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Sclerochronogical studies of modern coral cores from Glorieuse Island (Île Éparse): impact of recent extreme events on coral growth

Intermediate report

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1. INTRODUCTION

1.1. The actual knowledge about global changes

It is common knowledge that humans have had a major impact on global change for several centuries. Technological development and modernisation related to the exploitation of hydrocarbon resources are indeed responsible for rapid global warming. These changes are mainly due to greenhouse gas emissions (Calvin et al. 2023), which have been steadily increasing since the industrial revolution (Maktinez 2005). According to the latest IPCC report (Calvin et al. 2023), the surface temperature rose by 1.1 °C between 1900 and 2010. This increase affects the atmosphere, the oceans and the land disturbing their functioning. The number of impacts is countless, particularly on biodiversity and the ecosystem, for example through mass extinctions on land and in the sea (Calvin et al. 2023).

1.1.1. Global changes and repercussions

On the one hand, the frequency of extreme climate events such as droughts and heavy rainfall has increased, as have hurricanes and/or typhoons (Stocker et al. 2013). On the other hand, sea levels have risen due to the expansion of water and the melting of glaciers and permafrost soils (Douglas et al. 2000). These changes disrupt the resilience and resistance of an ecosystem (Patrick et al. 2022) and make it more vulnerable to other threats.

The oceans are considered the second most important carbon sink on Earth (Rehdanz et al. 2006), as they store carbon thanks to exchanges between the ocean and the atmosphere. However, as greenhouse gas emissions continue to rise, the carbon stored in the ocean is increasing, while rising temperatures are reducing the solubility of carbonate in seawater (Mcneil & Matear 2007). These opposing effects increase the impact of ocean warming. In addition, this lowers the pH value of the water and makes it more acidic.

1.1.2. From global scale to local disturbances, human-nature dependency

These global disturbances result in a number of local problems, such as coastal erosion (Leatherman 1990), shifts in community structure in coral reefs (Hughes et al. 2007), destructive fires in Australia (Bradstock et al. 2012), etc. Humans are directly dependent on these ecosystems (Fraser et al. 2003) as they need access to food, shelter and building materials. It is therefore crucial to preserve and protect nature. Unfortunately, this requires a reduction in CO_2 emissions. For example, trying to change consumer behavior can be a solution, especially in developed countries (Dubois & Ceron 2015).

1.2. Coral reefs, key ecosystems for biodiversity and for human services

1.2.1. Coral reef ecosystems

Coral reefs, which make up only 0.1 % of the global earth's surface and about 0.2 % of the ocean surface (Reaka-Kudla 1997), are home to 95,000 described species, which corresponds to 5 % of the world's known species and 35 % of known marine species (Reaka-Kudla 2005). Coral reefs are among the most productive ecosystems on earth (Odum & Odum 1955; Silveira et al. 2017) and can be seen as “rainforests” of the seas. This high production is likely due to an optimal nutrient recycling system supported by sponges (De Goeij et al. 2013) and holothuroids (Uthicke 2001). The three-dimensional growth structure of stony corals also plays an important role in creating shelters and increasing the exchange area between the benthic and open-water compartments (Graham & Nash 2013). Hermatypic (reef-building) corals are the mainstay species of coral reefs, building entire reefs framework and deliver the material for carbonate sediments. Using the photosynthetic ability of dinoflagellate algae called zooxanthellae, corals can utilise autotrophic nutrients, especially for the calcification process (Gattuso et al. 1999 ; Muller-Parker et al. 2015). Corals and algae are in an endosymbiotic relationship which benefits both of them.

All this biotic and abiotic production provides economic goods and services for millions of people around the world (Samonte-Tan 2008). They contribute to livelihoods, food security, security services and tourism, which are estimated to be worth 29.8 billion dollars per year worldwide (Samonte-Tan 2008). For certain countries, coral reefs are an important part of the economy and food supply. However, coral reefs are among the ecosystems that are most sensitive to global change and human impacts (Schellnhuber et al. 2016).

1.2.2. Coral reef threats linked to global warming

1.2.2.2. Coral bleaching

Last but not least, long heat waves can cause stress for the colonies (Anthony et al. 2007; Bigot & Quod 2000). This stress is caused by the release of the algal endosymbiont and the loss of the most important nutrient supply. If the heat wave continues, the coral is at risk of starvation. This is a major threat to all corals around the world and is known as coral bleaching (Vidal-Dupiol et al. 2009 ; Brown 1997), as the coral polyps turn white after shedding their zooxanthella. According to Vidal-Dupiol (2009), the cause of zooxanthellae shedding seems to be explained by the decrease in

Pdc lectin transcription after a severe stress phase. Pdc lectin is a protein that is thought to enable the recognition of Zooxanthella cells. However, there are not many studies looking at the physiological mechanism of this stress response in corals, making a comparison difficult. In 1998, the first global bleaching event was observed, leading to an average decline in hard coral cover from 32.5 % to 30 % between 1997 and 2002 (Souter et al. 2020). Since this event, two more global bleaching were observed in 2010 and 2016 (Moore et al. 2012 ; Hughes et al. 2017). Today, only 19 % of the coral population appears to be left (Tebbett et al. 2023). In addition, high mortality events such as coral bleaching could reduce functional diversity and make this ecosystem more vulnerable (Micheli et al. 2014). The IPCC 2023 report (Calvin et al. 2023) predicts a rise in global temperature of between 1.4°C and 4.4°C in less than 80 years, depending on the emissions scenario (SSP1-1.9 or SSP5-8.5). At this temperature, corals will probably no longer be able to maintain their symbionts and zooxanthellae will die due to frequent marine heat waves (Strychar & Sammarco 2009).

1.2.2.1. Additional global threats

The vulnerability of coral reefs could be compounded by cumulative factors: firstly, the decrease in water pH affects the growth of the hard coral skeleton (Venn et al. 2013) by increasing the threshold for calcareous precipitation (Allemand et al. 2011). Secondly, as mentioned above, climate change will increase the intensity and frequency of cyclones (Stocker et al. 2013). Normally, the recovery capacity of reefs allows them to recover from this type of event (Cheal et al. 2017). In reality, however, repetition weakens their resilience and makes them more vulnerable to future disturbances.

1.3. Lessons from studying coral skeleton

1.3.1. Coral skeletons are an archive of past environment

In this alarming context, understanding and monitoring changes in natural ecosystems is fundamental to determine the impact of humans on the environment. As mentioned earlier, coral reefs are one of the most threatened ecosystems in the world, and learning more about how they function will help us find solutions for their protection and conservation. It also sheds light on the potential impact on other ecosystems. The number of studies looking at the effects of climate change on coral reefs is constantly increasing (Thirukanthan et al. 2023). The study of coral reefs is divided into many fields, e.g. oceanography, evolutionary biology, ecology, geochemistry, etc. This disciplinary diversity allows us to get a global overview of environmental changes from different angles and at different scales.

1.3.1.1. Calcification process

In this study, we will analyse the coral calcareous skeleton, which could be seen in the field of paleontology and geochemistry. Coral calcification consists of the extracellular formation (Johnston 1980) of aragonite layers (Dana 1846). The calcification process takes place between the calicoblastic ectoderm (or sub calicoblastic) and the skeleton (Clode & Marshall 2002) and consists of a chemical reaction between the ion $Ca2^{+}$ and the mainly respired CO_2 (Erez 1978), producing $CaCO_3$ molecules. The calcium-saturated solution causes $CaCO_3$ to precipitate, forming aragonite crystals (Allemand et al. 2011). The Ca_2^{+} ion comes from sea water and is transported via an active ATP pump, the CO_2 from the coral respiration process and a little from sea-water DIC (Dissolved Inorganic Carbon) (Erez 1978 ; McCulloch et al. 2017) (**Annex 1**).

1.3.1.2. Variation in growth parameters

The growth of the coral skeleton depends on the species, the health of the colony and external parameters (Highsmith 1979). Among other things, the temperature of the ambient water plays an important role in the growth of the skeleton (Highsmith 1979 ; Lough 2008). The higher the temperature, the faster the calcification and growth rate, but the lower the skeletal density (Knutson et al. 1972) (**Figure 1**). In addition, it is possible to date corals from different locations by counting the annual density bands (Dodge & Vaišnys 1975; Berkowski & Belka 2008; Knutson et al. 1972) (**Annex 2**). However, during a coral bleaching event, calcification is halted, followed by growth rate (Druffel & Linick 1978 ; Barkley & Cohen 2016). This "stress band" can be recognised by an unusually dense band (**Annex 2**) or cavities, which means that coral polyps have died there.

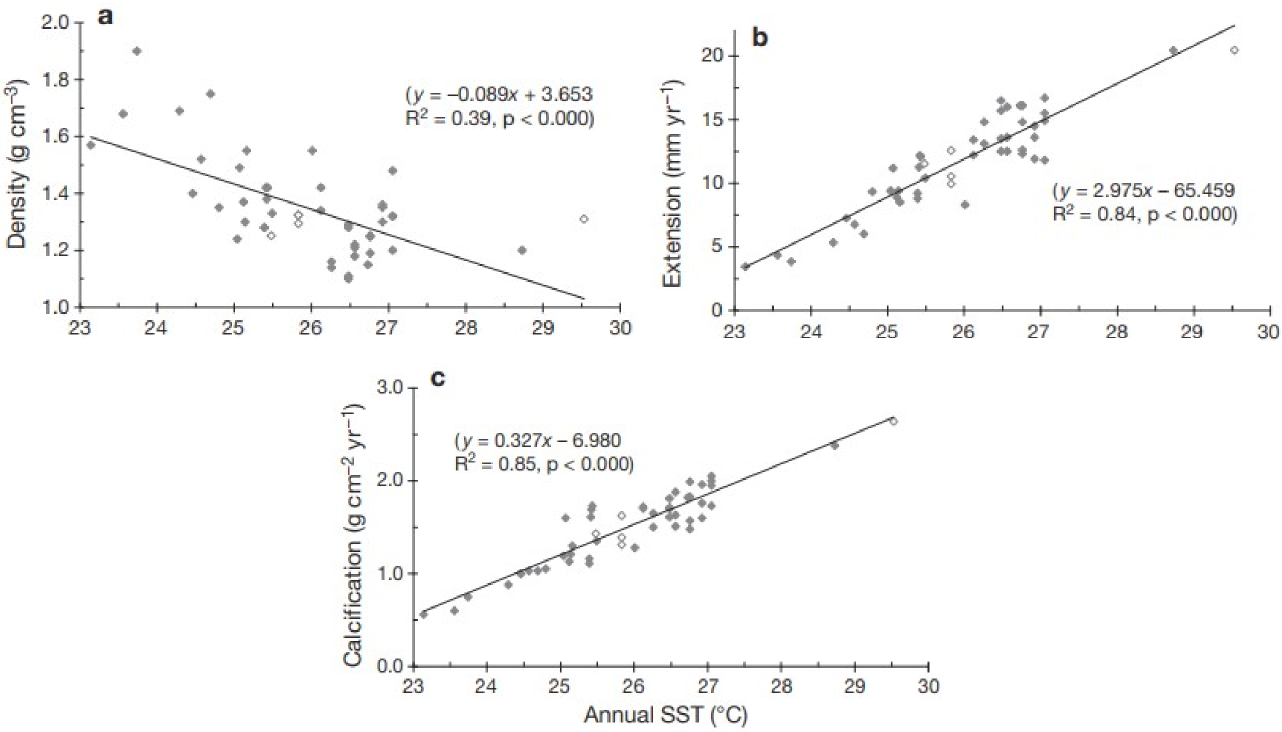

***Figure 1:** Porites spp. Porites growth data averaged across colonies from each of 49 reefs vs. annual average sea surface temperature (SST) for (a) density, (b) extension and (c) calcification. Linear regressions also shown. Open diamonds are data for 4 sites in the Arabian Gulf and 1 site at Lihir Island (figure and caption from Lough 2008)*

1.3.2. Coral skeleton as a SST thermometer

In parallel, it is possible to infer the temperature through the coral skeleton, which enables the reconstruction of past climate over time (Felis & Pätzold 2003). Paleoclimatic archives are important to record the climate in the past, before the global dominance of humans. The Sr/Ca ratio appears to be one of the most commonly used paleothermometers (Grove et al. 2013). When the coral skeleton forms aragonite, some elemental traces (here strontium) may be included in it. Depending on climatic fluctuations, the incorporation of trace elements in coral aragonite can change. Temperature has been shown a negative correlation with the amount of strontium included (DeLong et al. 2007). When the temperature rises, less strontium is incorporated (DeLong et al. 2007). However, not only temperature plays a role in this result, but also the "vital effect" can have a strong influence on it (Grove et al. 2013).

1.4. Indian Ocean is the fastest warming ocean in the world

Compared to other oceans, the Indian Ocean (IO) has the most complex hydrological system with a strong current inversion in the northern and central parts depending on the season (Molinari et al. 1990). Currently, the IO is the most affected by global warming due to rising CO2,(Alory and Meyers) and/or by natural seasonal climate variability such as ENSO and IOD events (Saji & Yamagata 2003 ; Roxy et al. 2014). As the name suggests, the IOD (Indian Ocean Dipole) consists of two poles, one in the west and one in the east of the IO (Saji et al. 1999). When the IOD is in the negative phase, the SST rises on the east side of the IO, while it cools on the west side. In contrast, the positive phase consists of an inversion of the pole, whereby the western pole is hotter than the eastern pole. These fluctuations are closely linked to ENSO variations (Stuecker et al. 2017) and affect local human and natural ecosystems. They are the cause of monsoons floods and droughts, cyclonic events and also significant heatwaves. For example, the first human-observed global coral bleaching events in 1998 coincided with strong El Niño events (Aronson et al. 2000) (**Figure 2**). During this positive ENSO phase, the water of the equatorial Pacific warms up strongly (Wang et al. 2017). Extreme drought events occurred in Australia (Chiew et al. 1998), causing forest fires and extreme local coral bleaching. The IPCC report (Calvin et al. 2023) predicts that inter-annual climate fluctuations such as ENSO or IOD events will increase with global change. The main problem for coral ecosystems is the heat packs that these events cause (**Figure 2**).

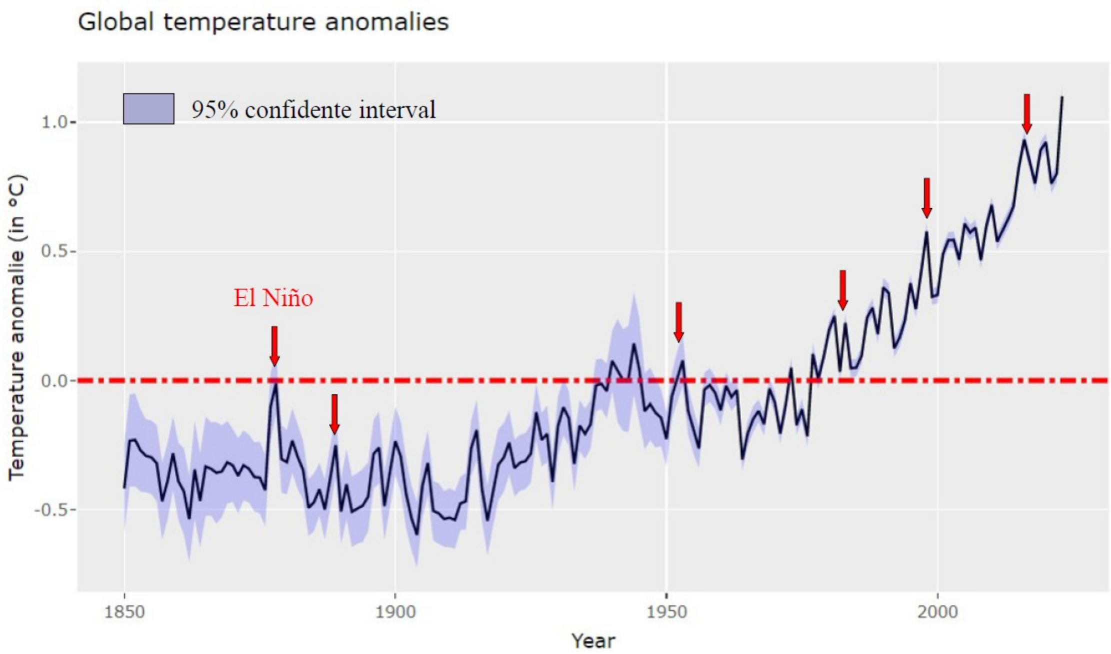

Figure 2*: Global temperature anomalies average since 1851. Red arrows represent strong El Niño events. From Felis & Pfeiffer (2016)*

1.5. Aims of this study

Most of the studies on coral reefs to date analyse some human-disturbed sites, which makes it difficult to isolate the effects of global change. The destructive impact of humans is a major threat to all types of ecosystems. Due to the coupling with other disturbance factors, both impacts cannot be clearly identified. The only way to identify only the effects of climate change is to analyse a reef that has not been impacted by humans. This type of site still exists today. For example, the French overseas territories, the so-called "Îles Éparses", are off-limits to most people. Furthermore, some marine protected areas have been established to preserve fish stocks and avoid human impact. This study therefore focuses on one of these islands, Glorieuses Islands, which has been protected by a marine nature park since 2012 (Ministerial Decree No. 2012-245 of February 22, 2012; Durville et al. 2004), and has limited access for research. Due to their importance for the reproduction of turtles and seabirds (Bocquet et al. 2016) and their protection from human impact, these islands are key areas for marine and terrestrial biodiversity, but also for studying the effects of global warming (Quod et al. 2007). However, the threat of global warming in this area is high due to the strengthening warm current from the south of the channel (Quod et al. 2007). The reef, which is mainly composed of hard corals and calcareous algae (Halimeda sp.) (Chabanet et al. 2016), has some long-lived massive corals (Porites sp.). The study of the growth of these colonies could make it possible to trace the local disturbances before the beginning of global warming. The aim of this study is therefore to capture the impact of rising temperature on coral growth and the response to heatwaves, by analysing the fluctuations in the density and composition of coral skeletons from Glorieuses Islands.

First, the CT scan method will be applied to coral cores to analyse and estimate growth and density fluctuations over a long period (1880 to 2019). Thanks to the length of the coral core (4 m), it is possible to cover a period of more than 100 years, which is a first for the western Indian Ocean. Next, we will analyse the effects of global warming by identifying the stress bands and tracking the frequency of their occurrence. We expect the frequency of stress bands to increase over time. This should reflect the increase in frequency and intensity of heat waves in the Indian Ocean. In parallel, the temperature will be estimated using the Sr/Ca ratio of the most recent sections to determine the temperature. We also plan to measure the temperature during the stress period using the stress bands via Very high-resolution laser analysis. This will allow us to determine a potential SST threshold for the corals of Glorieuses Islands. An increase in the SST bleaching threshold could be related to coral acclimatisation and/or adaptation to global warming (DeCarlo et al. 2019). The inter-annual events such as IOD and ENSO seem to play an important role in the occurrence of heat waves, so this study will also try to observe and understand their effects on coral growth and composition. Finally, special care will be taken to ensure that all analysis are as reproducible as possible to facilitate future coral core studies.

2. MATERIAL & METHOD

2.1. Study area

Glorieuse Islands are an archipelago in the west of the Indian Ocean (11°29'S, 47°23'E), more precisely in the north of the Mozambique Channel (Durville et al. 2004). This archipelago consists of two main islands, the "Grande Glorieuse" and the "Île du Lys", and is part of the five "Îles Éparses". This study focuses on the island of Grande Glorieuse, where the sample was taken. This island has an area of about 4 km2 and the marine habitat of the archipelago is characterized by fringing coral reefs and extensive shallow lagoon reefs between the islands (Chabanet et al. 2016) (**Figure 3**). The composition of the benthic compartment is unique compared to other Îles Éparses due to the dominance of the calcareous algae Halimeda sp. (Schleyer et al. 2018 ; Chabanet et al. 2016 ; Quod et al. 2007) and the higher presence of vertebrates. Among the corals, Chabanet et al. (2016) found 131 species of hard corals, while Quod et al. (2007) found between 40 and 90 species. However, the hard coral diversity of the Glorieuses is less significant than that of the neighboring reefs (Quod et al. 2007). This can be explained by the fact that the presence of a lot of sand sediment makes the installation of larvae more difficult (Moeller et al. 2017). About the ichthyological compartment, Glorieuses has the lowest diversity and biomass of fish compared to the other Îles Éparses (Chabanet et al. 2016). **Annex 3** from Chabanet et al. (2016) shows the distribution of the different compartments across all Îles Éparses.

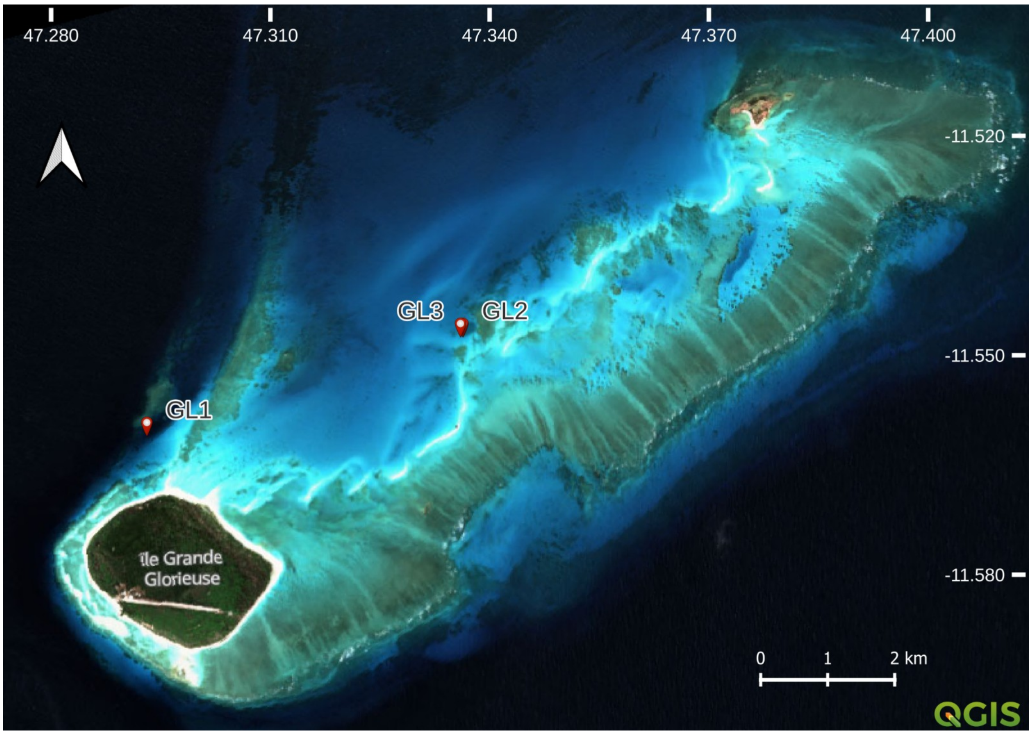

Figure 3*: Satellite picture of Glorieuses archipelago with locations of coral core samples*

2.2. Coral core's samples

The coral cores were taken as part of the Climate Eparse project led by Pr. Dr. Henrich Bruggemann and in collaboration with TAAF, CNRS, IRD and IFREMER. The main objective of this project is to study the evolution of SST during the last 300 years and the last millennium, and then to study the response of corals to these changes. Between April 4 and 30, 2019, a mission was carried out on board Marion Dufresne to study all the reefs of the Îles Éparses. Three Glorieuses coral cores of a multi-centennial colony of Porites sp. with a length of 60 cm (two cores) and 4 m were drilled with a drilling diameter of 8, 3.5 and 3.5 cm respectively (**Annex 4**). The pneumatic drill was operated with air tanks. The locations of the individual colonies are shown in **Figure 3**.

2.3. CT scan method

The CT scan method will be used to analyse the density variations of the coral skeleton. This method is non-destructive, allows visualisation of annual bands, the estimation of density, growth rate and calcification rate. In addition, stress bands can be clearly visualised. The core will be scanned at the Molecular Imaging North Competence Center (MOIN CC) of Kiel University thanks to the VivaCT 80 micro-CT (Scanco). The output is in the form of horizontal sections with a voxel resolution of 20 microns (DICOM files). The output unit is HU (Hounsfield units), which measures the radiological density of the structures observed in CT images (Hounsfield 1973).

2.4. CT scan analysis

The top of the core has already been scanned and preliminary anlysis has been done. CT files were compiled for visualisation using Fidji (ImageJ 1.54f) (Schindelin et al. 2012). To identify skeletal variations in density, orthogonal tools were used to obtain tangential slices (**Figure 4**). The dark areas represent low density and the white bands represent high density (negative). Since the density of the coral skeleton varies as a function of SST temperature, an alternation of white and dark bands is considered as one year. With this method, date estimates for the entire core can be made with an accuracy of one year. On the other hand, the density estimation was made thanks to Dr. Watanabe, who had previously calibrated the HU result to the density for current settings (**Figure 5**). Indeed, it is important to mention that the output values strongly depend on the scan settings (DeCarlo 2017). For replication, copy the details of the setting, or do not use the calibration presented here.

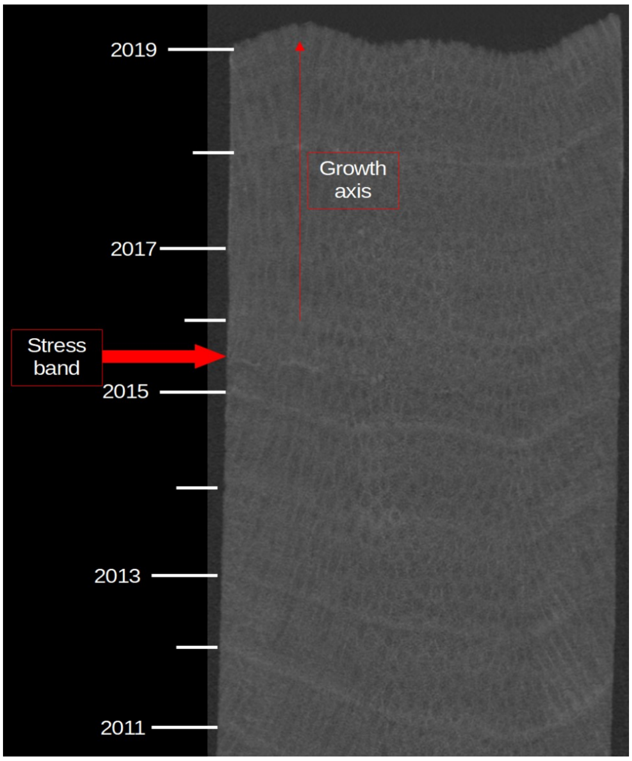

***Figure 4**: Same as figure 4. Showing the growth axis in tangential slice of top GLOM2 Coral core. To define growth axis, we observe the location of vertical polyps.*

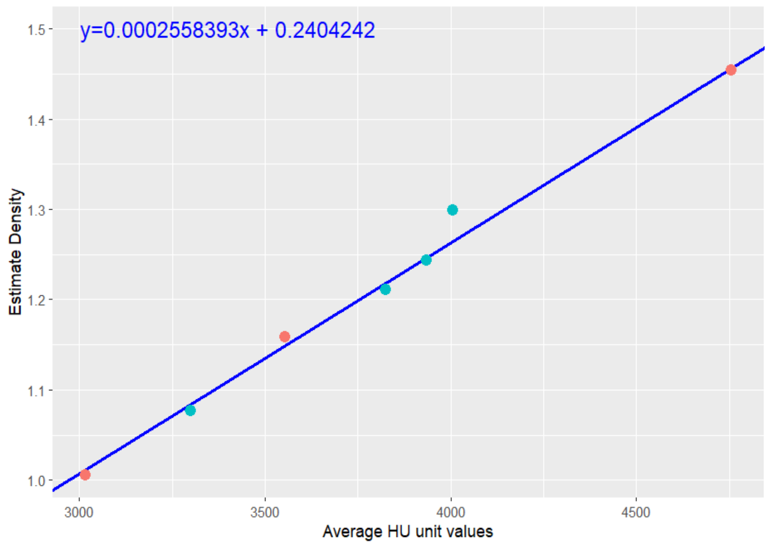

***Figure 5:** Density calibration graphic. Blue line represente the lineare regression between Estimated Density and Average HU unit values*

To illustrate the density fluctuations over time, some profile plots were created by drawing 50 pixel thick lines along the growth axis. In addition, the growth rate (in $mm.y^{-1}$) was estimated each year by measuring the length of each alternating high/low density band. Finally, the calcification rate (in $g.cm^{-2}.y^{-1}$) was calculated by multiplying the growth rate by the density. For each year, 6 replicates were performed to estimate the average and distribution.

As for the stress bands, the intra-annual bands with high density and/or traces of mortality were good indicators of coral bleaching. These positions were used for dating and all previous parameters were calculated. A comparison was made with IOD/ENSO events and stress band dating to observe the potential effects of seasonal climate events on coral skeletal density and to determine if there is a correlation with bleaching events (by stress bands).

2.5. Statistical analysis

The statistical analysis was performed with the R 4.3.1 language (R Core Team 2017) using the Rstudio 2023.03.1 interface. First, the most recent density bands were compared with the past bands. Twenty-year classes were formed and compared using PERMANOVA analysis. The classes are then compared in pairs. The same analysis is performed for the growth rate and the calcification rate. Statistical modelling is also planned to find relationships between skeleton growth and climate parameters. For the Sr/Ca ratio data, comparison with density will be done.

2.6. Strontium/Calcium ratio

A novel ICP-OES method with laser ablation will be done to determine the Sr/Ca ratio, and then the infer SST and the bleaching threshold in stress bands. Some powder samples will be taken with a micro-drilling machine with a resolution of 0.5 mm per drilling point. Thanks to the inductively coupled argon plasma, the powder is vaporized and emits a photon of a specific wavelength, which is received by the ICP-OES instrument (Kasper 2008) (see **Annex 5** for details of the method). First, a calibration will be performed by comparing the Sr/Ca ratio with a recent satellite database (NOAA). The average of all stress band events will be then calculated to obtain the SST threshold for bleaching, and thanks to the high resolution results, we plan to observe whether the bleaching threshold has changed over time.

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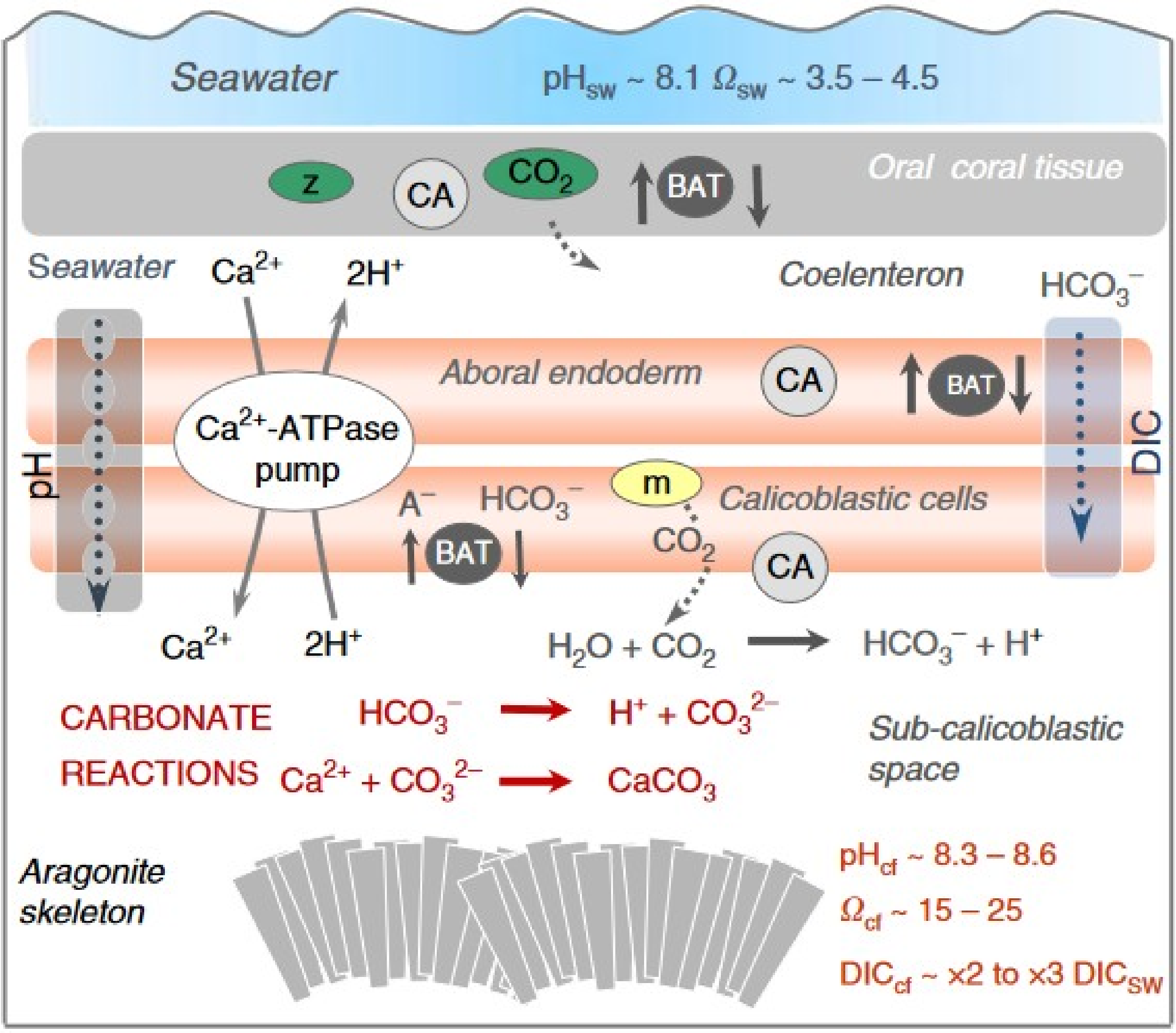
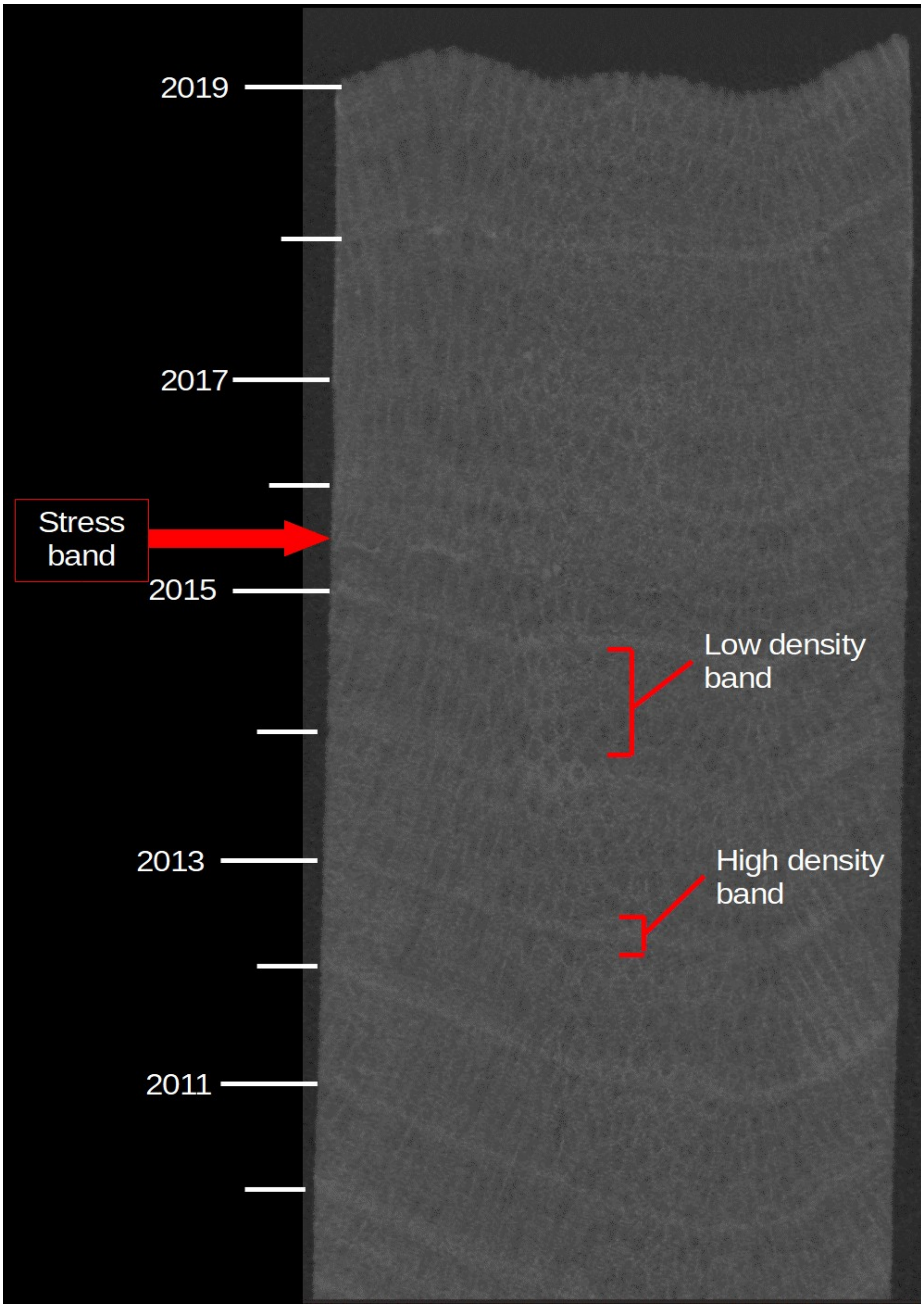
Table of Annexes

Annex 1: **Mechanisms involved in coral calcification** (Figure and caption taken from McCulloch et al. 2017)

Calcification occurs within the sub calicoblastic space from an initial seawater-derived fluid with additional metabolic sourced supply of DIC5–7. Elevation of calcifying fluid pHcf occurs via removal of protons from the calcification site by Ca2 þ ATPase exchangers. The carbonic anhydrases (CA) catalyse the forward reactions converting CO2 into HCO3 ions7,34. Transfer of DIC into the subcalicoblastic space may occur via diffusion of CO2 and/or by HCO3 pumping via bicarbonate anion transporters (BAT)5–7. The link between the activity of zooxanthellae located in the oral coral endoderm tissue to the generation of metabolic DIC within the aboral endoderm and calicoblastic cells (orange) and transport to the calcifying fluid remains uncertain5–7 (Figure modified from McCulloch et al. 2012)

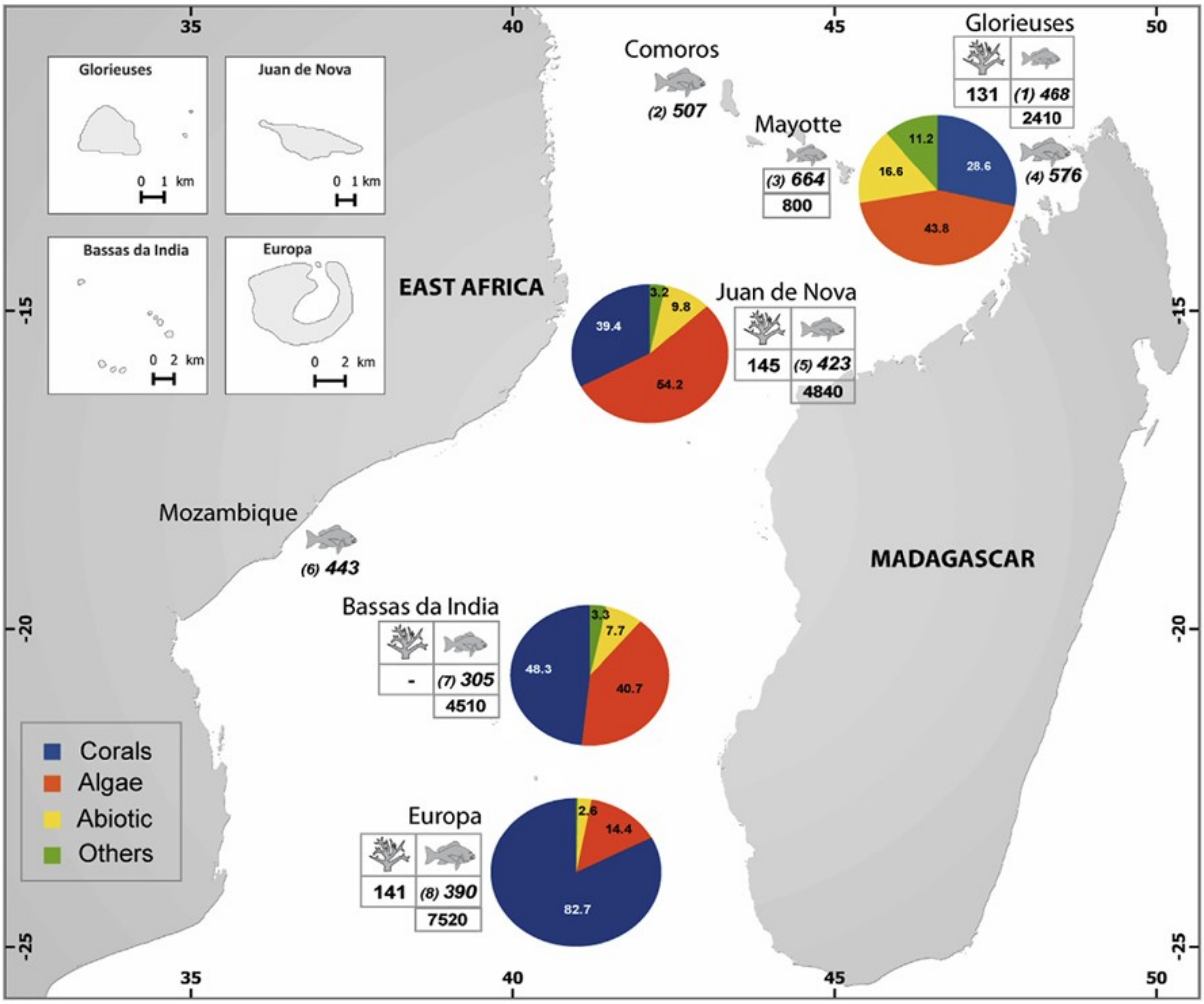


Annex 2: Tangential slice of a coral skeleton CT scan. Year estimation is based on density bands (on the left). A stress band can be observed near to 2016.



Annex 3: Comparison of benthic cover (coral, algae, abiotic and "others") and coral diversity per station (total number of species) in the Mozambique Channel including Iles Eparses, from Chabanet et al. (2016)

Fish parameters include diversity (total number of species) and biomass (kg/ha). Diversity is calculated from inventories using the theoretical coral fish diversity index (CFDI, Allen and Werner, 2002). From Chabanet et al. (2016).



Annex 4: List of core's sample information

Date	ID	Lat	Lon	Max deep (m)	Length	Thickness
20/04/19	GL1	11° 33,664'	47° 17,595'	15	60	8
21-23/04/2019	GL2	11° 32,852'	47° 20,189'	5	420	3.5
22-23/04/2019	GL3	11° 32,852'	47° 20,170'	5	60	3.5

Annex 5: Sr/Ca ratio protocol (from Kasper 2008)

1 mg of the sample material was dissolved in 1 ml HNO_3 2% and diluted with HNO_3 2% to a solution of 10 ml with a concentration of 8 ppm calcium. The ICP-OES works with an external error of <1% and an analytical precision in Sr/Ca determination of 0.15% RSD or 0.01 mmol/mol.