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Front Cover: Rice Bay Formation, looking southwest along Grotto Beach. Photograph by Sandy Voegeli.

Back Cover: Dr. John Milliman, The College of William and Mary. Keynote Speaker for the 13th Symposium. Photograph by Sandy Voegeli.

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TESTING THE DEEP FORM OF THE IVORY TREE CORAL, *OCULINA VARICOSA*, AS A PROXY FOR INTERMEDIATE/BOTTOM WATER VARIATION: OCULINA BANKS, FLORIDA, USA

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ABSTRACT

Deep-water corals grow worldwide and are noted for their ability to grow without the aid of algal symbionts at depths that can exceed 5000 m. Like zooxanthellate shallow-water species, deep-water corals are currently being assessed as potential paleoclimate archives. Because their environmental conditions are thought to be relatively more stable than that of shallow-water corals, and because they lack zooxanthellae, isotopic analyses of deep-water corals are thought to yield “cleaner” signals and serve as intermediate and bottom-water proxies for ocean circulation change, that then may be linked to changes in climate. *Oculina varicosa* is the dominant scleractinian coral on the Oculina Bank and the species responsible for construction of the extensive system of high-relief coral pinnacles and ridges off the east coast of central Florida. These corals grow at depths between 70 and 100 m and are subject to the combined effects of the Florida Current/Gulf Stream and Florida Straits upwelling water masses. This study compared the oxygen and carbon isotopic composition of a specimen of this species with a year-long record of surface temperature, bottom temperature, and bottom current velocity from the area in a pilot study to assess the species’ ability to geochemically sense fluctuations in these water masses. Oxygen isotopes ranged between -2.6 and 1.0 ‰ PDB, and carbon isotopes ranged between -6.9 and 2.1 ‰ PDB. Isotopic trends indicate a 2.5 to 3.0 cm per year growth cycle, nearly doubling previous estimates. Mean temperatures of aragonite precipitation calculated from two temperature equations derived for marine carbonates fell within 4.7 °C and 2.7 °C of the observed mean

bottom temperature when values of $\delta^{18}\text{O}_w$ were estimated as 0‰ and -0.5‰, respectively. Isotopic trends in *O. varicosa* generally reflect bottom temperature trends and periods of nutrient influx triggered by eddies from the Florida Current and upwelling from the Florida Straits. Discrepancies in derived precipitation temperatures might be attributed to isotope fractionation (which may render available temperature equations inapplicable); however, the similarity between the isotope and temperature profiles suggests fractionation might be constant, as seen in other corals. Alternatively, derived temperature discrepancies might be attributed to the expansion of a year-long record of bottom temperature to a 3-year record of coral growth, as well as the lack of seawater oxygen isotope data for the Oculina Banks region. By measuring bottom temperature over a longer time period and building a database of seawater $\delta^{18}\text{O}$ from multiple depths in this region, these two issues can be resolved.

INTRODUCTION

Coral Ecosystems and Biology

While corals typically inhabit shallow-marine tropical waters, recent research has explored the presence of deep-water coral ecosystems worldwide ranging from shelf to abyssal depth (Roberts et al., 2006). Although the existence of deep-water corals has been recognized for centuries, only recent technological developments have allowed for the detailed exploration and study of these ecosystems. To date, they have been documented globally, ranging from sparse colonies of individual hard- and soft-coral

species to dense frameworks that support major fisheries.

Deep-water corals are primarily azooxanthellate and rely on nutrients obtained directly from the water column. As a result, colonies are often found in association with pockets of high productivity, such as regions of upwelling, ocean circulation currents, and cold-water seeps (Roberts et al., 2006). However, some species are apozooxanthellate, or facultatively zooxanthellate, and can convert between a zooxanthellate and azooxanthellate growth form based on the existing environmental conditions. These species have been documented at depths ranging from 3 to 100 m in Bermuda and on the eastern Florida Shelf.

Isotope Analyses

In recent years, deep-water corals have been isotopically analyzed to determine their use as paleoclimate archives, with much of the work concentrating on the scleractinians *Lophelia pertusa* and *Desmophyllum dianthus*. The absence of zooxanthellae in these taxa and their position in deeper waters buffered from relatively dynamic surface conditions, were cited as indications that kinetic and vital effects would not be as strong a factor in the interpretation of their isotopes as has been the case with shallow-water corals. However, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the aragonite in deep-water corals have been found to be more depleted relative to their environment (Mikkelsen et al., 1982; Freiwald et al., 1997; Spiro et al., 2000). Wefer and Berger (1991) hypothesized that differences in the $\delta^{13}\text{C}$ signature of dissolved inorganic carbon (DIC) between shallow- and deep-water regions could be a potential cause. The same line of reasoning could also be applied to $\delta^{18}\text{O}$ from dissolved oxygen (DO). Although sinking organic matter would carry with it $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from the surface, remineralization and oxidation/reduction reactions occurring at the bottom are hypothesized to alter these values, particularly in areas affected by upwelling and deep-water circulation (Mooers and Feichter, 2005). Aragonite precipitation and feeding would integrate these values

within the coral skeleton with metabolic processes, potentially further fractionating the isotopes.

Differences in carbon and oxygen isotope composition, both between individuals of the same species and age, and between samples from the same individual, have been documented in several coral species, further complicating the interpretation of deep-water coral isotopes (Spiro et al., 2000; Smith et al., 2000; Smith et al., 2002). Variations revealed by UV fluorescence in the aragonitic microstructure of individual *Lophelia pertusa* are cited as a possible cause for such isotope differences. These variations are shown to be minimized when using secondary ion mass spectrometry (SIMS) and ion microprobe sampling procedures (Blamart et al., 2005).

Finally, when the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of deep-water corals are plotted against one another, they often form a near linear regression (Emiliani et al., 1978; Mikkelsen et al., 1982; Swart, 1983; Spiro et al., 2000; McConnaughey, 2003). Romanek et al. (1992) suggested that $\delta^{13}\text{C}$ signals from aragonite should be generated independently of temperature, an idea that was confirmed later by Smith et al. (2000). It was therefore hypothesized by Spiro et al. (2000) that the precipitation of both isotopes must be linked. They further concluded that because salinity and temperature are relatively stable in deep-water environments compared to that of shallow-water environments, and because photosynthesis is not a controlling factor for ahermatypic corals, the elimination of these variables would be expected to stabilize $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals in the aragonite. Isotopic composition should therefore be affected primarily by coral metabolism and not by independent, external variables.

Despite the apparent difficulties in interpreting the isotope records of deep-water corals, their potential as proxies of bottom water variation warrants further research, with emphasis on studying a wider variety of species. *Oculina varicosa* is an apozooxanthellate coral species common to the eastern Florida Shelf and is the ahermatypic reef builder of the Oculina Bank on the Florida Shelf margin. Little has been done to understand its biology and potential as an envi-

ronmental proxy; however the position of *Oculina* Banks on the margin of the Florida Shelf, combined with its exposure to the Florida Current above and upwelling from the Florida Straits below make it worthwhile to determine the potential of this species as a proxy for variation in these water masses.

OCULINA BANKS, FLORIDA

Oculina Banks is a north-south trending, deep-water reef structure extending nearly 170 km north to south along the eastern Florida shelf of the United States (Reed, 2002; Figure 1). The region is dominated by high-relief coral pinnacles, mounds, and ridges ranging in elevation from 3-35 m above the surrounding substrate. Substrates underlying the coral framework consist of sand and mud sediments, disarticulated coral debris, and oolitic limestone formed during the Holocene transgression (Macintyre and Milliman, 1970; Reed, 1980).

The high-relief structures are capped by colonies of the apozooxanthellate ivory tree coral, *Oculina varicosa* (sometimes misidentified as *Oculina valenciennesi*). Their distribution varies in depth from 70 to 100 m. At these depths they display their azooxanthellate deep-water morphology (Figure 2-3), with stem and branches generally less than 1 cm in diameter. This differs from their shallow-water zooxanthellate morphology found off the coast of Ft. Pierce and in Bermuda, where stem and branch diameters average 1.5 cm or more. *Oculina varicosa* has been known to expel its zooxanthellae during times of stress, and has been documented converting to its deep-water morphology after being transplanted from the shallows (Reed, 1981).

In this setting, bottom temperatures average 16.2 °C, but can decrease to as low as 7.4 °C during periods of upwelling from the Florida Straits (Reed, 1981; Smith, 1981; and Reed, 1983). Bottom currents average 8.6 cm s⁻¹ and can exceed 50 cm s⁻¹ when the Florida Current reaches its maximum velocity (Reed, 1981; and Hoskin et al., 1983).

Nutrient-rich water upwells from the

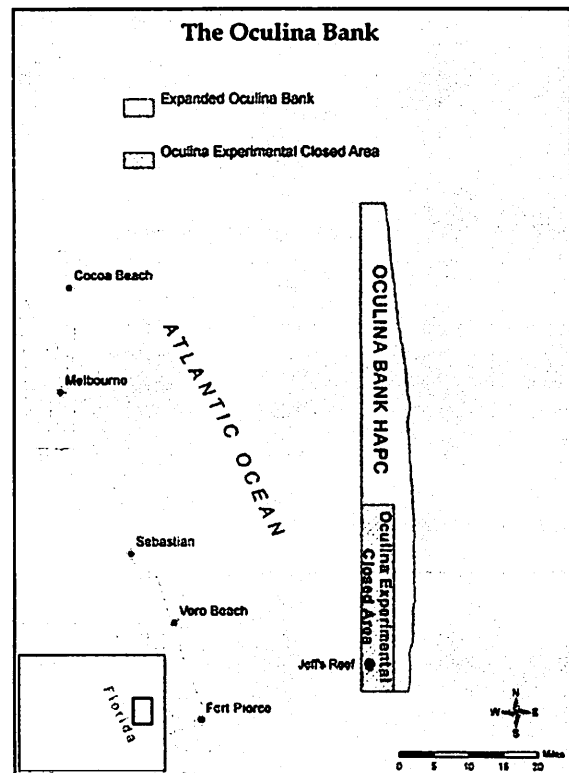


Figure 1. The Oculina Bank, FL (courtesy of A. Shepard, UNC-Wilmington).

Florida Straits periodically throughout the year, with stronger pulses during the winter months (Mooers and Fiechter, 2005; personal comm.). Surface eddies from the Florida Current/Gulf Stream have a 4-7 day frequency, and are more frequent in the winter. Using mesoscale numerical modeling of primary productivity based on physical and biologic observations in the region, Mooers and Fiechter (2005, personal comm.) predicted that while nutrient supplies are relatively constant throughout the year, nutrient loading would occur in the winter, suggesting a strong interaction between the upwelling and eddy water masses.

The combination of nutrient availability and the presence of the corals support a dense macroinvertebrate fauna, that in turn supports a diverse fish population including a number of economically important species (Reed, 2002). However, despite the designation of *Oculina* Banks as a Habitat of Particular Concern in 1984 (expanding from 315 km² to 1029 km² in 2000),

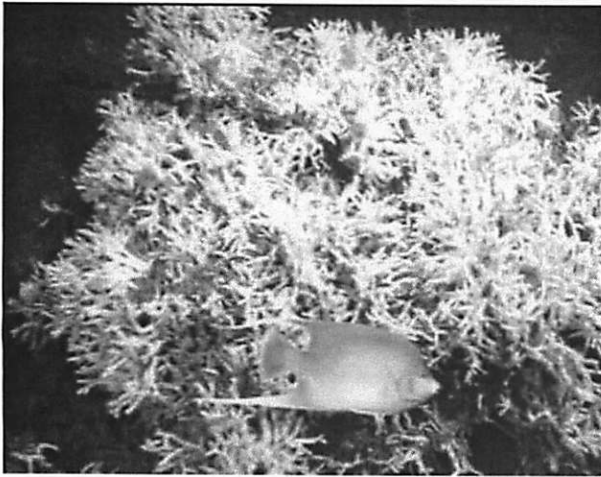


Figure 2. *Oculina varicosa* colony. Courtesy of NURC-UNCW.

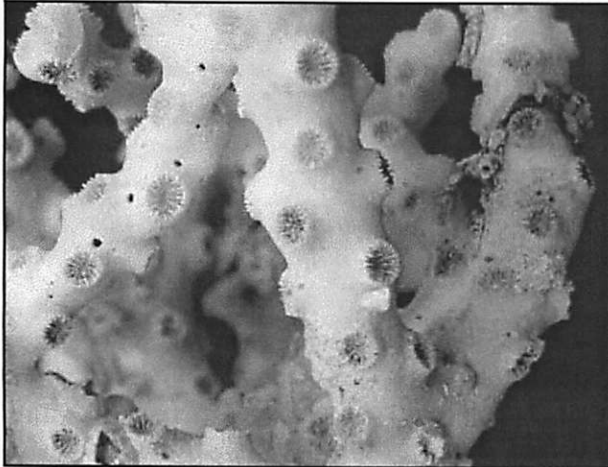


Figure 3. Individual *O. varicosa* corallites (average corallite diameter = 1.75 – 2.5 mm).

illegal bottom fishing and shrimp trawling have continued to damage the coral colonies.

Because few isotopic analyses have been undertaken using the azooxanthellate form of *Oculina varicosa*, this study addresses its potential as a useful proxy for temperature. Since shallow-water corals have yielded effective climatic signatures over time (albeit with some corrections), the ability of *O. varicosa* to exist in both shallow and deep regions (as opposed to *Lophelia pertusa* and *Desmophyllum dianthus*) might suggest that vital effects impacting equilibrium isotope concentrations in solely azooxanthellate species may not be a factor. Alternatively, the abil-

ity of *O. varicosa* to convert between growth morphologies may introduce a metabolic effect differing from those affecting azooxanthellate corals. However, because the Oculina Banks are situated in an environment dominated by movement of the Florida Current/Gulf Stream above and the upwelling from the Florida Straits below, the potential of isotopes recorded by *O. varicosa* to serve as a proxy monitoring the flow and interaction of these major water masses over time warrants an investigation of the isotopic composition of the species. By understanding the dynamics of these water masses, we may better understand their flow patterns and associated effects on the region as well as how they may have differed in the past. This paper presents the results of a pilot study using mass spectrometry to assess the capacity of *O. varicosa* as an effective paleo-oceanographic tool.

METHODS

Sample Collection

Oculina varicosa samples were collected on October 13, 2005 during a multibeam sonar cruise of Oculina Banks aboard the NASA *M/V LIBERTY STAR*. Samples were collected from Station 12 at Chapman's Reef (27° 36.764' N, 79° 58.444' W) at a depth of approximately 82 m using the Phantom S2 remotely operated vehicle (ROV).

Grab samples from this location included live and dead coral specimens, combined with silt and clay. Coral specimens were documented and cataloged for reposit at the Smithsonian Institute. Of these, specimen OB05-12 was shipped to the University of South Florida for the isotope analysis used in this study. This specimen measured 15.1 cm in total length and was composed of six branching stalks of various sizes. Although the specimen was non-living upon collection, it remained relatively free of encrusting organisms except at the base, an indicator of recent mortality in an area where encrusting organisms are common (Winston and Jackson, 1984).

Isotope Analysis

A single stem and associated branches of specimen OB05-12 was selected for isotope analysis based on its relatively straight growth. Powders were spot drilled every 0.25 cm along the length of the stem and along the initial few centimeters of each of the two branches with a Dremel[®] drill using a 0.8 mm bit. Drilling took place along the coral skeleton away from the septal margins to ensure the samples recorded branch/stem growth and not that of any corallites, which may have varying growth and/or precipitation rates that could influence the isotopic composition. Each drill site was initially prepared by lightly abrading the coral skeleton to remove the site mark and create a fresh drilling surface. Due to the brittle nature of the specimen, drill holes were kept shallow to prevent puncturing the skeleton to hollow voids within the stem. Distances for each drill sample were recorded beginning with 0 cm for the first sample; and sampling at the branches were given equidistant values from the 0 cm starting point as samples along the main stem. Drill powders were weighed on a mass balance to weights between 50 and 100 µg for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analysis, which was performed using a ThermoQuest[®] Delta+XL mass spectrometer using NBS-19 as the standard for PDB.

$\delta^{18}\text{O}$ values of the skeleton were used in two equations to estimate aragonitic precipitation temperatures:

$$T = 20.6 - 4.34(\delta^{18}\text{O}_c - \delta^{18}\text{O}_w)$$

Grossman and Ku, 1986

$$T = [(\delta^{18}\text{O}_c - \delta^{18}\text{O}_w) - 4.97] / -0.25$$

Smith et al., 2000

Although the Grossman and Ku (1986) equation was developed for use with gastropods and foraminifera, it formed the basis of the Smith and others (2000) equation developed for cold-water scleractinian coral species, and was therefore included in this study. Because $\delta^{18}\text{O}$ values of depths between 70 and 100 m were not available for this region, a 0 ‰ value was used as a default (Schmidt et al., 1999).

Environmental Data

A record of bottom conditions at 74.68 m was obtained from an instrumental array moored by Oregon Institute of Marine Biology/University of Oregon at Jeff's Reef for 340 days from April 2000 to March 2001. This array included an acoustic Doppler current profiler and temperature profiler that recorded environmental conditions at a frequency of 36 measurements per day (one recording per five minutes for the first fifteen minutes of every other hour). Sea-surface temperatures and meteorologic conditions for the same time period were collected from the National Data Buoy Center online archive of Buoy 41009, located 20 nautical miles east of Cape Canaveral, and the closest data buoy to Oculina Banks. Environmental conditions were recorded hourly, on the hour.

RESULTS

Oxygen and Carbon Isotopes

Isotope values from the coral specimen ranged between -2.6 and 1.0‰ for $\delta^{18}\text{O}$ and -6.9 and 2.1‰ PDB for $\delta^{13}\text{C}$ (Figures 4, 5). Samples without isotopic values indicate insufficient CO_2 produced from the powders to generate $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. Isotopic values for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ form a near linear regression when plotted against one another, with an r^2 of 0.92 (Figure 6). Temperatures of precipitation based on $\delta^{18}\text{O}_c$ for the Grossman and Ku (1986) equation and assuming a $\delta^{18}\text{O}_w$ of 0‰ ranged between 16.1 and 31.7 °C with a mean of 25.9 °C (Figure 7). Temperatures calculated from the Smith and others (2000) equation were slightly lower, ranging between 15.8 and 30.1 °C with a mean of 24.8 °C (Figure 8).

Environmental Temperature

Sea-surface temperatures from April, 2000 to March, 2001 recorded by Buoy 41009 ranged between 18.3 and 30.7 °C, with a mean of 24.0 °C (Figure 9). Bottom temperatures re-

corded at Jeff's Reef ranged from 12.0 to 29.0 °C, with a mean of 20.1 °C. An overall increase in SST occurred between April and August, 2000, followed by a decrease until late January, 2001 before increasing slightly between February and March, 2001.

Bottom temperatures displayed more volatility over the interval, but appear to show an overall increase from May to late October of 2000, before falling in November. Temperatures appeared to rise again between February and March, 2001. Average bottom currents remained between 5 and 20 cm sec⁻¹ throughout this interval, with regular, rapid fluctuations between these values (Figure 10). Current velocity peaked at

53.24 cm sec⁻¹ for the period studied on March 26, 2001, and was associated with several large bottom temperature fluctuations (varying between 3 and 13 °C) from March 23 to March 26, as well as an overall increase in bottom temperature. Coeval anomalies in sea-surface observations from Buoy 41009 were not apparent.

Tropical Storm Leslie passed approximately 50 km north of Oculina Banks on October 5-6, 2000, however wind speeds remained at 40 kt or less, and air pressures remained at 1007 mb and above (Franklin and Brown, 2000). An increase in current velocity to 12.8 cm sec⁻¹ occurs at this time, before quickly falling back to values less than 1 cm sec⁻¹.

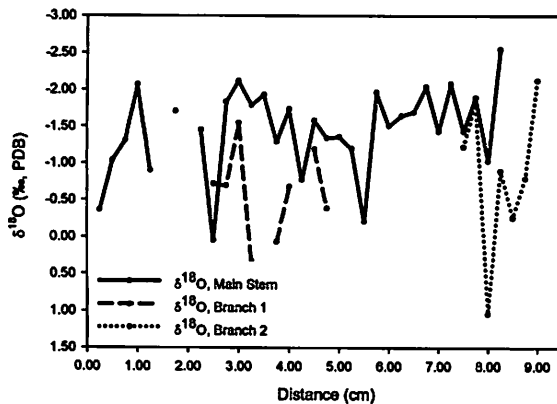


Figure 4. Oxygen isotope profile for main stem and branches of *O. varicosa*.

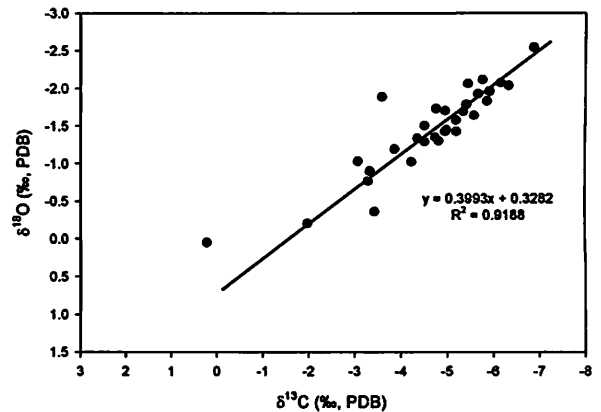


Figure 6. Cross plot of oxygen vs carbon isotopic values.

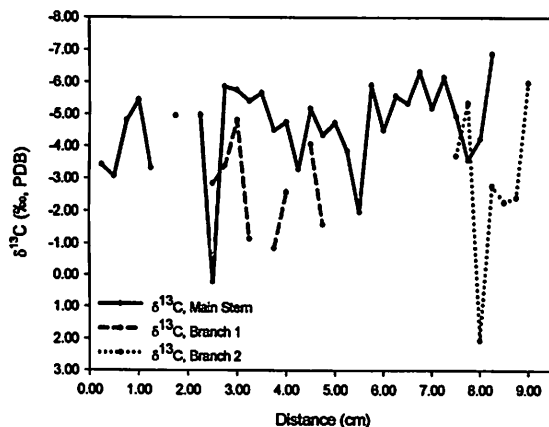


Figure 5. Carbon isotope profile for main stem and branches of *O. varicosa*.

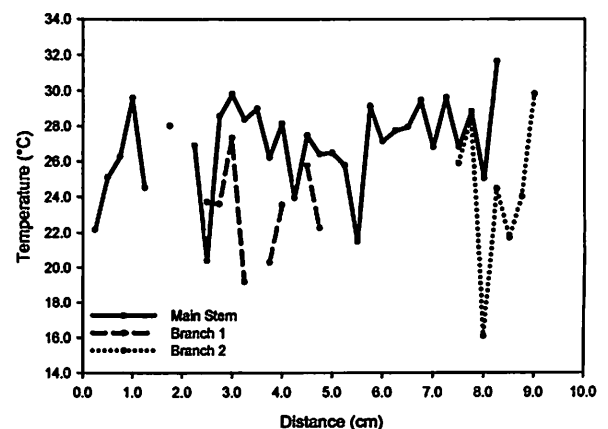


Figure 7. Temperature profile derived from Grossman & Ku, 1986 (assuming 0‰ for $\delta^{18}\text{O}_w$).

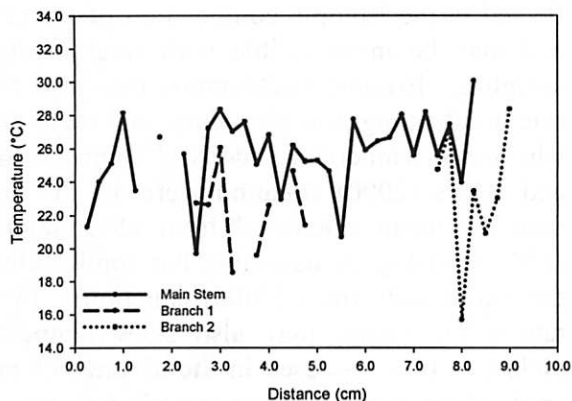


Figure 8. Temperature profile derived from Smith et al., 2000 (assuming 0‰ for $\delta^{18}\text{O}_w$).

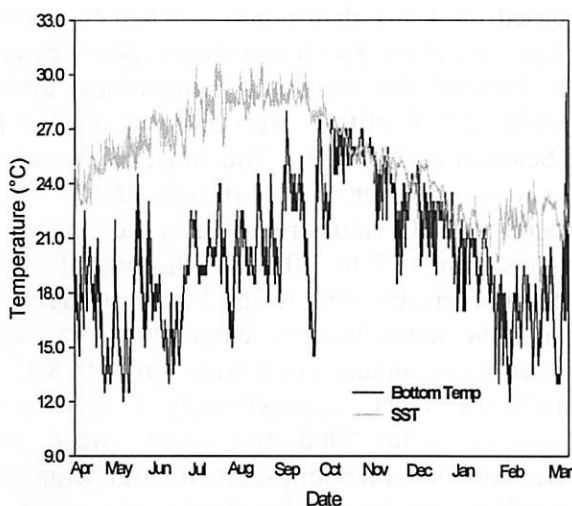


Figure 9. Bottom and surface temperature profiles for Jeff's Reef, Oculina Banks, April 2000 to March 2001.

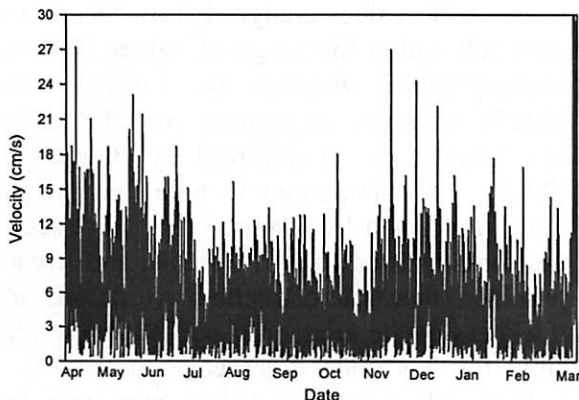


Figure 10. Bottom current profile for Jeff's Reef, Oculina Banks, April 2000 - March 2001.

DISCUSSION

Isotope Sampling

Preliminary analyses suggest the possibility of a 2-3 cm maximum annual growth cycle for *O. varicosa* as opposed to a 1.5 cm cycle observed by Reed (1981). Given that Reed's estimate was based on a transplanted individual, discrepancies in the growth rates should not be unexpected and may reflect stress induced by the relocation of the specimen. Future work that includes microsampling of the specimen used in this study will improve the sampling resolution and may help resolve this issue.

The differing isotopic values between main stem samples and parallel points on the branches of the coral specimen have two primary implications. First, the branches of the coral may grow at a different rate from the main stem, leading to an offset in isotopic values between the two at equal distances. If this is so, finer-scale microsampling should show similar patterns of isotopic fluctuation on different scales, and an estimate of the differences in growth rate can be inferred. However, because the skeletal microstructures of some cold-water scleractinian species have been shown to vary (Blamart et al., 2005), it is possible that fractionation based on these differences yields the isotopic variability seen here. UV fluorescence and SIMS/ion microprobe analysis should determine whether this is the case. Further complications resulting from variable growth rates and skeletal microstructural differences may be acting simultaneously and fine-scaled analysis of the isotopic variation in the microstructures must be resolved prior to establishing differences in growth rates.

Assessing Proxy Potential

The Grossman and Ku (1986) and Smith and others (2000) temperature equations calculated similar temperature results, with means varying by 1.1 °C. Because the Smith and others (2000) equation is essentially a fine-tuned version of the Grossman and Ku (1986) equation, the similarities in temperature results should be ex-

pected. Although the Grossman and Ku (1986) equation is commonly applied in paleotemperature studies, its development for use with foraminiferal and molluscan species suggests it may not be directly applicable for temperature reconstructions using cold-water corals. Its applicability over a number of such equations existing for tropical coral species is another problem to be addressed. Moreover, the Smith and others (2000) equation was established using estimates of $\delta^{18}\text{O}_w$ based on salinity averages reported by the World Ocean Atlas 2001 (Boyer et al., 2002) for the coral collection sites rather than observed *in situ* values. As $\delta^{18}\text{O}$ values are less commonly recorded and reported relative to other environmental parameters, such as temperature and salinity, particularly at depth, relatively little is known about their localized fluctuation over time in specific locations. In the absence of more tailored equations however, the Smith and others (2000) equation, which is slightly more appropriate to deep-water corals than the Grossman and Ku (1986) equation, must suffice.

Temperature fluctuations observed at Jeff's Reef for the April 2000-March 2001 observation period are much greater than those seen at the surface, likely resulting from Florida Straits upwelling throughout the year. Upwelling pulses may also be interpreted from the current profile, indicating a decrease in average current velocity through the summer followed by a mild increase in the winter, corresponding to upwelling frequency observations (Mooers and Fiechter, 2005; personal comm.). Because the range of temperature fluctuations in bottom waters is larger than that seen at the surface, and because anomalies in the bottom currents do not appear to correlate with surface conditions, it may be inferred that upwelling events do not reach the surface. Thus, the general assumption that increasing depth translates to more regulated environmental conditions is not supported, at least for this dynamic locality. While this assumption may hold for regions not affected by ocean currents, upwelling, and/or seeps, deep-water reefs are generally associated with and influenced by these conditions.

Regardless, these physical and chemical fluctuations in the bottom water should be re-

flected in the isotopic composition of the corals, and may be more visible with finer resolution sampling. Isotopic fractionation may also play a role in offsetting isotopic values, and may explain why mean temperatures derived from the Smith and others (2000) equation were 4.7 °C higher than the mean calculated from observations at Jeff's Reef (again, assuming the applicability of the Smith and others (2000) equation). Inaccurate $\delta^{18}\text{O}_w$ values may also skew temperature yields, as 0‰ was used in the absence of measured values of the ambient water's isotopic composition. NASA's Global Seawater $\delta^{18}\text{O}$ Database v1.14 reported a mean global isotopic value of -0.49‰ for depths between 70 and 100 m, based on 1,561 data points. When this average was used in the Smith and others (2000) equation, it lowered the estimated temperature mean to within 2.7 °C of the observed mean at Jeff's Reef (Schmidt et al., 1999). This must be viewed with caution however, for two reasons. First, the range of $\delta^{18}\text{O}$ values reported in the database extends from -6.7 to 2.0 ‰, with none of the data points corresponding to the Florida region. Second, the mean bottom temperature reported by Reed in an annual cycle from July 1978 to July 1979 was 16 °C, approximately 4 °C lower than observed in the 2000-2001 profile (Reed, 1981). Because no other long-term bottom temperature profiles exist for Oculina Banks, the variation in bottom temperature from year to year has not been established. Thus, given the current limitations, it may be safest to assume the true $\delta^{18}\text{O}_w$ mean for Oculina Banks is close to -0.49‰.

$\delta^{13}\text{C}$ values analyzed from *Oculina varicosa* fell within the range of values observed in *Desmophyllum dianthus* by Lutringer et al. (2005) and *Lophelia pertusa* from the northeastern Atlantic, as summarized by Blamart et al. (2005). It is important to note that microsampling performed by Blamart et al. produced values ranging from -0.7 to -15.3‰, and it was determined that microstructural variations in the thickness of the aragonitic skeleton were responsible for this wide divergence in values. The lighter carbon isotopic values measured in this study corresponds to that of marine organisms as discussed by Stahl (1979); however the heavier

values correspond more closely to standard values of marine HCO_3^- . Because marine plankton is isotopically light, ranging from -16 and -27‰, one might expect $\delta^{13}\text{C}$ values of *Oculina varicosa* to fall within their isotopic range. This effect, however, may be dampened by heavier DIC values, potentially imported to the region by upwelling events. By obtaining periodic $\delta^{13}\text{C}$ values of local DIC, it may be possible to determine how much fractionation is occurring in the coral. From there, culturing the species on a diet of known $\delta^{13}\text{C}$ and in a medium of known $\delta^{13}\text{C}$ of DIC can help determine whether fractionation is governed by vital or kinetic effects.

CONCLUSIONS

Preliminary analysis of *Oculina varicosa* indicates that it may serve as an effective proxy for intermediate and bottom-water change at Oculina Banks; however, further work must be undertaken to better understand both the environmental parameters and the species' biology in order to better interpret these isotopic data. Higher resolution sampling of the coral will better illustrate any cyclicity in growth patterns and growth rate differences between the branches and main growth axes, if indeed they are reflected in its isotopic composition. Measuring $\delta^{18}\text{O}$ values of the bottom water at Oculina Banks is vital to developing a more applicable temperature equation for the coral, particularly if more thorough sampling of bottom temperatures and isotopic composition of multiple specimens can be undertaken. Establishing values of $\delta^{13}\text{C}$ values of DIC of the water, as well as coral culturing experiments will aid in the understanding of any carbon isotopic fractionation. Finally, a better understanding of the physical regime at Oculina Banks, including longer-term profiles of bottom temperature, current velocity, and nutrient and/or organic matter concentrations will help provide a more solid foundation for comparison with isotopic data yielded by the corals.

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