

Changes in Bioenergetics Associated with Ocean Acidification and Climate Changes

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Abstract

Ocean global changes, including CO₂-triggered ocean acidification and warming as well as associated changes in physical and chemical environments affect metabolisms of marine organisms and increase their energetic demand to cope with the environmental stresses. Phytoplankton species grown under ocean acidification conditions alter their metabolic pathways, down-regulating their CO₂ concentrating mechanisms, up-regulating photorespiration and heat-dissipating processes and generating extra energy by degrading accumulated phenolic compounds, which are toxic and can be transferred to higher trophic levels, changing food quality. Calcifying algae, under influence of ocean acidification, need more energy to maintain their calcification and to synthesize UV screening compounds due to reduced thickness of the calcified "shell". Changes in the bioenergetics with exacerbating ocean global environmental issues will lead to ecological consequences and affect services of marine ecosystems.

Keywords: Algae; Calcification; Climate change; Diatoms; Growth; Ocean acidification; Photosynthesis; Phytoplankton; Warming; UV radiation

Introduction

Increasing atmospheric CO₂ concentration due to combustion of fossil fuels result continuous dissolution of anthropogenic CO₂ into the oceans, leading to ocean acidification (OA, declining pH in surface oceans). Increased availability of CO₂ in seawater may save energy for photosynthetic CO₂ fixers, but can increase energetic cost due to acidic stress caused by OA for all organisms that have adapted to the contemporary carbonate chemistry [1]. In view of the metabolic responses and associated energetics, changes in chemical and physical environments associated with OA and other ocean climate changes, such as warming and increasing exposures to solar UV radiation due to enhanced stratification (thinner upper mixing layer) for cells within this layer, may interactively (additive, synergistic or antagonistically) affect physiological processes and ecological functions of marine organisms.

Bio-calcification

Calcifying organisms are expected to need extra energy to sustain calcification processes with progressive OA, which are known to perform less efficiently under lowered pH. Corals, shellfishes and calcifying plankton as well as calcareous macroalgae usually produce thinner or less "skeleton" under OA conditions [2]. When calcifying

macroalgae (such as coralline algae) and microalgae (such as coccolithophores) are grown under OA, they calcify less and suffer more from solar UV radiation, then struggle to spend extra energy to synthesize UV-screening or absorbing compounds [3,4]. The calcified coverage has been demonstrated to shield of UV irradiances by over 25% in *Emiliania huxleyi* [3]. Even for zooplankton and/or other non-calcifying organisms, in future oceans or some natural shallow environments today where pH is low, they need extra energy to cope with acidic stress and other stressors, such as UV and warming. Increasing temperature may help to gain the extra energy for some species at higher latitudes and may synergistically lift the costs as well.

Photosynthesis and Growth

Marine photosynthesis drives marine biological CO₂ pump, that takes up over 1 million tons of CO₂ on global average from the atmosphere. Since CO₂ is the substrate of carboxylation, it is often thought that increased partial pressure of CO₂ in seawater leads to increased CO₂ availability, and therefore, enhances algal or cyanobacterial growth and stimulate primary productivity. In seaweeds (macroalgae) or seagrasses, excluding the calcifying species, this is usually true. In *Nori* (*Porphyra yezoensis*) and a green tide alga (*Ulva* sp.), elevated CO₂ remarkably enhanced their growth [5,6], with their CO₂ concentrating mechanisms (CCMs) being down-regulated. In diatoms, similar trend has been reported under laboratory conditions (low light and constant temperature), however, under high levels of sunlight, the diatoms grow much slower under the OA treatment compared to ambient CO₂ condition [7]. Mechanistically, down-regulation of CCMs under elevated pCO₂ can save energy for active uptake of inorganic C, the saved energy could be employed to stimulate growth under light-limiting condition and to exacerbate light stress under over-saturating light levels, leading to up-regulated photorespiration. That is, the changed carbonate chemistry due to OA is supposed to increase light stress, as indicated in enhanced non-photochemical quenching (NPQ) in surface phytoplankton assemblages in the South China Sea [7]. Nevertheless, increased NPQ under OA do not always couple with decreased growth or photosynthetic carbon fixation [6].

Perspectives

As global warming will cause upper mixed layer depths to decrease (enhanced surface ocean stratification) in the future ocean, plankton species within this layer will be exposed to higher daytime dose of solar radiation [8]. This in combination with OA can act synergistically to trigger additional light and/or UV stress and photo-damages, since

less upward transport of nutrients would restrain the planktons to synthesize defensive proteins or components.

Performance and biochemical compositions of primary producers directly or indirectly influence secondary producers. Phytoplankton species (diatoms and coccolithophores) grown under OA accumulate more phenolics within their cells, which lead to higher contents of phenolics in copepods who feed them [9]. This is caused by alterations in metabolic pathways (β -oxidation and the Krebs cycle) that are considered to provide extra energy to cope with acidic stress under OA treatment (Figure 1). Since phenolics are toxic, OA impacts through food chain may affect food quality. Taste of shrimps grown under OA was shown to deteriorates [10], though there is no evidence that these shrimps had higher phenolic compounds compared to the control (ambient CO_2 level). This aspect is certainly worth looking into from biochemical and molecular aspects, since degradation of extra phenolic compounds requires more related enzymes or higher activity of them, which then have imprints on expressions of genes.

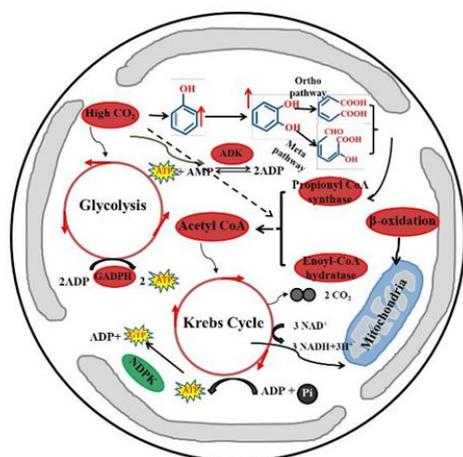


Figure 1: Ocean acidification up-regulated (red) and down-regulated (green) metabolic pathways in a calcifying microalga (*Emiliana huxleyi*) Jin et al. [9].

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