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# A biomarker perspective on coccolithophorid growth and export in a stratified sea

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ABSTRACT

Summer cruises to the Gulf of California and adjacent Eastern Tropical North Pacific between 2004 and 2008 provided data on non-bloom coccolithophorid abundance and production in nitrate-depleted surface waters. Using lipid biomarkers specific to the dominant coccolithophorids in this region, it was found that these organisms routinely exhibited maximum production rates at depths associated with subsurface chlorophyll features and the nitracline, as opposed to the N-depleted surface. Estimates of integrated coccolithophorid production, relative to bulk primary production, showed no systematic relationship to availability of the limiting macronutrient (nitrate) in the euphotic zone. Our observations suggest that, in sufficiently well-stratified settings, the nutrient-depleted and nutrient-replete portions of the euphotic zone may become so sharply partitioned and temporally stable that a coccolithophorid-favorable 'mid-to-low nutrient' niche is absent. Consequently, the relative abundance and production rate of coccolithophorids are low, and the relative contribution of alkenones to carbon export is driven by variability in the significantly larger bulk carbon component. Study of this region provides important insights into the ecology of these calcifying organisms in a warm, quiescent ocean. Our findings suggest that, if water columns akin to those surveyed become more common, coccolithophorid-derived inorganic carbon export may serve as a weaker positive feedback on atmospheric $CO_2$ than previously suggested.

## 1. Introduction

As a dominant producer of particulate inorganic carbon (PIC) in the global ocean (Baumann et al., 2004; Hay, 2004), coccolithophorids have received significant research focus for the last two decades. An increased understanding of coccolithophorid physiology (e.g. Müller et al., 2008), ecology (e.g. De Bernardi et al., 2005), and biogeochemical cycling (e.g. Balch and Utgoff, 2009) has provided important insights into fluctuations in the inorganic carbon pump, the evolution of past climates, and changes in the ecology and chemistry of the ocean in the face of rising atmospheric $CO_2$ (e.g. Zondervan et al., 2001). This last subject is of particular importance. The predictability of future climate change is dependant, in part, on the understanding of positive or negative feedbacks between algal calcite production and sea surface temperature (SST), upper ocean stratification, atmospheric $CO_2$ and ocean pH (Holligan and Robertson, 1996; Tyrrell, 2008; Beaufort et al., 2011). This situation has stimulated an effort to understand how modern coccolithophorid production relates to prognostic ocean parameters (e.g. Iglesias-Rodríguez et al., 2002; Cermeño et al., 2008). It remains unclear, however, which perspective is most relevant for the future ocean: bloom-dominated or steady-state/subsurface 'background' production. In oligotrophic surface waters, the low nutrient half-saturation constants and high light tolerance of coccolithophorids give them a competitive advantage over larger plankton such as diatoms (Tozzi et al., 2004; Litchman et al., 2007). These physiological attributes may also be a key component in coccolithophorids' successional niche in the North Sea (Head et al., 1998) and the North Atlantic (Lochte et al., 1993) blooms. However, coccolithophorids have also been observed or inferred to exhibit production maxima associated with the nitracline (Fernández et al., 1993; Prahl et al., 1993; Popp et al., 2006b), and it has been estimated that the bulk of global coccolithophorid production takes place under non-bloom conditions (Brown and Yoder, 1994). Currently, it is unclear to what extent nutrient gradients with depth, in stratified settings, provide the same coccolithophorid-favorable niche provided by temporal nutrient gradients in more regularly-mixed regions (e.g. Iglesias-Rodríguez et al., 2002).

Cruises to the Gulf of California (GC) were conducted in the summers of 2004, 2005 and 2008, with the latter cruise also

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extending to the Gulf's entrance zone (EZ) and the adjacent Eastern Tropical North Pacific (ETNP) (White et al., 2007, 2012; Malinverno et al., 2008). These cruises (Table 1, Fig. 1) provided an excellent opportunity to study the dynamics of coccolithophorid production in stratified water columns, across a broad temperature range, in a location where subsurface maxima in coccolithophorid abundance have been reported (Hernández-Becerril, 1987). Furthermore, estimates of coccolithophorid and diatom abundance in the GC from the summer of 2005 correspond to coccolithophorid:diatom ratios on the order of ~0.01–0.08 (chlorophyll a basis; Malinverno et al., 2008). This ratio is lower than expected for what should be a coccolithophorid-favorable high light, low nutrient setting. For comparison, ratios >1 (carbon basis) were observed along the majority of the longitudinal Atlantic Ocean transect surveyed by Cermeño et al. (2008). This difference suggests unusual coccolithophorid ecology in the GC, warranting further investigation.

We have estimated coccolithophorid production and export relative to key water column features including mixed layer and nutricline depth, net primary production (NPP), and chlorophyll a (ChlA) concentration profiles during these cruises. This information allowed the following questions to be addressed:

1. Is coccolithophorid production enhanced under stratified, nutrient-depleted conditions in our study area? If so, why is the relative coccolithophorid abundance so low?
2. Does any perceived dependence of production on nutrient conditions alter the contribution of these plankton to carbon export?

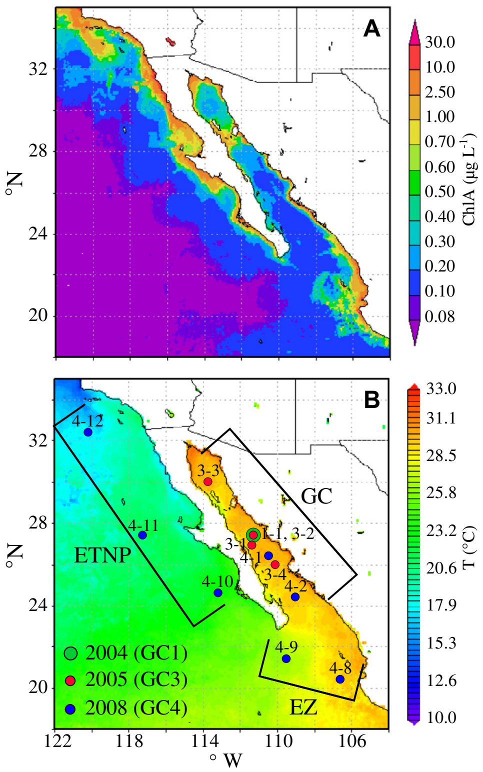

**Fig. 1.** Seasonal composites of Aqua MODIS level-3 4 km sea surface ChlA (μg L$^{-1}$) and 11 μm nighttime SST (°C) (A and B, respectively) in the Gulf of California for the summer (July–September) of 2005 (NASA Giovanni visualization). Sampling locations for 'GC' cruises 1 (2004), 3 (2005) and 4 (2008) are shown in B. Stations 4-8 and 4-9 are referred to herein as 'entrance zone' stations (EZ), and 4-10, 11, and 12 are referred to as 'ETNP'. The remaining stations are classified as 'GC'. See Table 1 for occupation coordinates and dates.

Using the compound-specific $^{13}$C incubation techniques developed by Popp et al. (2006a) and detailed further in Popp et al. (2006b), we employed $C_{37}$ alkenones as a sensitive tracer of coccolithophorid-specific production in this low-abundance, low PIC:particulate organic carbon (POC) setting. Alkenone biomarkers are unique to specific prymnesiophytes, and are largely produced by *Emiliania huxleyi* and members of the genus Gephyrocapsa (Volkman et al., 1980, 1995; Marlowe et al., 1984). These species are the predominant coccolithophorids in the Gulf of California (Thunell et al., 1996; Malinverno et al., 2008) and throughout the world ocean (Winter et al., 1994). The primary alkenones produced in marine settings, including the GC and adjacent ETNP, are the di- and tri-unsaturated 37-carbon methyl ketones K37:2 and K37:3. Using these two alkenones and previously reported cell abundances, we compare estimated coccolithophorid production and export to NPP and POC flux in the context of nutrient conditions and stratification.

**Table 1**
Summary of descriptive hydrographic parameters measured at stations in this study. Surface temperature is given as the mean temperature observed in the surface-most density bin over the course of station occupation (see Section 2.2). Mixed layer depth (density offset of 0.125 kg m$^{-3}$ from the surface value), top-of-nitracline depth ([$NO_3^-$] = 1 μmol L$^{-1}$) and 1% light level (vs. simultaneous surface PAR) are interpolated from the mean profiles described in Section 2.2 (Supplemental data). Uncertainty values are given as half the depth range between the two density bins bracketing the interpolated values. ChlA maximum depths are given as the average depth of the density bin with the highest average ChlA fluorescence (Supplemental data), and uncertainty is given as the standard deviation of depth of this isopycnal.

| Station | Occupation date | Lat (°N) | Lon (°W) | SST (°C) | Mean mixed layer depth (m) | ± | Nitracline depth (m) | ± | Depth of 1% light (m) | ± | DCML depth (m) | ± | Averaged casts |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Gulf of California (GC)* | | | | | | | | | | | | | |
| 1-1 | July 13–15 2004 | 27.50 | 111.33 | 28.5 | 6 | 2 | 23 | 1 | 19 | 1 | 26 | 2 | 15 |
| 3-1 | August 5–7 2005 | 27.02 | 111.42 | 30.9 | 4 | 0 | 47 | 7 | 43 | 1 | 32 | 4 | 12 |
| 3-2 | July 27–30 2005 | 27.50 | 111.33 | 29.4 | 8 | 1 | 33 | 4 | 29 | 1 | 34 | 2 | 7 |
| 3-3 | July 31–August 3 2005 | 30.10 | 113.87 | 30.1 | 5 | 1 | 33 | 2 | 34 | 1 | 32 | 3 | 9 |
| 3-4 | August 3–5 2005 | 26.07 | 110.12 | 29.8 | 14 | 3 | 46 | 3 | 42 | 1 | 44 | 3 | 9 |
| 4-1 | July 11–13 2008 | 26.50 | 110.50 | 28.8 | 9 | 2 | 35 | 5 | 42 | 1 | 35 | 6 | 16 |
| 4-2a | July 14–16 2008 | 24.50 | 109.00 | 29.4 | 10 | 0 | 36 | 3 | 55 | 0 | 39 | 6 | 19 |
| 4-2b | July 22–24 2008 | 24.50 | 109.00 | 29.7 | 8 | 2 | 40 | 9 | 45 | 2 | 46 | 1 | 14 |
| *Entrance zone (EZ)* | | | | | | | | | | | | | |
| 4-8 | July 18–21 2008 | 20.50 | 106.50 | 29.5 | 8 | 1 | 69 | 1 | 67 | 1 | 60 | 8 | 19 |
| 4-9 | July 25–27 2008 | 21.50 | 109.50 | 28.8 | 8 | 1 | 34 | 3 | 44 | 1 | 43 | 4 | 16 |
| *Eastern Tropical North Pacific (ETNP)* | | | | | | | | | | | | | |
| 4-10 | July 28–31 2008 | 24.70 | 113.30 | 24.2 | 9 | 1 | 40 | 10 | 47 | 2 | 50 | 3 | 17 |
| 4-11 | August 1–3 2008 | 27.50 | 117.50 | 21.0 | 12 | 3 | 51 | 3 | 42 | 1 | 50 | 6 | 15 |
| 4-12 | August 5–7 2008 | 32.50 | 120.50 | 16.9 | 15 | 3 | 22 | 3 | 32 | 1 | 23 | 4 | 14 |