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Ecophysiology of the calcifying marine alga *Emiliana huxleyi*

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Summary

Using a combined morphological and immunological approach, it was found that two major calcified types of the coccolithophorid *Emiliania huxleyi* are unequally distributed over the oceans. The small type, called type A (3-5 μm in diameter), was widespread in the Atlantic region. In contrast, for reasons yet unknown, the larger type B (5-8 μm in diameter) had a far more restricted distribution; this type was only encountered in the North Sea. Recent experiments indicate that type B is a polyploid of type A.

Emiliania huxleyi types A and B showed considerable differences in cell and growth characteristics. Type B grew faster than type A at low photon flux densities (PFD $<20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). Type B cells had higher calcium carbonate and organic matter contents, higher chlorophyll fluorescence and higher side-scatter properties. Considering the effects of PFD, temperature and phosphate concentration on cell and growth characteristics, the diel variability in these parameters, induced by the L:D cycle, was significant.

On the basis of calcite carbon/organic carbon production ratios, it was concluded that growth of both *E. huxleyi* types under light limitation is a sink for carbon dioxide. In contrast, growth of both types under phosphate limitation produced carbon dioxide. Growth of natural *E. huxleyi* populations (typical concentrations between 0.5 and 50 million cells l^{-1}) under phosphate limitation could increase the carbon dioxide concentration $[\text{CO}_2\text{aq}]$ of surface water with $0.05\text{-}0.5 \mu\text{mol l}^{-1} \text{d}^{-1}$.

It was demonstrated that in the dark significant net dissolution of calcium carbonate ($>10\%$ of standing stock in 8 h) can take place despite the fact that the ambient sea water is supersaturated with calcium carbonate. Bacterial activity, cell division and lysis processes may all contribute to the dissolution. On the other hand, it was shown that calcium carbonate production can continue in the dark and that phosphate limitation stimulates this dark production. The results imply that calcification measurements should extend over a complete L:D cycle (24 h).

Another aspect is the detachment of coccoliths from the *E. huxleyi* cell. It was found that coccoliths become detached during the cell division process. Numbers of detached liths also increased during the decline of an *E. huxleyi* population due to grazing activity or lyses of cells.

In outdoor enclosures which varied in their phosphate loadings, standing stocks of organic matter, calcium carbonate, and numbers of *E. huxleyi* cells and detached liths were measured over an extended period covering initial, exponential and declining stages of *E. huxleyi* blooms. In enclosures with low and intermediate phosphate loadings, intense blooms of *E. huxleyi* type A developed. In contrast, *E. huxleyi* numbers stayed low in enclosures with high phosphate concentrations and in unfertilized enclosures. Accurate calculations based on the daily net changes in organic matter and calcium carbonate standing stocks in the enclosure with the low phosphate loading revealed that the phytoplankton community, including an *E. huxleyi* bloom of 30 million cells l^{-1} , had decreased the partial pressure of carbon dioxide (pCO_2) from 250 to 150 ppm. In comparison, a non-calcifying phytoplankton

community reaching the same organic matter mass (about 0.8 g C m^{-3}) would have reduced pCO_2 from 250 to 130 ppm. It was concluded that *E. huxleyi* decreases the concentration of carbon dioxide in surface waters, but to a smaller extent than non-calcifying phytoplankters with the same organic matter content would have done.

In order to find out whether the formation of *E. huxleyi* blooms in the outdoor enclosures was controlled by nutrients (bottom-up) or by predators (top-down), a novel method was applied to determine in situ species specific gross growth rates of phytoplankton. Initial studies with laboratory cultures showed that gross growth rates calculated on the basis of diel changes in cellular DNA content were in close agreement with the measured growth rates (based on cell counts). Subsequently, the same calculations were applied to *E. huxleyi* populations in the different enclosures. Results showed no differences in gross growth rates among different enclosures. In contrast, loss rates differed significantly. In enclosures with low and intermediate phosphate concentrations loss rates were low, allowing extensive blooming of *E. huxleyi*, whereas in the enclosure with high phosphate concentrations and in the unfertilized oligotrophic enclosure losses were high, preventing blooming of *E. huxleyi*. Clearly, losses, or rather the lack of such, determined the success of *E. huxleyi* blooming and nutrient conditions affected the *E. huxleyi* loss rates, probably because they affected the growth rates of other phytoplankton species.

Cell cycle studies of *E. huxleyi* revealed that photon flux density (PFD) exerts control only on the G_1 phase and not on the S and G_2M phases of the DNA synthesis cycle. Temperature affects the G_2M phase (and probably also the other phases). In addition to environmental control, an internal *E. huxleyi* clock seems involved in the regulation of cell cycle processes.

