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New insights on Antarctic gorgonians' age, growth and their potential as paleorecords

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ABSTRACT

Antarctic benthic communities have long been regarded as relicts of the past, since they have developed in a very stable environment and are formed by slow-growing and extraordinary long-lived organisms. However, little is known about the life history traits of gorgonian species, which are considered key components of the Antarctic benthos. In this study, age, Radial Growth Rates (RGR) and skeletal composition of *Thouarella variabilis*, *Fannyella abies* and *Fannyella rossii* colonies (Octocorallia, Primnoidae) that inhabit Antarctic shelf waters were examined. The radioisotopes ^{14}C and ^{210}Pb used for dating revealed that these colonies are long-lived, with ages spanning from 50 to 1100 years, thus confirming the archaic character of the Antarctic ecosystem. Some RGR obtained are among the lowest rates ever reported for primnoid species and gorgonians as a whole, with *Thouarella* species showing rates of 5.08 $\mu m\ yr^{-1}$. Growth ring deposition seemed to occur every 2–3 years on average, although this result cannot be confirmed. Irregularities in the growth rings could be observed under the Scanning Electron Microscope (SEM) as fluctuations in the skeletal composition, which may be indicative of changes in the environmental conditions, most possibly primary production.

1. Introduction

Antarctic benthic communities are archaic in structure and function, and can be compared to Paleozoic and deep-sea assemblages in their ecological functioning (Aronson et al., 2007). Primnoid gorgonians are, next to sponges, key components of such communities, playing an important role in structuring those habitats (Brandt et al., 2007). Indeed, an astonishingly diverse fauna of ophiuroids, asteroids, echinoids, pycnogonids, isopods, amphipods, nemerteans and gastropods can be found living in association with these sessile organisms (Arntz et al., 1992). However, and despite their key role in those benthic communities, gorgonians are among the least studied group of Antarctic macrofauna and little is known about their life history traits beyond taxonomic features (Gili et al., 2001).

Like any other modular organism, Primnoids – and octocorals in general – grow through the iterated replication of individual modules to form large, integrated individuals or colonies (Lasker et al., 2003). Estimation of age and growth rates of gorgonian species has generally been carried out by analysing the skeleton density bands observed in thin cross-sections at the base of the colony. Primnoids deposit a 2-part skeleton of calcium carbonate ($CaCO_3$) and gorgonin at different densities, resulting in apparent rings or bands (Barnes and Lough, 1993; Goldberg, 1976; Sherwood et al., 2005b). The reasons for such variations have been speculated upon, for which different suggestions have been made: (1) greater food availability during certain times of the year (Sherwood et al. 2005a, 2005b), (2) variations in the extent of the protein tanning (Goldberg, 1976) or even (3) structural requirements of the species (Lewis et al. 1992). An annual periodicity in the deposition of these bands has been reported in many species worldwide, like *Muricea californica* and *Muricea fructicosa* in Californian waters (Grigg, 1974), *Plexaura* sp. from Florida Reefs (Ward-Paige et al., 2005) and the Mediterranean red coral *Corallium rubrum* (Marschal et al., 2004; Weinbauer et al., 2000). More recently, radiometric dating techniques applied to the skeleton of the Primnoid species *Primnoa resedaeformis*, or the antipatharians *Stauropathes artica* and *Keratosis ornata*, revealed that these organisms are extraordinary long-lived and display a very defined pattern regarding the deposition of annual rings (Sherwood and Edinger, 2009; Sherwood et al., 2005b). Although no study has ever focused on Antarctic gorgonian's longevity, many marine sponges dwelling in Antarctic waters have proven to be extraordinary long-lived (Arntz et al., 1992; Dayton et al., 2013; Fallon et al., 2010), suggesting similar or even higher lifespans for Primnoid gorgonians.

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Previous works have revealed the likelihood that long-lived gorgonians and corals may have in explaining past environmental conditions through chemical traces left in their skeletons (Druffel, 1997; Sherwood et al., 2009; Thresher et al., 2010). In this sense, skeleton chemistry analyses performed over tropical species have revealed differences in daily light fluctuations (Lewis et al., 1992), lunar cycles and monthly tidal pressures (Risk et al., 2002; Tracey et al., 2007), surface productivity variations (Sherwood et al., 2005b) and annual seawater temperature oscillations (Thresher et al., 2010; Weinbauer et al., 2000).

Following the possibilities brought up by modern technologies, this study aims to investigate the longevity of Antarctic gorgonians through the analysis of their skeleton, understanding at the same time their growth patterns by analysing the skeletal composition of three Primnoid species that inhabit the shelf waters of the Antarctic realm.

2. Materials and methods

2.1. Study area

Gorgonians used in this study were sampled over the continental shelf of Weddell and Ross Seas (Fig. 1). The Antarctic continental shelf covers an area of over 4 million sq km, with depths ranging between 400 and 500 m, although depths over 1000 m have been recorded in specific regions (Dayton, 1990). The unusual depth of the Antarctic continental shelf resulted from ice grounding and scouring during the last glacial maximum and the consequent isostatic depression of the continent (Clarke, 1996). Antarctica's shelf environment is dominated by a marked seasonality, which is regulated by the extent of the sea-ice. The regression of the ice cover increases the amount of light reaching the seabed, and allows for a strong summer pulse of primary production (Clarke and Leakey, 1996b; Turner et al., 2009). In general, phytoplankton begins to bloom in mid-November, just as the area of open water and the availability of light begins to increase and eventually peaks in late December. After blooming for approximately six weeks, phytoplankton growth rates begin to diminish. At this time, loss processes such as grazing and sinking exceed rates of growth, causing Chl a abundance and primary production to decline steadily (Arrigo et al., 2008).

Sea-ice dynamics also play a key role in shaping the seafloor by providing large ice-rafted boulders (drop-stones) and patches of hard substratum, which later become suitable for the settlement of benthic organisms (Clarke, 1996). The seawater temperature is typically very low and stable, ranging between -1 and $+1$ °C. These conditions provoke that many taxa, elsewhere considered to

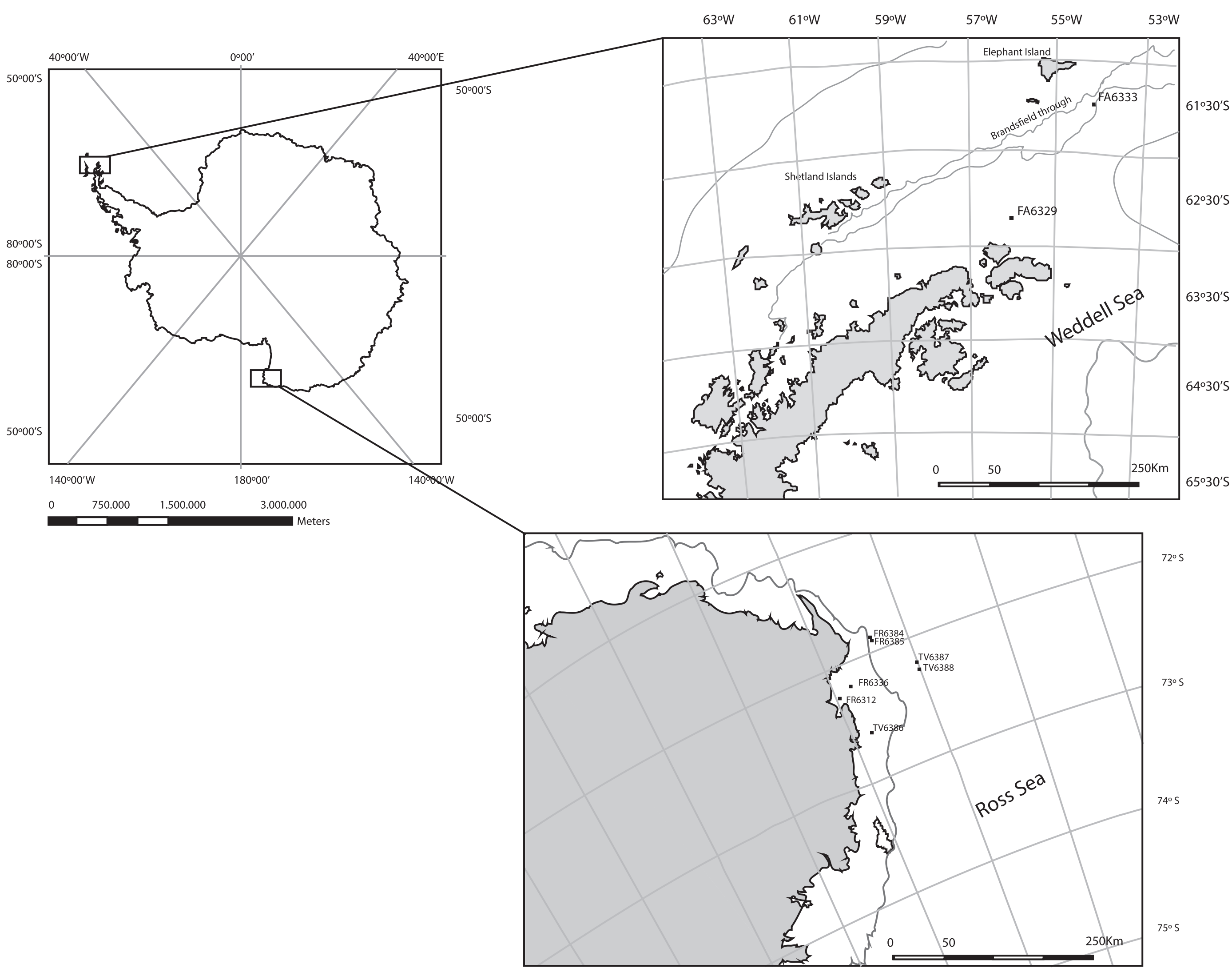

Fig. 1. Sampling locations.