New insights about Antarctic gorgonians (Octocorallia, Primnoidae) age, growth and their potential as a paleorecords
To strive, to seek, to find, and not to yield

Ulysses, Lord Tennyson (1842)
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ABSTRACT - Antarctic benthic communities have long been defined to be formed by slow-growing and extraordinary long-lived organisms. However, little is known about life history traits of gorgonians – key components of the Antarctic benthos. In this study, colonies of *Thouarella variabilis* (Wright and Studer, 1889), *Fannyella abies* (Broch, 1965) and *Fannyella rosii* Gray, 1872 have been used as target species in order to estimate ages, growth rates and identify their skeletal composition. The radioisotopes $^{14}$C and $^{210}$Pb used for dating have revealed these colonies to be long-lived with ages spanning from 50 to 1100 years. Radial Growth Rates in this study have also showed to be the slowest rate ever reported for gorgonians (about 6.4 µm yr$^{-1}$) with apparent growth ring deposition every 2 years. Irregularities in the growth rings were observed also observed as fluctuations in skeletal composition, which may be indicative of changes in the environmental conditions.

INTRODUCTION

Surrounded by the Antarctic Circumpolar Current, the continent of Antarctica has remained isolated from elsewhere since the opening of the Drake Passage about 40Myr ago (Brandt *et al.* 2007). The conditions observed in Antarctica today are a consequence of a crucial fact that happened 34 Myr ago: the onset of Antarctic glaciation (Arntz *et al.* 2005; Thatje *et al.* 2005; Trush *et al.* 2006). Since then, sea ice conditions have created a unique, stable environment where life has evolved to survive in extreme cold circumstances.

But extremely cold does not imply that Antarctica has to be perceived as a dead desert. In general, the Antarctic benthic environment is characterised by the presence of highly diverse tridimensional structured communities composed by numerous species of sponges, anemones, ascidians, cnidarians, briozoans, polychaetes and echinoderms (Brandt *et al.* 2007; Clarke, 2008). Up to date, more than 4000 species have been described in the waters of Antarctica (Clarke, 2008), making the Southern Ocean one of the most diverse areas on Earth. In fact, recent calculations estimate that about 1700 species are still waiting to be described (Gutt *et al.* 2004), since most of the deep-sea of Antarctica is still unexplored.
The biomass produced by benthic communities is often compared to those observed in temperate waters (Clarke, 2008). However, those high benthic biomasses recorded must not be considered only as a direct consequence of the high productive conditions present in Antarctica’s euphotic zone, but rather as a result of a combination with other factors such as slow growth, delayed sexual maturity, longevity of the fauna and low predation pressure (Arntz et al. 1992).

Considering the apparent food scarcity, the different benthic groups represented in Antarctica reach surprisingly much greater sizes than their counterparts in warmer waters (Thomas, 2004). Gigantism appears to be a common feature amongst polar benthic organisms, both Arctic and Antarctic. Low temperatures certainly slow metabolic rates to the extent that growth rates are slow enough to enable organisms to grow large and live longer (Aronson and Blake, 2001; Thomas, 2004; Brey and Clarke 1993). In fact, many Antarctic marine invertebrates are extraordinarily long-lived (Arntzt et al. 1992). Current research of longevity in Antarctic benthos has generally focused on one of the most dominant taxa: sponges. In this sense, the Antarctic lollipop sponge *Stylocordyla borealis* can live up to 150 years, while adult sponges of the genera *Rossellidae* are thought to be at least 300 years old. Specimens of this latter group can reach up to 2m in height, with lifespans estimated to be over 10,000 years (Thomas, 2004). Dayton et al. (2013) also documented exceptional growth of the hexactinellid sponge *Anoxycalyx joubini*.

Cnidarians, especially Hydrozoans and Anthozoans are, next to sponges, key components of the Antarctic benthic communities, and are considered to play a very important role in structuring the benthic habitats (Brandt et al. 2007). In the Weddell Sea, anthozoans are the third dominant taxon in shelf communities, accounting for 10% of the individuals (Starmans et al. 1999). Associated with these sessile organisms, an astonishingly diverse fauna of ophiuroids, asteroids, echinoids, pycnogonids, isopods, amphipods, nemerteans and gastropods can be also found (Arntzt et al. 2005).

However, and despite their presence and role in Antarctic benthic communities, gorgonians are among the least studied group of Antarctic marine macrobenthic fauna, and little is known about their life history traits beyond taxonomic features (Gili et al. 2001). Studies focused in their trophic ecology have contributed to increase our knowledge about their diet. According to Orejaset al. (2000), gorgonians feed on the
fine fraction of the seston, which are bacteria, nano- and picoplankton, unicellular organisms and organic detritus. Thus, despite living in an extreme environment, these organisms rely on different food resources to attenuate the effects of seasonal fluctuations in primary production, a strategy named trophic plasticity (Gili et al. 2000, Sherwood et al. 2008). However, nothing is known about how long Antarctic gorgonians live, how do they grow and which factors may influence their life history.

Gorgonians, as modular organisms, grow through the iterated replication of individual modules to form large, integrated individuals or colonies (Lasker et al. 2003). Growth and development in gorgonians has been studied by measuring colony height (this is the case for the Mediterranean gorgonian Paramuricea clavata; Coma et al. 1998) or by determining the hierarchy and branching pattern (in the case of the tropical gorgonian Pseudopterogorgia elisabethae; Lasker et al. 2003). To date, estimation of age and growth rates of gorgonians and coral species in general has been carried out by observing skeleton density bands in thin cross-sections of the base of the colony. Indeed, growth bands of red coral Corallium rubrum were already described a century ago (Marshal et al. 2004).

Similar to terrestrial trees, gorgonians build their skeletons by secreting walls of calcium carbonate (CaCO₃) at different densities throughout the whole year, which in the end they show up as rings or bands (Barnes and Lough, 1993). Mineralisation of a calcitic skeleton is a very old process in evolutionary terms, which appears to have first evolved at the start of the Cambrian period 450 Myr ago (Roberts et al. 2009). Through evolution, the complexity and diversity of calcification processes in marine invertebrates have changed. Indeed, in gorgonians species, the rings appear as couplets of alternating bands of calcite/gorgonin (Sherwood et al. 2005a; 2012) deposited around a central, hollow, chambered canal (Lewis et al. 1992). Moreover, in single individuals, different regions can be identified in terms of composition and calcification modes: 100% calcite and 100% gorgonin or a varying degree of both (Sherwood and Risk 2007, Edinger and Sherwood, 2012).

Annual periodicity of these bands is firmly established in some species like the Californian species Muricea californica and Muricea fructicosa (Grigg 1974), Porites lobata from the South-Western Pacific Ocean (Beck et al. 1997) and the Mediterranean Corallium rubrum (Weinbauer et al. 2000, Marshall et al. 2001). More recently, studies
based on radiometric dating techniques on the primnoid gorgonian *Primnoa resedaeformis*, and the antipatharians *Stauropathes artica* and *Keratosis ornata* from the Labrador Searevealed also to have an annual rings deposition pattern (Sherwood *et al.* 2005a; Sherwood and Edinger 2009; Andrews *et al.* 2002).

Growing evidence supports that counting rings could be an easy way to estimate gorgonian age and growth patterns. Nevertheless, since deviations from this trend have been observed this cannot be applied to all species. This is the case of the genera *Paramuricea*, which seem to produce rings once every decade (Sherwood and Edinger, 2009). Furthermore, in some cases a clear periodicity in the growth banding cannot be observed since the rings somehow appear with irregular and ambiguous appearances (Andrews *et al.* 2002; Risk *et al.* 2002).

Conversely, other studies focused on whether periodic variations in skeletal composition could be used to determine the coral’s age (*Keratosis* sp. from Tasmanian waters; Thresher *et al.* 2009). Although no annual deposition has been identified, this work proved that the composition of the skeleton could yield valuable information about climatic events such as the Antarctic reflection of ENSO and the Southern Annular Mode. In this sense, growth rings seem to be clues from the past that record the chemical and physical conditions that existed in the surrounding waters at the time of skeletal accretion (Druffel, 1997). Thus, they provide a complete diary of natural history that can tell us about daily light variations (Lewis *et al.* 1992), lunar cycles and monthly tidal pressures (Risk *et al.* 2002; Tracey *et al.* 2007), surface productivity variations (Sherwood *et al.* 2005) and annual seawater temperature variations (Corrège *et al.* 2000; Weinbauer *et al.* 2000; Glyn and Wellington, 1983; Saenger *et al.* 2008). The advantages against other proxies, like sediments, are the absence of mixing processes along the corals' skeleton, which can record the environmental conditions from centuries to thousand years with a high temporal resolution (Beck *et al.* 1997).
AIMS OF THE STUDY

The works mentioned above have set the baseline for the present study, which focuses on the growth of Antarctic gorgonians and their environment. It is a pioneering work, because most of this type of research has generally been aimed for tropical and temperate corals.

Essentially, this study pretends to investigate the longevity of Antarctic gorgonians and to understand the growth patterns of gorgonians of the genus *Fannyeella* and *Thouarella* that inhabit shelf waters of Antarctica in terms of radial growth and skeletal composition. In this line, the following objectives were defined:

1. To determine the age of a set of Antarctic gorgonians, for which little is known about their lifespan or their life cycle. Given that there is a growing support for longevity as a key feature to understand the ecology of Antarctic organisms (Arntz *et al.* 1997) and Peck and Borrington(2013) suggested that growth in Antarctic gorgonians is about 5-10 times slower than their temperate counterparts, Antarctic gorgonians are thought to be slow-growing and long-lived too. This objective was addressed via dating the colonies using radiometric techniques.

2. To estimate the periodicity of the growth rings. Given the evidences for annual periodicity in ring production for other temperate and tropical species (Sherwood *et al.* 2005a; Grigg, 1974; Beck *et al.* 1997; Marshall *et al.* 2001, Andrews *et al.* 2002), one would suspect that growth rings in Antarctic gorgonians should form annually due to the marked seasonality of the Antarctic environment. This objective was addressed counting the growth rings and validating their periodicity with the dating results.

3. To investigate whether the skeletal composition reflects the growth variations observed in growth rings, which could lead to the interpretation of past environmental conditions at the time of the skeleton’s formation. This objective was addressed performing EDX microanalyses with Scanning Electron Microscope.
MATERIALS AND METHODS

Study area

Sampling of gorgonians for this study was carried out in the continental shelf of Weddell and Ross Seas. In general, Antarctic continental shelves cover an area of 4.59 million km² with depths ranging between 400-500m, although they can reach more than 1000m depth at certain places (Dayton 1990 in Brandt et al. 2007). These shelves are primarily composed of soft siliceous sediments of glacial-marine origin (glacial till, gravels, sands and biogenic deposits), since Antarctica lacks a typical fluvial sediment supply (Clarke, 1996). Some of them may be very old in age like the seabed of Weddell Sea, which dates back to the Middle Jurassic (Brandt et al. 2007). Shelf waters include a variety of water masses whose characteristics provide a fairly uniform cold environment for benthic organisms. These water masses include Antarctic Bottom Waters (AABW), Antarctic Intermediate Waters (AAIW) and Antarctic Mode Waters (AAMW) (Turner et al. 2009).

The role that ice plays in the dynamics of Antarctica makes this continent different to any other place in the world, shaping the environment of the Southern Ocean since the consolidation of the Antarctic Ice sheet 34 Myr ago (Arntz et al. 2005; Thatje et al. 2005; Trush et al. 2006). It exerts its influence driven by the seasonal difference in insulation, which induces changes in the extent of the sea-ice of about 17×10⁶ km² (Clarke, 1988). This may have a profound effect on primary production, and over the Antarctic marine ecosystem as a whole. Although there are some highly productive areas, the Southern Ocean is in general an oligotrophic environment, with an estimated annual production of 41gC·m⁻²·yr⁻¹ (Orejas et al. 2000).

In relation to this, Turner et al. (2009) defined three main areas in the Southern Ocean in terms of productivity. Colonies analysed in this study inhabit the southernmost zone, which comprises the permanent ice shelf waters. This area encompasses the inner areas of Weddell and Ross Seas, where primary production is limited to a short but intensive season.

As austral winter advances, marine life is forced to survive under extreme conditions, mainly due to the formation of sea-ice, a dramatic decline in solar radiation and a consequent reduction in food availability. Many scientists have long attributed this resource limitation to be a key constrain for polar marine fauna, which has to rely on
short spring/summer blooms (Clarke, 1988). However, low concentrations of particulate matter in winter are compensated by the increase in water clarity, important in promoting next early spring benthic microalgal bloom (Clarke and Leakey 2009). In addition, the material released during the ice melting provides an important food source for macrobenthos (Clarke and Leakey, 2009) which will be available for the whole year thanks to advection and resuspension processes (Gili et al. 2001). Sea-ice not only exerts a control over primary production, it also regulates the amount of light reaching the seafloor by providing large ice-rafted boulders (drop-stones) and patches of hard substratum that are suitable for the settlement of benthic organisms (Clarke, 1996). In this sense, Antarctic gorgonians are usually found dwelling in complex megafaunal communities, mainly attached to exposed rocky outcrops or basaltic rocks of oceanic spreading centres (Brandt et al. 2007).

Species analysed

The target species in this study were *Thouarella variabilis* (Wright and Studer, 1889), *Fannyella rosii* (Gray 1872) and *Fannyella abies* (Broch 1965). All these species of cnidaria belong to the subclass Octocorallia, family *Primnoidae*. According to Cairns and Bayer (2009), primnoids originated in the Antarctic, where they are the dominant gorgonian family (16 genera). Furthermore, according to Zapata-Guardiola (2013) 81% of primnoids are endemic to the Southern Ocean, especially in the Antarctic sector (61%).

A general feature of primnoids is that their polyps are more or less covered by an armour of scale-like slerites (Watling et al. 2011). Primnoidae species, share with other calcaxonians the feature of having a solid axis composed of large amounts of non-scleritic calcareous material, which allow them to live in the high hydrodynamic environments of the bathyal slope (Watling et al. 2011; Lewis et al. 1992; Roberts et al. 2009). In fact, as suspension feeders, they depend on current advection processes that enable continuous water renewal close to the bottom and the resuspension of particulate matter (Gili et al. 2001).

*Thouarella* is one of the most diverse primnoid genera (Cairns, 2006) and the best represented in Antarctic and sub-Antarctic waters with 29 species, 8 of them reported in the Southern Ocean (Zapata-Guardiola and López-González, 2010). Nevertheless, it
is a truly cosmopolitan genera, as it is present not only in Southern Ocean, but South Africa, off Chile, western Atlantic from Burdwood Bank to northern Florida, Japan, Aletuan Islands with a depth range of 60-1500m (Watling et al. 2011; Cairns and Bayer, 2009).

*Fannyella* species’ distribution is limited to Antarctica and it has been observed in Weddell and Ross seas, South Shetland Islands, Antarctic Peninsula, Coates Land (Cairns and Bayer, 2009). According to Watling et al.(2011), species of *Fannyella* seem to be associated with Antarctic Bottom and Intermediate Waters, showing a smaller depth range compared to the genus *Thouarella* (46-852m) (Cairns and Bayer, 2009).

**Sample collection**

Live colonies of *Fannyella abies* (FA 6329 and FA6333) were collected using a bottom trawl in 2006-2007 during the ANT XXIII-8 CLIMANT expedition. These gorgonians were sampled from the Weddell Sea at depths of 243 and 293m respectively. *Fannyella rosii* colonies (FA6312, FA6336, FA6384, FA6385) were collected from the Ross Sea in 2004 during the VLT (Italica XIX) and TAN 2004 cruises using and Agassiz trawl and aORHT sampling device.

*Thouarella variabilis* specimens (TV6386, TV6387 and TV6388) were collected from the Ross Sea with a OGT (Orange Roughly Trawl) at depths of 126,5and 525,5 metres in 2004 during the TAN 0402 campaign on board of New Zealand’s RV *Tangaroa*.

**Ring counting**

Previous to dissection, collected colonies were air-dried and living tissue was removed. About 5-6 disks of 2mm thick in thickness were cut from the first centimetre of each basal section using an ISOMET low speed saw at Servei de Làmina Prima (Faculty of Geology, University of Barcelona).

One basal section of each colony was chosen for ring counting using an stereo microscope. To avoid bias in ring counting, stillpictures from each section were taken with a Moticam 2300 camera mounted on Olympus Stereoscope SZ60 at x1.5 and x6.3 (Fig.2). To avoid subjectivity, rings from each of the colonies photographed were counted by three different observers. Additionally, maximum radius was measured from still images using using Macnification® software.
Parallel to this, another basal section of each colony was coated with gold palladium (AuPd) prior to its examination with a Scanning Electron Microscope. SEM analyses were carried out with a Hitachi S-3500N at the Marine Science Institute in Barcelona (ICM-CSIC). Rings counting were done following the same procedure as with the optical microscope. SEM pictures were taken at 20Kv, dwell time 100s and at x500 (Fig.2).

Additionally, those same samples were used to analyse the skeleton’s geochemistry. Electron Dispersive X-ray microanalyses (EDX) were performed at 15-30Kv, 1.2 kcps in backsattered mode, following a horizontal path along the radius. Each path was formed by a series of 257μm-long continuous line scans that quantified the chemistry of the sample every 2.5μm. The chosen procedure aimed to the highest possible resolution to best represent the continuous fluctuations in the concentration of each element in the skeleton of the gorgonians, rather than performing specific point analysis. Element concentrations are given in normalised %. The examined elements were those detected in the skeletons were Calcium (Ca), Magnesium (Mg), Strontium (Sr) and Bromine (Br). No other elements were detected nor were studied.

Radiometric dating

The age of the gorgonians was determined using radiometric techniques with two different isotope tracers, $^{14}$C and $^{210}$Pb. Both of these isotopes are known to get incorporated into the skeletal matrix at time of formation (Druffel, 1997; Druffel and Bauher, 2000; Andrews et al. 2002).

Carbon-14

$^{14}$C dating was performed on the organic content (gorgonin) of each colony in order to avoid any sign of carbon contamination. Basal sections of each of the specimens were decalcified in 5% HCl solution for 3 weeks following Sherwood et al. (2005a) procedure. As our interest was to date a few different growth bands in a colony, 7 to 16 rings were teased apart (Fig. 3) and decalcified in 5% HCl for two more days. Once calcite had dissolved completely, samples were cleaned in Milli-Q water, air-dried and weighted using a Mettler Toledo MX5 microbalance. At least 2 rings per colony were selected (one from inner zone and one from the edge) ensuring that the minimum weight for radiocarbon analyses was met (1-3mg). Samples were analysed with a Mass
Spectrometry Accelerator (AMS) at CNA laboratory (Centro Nacional de Aceleradores, Seville).

Before Present ages (BP) were calibrated using marine curves and corrected for local reservoir effects using the CALIB® software. This is essential because organisms from marine and lacustrine environments have been exposed to different levels of $^{14}$C than their counterparts in the atmosphere (Mangerud, 1972). A maximum local reservoir correction factor ($\Delta R$) of 1400 years was proposed by Gordon and Harkness (1992) for high latitudes of Antarctica, however, a more adjusted $\Delta R$ of 928±29 years was used in our samples averaging published data from the Marine Reservoir Correction Database (http://calib.qub.ac.uk/marine/) in accordance with survey coordinates. According to Hall et al. (2010), the Southern Ocean reservoir age has not varied significantly during the last 6000 BP years. Therefore, we assume that the reservoir correction factor of 928±29 years is constant.

Radiocarbon analyses of Antarctic gorgonians embrace several limitations due to the nature of the samples and the nature of the environment. These limitations include: (1) the need for a minimum sample weight to perform the analysis; (2) the complexity to calculate ages from contemporaneous rings (younger than 400 BP years) because of the time-dependent global ocean reservoir correction of about 400 BP years incorporated by the marine calibration curve (Stuiver and Reimer, 2005); and (3) the signal of nuclear bomb testing in 1950s that opens the possibility for multiple calibration ages (Sherwood et al. 2006).

**Lead-210**

Two rings per colony were selected for $^{210}$Pb dating, selecting fragments coincident with those used for $^{14}$C dating. Rings were cut with a scalpel and teased apart with tweezers, weighted and sent for lead-210 analyses. Lead-210 activity was analysed with gamma spectrometry at the Radioisotope Service from the University of Seville. This technique is only useful for materials with less than 150 years of age since Lead-210 is a very radioactive isotope with a half-life span of 23.26 years. It is incorporated into the skeletal matrix at the time of formation, when new tissue is added over the external part of the skeleton. The activity of Lead-210 decreases in time to the point at which the activity of $^{210}$Pb equals the activity of Ra-226, a naturally occurring calcium substitute, reaching an equilibrium ratio of 1 (Andrews et al. 2005,
Tracey et al. 2007). Beyond this point no dating is possible with $^{210}$Pb and indicates that samples are older than 150 years.

Data analyses

Skeleton age was calculated subtracting the year of collection (2004 or 2007) to the 97% probability age given by the CALIB® software. Radial growth rates (RGR), understood as the yearly increase of the radius, were estimated dividing the measured radius by colony age, assuming this rate has been constant throughout the life of the organisms. Descriptive statistics were applied using the Rstudio® software in order to describe the basic skeletal composition. The relationship among elements was examined with regression analyses and non-parametric Kendall’s rank correlation.

Because of the non-stationary character of the data series acquired with the microanalyses, spectral analyses (FFT) could not be used to study the periodicity of the variation in element concentrations; since these kind of analyses assume that the observations are equidistant in time. For this reason, window integrated values were calculated in order to reduce data noise and smooth the pattern of the time series (window length = 10 points).
RESULTS

Radiometric analyses

A summary of the radiometric dating results is presented in Table 2, including suggested colony ages after correcting for the reservoir effect. Radiocarbon analyses estimate an age of 1100 years for the gorgonian TV6388, corresponding to the species *Thouarella variabilis*. This seems to be the oldest gorgonian ever dated after a *Primnoa resedaeformis* specimen of 700 years dated by Sherwood et al. (2006). Specimens of *Fannyella abies* (FA6329) and *Fannyeella rosii* (FA6336) resulted to be also very old, with ages of 329 and 354 years respectively. The age of the individual FA6312 was at the edge of radiocarbon calibration, leading to believe that its age is very close to 300 years.

The *T. variabilis* sample TV6387 could not be dated because separated rings did not weight enough for radiocarbon dating analyses. Ages of outer rings (sample code -1) of all colonies could also not be calibrated because $^{14}$C concentrations were higher than the standard reference year of 1950 (“pre-nuclear”) and are therefore affected by nuclear bomb testing.

When $^{14}$C ages could not be calibrated, $^{210}$Pb analyses were used to validate the results. $^{210}$Pb activity at the core of most of the skeletons analysed is in equilibrium with $^{226}$Ra, so almost all colonies used in this study are older than 150 years. Specifically, colonies FA6333, FA6312 and TV6386 must have ages greater than 150 but less than 400 BP years, which is the lower limit of calibration for $^{14}$C ages. $^{210}$Pb dating also suggests a lifespan of 50 and 58 years for the *F. rosii* specimens FA6384 and FA6385 respectively.

Growth characteristics and ring deposition

After the examination of still images, rings appeared to be diffuse and irregular. Table 3 shows the average ring counts for both stereomicroscope and SEM images. Counts from the three observers were very similar with an average error of ±16. Stereomicroscope counts ranged from 60 to 145, while SEM counts were above 100 rings in all cases. Samples FA6333, FA6384 and FA6385 did not show rings under SEM observation.
Radiometric techniques did not validate an annual periodicity of the rings. However, colonies of known age (TV6388, FA6329 and FA6336) showed rings under the SEM that seemed to be deposited biannually.

Independently from the appearance or periodicity of the rings, after determining the age of 4 rings in colony TV6388 and measuring the increase in distance and surface between them, the observed radial growth seemed to remain constant throughout the life of the gorgonian ($R^2=0.99$)(Fig.4).

A major methodological constrain in having more accurate growth estimations has been the size of the basal sections. Subsequently, only two rings per colony could be dated in most cases but except of *Thouarella variabilis* TV6388 with a radius that doubled the rest of the colonies (5577.03µm). However, radial growths rates (RGR) are presented in Table3 and are indicative for the measured radius. RGR in *T. variabilis* 6388 was 4.8µm yr$^{-1}$, while the average for the longest colonies in this study seems to be 6.4 µm yr$^{-1}$. Paradoxically, radial growth rate of FA6384 and FA6385 reported by $^{210}$Pb dating is 48 and 51 µm yr$^{-1}$ respectively.

**Skeletal composition**

A summary of the microanalyses performed is shown in Table 5. Although the ratio of each element versus Calcium varied widely among colonies, results suggest that the basic mineralogy of the skeletons is based on a low magnesium calcite (MgCO$_3$) deposition. Magnesium concentrations were very low in all cases, ranging between 0.62 and 3.03% of the skeleton’s mass. The measured concentrations of minor elements such as Strontium (Sr) and Bromine (Br) ranged between 15 to 44% and 20 to 44% respectively. The species of gorgonian used for this study seem to incorporate Sr in relatively high quantities: This is the case of TV6387, TV6386 and FA6333, whose skeletons appear to be formed by strontianite (SrCO$_3$) rather than calcite (CaCO$_3$). Bromine concentrations were also surprisingly high in colonies of *T. variabilis* TV6386 and TV6387, accounting for more than 40%.

Coarse-resolution regression analyses of skeletal composition confirm that elements are not found in random concentrations. A strong negative correlation between Sr/Ca and Br/Ca ($R^2$ values of 0.78 and 0.68 respectively) was found (Fig.5). Conversely, Mg showed no correlation with any of the other elements and its incorporation seems to be
rather stochastic. In addition, when aligning the microanalyses data with the stereomicroscope images, bromine variations appear to coincide with gorgonin layers (Fig.6).

*Data series of the different elements*

Given the low concentrations of Mg and the inexistent relationship with the other elements, it was excluded from further examination.

A closer look to the concentration of the other three elements across the radius indicates that a certain degree of variability exists, although no periodicity can be determined yet. Plots of the smoothed data series (Fig.7 a-f) exhibit abrupt variations in skeletal composition regarding Ca and Sr in certain points in the radius. Data evidences that colonies change the use of calcium for strontium as its basic building material and vice versa. This seesaw pattern is present in most colonies and it is very clear in sample *Fannyellaabies* FA6329 from the Weddell Sea (Fig.7-d), in which this alternation in the calcification mode appears at least 3 times along the radius. Furthermore, the pattern observed in the individual FA6329 is significantly correlated with the gorgonian of similar age *Fannyellarosii* FA6336 for both calcium (p-value=0,0001) and strontium (p-value=0,0002). However, although there is no correlation in Ca and Sr between FA6329 and FA6312, the significant correlation between the latter and FA6336 may be indicating the same events with slightly different lags.

Conversely, the younger colonies FA6384 and FA6385 (Fig. 7 e and f) show a different pattern, with smoother fluctuations. Comparisons of Ca and Sr elements between both specimens show that there is also a positive correlations between the concentration of such elements (p-value=0,02 for Ca and 0,01 for Sr).
DISCUSSION

Methodology

Both radiometric analyses (\(^{14}\)C and \(^{210}\)Pb) greatly differ from each other in the scales that they work, and the methods they use for age calculations and subsequently, the ages they estimate. Though it is beyond the scope of this work to deepen in the technicalities of each, we will evaluate their performance and limitations when dating Antarctic organisms.

As it has previously been mentioned, the radiocarbon method does work well when colonies to be dated exceed certain age for BP ages’ calibration. Moreover, we found indispensable to have knowledge about precise reservoir correction factors, and radiocarbon content in general, of the study area. Otherwise, no matter how accurate the results are, they will not be useful because of growing calibration limitations. In the particular case of Antarctica, very little information is available about \(^{14}\)C content in Southern Ocean waters and its biota (Michel and Druffel, 1983; Gordon and Harkness, 1997) leaving little to compare with our gorgonians. Nevertheless, radiocarbon concentrations and ages reported in this study are in fact valuable information about modern \(^{14}\)C values from both Weddell and Ross basins and in new a studied group: gorgonians.

Alternatively, \(^{210}\)Pb performed well in young colonies (FA6384, FA6385). However, given the temporal scale at which the gorgonians used in this study lived, \(^{210}\)Pb has proved to be very limited. Indeed, colonies TV6388, TV6386, FA6329, FA6312, FA6336, FA6333 exceeded the age for Lead-210 dating. It is important to note that 210Pb was useful to validate the radiocarbon results and vice versa. For example, when radiocarbon ages of FA6384 and FA6385 could not be calibrated because of the modern character of the rings, \(^{210}\)Pb succeeded in giving an age. Similarly, the radiocarbon technique estimated an age for the older colonies that are out of the range of \(^{210}\)Pb dating. Therefore, the two techniques are compatible and complement each other.

Weight and volume of the samples has been a major limitation in this study, with only two measurements to be carried out in each sample due to the nature of the gorgonian’s skeleton. Separating the rings in very small sections leaves very little material for dating analyses. Thus, increasing the number of measurements could improve the performance.
of both tracers and the accuracy of the results as a whole. In the specific case of Lead-210, having more measurements along the radius would inform us better about the equilibrium point between $^{210}\text{Pb}$ and $^{226}\text{Ra}$ (i.e. at which point the colony is older than 150 years). For these reasons, we find advisable to carefully examine the possibilities and limitations of each dating technique prior to propose any dating.

Ages

Results yielded by this study provide convincing evidence that Antarctic gorgonians are extraordinary long-lived animals, which is in agreement with other reported long-lived marine organisms not only from Antarctica, but from other oceans (Table 6). The inability to date the colonies TV6387 and TV6386 complicates the inter-genera comparisons, as only one $T. \text{variabilis}$ specimen could actually be dated (TV6388). However, the average radial growth of 6.4$\mu$m yr$^{-1}$ calculated from the longest colonies could indicate that the organisms not dated could also be from a similar age. This in fact could lead us to believe that longevity of Antarctic primnoids must be a general feature with no big differences between species or genera.

Ages of TV6388, FA6329 and FA6336 are comparable to those of other primnoids from other ocean basins such as specimens of $\text{Primnoa resedaeformis}$ of 700 and 300 years (Sherwood et al. 2006; Risk et al. 2002). Likewise, black corals $\text{Leiopathes glaberrima}$ and $\text{Antipathes dichotoma}$ (both Antipatharians) have also been known to grow remarkably old, exceeding ages of 2000 years (Druffel et al. 1990). On the other hand, $\text{Fannyella rosii}$ specimens 6384 and 6385 seem to be in the same age range as $\text{Thouarella variabilis}$, with 60-year old organisms reported by Zapata-Guardiola (2014).

Ring deposition

Prior to this study, it was assumed that growth rings from Antarctic gorgonians were produced annually, as mentioned in Zapata-Guardiola (2014). After determining the age of the colonies with radiometric techniques, the reported ages a priori did not match the ring counts. Yet, visual inspection of images revealed the rings were quite irregular. Moreover, under SEM observation, gorgonians of the genus $\text{Thouarella}$ showed clear structures while $\text{Fannyella}$ specimens appeared to have a denser, proteinaceous skeleton with few or no-rings appreciable. Thus, the miss-match between the counts and the age validation can be explained by the following reasons:
1) The counting precision largely depends on the quality of the section. As a result, counting rings from both stereomicroscope and SEM images were not as useful as we expected to determine the ages of the colonies and to do comparisons between specimen.

2) The condensed appearance of the rings under the naked eye as mentioned in other works (Noé and Dullo, 2006).

Contrary to the abundant literature in the field (some examples can be found in Sherwood et al. 2005; Andrews et al. 2002; Sherwood and Edinger, 2009; Risk et al. 2002; Zapata-Guardiola, 2013; Wilson et al. 2002) average ring deposition in Antarctic gorgonians appeared to be 1 every 2 years for those specimens whose rings were visible under the Scanning Electronic Microscope, in the same way that happens with the black corals *Lepidisis* spp. (Tracey et al. 2007). According to this, we speculate that ring deposition of the gorgonians used in this work presumably follows a pattern determined with some sort of internal clock that governs activities like reproduction rather than the Antarctic environmental seasonality. This theory has already been suggested by Tracey et al. (2007), who suggest that the energy spent in gametogenesis would likely influence ring deposition in black corals. Few works have suggested a two year cycle for the maturation of oocytes in *T. variabilis* (Brito, 1997; Zapata-Guardiola, 2013): However, larvae have been found in all seasons supporting the hypothesis of a continuous gametogenesis process in such species (Zapata-Guardiola, 2013).

**Growth**

In general, the radial growth rate observed in this study was as slow as it might be expected for organisms living under extremely low temperatures. Similar to some of the slowest-growing deep-sea corals (Table 6), gorgonians under this study showed slower growth than Antipatharians, whose growth rates are about of 15µm yr⁻¹ (Sherwood and Edinger, 2009). Therefore, this study confirms that growth of Antarctic gorgonians can be about 10 times slower than their temperate counterparts as suggested by Peck and Borrington (2013).

When comparing the younger *Fannyella rosii* colonies (FA6384 and FA6385) with the rest of gorgonians in this study, their lifespans showed differences of an order of magnitude. A preliminary hypothesis to explain this fact could be that the growth...
rate would not be constant through time and that it may be faster in younger individuals as mentioned by Risk et al. (2002). It is reasonable to think that younger gorgonians are under strong selective pressure, so they may grow faster to be less vulnerable. Consequently, the energetic investment of these animals would be focused in growth rather than other functions such as reproduction.

This completely contradicts our own results for *Thouarellavariabilis TV6388*, whose growth seems significantly constant at a rate of 4.8 µm yr\(^{-1}\). Unfortunately, we do not know the growth rate of TV6388 at the time when it was 50 years old. Due to methodological limitations, the radiocarbon measurement at the core of this specimen may include several decades if not hundred years. Interestingly, Dayton et al. (2013) also witnessed an extraordinary growth spurt and an increment in mass of about 30% for *Anoxycalyx joubini* in only 13 years. Although there is no clear explanation for this sudden growth, authors suggested that it could be related to increases in plankton concentration or variations in its composition.

Data such as that provided by Matsumoto (2007) give support to the constant growth hypothesis, in this case after studying the growth of the deep-water *Primnoa pacifica*, which below some threshold temperature, it showed relatively constant growth rates in diameter of around 0.1-0.2 mm yr\(^{-1}\). Certainly, both facts are not mutually exclusive. We believe that there must be a faster growth rate in young colonies (< 70 yrs.) and from a certain moment, growth stabilizes and remains fairly constant. Our hypothesis is supported by the Antarctic environmental setting that creates stability and undisturbed conditions, not only in terms of temperature but also in food availability (Gili et al. 2001; Turner et al. 2009).

Indeed, the continuous resuspension of the organic matter from summer blooms creates suitable trophic conditions constant almost the entire year (Smith et al. 2006 and Gili et al. 2001), allowing for constant growth and reproduction (Zapata-Guardiola, 2013).

**Skeletal composition and data series**

Our work has provided some insights to the knowledge of the composition of Antarctic gorgonians skeletons. Our results show that there are at least two groups that differ in absolute skeletal composition:
a) Calcium carbonate – Colonies FA6312, FA6329, FA6384, FA6385 and TV6388 showed very similar elements concentrations. All of them could be included in the group of low-magnesium calcite “builders” such as *Plexaura flexuosa*, *Muricea muricata*, and *Eunicea turniforti* (Lewis et al., 1992).

b) Strontium carbonate – Colonies TV6386, TV6387 and FA6333 showed higher Sr and Br concentrations. Many marine invertebrates also use Sr to build up their body shells such as *Acantharians* (Radiolaria), gastropods, cephalopods and corals (De Decker, 2004; Bettencourt and Guerra, 2000).

On the other hand, since bromine has been observed in gorgonin layers, its presence can be attributed to a feature of monobromotyrosine or dibromotyrosine, both iodinated invertebrate scleroproteins (Ehlrich, 2010). Similarly, Br has been reported in several marine organisms such as in fatty acids of sponges *Xestospongia* sp., while bromoindoles are also common in the Antarctic sponges of the genus *Psannopema* (Gribble, 1999). Thus, it is not surprising to find this element in Antarctic gorgonians. Given the relation between bromine and gorgonin, variations in the amount of that element as well as the thickness of gorgonin layers, could reflect productivity variations (Risk et al. 2002, Sherwood et al. 2008, Sherwood et al. 2005b).

Many authors such as Druffel(1997), Saengeret al. (2008), Weinbaueret al. (2000), and Thresher et al. (2007, 2010) have long suggested that there is a clear link between the skeletal composition and the growth rate. But what factors can explain the observed fluctuations in both growth and skeletal composition? Most of literature directly relates temperature to the incorporation of Sr and Ca (Thresher et al. 2007, 2009, 2010; Weinbauer and Velimorov, 1995) and there is a purely chemical-based explanation behind. Calcium and Strontium are two of the most abundant and constant elements in seawater present as free ions Ca$^{++}$ and Sr$^{++}$. Both are very similar chemically in terms of weight and size (Sr is only 13% larger than Ca) (Cohen and McConnaughey, 2003). Active transcellular transport of both ions occurs enzymatically via the Ca$^{++}$-ATPbase “pump”. The enzyme has a higher affinity for Ca$^{++}$ than for Sr$^{++}$ (Cohen and McConnaughey, 2003) which explains why the majority of the studied gorgonians had more Ca than Sr. Strontium carbonate (SrCO$_3$) however, is less soluble than calcium carbonate (CaCO$_3$) and solubility is largely determined by the size of the ion and dependent on temperature (Atkins, 1993). Indeed, Thresher et al. (2010)
suggested a positive association between Sr/Ca and temperature for both Antarctic and non-Antarctic specimens (the lower the temperature, the higher the ratio).

If that stands to be right, the observed peaks in Sr/Ca would be indicative of intense and abrupt temperature variations in shelf waters of both Ross and Weddell Seas over the last 300 years as seen in FA6329, FA6312 and FA6336. Although we still fail to attribute a date to these events, we suspect from the width of the signal and the age of the colony that they must have lasted several years or even decades. Similarly, Ross Sea colonies FA6384 and FA6385 had environmental conditions over the last 50 years that seem to have been quite constant.

Unfortunately, temperature records from Antarctica are scarce in space and do not extent far back in time, thus not allowing comparisons between our results and seawater temperatures in the same way Beck et al. (1992) did in their work. However, our results certainly ensure that significantly correlated colonies are reproducing the same environmental history. Given the long-standing idea of gorgonians’ and corals in general- sensitivity to their environment (Beck et al. 1992; Heikoop et al. 2002; Weinbauer and Velimorov, 1995) there are enough hints to speculate that these events could be related to the Antarctic reflection of broad-scale climatic patterns as seen in Thresher et al. (2009). In fact, large amount of studies support that broad-scale climatic patterns such as El Niño-Southern Oscillation or the Southern Annular Mode can induce inter-annual temperature anomalies or changes in sea-ice extent and productivity (Loeb et al. 2009; Ledley and Huan, 1997; Yuan, 2004; Hanna, 2001).

Therefore, indirect effects related to such processes may explain the fluctuations of the elements’ fluctuations in the target colonies. Nevertheless, further research is needed to confirm it.
CONCLUSIONS

This work is an insight of a broader study that contemplates different techniques in the study of age and growth in gorgonians. To better describe the longevity and growth of Antarctic gorgonians it would require to expand the research to other species, and use a larger number of colonies if the aim is to define a general growth rate for each species.

- Long-lived gorgonians: Lifespans reported in this study are among the oldest ever observed in gorgonians, ranging from 50 to 1100 years. This is in agreement with the long-standing idea of longevity in Antarctic benthic fauna.

- Slow growth rates: the majority of the colonies studied exceeded 150 years in age, showing some of the slowest growth rates in gorgonians ever recorded (about 6.4 µm yr^{-1}). In addition, the presence of two colonies of 50 years old and faster growth rates (about 50 µm yr^{-1}) suggests the idea that gorgonians grow faster in earlier life stages and their growth rates stabilize and remains constant after a certain moment.

- Growth rings not annual: growth bands in specimens of *Thouarella variabilis*, *Fannyella rosii* and *Fannyella abies* are not annual and thus cannot be used to determine the age of the colony. Nevertheless, preliminary results indicate that growth rings observed under SEM could be biannual.

- Growth rates of Antarctic gorgonians similar to rates of counterparts of deep sea: overall, the lifespans and growth rates observed in this work are only comparable to those species living in the deep ocean. Both environments, Antarctica and the deep ocean, offer constant low temperatures and lack major disturbances such as predation, thus creating a stable environmental that is suitable for benthic species to live long.

- Necessity to carry out further studies: Given that information about growth and longevity of habitat-structuring organisms such as gorgonians is essential for the conservation of Antarctic habitats, further research is needed to better understand their life history. This should involve other species and include larger number of colonies.

- Usefulness of primnoids as environmental proxies: from a paleoenvironmental perspective, the results presented here suggest that gorgonians, which have been growing for hundreds to thousands of years, have actually recorded past environmental conditions in their skeleton. Positive correlations among specimens
sustain the reproducibility of similar patterns in different colonies, meaning that each colony could be recording the same events in its own skeleton. For this reason, gorgonians promise to be valuable proxies about the recent environmental history of Antarctica with a high temporal resolution.

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Annex
Figure 1. Sampling area. Georeferenced map extracted from The International Bathymetric Chart of the Southern Ocean (IBCSO) Version 1.0 (Arndt et al. 2013).
Figure 2. Section of images a) Optical microscope; b) Scanning Electron Microscope showing growth rings of Thouarella 6388.

Figure 3. a) Basal section of Thouarella in 5% HCl solution. b) and c) Process of teasing apart the rings for both Thouarella and Fannyella.

Figure 4. a) Image of dated rings of Thouarella 6388. b) Radial growth of TV6388
Figure 5. Bromine concentrations along the radius of  

a) *Fannyella abies* 6329  
b) *Fannyella rosii*
Fig. 6. Relation of bromine and strontium versus calcium
Figure 7. Top: Smoothed time series for Ca and Sr. Bottom: Ratio Sr/Ca. a) TV6388, b) FA6336, c) FA6312, d) FA6329, e) FA6384, f) FA6385.
Table 1. Data of specimens used in this study. Depth in meters below the sea level, coordinates expressed as DDM. Gear acronyms: BT= Bottom Trawl, ORHT= Orange Roughly Trawl, OGT=Orange Roughly Trawl.

<table>
<thead>
<tr>
<th>Species</th>
<th>Id</th>
<th>Year</th>
<th>Survey</th>
<th>Ocean Basin</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Depth</th>
<th>Gear</th>
</tr>
</thead>
<tbody>
<tr>
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<td>FA6329</td>
<td>2007</td>
<td>ANT XXIII-8</td>
<td>Weddell Sea</td>
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<td>55º58.45'W</td>
<td>-243</td>
<td>BT</td>
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<tr>
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<td>2006</td>
<td>ANT XXIII-8</td>
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<td>54º7.19'W</td>
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<td>BT</td>
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<tr>
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<td>FA6312</td>
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</tr>
<tr>
<td><em>Fannyella rossi</em></td>
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<td>VLT (Italica XIX)</td>
<td>Ross Sea</td>
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<td>170º24.9’E</td>
<td>333-332</td>
<td>Agassiz</td>
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<td><em>Fannyella rossi</em></td>
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<td>TAN2004</td>
<td>Ross Sea</td>
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<td>-324</td>
<td>ORHT</td>
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<tr>
<td><em>Thouarella variabilis</em></td>
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<td>TAN0402</td>
<td>Ross Sea</td>
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<td>170º30.5’E</td>
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<td>OGT</td>
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<td><em>Thouarella variabilis</em></td>
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<td>OGT</td>
</tr>
<tr>
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<td>2004</td>
<td>TAN0402</td>
<td>Ross Sea</td>
<td>72º9.35’S</td>
<td>172º9.35’E</td>
<td>-525</td>
<td>OGT</td>
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Table 2. Radiometric results. The stable carbon isotope ($\delta^{13}$C) abundances are expressed in ‰. Radiocarbon age given in years before present (BP) where “present” is defined as AD 1950. BP errors are presented with a standard deviation of 2 sigma (95% probability), and are based on combined measurements of the sample, the background, and the standard of modern reference. Calibrated ages represent an age range of the Gregorian calendar (Anno Domini) and includes correction for local reservoir effects ($\Delta$R=928 ± 29 years). The $^{210}$Pb excess activities are expressed in Bq/kg. Colony age in years.

<table>
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<tr>
<th>Species</th>
<th>Sample nº</th>
<th>$\delta^{13}$C</th>
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<th>Cal. Age range AD</th>
<th>$^{210}$Pb excess</th>
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<td>&lt;7</td>
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<td>&gt;150</td>
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<td>80±5</td>
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Table 3. Summary of growth features of colonies used in this study. Radius length expressed in µm, colony age in years and Radial Growth Rate in µm yr\(^{-1}\); RGR average calculated from colonies FA6329, FA6336 and TV6388. *RGR given by \(^{210}\)Pb analysis.

<table>
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<tr>
<th>Sample ID</th>
<th>Radius</th>
<th>Colony age</th>
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<td>77</td>
<td>111</td>
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<td>7.7</td>
<td>74</td>
<td>126</td>
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<td>48*</td>
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<td>FA 6385</td>
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<td>51*</td>
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Table 4. Average element concentration in normalized %.

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Table 5. Inter-specimen elements’ correlation.

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<td>p-value</td>
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<td>p-value</td>
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Table 6. Review of reported/observed lifespan in octocorals *Subfossil. Depth in meters below the sea level, Lifespan in years and Radial Growth Rate in mm yr$^{-1}$. * Radial growth rate of gorgonians in this study expressed as µm yr$^{-1}$

<table>
<thead>
<tr>
<th>Species</th>
<th>Area</th>
<th>Depth</th>
<th>Lifespan</th>
<th>RGR</th>
<th>Technique</th>
<th>Reference</th>
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<tr>
<td><em>Coralium secundum</em></td>
<td>Hawaii</td>
<td>50-450</td>
<td>68-75</td>
<td>0.17</td>
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<td>Roark et al. 2006</td>
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<td>180</td>
<td>0.11</td>
<td>$^{210}$Pb</td>
<td>Druffel et al. 1990</td>
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<tr>
<td><em>Leiopathes glaberrina</em></td>
<td>Atlantic Ocean</td>
<td>250±70</td>
<td>0.5</td>
<td>Aminoacid racemization</td>
<td>Goodfriend 1997</td>
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<tr>
<td><em>Antipathes dichotoma</em></td>
<td>2377*</td>
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<td></td>
<td></td>
<td>Druffel et al. 1995</td>
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<tr>
<td><em>Corallium noibae</em></td>
<td>807, 450-</td>
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<td><em>Halipteris willemoesi</em></td>
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<td>Wilson et al. 2002</td>
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<td>Noé and Dullo 2006</td>
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<td>Andrews et al. 2005</td>
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<td>Noé et al. 2008</td>
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<td>30</td>
<td>0.4</td>
<td>Ring counting</td>
<td>Grigg, W.R. 1974</td>
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<td>&lt;10</td>
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<td>Matsumoto 2005</td>
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<td>Sherwood et al. 2005</td>
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<td>Sherwood et al. 2006</td>
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<td>Sherwood et al. 2009</td>
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<td><em>Primnoa resedaeformis</em></td>
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<td>400-900</td>
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<td>0.8</td>
<td>$^{14}$C, $^{210}$Pb, ring counting</td>
<td>Sherwood and Edinger 2009</td>
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<td><em>Paramuricea spp.</em></td>
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