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Stable carbon isotopes ($\delta^{13}\text{C}$) in corals: An experimental approach and applications for paleoceanography

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Scleractinian corals obtain fixed carbon via photosynthesis by their endosymbiotic algae (zooxanthellae) and via heterotrophy (injection of zooplankton, $\delta^{13}\text{C} \approx -17$ to -22‰). Carbon dioxide (CO_2) used for photosynthesis is obtained from seawater ($\delta^{13}\text{C} \approx 0\text{‰}$) or from respired CO_2 within the coral host. The $\delta^{13}\text{C}$ of the carbon used in the formation of the underlying coral skeleton is fractionated as a result of both of these metabolic processes. As photosynthesis increases, fractionation decreases, and the $\delta^{13}\text{C}$ of the CO_2 available for skeletogenesis should increase. At the time that I was conducting this research, the generally observed decreases in coral skeletal $\delta^{13}\text{C}$ with depth and with seasonal decreases in solar irradiance suggested that this was true. However, these trends were not always observed and direct experimental evidence did not exist. Second, as heterotrophy increases the amount of low $\delta^{13}\text{C}$ respired CO_2 available for skeletogenesis should increase, and the $\delta^{13}\text{C}$ of the skeleton decrease. Corals are known to be active feeders though the proportionate contribution of heterotrophically-derived carbon to the skeleton remains unclear. Using experiments and field surveys, I tested the following hypotheses: 1- As light levels increase skeletal $\delta^{13}\text{C}$ increases, and 2- As heterotrophy increases, skeletal $\delta^{13}\text{C}$ decreases.

Effect of Light and Photosynthesis on Coral $\delta^{13}\text{C}$

To test the effect of light on skeletal $\delta^{13}\text{C}$, three experiments and one survey were conducted. Experimentally, *Pavona clavus* and *Pavona gigantea* corals were reared under ambient and very low light levels in the field at two depths in Panama. *Porites compressa* corals were reared under four light levels in outdoor seawater tanks while additional *P. compressa* and *Porites lobata* corals were reared under field conditions at 1.7, 5, and 8.3 m depth in Hawaii. A survey of bleached and non-bleached *P. compressa* and *M. verrucosa* corals following the 1996 bleaching event in Kaneohe Bay, HI was also conducted.

In the experiments, decreases in light levels due to shading or depth resulted in a significant decrease in skeletal $\delta^{13}\text{C}$ [1, 2, 3, 4]. Further inspection of the data confirms that it is the changes in photosynthesis itself that drive the changes in $\delta^{13}\text{C}$. Skeletal $\delta^{13}\text{C}$ was lower in bleached than in non-bleached corals growing under the same conditions and location. Skeletal $\delta^{13}\text{C}$ also decreased at higher than normal light levels most likely due to photoinhibition. Thus decreases in photosynthesis due to reduced light levels, due to bleaching induced decreases in chlorophyll *a* concentrations, or due to photodamage induced decreases in functional chlorophyll *a*, results in significant $\delta^{13}\text{C}$ decreases.

Effect of Heterotrophy and Respiration on Coral $\delta^{13}\text{C}$

To test the effect of heterotrophy on skeletal $\delta^{13}\text{C}$ *P. clavus* and *P. gigantea* corals were reared under ambient or reduced zooplankton levels in the field at two depths in Panama. Here, the addition of natural concentrations of zooplankton to the diet resulted in decreases in skeletal $\delta^{13}\text{C}$ for both species [1]. The proportionate effect of heterotrophy on skeletal $\delta^{13}\text{C}$ was greater at depth and in *P. gigantea*. This is consistent with results from recent feeding experiments [4]. However, tank-reared *P. compressa* revealed that at unnaturally high feeding rates, enhanced nitrogen supply in the diet can disrupt the coral-algal symbiosis, stimulate zooxanthellae growth and photosynthesis, and cause an increase in skeletal $\delta^{13}\text{C}$. It is proposed that under natural field conditions corals feed on zooplankton below this 'nutrient threshold' and that increases in heterotrophy should result in decreases skeletal $\delta^{13}\text{C}$ values.

Summary

Changes in photosynthesis and heterotrophy have a significant effect on coral skeletal $\delta^{13}\text{C}$. In shallower corals, photosynthesis drives the bulk of the variation in $\delta^{13}\text{C}$. Thus the skeletal $\delta^{13}\text{C}$ records from shallow corals in non-upwelling regions where zooplankton concentrations are relatively constant should represent a reliable proxy of light variability. Due to the complexity associated with nutrients and heterotrophy, $\delta^{13}\text{C}$ records from upwelling regions or deep corals are still difficult to resolve. In addition, boron isotope data indicate that pH levels do not vary with changes in photosynthesis or heterotrophy [5] suggesting that metabolically driven $\delta^{13}\text{C}$ fractionation during skeletogenesis is not pH driven.

References

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