Biogeochemical implications of comparative growth rates of *Emiliania huxleyi* and *Coccolithus* species
C. J. Daniels, R. M. Sheward, and A. J. Poulton

Daniels *et al.* present data about calcification and growth of 4 strains/ species of coccolithophorids during exponential growth and about species abundances in field samples. They use these data to evaluate the potential contribution of each species to calcite production in mixed populations. The work is new and of interest for a wide audience and the manuscript is well written, though too sparse in information at times. Also, I have concerns about the way the authors interpret their results in terms of species contributions to community calcite production in the field.

Sparseness of information. This paper tries to make the case that lab rat species *E. huxleyi* may not be as an important contributor to calcite production in the Northern Atlantic as is commonly believed or implied. It is important that myopic viewpoints get challenged; the amount of research effort devoted to a certain species doesn't proof its importance. However, in order to make their challenge convincing, the authors should evaluate a much wider selection of published data, e.g. including those of Bach *et al.*, Hoppe *et al.*, Rodriguez-Iglesias *et al.* and many older publications, especially since the per-capita growth rate and cellular calcite content reported for *E. hux* in this manuscript are substantially lower than those reported in many other papers. I find the author's reply to the same issue raised by the editor not compelling (most published data would not be comparable with the author's data due to a difference in growth conditions) and even contradicting their own application of lab results to estimate calcite production in field populations, as those mixed populations are highly unlikely facing growth conditions that are comparable to those maintained in the lab. Publications that have appeared in the context of OA all report on the performance of coccolithophorids at present day ocean carbonate system conditions; this voids the author's second objection. With those alternative data, the authors may come to conclusions that are qualitatively similar but quantitatively much less pronounced. In addition, the authors consider only 2 *E. hux* strains; Read *et al.* (doi:10.1038/nature12221) have recently shown light on the large diversity in metabolic potential among *E. hux* strains. This makes the foundation of the author's case rather fragile.

The authors also provide too little information about the growth conditions in their lab experiments. I couldn't find the composition of "enriched seawater K/20 medium (modified from Keller et al., 1987)" anywhere – what are the concentrations of P and N species? which is the nutrient that ultimately becomes limiting for growth? This is a serious omission, albeit easily remedied. In the same vein, the manuscript lacks a physico-chemical characterization of the samples from the North Atlantic.

The authors probably didn't find statistically significant differences in the measures among treatments in Table 1 and therefore decided to give means and SDs instead of individual measurements. Frustratingly, this is a too common practice, which can seriously limit the value of results for readers with different research questions either now or later when insights in a field will have evolved. You did the work, so why limit the credit you could potentially receive for it? Those data could easily be included in Table 2 once 3 unnecessary columns are deleted. The column with daily irradiance should be deleted because it is redundant (and presented with reduced precision – *cf.* significant figures of column 2) and the columns with standard deviations

are potentially misleading (the SDs refer to the variability in instrumental readings, not biological quantities).

Finally, the presentation of the computational method needs elaboration. Keep Equation 1 (in which numerator and denominator should change places!), but add the form that is actually used,

$$\%CP_c = \frac{r_c c_c n_c}{r_c c_c n_c + 1} \times 100\%$$

with $c_c = C_c / C_e$, $r_c = \mu_c / \mu_e$ and $n_c = N_c / N_e$, in which the subscripted '*c*' and '*e*' stand for *Coccolithus* and *Emiliania*, respectively. r_c is the growth rate of *Coccolithus* relative to that of *Emiliania* (expressing relative growth rates and species abundances as percentages instead of fractions is not only ugly but also confusing). Based on this recast equation, I'd suggest (1) to use corresponding measures, i.e. n_c instead of n_e (=1-n_c) with r_c, and (2) to simplify Figure 3 (but see next section), since varying r_c, n_c or c_c gives identical results (hence, the contour curves in Figure 3 are straight lines). Unfortunately, the nonlinear relationship between $\%CP_c$ and any of these relative measures is obscured in Figure 3. I think a plot with $c_c n_c$ on the x-axis, $\%CP_c$ on the y-axis and r_c representing contour curves is more informative, while the number of panels is reduced from 6 to 2 (you could add dotted curves to display the information of Table 1 including the +/1 SD curves).

Relative contribution to calcite production. The value of the authors' method for the estimation of species contributions to calcite production in mixed field populations depends on the reliability of 4 assumptions, of which 3 are implied; these must be made explicit and evaluated. First, the relative abundance of species in mixed field populations is constant. I would like to see some back up with literature references showing that community dynamics are sufficiently slow to warrant the assumption approximately holds for a meaningful time interval. (It is very confusing to mention 'steady state' in this context, as there isn't a dynamic model; e.g. with relative population densities as state variables, a steady state means populations are growing exponentially, whereas with absolute population densities, it means that the loss rate (mortality, sinking, grazing) equals the population growth rate. Also, it is confusing to link 'steady state' with a variable relative growth rate.)

Second, the authors implicitly assume that the strains in mixed field populations are the same or behaving physiologically similar to the ones in their lab studies. The authors try to overcome the constraints of this assumption by considering cellular calcite contents that may differ up to 1 SD from the means in their calculations. However, they do not provide support that this level of variation would cover the variability in cellular calcite content among strains and environments (I doubt it does, as 1 SD corresponds to only 15-30% of the mean.

Third, the authors implicitly assume that lab and field growth conditions (the reader remains uninformed about the latter) are similar, thought those conditions are likely very different.

Related to this, the authors also implicitly assume that the relative growth rate is independent of the availability of the limiting nutrient, i.e. the relative maximum growth rate equals the ratio of the growth rates of the 2 species involved regardless of environmental conditions as long as the relative abundance is constant. This assumption is too heroic for my taste. A species can have a

relatively low maximum growth rate and relatively high growth rate at low resource densities, and vice versa. Taking the Monod or Holling type 2 model as an example (other models such as Droop's cell quota model lead to analogous results),

$$\mu_{sp} = \mu_{\max,sp} \frac{X}{X + K_{sp}}$$

(X is the limiting nutrient concentration; K_{sp} is the half saturation constant for the limiting nutrient), the growth rate of *Coccolithus* relative to *Emiliania* becomes

$$r_c = \frac{\mu_{\max,c}\left(X + K_e\right)}{\mu_{\max,e}\left(X + K_c\right)}$$

implying that r_c ranges between $\mu_{\max,c}/\mu_{\max,e}$ (high nutrient concentrations; $X \gg K_{sp}$) and $\mu_{\max,c}K_e/\mu_{\max,e}K_c$ (very low nutrient concentrations; $X \ll K_{sp}$). Since K values could differ by more than an order of magnitude, the range of relative growth rates that should be considered in the authors' evaluation is much wider than the range they consider to be relevant (e.g. in Figure 3). Assuming values for K_{sp} are unknown, this undermines a major line of reasoning in the manuscript, unless the authors have additional information, such as estimates for loss rates through sediment trap data (in steady state, the relative growth rate is equivalent to the ratio of the loss rates of the 2 species).

Other comments

line 157-160: a difference in irradiance between this study and that of others cannot explain the relatively low growth rate found in this study. Beyond 100 mumol photons/sec m^2 irradiance is ad libitum for all 4 strains/species: there is no increase in temperature corrected growth rates as irradiance levels increase beyond this level (I did a crude temperature correction with the parameters estimated from growth rate vs temperature by linear regression (each strain/species separately); growth rates at irradiance levels < 100 mumol/ sec m^2 and 244 mumol/ s m2 excluded from the fit for obvious reasons). I would give an explanation based on strain variability more credibility. The fact that the temperature response curves appear linear rather than exponentially increasing (as with Q10, Arrhenius) is interesting and might merit a bit of thought and elaboration.

I like the author's use of molar units rather than the mass units commonly used.

line 136. Langer (also) gives growth rates for *C. pelagicus.*

Please define 'relative growth rate' the first time it appears in the text.