



## Numerical modelling of physiological and ecological impacts of ocean acidification on coccolithophores

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### ABSTRACT

Ocean surface acidification due to increasing atmospheric CO<sub>2</sub> concentration is currently attracting much attention. Coccolithophores distribute widely across the world's oceans and represent a carbon sink containing about 100 million tonnes of carbon. For this reason, there is concern about dissolution of their shells, which are made of calcium carbonate, due to decreasing pH. In this study, intracellular calcification, photosynthesis, and mass transport through biomembranes of *Emiliania huxleyi* were modelled numerically for understanding biological response in calcifying organisms. Unknown parameters were optimised by a generic algorithm to match existing experimental results. The model showed that the production of calcium carbonate rather than its dissolution is promoted under an acidified environment. Calcite remains at saturation levels in a coccolith even when it is below saturation levels in the external seawater. Furthermore, a coccolith can dissolve even in water where calcite saturation exceeds 1, because the saturation may be below the threshold level locally around the cell membrane. The present model also showed that the different calcification rates of *E. huxleyi* with respect to rising CO<sub>2</sub> concentrations reported in the literature are due to differences in experimental conditions; in particular, how the CO<sub>2</sub> concentration is matched. Lastly, the model was able to reproduce differences in calcification rates among coccolithophore species. The above biochemical-kinetic model was then incorporated into an ecosystem model, and the behaviour of coccolithophores in the ecosystem and the influence of increases in CO<sub>2</sub> concentration on water quality were simulated and validated by comparison with existing experimental results. The model also suggests that increased CO<sub>2</sub> concentration could lead to an increase in the biomass ratio of coccolithophores to diatoms at high CO<sub>2</sub> concentrations, particularly in oligotrophic environments, and to a consequent decrease in pH due to calcium dissolution.

### 1. Introduction

The pH of the ocean decreases from about 8.2 to 8.1 over the past 200 years by oceanic absorption of atmospheric CO<sub>2</sub>. Atmospheric CO<sub>2</sub> concentration will possibly exceed 1000 ppm by 2100 if anthropogenic CO<sub>2</sub> emissions continue to rise, leading to a further decrease in oceanic pH of 0.3 to 0.4 (Orr et al., 2005). Absorption of CO<sub>2</sub> by oceans increases bicarbonate (HCO<sub>3</sub><sup>-</sup>) levels and causes a decrease in carbonate ions (CO<sub>3</sub><sup>2-</sup>) (Riebesell et al., 2000). This decrease in CO<sub>3</sub><sup>2-</sup> decreases the saturation of calcium carbonate (CaCO<sub>3</sub>), which makes up calcite and aragonite. Aragonite, generated by organisms such as corals and foraminifers, dissolves more easily than calcite, generated by organisms

such as foraminifers and coccolithophores; however, both forms are vulnerable to increases in CO<sub>2</sub> concentration (Feely et al., 2004).

It is known that calcification in marine organisms greatly depends on oceanic calcium carbonate saturation (Riebesell et al., 2000; Zondervan et al., 2002), and it has been predicted that aragonite will be depleted from the surface layer of high-latitude oceans by around 2050 (Orr et al., 2005). It is thought that some calcifying organisms have already been affected by this decrease. About half of all calcification on Earth occurs in coccolithophores, corals, and calcareous algae (Shiraiwa, 2001), and it is therefore important to understand the influence of ocean acidification on these calcifying organisms.

Coccolithophores are unicellular phytoplankton that live around the

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world in the surface layer at latitudes of up to about 60° in both hemispheres. These organisms form a shell of calcium carbonate called a coccolith inside their body, which becomes attached to the cell surface. The amount of carbon fixed by coccoliths is estimated to be about 100 million tonnes per year CO<sub>2</sub> equivalent, and this is expected to have a huge influence on the carbon cycle on Earth (Fujiwara and Tsuzuki, 2007).

Coccolithophores utilise two carbon fixation routes, photosynthesis and calcification. Calcification consumes HCO<sub>3</sub><sup>-</sup> and produces CO<sub>2</sub>, and photosynthesis consumes CO<sub>2</sub>. Calcification requires the energy generated by photosynthesis, and this exchange is promoted by the CO<sub>2</sub> produced by calcification (Nimer and Merrett, 1992). It is well known that calcification is a strategy for promoting photosynthesis in the ocean, which has a scarcity of CO<sub>2</sub> and an abundance of HCO<sub>3</sub><sup>-</sup> (Roer et al., 1980; Suzuki, 1997).

It is thought that the molar ratio of organic to inorganic carbon produced by coccolithophores is about 1:0.8. This means that even though photosynthesis absorbs CO<sub>2</sub>, almost the same amount of CO<sub>2</sub> is produced by the synthesis of the coccoliths. In the case that proliferation of other photosynthetic organisms is suppressed by a bloom of coccolithophores, the ocean may discharge CO<sub>2</sub> into the atmosphere, instead of absorbing it. In fact, during a mass bloom of *Emiliania huxleyi* in the Bering Sea in 2000, the partial pressure of CO<sub>2</sub> in the surface water increased to 450 μatm, which was greater than the atmospheric level of 370 μatm, and the ocean ultimately released CO<sub>2</sub> into the atmosphere (Murata and Takizawa, 2002).

Diatoms also form shells and are distributed throughout high-nutrient environments in high-latitude regions. Like coccolithophores, they also play an important role in the oceanic carbon cycle compared with shell-less phytoplankton species because their shell acts as a weight that transports material efficiently in the vertical direction. The difference between the two planktons is that the shell in diatoms consists of vitreous silicate. This suggests that diatoms assimilate only carbon, and areas where diatoms are the dominant species absorb CO<sub>2</sub>, implying that the dominant species at a site has a large influence on the local carbon cycle. It is therefore important, both for the ocean and for climate change, to estimate increases and decreases in coccolithophore population and calcification, and the effects they have on other organisms.

The saturation state of calcium carbonate is given by  $\Omega = [\text{Ca}^{2+}][\text{CO}_3^{2-}]/K_{\text{sp}}$ , where  $K_{\text{sp}}$  is a solubility product constant. It has been conjectured that when  $\Omega$  decreases due to a decrease in CO<sub>3</sub><sup>2-</sup>, calcifying organisms such as coral and coccolithophore are greatly affected and decrease as a result (Iglesias-Rodriguez et al., 2008). The effect of increased CO<sub>2</sub> concentrations on oceanic coccolithophores, such as *E. huxleyi* and *Gephyrocapsa oceanica*, was recently investigated, and a decrease in calcification was found to have occurred at high CO<sub>2</sub> concentrations (Riebesell et al., 2000; Zondervan et al., 2002). However, observational results have shown that coccolithophores proliferate even if calcification decreases, due to the increase in photosynthesis. Since the affinity of coccolithophores to CO<sub>2</sub> is lower than other phytoplanktons, photosynthesis is expected to increase with an increase in CO<sub>2</sub> under conditions where CO<sub>2</sub> is its limiting factor.

Falter et al. (2013) suggested that physical and biological controls on the carbonate chemistry are important processes on the effects of metabolism.

It has been demonstrated that some species do not necessarily decrease under rising CO<sub>2</sub> concentrations. Langer et al. (2006) showed that the amount of calcification by *Pleurochrysis carterae* remains virtually unchanged and that calcification by *Coccolithus pelagicus* follows a nonlinear curve that exhibits maximum calcification at present CO<sub>2</sub> concentrations. *Pleurochrysis carterae* exhibited some kind of adaptation, with the calcification initially decreasing and then increasing again in an experiment at Shizuoka University (Casareto et al., 2009). It is understood that acidification of the ocean by CO<sub>2</sub> has various effects on oceanic calcifying organisms.

Some experiments have shown that coccolithophores can dissolve even if  $\Omega > 1$  in the environment (Riebesell et al., 2000; Langer et al., 2006). External water quality cannot explain this dissolution of the coccolith, because conditions of supersaturation persist until the CO<sub>2</sub> concentration exceeds about 1500 ppm. There is a possibility that  $\Omega < 1$  conditions exist locally in the environment near the cell membrane (Sekino et al., 1996). Although calcification also depends on light, the calcite saturation level near the cell membrane may more readily drop to 1 or less at night (Linschooten et al., 1991; Shiraiwa, 2001). It is therefore thought that intracellular biochemical reactions such as photosynthesis and calcification do not simply depend on the external water quality conditions. In other words, it is possible that intracellular water quality conditions and mass transfers through biomembranes could be important factors that control these reactions, and could cause differences between species and experimental conditions. Although several numerical models for treating coccolithophores have been proposed previously, such as by Gregg and Casay (2007), Fujii and Chai (2006), and Bernard et al. (2008), these considered reactions to be dependent on only external environmental conditions and did not consider intracellular conditions.

The objective of the present study is to model the biochemical reactions inside the coccolithophore cells, and to simulate how photosynthesis, calcification, dissolution of the coccolith, and other processes respond to ocean acidification. In addition, an ecosystem model that includes the above biochemical model single coccolithophores is developed and the dynamics and environmental interactions of coccolithophores with other organisms such as diatoms as the CO<sub>2</sub> concentration increases are investigated.

## 2. Method and materials

### 2.1. Overall model concept

Although there are many species of coccolithophores, *E. huxleyi*, which has a wide distribution and has been the subject of much research, was selected for this study. Schematic diagrams of the coccolithophore intracellular model and the ecosystem model are shown in Figs. 1 and 2, respectively. In Fig. 1, PHY<sub>1</sub> and COC denote the biomasses of coccolithophore and coccolith, respectively. Boxes inside the shaded areas represent water quality factors, which also vary in the kinetics of the carbonate system. In Fig. 2, PHY, ZOO, POM, DOM, DIN, and DO denote phytoplankton, zooplankton, particulate organic matter, dissolved organic matter, and dissolved oxygen, respectively. Boxes inside the shaded area represent water quality factors the same as in the intracellular model.

Although the time scale of the intracellular reactions is far < 1 s, carbonic acids cannot be assumed to be in equilibrium since equilibration takes tens of seconds, and chemical equations of carbonic system kinetics were solved accordingly. Fig. 3 shows the time scales of the model reactions in the present study with the loops indicating iterations for time adjustment.

### 2.2. Intracellular biochemical model of coccolithophores

#### 2.2.1. Model description

Photosynthesis in coccolithophores is performed intracellularly by the chloroplasts. At the same time, the coccolith vesicle outside the cytoplasm creates coccoliths on a substrate plate made of acidic polysaccharide. The intracellular reactions are governed by the water quality in the vesicle and the cytoplasm and the amounts of H<sup>+</sup>, HCO<sub>3</sub><sup>-</sup>, and CO<sub>2</sub> that pass through the membranes of the vesicle and the cell. The completed coccolith adheres to the exterior of the cell membrane and is affected by the extracellular water quality.

Considering these factors, we divided the domain into four partitions: (a) coccolith vesicle, (b) cytoplasm excluding the vesicle, (c) cell periphery, and (d) external water, as shown in Fig. 4, and modelled the

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