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This project generally questioned causes of variation of the stable oxygen and carbon isotopes in coral skeletons. Scleractinian corals construct extremely durable and well conserved aragonite skeletons. Corals, which can live for centuries, therefore provide a powerful and high resolution tool for the reconstruction of climate variations and crucial ecological parameters. Time-series profiles of skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, for example, allow for reconstruction of sea surface temperature (SST) and global (climate) change. However, several biological and environmental factors have been shown to affect the reading of coral skeletal $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ paleorecords. These sources of variation are caused by factors covering a range of scales. Consequently, the interpretation of proxies from the coral skeleton is less straightforward than previously assumed. The research comprised general questions of how stable isotope fractionation in the coral skeleton varies with skeletal growth rate, coral morphology, colony topography, coral physiology and taxonomy.

Basic questions on the magnitude of variation between replicate $\delta^{18}\text{O}$ time series from coral skeleton and whether there are colony or species specific effects on skeletal isotope fractionation had still to be answered. We thus compared a total of twelve short $\delta^{18}\text{O}$ time-series of skeletal depth profiles taken from six colonies of three species of the coral *Porites* spp (Fig. 1). The massive coral *Porites* is one of the most common species used in paleoclimate reconstruc-

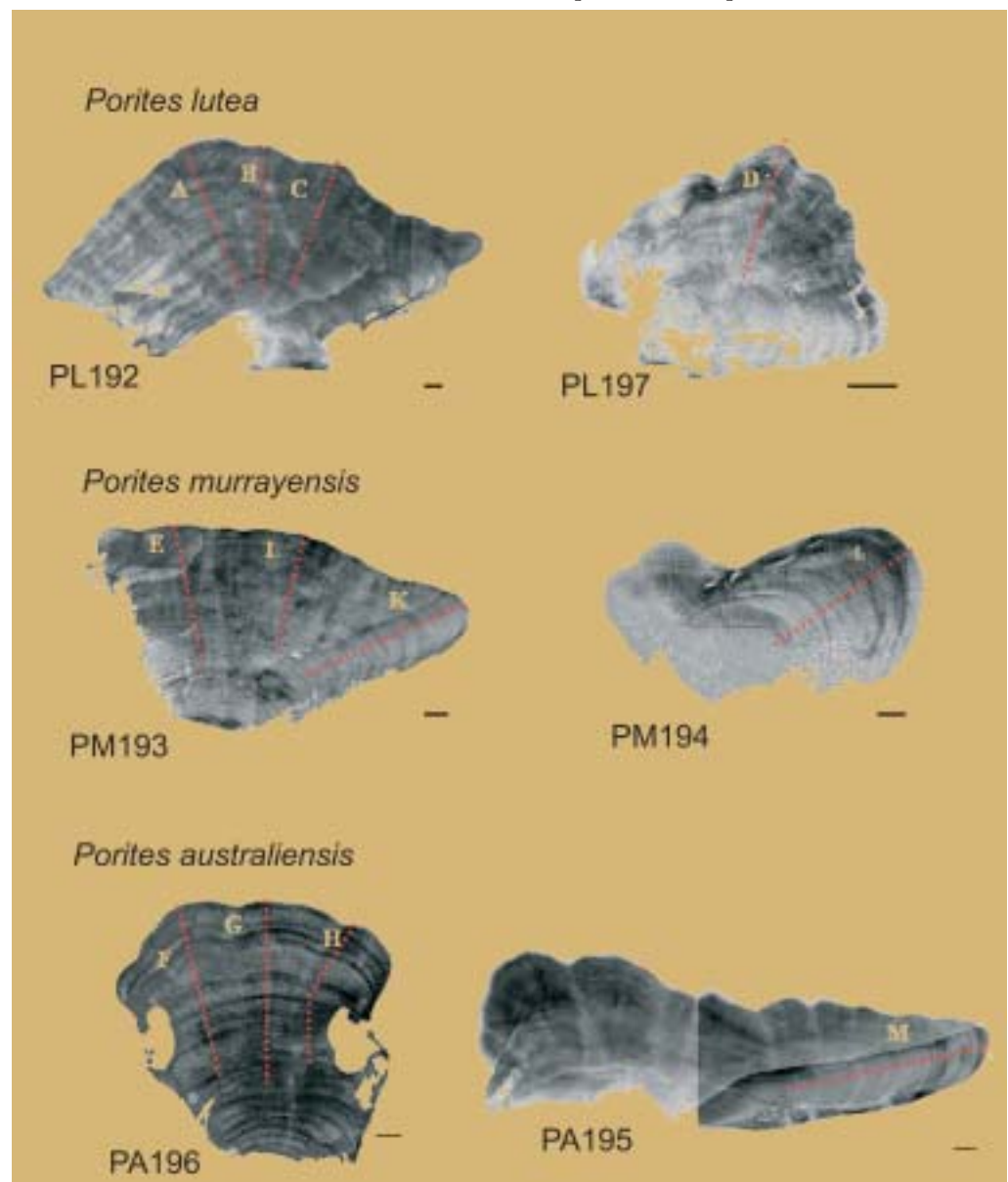


Fig. 1 X-ray photographs of \pm 5 mm thick coral slabs of *Porites lutea*, *murrayensis* and *australiensis*. Dotted red lines indicate trajectories for drilling $\delta^{18}\text{O}$ time-series. Scale bars = 1 cm.

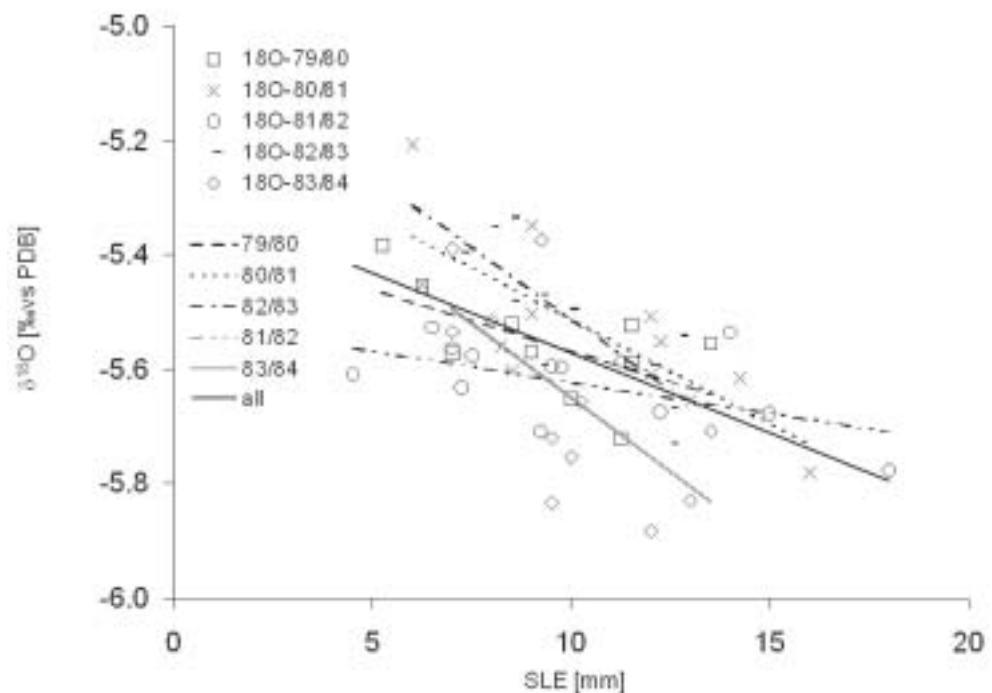


Fig. 2 Mean annual $\delta^{18}\text{O}$ signals versus yearly skeletal linear extension (SLE). Linear regression line between $\delta^{18}\text{O}$ and SLE.

tion and understanding other than environmental sources of variation is pivotal to interpreting this climate proxy. The comparison of replicate profiles on intra-, intercolony and between species scale revealed that the skeletal $\delta^{18}\text{O}$ signal of *Porites* is not influenced by between colony or species effects as has been assumed in earlier studies. Results rather showed that non-environmentally induced variation is a function of skeletal linear extension (Fig. 2) and may further be due to methodological constraints related to the three-dimensional structure of the skeleton, sampling resolution and variation in time-averaging between samples.

Another question addressed was the intra-colony variation within the Caribbean coral *Madracis* spp. Preliminary investigations on stable isotope composition over the colony surface revealed an enormous variation in the $\delta^{13}\text{C}$ of $> 6\text{‰}$ within a single colony of *Madracis formosa*. This led to a more in depth study of skeletal $\delta^{18}\text{O}$ and $\delta^{18}\text{C}$ from different species and depths of *Madracis*. The combined signal of skeletal $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was shown to be a good indicator for physiological plasticity and adaptation of zooxanthellate corals to distinct depth and light regimes.

The question arose if the depth-specialist species of *Madracis* compensate a decrease in photosynthesis with increasing water depth by shifting to more heterotrophic feeding as suggested for other reef corals. To address this, tissue samples of branching *Madracis* were sampled over a depth gradient from 5 to 50 m, and polyp tissue and zooxanthellae were separated for analyses of $\delta^{13}\text{C}$. Further $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of holobiont tissue were analyzed. This set of data allowed for interpreting the carbon and nitrogen assimilation and resource partitioning between polyp and zooxanthellae at respective depths. The stable isotope data indicated, that the shallow water specialist *Madracis mirabilis* is DIN (dissolved inorganic nitrogen) restricted over its entire depth range from 5 to 20 m. The DIN limitation actually hints at very high rates of photosynthesis. On the other hand photosynthesis was not DIC limited at these shallow depths as indicated by the carbon isotopic signals. Comparisons of polyp and zooxanthellae $\delta^{13}\text{C}$ on intra-colony scale, between upward facing branch tips and sideward facing position further down at a branch, revealed that at all depths particle capture was higher at the tip of a colony. This must be related to flow regimes forming around a colony and its branches with particle encounter rates being lower at the side of a branch and thus decreasing the success of prey capture. Most strikingly, there was no indication from $\delta^{13}\text{C}$ of polyp and zooxanthellae, that the depth specialist species of *Madracis* compensate for the inevitable loss of carbon assimilation due to a reduced photosynthetic rate by increasing their heterotrophic food uptake at increasing water depth. This raises new questions of what other energy supply or "energy saving mechanisms" apply in these reef corals specialized to the low-light environment at depths of 50 m or more.