Stable Carbon Isotopes ($\delta^{13}C$) in Coral Skeletons

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Introduction

Following the highly publicized 1998 El Niño event, interest in how climatic events in the tropics affects global climate has grown. However, an understanding of the long-term natural variability in tropical climates is only beginning to emerge. Long-term instrumental records documenting tropical ocean climate are sparse or non-existent in some areas. Therefore, scientists depend upon proxy climate records. The isotopic signatures of coral skeletons offer a suite of proxy records for potentially reconstructing past tropical climate over the last few centuries. Our ability to model and understand current climate and to predict future climate conditions depends on a solid understanding of past climate.

Recent research suggests that stable isotope records, trace element, and minor element content in the calcium carbonate skeleton of scleractinian corals can be used to reconstruct sub-annual to centennial time-scale variation in past climate at tropical and subtropical latitudes (Beck et al., 1992; Cole et al., 1993; Dunbar et al., 1994; Druffel, 1997; Fairbanks et al., 1997). The stable oxygen isotope signature ($\delta^{18}O$) in reef corals is a reliable recorder of sea surface temperatures (Weber and Woodhead, 1972; Dunbar et al., 1994; Wellington et al., 1996) and salinities in some regions (Cole et al., 1993; Linsley and Dunbar, 1994; Swart et al., 1996a). However, an understanding of the long-term variation in seasonal cloud cover (solar irradiance) and upwelling are critical for a more complete understanding of tropical climate globally. Cloud cover plays a large role in the global heat budget yet is one of the primary unknowns in climate models and is missing from most paleo-records. Stable carbon (the per mil deviation of the $^{13}C/^{12}C$ ratio relative to the PDB-1 standard called $\delta^{13}C$) in coral skeletons shows some promise as a proxy-recorder of past solar irradiance levels and nutrient-rich upwelling events, and is measured simultaneously with $\delta^{18}O$.

Carbon isotopes are believed to be predominantly fractionated by metabolic processes making it difficult to use them as a climate indicator. In an effort to understand the effect of metabolic processes on skeletal $\delta^{13}C$, I have experimentally tested the effects of light (which drives photosynthesis) and heterotrophy (coral feeding) on coral skeletal $\delta^{13}C$. The results of this work indicate that: 1) $\delta^{13}C$ in corals is a complicated tracer that responds to both changes in light and heterotrophy, 2) $\delta^{13}C$ skeletal records from shallow growing coral in non-upwelling regions hold promise as paleo-recorders of changes in solar irradiance levels, and 3) further research is needed in order to better understand how $\delta^{13}C$ varies with heterotrophy and other environmental parameters (i.e. spawning and dissolved inorganic carbon of seawater (DIC)) before it can be more widely used as a climate proxy-recorder.

Background

In symbiotic coral, skeletal $\delta^{13}C$ is believed to be predominantly influenced by metabolic processes such as photosynthesis and respiration in the coral polyp (Swart, 1983; McConnaughey, 1989a; Allison, 1996; McConnaughey et al., 1997; Grottoli and Wellington, 1999). Therefore, environmental variables influencing coral metabolism should also affect skeletal $\delta^{13}C$ levels.

Coral polyps acquire carbon primarily by two mechanisms: 1) ***photosynthesis*** [dissolved inorganic carbon in seawater (mean $\delta^{13}C$ of 0‰) is fixed by endosymbiotic algae called zooxanthellae], and 2) ***heterotrophy*** [ingestion of zooplankton with a mean $\delta^{13}C$ of -15 to -21‰ or lower (Rau et al., 1990; Grottoli-Everett, 1998)].

Photosynthesis is a light driven metabolic reaction that causes isotopic fractionation (McConnaughey, 1989a; McConnaughey et al., 1997). The bulk of photosynthetically fixed carbon is translocated from the zooxanthellae to the coral host (e.g. Falkowski et al., 1984; Muscatine et al., 1984; Spencer Davies, 1991). As the rate of photosynthesis increases, skeletal $\delta^{13}C$ increases (Swart, 1983; McConnaughey, 1989a; Porter et al., 1989; McConnaughey et al., 1997). Conversely, as photosynthesis decreases, skeletal $\delta^{13}C$ decreases (Porter et al., 1989). Thus, coral skeletal $\delta^{13}C$ should reflect changes in solar irradiance levels.

Some observational data strongly support this hypothesis. Skeletal $\delta^{13}C$ in corals decreases with depth (light decreases) (e.g. Weber et al., 1976; Bosscher, 1992; Carriquiry et al., 1994; Grottoli, 1999) and varies seasonally in accordance with seasonal changes in light

levels associated with cloud cover (e.g. Fairbanks and Dodge, 1979; Cole and Fairbanks, 1990; Carriquiry et al., 1994; Grottoli-Everett, 1998; Grottoli and Wellington, 1999). While these studies support the idea that light is a driving force in the variation of skeletal $\delta^{13}C$ composition, none addresses the issue experimentally, and

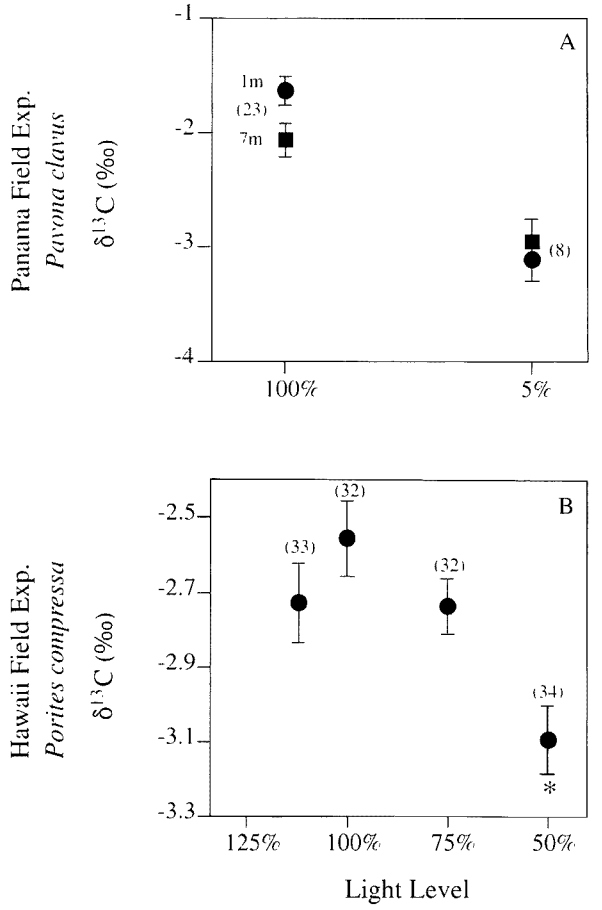

Figure 1: (A) In field-reared Panamanian Pavona clavus *coral, mean skeletal $\delta^{13}C$ (± 1SE) significantly decreased by an average of 1.18‰ as light decreased (ANOVA $p<0.001$). Sample size of each mean (indicated in brackets) for shallow (●) and deep (■) treatments are the same. (B) In tank-reared* Porites compressa *corals, mean skeletal $\delta^{13}C$ (± 1SE) significantly decreased by 0.54‰ when light decreased from 100% to 50% (ANOVA $p<0.0001$,* A. posteriori *Tukey Test $p<0.05$; * indicates the mean that significantly differs from all other means). $\delta^{13}C$ decreased non-significantly as light increased above 100% most likely as a result of photoinhibition. Sample size of each mean indicated in brackets. Location, experiment type, and coral species are listed to the left of each graph. From Grottoli-Everett, 1998; Grottoli and Wellington, 1999.*

none addresses the contribution of zooplankton to the $\delta^{13}C$ signature. Coral are active heterotrophs (Coles, 1969; Sebens et al., 1996; Grottoli-Everett, 1998) and ingestion of naturally occurring zooplankton can have a significant effect on skeletal linear extension (Wellington, 1982; Sebens, pers. comm.). Given that marine zooplankton have low $\delta^{13}C$ values relative to coral skeletons, ingestion of zooplankton by corals should be accompanied by a decrease in the $\delta^{13}C$ of coral skeletons. Recent observations by Felis et al. (1998) indicate that increases in heterotrophy associated with seasonal deep water mixing and plankton blooms lead to decreases in skeletal $\delta^{13}C$. Thus, both solar irradiance and zooplankton ingestion should have a significant effect on skeletal $\delta^{13}C$.

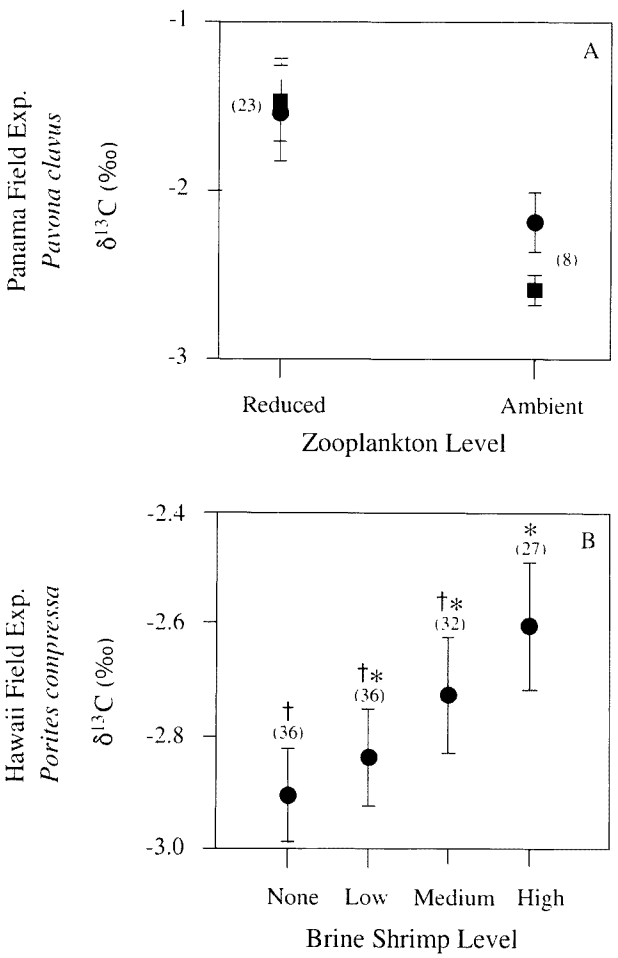

Figure 2: (A) Mean skeletal $\delta^{13}C$ (± 1SE) increased significantly by an average of 0.88‰ when zooplankton levels were reduced (ANOVA $p<0.0001$). Sample size of each mean indicated in brackets are the same for shallow (●) and deep (■) treatments. Zooplankton were excluded in the reduced zooplankton treatments with a 95 µm Nitex mesh. (B) Mean skeletal $\delta^{13}C$ (± 1SE) increased significantly by 0.31‰ as brine shrimp levels increased (ANOVA $p<0.016$). Means with similar symbols (or †) do not significantly differ from each other (*a posteriori *Tukey Test $p<0.05$). Sample size of each mean indicated in brackets. Location, experiment type, and coral species are listed to the left of each graph. From Grottoli-Everett, 1998; Grottoli and Wellington, 1999.*

Research

The goal of my dissertation research was to experimentally evaluate the effect of light and zooplankton on coral skeletal $\delta^{13}C$ via the following hypotheses: 1) as light levels decrease, $\delta^{13}C$ decreases, and 2) as heterotrophy decreases $\delta^{13}C$ increases. By growing corals under controlled conditions and manipulating both light and heterotrophy levels, their effects on skeletal $\delta^{13}C$ values

could be isolated. Although skeletal carbon isotopes may vary due to changes in the isotopic composition of DIC in seawater (Swart et al., 1996b), dissolved organics and bacteria (Sorokin, 1973; Muscatine and Porter, 1977), or spawning (Gagan et al., 1994; Gagan et al., 1996), these factors were constant across all treatments in both experiments and therefore did not interfere with the interpretation of the present data. In addition, skeletal $\delta^{13}C$ may vary due to changes in kinetic (non-metabolic) fractionation (McConnaughey, 1989a, b). However, examination of the skeletal $\delta^{18}O$ data reveals that kinetic fractionation did not interfere with the interpretation of the present $\delta^{13}C$ data (Grottoli-Everett, 1998; Grottoli and Wellington, 1999).

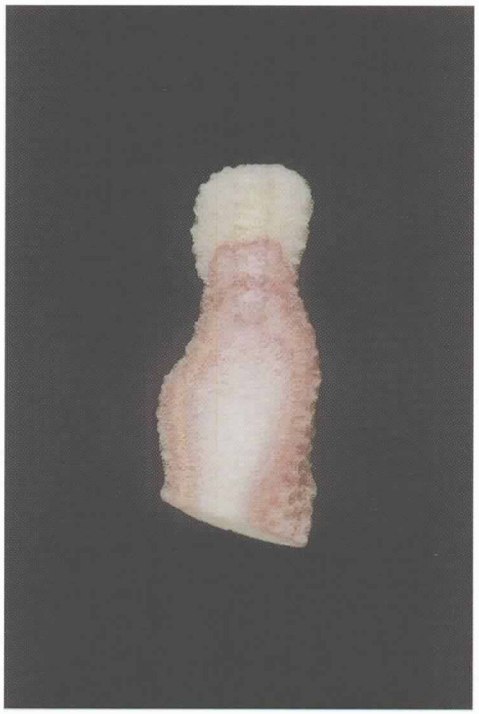

Figure 3: Cross-section of Porites compressa *fragment from The Point Reef collected at 2 m depth. Stain lines from bottom to top correspond to 2 August 1996, 17 October 1996, and 22 November 1996. Coral fragment was collected on 2 March 1997 (top of fragment). Sequential 2 mm skeletal samples were extracted along the major axis of growth between the bottom stain line and tip of the coral fragment (indicated by resulting shallow furrow) yielding a ~ monthly sampling resolution. Distance from bottom stain line to tip of fragment is 1.5 cm.*

Effect of light on coral skeletal $\delta^{13}C$

Large decreases in light resulted in significant decreases in skeletal $\delta^{13}C$ of field-reared Panamanian *Pavona clavus* (Figure 1a) and *Pavona gigantea* (not shown) at both shallow (1m) and deep sites (7m). Degree and range of $\delta^{13}C$ response to light varied as a function of species and depth. In tank reared Hawaiian *Porites compressa* coral, decreases in light from 100% also resulted in a significant decrease in $\delta^{13}C$ (Figure 1b). This is consistent with the first hypothesis. In addition, increases in light above 100% also resulted in a slight decrease in *P. compressa* skeletal $\delta^{13}C$ (Figure 1b). This appears to be a photoinhibitive effect whereby very high light levels may actually lead to decreases in photosynthesis (Barnes and Taylor, 1973; Erez, 1978; Harriott, 1998).

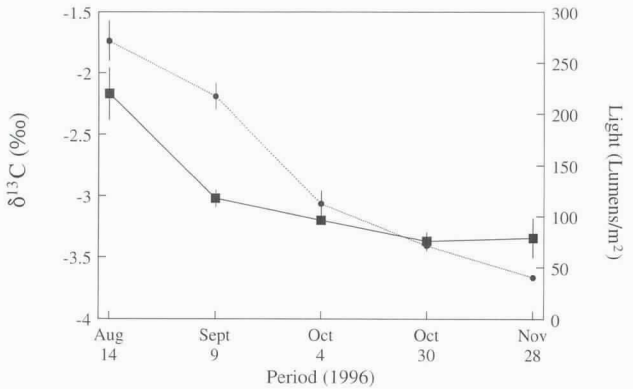

Figure 4: Skeletal $\delta^{13}C$ decreased as light decreased due to seasonal increases in cloud cover. Mean skeletal $\delta^{13}C$ (± 1SE) (solid line with ■) in Hawaiian Porites compressa *(n=4) decreased from August to November as mean daily irradiance levels decreased (lumens/m² ± 1SE; dashed line with ●) (lumens/m² = 176 * $\delta^{13}C_{pdb}$ + 672, $r^2 = 0.79$, $n = 5$, $p < 0.04$, Pearson correlation coefficient = 0.89). Modified from Grottoli, 1999*

Effect of heterotrophy on coral skeletal $\delta^{13}C$

In field-reared corals, *reduction* of naturally occurring zooplankton resulted in a significant mean *increase* in $\delta^{13}C$ of 0.88l (Figure 2a). This is consistent with the second hypothesis. In contrast, *increases* in heterotrophically acquired brine shrimp in tank-reared corals resulted in small but equally significant increases in $\delta^{13}C$ of 0.31‰ (Figure 2b). Brine shrimp and zooplankton both have similar low $\delta^{13}C$ values relative to coral and are both a rich source of nitrogen (C:N ratios < 5). So, why does skeletal $\delta^{13}C$ increase with increases in brine shrimp in the tank-reared coral but decreases with increases in zooplankton (to ambient levels) in the field (Figure 2)? I suspect it is because coral in the tanks were fed very high concentrations of brine shrimp (6 - 90 times greater than naturally occurring concentrations of zooplankton on the reef) thus exposing the coral to extremely high levels of nitrogen. Nitrogen alone, not phosphorus, limits zooxanthellae biomass in corals (Falkowski et al., 1993). High concentrations of nitrogen have been shown to lead to increased zooxanthellae concentrations (pigmentation), increased photosynthesis, and decreased skeletal growth in corals (Falkowski et al., 1993; Cook et al., 1994; Snidvongs and Kinzie, 1994; Marubini and Davies, 1996; Stimson, 1997). In fact, increases in pigmentation and significant decreases in skeletal extension were observed in the brine shrimp-fed corals but not in the field-reared coral that were exposed to zooplankton. These observations support the notion that coral have a "nutrient threshold". Under normal, low nitrogen conditions, zooxanthellae growth rate is limited and increases in zooplankton lead to a decrease in skeletal $\delta^{13}C$. At nitrogen levels above the

"nutrient threshold", zooxanthellae activity and photosynthesis greatly increase leading to an increase in skeletal $\delta^{13}C$, and swamping the low $\delta^{13}C$ signal of the brine shrimp themselves. Overall, what is clear is that heterotrophic input has a significant effect on coral skeletal $\delta^{13}C$.

Applications for paleoclimate reconstruction

Approximate monthly resolution $\delta^{13}C$ measurements were made from a *Porites compressa* corals collected at 2m depth from Kaneohe Bay, Hawaii (a non-upwelling region). Decreases in $\delta^{13}C$ from August to November were significantly correlated with decreases in light levels measured *in situ* with light loggers over the same time period (Figures 3, 4). As light levels decreased with the onset of the rainy season, $\delta^{13}C$ decreased. Changes in light accounted for almost 80% of the variation in $\delta^{13}C$ in the coral skeleton at this location. The remaining 20% of the variation was probably due to changes in heterotrophy, $\delta^{13}C$ of the DIC, spawning, or some combination of these factors. These results suggests that in shallow coral from non-upwelling regions, light seems to be the major factor controlling skeletal $\delta^{13}C$ variation.

Summary

Coral skeletal $\delta^{13}C$ is significantly influenced by heterotrophy and light levels. First, this research shows the first experimental evidence that heterotrophic input has a significant effect on $\delta^{13}C$ in coral skeletons. Further research is needed to decouple the nutrient versus zooplankton effect on skeletal $\delta^{13}C$. Second, decreases in light by at least 50% led to a statistically significant decrease in mean skeletal $\delta^{13}C$ in all 3 species of corals studied. Since cloud cover reduces sunlight levels by ~50%, such changes in light levels should be detectable in the coral skeletal $\delta^{13}C$ signature. High-resolution analysis of the intra-annual variation in skeletal $\delta^{13}C$ composition of shallow *Porites compressa* corals in Hawaii indicates that skeletal $\delta^{13}C$ responds primarily to seasonal changes in sunlight. These results suggest that we can optimize our ability to acquire a paleorecord of solar irradiance levels by choosing a shallow coral from a non-upwelling region. Due to the complexity associated with nutrients and heterotrophy, the $\delta^{13}C$ record from upwelling region corals is still difficult to resolve. Overall, this work increases our knowledge of how light and heterotrophy affect coral physiology and the $\delta^{13}C$ of coral skeletons.

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