Oxygen and Heterotrophy Affect Calcification of the Scleractinian Coral *Galaxea fascicularis*

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Heterotrophy is known to stimulate calcification of scleractinian corals, possibly through enhanced organic matrix synthesis and photosynthesis, and increased supply of metabolic DIC. In contrast to the positive long-term effects of heterotrophy, inhibition of calcification has been observed during feeding, which may be explained by a temporal oxygen limitation in coral tissue. To test this hypothesis, we measured the short-term effects of zooplankton feeding on light and dark calcification rates of the scleractinian coral *Galaxea fascicularis* (n = 4) at oxygen saturation levels ranging from 13 to 280%. Significant main and interactive effects of oxygen, heterotrophy and light on calcification rates were found (three-way factorial repeated measures ANOVA, $p<0.05$). Light and dark calcification rates of unfed corals were severely affected by hypoxia and hyperoxia, with optimal rates at 110% saturation. Light calcification rates of fed corals exhibited a similar trend, with highest rates at 150% saturation. In contrast, dark calcification rates of fed corals were close to zero under all oxygen saturations. We conclude that oxygen exerts a strong control over light and dark calcification rates of corals, and propose that in situ calcification rates are highly dynamic. Nevertheless, the inhibitory effect of heterotrophy on dark calcification appears to be oxygen-independent. We hypothesize that dark calcification is impaired during zooplankton feeding by a temporal decrease of the pH and aragonite saturation state of the calcifying medium, caused by increased respiration rates. This may invoke a transient reallocation of metabolic energy to soft tissue growth and organic matrix synthesis. These insights enhance our understanding of how oxygen and heterotrophy affect coral calcification, both in situ as well as in aquaculture.

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