

Solenosmilia variabilis-bearing cold-water coral mounds off Brazil

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Abstract Cold-water corals (CWC), dominantly *Desmophyllum pertusum* (previously *Lophelia pertusa*), and their mounds have been in the focus of marine research during the last two decades; however, little is known about the mound-forming capacity of other CWC species. Here, we present new ²³⁰Th/U age constraints of the relatively rarely studied framework-building CWC *Solenosmilia variabilis* from a mound structure off the Brazilian margin combined with computed tomography (CT) acquisition. Our results

show that *S. variabilis* can also contribute to mound formation, but reveal coral-free intervals of hemipelagic sediment deposits, which is in contrast to most of the previously studied CWC mound structures. We demonstrate that *S. variabilis* only occurs in short episodes of < 4 kyr characterized by a coral content of up to 31 vol%. In particular, it is possible to identify distinct clusters of enhanced aggradation rates (AR) between 54 and 80 cm ka⁻¹. The determined AR are close to the maximal growth rates of individual *S. variabilis* specimens, but are still up to one order of magnitude smaller than the AR of *D. pertusum* mounds. Periods of enhanced *S. variabilis* AR predominantly fall into glacial periods and glacial terminations that were characterized by a 60–90 m lower sea

Electronic supplementary material

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level. The formation of nearby *D. pertusum* mounds is also associated with the last glacial termination. We suggest that the short-term periods of coral growth and mound formation benefited from enhanced organic matter supply, either from the adjacent exposed shelf and coast and/or from enhanced sea-surface productivity. This organic matter became concentrated on a deeper water-mass boundary between South Atlantic Central Water and the Antarctic Intermediate Water and may have been distributed by a stronger hydrodynamic regime. Finally, periods of enhanced coral mound formation can also be linked to advection of nutrient-rich intermediate water masses that in turn might have (directly or indirectly) further facilitated coral growth and mound formation.

Keywords Cold-water corals · South Atlantic · $^{230}\text{Th}/\text{U}$ · Computed tomography

Introduction

Framework-building scleractinian cold-water corals (CWC) are one of the most important ecosystem engineers of the deep sea (e.g. Freiwald 2002; Roberts et al. 2006; Frank et al. 2011; Hebbeln et al. 2019; Raddatz and Rüggeberg 2019). The initial settlement of CWCs generally occurs on continental slopes and shelves, seamounts or oceanic ridges (Roberts et al. 2006). CWCs have been able to form reef- and mound-like structures on the European (Roberts et al. 2009) and African (Wienberg et al. 2018) continental margin, the Mediterranean (e.g. Freiwald et al. 2009), the Caribbean and in the Gulf of Mexico (e.g. Hebbeln et al. 2014), on the continental margin off South America in the South Atlantic (Viana et al. 1998; Sumida et al. 2004) and have also been reported from the Indian Ocean (e.g. Western Australia, Trotter et al. 2019) and the NE Pacific (e.g. Lumsden et al. 2007). The main constructors of coral mounds are the framework-building CWCs *Desmophyllum pertusum* (new combination of the former species *Lophelia pertusa* as suggested by Addamo et al. (2016), that still needs further validation) and *Madrepora oculata*. Coral mound development strongly depends on the proliferation of the scleractinian CWC species and is a result of the balance between coral growth and sediment input. Furthermore, coral mounds are typically characterized by a composition of > 50% hemipelagic sediments and loose interspersions of coral fragments and other shell-building organisms (Titschack et al. 2015; Wienberg and Titschack 2017). They can be subdivided into (I) “active” mounds that are characterized by a flourishing coral community and ongoing mound aggradation and (II) “dormant” mounds, which are currently not covered by a vivid coral community and exhibit

no significant mound aggradation (Wienberg and Titschack 2017). Here, we follow the terminology of these seabed structures by Wienberg and Titschack (2017) which implies that all three-dimensional structures formed at least periodically by CWCs are termed coral mounds.

Off Brazil, CWC mounds were reported first by Viana et al. (1998) and Sumida et al. (2004). Since then there is growing evidence that the Brazilian continental slope is an important region of vital CWC habitats characterized by a high biodiversity (Kitahara 2006, 2007; Pires 2007; Pires et al. 2014; Carvalho et al. 2016). In particular, on the Brazilian continental margin *D. pertusum*, *Enallopsammia rostrata* and *S. variabilis* are the known framework-building corals (Fig. 1; Freiwald et al. 2017 and references therein; Pires 2007). CWC mounds along the continental slope are found at intermediate water depth between 500 and 1000 m and are up to 70 m in height and 180–360 m in width (Arantes et al. 2009; Sumida et al. 2004; Viana et al. 1998). Mound formation driven by the growth of the CWC *D. pertusum* is documented during the last 25 kyr in the Campos and Santos Basin (Mangini et al. 2010; Henry et al. 2014). In contrast, little is known about the mound-forming potential of *S. variabilis* corals. In general, *S. variabilis* occurrences have been reported from the Atlantic, Pacific and Indian Ocean (Fig. 1, Zibrowius 1973, 1980; Cairns 1995; Freiwald et al. 2017; Trotter et al. 2019) and are often associated with *D. pertusum* occurrences, but at greater water depth (Zibrowius 1980; Zibrowius, pers. comm.; Roberts et al. 2009; Freiwald et al. 2017). Best studied are the *S. variabilis* occurrences from the SW Pacific in water depths ranging from 220 to 2165 m with densest aggregations between 1000 and 1300 m off New Zealand and Australia (Koslow et al. 2001; Tracey et al. 2011; Bostock et al. 2015; Fallon et al. 2014; Thresher et al. 2014). The environmental controlling factors of modern *S. variabilis* reefs are not well studied. However, *S. variabilis* occurrences appear typically between 3 and 4 °C, which is at least 3 °C colder than flourishing *D. pertusum* mounds (Fallon et al. 2014; Flögel et al. 2014; Gammon et al. 2018). Moreover, *S. variabilis* habitats are found in less aragonite saturated waters (Thresher et al. 2011; Bostock et al. 2015; Gammon et al. 2018) compared to flourishing *D. pertusum* reefs and mounds (Flögel et al. 2014). Nevertheless, whether these different ecological tolerances enable *S. variabilis* to form mounds is unknown. Moreover, a comparison of different framework-building CWCs may further help to constrain factors that promote or inhibit mound formation.

Here, we present a mound that is periodically formed by the CWC *S. variabilis* and (1) reconstruct its temporal development and (2) discuss the environmental controlling factors favourable for its formation. Our study is based on a combination of computed tomography (CT) acquisitions of

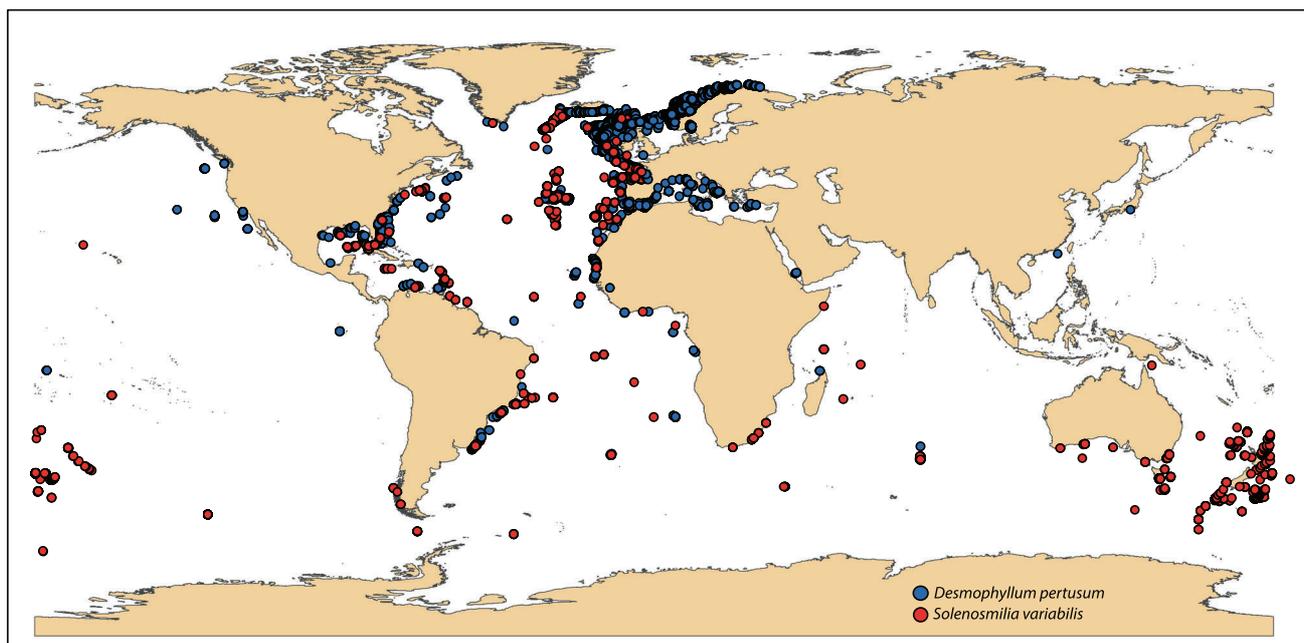


Fig. 1 Global distribution of the scleractinian framework-building cold-water corals *Desmophyllum pertusum* (blue) and *Solenosmilia variabilis* (red). Data taken from various sources: NIWA Invertebrate

Collection; UNEP Dataset, Freiwald et al. 2017; GloSS Dataset, Freiwald (Unpublished)

a sediment core retrieved from the top of a 25 m high mound structure (Bowie Mound, Fig. 2, Bahr et al. 2016) and ²³⁰Thorium/Uranium age determinations on the coral fragments.

Local hydrography

The ocean circulation along the continental slope of South America at 20° S is dominated by the anticyclonic subtropical gyre (Stramma and England 1999; Fig. 2). The Salinity Maximum Water (SMW, 24 °C, $\sigma_\theta \sim 25.2$) forms by excess evaporation in the tropics (Worthington 1976) and is transported westward towards the South American coast by the South Equatorial Current (SEC). The SEC bifurcates upon reaching the South American shelf break at approximately 10°–14° S, continuing northwards as the North Brazil (Under) Current and southwards as the Brazil Current (Stramma and England 1999; Rodrigues et al. 2007). SMW occupies the upper 200 m between 12° S and 22° S (Mémery et al. 2000). River waters mix with SMW in shelf areas to form lower salinity Subtropical Shelf Water (SSW; Piola et al. 2002; Venancio et al. 2014). Below the SMW, steadily decreasing temperatures and salinities (20 °C, 36.0 psu to 5 °C, 34.3 psu) mark the presence of South Atlantic Central Water (SACW) with contributions from formation areas in the southwest Atlantic and the South Indian Ocean (Stramma and England 1999; Sverdrup et al. 1942). The SACW is underlain by the Antarctic Intermediate Water

(AAIW), which bathes the *S. variabilis*-bearing Bowie Mound at 866 m water depth (Fig. 2). Here, the AAIW forms a low salinity layer (< 34.4 psu) due to the subduction of cooled surface water of the Antarctic Circumpolar Current between the Antarctic Polar Front (APF) and the Subantarctic Front (SAF), particularly in the vicinity of the Drake Passage and Falkland Current loop. Some AAIW is also supplied to the South Atlantic from the Indian Ocean via the Agulhas Current (Stramma and England 1999). Upper North Atlantic Deep Water (UNADW) is found below AAIW north of 26° S and can be recognized on the basis of higher oxygen concentrations and salinities compared to AAIW (Mémery et al. 2000).

Methods

During research expedition M125 with the German research vessel METEOR, we retrieved the 5.86-m-long gravity core M125-34-2 (positioning secured by Ultra-Short-Baseline system, POSIDONIA) from the top of the 25 m high “Bowie mound” structure in 866 m water depth at 21°56.957' S and 39°53.117' W located within a province of mound-like structures (Fig. 2, Bahr et al. 2016). CT images were performed for the sedimentological characterization of the deposits and subsequent ²³⁰Th/U age determinations to temporally constrain mound formation phases and determine mound AR. Additional on-board Conductivity-Temperatures Depth (CTD) profiles at the

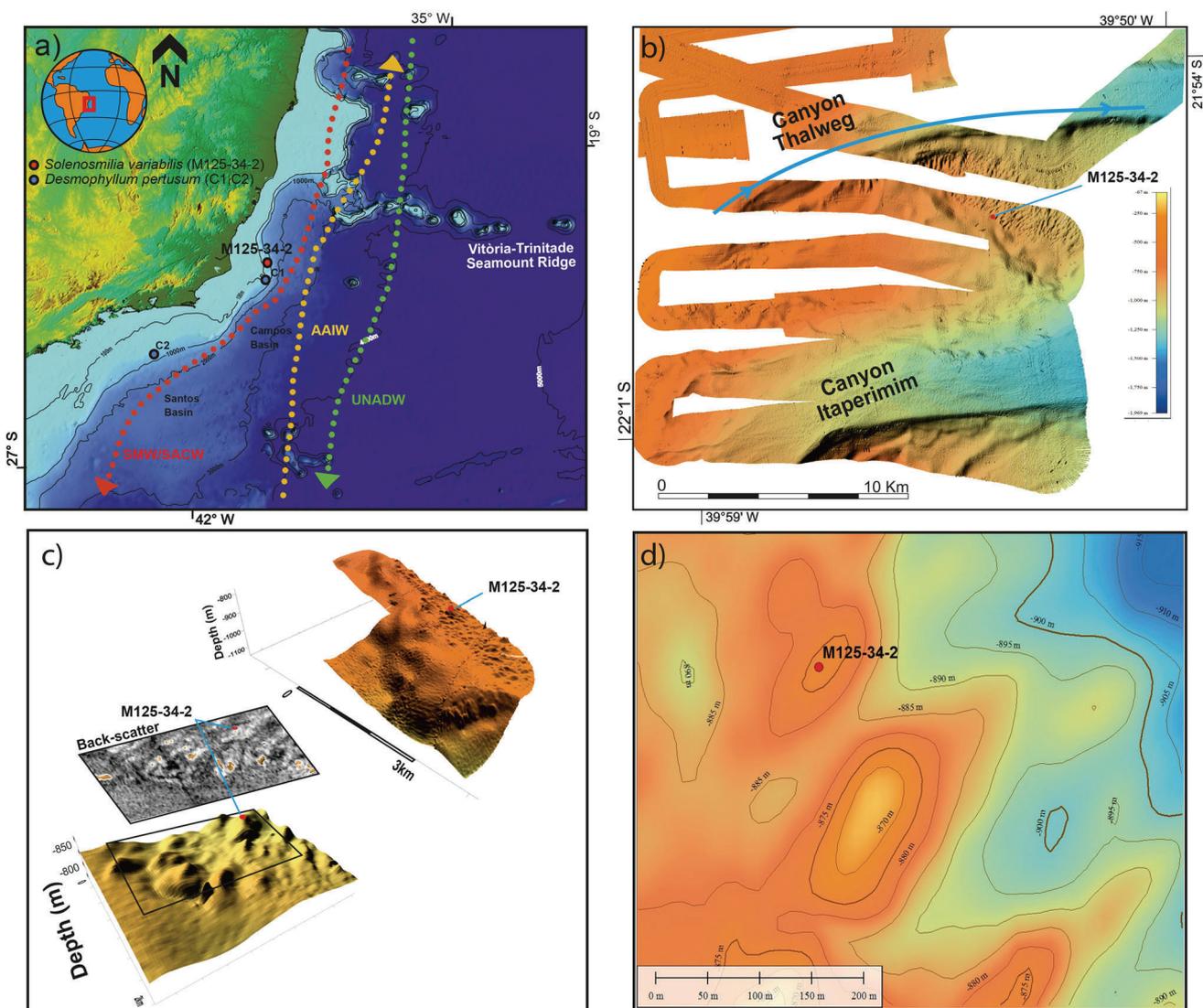


Fig. 2 a Map of study area showing the locations of sediment core M125-34-2 retrieved during research cruise M125 with RV Meteor and two other cold-water coral *D. pertusum*-bearing sediment cores (C1 and C2) investigated by Mangini et al. (2010) and Henry et al. (2014). b Bathymetric map of the coral mound province on the slope of the Campos Basin and the Bowie Mound sampled for this study (Bahr et al. 2016). c Close-up of the bathymetry coral mound

Campos Basin over the Bowie Mound were collected to determine the modern hydrography.

CTD

A down-slope transect of seven CTD profiles were measured with a Seabird SBE 9 device fitted with two temperature sensors, two conductivity sensors, a pressure sensor, an oxygen sensor and a fluorometer together with a Seabird SBE 11 plus V 5.2 deck unit. Data were taken from the downcasts. In addition to the on-board measured seawater parameters, all carbonate system parameters were

calculated from existing global datasets (Global alkalinity and TCO₂; Goyet et al. 2000) with CO₂sys (Lewis and Wallace 1998).

province and the Bowie mound (to right) revealing up to 25 m high mound structures, the resulting backscatter image highlighting differences in the hardness (upper panel, left) of the seafloor and its topography (lower panel, left). d Detailed multibeam map of the Bowie Mound indicating the core location M125-34-2. The bathymetry was generated with an EM 122 and 702 multibeam echo sounder and a parasound system (MBPS, Bahr et al. (2016)

²³⁰Th/U age determinations

The sediment surface of station 34 reveals no living corals, but heavily coated and partly dissolved fossil coral fragments of mostly *S. variabilis*, which were not suitable for ²³⁰Th/U age determinations. Samples from the sediment core were selected according to the depositional intervals with enhanced/reduced coral abundances (Section 2.5)

identified within the CT images. Prior to analyses, all coral samples were cleaned mechanically to remove any contaminants from the skeleton surface (e.g. epibionts, borings, ferro-manganese crusts and coatings) and were then cleaned chemically using weak acid leaching and water rinsing according to the procedure described in Frank et al. (2004), recently updated by Wefing et al. (2017). The measurements were taken at the Institute for Environmental Physics at Heidelberg University (IUP, Germany) on a multi-collector inductively coupled plasma mass spectrometer (ThermoFisher Neptune plus; Wefing et al. 2017). The reproducibility of mass-spectrometric measurements was assessed using the reference material HU-1 (Cheng et al. 2000). In total 36 coral ages have been measured. The ^{232}Th concentrations of all analysed corals ($N = 34$ *S. variabilis* and $N = 2$ *M. oculata*) were always < 4 ppb, which is indicative of minor residual contamination with Th either non-carbonate phases (detritus and coating) or seawater. Nevertheless, a correction for initial ^{230}Th was applied prior to age determination using a $^{230}\text{Th}/^{232}\text{Th}$ activity ratio of 8 ± 4 (e.g. Mangini et al. 2010; Wefing et al. 2017).

The $^{234}\text{U}/^{238}\text{U}$ activity ratio of all the corals (given as $\delta^{234}\text{U}$, i.e. ‰ deviation from secular equilibrium) plot within uncertainty in a narrow band of $\pm 10\%$ compared to the value of modern seawater (146.8‰, Fig. 3, electronic supplementary material, Andersen et al. 2010), suggesting closed system behaviour for the exchange of U between the skeletons and seawater or the embedding sediment matrix. Hence, all ages given below are considered reliable.

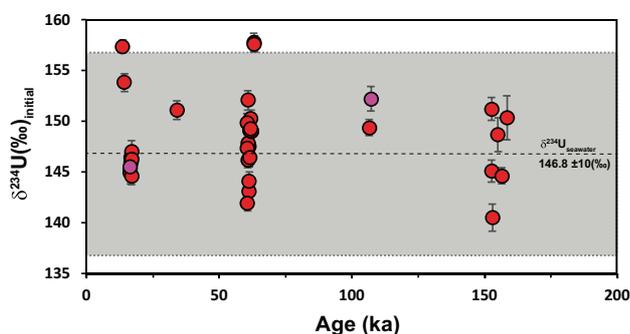


Fig. 3 Calculated $\delta^{234}\text{U}_{\text{initial}}$ of the $^{230}\text{Th}/\text{U}$ dates *Solenostoma variabilis* (red) and *Madrepora oculata* (purple) fragments. All samples plot within uncertainty into the $146.8 \pm 10\%$ envelope (Andersen et al. 2010) and can therefore be considered as reliable. If not visible uncertainties of the $^{230}\text{Th}/\text{U}$ ages and the $\delta^{234}\text{U}_{\text{initial}}$ values are smaller than the dots (see electronic supplementary material)

Computed tomography measurements

Before opening (cut frozen to avoid core disturbances), sediment core sections were imaged using a CT scanner system (SOMATOM Definition Flash) as described in Skornitzke et al. (2019). Briefly, sediment core sections of 1 m in length and 12 cm in diameter were manually aligned with the main axes of the CT scanner's coordinate system using the integrated laser sight system of the CT scanner. Subsequently, image acquisitions were conducted with 140 kV_p tube potential and 570 mAs tube current-time product with a pitch of 0.4. The reconstructions of the images were performed iteratively (ADMIRE, Siemens Healthineers) using a sharp kernel (I70 h level 3), a slice thickness/increment of 0.5 mm/0.3 mm, and an isotropic voxel size of 0.35 mm. Further data processing was carried out according to Titschack et al. (2015) using the ZIB edition of the Amira software (Stalling et al. 2005). Briefly, the measured core sections were virtually reunited and the core liner and artefacts due to the coring process were removed (2 mm of the core rim). Furthermore, coral clasts were segmented and separated with the ContourTreeSegmentation module (threshold: 1400; persistence value: 1150) and macrofossils > 2 cm were visualized as surfaces in 3D (for further methodological details see Titschack et al. 2015).

Results

Local hydrography and seawater characteristics

Maximum salinities of 37.3 psu were measured in the upper 20 m of the study area. Warm (> 20 °C) and saline (> 36 psu) SMW occupies the upper 150 m and below this, a steady decline in both temperature and salinity marks the presence of SACW (Fig. 4). The AAIW salinity minimum (34.3 psu) is centred at ~ 900 m (Fig. 4). The AAIW also exhibits the lowest oxygen concentrations in the study area (< 4.2 mL L⁻¹). An increase in oxygen concentrations and salinity below ~ 1400 m indicate the contribution of UNADW to the deeper slope region (Fig. 4). At the depths of the coral mound (866 m, taken from Station 25-1 and Station 24-1), potential temperature is 4.3 °C, salinity is 34.34 psu, potential density is 27.23 kg m⁻³, and oxygen concentration is 4.60 mL L⁻¹ (Fig. 4; Bahr et al. 2016). The Bowie Mound is thus bathed predominantly in AAIW. According to existing datasets (Station 15041, 39.5° W, 21.5° S, 900 m water depth; Goyet et al. 2000), the AAIW at 900 m water depth has a total alkalinity (TA) of 2287 $\mu\text{mol kg}^{-1}$, dissolved inorganic carbon (DIC) of 2194 $\mu\text{mol kg}^{-1}$, carbonate ion

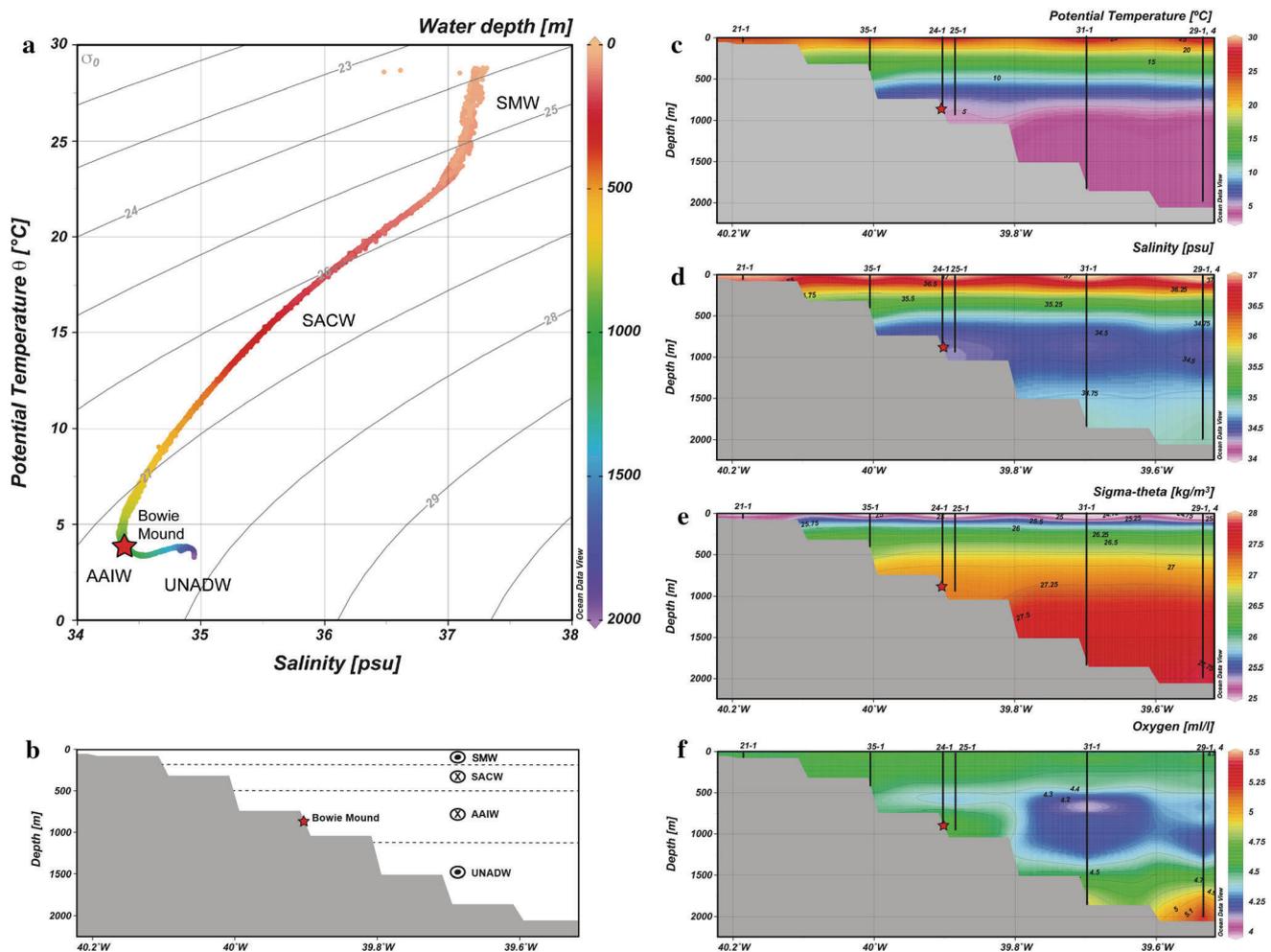


Fig. 4 **a** Temperature–salinity–depth (TSD) plot including isopycnals of σ_θ of the seven CTD casts in the study area. Red star marks the position of Bowie Mound. Identified water masses are Salinity Maximum Water (SMW), South Atlantic Central Water (SACW), Antarctic Intermediate Water (AAIW), and Upper North Atlantic Deep Water (UNADW). **b** Downslope section including depth

concentrations (CO_3^{2-}) of $79 \mu\text{mol kg}^{-1}$, a pH value of 7.97 and an aragonite saturation (Ω) of 1.2.

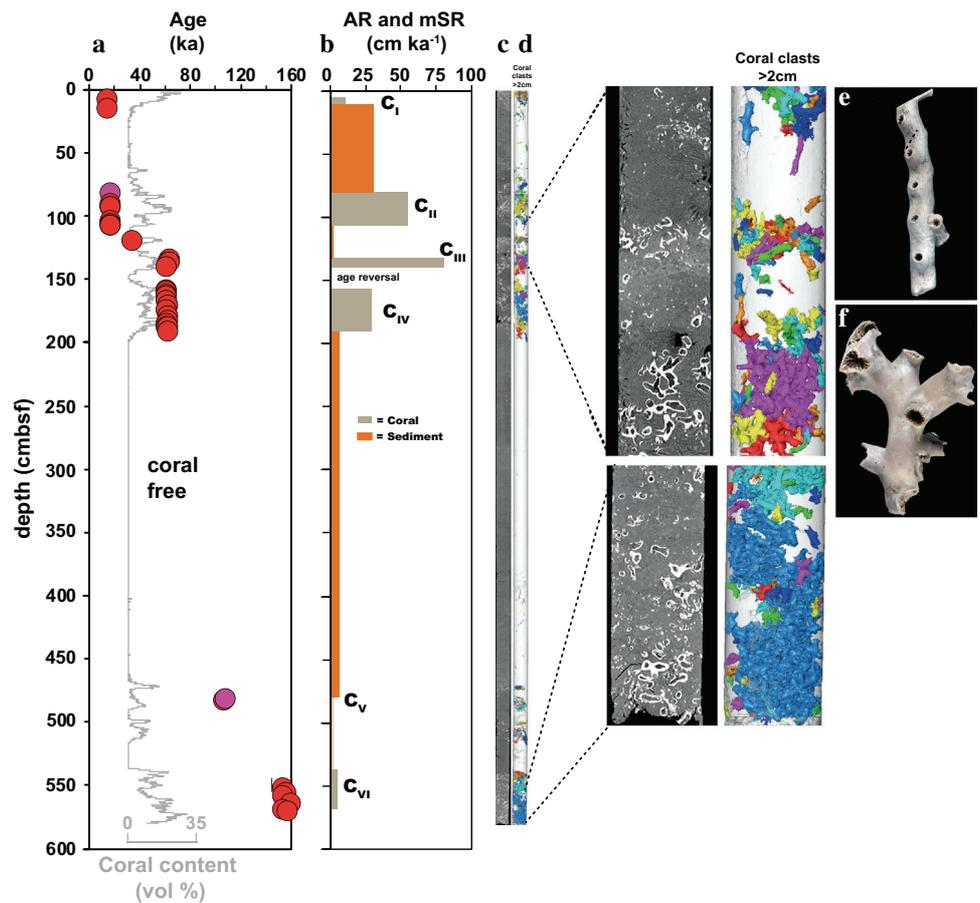
Macrofossils clast size and coral content

The sediment core is characterized by coral-bearing and non-coral-bearing intervals. The sediment is dominantly olive greyish silty clay. Coral-bearing intervals are indicated by the presence of *S. variabilis* and to a minor degree *M. oculata* as the major macrofossils (clast length > 2 cm), whereas other taxa occur only in very rare quantities (bivalves, gastropods, pteropods). Throughout the entire core, the coral content varies between 0 and 31 vol%. Six coral-bearing intervals (C_I – C_{VI}) were identified within the core (Fig. 5). In detail, C_I occurs between 5.5 and 13 cm with an average coral content of 9 vol% and maximum of 19 vol%.

intervals of the ambient water masses and their flow directions. To the right, down-slope sections of the study area showing **c** potential temperature, **d** salinity, **e** potential density, and **f** oxygen concentrations. In each case the red star marks the seawater properties at the depth of the Bowie Mound. Figures were generated using Ocean Data View (Schlitzer 2017)

C_{II} is located at 80–105 cm with an average coral content of 13 vol% and a maximum of 23 vol%. Between 131.5 and 138 cm C_{III} exhibits coral contents of on average 14 vol% and a maximum 16 vol%. C_{III} is separated from C_{IV} by a thin coral-free interval at about 150 cm core depth. Interval C_{IV} (157 cm to 190 cm) reveals coral contents of on average 11 vol% and maximal 23 vol%. The subsequent interval C_V between 479.5 and 480.5 has only a minor coral content of maximal 3 vol%, whereas the last interval C_{VI} from 549.5 to 568 cm exhibits coral contents with an average of 13 vol% and up to a maximum of 31 vol% at 576 cm.

Fig. 5 **a** Downcore $^{230}\text{Th}/\text{U}$ ages of the analysed coral fragments *Solenosmilia variabilis* (red) and *Madrepora oculata* (purple) of sediment core M125-34-2. **b** The calculated aggradation rates (AR) of the different age clusters in cm ka^{-1} (orange) and the coral content in vol% (grey) are plotted against core depth. Note for the calculation of the AR both coral species were used. Also shown are the results of the CT-scans with **c** sediment surfaces images as well as **d** bioclasts > 2 cm. The two smaller figures to the right depict representative intervals of alternating coral-bearing and non-coral-bearing intervals. Below, a picture of the two cold-water corals *Madrepora oculata* (**e**) and *Solenosmilia variabilis* (**f**) with clearly different morphologies, which are identifiable on CT images. Uncertainties of the $^{230}\text{Th}/\text{U}$ ages are smaller than the dots (see electronic supplementary material)



Age constraints

The $^{230}\text{Th}/\text{U}$ ages increase from 13.65 to 158.41 ka with core depth (Figs. 3 and 5) while the identified coral intervals correspond to six age clusters (Fig. 5). The youngest cluster C_I provides ages of 13.65 and 14.34 ka for its 7.5 cm of coral-bearing sediment. The subsequent 67 cm of hemipelagic sediment corresponds to 2.2 kyr according to the coral ages of C_{II} , which span from 16.54 to 17.01 ka. The next 20 cm sedimentation without corals covers a period of > 40 kyr. The following coral-bearing unit C_{III} between 131.5 and 138 cm appears to be of identical or even older age compared to C_{IV} . C_{III} yields four ages between 61.15 and 63.19 ka, whereas C_{IV} (158 and 190 cm) is constrained by 17 dates revealing ages between 60.53 and 62.2 ka, indicating a minor age reversal. Therefore, C_{III} has to be considered with caution (Figs. 2, 5) till additional cores or further seismic data that support this finding become available. Coral from unit C_V yield ages of 106.62 and 107.14 ka and are separated from the previous unit by 3.9 m of hemipelagic sediments deposited again roughly in 40 kyr. The final coral-bearing unit C_{VI} near the core base at 550 cm covers a time span ranging from 152.61 to

156.61 ka (N = 6; Fig. 5; Electronic supplementary material). Overall, short periods of coral growth and mound formation are followed by tens of thousands of years of coral absence, dominated by hemipelagic sedimentation.

Aggradation (AR) and sedimentation rates (SR)

The 36 coral ages obtained build the chronostratigraphic basis to investigate the vertical mound aggradation. We use the concept proposed by Titschack et al. (2015) and Wienberg et al. (2018) for mound formation by framework-forming corals *D. pertusum* and *M. oculata*. Coral-bearing intervals of the Bowie Mound can clearly be identified as they are sharply separated by coral-free deposits. AR were calculated for each coral-bearing interval (including ages from all dated species, hence also *M. oculata* samples) using the youngest and oldest age and the total thickness of the interval. The resulting AR for the coral-bearing intervals are 11 cm kyr^{-1} (C_I), 54 cm kyr^{-1} (C_{II}), 80 cm kyr^{-1} (C_{III}), 29 cm kyr^{-1} (C_{IV}), 2 cm kyr^{-1} (C_V) and 5 cm kyr^{-1} (C_{VI}) resulting in a mean AR of 30 cm kyr^{-1} and a median value of 20 cm kyr^{-1} (including C_{III} , Fig. 5).

The intervals without corals can be assumed to reflect continuous sedimentation for which the minimal rates are given by the age difference of the oldest and youngest coral enclosing the section (matrix sedimentation rate, mSR). In the intervals between the coral-bearing units C_{III} and C_{IV} the prominent age reversal inhibits the calculation of a mSR. Overall, mSR is mostly lower than the coral AR and varies between 0.5 and 30 cm kyr⁻¹ with an mean of 8 cm kyr⁻¹ and a median value of 2 cm kyr⁻¹ (Fig. 5). In detail, mSR is 30 cm kyr⁻¹ between C_I/C_{II} and 0.7–0.5 cm kyr⁻¹ between C_{II}/C_{III} (interrupted by one single coral at 117 cm with an age of 34.034 ± 0.144 ka). Subsequently, mSR varies between 6 cm kyr⁻¹ between coral units C_{IV}/C_V and 2 cm kyr⁻¹ between coral units C_V/C_{VI} .

Discussion

Coral mounds off Brazil: temporal development

The first evidence on the temporal occurrence of *S. variabilis* corals off Brazil presented here strongly supports the findings of Mangini et al. (2010) and Henry et al. (2014) and highlights that CWC mound formation at Bowie Mound shows a tendency to occur in relatively short pulses of < 4 kyr. This is different from the general formation systematics of CWC mounds in the NE Atlantic Ocean where formation phases during the last 500 kyr occur on interglacial/glacial time scales, predominantly during interglacials at latitudes above 45° N and mainly during glacials at low latitudes less than 37° N (Rüggeberg et al. 2007; Eisele et al. 2011; Frank et al. 2011; Raddatz et al. 2014, 2016; Wienberg et al. 2009, 2010) with continuous formation phases of > 50 ka (e.g. Wienberg et al. 2018).

Off Brazil, very little information exists with respect to the growth of framework-forming CWCs and the formation of coral mounds. A first study on the temporal occurrence of *D. pertusum* and *M. oculata* has been obtained by Mangini et al. (2010). They pointed out that corals tend to occur within Termination I and are synchronous with the Younger Dryas (YD) cold reversal and Heinrich event 1 (H1). Similar findings have been made for the Mediterranean Sea (McCulloch et al. 2010; Fink et al. 2015; Taviani et al. 2019; Vertino et al. 2019; Wang et al. 2019).

Desmophyllum pertusum versus *Solenosmilia variabilis*: the influence of the coral species on mound formation

Growth rates of individual *S. variabilis* have been determined to vary between 0.8 and 1.25 mm yr⁻¹ in live caught field samples (Fallon et al. 2014) and between 0.5 and 3 mm yr⁻¹ (1.5 mm on average) in cultivation experiments

(Gammon et al. 2018). These growth rates are similar to the AR determined here (30 cm kyr⁻¹) and for *S. variabilis* reefs on SW Pacific seamounts (21 cm kyr⁻¹; Fallon et al. 2014). In comparison, *D. pertusum* mounds off Brazil exhibit ARs an order of magnitude higher with rates of up to 280 cm kyr⁻¹. The reason for this may be the higher growth rate of *D. pertusum*. Norwegian and last glacial Mauritanian CWC mounds reveal the highest AR of up to 1600 cm ka⁻¹ (Titschack et al. 2015; Wienberg et al. 2018), which is in the same order of magnitude to the growth rate of individual *D. pertusum* with up to 2.7 cm yr⁻¹ (e.g. Gass and Roberts 2011) and therefore may represent maximal CWC mound AR (Titschack et al. 2015). Thus, even though *S. variabilis* mounds are characterized by a reduced AR compared to *D. pertusum* mounds, the Bowie mound may represent nearly maximal AR of *S. variabilis*-bearing coral mounds.

Furthermore, the AR are determined in order to obtain additional information on the processes of mound formation from the species *S. variabilis*. In *D. pertusum* mounds phases of sustained coral growth are characterized by active mound formation and phases when coral growth is absent are characterized by a very low AR or even erosion (Rüggeberg et al. 2007; Frank et al. 2009; Mienis et al. 2007; Titschack et al. 2015; Wienberg et al. 2018). In contrast to most of the previously studied sedimentary *D. pertusum* mound sequences from the North Atlantic and also off Brazil (e.g. Mangini et al. 2010; Frank et al. 2011 and references therein; Henry et al. 2014; Wienberg and Titschack 2017), Bowie Mound sediments reveal intermittent intervals of sediment deposition during phases of coral absence. In particular, Bowie Mound tends to be a sediment mound with punctuated occurrences of corals possibly consolidating the sedimentary environment. This is because the amount of sediment is greater than the coral-bearing units, which is different to *D. pertusum* and *M. oculata* mounds (Fig. 5), in which intervals solely consisting of matrix sediments are usually absent (Frank et al. 2011; Titschack et al. 2015; Wienberg et al. 2018). The calculated mSR at Bowie Mound in such coral-free intervals is considerably lower (8 vs. 30 cm kyr⁻¹) than within coral-bearing intervals. The mSR of matrix sediments is calculated based on the constraining coral ages, which might introduce a slight bias in the calculated SR as previous studies have shown that matrix sediments and corals may exhibit considerable age offsets of several hundred years (López Correa et al. 2012). However, this observation mirrors previous studies from the E Brazilian margin where glacial sedimentation is up to 50 cm kyr⁻¹, and thus an order of magnitude higher than Holocene sedimentation (Mahiques et al. 2004, 2007). During sea-level lowstands, the Brazilian shelf was almost entirely exposed leading to enhanced terrigenous input and increased sedimentation

rates on the outer shelf (Mahiques et al. 2010; Albuquerque et al. 2016). At Bowie Mound, the increased sediment supply during glacial phases is baffled by the CWC framework leading to higher AR. This is well documented for *D. pertusum* mounds, where formation benefits from strong bottom currents (Rüggeberg et al. 2005; Huvenne et al. 2009; Raddatz et al. 2011) that enhance organic matter supply accompanied by increased sediment input, which is baffled in the coral framework causing enhanced mound aggregation (Huvenne et al. 2009; Mienis et al. 2007; Titschack et al. 2015). Therefore, our results may also point to a highly dynamic sedimentation regime, but also highlight that other CWCs, such as *S. variabilis*, have the ability to baffle sediment, resulting in short pulses of relatively rapid mound formation (Fig. 5).

Today bottom currents along the Brazilian shelf peak near 800 m water depth and occasionally exceeds 33 cm s^{-1} associated with the AAIW (Silveira et al. 2004). Therefore, during periods with 60–90 m lower sea-level Bowie Mound may have been exposed to stronger hydrodynamic conditions and a different intermediate water-mass regime that favoured sediment and organic-matter supply to the corals. However, as we are not aware of any flow speed experiments carried out on *S. variabilis*, it is unknown whether high current intensities increase or reduce the growth of *S. variabilis*. *Desmophyllum pertusum* captures food more efficiently under slower flow velocities (Purser et al. 2010) and occurs at sites with flow speeds varying between 5 and 15 cm s^{-1} (Duineveld et al. 2007; Mienis et al. 2007). However, there are also reports of very large *D. pertusum* colonies that were able to survive at very high flow velocities of 60 cm s^{-1} (Mienis et al. 2014). Thus, we suggest that an increase in flow velocities associated with a deepening of the water-mass interface between SACW and AAIW relative to Bowie Mound during glacial periods rather actively supported than diminished CWC growth (see below).

Paleoenvironmental controls on *S. variabilis*-bearing mounds

The present physical properties of the AAIW with a sea-water pH of 7.97, an aragonite saturation (Ω) of 1.2 (Goyet et al. 2000), bottom-water temperature of $4.3 \text{ }^\circ\text{C}$ (Fig. 2; Bahr et al. 2016), salinity values of 34.3 psu and an oxygen concentration of 4.2 mg L^{-1} do not necessarily explain the currently non-active state of *S. variabilis*-bearing mounds off Brazil. Even though framework-forming CWCs may tolerate a wide range of environmental conditions, recent studies demonstrate that flourishing CWC habitats appear to be controlled by very specific environmental and oceanographic conditions (e.g. Dullo et al. 2008; Flögel et al. 2014; Hennige et al. 2014a, b), which appear to be

species-specific (Wienberg and Titschack 2017). However, along the European Continental Margin flourishing CWC reefs and mounds occur in a narrow seawater density range of $27.5 \pm 0.15 \text{ kg m}^{-3}$ (Dullo et al. 2008; De Mol et al. 2011; Rüggeberg et al. 2011; Flögel et al. 2014; Somoza et al. 2014; Sánchez et al. 2014). This density envelope forms due to large differences between two ambient water masses generating a strong pycnocline that favours the accumulation of organic matter from sea-surface productivity and is critical for the food supply to the corals (White et al. 2007; Dullo et al. 2008; White and Dorschel 2010). Periods of enhanced aggradation at Bowie mound predominantly fall into distinct glacial intervals and glacial terminations characterized by a lower sea level of about 60–90 m (Fig. 6; Rohling et al. 2014) implying a deepening of the water-mass boundary between the SACW and the AAIW. Such a water-mass stratification may favour the supply of particulate organic matter (POM) from high sea-surface productivity settling at the pycnocline or water-mass boundaries and then getting distributed by strong internal waves or along-slope bottom currents (Mienis et al. 2007; White et al. 2007; Rüggeberg et al. 2016). On the Brazilian shelf the organic-matter (OM) transport is controlled largely by sea-level changes (Albuquerque et al. 2016) and is locally enhanced due to strong sea-surface productivity (see below). Scleractinian CWCs have been observed in a number of field and laboratory studies to feed on a range of different food sources varying from particulate to dissolved OM (Van Oevelen et al. 2016a, b; Mueller et al. 2014; Gori et al. 2014; Duineveld et al. 2007; Kiriakoulakis et al. 2005). Here, we can only speculate which type of OM may have been the primary source for enhanced CWC growth and thus mound formation. A recent study reveals that the upper and middle slope off Brazil (Camps Basin) between 400 and 1300 m water is characterized by high total organic carbon and labile lipids concentrations (Cordeiro et al. 2018) possibly originating from enhanced primary productivity due to increased SACW upwelling on the continental shelf (Carreira et al. 2012) and thereby providing high food quality for heterotrophic organisms.

High latitude linkages

Enhanced *S. variabilis* mound formation occurs mostly during specific intervals of a glacial period, which are characterized by sea levels of 60–90 metres below present, increased dust supply recorded in Antarctic ice cores and increased Fe input in Southern Ocean sediments (Fig. 6; Rohling et al. 2014; Lambert et al. 2012; Martínez-García et al. 2014). Furthermore, these periods are in turn accompanied by changes in the latitudinal winds zones and high latitudinal upwelling in the South Atlantic (Anderson

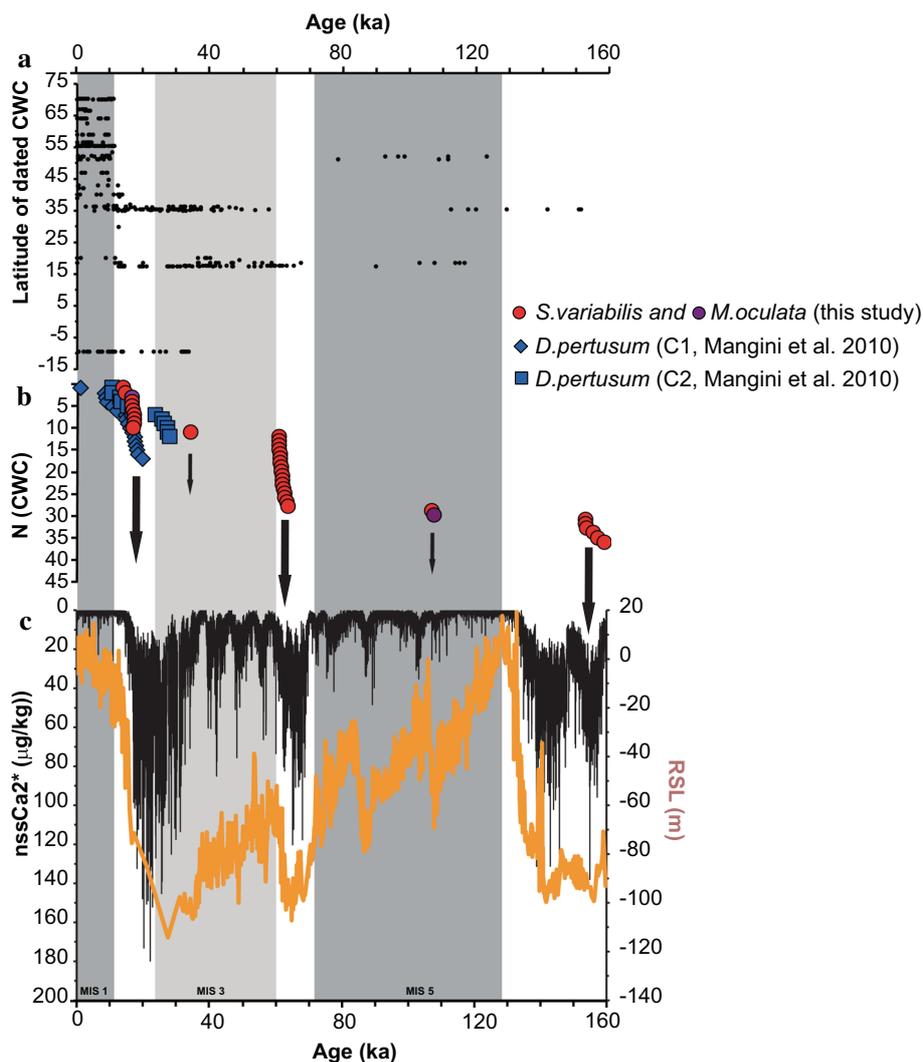


Fig. 6 **a** Corals ages taken from different latitudes are taken from various publications (Lindberg et al. (2005); López Correa et al. 2012; Lindberg and Mienert 2005a, b; Lindberg et al. 2007; Raddatz et al. 2014, 2016; Titschack et al. 2015; Hovland et al. 1998; Hovland and Mortensen 1999; Schröder-Ritzrau et al. 2005; Mikkelsen et al. 1982; Douarin et al. 2013; Mienis et al. 2009; Frank et al. 2009, 2004; Dorschel et al. 2007; Eisele et al. 2011; De Mol et al. 2011; Wienberg et al. 2009, 2010; Wienberg et al. 2018a, b; Frank et al. 2011; McCulloch et al. 2010; Wefing et al. 2017; $N \geq 600$) and are plotted without uncertainties. **b** The coral ages of Mangini et al. (2010, *D. pertusum*, blue) and this study (*S. variabilis*, red and *M. oculata*

et al. 2009). Changes of polar upwelling in the Southern Ocean generally lead to a change in the chemical signature and nutrient enrichment of intermediate water masses (Anderson et al. 2009; Kiefer et al. 2006; Sarmiento et al. 2004; Spero and Lea 2002), which can also be traced at lower latitudes (Poggemann et al. 2017). Nevertheless, there is an ongoing debate, if there was an enhanced or reduced AAIW during glacial periods (Pahnke et al. 2008; Muratli et al. 2010; Ronge et al. 2015).

purple) are plotted as numbers at age. Uncertainties of the $^{230}\text{Th}/\text{U}$ ages are smaller than the dots (Supplementary Table 1). **c** To track changes of the southern High latitude the sea-salt free Ca^{2+} concentration in the DOME C (EPICA) ice core from Lambert et al. (2012, black) is plotted as well as the sea-level curve of Rohling et al. (2014, orange). Black arrows indicate periods of mound formation pulses associated with sea-level stands 60–90 m lower than today and an enhanced dust input at the higher latitudes. Marine Isotope Stages (MIS) boundaries are taken from Lisiecki and Raymo (2005), except for the Pleistocene/Holocene boundary at 11.7 ka (Walker et al. 2012)

However, biogeochemical dynamics such as the carbonate ion concentration and nutrients have been identified to contribute to CWC growth (Davies and Guinotte 2011; Findlay et al. 2014). Furthermore, it was shown that nutrient enrichments make scleractinian corals less sensitive to changes in seawater aragonite saturation (Langdon and Atkinson 2005), similar to what has been shown for food availability in CWC cultivation experiments (Büscher et al. 2017). Hence, it may be reasonable to speculate that such additional nutrient enrichments made Brazilian CWC

less sensitive to the generally CO₂ enriched AAIW (Allen et al. 2015) and thereby fostered CWC mound formation. Moreover, nutrient-rich intermediate water masses may have also fed thermocline waters at low latitudes (Raddatz et al. 2017), especially in upwelling regions (Kiefer et al. 2006; Sarmiento et al. 2004; Spero and Lea 2002). Such a scenario would also have ultimately facilitated CWC growth by increasing sea-surface productivity. Thus, even though the reason remains unclear, our data points to a linkage between Brazilian coral provinces and changes in the biogeochemical dynamics of intermediate water masses of southern origin.

Overall, our findings reveal that also other CWCs besides *Desmophyllum pertusum* and *Madrepora oculata* may at least contribute to the formation of large mound-like structures. However, as this study is only based on one sediment core, there is an urgent need to further sample different mounds (formed by different species) and mound provinces from different latitudes and different water depths along the Brazilian/Argentinian margin to clarify whether SE American coral mounds may have moved their biogeographical limit and/or water depth through time, similar to their North Atlantic counterparts.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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