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From laboratory manipulations to earth system models: predicting pelagic calcification and its consequences

A. Ridgwell[1], **D. N. Schmidt**[2], **C. Turley**[3], **C. Brownlee**[4], **M. T. Maldonado**[5], **P. Tortell**[5,6], **and J. R. Young**[7]

[1]School of Geographical Sciences, University of Bristol, UK
[2]Department of Earth Sciences, University of Bristol, UK
[3]Plymouth Marine Laboratory, Plymouth, UK
[4]Marine Biological Association, Citadel Hill, Plymouth, UK
[5]Department of Earth and Ocean Sciences, University of British Columbia, Vancouver, Canada
[6]Department of Botany, University of British Columbia, Vancouver, Canada
[7]Palaeontology Department, The Natural History Museum, London, UK

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Correspondence to: A. Ridgwell (andy@seao2.org)

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Abstract

The variation in pH-dependent calcification responses of coccolithophores paint a highly incoherent picture, particularly for the most commonly cultured “species”, *Emiliania huxleyi*. The disparity between magnitude and even sign of the calcification change at higher CO_2 (lower pH), raises challenges to quantifying future carbon cycle changes and feedbacks, by introducing significant uncertainty in parameterizations used for global models. Putting aside the possibility of methodological differences that introduce an experimental bias, we highlight two pertinent observations that can help resolve conflicting interpretations: (1) a calcification “optimum” in environmental conditions (pH) has been observed in other coccolithophore species, and (2) there exists an unambiguous direction to the CO_2-calcification response across mesocosm and shipboard incubations. We propose that an equivalence can be drawn between integrated ecosystem calcification as a function of pH (or other carbonate system parameter such as calcite saturation state) and a widely used description of plankton growth rate vs. temperature – the “Eppley curve”. This provides a conceptual framework for reconciling available experimental manipulations as well as a quasi-empirical relationship for ocean acidification impacts on carbonate production that can be incorporated into models. By analogy to the Eppley curve temperature vs. growth rate relationship, progressive ocean acidification in the future may drive a relatively smooth ecosystem response through transition in dominance from more to less heavily calcified coccolithophores in addition to species-specific calcification changes. However, regardless of the model parameterization employed, on a century time-scale, the CO_2-calcification effect is a minor control of atmospheric CO_2 compared to other C cycle feedbacks or to fossil fuel emissions.

1 Introduction

Concerns were raised in the late 1990s that reductions in the carbonate ion (CO_3^{2-}) concentration and pH of the surface ocean resulting from the uptake of fossil fuel CO_2 from the atmosphere, might adversely affect the ability of marine plankton such as coccolithophorids and foraminifera to produce calcium carbonate ($CaCO_3$) shells (Wolf-Gladrow et al., 1999). The wide availability of physiologically well characterized strains of calcifying phytoplankton in long-term culture enabled the impact of ocean acidification to be tested. Early laboratory experiments carried out on the most abundant modern species of coccolithophorid, *Emiliania huxleyi*, in which the pH of the growth medium was decreased by addition of acid, produced varying calcification responses (Buitenhuis et al., 1999; Nimer and Merrett, 1993). However, the chemical conditions used in many of the manipulations deviated substantially from either modern or possible future geochemistry. Subsequent laboratory experiments using *E. huxleyi* manipulated pH to simulate a more "realistic" range of glacial and future CO_2 changes, and showed a clear overall decrease in carbonate production across low pH treatments compared to the control (i.e., current ocean pH) together with the occurrence of malformed liths (calcium carbonate plates) (Riebesell et al., 2000; Zondervan et al., 2001). This result was consistent with contemporary ship-board experiments in the NE Pacific conducted with either acid/base additions or CO_2 bubbling which also showed a clear decrease in calcification at elevated CO_2 (Riebesell et al., 2000).

A strong CO_2-dependence of calcification rates has significant implications for ocean carbon cycling and would provide a negative feedback on atmospheric CO_2 increases (Ridgwell et al., 2007b; Zondervan et al., 2001), since calcification decreases seawater alkalinity and releases CO_2 from bicarbonate (HCO_3^-) in the upper ocean. Changes in the production of biogenic $CaCO_3$ minerals at the ocean surface could potentially also affect the transport of particulate organic carbon (POC) to depth (Armstrong et al., 2002; Klaas and Archer, 2002) and act to increase atmospheric CO_2 via a reduction in the efficiency of the biological pump. An important CO_2-dependence of particulate organic carbon production by coccolithophores was also observed (Zondervan et al., 2001), and this could provide a further (negative) feedback to rising atmospheric CO_2.

Subsequent experiments carried out on *E. huxleyi*, both in the laboratory (Feng et al., 2008; Sciandra et al., 2003) and in mesocosms (Delille, et al., 2005; Engel et al., 2005) generally supported a strong and detrimental impact of ocean acidification on calcification. Studies of the relationship between coccolithophore assemblages to ocean geochemistry also provide evidence of a relationship between coccolithophorid calcification and carbonate chemistry (e.g., Cubillos et al., 2007; Tyrell et al., 2008; Beaufort et al., 2008).

However, in a series of very recent laboratory experiments, Iglesias-Rodriguez et al. (2008a) and Shi et al. (2009) report quite the opposite response to many previous experiments – increased rather than decreased calcification at higher ambient CO_2 (and lower pH). Interspecific variability in the CO_2-sensitivity of calcification has previously been documented. For example, *Coccolithus pelagicus* and *Calcidiscus leptoporus* grown in laboratory mono-cultures exhibit no consistent trend in calcification as a function of CO_2 (Langer et al., 2006), while *Gephyrocapsa oceanica*, a species with close ancestoral links with *E. huxleyi*, responds with a very substantial decrease in calcification under high CO_2 (low pH) conditions (Riebesell et al., 2000; Zondervan et al., 2001).

It is important to resolve this apparent incongruence in calcification responses to simulated ocean acidification if we are to draw reliable implications from experimental manipulations regarding expected future CO_2-dependent changes in marine ecosystems. Global carbon cycle models used for predicting future fossil fuel CO_2 impacts base their parameterizations for calcification closely on such results (e.g., Gehlen et al., 2007; Heinze, 2004; Hofmann and Schellnhuber, 2009; Ridgwell et al., 2007a, b), and these model predictions will be unreliable if rooted in unrepresentative or misunderstood laboratory observations.

In this paper we summarize and assess the current state of knowledge provided by experimental manipulations of coccolithophores (Sect. 3) and propose a new framework for reconciling experimental observations and making future predictions (Sect. 4). We start with an overview of the importance to atmospheric CO_2 of ocean acidification impacts on pelagic calcification and how this is currently treated in models (Sect. 2), and end with brief conclusions and perspectives (Sect. 5).

2 Global carbon cycle impacts of ocean acidification

By precipitating calcium carbonate ($CaCO_3$) from sea-water, marine organisms affect the global carbon cycle and thus climate system. In the net chemical reaction for creating carbonate shells and skeletons:

$$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_{2(aq)} + H_2O \qquad (1)$$

dissolved inorganic carbon in seawater, in the form of bicarbonate ions (HCO_3^-) which itself cannot interact directly with the atmosphere, is converted into dissolved CO_2 ($CO_{2(aq)}$) as a consequence of the removal of alkalinity (as Ca^{2+}) during calcification. Thus, the process of calcification acts to increase the concentration of $CO_{2(aq)}$ at the ocean surface and hence acts as a brake on the transfer of fossil fuel CO_2 from the atmosphere into the ocean. Consequently, reducing the rate of calcification globally would accelerate the rate of uptake of fossil fuel CO_2 from the atmosphere, providing a negative feedback on climate change.

There is a second reason for correctly representing the carbonate production response to ocean acidification in models – because mineral $CaCO_3$ is much denser than the soft body parts of plankton, the presence of $CaCO_3$ in aggregates with organic matter may be important in accelerating the rate of sinking (Armstrong et al., 2002; Klaas and Archer, 2002). In this "ballast hypothesis", any reduction in calcification by plankton at the ocean surface would increase the time that POC was suspended in the warm upper ocean and increase the likelihood of its being consumed by the more numerous and more active bacteria present there (Turley and Mackie, 1994). A reduction in the efficiency of the biological pump would create a positive feedback on rising atmospheric CO_2.

Only a few global models have so far been applied to quantifying the importance of changing pelagic carbonate production on the oceans ability to sequester CO_2. Although the CO_2-calcification feedback was initially assessed in box models (Barker et al., 2003), the first ocean GCM to account for this effect was the HAMOCC model (Six and Maier-Reimer, 1996), in which Heinze (2004) parameterized the net ecosystem $CaCO_3$:POC rxport ratio ($R^{CaCO_3/POC}$) as a function of the ambient $CO_{2(aq)}$ concentration (($CO_{2(aq)}$)):

$$R^{CaCO_3/POC} = R_{max}^{CaCO_3/POC} \cdot \left(1 - 0.012 \cdot \left(CO_2 - CO_{2(0)}\right)\right) \quad (2)$$

where CO_2 is the current $CO_{2(aq)}$ concentration (μmol l^{-1}), $CO_{2(0)}$ is preindustrial ($CO_{2(aq)}$), and $R_{max}^{CaCO_3/POC}$ is assigned a value of 0.15. (Further modifications are made in the model to $R^{CaCO_3/POC}$ according to inferred diatom productivity.) The strength of the relationship between $CaCO_3$:POC and ($CO_{2(aq)}$) was taken directly from the *E. huxleyi* manipulation response reported by Zondervan et al. (2001).

Gehlen et al. (2007), in the ocean GCM/biogeochemical model OCM-PISCES (Gehlen et al., 2006) , generalized their parameterization of the CO_2-calcification response by including the newly available results of mesocosm experiments (Delille et al., 2005) in addition to laboratory manipulations (Zondervan et al., 2002). For the form of the empirical fit to the observed data, Gehlen et al. (2007) assumed a hyperbolic function for their parameterization, akin to the Monod equation relating phytoplankton growth to nutrient concentrations:

$$R^{CaCO_3/POC} = R_{max}^{CaCO_3/POC} \cdot \frac{(\Omega_c - 1)}{K_{max} + (\Omega_c - 1)} \quad (3)$$

where $R_{max}^{CaCO_3/POC}$=0.8 and K_{max} is assigned a value of 0.4.Ω_c is the ambient saturation state with respect to calcite.

Ridgwell et al. (2007a, b) utilized established abiotic precipitation thermodynamics as the basis for their description of marine carbonate production, in an equation of the form:

$$R^{CaCO_3/POC} = R_{max}^{CaCO_3/POC} \cdot (\Omega - 1)^{\eta} \tag{4}$$

where η is a power setting the non-linearity of the calcification response to changes in ambient saturation state. ($R^{CaCO_3/POC}$ is zero for $\Omega_c<1.0$.) In Ridgwell et al. (2007b), the implications of a range of potential values for η were considered, spanning the reported responses in a variety of different experimental manipulations and consistent with observed ocean geochemical distributions. The central estimate was with η=0.81.

Finally, in a recent study, Hofmann and Schellnhuber (2009) incorporate the box-model parameterization of Barker et al. (2003) into the ocean-atmosphere-sea ice-biogeochemistry model "POTSMOM-C" (Hofmann and Schellnhuber, 2009):

$$R^{CaCO_3/POC} = e^{0.0083 \cdot \left(CO_3^{2-} - CO_{3(0)}^{2-}\right)} \tag{5}$$

where CO_3^{2-} is the current ambient carbonate ion concentration (μmol l^{-1}) and $CO_{3(0)}^{2-}$ is assigned a value of 150 μmol l^{-1}.

As might be expected with different ocean GCMs utilizing different parameterizations for the calcification response to acidification, there is no agreement as to the predicted strength of the CO_2-calcification feedbacks or the additional quantity of fossil fuel CO_2 taken up by the ocean by the year 2100 due to reduced calcification, with estimates ranging from 5.9 and 23.4 PgC (Fig. 1). However, in constructing the CO_2-calcification parameterizations in the models, each study was also informed by different sub-sets of available experimental observations. We are left asking: How important is the uncertainty in the calcification response to ocean acidification in the range of estimates of future ocean CO_2 uptake? And: How important to the CO_2 predictions is the form of the equation that is chosen ("structural" uncertainty)? The uncertainty in the CO_2-calcification dependence can be reduced with more and improved experiments, while models can be refined through better construction. But, which would be more effective in improving future CO_2 predictions?

Some insight into the sources of predictive uncertainty can be made using a single model and parameterization, but with an ensemble of differing model CO_2-calcification sensitivities accounting for the broad range of calcification responses observed in laboratory manipulation experiments. In just such a modeling exercise, the predictions of enhanced year 2100 CO_2 uptake were found to span 5.4 PgC to 25.7 PgC, with an ensemble mean of 17.2 PgC (Ridgwell et al., 2007b). This range of predictions exceeds that variability between different models, suggesting that the uncertainty in species calcification response and their relative importance for carbonate production globally is likely dominating the overall uncertainty in model predictions of fossil fuel CO_2 uptake by the ocean (Fig. 1).

Fewer global ocean models have assessed CO_2-calcification together with "ballasting". Hofmann and Schellnhuber (2009) found a ~6 PgC (27%) reduction in CO_2 uptake by the ocean due to reduced $CaCO_3$ ballasting. Other studies have hinted that as much as 80% of the CO_2-calcificiation feedback could be negated (Heinze, 2004), while Barker et al. (2003) predict a reversal, with more fossil fuel CO_2 overall residing in the atmosphere. However, the importance of mineral ballasting in the transport of organic matter to depth is currently highly uncertain (Francois, et al., 2002; Passow and De La Rocha, 2006).

3 Reconciling observed coccolithophorid manipulation responses

The potential carbon cycle roles and feedbacks with climate involving the production and fate of calcite liths requires that we identify the sign of the response of pelagic carbonate production to ocean acidification and ideally, tightly constrain the magnitude of the response. To this end, and to help make better sense of experimental observations and improve model parameterizations, we have compiled the pertinent details of available coccolithophorid manipulations and their differing calcification responses to elevated CO_2 and lower pH (Table 1). While irradiance levels and nutrient regime may vary substantially between experiments and potentially be important (Riebesell et al., 2008), we will concentrate in this paper on: species (and strain), experimental design, and chemistry manipulation. Because there is no common baseline CO_2 concentration that is used across all experiments, nor consistent degree of acidification (or CO_2 concentration increase/decrease) in the experimental manipulation, or even a single unit for reporting calcification, we have characterized the calcification response qualitatively rather than quantitatively, as described in Table 1.

This compilation can be used to test the explanation proposed by Iglesias-Rodriguez et al. (2008a, b) – that the difference between the chemical manipulations performed is critical, with direct acid/base manipulating pH (e.g., Riebesell et al., 2000, Zondervan et al., 2001) inducing an erroneous response to ocean acidification compared to CO_2 bubbling (e.g., Iglesias-Rodriguez et al., 2008a). The basis of this argument is that while both types of manipulations are capable of producing the same pH or pCO_2 changes, bicarbonate (HCO_3^-) concentrations will differ (Iglesias-Rodriguez et al., 2008b; Shi et al., 2009) which could potentially influence the response of both organic and inorganic carbon fixation if HCO_3^- is the substrate used (Buitenhuis et al., 1999; Paasche, 2002).

The carbonate parameters resulting from simulated CO_2 bubbling (changing total dissolved carbon, DIC) and acid/base addition (changing alkalinity, ALK) are summarized in Table 2. We argue that the differences in carbonate parameters between the different manipulations are not critical. For instance, going from "preindustrial" (278 ppm) to approximately year 2100 CO_2 (twice modern, 780 ppm) produces a 17% increase in HCO_3^- concentrations by CO_2 bubbling, and about half this due to acid/base addition, while all other carbonate parameters are very comparable between manipulation methods. If bicarbonate ion concentration changes dominate the calcification response, manipulation experiments carried out by acid/base addition will, if anything, underestimate acidification impacts. Otherwise, if ($CO_{2(aq)}$), (CO_3^{2-}) and/or (H^+) (pH) are important, experimental bias will be minimal. The generation of a reversed response seems unlikely.

Considering all reported coccolithophorid observations and associated experimental details (Table 1), there is no evidence of any systematic correlation between the direction of calcification response under simulated future conditions and type of chemical manipulation. Furthermore, shipboard incubations in which chemical manipulation was carried out by both methods exhibit similar suppressions of carbonate production at higher CO_2 (Riebesell et al., 2000). Very recent laboratory experiments performed on *E. huxleyi* (strain: PLY M219) also support a general method-independence (Shi et al., 2009). Thus, we rule out the possibility of a consistent methodological bias between CO_2 bubbling and acid/base addition that produces a spurious calcification response in one direction or the other.

Also notable in our compilation are differences in the strain of *E. huxleyi* used. The coccolithophorid *E. huxleyi* is in fact thought to be a "species complex", encompassing a wide range of genotypic variation. This is suggested by the extraordinarily broad ecological and biogeographic distribution of the species, and by its morphological variability (Paasche, 2002). This inference has been supported by a range of culture experiment work, (e.g. Brand, 1982; Young and Westbroek, 1991), and molecular genetic studies (Schroeder et al., 2005; Iglesias et al., 2006). It is now conventionally recognized that *E. huxleyi* includes at least five morphologically discrete varieties or sub-species (Young et al., 2003). However, it is likely that this is a gross simplification since both field and culture observations reveal considerably more variability, not least in degree of calcification of coccoliths (Young, unpublished data) (Fig. 2). Arguably we should regard *E. huxleyi* as a diverse assemblage of genotypes with highly variable calcification characteristics and ecological adaptations.

Given that different investigators have used different strains of *E. huxleyi* (Table 1), much of the incongruence between observed responses across studies could result from differing ecological adaptation (ecotypes). Additionally, the strains used have been in culture for differing periods ranging from several years to decades and may have partially adapted after capture to the altered chemical conditions in the stock medium. Thus, the intra-species variability across experiments on *E. huxleyi* may be analogous to less controversial interspecific variability that has been reported amongst obviously different species (e.g., Langer et al., 2006).

4 An "Eppley Curve" for pelagic calcifiers?

Individual phytoplankton species generally exhibit a pronounced growth response curve to temperature; with a growth rate maximum (μ_{max}) corresponding to optimum conditions (Fig. 3). Sampling just a few species taken from differing environments creates the potential for conflicting experimental observations, depending upon the position of the experimental growth position relative to the species optimum (i.e. above or below). It is thus possible to find a temperature which exceeds the optimum of a cold-adapted species leading to slower growth rates with increasing temperature, while a warm-adapted species might exhibit increased growth rates (experimental temperature is below the optimum). That the plankton growth response to changes in temperature (hereafter, the "T-growth" response) has not caused confusion or difficulties for global modelers may be ascribed to the work of Eppley (1972), who noted that *given a sufficiently large species sample size*, the envelope of the individual growth-temperature response curves could be delineated by a simple function of temperature (Fig. 4):

$$\mu_{\text{max}} = 0.59 \cdot e^{0.0633 \cdot T} \tag{6}$$

This equation encapsulates the progressive transition in dominance amongst different plankton species as a function of changing temperature, and hence, allows the net community growth rate to be simply approximated in models. The Eppley curve thus negates the need to resolve the potential presence and specific characteristics of hundreds of individual species, by instead focusing on the community level response. Although the accuracy of this approximation becomes somewhat degraded in conditions of rapid species transition and dominance such as during a spring bloom (Moisan et al., 2002), global models invariably utilize the Eppley function (e.g., Aumont et al., 2003; Schmittner et al., 2008; Six and Maier-Reimer, 1996). Recent re-analyses based on larger data-sets have not led to any significant change in the details of this equation (Bissinger et al., 2008).

We propose for the purposes of encapsulating a net ecosystem calcification response to ocean acidification in models, equivalence between the T-growth and CO_2-calcification behaviors can be drawn. In doing this, we recognize that pH-calcification or saturation-calcification (or other relationships with carbonate chemistry) may be equally (or more) applicable. We take CO_2 concentration for illustration. The equivalent CO_2-calcification parameters are shown in Figs. 3 and 4.

The barrier to deducing the net community plankton calcification response vs. CO_2 (and pH) is the small sample size available. To date, only in a single experiment carried across future-relevant carbonate chemistry changes (Langer et al., 2006) has a clear calcification 'optimum' been observed (Table 1) – the remainder of the data-set, at best, is sampling incomplete portions of an optimum curve. It also seems likely that calcification optima, if generally existing, are relatively broad compared to existing growth-temperature relationships in the ocean and may have a highly protracted (or non-existent) "tail" of declining calcification at lower CO_2 (higher pH) than the optimum. From the paucity of available laboratory mono-specific manipulations and in light of the differing experimental conditions, even the sign of the CO_2-calcification response cannot be unambiguously assigned, unlike the case for the T-growth relationship for which 162 culture responses were originally available to define the response envelope (Eppley, 1972). However, we note that the responses observed in shipboard incubations (Riebesell et al., 2000) and mesocosm experiments (Delille et al., 2005; Engel et al., 2005), all manipulations with natural plankton assemblages, appear highly consistent in showing substantial decrease in community carbonate production at higher CO_2 (Table 1). We suggest these observations can be reliably taken to inform the sign of the CO_2-calcification curve and that at progressively higher CO_2 net community calcification will generally be lower.

The apparently increased CO_2 sensitivity of carbonate production of natural assemblages relative to laboratory cultures (Table 1, Ridgwell et al., 2007b) provides some support for our interpretation. This may reflect an amplification of acidification impacts on carbonate production via changes in the species and ecotype composition of calcifying phytoplankton assemblages, in addition to direct physiological impacts on the calcification of individual species. The co-variation between saturation state and morphotype of *E. huxleyi* observed across the Subantarctic and Polar Fronts in the Southern Ocean, with less heavily calcified ecotypes dominant at lower saturation state is also consistent with our model (Cubillos et al., 2007). In addition, Tyrell et al. (2008) argued that the absence of *E. huxleyi* in the Baltic but presence in the Black Sea cannot be explained by salinity or temperature but could be a result of calcite saturation state, while Beaufort et al. (2008) inferred that size and weight of coccoliths of Isochrysidales (e.g., *E. huxleyi* and *Gephyrocapsa*) through the Pacific Ocean correlates with carbonate system parameters, and especially alkalinity.

The most important impact of ocean acidification may thus occur through a shift in the dominance of one ecotype or species over another and hence a change in net ecosystem carbonate production, rather than through a physiological response induced in any particular ecotype and individual species. Indeed, the difference in CO_2-growth rate relationships between two distinct monoclonal cultures of *E. huxleyi* reported by Iglesias-Rodriguez et al. (2008a) hints at the possibility of succession by less heavily calcified ecotypes in the open ocean. In these experiments, the less calcified strain (MBA 61/12/4) exhibits less growth rate sensitivity to higher CO_2 conditions (M.D. Iglesias-Rodriguez, personal communication, 2008) than the more heavily calcified strain (CAWPO6) and under the 750 ppm CO_2 treatment, MBA 61/12/4 becomes the faster growing strain. Preferential suppression of cell division rate of more heavily calcified ecotypes at higher CO_2 is consistent with the observations of Cubillos et al. (2007) and hints at the possibility of succession by less heavily calcified ecotypes in the open ocean in the future.

This potential response of coccolithophorid populations is in contrast to many other marine calcifiers, such as corals, for which any increase in dominance of less heavily calcified species would increase the vulnerability of reefs to physical and bio-erosion

(Manzello et al., 2008). A species dominance adaptive response is also not possible for populations of carbonate shell forming species facing under-saturated conditions in the future, such as pteropods in the Southern Ocean (Orr et al., 2005), as all shell-forming species would be similarly vulnerable. Thus, calcifying (phyto-) plankton may be relatively unique in being able to respond to continuing ocean acidification without causing fundamental ecosystem disruption.

5 Conclusions and perspectives

We conclude that the extraordinary diversity in calcification behavior and environmental sensitivity exhibited by the different ecotypes of *E. huxleyi* make laboratory studies with mono-specific cultures prone to producing conflicting results. It is thus unclear how well the observed responses can inform us about the net impact of higher CO_2 (lower pH) on diverse, natural assemblages in situ. Mesocosm experiments and shipboard manipulations carried out in a variety of oceanic regions are then vital if we are to improve our predictive capabilities of phytoplankton calcification and their role in the cycling of carbon in a future high-CO_2 world. However, laboratory studies will continue to provide key information on the range of potential responses of different ecotypes and on the mechanisms by which the response to changes in CO_2 chemsitry occurs.

Drawing a parallel between the calcification response to ocean acidification and the "Eppley curve" for net ecosystem growth rate behavior with changing temperature is consistent with: monoclonal laboratory observations of preferential growth rate suppression in more heavily calcified species (Iglesias-Rodriguez et al., 2008a), transitions from more to less heavily calcified morphotypes across saturation gradients in the ocean (Cubillos et al., 2007), and a greater net calcification response in natural plankton assemblages relative to mono-specific cultures (Ridgwell et al., 2007b). This leads us to a recommendation for the form of the parameterization to be used in future ocean carbon cycle modeling, although the observational data needed to constrain the steepness of the CO_2-calcification response and hence the parameter values in this equation are currently insufficient. Better experimentally-based understanding of acidification impacts at both the organism and ecosystem level and how this translates to the global scale is essential for improvements to be made in model predictions of future fossil fuel CO_2 uptake.

Regardless of the form and sensitivity of the calcification parameterization, it should be recognized that the direct impact of calcification changes on atmospheric CO_2 through the remainder of this century is relatively small compared to anticipated annual emissions as well as to other carbon cycle feedbacks. For instance, yearly emissions of CO_2 from the burning of fossil fuels and cement production currently stands at some 7.2 PgC yr^{-1} (IPCC, 2007) – this is of comparable magnitude to the entire 100-year integrated impact of reduced calcification of ~6–23 PgC. The predicted year 2100 repartitioning of CO_2 from atmosphere to ocean due to reduced calcification is also dwarfed by the anthropogenic CO_2 inventories of the ocean and atmosphere, which even in 1994 stood at 118 and 165 PgC, respectively, as well as by the importance of feedbacks such as between temperature and CO_2 solubility.

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Table 1. Synthesis of available coccolithophorid calcification carbonate chemistry manipulation experiments.

Species	Strain (Clone)	Isolation date and location	Experimental design	Ambient light environment [a]	Carbonate chemistry manipulation	Calcification response [b]	Calcification response [c]	Reference [j]
Emiliania huxleyi	NZEH (CAWPO6)	1992 South Pacific	laboratory culture	12:12 h L:D 150 μmol m^{-2} s^{-1}	CO$_2$ bubbling	↑	↑	*1*
Emiliania huxleyi	MBA 61/12/4	1991 North Atlantic	laboratory culture	12:12 h L:D 150 μmol m^{-2} s^{-1}	CO$_2$ bubbling	↑	↑	*1*
Emiliania huxleyi	PML B92/11A	1992 North Sea	laboratory culture	18:6 h L:D 150 μmol m^{-2} s^{-1}	acid/base	n/a	↓	*2,5*
Emiliania huxleyi	PML B92/11A	1992 North Sea	laboratory culture	24:0 h L:D 150 μmol m^{-2} s^{-1}	acid/base	n/a	↓	*2,5*
Emiliania huxleyi	CCMP 371	1987 Sargasso Sea	laboratory culture	12:12 h L:D 50 μmol m^{-2} s^{-1}	CO$_2$ bubbling	↔	↓	*3*
Emiliania huxleyi	CCMP 371	1987 Sargasso Sea	laboratory culture	12:12 h L:D 400 μmol m^{-2} s^{-1}	CO$_2$ bubbling	↓	↓	*3*
Emiliania huxleyi	TW1	2001 W Mediterranean	laboratory culture	24:0 h L:D 570 μmol m^{-2} s^{-1}	CO$_2$ bubbling	n/a	↓	*4*
Emiliania huxleyi	88E	1988 Gulf of Maine	laboratory culture	24:0 h L:D 50 μmol m^{-2} s^{-1}	acid/base	n/a	↔[d]	*9*
Emiliania huxleyi	Ch 24-90	1991 North Sea	laboratory culture	16:8 h L:D 300 μmol m^{-2} s^{-1}	CO$_2$ bubbling	n/a	↔[e]	*10*
Emiliania huxleyi	NZEH (PLY M219)	1992 South Pacific	laboratory culture	24:0 h L:D 150 μmol m^{-2} s^{-1}	acid/base	↑	↑	*11*
Gephyrocapsa oceanica	PC7/1	1998 Portuguese shelf	laboratory culture	18:6 h L:D 150 μmol m^{-2} s^{-1}	acid/base	n/a	↓	*2,5*
Calcidiscus leptoporus	AC365	2000 South Atlantic	laboratory culture	16:8 h L:D 350 μmol m^{-2} s^{-1}	acid/base	n/a	↓[f]	*6*
Coccolithus pelagicus	AC400	2000 South Atlantic	laboratory culture	16:8 h L:D 350 μmol m^{-2} s^{-1}	acid/base	n/a	↔	*6*

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Table 1. Continued.

Species	Strain (Clone)	Isolation date and location	Experimental design	Ambient light environment [a]	Carbonate chemistry manipulation	Calcification response [b]	Calcification response [c]	Reference [j]
Emiliania huxleyi [g]	n/a	n/a (North Sea)	mesocosm [h]	95% of ambient surface irradiance	CO_2 bubbling	n/a	↓[i]	*7,8*
subarctic North Pacific natural assemblages	n/a	n/a (N. Pacific)	ship-board incubation	30% of ambient surface irradiance	CO_2 bubbling	n/a	↓[i]	*2*
subarctic North Pacific natural assemblages	n/a	n/a (N. Pacific)	ship-board incubation	30% of ambient surface irradiance	acid/base	n/a	↓[i]	*2*

[a] Light:dark irradiance cycle in hours light vs. dark per 24 h cycle; irradiance as the photon flux density associated with the 'light' period. [b] Sign of the calcification response of plankton at elevated (~×2 to ×3) compared to modern CO_2. The size of the arrow indicates the sensitivity of calcification response in a simple: "very low" (↓), "low" (↓), "medium" (↓), "high" (↓) classification, with "medium" representing an approximate halving (or doubling) of calcification in resposne to a ca. ×2–3 increase in CO_2. Red represents a decrease in calcification in response to higher CO_2 (lower pH), while blue (↑) is a calcification increase. Green (↔) is no significant change. The calcification change is calculated from observations reported in units of mol (or g) of $CaCO_3$ (or C) per cell. [c] As [b], except change in calcification in units of mol (or g) of $CaCO_3$ (or C) per cell per day (or hour). The difference between [b] and [c] reflects any change in growth rate (μ, d^{-1}) at elevated CO_2. [d] "Optimum" CO_2-calcification response curve with no consistent trend with CO_2. Experimental carbonate chemistry modification was qualitatively very different from the effect of increased CO_2 alone and some treatments had very low DIC, questioning its applicability to future conditions in the ocean. [e] Results of the constant alkalinity experiment, which was the only manipulation similar to the effect of future CO_2 addition. However, alkalinity used (1214 μ·eq l^{-1}) was only about half that found in the modern open ocean, questioning its applicability. [f] "Optimum" CO_2-calcification response curve – no consistent trend with CO_2, but reduced calcification at 800–900 ppm compared to modern CO_2. [g] *Emiliania huxleyi* was the dominant (calcifying) plankton species in the induced mesocosm bloom. [h] Enclosed body of seawater in each mesocosm was approximately 11 000 L volume. [i] Reported as an integrated production rate in units of mol (or g) carbon per unit volume per unit time. [j] References: (1) Iglesias-Rodriguez et al. (2008), (2) Riebesell et al. (2000), (3) Feng et al. (2008), (4) Sciandra et al. (2003), (5) Zondervan et al. (2001), (6) Langer et al. (2006), (7) Delille et al. (2005), (8) Engel et al. (2005), (9) Nimer and Merrett (1993), (10) Buitenhuis et al. (1999), (11) Shi et al. (2009).

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Table 2. Behaviour of carbonate parameters in response to CO_2 bubbling vs. acid/base manipulation. Numbers in **bold** assume a CO_2 bubbling like change, i.e., ALK is held constant and pCO_2 adjusted. Numbers in normal text assume ALK is changed in order to match the pH change. Numbers in *italics* assume ALK is changed in order to match the pCO_2 change. The carbonate chemistry starting point (278 ppm) is shaded in grey. Calculations assume a temperature of 20°C and salinity of 35 PSU and atmospheric pressure (0 m water depth), and 0 μmol kg^{-1} (PO_4^{3-}) and (H_4SiO_4), and were made using the "CO2SYS" program (Lewis and Wallace, 1998), with K_1 and K_2 from Mehrbach et al. (1973) as refit by Dickson and Millero (1987) and K_{SO_4} from Dickson (1990).

Target pCO_2 (μatm)	DIC (μmol kg^{-1})	ALK (μmol kg^{-1})	($CO_{2(aq)}$) (μmol kg^{-1})	(HCO_3^-) (μmol kg^{-1})	(CO_3^{2-}) (μmol kg^{-1})	$pH_{(SWS)}$	Ω (calcite)
190.0	**1882.2**	**2300.0**	**6.1**	**1587.7**	**288.4**	**8.294**	**6.90**
198.1	1967.3	2397.5	6.4	1659.7	301.2	8.294	7.20
190.0	*1967.3*	*2411.8*	*6.1*	*1649.8*	*311.4*	*8.311*	*7.45*
278.0	**1967.3**	**2300.0**	**9.0**	**1725.5**	**232.8**	**8.165**	**5.57**
278.0	1967.3	2300.0	9.0	1725.5	232.8	8.165	5.57
278.0	*1967.3*	*2300.0*	*9.0*	*1725.5*	*232.8*	*8.165*	*5.57*
390.0	**2037.1**	**2300.0**	**12.6**	**1836.5**	**188.0**	**8.045**	**4.50**
377.0	1967.3	2224.0	12.2	1773.7	181.4	8.045	4.34
390.0	*1967.3*	*2216.3*	*12.6*	*1778.4*	*176.3*	*8.031*	*4.22*
560.0	**2104.2**	**2300.0**	**18.1**	**1940.0**	**146.1**	**7.912**	**3.49**
523.6	1967.3	2154.8	16.9	1813.8	136.6	7.912	3.27
560.0	*1967.3*	*2142.1*	*18.1*	*1820.6*	*128.7*	*7.884*	*3.08*
780.0	**2158.8**	**2300.0**	**25.2**	**2019.9**	**113.7**	**7.786**	**2.72**
710.2	1967.3	2100.8	22.9	1840.7	103.7	7.786	2.48
780.0	*1967.3*	2085.8	25.2	1847.0	95.1	7.747	2.27

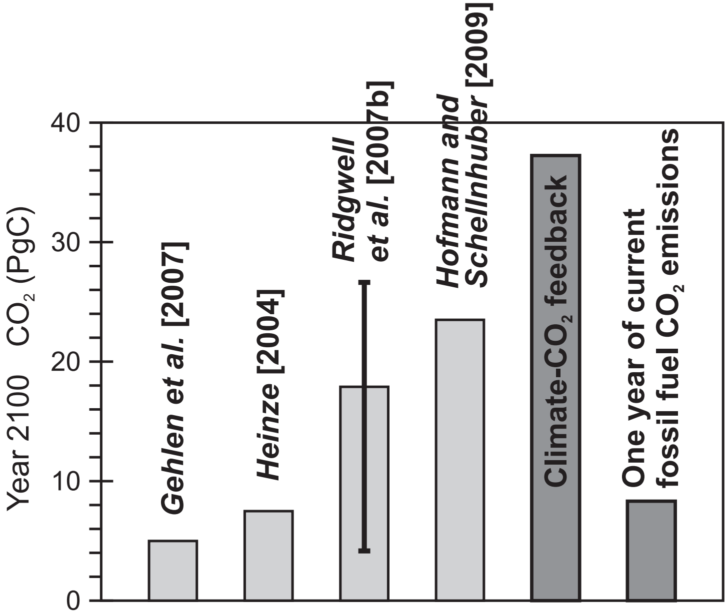

Fig. 1. Predicted strength of the CO_2-calcification feedback.
Model predictions for increased CO_2 uptake by the ocean by the year 2100 due to reduced calcification, and contrasted to a single year of CO_2 emissions at current rates as well as to an estimate of the year 2100 strength of CO_2-climate feedback (the additional CO_2 remaining in the atmosphere due to ocean surface warming and changes in circulation) (Cao et al., 2009). Note that the assumed CO_2 emissions or atmospheric concentration trajectory differ somewhat between studies, although all are loosely "business as usual". There is also no consistency between the studies as to whether climate feedbacks are included or not.

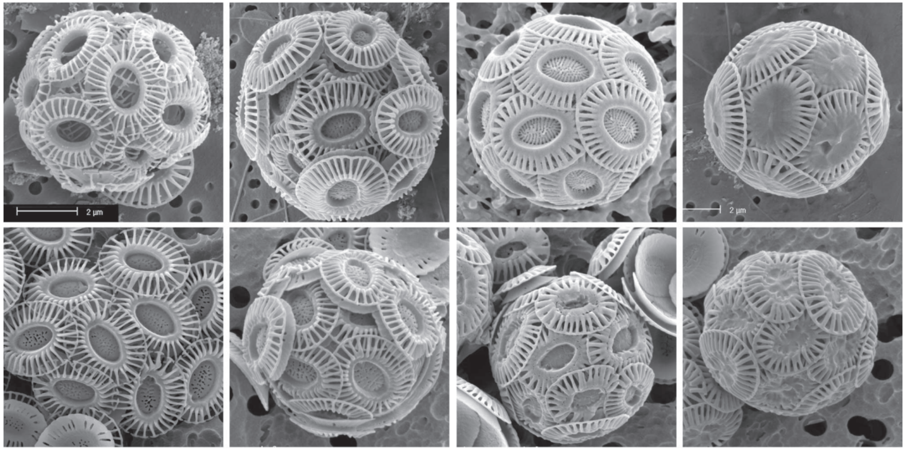

Fig. 2. Observed natural and laboratory variability in *Emiliania huxleyi* calcification. Top row: Emiliania huxleyi from plankton samples showing highly variable calcification, and with no sign of overgrowth or etching. Bottom row: four different *Emiliania huxleyi* strains grown under similar conditions and illustrating range of variability shown between strains. All images taken at the same magnification.

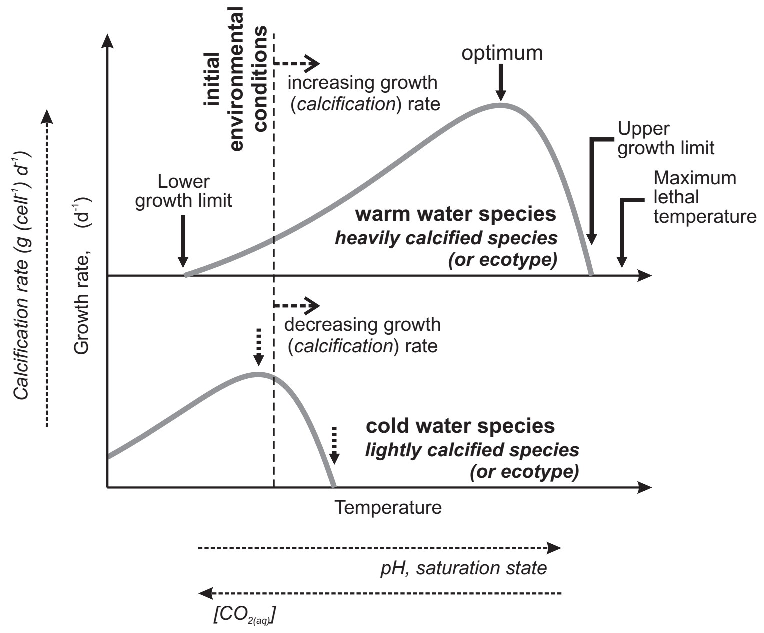

Fig. 3. Environmental optima. Idealized temperature growth model for a warm water and a cold water species with environmental niche divided into optimum growth, reproductive range, growth limits and lethal conditions. Modified from Schmidt et al. (2006). Shown for illustration is our proposed analogy for the CO_2-calcification system (axis labels in *italics*). Also illustrated is a hypothetical initial environmental condition (temperature or *saturation state*) for two different species (or ecotypes), which is subsequently manipulated (higher) and the growth (or calcification) rate change measured.

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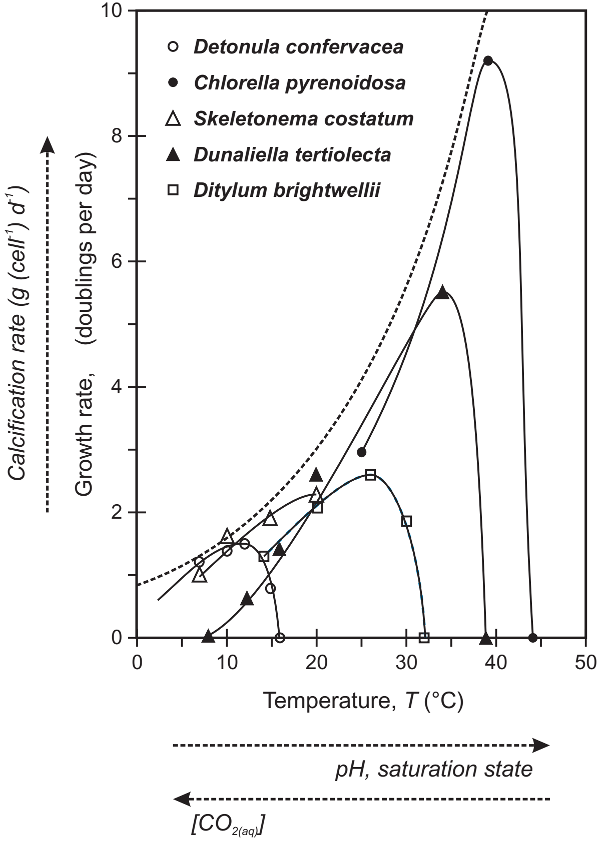

Fig. 4. Eppley curve encapsulation of temperature-growth behavior. Growth rates vs. temperature curves (solid lines) for five unicellular algae with different temperatyure optima (redrawn from Eppley, 1972). Shown is the Eppley curve (dashed line) together with its equation. Shown for illustration is our proposed analogy for the CO_2-calcification system (axis labels in *italics*).

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