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Age, Growth Rates, and Paleoclimate Studies of Deep-Sea Corals

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AGE, GROWTH RATES, AND PALEOCLIMATE STUDIES IN DEEP SEA CORALS OF THE USA

Nancy Grumet Prouty[1], E. Brendan Roark[2], Allen A. Andrews[3], Laura F. Robinson[4], Tessa Hill[5], Owen Sherwood[6], and Branwen Williams[7], Thomas Guilderson[8,9], & Stewart Fallon[10]*

[1]U.S. Geological Survey (* Corresponding Author: NProuty@usgs.gov)

[2]Texas A&M University

[3]NMFS Pacific Islands Fisheries Science Center

[4]University of Bristol

[5]University of California at Davis

[6]University of Colorado, Boulder

[7]Claremont Colleges

[8]Lawrence Livermore National Laboratory

[9]University of California, Santa Cruz

[10]Australian National University

I. Introduction

Deep-water corals are some of the slowest growing, longest-lived skeletal accreting marine organisms. These habitat-forming species support diverse faunal assemblages that include commercially and ecologically important organisms. Therefore, effective management and conservation strategies for deep-sea corals can be informed by precise and accurate age, growth rate, and lifespan characteristics for proper assessment of vulnerability and recovery from perturbations. This is especially true for the small number of commercially valuable, and potentially endangered, species that are part of the black and precious coral fisheries (Tsounis et al. 2010). In addition to evaluating time scales of recovery from disturbance or exploitation, accurate age and growth estimates are essential for understanding the life history and ecology of these habitat-forming corals. Given that longevity is a key factor for population maintenance and fishery sustainability, partly due to limited and complex genetic flow among coral populations separated by great distances, accurate age structure for these deep-sea coral communities is essential for proper, long-term resource management.

The importance of accurate age and growth characteristics has another important utility in marine sciences. Many deep-sea corals have been useful as biogeochemical proxies that provide a unique view of marine climate and environmental change over time (e.g., Adkins et al. 1998, Robinson et al. 2005, LaVigne et al. 2011). Similar to trees on land, many corals have concentric growth rings that allow scientists to track growth patterns, which can be used to look back into climate history over the coral's lifespan using stable and radio-isotope techniques. Here we summarize recent developments in determining age and growth characteristics for structure-forming deep-sea corals, many of which are vulnerable to disturbance, with highlights on recent advances in paleoclimate reconstruction efforts using deep-sea corals.

II. Age and Growth Rates

Age and growth rates of deep-sea corals have been determined by methods that differ greatly in approach and experimental design. These methods include tagging and outgrowth observations (often limited to shallower depths; Grigg 1976, Stone and Wing 2001, Peck and Brockington 2013), sclerochronology (counting of growth rings in the axial skeleton; Grigg 1974, Wilson et al. 2002, Marschal et al. 2004, Tracey et al. 2007, Aranha et al. 2013), and by radiometric techniques (Uranium/Thorium, Lead-210 and radiocarbon (^{14}C) dating; Cheng et al. 2000, Adkins et al. 2002, Andrews et al. 2009, Roark et al. 2009, Carreiro-Silva et al. 2013, Aranha et al. 2014).

When evaluating reported age and growth rates, it is important to evaluate the strengths and weakness of each method along with its applicability to the potential lifespan (**Figure 1**). These may include the limits of methodological dating and precision, as well as skeletal morphology and mineralogy. For example, in traditional tagging studies it is difficult to get accurate in-situ measurements and it can take many years to see measurable growth (Grigg 1976). Sclerochronology can provide estimates of age from visible growth rings in the skeletal structure (**Figure 2**), but this approach requires validation of the ring formation periodicity (Andrews et al. 2002; Sherwood et al. 2005). Radiometric techniques have different ranges for effective dating and usually require assumptions. With recent advances in Uranium/Thorium dating, it is possible to determine the age of aragonitic (a form of calcium carbonate) corals from less than a few decades old up to 600,000 years in age (Cheng et al. 2000). Typical uncertainty is variable and dependent upon various factors, but recent developments have reduced the uncertainty (Edwards et al. 1987, McCulloch and Mortimer 2008). Lead-210 dating is typically applicable to the last ~100 years with uncertainties as low as ± 10 years and is most applicable to determining a mean growth rate for the entire colony (Andrews et al. 2009). The range of conventional radiocarbon dating is from modern time (defined as 1950 AD) to ~50,000 years BP. While the method is effective, challenges exist in most applications because the atmospheric concentration of radiocarbon has varied over time (Stuiver and Brazunias 1993, Reimer et al., 2009). In the marine environment, radiocarbon ages are also corrected for the difference between the atmospheric radiocarbon content and the local radiocarbon content of the surface ocean, also known as a "reservoir correction." Age determination in deep-sea corals using radiocarbon dating is most applicable to growth occurring over centuries to millennia for living specimens, and extends into fossil specimens in the 10's of thousands of years

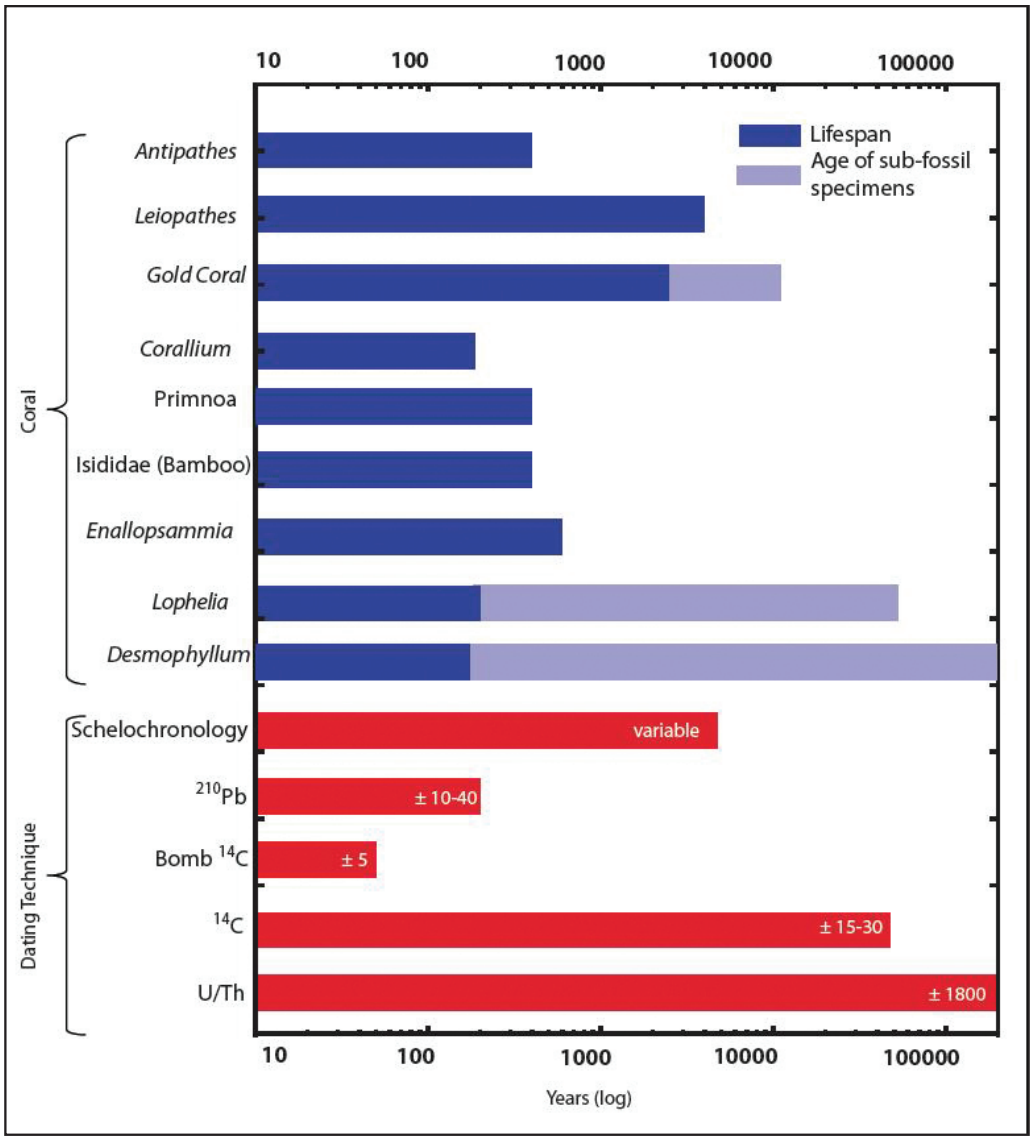

Figure 1. *Maximum lifespan (years) of several key deep-sea corals (blue), and the relative time span of efficacy for different dating techniques (red). Typical dating uncertainties listed for dating techniques.*

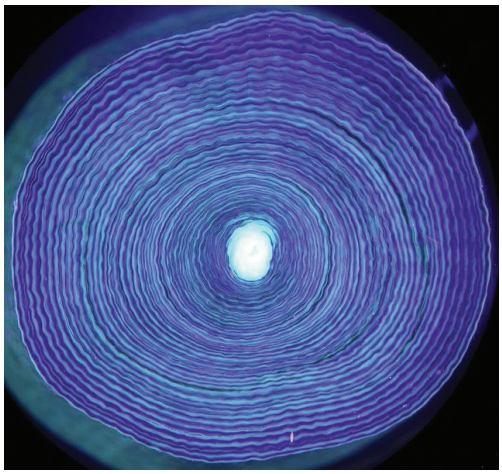

Figure 2. *Ultraviolet light illuminates the growth rings in a cross-section of a 44-year-old deep-sea coral (*Primnoa resedaeformis*) collected off the coast of Newfoundland at 400 meters. Similar to trees, cross-sections reveal coral-growth rings (photo by Owen Sherwood).*

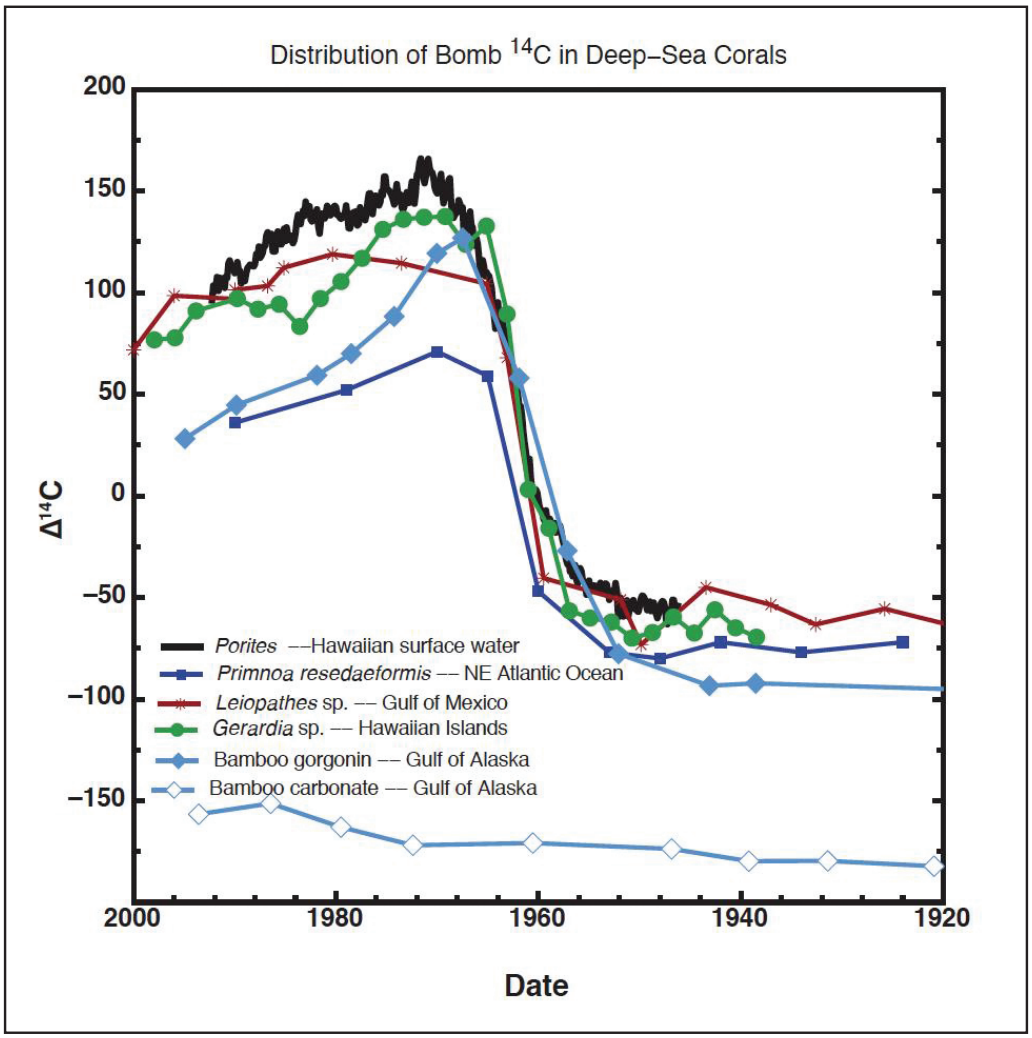

Figure 3. *Distribution of bomb-derived radiocarbon ($\Delta^{14}C$) in proteinaceous deep-sea corals illustrating the uptake and delivery of elevated $\Delta^{14}C$ in food sources (e.g., rapidly exported surface derived organic matter) to the deep-sea coral community. In comparison, the $\Delta^{14}C$ of the carbonate portion of the bamboo coral is not elevated and reflects the influence of ambient water with a $\Delta^{14}C$ signature equivalent to the surrounding dissolved inorganic carbon pool.*

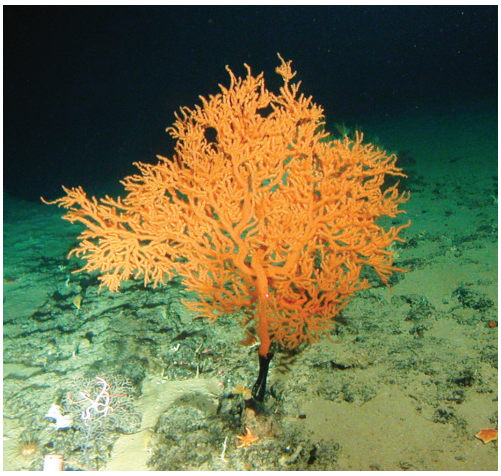

Figure 4. *Hawaiian black coral* Leiopathes annosa. *This species includes the oldest known coral. Photo credit: Hawaii Undersea Research Laboratory (HURL).*

(Guilderson et al. 2005). A second form of radiocarbon dating for some living deep-sea corals involves the identification of the anthropogenic bomb-radiocarbon signal from the testing of thermonuclear devices in the 1950s and 1960s. This method is sometimes referred to as bomb radiocarbon dating (**Figure 3**; Roark et al. 2005, Sherwood et al. 2005), which also has applications in the validation of fish age (Andrews et al. 2012).

Black coral

Black coral (**Figure 4**) represent a group of organisms that are some of the deepest dwelling and longest-lived species. Several species live in US territorial waters and most have been long lived (centuries to millennia). Wagner et al. (2012) summarized information on black coral growth and longevity. Longevity is particularly important within the black coral fishery (Parish et al., and Wagner et al. this volume) because age and growth rates are needed to determine sustainable yields. These typically shallower dwelling species appear to be faster growing than deeper species and growth rates have been measured based on axial extension rates, growth rings, radiocarbon (^{14}C) and lead-210 dating (Grigg 1976, Roark et al. 2006, Love et al. 2007, Risk et al. 2009). Estimated longevities for sampled Antipathes spp. ranged from ~ 12 - 140 years (Wagner et al. 2012). In contrast, deepwater black corals from Hawaii (*Leiopathes annosa*, reported as *Leiopathes* spp.) were found to have a potential lifespan in excess of 4000 years with a radial growth rate of less than 10 $\mu m \cdot yr^{-1}$ (Roark et al. 2006, 2009). Similar estimated growth rates and longevities (400 – 2100 years) have been reported for *Leiopathes* from the Gulf of Mexico (Prouty et al. 2011) and the southeastern United States (Williams et al. 2007), with variable growth rates documented from populations in the Azores (Carreiro-Silva et al. 2013).

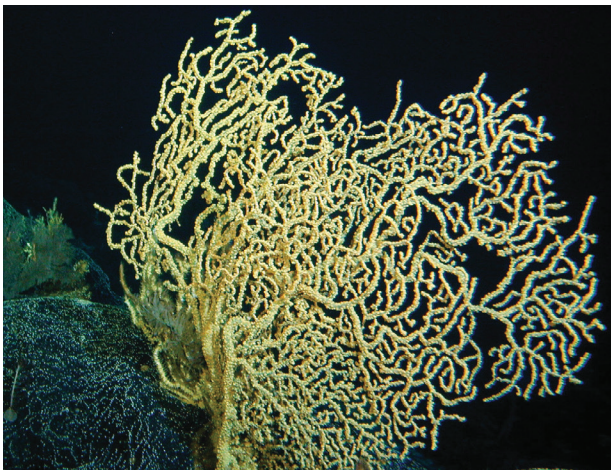

Figure 5. *The Hawaiian gold coral* Kulamanamana haumeaae. *Photo credit: HURL.*

Gold coral

The proteinaceous colonial parazoanthids (formerly known as *Gerardia* spp.), commonly referred to as gold corals, have similar longevity to that of *Leiopathes*. Numerous specimens (n=23) of the Hawaiian gold coral (*Kulamanamana haumeaae*) (**Figure 5**) dated by radiocarbon show lifespans up to 2740 years with an average radial growth rate of 41 ± 20 $\mu m \cdot yr^{-1}$ (Roark et al., 2006, 2009, Parish and Roark, 2009). These results are not in agreement with shorter lifespan estimates (max age ~70 years) and faster radial growth rates (~1 $mm \cdot yr^{-1}$) from presumed annual growth rings (Grigg 1974). A gold coral (identified as *Gerardia* sp.) specimen from Little Bahamas Bank in the Atlantic Ocean dated by amino acid dating (~250 ±70 years; Goodfriend et al., 1997) and by radiocarbon (1800 ±300 years; Druffel et al., 1995) also revealed similar age and growth discrepancies. Using radiocarbon and stable isotopes ($\delta^{13}C$, $\delta^{15}N$), Roark et al. (2009) showed that *K. haumeaae* are feeding almost exclusively on recently transported particulate organic carbon from surface waters and that skeletal growth utilizes this carbon. An in

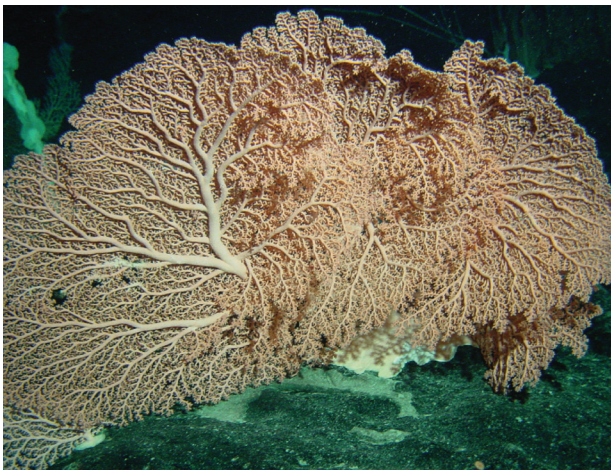

Figure 6. *The Hawaiian precious coral* Corallium laauense *(=*Hemicorallium laauense*). In the past, this species has been harvested for jewelry in Hawaii. Photo credit: HURL.*

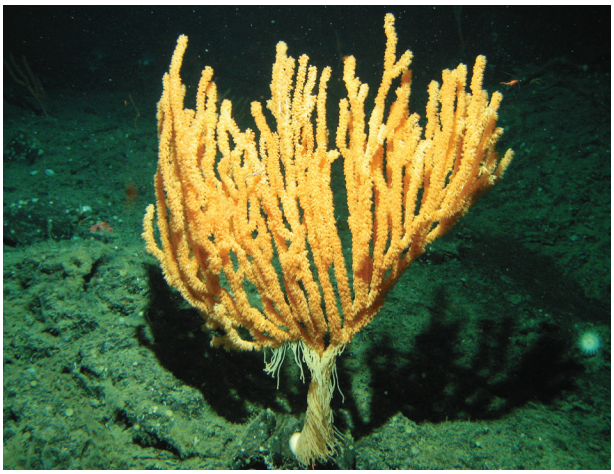

Figure 7. *The bamboo coral,* Isidella tentaculum*, from Giacomini Seamount in the Gulf of Alaska. Photo credit: NOAA and the Woods Hole Oceanographic Institution Alvin Group.*

situ tagging study by Parrish and Roark (2009) observed no measurable change in the size of Hawaiian gold coral colonies over nine years, which is consistent with the slow growth, long-lived age estimates using radiocarbon dating. Based on radiocarbon results, and counter indicative to sclerochronology estimates, the Western Pacific Fishery Management Council implemented a 5-year moratorium on gold coral harvesting in 2008, which was subsequently extended through 2018.

Precious coral

Corals in the Family Coralliidae (e.g., pink and red corals in the genus *Corallium*) have been a historical part the precious coral (**Figure 6**) fishery in many parts of the world, primarily in the Mediterranean and western north Pacific (Bruckner and Roberts 2009). Most of these fisheries have been strongly impacted by fishing effort that exceeds sustainable growth. Age estimates based on a variety of petrographic (carbonate structure) and organic band counting are generally consistent with ages estimated using radiometric techniques. Colony age estimates range between 50 and 180 years, with radial growth rates less than 1 $mm \cdot yr^{-1}$ (Druffel et al. 1990, Marschal et al. 2004, Andrews et al. 2005, Roark et al. 2006, Luan et al., 2013). In addition, deeper water *Corallium* species appear to grow more slowly than shallower species (Roberts et al. 2009), making them more vulnerable to exploitation. This has led to cautionary measures in some regions where deep-water *Corallium* is known to exist (DeVogelaere et al. 2005).

Bamboo and other octocorals

Radiocarbon and bomb-radiocarbon dating of living bamboo corals (Family Isididae) (**Figure 7**) range from 50 to 420 years and radial growth rates ranging 50 to 100 $\mu m \cdot yr^{-1}$ (Roark et al., 2005, Sherwood et al., 2009, Hill et al., 2011, Sinclair et al., 2011, Thresher et al. 2011, Farmer et al., 2015). Based on the timely response of the bomb radiocarbon signal, it is likely that there is a correspondence of growth with surface water productivity. A recent innovation in lead-210 dating using a higher

resolution approach provided age estimates of 50 to 100 years for bamboo coral in the NE Pacific (Andrews et al. 2009). Given that radial growth rates for this group appear to be less than 200 μm·yr^{-1}, this group is susceptible to disturbance and removal because recovery would take decades.

Red tree corals (Family Primnoidae) can reach over 2 m in height and are among the most important habitat-forming gorgonian corals in the Northeast Pacific and Northwest Atlantic. Maximum ages of live-collected red tree coral specimens from Eastern Canada (*Primnoa resedaeformis*) were ~ 78 -100 years (Sherwood et al., 2005, Sherwood and Edinger 2009) and from the Northeast Pacific (*Primnoa pacifica*) were ~ 119-185 years (Andrews et al., 2002, Aranha et al. 2014). Estimated average radial growth rates of *P. pacifica* of 320-360 μm·yr^{-1} were faster than those of the sister species, *P. resedaeformis*, in the Atlantic (Aranha et al. 2014). Sub-fossil (i.e., dead corals whose remains are not fully fossilized) specimens of *P. resedaeformis* were estimated to be at least 700 years old (Sherwood et al., 2006).

Ages and radial growth rates of other deepwater gorgonian corals have been reported for *Muricella* sp. (Family: Acanthogorgiidae; ~50 and 100 years; 100-200 μm·yr^{-1}) from the 100 m depth range in the tropical Pacific (Williams and Grottoli, 2010); and from the Northeast Atlantic, *Paramuricea* sp. (Family: Plexauridae; ~ 70 – 100 years; 92-205 μm·yr^{-1}; depth 814-850 m) and *Paragorgia arborea* (Family: Paragorgiidae; 80 years; 830 μm·yr^{-1}; depth 814-850 m) (Sherwood and Edinger 2009). From the Gulf of Mexico, Prouty et al. (2014b) reported life spans of over 600 years for *Paramuricea biscaya*, with radial growth rates between 0.34 μm yr^{-1} and 14.20 μm yr^{-1} and linear growth rates from 0.019 cm yr^{-1} to over 1 cm yr^{-1}.

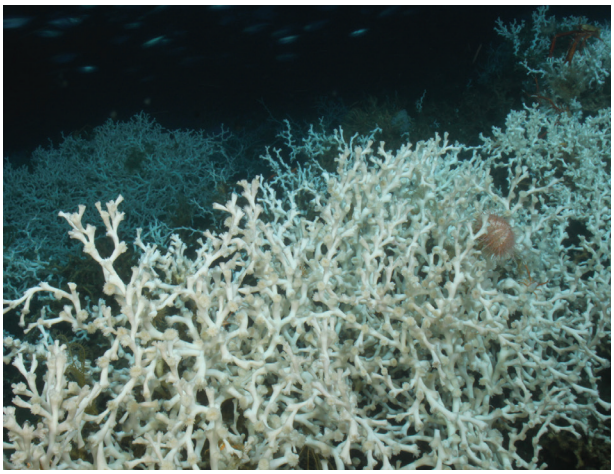

Figure 8. *Stony coral* Lophelia pertusa *in the Gulf of Mexico. Photo credit: NOAA & Bureau of Ocean Energy Management Lophelia II Project.*

Stony corals

A few species of scleractinian corals, especially *Lophelia pertusa* (**Figure 8**), *Solenosmilia variabilis*, and *Oculina varicosa*, (and to a lesser extent *Enallopsammia rostrata*, *E. profunda*, *Madrepora oculata* and *Goniocorella dumosa*) create deepwater coral reefs or bioherms. These massive and ancient structures can be up to 30 m high and 10's of kilometers in length (Reed 2004, Roberts et al. 2009). *Lophelia* reefs from lower latitudes, like those off of NW-Africa, the Mid-Atlantic Ridge and the Western Mediterranean Sea, indicate their structural growth represents 50,000 years of accumulation, according to U/Th dating (Schroder-Ritzrau et al., 2005). Higher latitude *Lophelia* carbonate mounds, appear to have gone through alternating cycles of accumulation and die off over periods of centuries that appear to be tied to changes in oceanographic conditions associated with glacial-interglacial cycles (Roberts et al. 2009) and the North Atlantic sub-polar gyre (Douarin et al. 2013). Individual colonies of *L. pertusa* from bioherms in the northeastern

Atlantic exhibited axial growth rates of 5-26 mm·yr^{-1} based on in situ measurements, aquaria observations, isotopic analyses and estimates of age inferred from growth on artificial structures (Mortensen and Rapp 1998, Mortensen 2001, Gass and Roberts 2006). Results with transplanted *L. pertusa* in the Gulf of Mexico exhibited axial growth rates of up to 16 mm·yr^{-1} with new polyps exhibiting higher growth rates and more mature polyps at rates of ≤5 mm·yr^{-1} (Brooke and Young, 2009). Observations of *L. pertusa* colonies on oil rigs and shipwrecks in the northern Gulf of Mexico (320-995 m depths) yielded minimum calculated growth rates ranging from 3.2 to 32.3 mm·yr^{-1} (Larcom et al. 2014).

Azooxanthellate *Oculina varicosa* has a geographically restricted distribution and forms reef-like structures in relatively shallow water (70 – 100 m). An axial branch growth rate of 16.1 mm·yr^{-1} was measured in-situ for *O. varicosa* at 80 m depth (Reed 1981). Similar axial growth rates were found for *Madrepora oculata* (14.4 ± 1.1 mm·yr^{-1}) using lead-210 dating for samples collected off Norway (Sabatier et al., 2011).

Solenosmilia variabilis is the dominant reef-building coral on seamounts in the southwest Pacific, where it occurs at depths significantly deeper than the Northern hemisphere *L. pertusa* reefs. Fallon et al. (2014) reported growth rates of from 0.84 – 1.25 mm·yr^{-1} linear extension for colonies collected between 958 and 1,454 m. The authors estimated a coral accumulation rate of ~ 0.27 mm·yr^{-1}, indicating that recovery from trawl damage would likely be extremely slow. Neil et al. (2011) found similar linear growth rates for *S. variabilis* in on Chatham Rise in New Zealand (ranging from 0.3 to 1.3 mm·yr^{-1}) and estimated that it could take 380 to 1,700 years for colonies to grow to a maximum height of 1 m.

Enallopsammia rostrata (Family Dendrophylliidae) is an aborescent stony coral that creates massive dendritic colonies up to 1 m wide and 0.5 m tall. Uranium-thorium dating of specimens from the Line Islands (Houlbreque et al., 2010), and lead-210 dating of a single North Atlantic specimen, have documented longevity up to ~600 years with axial extension rates of 5 mm·yr^{-1} a radial growth rate of ~0.07 mm·yr^{-1} near its base (Adkins et al., 2004). The structure of *E. rostrata* is prone to 'shedding' (natural limb loss) and as a consequence accurate estimates of axial growth rates are difficult to determine.

Other members of the stony corals have different growth structures. The solitary cup coral *Desmophyllum dianthus* has a slow axial extension rate of 0.5-2.0 mm·yr^{-1} based on lead-210, radiocarbon, and U/Th dating techniques (Cheng et al., 2000, Adkins et al., 2002, 2004).

III. Paleoclimate and Paleoenvironmental Studies using Deep-Sea Corals

The utility of deep-sea corals in understanding past climate variability is closely tied to accurately dating the corals specimens (Robinson et al., 2014). Equally important is the development of environmental proxies for the temperature and elemental composition of the water in which the coral grew. As such, a fundamental goal in deep-sea coral paleoclimate research has been to determine how environmental conditions are captured in the coral skeleton records. Both solitary and colonial, as well as calcitic and proteinaceous deep-sea coral species, are being used for climate change studies. Increased geographic distribution of sampling, coupled with advances in micro-analytical sampling techniques and recognition of novel

biogeochemical proxies, have advanced the field and are providing insights on climate variability at century to millennial time-scales.

Paleothermometry

Deep ocean circulation plays a vital role in modulating and stabilizing the Earth's climate system, because the deep ocean stores and transports heat. Using radiocarbon captured within the skeletons of deep-sea corals, researchers have examined how the ocean has behaved in the past, in terms of rates of circulation and carbon exchange between different water bodies (e.g., Mangini et al., 1998, Frank et al., 2004). Evidence from deep-sea coral records indicate that the deep ocean circulation can change abruptly, on timescales as short as 10 years (Adkins et al., 1998, Eltgroth et al., 2006). Such changes may have a major impact on global temperatures (Robinson et al., 2005), atmospheric carbon concentrations (Burke and Robinson, 2012), and deep-sea organisms (Sutherland et al., 2012). Recent studies also indicate that tracers, such as the isotopic composition of neodymium from living and fossil deep-sea coral species (*L. pertusa*, *D. dianthus* and *M. oculata*), may have value in reconstructing ocean circulation patterns, particularly those operating during the last 10,000 years (van de Flierdt et al., 2006, 2010, Copard et al., 2012, Lopez Correa et al., 2012, Montero-Serrano et al. 2013).

To understand historical climate and ocean circulation changes, it is critical to reconstruct changes in seawater temperature. Ocean temperature reconstructions are challenging because biological processes also affect skeletal chemical compositions. The chemical composition of the skeleton is thus controlled by two main factors: 1) the external environment (e.g., temperature), and 2) biological activity (referred to as 'vital' effects). In deep-sea corals, these vital effects may be larger than environmental controls in elemental tracers, such as oxygen isotopes ($\delta^{18}O$) or trace metal ratios (e.g., Mg/Ca), which are typically used as temperature proxies in other marine organisms. However, by taking an average of multiple analyses it is possible to calculate environmental temperatures from single specimens based on direct and indirect comparisons (Smith et al., 2000, Adkins et al., 2003, Hill et al, 2011). Additional methods that show promise for temperature reconstruction include the ratio of Mg/Li in coral skeletons (Case et al, 2010, Montagna 2014) and "clumped" carbon and oxygen isotopes that act independently of vital effects (Thiagarajan et al., 2011). One important caveat for all of these methods is that calculated uncertainties for the paleothermometry estimates can range from 0.5 to 2°C. The utility of reconstructing small-scale temperature changes in the deep-sea is limited by the precision of the technique as well as temporal precision and accuracy. Efforts are underway by a number of research groups to increase the precision and resolution with which deep-water temperatures can be reconstructed.

Nutrient and trophic level proxies

Proteinaceous deep-sea corals, such as black corals, gorgonians (e.g., *Primnoa* spp.), and the colonial zoanthids gold corals (formerly known as *Gerardia* sp.), derive their skeletal protein from recently exported particulate organic matter from the surface. From a compositional perspective, these corals are somewhat analogous to sediment traps, integrating the geochemical signature of recently exported organic matter into their slow growing skeletal structure. Useful geochemical signatures captured in skeletal protein include radiocarbon and stable carbon

($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes, which can be used to reconstruct nutrient sources and cycling as well as food web (trophic) dynamics through time. Elemental composition, such as phosphorus and barium, in both stony corals and gorgonians, can also be used in studies of seawater nutrients variability.

Nitrogen

With sufficient understanding of the nitrogen dynamics of a particular region, including the $\delta^{15}N$ of sinking and suspended particulate organic matter, skeletal $\delta^{15}N$ may be used in reconstructions of local trophic and/or nutrient dynamics. In the Gulf of Mexico and the South Atlantic Bight, marked increases over the past 75 years in coral skeletal $\delta^{15}N$ exceed 3‰, indicating there has been a higher contribution of terrestrial effluent to the deep sea (Williams et al. 2007). In the western tropical Pacific, multi-decadal decreases in $\delta^{15}N$ values from specimens at the base of the euphotic zone suggest a gradually shallowing of the nutricline (nutrient gradient) (Williams and Grotolli 2010). Off Tasmania, records of bulk $\delta^{15}N$ indicate relatively stable nutrient and trophic conditions over the past 250 years (Sherwood et al. 2009). In instances where the cause of skeletal stable isotopic variability is ambiguous, analysis of the $\delta^{15}N$ of amino acids ($\delta^{15}N$-AA) has emerged as a powerful tool to separate and independently track the effects of source nutrients, trophic transfers and microbial activity (McCarthy et al., 2007, Prouty et al., 2014a). Using *Primnoa resedaeformis* samples from Nova Scotia, Canada, Sherwood et al. (2011) pioneered the application of $\delta^{15}N$-AA to deep-sea corals, demonstrating a nutrient regime shift in the western North Atlantic since the 1970s. These studies underscore the broad potential for proteinaceous deep-sea corals in paleoceanographic studies linking nutrient and trophic variability to changes in global climate.

Phosphorous and Barium

In addition to using isotopic studies from proteinaceous corals as proxies for nutrient input to the deep sea, two elements that have also been used are phosphorus and barium. Phosphorus is a key nutrient in global primary productivity. It is utilized by organisms at the ocean surface and concentrates at depth. As a result, variations in seawater phosphorus reflect changes in surface ocean biological production and cycling (Montagna et al. 2006). As a proxy for seawater phosphate, phosphorus to calcium (P/Ca) ratios have been studied in the deep-sea coral *D. dianthus* (Montagna et al. 2006, Anagnostou et al. 2011). These global studies have shown a relationship between seawater phosphate and coral skeletal P/Ca ratios (Montagna et al. 2006, Anagnostou et al. 2011), suggesting that coral P/Ca has the potential to reconstruct variations in biological productivity on annual to decadal time-scales. Seawater barium, which also displays nutrient-like behavior in seawater, such that coral Ba/Ca ratios have the potential to trace the history of intermediate and deep-water refractory (slowly decomposed) nutrients, such as silica (Anagnostou et al. 2011, LaVigne et al. 2011, Sinclair et al. 2011).

Ocean Acidification

Ocean acidification is predicted to have profound implications for marine ecosystems partly because carbonate ions are an essential part of coral calcification. Changes to carbonate ion chemistry may particularly affect deep-water corals because carbonate levels are already low (Guinotte et al., 2006, Turley et al., 2007, Thresher et al., 2011). Instrument and modeling studies indicate

that seawater carbonate chemistry (carbon dioxide, pH, total dissolved inorganic carbon and alkalinity) is changing due to uptake of anthropogenic carbon dioxide (CO_2) from the atmosphere. In addition, it is likely that there were large changes during major climate events of the past. One way to examine the response of the ocean and deep-sea corals to large perturbations to the carbon cycle is to use geochemical proxies that record pH within the coral skeletons.

Boron isotopes ($\delta^{11}B$) in biogenic carbonates have been established as a proxy for seawater pH due to preferential uptake of the borate ion relative to boric acid as a function pH (Vengosh et al. 1991, Hemming and Hanson 1992). Experimental relationships between pH and $\delta^{11}B$ have been determined in both surface and deep-water scleractinian corals indicating a relationship between carbonate $\delta^{11}B$ and seawater pH (Reynaud et al., 2004, Blamart et al., 2007, Maier et al., 2009, Trotter et al., 2011, McCulloch et al., 2012a). However, $\delta^{11}B$ values higher than predicted for seawater pH have been observed in these studies (e.g., Vengosh et al., 1991, Blamart et al., 2007, Trotter et al., 2011). In an effort to reconcile these observations, scientists have found that aragonitic ($CaCO_3$) forming corals (e.g., stony corals) are able to regulate internal pH at the site of calcification (McCulloch et al., 2012a, 2012b). This may explain how some deep-sea corals can calcify at levels below the aragonite saturation horizon, which suggests deep-sea corals may be influenced less by decreasing seawater pH than originally thought (McCulloch et al., 2012a, 2012b; Hennige et al. 2015). Therefore, one must be cognizant of the fact that the research is evolving and presently there are conflicting results.

Challenges

The geochemical archives derived from deep-sea corals have enormous potential to help scientists decipher and describe changes and variability of paleoenvironmental and paleoceanographic conditions through time. However, it is inherently difficult to determine the accuracy of predictive relationships in the coral skeleton relative to the seawater environment from field data. Analyses of deep-water taxa are constrained by the challenges of collecting and sampling the organisms and sparse environmental data for use in validating relationships in ambient deep-sea environmental conditions. Deep-sea coral research is still in its infancy in terms of understanding variability between locations, depth strata, as well as taxonomic orders. For example, Thresher et al. (2010) suggest that adaptation to local conditions and hence a role for physiology at higher taxonomic levels may occur in deep-sea corals. Therefore challenges still exist to better constrain the species-dependent effect and to identify the causes of inter-species differences and intra-colony age and growth variability (Carreiro-Silva et al. 2013).

Studies employing advanced micro-analytical techniques have confirmed that micrometer scale heterogeneity influences the geochemical signal in deep-sea corals. Recent studies on stony corals show that the main differences in minor/trace element compositions, stable isotopes and organic compounds occur between calcification centers and fibrous aragonite (Gagnon et al 2007, Rollion-Bard et al., 2009, López Correa et al., 2010). Biomineralization processes exerting a strong biological control on the skeletal formation can overwhelm signals caused by environmental conditions (Adkins et al., 2003, Gagnon et al 2007). Systematic studies of the isotopic and

trace metal variation in various biocarbonates, combined with detailed studies of deep-sea coral skeletal structure are critically needed to decipher the role of "vital effects" on the application of these proxies to paleoclimate studies.

IV. New Directions

There are several new directions being pursued in an attempt to successfully use deep-sea corals as reliable archives of seawater chemistry and oceanographic proxies to climate change research. Given that many common tracers in the carbonate skeletons of deep-sea corals are strongly affected by physiological processes during biomineralization (i.e., "vital effects"), there is a need to increase our knowledge of the characteristics and mechanisms of vital effects. In other words, how can we tease apart the strong biological fractionation that is superimposed on the environmental signal? Focused studies, such as addressing the question of how the fluid reservoir from which calcification occurs is linked to the surrounding seawater, are becoming increasingly important as we refine our understanding of the various coral calcification models and strategies to reduce bias from vital effects. The introduction of micro-analytical sampling techniques, such as micromilling, ion microprobes, laser-ablation and highly focused synchrotron radiation, has made it possible to investigate coral intraskeletal variability of trace element and stable isotopic compositions directly related to the ultra-structure of the skeleton (Rollion-Bard et al., 2009, Thresher et al., 2009, 2010, Case et al 2010, López Correa et al., 2010, Sinclair et al., 2011). Therefore, we need to couple these high-resolution measurements to increase knowledge of present day processes affecting the coral communities.

As previously mentioned, from a compositional perspective, proteinaceous corals are somewhat analogous to sediment traps since they depend on surface-derived particulate organic matter. Therefore, age and growth studies should be accompanied by sediment trap studies that can clarify how the elemental and isotopic composition of particulate organic matter (i.e., food source) is captured or represented in the deep-sea coral skeletal chemistry. Additional focused studies should include the collection of appropriate coral specimens along with food sources and particulate and dissolved nutrients from the same location to clarify our understanding of feeding habits, prey type, timing and seasonality, as well as the impact of microbial activity of food sources on geochemical signatures encoded in corals. Examination of new specimens from different nutrient and oceanographic regimes, integration of isotopic and trace elemental geochemical signals, and use of new techniques such as the $\delta^{15}N$ of skeletal amino acids will aid in understanding past nutrient and trophic dynamics in the oceans, including reconstructions of source nitrogen variability and phytoplankton trophic and community structure.

A paramount challenge to the application and utilization of paleoenvironmental reconstructions using deep-sea corals is the precision, fidelity, and resolution of independently derived age-models (e.g., Komugabe et al., 2014), regardless of whether they are radiometric or based on sclerochronology. A particularly challenging time period is the 'near instrumental' period of the last several hundred years where radiocarbon is insensitive and sample size requirements make Th/U, in general, untenable for a well resolved chronology. Anthropogenic tracers with known or reconstructed emission histories (e.g., Pb, Pb-isotopes, As, Cd, Hg) and proxies of

disturbance events of known age may provide regional tie points (e.g., Schuster et al., 2002, Kelly et al., 2009) that could be coupled to radiometric chronologies. For example, Andrews et al. (2009) applied a refined lead-210 dating technique to yield relatively high-precision growth rate and age determinations for bamboo corals living during the last 100 years. Inter-disciplinary studies that use multiple chronological approaches with cross-validation of sclerochronological features are also necessary. Validation of the timing and cause of sclerochronological features have the potential to refine chronologies. Advances in deep-sea coral research continue to highlight the growing importance of deep-sea corals as reliable marine archives of climate change and other environmental cycles. Like their shallow-dwelling counterparts, deep-sea corals have also proven to be important archives of past ocean variability. While challenges still exist to providing reliable, reproducible records of climate variability, recent advances provide new opportunities and directions to close this gap.

Information on growth rate and life span of deep-sea corals is essential for conservation and management because the life history of these prominent organisms is either poorly understood or unknown. Validated age and growth of these organisms is the most fundamental information on susceptibility to disturbance or removal. Early estimates of age and longevity have been roughly determined, but more advanced techniques hold promise in not only determining longevity, but variations in growth through ontogeny (Andrews et al. 2009, Roark et al. 2009, Carriero-Silva et al. 2013). Assessment of the vulnerability of these long-lived, habitat-forming organisms to both natural and anthropogenic perturbations is of paramount importance because recovery may involve life history aspects that are not currently considered. Once some or many of these coral species are lost to damage or removal, many are not likely to return within our lifetime. Even in terms of minor damage, some arborescent corals have shown little to no recovery in nearly a decade of no disturbance (Krieger 2002, Williams et al. 2010). In addition, there is evidence that energy may be focused on regenerative growth within the broken colony in lieu of reproductive effort (Waller and Tyler 2005). For the longest-lived members of the deep-sea corals, perhaps it is prudent to take on a perspective of value in terms of world heritage, analogous to ancient terrestrial forests.

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