Poorly recognized diversity of PIC to POC ratios underpins the role of coccolithophores in the marine carbon cycle

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Throughout their evolutionary history, coccolithophores have shown a spectacular array of diversity in coccolith morphology, coccosphere architectures and cell size that leads to specific cellular PIC (particulate inorganic carbon, calcite) and POC (organic carbon, biomass) characteristics for each species. As biogenic calcite production is a source of CO₂ and biomass production is a sink of CO₂, there has been extensive investigation into the physiological and environmental influences on PIC:POC and development of its use as a major biogeochemical trait for this plankton group. However, as much of our knowledge of coccolithophore PIC:POC stems from laboratory experiments on a limited selection of species in culture (i.e. *Emiliania huxleyi*) and from bulk analysis of field population samples that integrates the PIC and POC of all species present in the assemblage, the diversity of PIC:POC across coccolithophore species remains poorly quantified. This limits our ability to identify which species, taxonomic or functional groups contribute more (or less) significantly to community calcite and biomass production, and therefore the biogeochemical and ecological consequences of species extinctions, range shifts or changes in productivity due to climate or biotic pressures.

Here, we present recent insights into the PIC and POC diversity of extant coccolithophores and fossil calcareous nannoplankton by quantifying the morphology of thousands of individual coccospheres from laboratory cultures, filtered surface sea water samples, and well-preserved marine sediments. Across individual cells, PIC:POC show a very broad range from ~20:1 (e.g., heavily calcified cells of *Braarudosphaera*) to ~1:20 (e.g., lightly calcified cells of *Kilwalithus*), though the majority of individual cells typically lie between a PIC:POC of 2:1 and 1:2. Taxa that may appear to be "heavily calcified" (e.g. *Umbilicosphaera*) can have a lower cellular PIC:POC than expected if they are associated with larger cells (and therefore more POC) and vice versa. The intraspecies range in PIC:POC can also be substantial, as it is a function of variability in coccolithsize and morphology, the number of coccoliths per cell, and cell size. All these parameters have been shown to be influenced at a cellular level by environmental factors and at a population level by the mixing of ecotypes or morphotypes with different morphological characteristics and physiological states. Overlapping PIC:POC ranges for many species indicates the potential for some degree of 'functional redundancy' in coccolithophore communities providing that the ecophysiology of replacement species does not differ substantially. The remarkable diversity of PIC:POC across coccolithophores past and present strongly suggests that a "one-sizefits-all" approach to coccolithophore PIC:POC

is not sufficient to capture the biogeochemical and ecological consequences of changes in community structure, species productivity or biogeography.