

The Geochemistry of Coral Biomineralization: Using Boron Isotopes to Understand the Cost of Resilience in a Changing Ocean

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Coral calcification is both sensitive to environmental changes and buffered from these changes through the physiology of biomineralization. The mechanisms governing this balance determine how corals respond to ocean acidification and control the sensitivity of many paleoclimate proxies. One such promising proxy in corals and other marine calcifiers is skeletal boron isotopes, which are used to reconstruct ocean pH changes over geologic time. Because boron isotopes reflect calcifying fluid chemistry, understanding how boron responds to a wide range of CO₂ chemistry conditions can improve this paleoclimate proxy while also elucidating environmental controls on biomineralization. We show that skeletal boron isotopes are not a simple indicator of seawater pH but are also sensitive to the total dissolved inorganic carbon (DIC) concentration of seawater in the cultured cold-water coral *Balanophyllia elegans*. A general geochemical model of calcification, which includes boric acid diffusion across cell membranes, accurately predicts both this new DIC effect and the behavior of the boron paleo-pH proxy. Contrary to previous studies, our results demonstrate that skeletal boron isotopes do not necessarily reflect calcifying fluid pH, which remains nearly constant in the species studied here. This constant calcifying fluid pH implies similar calcification rates during ocean acidification, which may explain the resilience of *B. elegans* to ocean acidification. Nevertheless, this resilience comes at an energetic cost because our model shows that calcification becomes less efficient as seawater becomes more acidic.