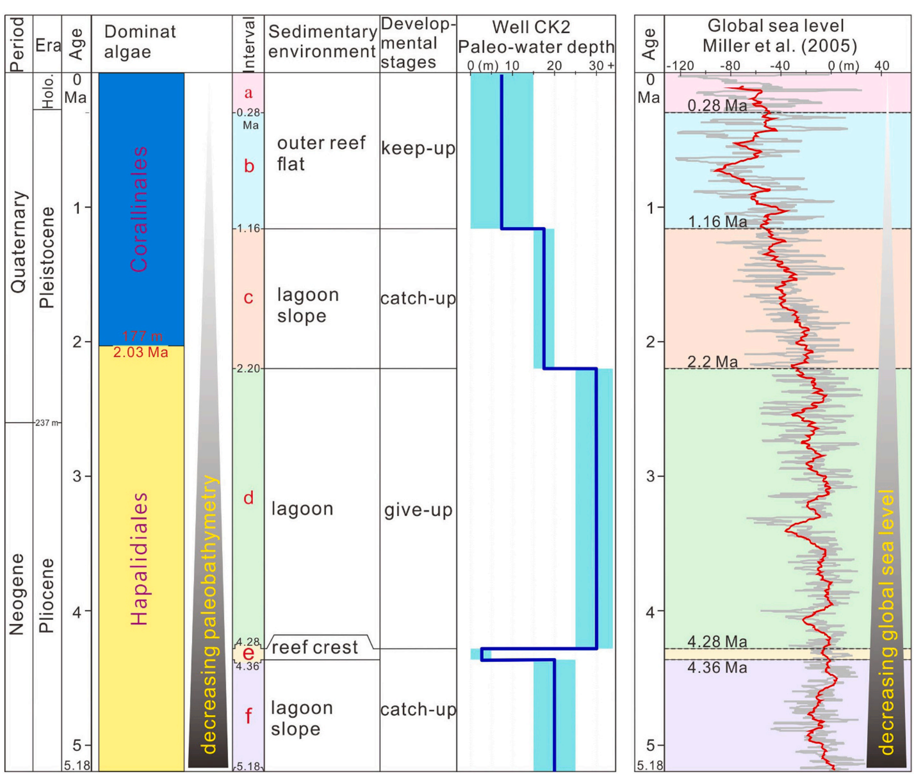

Fig. 6. Paleo-water depth, sedimentary environment, and developmental stage of coral reef estimate based on coralline algal assemblages in the South China Sea. Paleo-water depth is based on the comparison of coralline algal assemblages in Well CK2 with modern coralline algae. Sedimentary environment and developmental stage are results of combination of variations in biological assemblages and paleo-water depth. The eustatic curves are from Miller et al. (2005).

Pliocene (Fig. 6). According to the abundance of coral, we gave a supplementary explanation to the paleo-water depth of the interval where coralline algae were absent. Through the above findings, the sedimentary environment was built in the investigated core.

4.1.1. Interval a (0–30 m; 0–0.28 Ma)

Acropora dominates the biological assemblage with sporadic *Lithophyllum* in this interval. In most of the Mediterranean, *Lithophyllum* attaches to rocks at depths of 10–12 m and forms algal nodules (Adey, 1986; Braga and Aguirre, 2004). This is consistent with indications of mid-high wave energy conditions seen in the Atol das Rocas in the equatorial South Atlantic (Gherardi and Bosence, 2005). As in modern algae in areas like the Mediterranean and the Atol das Rocas, Interval a is likely a shallow water (ca. 10 m) deposit which accumulated on an outer reef flat.

4.1.2. Interval b (30–80 m; 0.28–1.16 Ma; Lithoporella-Lithophyllum assemblage)

Lithoporella and *Lithophyllum* dominate the algal assemblage in this interval, which indicates shallow water conditions. *Lithophyllum* dominated assemblages occur in shallow water in mid- to low-latitude environments (Aguirre et al., 2000; Braga and Aguirre, 2004). *Lithophyllum* can build large "trottoirs" in the intertidal zone of the northern and western Mediterranean (Adey, 1986; Braga and Aguirre, 2001). In most of the Mediterranean, *Lithophyllum* attaches to rocks at depths of 10–12 m and forms algal nodules (Adey, 1986; Braga and Aguirre, 2004). The species of *Lithophyllum byssoides* is widely distributed in the lower midlittoral zone and is found in thin vertical intervals just a few centimeters above mean sea level (Blanfuné et al., 2016). Consequently, the *Lithoporella-Lithophyllum* assemblage is considered to be indicative of a water depth shallower than 15 m. Interval b must also be a shallow water deposit that accumulated on an outer reef flat.

4.1.3. Interval c (80–200 m; 1.16–2.20 Ma; Mesophyllum-Lithophyllum assemblage)

Compared to Interval b, Interval c is characterized by an increase in Hapalidiales and in coral diversity, suggesting a deeper environment. In the Ryukyu Group, the first occurrences of *Mesophyllum* is at about 15 m of water depth (Iryu, 1992), and can be as deep as 30 m (Iryu et al., 1995). The abundance of coral is relatively high in this interval. *Lithophyllum* is also a representative of shallow water environment. Therefore, this algal assemblage may represent a moderate water depth from 15 to 20 m. Interval c must be a deep-water deposit that accumulated on a lagoon slope.

4.1.4. Interval d (200–309 m; 2.20–4.28 Ma; Lithothamnion assemblage)

As the most common genera of the Hapalidiales, *Mesophyllum* and *Lithothamnion* are representative of deep water environments below 20 m, even up to 100 m (Adey, 1986; Braga and Aguirre, 2004). They are reported to occur together below 20–40 m of water depth (Coletti and Basso, 2020). They often grow with each other, but this intergrowth is not found in Well CK2. As suggested by modern coralline algal distribution (Adey, 1986; Lund et al., 2000), *Lithothamnion* generally occur deeper than *Mesophyllum*. Thus, Interval d deposited in deeper water than Interval c. This is also suggested by coral abundance. Interval d displays a reduced coral abundance in comparison to Interval c. The emergence of microbialites at 230 m (2.47 Ma) indicates less-illuminated conditions, another sign of a rapidly deepening environment (Iryu et al., 2010). This further corroborates the deep water sedimentary environment. Overall, this assemblage indicates a water depth of more than 25 m, potentially much deeper. Interval d suggests a deep-water deposit that accumulated in a lagoon.

4.1.5. Interval e (309–312 m; 4.28–4.36 Ma; Spongites assemblage)

Spongites assemblage is characteristic of a very shallow environment, probably the shallowest recorded into the core. This interval also has an apparent unconformity (Wang et al., 2018), indicating that the relative water depth had dropped to the lowest level. This interval probably testifies to a major regressive event in the region. The investigative results of Well CK2 are similar to those of the North Island of New Zealand, where the rhodoliths grow under moderate to strong hydrodynamic conditions and exhibit a spheroidal-to-ellipsoidal shape, indicating a shallow-water environment (Basso et al., 2009). Rhodoliths have been confirmed as the main pioneer flora in the development of new carbonate platforms in southwest New Caledonia (Payri and Cabioch, 2003). Spheroidal rhodoliths can develop only when they reach a balance between regular overturning frequencies, and large rhodoliths are stable even under relatively strong currents (Basso, 1998). Rhodolith morphology together with the dominance of *Spongites*, a genus that is known to occur in very shallow settings (Vidal et al., 2003; Keats et al., 1994), suggest a remarkably shallow sedimentary environment such as the reef flat/reef crest, possibly around 5 m of water depth.

4.1.6. Interval f (341–312 m; 5.18–4.36 Ma; Mesophyllum assemblage)

This interval is dominated by *Mesophyllum* assemblage indicative of a relatively deep water environment, which means that sea level was rising at this time. This genus commonly occurs in deep-water and intermediate depth assemblages and appears frequently in the coralline algal assemblage of the Ryukyu Group (from 15 to 30 m) (Iryu, 1992), the Great Barrier Reef in the Pleistocene (Braga and Aguirre, 2004), the Sommieres Basin in the early Miocene (Coletti et al., 2018), and the modern coral reefs of eastern Australia (Lund et al., 2000). In the early Pliocene corals were rare, or absent. This evidence points to a deep water environment during carbonate deposition on the lagoon slope, probably ranging from 15 to 25 m of water depth.

Overall, the Plio-Pleistocene water depths indicated by coralline algae suggest a process of water depths going from deep to shallow, then shallow to deep, and gradually to final shallow depths. These findings clearly indicate shallowing upward on a long-term scale (Fig. 6).

4.2. The relationship between paleo-water depth in coral reefs of the South China Sea and global sea level since the Pliocene

The high-resolution record of benthic isotope data from ODP Site1146, South China Sea, shows a long-term cooling process accompanied by the intensification of the Asian winter monsoon from ~7 to 5.5 Ma, and temporary Northern Hemisphere glaciations that led to a cooling climate peaking at 6.0–5.5 Ma (Holbourn et al., 2018). This significant event began to reverse in the Pliocene at 5.3 Ma (Sniderman et al., 2016). Meanwhile, eustatic curves also showed significant changes in this time period, rising rapidly from 5.3 Ma to 5.1 Ma and maintaining a long-term highstand level between 5.1 Ma and 3.7 Ma. Overall, the Pliocene global average sea level was about 20 m higher than the present, and the temperature was 2 °C–3 °C higher than the present (Ravelo et al., 2004). After that highstand, sea level dropped gradually with the development of polar ice sheets. During the Quaternary, sea level rose and dropped periodically due to the cyclic retreat and build-up of polar ice sheets (Haq et al., 1987; Miller et al., 2005).

Our results are consistent with the global trends displayed by Miller et al. (2005) in $\delta^{18}O$ curves (Fig. 6). During the Pliocene, the climate was warm and the sea level was higher than it is now. In Well CK2, *Mesophyllum* assemblage is relatively developed in the early Pliocene, indicating relatively deep water conditions. At 4.28–2.6 Ma, *Lithothamnium* assemblage occurs in a deeper water environment. Nevertheless, the lowest paleo-water depth is recorded at 4.36–4.28 Ma, which may be related to a major regressive event in the region caused by a short term fluctuation in global sea-level (Miller et al., 2005). The global sea level fell in the short term at 4.25–4.05 Ma, then began to rise (Miller et al., 2005). Our study shows that *Lithothamnium* became the dominant genus at 4 Ma while the global sea level was rising. During the global climate transition from the late Pliocene to early Pleistocene, the global sea surface temperature (GSST) began to decrease. At 2.7 Ma, the maximum amount of ice in the Arctic ice sheet was reached (Bai et al., 2015). The Pleistocene is characterized by large-amplitude (up to 120 m) sea level change (Miller et al., 2005). At 2.55–2.37 Ma (236–226 m) in Interval d, coralline algae are absent, which may be due to dramatic sea level rise. This is also reflected in the abundance of corals, which are rare/present. The subsidence rate around the Xisha Uplift has not changed significantly since the Pliocene (Wu et al., 2014). Consequently, the paleo-water depths in Well CK2 are mainly the result of the global sea-level changes.

4.3. The relationship between coral reef development in the South China Sea and paleo-water depth

Coral reef systems vary with sea-level fluctuations or water depth, and are extremely sensitive to water chemistry and physical factors (Abbey et al., 2011, and references therein). Corals thus record the past ambient conditions of a region. Studies of coral reef records and sea-level changes have revealed three main types of relationships between coral reef development and sea level (Neumann and Macintyre, 1985, 1) a keep-up stage, which means that coral reefs keep pace with rising sea level. Reef assemblages are composed of shallow water and high-energy biota communities; (2) a catch-up stage, which means that coral reef growth cannot initially keep up with rising sea level but stabilizes after the coral reef growth catches up with the sea level. This reef assemblage usually starts with deep water biota that are gradually replaced by shallower biota assemblages; and (3) a give-up stage, which means that coral reef growth cannot keep up with rising sea level. This situation eventually leads to the phenomenon of slow development or even the drowning of coral reefs. Reef assemblages are usually composed of deep water communities.

In Well CK2, four distinct coral reef development stages were recognized based on the relationship between coral reef development and water depth. These stages included a catch-up stage at 5.18–4.28 Ma; a give-up stage at 4.28–2.2 Ma; a reef growth during a catch-up stage at 2.2–1.16 Ma; and a keep-up stage between 1.16 Ma and 0 Ma. At 5.18–4.28 Ma, this stage was characterized by *Mesophyllum* assemblage indicating deep water being replaced by *Spongites* assemblage indicating shallow water, showing a shallowing upward process, in which the development of coral reef is in a catch-up stage. At 4.28–2.2 Ma, *Lithothamnium* indicated that deep water conditions developed after the interval characterized by *Spongites* dominated rhodoliths. Among them, the relatively high sea levels caused coral reefs to drown and reduced the sedimentation rate (average ~ 57 m Myr^{-1}) at 4.28–2.6 Ma. Especially at 2.55–2.37 Ma, the global sea level rose rapidly, which was indicated by the absence of corals and coralline algae in Well CK2. Overall, this section may represent a time when the sea level was rising too rapidly for the coral reef to catch up, which would be a deepening upward process while the development of coral reef was in a give-up stage. Later (after 2.2 Ma), the coralline algae changed from *Lithothamion* to *Mesophyllum* as the lagoon slope/ramp expanded. With the rapid development of coral reefs, *Mesophyllum-Lithophyllum* assemblage became the dominant flora, indicating a change in water depth from deep to shallow and an increasing sedimentation rate (Fig. 3). After ~2 Ma (175 m), the paleo-water depth had fallen to a level suitable for coral reef development and corals developed in abundance as indicated by shallow-water coralline algal assemblages. During this period, the global sea level was at a relatively stable stage 28 m below current sea level (Miller et al., 2005). A sudden increase in sedimentation rate during the interglacial period ~1.42–1.39 Ma is indicated by abundant coral framestones. At this time the global sea level was 19.7 m lower than the current sea level (Miller et al., 2005). Overall, this sequence suggests that coral reefs developed rapidly in the wake of rising sea levels in a catch-up stage growth trend. After 1.16 Ma, the algal assemblage is mainly dominated by *Lithoporella* and *Lithophyllum*, indicating shallow outer reef flat conditions. The abundance of coral is present. Overall, the development of coral reef was in a keep-up stage. Due to the influence of the glacial-interglacial cycle (Hansen et al., 2013), the development of coral reefs experienced dramatic fluctuations. Nevertheless, the effect of glacial-interglacial cycles on the development of coral reefs will require further in-depth research, especially for the time period after 1.16 Ma.

5. Conclusions

Nine coralline algal genera and five coralline algal assemblages were identified in the Plio-Pleistocene section of the core of Well CK2 from the Yongle Atoll of the Xisha Islands. The *Mesophyllum* assemblage, which developed from 5.18 to 4.36 Ma, is characteristic of deep-water settings. The *Spongites* assemblage is representative of a shallow water (<5 m) reef flat/reef crest that existed from 4.36 to 4.28 Ma. The *Lithothamnion* assemblage indicates deeper water conditions, which may have developed into a platform zone below 25 m after a rapid rise in sea level from 4.28 to 2.20 Ma. The *Mesophyllum-Lithophyllum* assemblage indicates shallower reef settings (15–20 m) from 2.2 to 1.16 Ma, suggesting a shallowing upward of the depositional environment. The *Lithoporella-Lithophyllum* assemblage represents shallow reef conditions (0–15 m) from 1.16 to 0 Ma . At 5.18–4.28 Ma, the overall process of coral reef development in the South China Sea was in a catch-up stage. At 4.28–2.2 Ma, the South China Sea entered a rapid transgressive stage characterized by the dominant *Lithothamnion* assemblage. The development of coral reefs was very slow. Reefs during this period were in a give-up stage. At 2.2–1.16 Ma, abundant corals developed and formed relatively thick reef frameworks. The development of coral reefs was basically in accordance with decreasing sea levels during this period, so the development of coral reefs was in a catch-up stage. After 1.16 Ma, sea level fluctuated dramatically due to the effect of glacial-interglacial cycles. Since then, coral reefs have been in a keep-up stage on a long-term scale. Based on the distributed characteristics of coralline algae/assemblages from Well CK2 in the South China Sea, we concluded that the development of coral reefs in the South China Sea was mainly influenced by the global sea levels and that fossil coralline algae can provide valuable information about paleo-water depths.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

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