Elevated CO_2 Enhances Otolith Growth in Young Fish

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A large fraction (0.3 to 0.5) of the carbon dioxide (CO_2) added to the atmosphere by human burning of fossil fuels enters the ocean (*1*). This causes ocean acidification by increasing the concentrations of oceanic CO_2, bicarbonate (HCO_3^-) and hydrogen (H^+) ions and decreasing the concentration of carbonate (CO_3^{2-}) ion and hence the saturation state of calcium carbonate (Ω) (*1*). Addition of CO_2 to the atmosphere and ocean may thus influence the rates of formation and dissolution of aragonite and calcite, biominerals that are critical to diverse marine taxa. Although some recent studies have shown that elevated CO_2 enhances structural calcification in coccolithophores and invertebrates, most studies have shown a slowing of structural calcification (*2*). Otoliths are bony structures used by fish to sense orientation and acceleration and consist of aragonite-protein bilayers, which document fish age and growth. We hypothesized that otoliths in eggs and larvae reared in seawater with elevated CO_2 would grow more slowly than they do in seawater with normal CO_2. To test our hypothesis, we grew eggs and prefeeding larvae of white sea bass (*Atractoscion nobilis*) under a range of CO_2 concentrations and measured the size of their sagittal otoliths by using a scanning electron microscope (Fig. 1, A to C) (*3*).

In each experiment, we incubated eggs and larvae in seawater under control (380 μatm of CO_2, 1 atm = 101.325 kPa) and treatment (993 or 2558 μatm of CO_2) atmospheres. Initial experiments 1 and 2 used 2558 μatm of CO_2 to test whether elevated CO_2, resulting in aragonite undersaturation in the seawater, affected otolith size. Experiments 3 and 4 used 993 μatm of CO_2, an atmospheric concentration ~2.5 times the present concentration that may occur by 2100 (*4*). Contrary to expectations, the otoliths of fish grown in seawater with high CO_2, and hence lower pH and $\Omega_{aragonite}$, were significantly larger than those of fish grown under simulations of present-day conditions (Fig. 1D and table S1). For 7- to 8-day-old fish grown under 993 and 2558 μatm of CO_2, the areas of the otoliths were 7 to 9% and 15 to 17% larger, respectively, than those of control fish grown under 380 μatm of CO_2. Assuming otolith density is constant and that volume is proportional to area$^{1.5}$ (*3*), we estimate otolith masses were 10 to 14% and 24 to 26% greater, respectively, for fish under 993 and 2558 μatm of CO_2. The dry mass of fish did not vary with CO_2 (*3*), and thus fish of the same size had larger otoliths when grown under elevated CO_2.

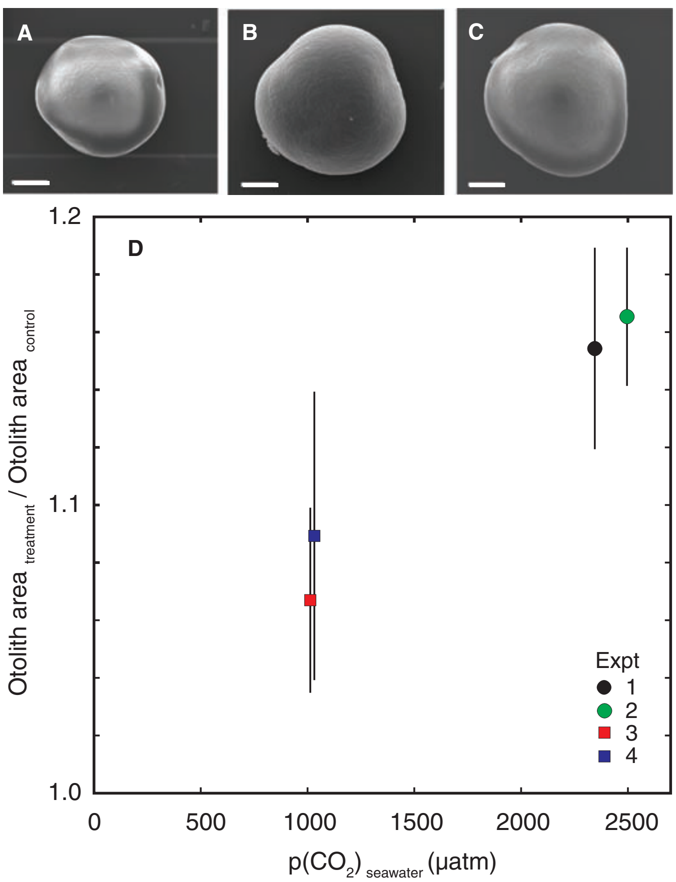

Fig. 1. Dorsal view of sagittal otoliths of 7-day-old white sea bass grown at (**A**) 430, (**B**) 1000, and (**C**) 2500 μatm $p(CO_2)_{seawater}$. Scale bars indicate 10 μm. (**D**) Ratio (treatment/control) of otolith area in relation to $p(CO_2)_{seawater}$. Mean ratios and their associated uncertainties (*3*) are plotted. The control level $p(CO_2)_{seawater}$ was ~430 μatm [$p(CO_2)_{atmosphere}$ ~ 380 μatm], for which otolith area ratio = 1.

Our results are consistent with young fish being able to control the concentration of ions (H^+ and Ca^{2+}), but not the neutral molecule CO_2, in the endolymph surrounding the otolith. Gases in tissues of fish eggs and larvae equilibrate rapidly with seawater by cutaneous exchange (*5*) but may also be affected by acid-base regulation (*6*). In the endolymph, with constant pH, elevated CO_2 increases CO_3^{2-} concentration and thus the $\Omega_{aragonite}$, accelerating formation of otolith aragonite. This is a fundamentally different effect of elevated CO_2 on marine biomineralization than those in previous reports on acidification (*1*, *2*).

We do not know whether our results apply to other taxa with aragonite sensory organs, such as squid and mysids (statoliths) or other fish species. Nor do we know whether larger otoliths have a deleterious effect, although we do know that asymmetry between otoliths can be harmful (*7*).

Our results indicate the need to understand the diverse effects of elevated CO_2 on biomineralization over taxa and developmental stages. The specific effects of elevated CO_2, not simply acidification, should be considered. Calcification and dissolution of calcium carbonate occur sequentially and often at different locations and under different conditions. Whatever the organism, to predict the effects of elevated CO_2, we need to know the mechanisms of production and dissolution and their relationships to changing seawater chemistry.

References and Notes

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Supporting Online Material
www.sciencemag.org/cgi/content/full/324/5935/1683/DC1
Materials and Methods
SOM Text
Table S1
References

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