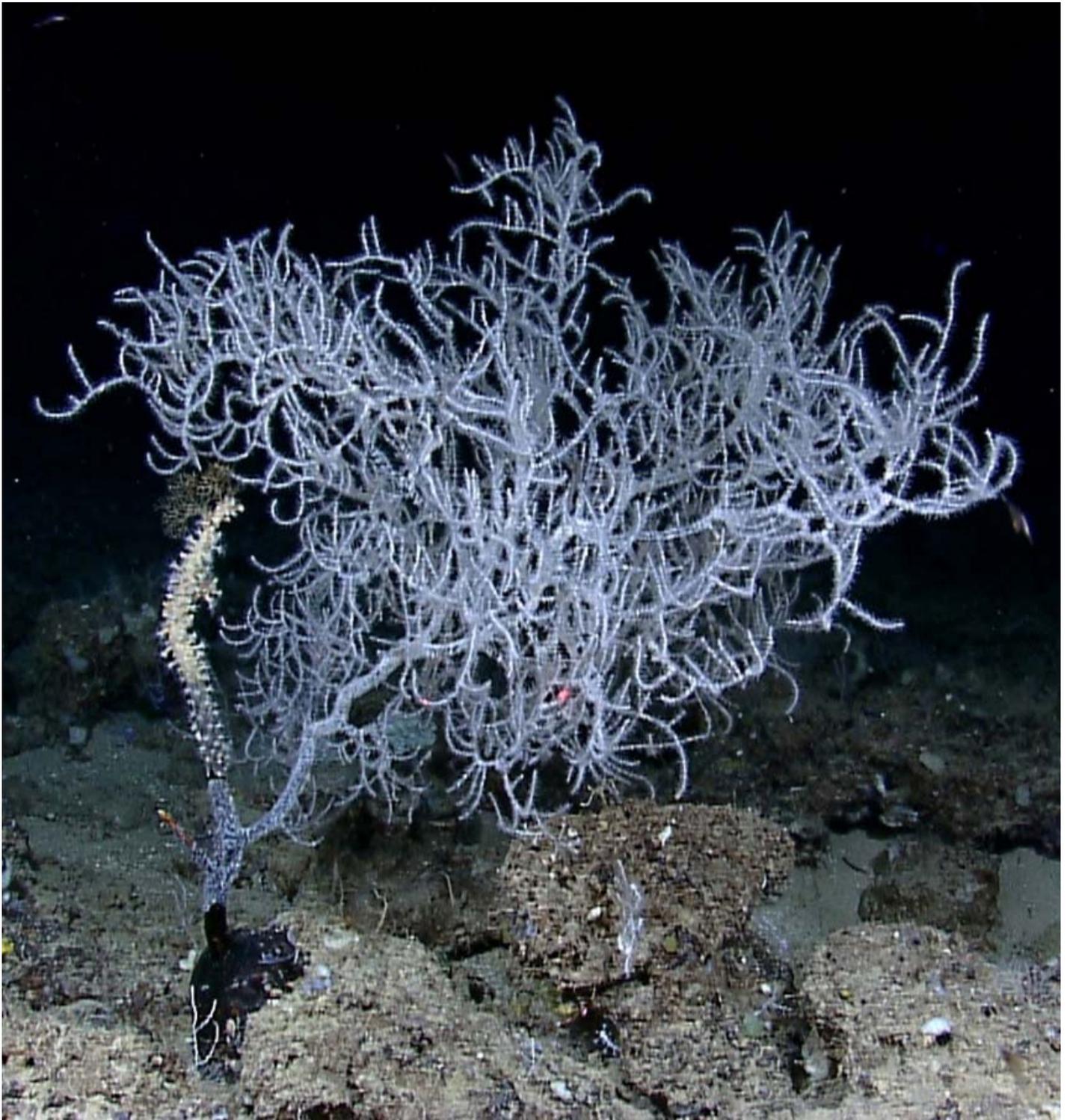


Age, Growth Rates, and Paleoclimate Studies in Deep-Sea Corals of the United States

Chapter 10 in The State of Deep-Sea Coral and
Sponge Ecosystems of the United States Report

Recommended citation: Prouty NG, Roark EB, Andrews AH, Robinson LF, Hill T, Sherwood O, Williams B, Guilderson T, Fallon S (2017) Age, Growth Rates, and Paleoclimate Studies in Deep-Sea Corals of the United States. In: Hourigan TF, Etnoyer, PJ, Cairns, SD (eds.). The State of Deep-Sea Coral and Sponge Ecosystems of the United States. NOAA Technical Memorandum NMFS-OHC-4, Silver Spring, MD. 22 p.
Available online: <http://deepseacoraldata.noaa.gov/library>.



Leiopathes black coral colony on the West Florida escarpment in the Gulf of Mexico. Red lasers visible near the middle of the image indicate that the basal axis of the colony is about 1.7 cm in diameter. This measurement suggests the coral colony is between 400-1000 years old, based on published growth rates for black corals in the Gulf of Mexico (Prouty et. al, 2011). Black corals in the genus *Leiopathes* are among the longest-lived marine organisms, reaching ages of thousands of years. Courtesy of the NOAA Office of Ocean Exploration and Research.



AGE, GROWTH RATES, AND PALEOCLIMATE STUDIES IN DEEP-SEA CORALS OF THE U.S.

Nancy G. Prouty^{1*},
E. Brendan Roark²,
Allen H. Andrews³,
Laura F. Robinson⁴,
Tessa Hill⁵, Owen
Sherwood⁶, Branwen
Williams⁷, Thomas
Guilderson⁸, and
Stewart Fallon⁹



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

¹ Pacific Coastal and Marine Science Center, U.S. Geological Survey, Santa Cruz, CA

* Corresponding Author:
NProuty@usgs.gov

² Department of Geography, Texas A&M University, College Station

³ NOAA Pacific Islands Fisheries Science Center, Honolulu, HI

⁴ School of Earth Sciences, University of Bristol, U.K.

⁵ Bodega Marine Laboratory, University of California, Davis

⁶ Institute of Arctic and Alpine Research, University of Colorado, Boulder

⁷ W.M. Keck Science Department, Claremont Colleges, Claremont, CA

⁸ Lawrence Livermore National Laboratory; University of California, Santa Cruz, CA

⁹ Research School of Earth Sciences, Australian National University, Canberra, Australia



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 Braziunas 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 tens of thousands of years (Guilderson et al. 2005). A second form of radiocarbon dating for some living deep-sea corals involves the identification of the

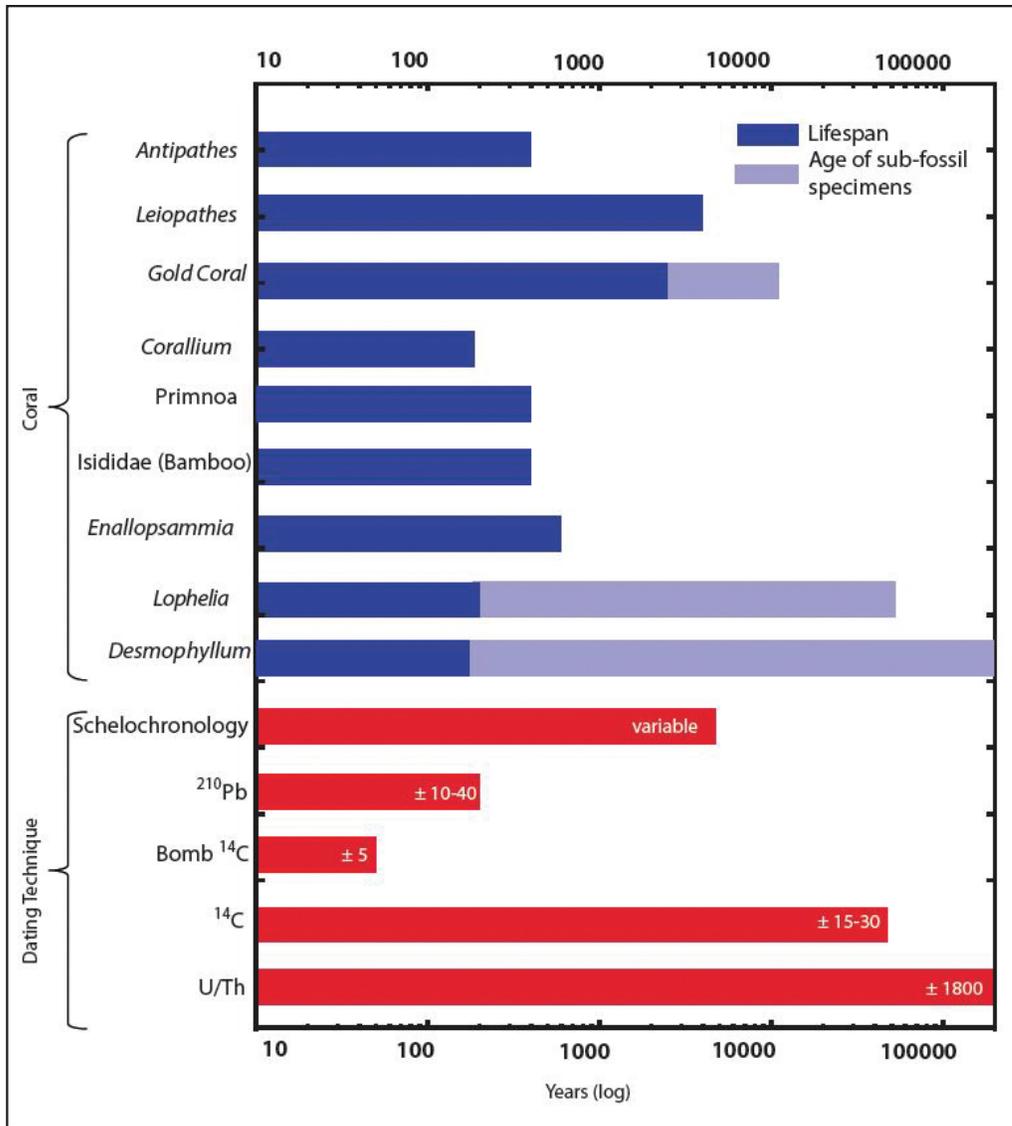
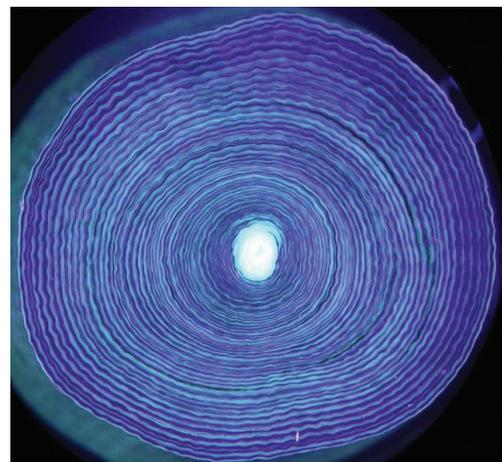


Figure 1. Maximum lifespan (years) of several key deep-sea corals (blue), and the relative time span of efficacy for different dating techniques (red). Typical dating uncertainties listed for dating techniques.

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).



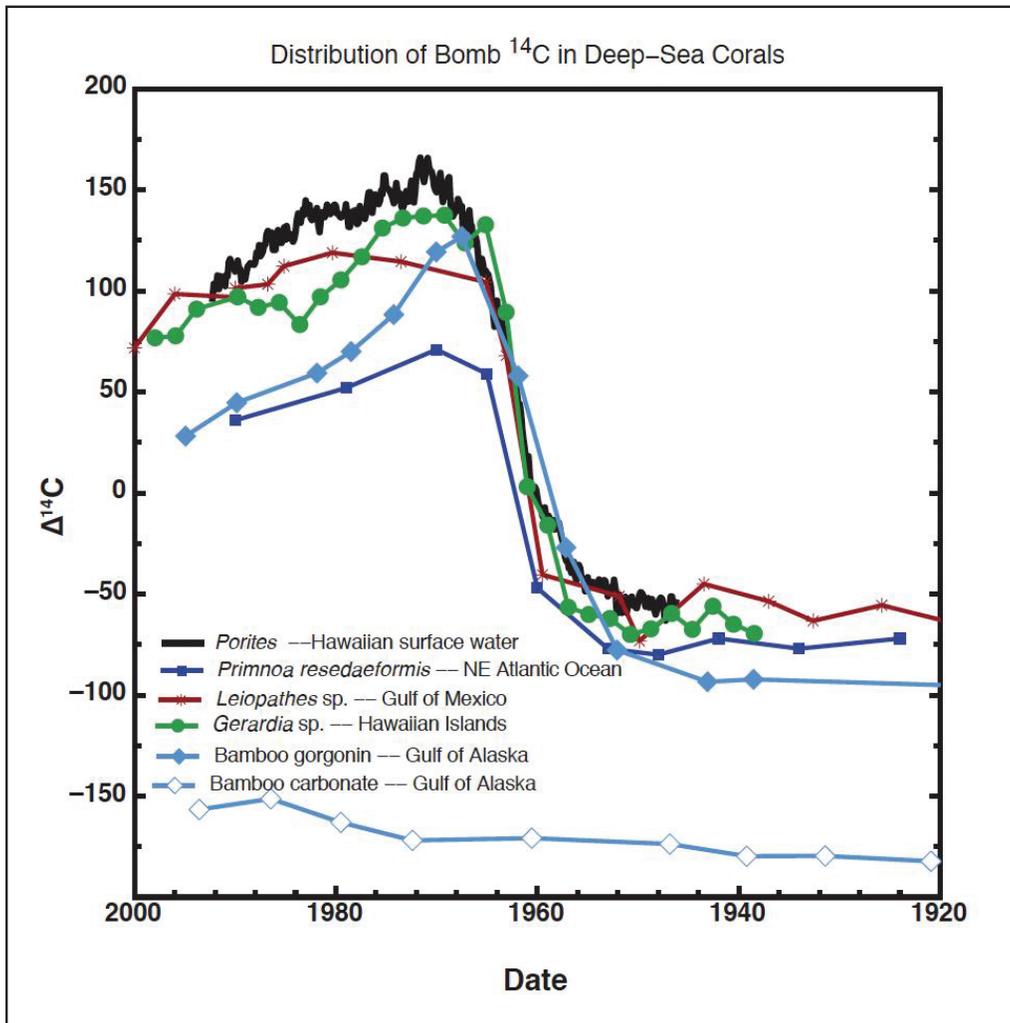
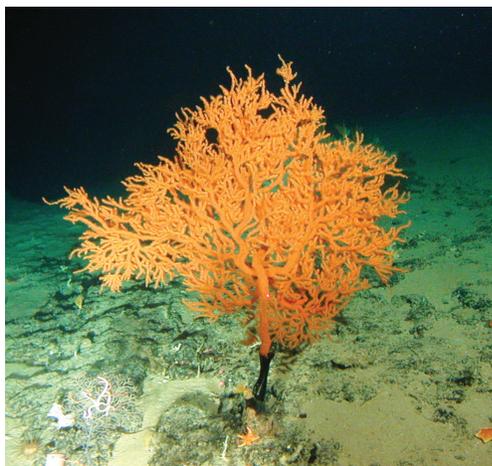


Figure 3. Distribution of bomb-derived radiocarbon ($\Delta^{14}\text{C}$) in proteinaceous deep-sea corals illustrating the uptake and delivery of elevated $\Delta^{14}\text{C}$ in food sources (e.g., rapidly exported surface derived organic matter) to the deep-sea coral community. In comparison, the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



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).

II.1. 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 U.S. 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 (Parrish 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 longevity 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 $10 \mu\text{m}\cdot\text{yr}^{-1}$ (Roark et al. 2006, 2009). Similar estimated growth rates and longevity (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).

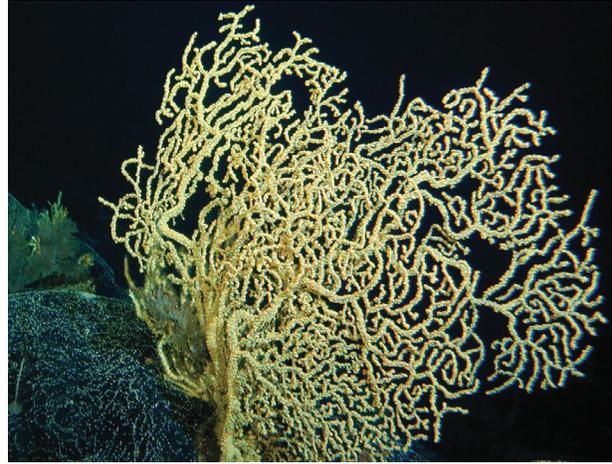
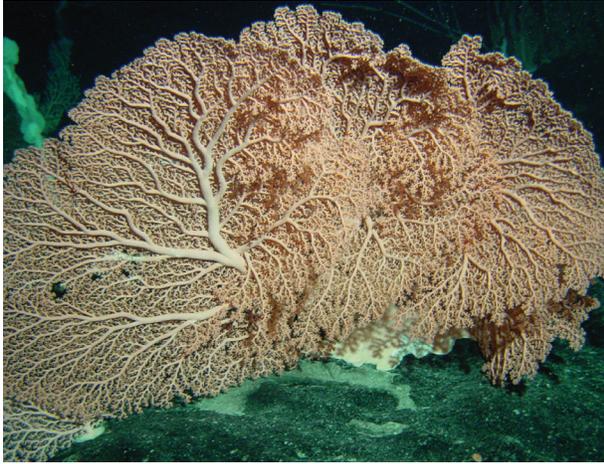


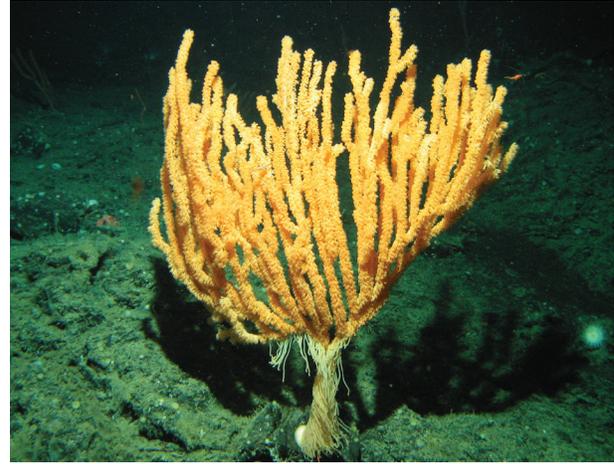
Figure 5. The Hawaiian gold coral *Kulamanamana haumea*. Photo credit: HURL.

II.2. 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 haumea*) (Figure 5) dated by radiocarbon show lifespans up to 2740 years with an average radial growth rate of $41 \pm 20 \mu\text{m}\cdot\text{yr}^{-1}$ (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 ($\sim 1 \text{ mm}\cdot\text{yr}^{-1}$) 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 ($\sim 250 \pm 70$ 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 ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), Roark et al. (2009) showed that *K. haumea* 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.

II.3. Precious Coral

Corals in the Family Coralliidae (e.g., pink and red corals in the genus *Corallium*) have been a historical part of 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 $1 \text{ mm}\cdot\text{yr}^{-1}$ (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).

II.4. Bamboo & Other Octocoral

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 $100 \text{ }\mu\text{m}\cdot\text{yr}^{-1}$ (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 $200 \mu\text{m}\cdot\text{yr}^{-1}$, 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 $320\text{-}360 \mu\text{m}\cdot\text{yr}^{-1}$ 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; $100\text{-}200 \mu\text{m}\cdot\text{yr}^{-1}$) 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; $92\text{-}205 \mu\text{m}\cdot\text{yr}^{-1}$; depth 814-850 m) and *Paragorgia arborea* (Family: Paragorgiidae; 80 years; $830 \mu\text{m}\cdot\text{yr}^{-1}$; 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 $0.34 \mu\text{m yr}^{-1}$ and $14.20 \mu\text{m yr}^{-1}$ 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 and Bureau of Ocean Energy Management Lophelia II Project.

II.5. Stony Coral

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.

III.1. 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 ($\delta^{18}\text{O}$) 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.

III.2. 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 ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) 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.

III.2.i – Nitrogen

With sufficient understanding of the nitrogen dynamics of a particular region, including the $\delta^{15}\text{N}$ of sinking and suspended particulate organic matter, skeletal $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ of amino acids ($\delta^{15}\text{N-AA}$) 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 $\delta^{15}\text{N-AA}$ 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.

III.2.ii – 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 used 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).

III.3. 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 (CO₂) 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 ($\delta^{11}\text{B}$) 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 of pH (Vengosh et al. 1991, Hemming and Hanson 1992). Experimental relationships between pH and $\delta^{11}\text{B}$ have been determined in both surface and deep-water scleractinian corals, indicating a relationship between carbonate $\delta^{11}\text{B}$ and seawater pH (Reynaud et al. 2004, Blamart et al. 2007, Maier et al. 2009, Trotter et al. 2011, McCulloch et al. 2012a). However, $\delta^{11}\text{B}$ 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 (CaCO₃) 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.

III.4. 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 $\delta^{15}\text{N}$ 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.

V. Literature Cited

- Adkins JF, Cheng H, Boyle EA, Druffel, ERM, Edwards RL (1998) Deep-sea coral evidence for rapid change in ventilation of the deep North Atlantic 15,400 years ago. *Science* 280: 725-728
- Adkins JF, McIntyre K Schrag DP (2002), The salinity, temperature, and $\delta^{18}\text{O}$ of the glacial deep ocean. *Science*, 298: 1769–1773
- Adkins JF, Boyle EA, Curry WB, Lutringer A (2003) Stable isotopes in deep-sea corals and a new mechanism for “vital effects”. *Geochim Cosmochim Acta* 67: 1129-1143
- Adkins JF, Henderson GM, Wang Sl, O’Shea S, Mokadem (2004) Growth rates of the deep-sea scleractinia *Desmophyllum cristagalli* and *Enallopsammia rostrata*. *Earth Planet Sci Lett* 227:481–490
- Anagnostou E, Sherrell RM, Gagnon A, LaVigne M, Field MP, McDonough WF (2011) Seawater nutrient and carbonate ion concentrations recorded as P/Ca, Ba/Ca, and U/Ca in the deep-sea coral *Desmophyllum dianthus*. *Geochim Cosmochim Acta* 75(9): 2529-2543



- Andrews AH, Cordes EE, Mahoney MM, Munk K, Coale KH, Cailliet GM, Heifetz J (2002) Age, growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. *Hydrobiologia* 471:101-110
- Andrews AH, Cailliet GM, Kerr LA, Coale KH, Lundstrom C, DeVoglaere A. (2005) Investigations of age and growth for three species of deep-sea coral from the Davidson Seamount off central California. In: Cold-water Corals and Ecosystems. Eds: A Freiwald and JM Roberts. Proceedings of the Second International Symposium on Deep Sea Corals. Erlangen, Germany. September 8-13 2003. Springer Berlin Heidelberg NY 965-982pp
- Andrews AH, Stone RP, Lundstrom CC, DeVoglaere AP (2009) Growth rate and age determination of bamboo corals from the northeastern Pacific Ocean using refined ²¹⁰Pb dating. *Mar Ecol Prog Ser* 397:173–185
- Andrews AH, DeMartini EE, Brodziak J, Nichols RS, Humphreys RL (2012) A long-lived life history for a tropical, deepwater snapper (*Pristipomoides filamentosus*): bomb radiocarbon and lead–radium dating as extensions of daily increment analyses in otoliths. *Can J Fish Aquat Sci* 69:1850-1869, 10.1139/f2012-109
- Aranha R, Edinger E, Layne G, Piercey G (2014) Growth rate variation and potential paleoceanographic proxies in *Primnoa pacifica*: Insights from high-resolution trace element microanalysis. *Deep-Sea Res Pt II* 99:213-226
- Blamart D, Rollion-Bard C, Meibom A, Cuif JP, Juillet-Leclerc A, Dauphin Y (2007) Correlation of boron isotopic composition with ultrastructure in the deep-sea coral *Lophelia pertusa*: Implications for biomineralization and paleo-pH. *Geochem Geophys Geosyst* 8(12): Q12001, doi: 10.1029/2007GC001686
- Brooke SD, Young CM (2009) In situ measurement of survival and growth of *Lophelia pertusa* in the northern Gulf of Mexico. *Mar Ecol Prog Ser* 397:153-161
- Bruckner AW, and Roberts GG (eds). (2009) Proceedings of the First International Workshop on *Corallium* Science, Management, and Trade. NOAA Tech Memo NMFS-OPR-43 and CRCP-8, Silver Spring, MD 153 p.
- Burke A, Robinson LF (2012) The Southern Ocean's role in carbon exchange during the Last Deglaciation. *Science* 335: 557-561
- Carreiro-Silva M, Andrews AH, Braga-Henriques A. de Matos V, Porteiro FM, Santos RS (2013) Variability in growth rates of long-lived black coral *Leiopathes* sp. from the Azores (Northeast Atlantic) *Mar Ecol Prog Ser* 473: 189–199
- Case DH, Robinson LF, Auro ME, Gagnon AC (2010) Environmental and biological controls on Mg and Li in deep-sea scleractinian corals. *Earth Planet Sci Lett* 300: 215-225
- Cheng H, Adkins J, Edwards RL, Boyle EA (2000), U-Th dating of deep-sea corals, *Geochim Cosmochim Acta* 64: 2401–2416
- Copard K, Colin C, Henderson GM, Scholten J, Douville E, Sicre MA, Frank N (2012) Late Holocene intermediate water variability in the northeastern Atlantic as recorded by deep-sea corals. *Earth Planet Sci Lett* 313, 34-44
- DeVoglaere AP, Burton EJ, Trejo T, King CE, Clague DA, Tamburri MN, Cailliet GM, Kochevar RE, Douros WJ (2005) Deep-sea corals and resource protection at the Davidson Seamount, California, U.S.A. pp. 1189-1198. In: Cold-water Corals and Ecosystems. Eds: A Freiwald and JM Roberts. Proceedings of the Second International Symposium on Deep Sea Corals. Erlangen, Germany. September 8-13 2003. Springer Berlin Heidelberg NY 965-982pp



- Druffel ERM, King LL, Belostock RA, Buesseler KO (1990) Growth rate of a deep-sea coral using Pb-210 and other isotopes. *Geochim Cosmochim Acta* 54:1493–1500
- Druffel ERM, Griffin S, Witter A, Nelson E, Southon J, Kashgarian M, Vogel J (1995) *Gerardia*: Bristlecone pine of the deep-sea? *Geochim Cosmochim Acta* 59(23): 5031-5036
- Edwards RL, Chen JH, Ku L, Wasserburg GJ (1987) Precise timing of the last interglacial period from mass spectrometric determination of thorium-230 in corals. *Science* 236:1547–1553
- Eltgroth S, Adkins JF, Robinson LF, Southon J, Kashgarian M (2006) A Deep-sea coral record of North Atlantic radiocarbon through the Younger Dryas. *Paleoceanography* 21: 10.1029/2005PA001192
- Expedition Scientists (2005) Modern carbonate mounds: Porcupine drilling. IODP Prel. Rept., 307. doi:10.2204/iodp.pr.307.2005
- Farmer JR, Robinson LF, Hönisch (2015) Growth rate determinations from radiocarbon in bamboo corals (genus *Keratoisis*) Deep Sea Research Part I: Oceanographic Research Papers 105: 124-40
- Frank N, Paterne M, Ayliffe L, van Weering T, Henriot JP, Blamart D (2004) Eastern North Atlantic deep-sea corals: tracing upper intermediate water Delta C-14 during the Holocene. *Earth Planet Sci Lett* 219: 297-309
- Gagnon AC, Adkins JF, Fernandez DP, Robinson LF (2007) Sr/Ca and Mg/Ca vital effects correlated with skeletal architecture in a scleractinian deep-sea coral and the role of Rayleigh fractionation. *Earth Planet Sci Lett* 261: 280–295
- Gass SE, Roberts JM (2006) The occurrence of the cold-water coral *Lophelia pertusa* (Scleractinia) on oil and gas platforms in the North Sea: Colony growth, recruitment and environmental controls on distribution. *Mar Pollut Bull* 52: 549-559
- Goodfriend GA (1997) Aspartic acid racemization and amino acid composition of the organic endoskeleton of the deepwater colonial anemone *Gerardia*: determination of longevity from kinetic experiments. *Geochim Cosmochim Acta* 61:1931–1939
- Grigg RW (1974) Growth rings: annual periodicity in two gorgonian corals. *Ecology* 55:876–881
- Grigg RW (1976), Fishery management of precious and stony corals in Hawaii, Rep. UNIH-SEAGRANT-TR-77-03, 48 pp., Univ. of Hawaii Sea Grant Progr., Honolulu.
- Guilderson TP, Cole JE, Southon JR (2005) Pre-bomb Suess effect in Cariaco Basin surface waters as recorded in hermatypic corals. *Radiocarbon* 47:57–65.
- Guinotte J, Orr J, Cairns S, Freiwald A, Morgan L, George R (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? *Front Ecol Environ* 4(3): 141-146
- Hennige SJ, Wicks LC, Kamenos NA, Perna G, Findlay HS, Roberts JM (2015) Hidden impacts of ocean acidification to live and dead coral framework. *Proc. Royal Soc. B* 282: 20150990
- Hemming N, Hanson G (1992) Boron isotopic composition and concentration in modern marine carbonates. *Geochim Cosmochim Acta* 56(1): 537-543



- Hill TM, Spero HJ, Guilderson, TP, LaVigne M, Clague D, Macalello S, Jang N (2011) Temperature and vital effect controls on bamboo coral (Isididae) isotope geochemistry: A test of the “lines method”. *Geochem Geophys Geosyst* 12: Q04008
- Houlbreque F, McCulloch M, Roark B, Guilderson T, Meibom A, Kimball J, Mortimer G, Cuif JP, Dunbar R (2010) Uranium-series dating and growth characteristics of the deep-sea scleractinian coral: *Enallopsammia rostrata* from the Equatorial Pacific. *Geochim Cosmochim Acta* 74:2380–2395
- Kelly AE, Reuer MK, Goodkin NF, Boyle EA (2009) Lead concentrations and isotopes in corals and water near Bermuda, 1780–2000,” *Earth Planet Sci Letters* 283: 93–100
- Komugabe AF, Fallon SJ, Thresher RE, Eggins SM (2014) Modern Tasman Sea surface reservoir ages from deep-sea black corals. *Deep Sea Research Part II: Topical Studies in Oceanography* 99:207-212
- Krieger KJ (2002) Coral (*Primnoa*) impacted by fishing gear in the Gulf of Alaska. pp. 106-116. In: *Proceedings of the First International Symposium on Deep Sea Corals*. Eds: JHM Willison, J Hall, SE Gass, ELR Kenchington, P Doherty, M Butler. Ecology Action Center, Halifax, Canada
- Larcom EA, McKean DL, Brooks JM, Fisher CR (2014) Growth rates, densities, and distribution of *Lophelia pertusa* on artificial structures in the Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers* 85:101-109
- LaVigne M, Hill TM, Spero HJ, Guilderson TP (2011) Bamboo coral Ba/Ca: Calibration of a new deep ocean refractory nutrient proxy. *Earth Planet Sci Lett* 312(3): 506-515
- López Correa, M, Montagna P, Vendrell B, McCulloch M, Taviani M (2010) Stable isotopes ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$), trace and minor element compositions of Recent scleractinians and Last Glacial bivalves at the Santa Maria di Leuca deep-water coral province, Ionian Sea. *Deep-Sea Res II* 57 (5/6): 471-486; doi:10.1016/j.dsr2.2009.08.016
- López Correa M, Montagna P, Joseph N, Ruggeberg A, Fietzke J, Flogel S, Dorschel B, Goldstein SL, Wheeler A, Freiwald A (2012) Preboreal onset of cold-water coral growth beyond the Arctic Circle revealed by coupled radiocarbon and U-series dating and neodymium isotopes. *Quaternary Sci Rev* 34: 24-43
- Love MS, Yoklavich MM, Black BA, Andrews AH (2007) Age of black coral (*Antipathes dendrochristos*) colonies, with notes on associated invertebrate species. *Bull Mar Sci* 80(2):391-400
- Luan NT, Rahman MA, Maki T, Iwasaki N, Hasegawa H (2013) Growth characteristics and growth rate estimation of Japanese precious corals. *J. Exp. Marine Biology & Ecology*. 441:117-125
- Maier C, Hegeman J, Weinbauer MG, Gattuso JP (2009) Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. *Biogeosciences* 6(8): 1671-1680
- Mangini A, Lomitschka M, Eichstadter R, Frank N, Vogler S, Bonani G, Hajdas I, Patzold J (1998) Coral provides way to age deep water. *Nature* 392: 347-348
- Marschal C, Garrabou J, Hermelin JG, Pichon M (2004) A new method for measuring growth and age in the precious red coral *Corallium rubrum* (L.). *Coral Reefs* 23: 423–432



- McCarthy M, Benner R, Lee C, Fogel M (2007) Amino acid nitrogen isotopic fractionation patterns as indicators of heterotrophy in plankton, particulate, and dissolved organic matter. *Geochim Cosmochim Acta* 71: 4727-4744
- McCulloch MT, Mortimer G (2008) Applications of the ^{238}U - ^{230}Th decay series to dating of fossil and modern corals using MC-ICPMS. *Aust J Earth Sci* 55: 955-965
- McCulloch MT, Falter J, Trotter J, Montagna P (2012a) Coral resilience to ocean acidification and global warming through pH up-regulation. *Nature Climate Change* doi: 10.1038/nclimate1473
- McCulloch MT, Trotter J, Montagna P, Falter J, Dunbar R, Freiwald A, Foerster N, Correa ML, Maier C, Ruggeberg A, Taviani M (2012b) Resilience of cold-water scleractinian corals to ocean acidification: Boron isotopic systematics of pH and saturation state up-regulation. *Geochim Cosmochim Acta* 87: 21-34 doi: 10.1016/j.gca.2012.03.027
- Montagna P, McCulloch M, Taviani M, Mazzoli C, Vendrell B (2006) Phosphorus in cold-water corals as a proxy for seawater nutrient chemistry. *Science* 312: 1788-1791, doi: 10.1126/science.1125781
- Montagna P, McCulloch M, Douville E, López Correa M, Trotter J, Rodolfo-Metalpa R, Dissard D, Ferrier-Pagès C, Frank N, Freiwald A, Goldstein S, Mazzoli C, Reynaud S, Rüggeberg A, Russo S, Taviani M (2014) Li/Mg systematics in scleractinian corals: Calibration of the thermometer. *Geochimica et Cosmochimica Acta* 132:288-310
- Montero-Serrano J-C, Frank N, Tisnérat-Laborde N, Colin C, Wu C-C, Lin K, Shen C-C, Copard K, Orejas C, Gori A, De Mol L, Van Rooij D, Reverdin G, Douville E (2013) Decadal changes in the mid-depth water mass dynamic of the Northeastern Atlantic margin (Bay of Biscay). *Earth Planet Sc Lett* 364:134-144
- Mortensen PB, Rapp HT (1998) Oxygen and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia pertusa* (L) (Anthozoa: Scleractinia): implications for determination of linear extension rates. *Sarsia* 83: 433-446
- Mortensen PB (2001) Aquarium observations on the deepwater coral *Lophelia pertusa* (L., 1758) (Scleractinia) and selected associated invertebrates. *Ophelia* 54:83-104
- Neil H, Tracey D, Clark MR, Marriot P (2011) Age and growth of habitat-forming *Solenosmilia variabilis* – an assessment of recovery potential. Presentation and abstract. In: “Understanding, Managing and Conserving our Marine Environment”, NZMSS Conference, Stewart Island, New Zealand, 5-8 July 2011.
- Parrish FA, Roark EB (2009) Growth validation of gold coral *Gerardia* sp. in the Hawaiian Archipelago. *Mar Ecol Prog Ser* 397:163-172
- Parrish FA, Baco AR, Kelley C, Reiswig H (this volume) State of Deep-Sea Coral and Sponge Ecosystems of the U.S. Pacific Islands Region. In: Hourigan TF, Etnoyer PJ, Cairns SD (eds.). State of Deep-Sea Coral and Sponge Ecosystems of the United States. NOAA Technical Memorandum NMFS-OHC-4, Silver Spring, MD
- Peck LS, Brockington S (2013) Growth of the Antarctic octocoral *Primnoella scotiae* and predation by the anemone *Dactylanthus antarcticus*. *Deep Sea Research Part II: Topical Studies in Oceanography* 92:73-78



- Prouty NG, Roark EB, Buster NA, Ross SW (2011) Growth-rate and age distribution of deep-sea black corals in the Gulf of Mexico. *Mar Ecol Prog Ser* 423:101-115
- Prouty NG, Roark EB, Koenig AE, Demopoulos AWJ, Batista FC, Kocar BD, Selby D, McCarthy MD, Mienis F (2014a) Deep-sea coral record of human impact on watershed quality in the Mississippi River Basin. *Global Biogeochemical Cycles*, DOI: 10.1002/2013GB004754
- Prouty, N.G. Fisher, C.R., Demopoulos, A.W.J., Druffel, E. (2014b) Growth rates and ages of deep-sea corals impacted by the Deepwater Horizon oil spill. *Deep-Sea Res II*. 10.1016/j.dsr2.2014.10.021
- Reed JK (1981) In situ growth rates of the scleractinian coral *Oculina varicosa* occurring with zooxanthellae on 6-m reefs and without on 80-m banks. *Proc.4th Int. Coral Reef Symp.* 2: 201-206
- Reed JK (2004) General description of deep-water coral reefs of Florida, Georgia and South Carolina: A summary of current knowledge of the distribution, habitat, and associated fauna. A Report to the South Atlantic Fishery Management Council, NOAA, NMFS, 71 p
- Reimer PJ, Baillie MGL, Bard E, Bayliss A, Beck JW, Blackwell PG, Bronk Ramsey C, Buck CE, Burr GS, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Hajdas I, Heaton TJ, Hogg AG, Hughen KA, Kaiser KF, Kromer B, McCormac FG, Manning SW, Reimer RW, Richards DA, Southon JR, Talamo S, Turney CSM, van der Plicht J, Weyhenmeyer CE (2009) IntCal09 and Marine09 radiocarbon age calibration curves, 0-50,000 years cal BP. *Radiocarbon* 51(4), 1111-1150
- Reynaud S, Hemming N, Juillet-Leclerc A, Gattuso, J (2004) Effect Of pCO₂ and temperature on the boron isotopic composition of the zooxanthellate coral *Acropora* sp. *Coral Reefs* 23(4): 539-546 doi: 10.1007/s00338-004-0399-5
- Risk MJ, Sherwood OA, Nairn R, Gibbons C (2009). Tracking the record of sewage discharge off Jeddah, Saudi Arabia, since 1950, using stable isotope records from antipatharians. *Mar. Ecol. Prog. Ser.* 397:219–226
- Roark EB, Guilderson TP, Flood-Page S, Dunbar RB, Ingram BL, Fallon SJ, McCulloch M (2005), Radiocarbon-based ages and growth rates of bamboo corals from the Gulf of Alaska, *Geophys Res Lett* 32: L04606, doi:10.1029/2004GL021919
- Roark EB, Guilderson TP, Dunbar RB, Ingram BL (2006) Radiocarbon-based ages and growth rates of Hawaiian deep-sea corals. *Mar Ecol Prog Ser* 327:1-14
- Roark EB, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA (2009) Extreme longevity in proteinaceous deep-sea corals. *PNAS* 106(13):5204-5208
- Roberts JM, Wheeler A, Freiwald A, Cairns S (2009) *Cold-water Corals: The Biology and Geology of Deep-sea Coral Habitats*. Cambridge University Press, Cambridge, 367pp
- Robinson LF, Adkins JF, Keigwin LD, Southon J, Fernandez DP, Wang SL, Scheirer DS (2005) Radiocarbon variability in the Western North Atlantic during the last deglaciation. *Science* 310:1469-1473
- Robinson LF, Adkins JF, Frank N, Gagnon AC, Prouty NG, Roark EB, van de Fliedert T (2014) The geochemistry of deep-sea coral skeletons: A review of vital effects and applications for palaeoceanography. *Deep-Sea Res Pt II* 99:184-198



- Rollion-Bard C, Vigier N, Meibom A, Blamart D, Reynaud S, Rodolfo-Metalpa R, Martin S, Gattuso JP (2009) Effect of environmental conditions and skeletal ultrastructure on the Li isotopic composition of scleractinian corals. *Earth Planet Sci Lett* 286(1):63-70
- Sabatier, P; Reyss, Jean-Louis; Hall-Spencer, Jason; Colin, Christophe; Frank, Norbert; Tisnerat-Laborde, Nadine; Bordier, L; Douville, Eric (2012) ^{210}Pb - ^{226}Ra chronology reveals rapid growth rate of *Madrepora oculata* and *Lophelia pertusa* on world's largest cold-water coral reef. *Biogeosciences*, 9:1253–1265
- Schröder-Ritzrau A, Freiwald A, Mangini A (2005) U/Th dating of deep-water corals from the eastern North Atlantic and the western Mediterranean Sea. In: Freiwald A, Roberts JM (eds) *Cold-water corals and ecosystems*. Springer, Heidelberg, 157–172pp
- Schuster PF, Krabbenhoft DP, Naftz DL, Cecil LD, Olson ML, Dewild JF, Susong DD, Green JR, Abbott ML (2002) Atmospheric mercury deposition during the last 270 years: A glacial ice core record of natural and anthropogenic sources. *Environ Sci Technol* 36:2303-2310
- Sherwood OA, Edinger EN (2009) Ages and growth rates of some deep-sea gorgonian and antipatharian corals of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences* 66:142-152
- Sherwood OA, Scott DB, Risk MJ, Guilderson TP (2005) Radiocarbon evidence for annual growth rings in the deep-sea octocoral *Primnoa resedaeformis*. *Mar Ecol Prog Ser*, 301:129-134
- Sherwood OA, Scott DB, Risk MJ (2006), Late Holocene radiocarbon and aspartic acid racemization dating of deep-sea octocorals. *Geochim Cosmochim Acta* 70:2806-2814
- Sherwood O, Thresher R, Fallon S, Davies D, Trull T (2009), Multi-century time-series of ^{15}N and ^{14}C in bamboo corals from deep Tasmanian seamounts: evidence for stable oceanographic conditions *Mar Ecol Prog Ser* 397:209-218
- Sherwood O, Lehmann M, Schubert C, Scott D, McCarthy M (2011), Nutrient regime shift in the western North Atlantic indicated by compound-specific ^{15}N of deep-sea gorgonian corals. *PNAS* 108(3), 1011-1015, doi/10.1073/pnas.1004904108.
- Sinclair DJ, Williams B, Allard G, Ghaleb B, Fallon S, Ross SW, Risk M (2011) Reproducibility of trace element profiles in a specimen of the deep-water bamboo coral *Keratoisis* sp. *Geochim Cosmochim Acta* 75(18): 5101-5121 doi: 10.1016/j.gca.2011.05.012
- Smith JE, Schwarz HP, Risk MJ (2000) Paleotemperatures from deep-sea corals: Overcoming 'vital effects'. *Palaios* 15:25-32
- Stone R and Wing B (2002) Growth and recruitment of and Alaskan shallow-water gorgonian. pp. 88-94. In: *Proceedings of the First International Symposium on Deep Sea Corals*. Eds: JHM Willison, J Hall, SE Gass, ELR Kenchington, P Doherty, M Butler. Ecology Action Center, Halifax, Canada
- Stuiver M, Quay PD (1981) Atmospheric ^{14}C changes resulting from fossil fuel CO_2 release and cosmic ray flux variability. *Earth Planet Sci Lett* 53:349–362
- Stuiver M, Braziunas TF (1993). Modeling Atmospheric C-14 Influences and C-14 Ages of Marine Samples to 10,000 BC. *Radiocarbon*, 35(1):137-189



- Sutherland WJ, Aveling R, Bennun L, Chapman E, Clout M, Côté IM, Depledge MH, Dicks LV, Dobson AP, Fellman L, Fleishman E, Gibbons DW, Keim B, Lickorish F, Lindenmayer DB, Monk KA, Norris K, Peck LS, Prior SV, Scharlemann JPS, Spalding M, Watkinson AR (2012) A horizon scan of global conservation issues for 2012, *Trends in Ecology and Evolution*, doi:10.1016/j.tree.2011.10.011
- Thiagarajan N, Adkins J, Eiler J (2011). Carbonate clumped isotope thermometry of deep-sea corals and implications for vital effects. *Geochim Cosmochim Acta* 75:4416-4425
- Thresher RE, MacRae CM, Wilson NC, Fallon S (2009) Feasibility of age determination of deep-water bamboo corals (Gorgonacea; Isididae) from annual cycles in skeletal composition. *Deep-Sea Res Part I* 56(3):442-449
- Thresher RE, Wilson NC, MacRae CM, Neil H (2010) Temperature effects on the calcite skeletal composition of deep-water gorgonians (Isididae). *Geochim Cosmochim Acta* 74:4655-4670
- Thresher R, Tilbrook B, Fallon S, Wilson N, Adkins J (2011) Effects of chronic low carbonate saturation levels on the distribution, growth and skeletal chemistry of deep-sea corals and other seamount megabenthos. *Mar Ecol Prog Ser* 442:87-99 doi: 10.3354/meps09400
- Tracey D, Neil H, Marriott P, Andrews AH, Calliet GM, Sanchez JA (2007) Age and growth of two genera of deep-sea bamboo corals (Family Isididae) in New Zealand waters. *B Mar Sci* 81:393-408
- Trotter J, Montagna P, McCulloch M, Silenzi S, Reynaud S, Mortimer G, Martin S, Ferrier-Pagès C, Gattuso JP, Rodolfo-Metalpa R (2011) Quantifying the pH vital effect in the temperate zooxanthellate coral *Cladocora caespitosa*: Validation of the boron seawater pH proxy. *Earth Planet Sci Lett* 303: 163-173 doi:10.1016/j.epsl.2011.01.030
- Tsounis G, Rossi S, Grigg, R, Santangelo G, Bramanti L, Gili JM (2010) The exploitation and conservation of precious corals. *Oceanogr Mar Biol Annu Rev* 48:161-212
- Turley C, Roberts J, Guinotte J (2007) Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? *Coral Reefs* 26(3):445-448
- van de Flierdt T, Robinson LF, Adkins JF, Hemming SR, Goldstein SL (2006) Temporal stability of the neodymium isotope signature of the Holocene to Glacial North Atlantic. *Paleoceanography* 21, 10.1029/2006PA001294
- van de Flierdt T, Robinson LF, Adkins JF (2010) Deep-sea coral aragonite as a recorder for the neodymium isotopic composition of seawater. *Geochim Cosmochim Acta* 74:6014-6032
- Vengosh A., Kolodny Y., Starinsky A., Chivas A, McCulloch, M (1991) Coprecipitation and isotopic fractionation of boron in modern biogenic carbonates. *Geochim Cosmochim Acta* 55(10):2901-2910
- Wagner D, Luck DG, Toonen RJ (2012) The biology and ecology of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). *Adv Mar Biol* 63:67-132



Wagner D, Opresko DM, Montgomery AD, Parrish FA (this volume) An Update on Recent Research and Management of Hawaiian Black Corals. In: Hourigan TF, Etnoyer PJ, Cairns SD (eds.). State of Deep-Sea Coral and Sponge Ecosystems of the United States. NOAA Technical Memorandum NMFS-OHC-4, Silver Spring, MD

Waller RG, Tyler PA (2005) The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic Ocean. *Coral Reefs* 24:514-522

Williams B, Risk M, Ross S, Sulak K (2007) Stable isotope records from deep-water antipatharians: 400-year records from the south-eastern coast of the United States of America. *Bull Mar Sci* 81(3):437-447

Williams B, Grottoli A (2010) Recent shoaling of the nutricline and thermocline in the western tropical Pacific. *Geophys Res Lett* 37: L22601 doi:22610.21029/22010GL044867

Williams A, Schlacher TA, Rowden AA, Althaus F, Clark MR, Bowden DA, Stewart R, Bax NJ, Consalvey M, Kloser RJ (2010) Seamount megabenthic assemblages fail to recover from trawling impacts. *Marine Ecology* 31:183-199

Wilson MT, Andrews AH, Brown AL, Cordes EE (2002), Axial rod growth and age estimation of the sea pen, *Halipteris willemoesi* Kölliker. *Hydrobiologia* 471:133- 142