

Reconstructing calcification in ancient coccolithophores: Individual coccolith weight and morphology of *Coccolithus pelagicus* (sensu lato)

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ABSTRACT

We have adapted an existing method to estimate coccolith calcite weight using birefringence (Beaufort, 2005) to suit the large coccoliths of *Coccolithus pelagicus*, which are only partially birefringent under cross-polarised light microscopy. Fossil and sediment trap material from the South Tasman Rise region of the Southern Ocean was used for calibration and validation. Our approach was tested with only the coccolith central area (CA) considered for measurement, to avoid relying on the less robust proximal shields. Thus our results are relative and intend to quantify intra-specific variations in volumetric calcite weight, expressed as a Weight Index (WI). Our results were overall consistent with mass estimation based on distal shield lengths. However, the WI approach clearly has the advantage in exploring allometric scaling between coccolith size and weight, as well as in measuring the degree of calcification in similarly sized morphotypes. Combining WI and morphometry data (distal shield length, DSL), we demonstrate subtle, but statistically significant changes in shape and thus calcification degree both within and between the tested *Coccolithus* populations. Most strikingly, it appears that modern *Coccolithus* populations in the Southern Ocean are, on average, more heavily calcified than their fossil counterparts.

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1. Introduction

At present, one of the most far-reaching perturbations of the marine environment is caused by the increased absorption of fossil-fuel CO₂ into the ocean, making it the second largest reservoir for anthropogenic carbon dioxide after the atmosphere itself (Riebesell et al., 2007). Current atmospheric CO₂ concentrations (pCO₂) are unprecedented for at least the past 800,000 years (Siegenthaler et al., 2005). The Southern Ocean is one of the most important areas of storage of anthropogenic carbon (e.g. Sabine et al., 2004), as well as being a region of air–sea flux of anthropogenic CO₂, with one third to half of the global uptake occurring south of 30°S (Orr et al., 2001; Takahashi et al., 2009). With continued CO₂ uptake, the Southern Ocean will likely see a reduction of carbonate, eventually leading to the undersaturation of calcium carbonate in the next 40 years (Orr et al., 2005; McNeil and Matear, 2008), which is likely to affect processes sensitive to seawater carbonate chemistry, such as calcification.

Recognition of the phenomenon of lowered ocean pH due to the oceanic uptake of excess pCO₂, (Caldeira and Wickett, 2003; The

Royal Society, 2005; Doney et al., 2009) has stimulated widespread research aimed at understanding its impact on calcifying marine biota. Specific focus has been given to corals (Langdon and Atkinson, 2005; Tribollet et al., 2009), foraminifera (Moy et al., 2009; Dissard et al., 2010), and coccolithophores (Riebesell et al., 2000; Delille et al., 2005; Langer et al., 2006; Beaufort et al., 2011). One major outcome is the recognition of significant species-specific, as well as strain-specific (e.g. Langer et al., 2009) responses within taxonomic groups and between groups of organisms (Ries et al., 2009), preventing straightforward extrapolations of documented responses to future scenarios of climatic change. Ultimately, it is crucial to understand the effects of ocean acidification on entire biological communities (Riebesell et al., 2008; Ries et al., 2009).

Changes in calcification by marine calcifiers can be estimated in terms of (a) calcite weight of individuals (applied in paleo-studies) and/or (b) calcification rates (mostly used in experimental or field observations within modern populations). Recently, Moy et al. (2009) compared average shell weights of the foraminifer *Globigerina bulloides* (estimated from ~50 hand-picked shells per sample within a narrow size range of 300–355 μm) from sediment trap samples, with those in Holocene sediments, documenting a significant reduction in weight from Holocene to modern shells in the Southern Ocean. This prompted further research into other calcifying organisms preserved

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in the same material—e.g. pteropods (aragonitic planktonic gastropods, e.g. Howard et al., 2011) and more recently coccolithophores (calcifying haptophyte algae) for which research is currently under way. However, individual coccoliths—the calcareous scales formed by coccolithophores—cannot be physically weighed due to their small size.

1.1. Coccolith calcite weight estimates: how and why?

The degree of calcification by coccolithophores and their response to a decrease in ocean pH have been examined in both laboratory studies and in the stratigraphic record, using a variety of methodologies. In sedimentary records, average coccolith mass has been estimated by Halloran et al. (2008) from total calcite mass and particle size distributions. Beaufort and Heussner (1999), and later Young and Ziveri (2000), developed a species-specific approach for estimating the contribution of each coccolithophore species to the total sedimentary calcite flux, calculating coccolith volume using size measurements and a shape factor derived from coccolith cross profiles of different species.

Another method for estimating individual coccolith weight is through birefringence (Beaufort, 2005), which exploits the optical properties of minerals such as calcite. This method relies on the conversion of the birefringence of a coccolith image captured in cross-polarised light—expressed in mean grey level (mean GL)—into picograms (pg), by a previously calibrated transfer function (Fig. 1). Calcite is one of the most birefringent minerals (Beaufort, 2005), hence providing a reliable method for estimating individual coccolith weight, with the advantage of being consistent and widely applicable. It is the only method to date able to measure intra-specific variability of coccolith weight (Beaufort, 2005). However, some coccoliths of the family Coccolithaceae and many other nannoliths may need a correcting factor due to the orientation of their crystallographic axes, which renders flat-lying coccoliths partially non-birefringent. Here, we present a modified birefringence weight estimation method and

apply the approach to the genus *Coccolithus* (Fig. 2). This ancient genus (first fossil occurrence ~63 Ma; Haq and Lohmann, 1976) is of particular interest because the modern subspecies *C. pelagicus* ssp. *braarudii*, in stark contrast to other coccolithophore species, appeared unaffected by perturbations of pH and high pCO₂ in short-term culture experiments (Langer et al., 2006). This apparent insensitivity may indicate retained adaptation to higher levels of past pCO₂ (Henderiks and Rickaby, 2007). However, Müller et al. (2009) found that long-term exposure to high levels of pCO₂ does have an effect on calcification and growth rate in *C. pelagicus* ssp. *braarudii* (strain RCC 1200). Therefore it remains crucial to further study natural responses of this species to changes in pCO₂ throughout the fossil record.

1.2. Species concept

Although *Coccolithus pelagicus* is recorded in fossil material since the Paleocene, this long fossil record is based on a very broad species concept (Geisen et al., 2004). Geisen et al. (2002) proposed that at the present day this genus consists of two extant subspecies: *C. pelagicus* ssp. *pelagicus* (Wallich, 1877) Schiller, 1930 and *C. pelagicus* ssp. *braarudii* (Gaarder, 1962) Geisen et al., 2002. Saez et al. (2003) describe these subspecies as having discrete but partially overlapping geographical ranges, with *C. pelagicus* ssp. *pelagicus* occurring in the subarctic region and coccolith size ranging from 6 to 11 μm, and the larger *C. pelagicus* ssp. *braarudii* (coccolith size 10–16 μm) present in temperate latitudes. More recently, Parente et al. (2004) described a third morphotype, *C. pelagicus* ssp. *azorinus*, ranging in size from 14 to 16 μm. However, so far genetic evidence has only established *C. pelagicus* ssp. *pelagicus* and *C. pelagicus* ssp. *braarudii* as subspecies (De Vargas et al., 2007).

It is likely that *C. pelagicus* ssp. *braarudii* is the predominant extant species present in the Southern Ocean today. Morphometric analysis of our samples shows a coccolith size variation of 10–16 μm. Even though the possible presence of the large morphotype *C. pelagicus*

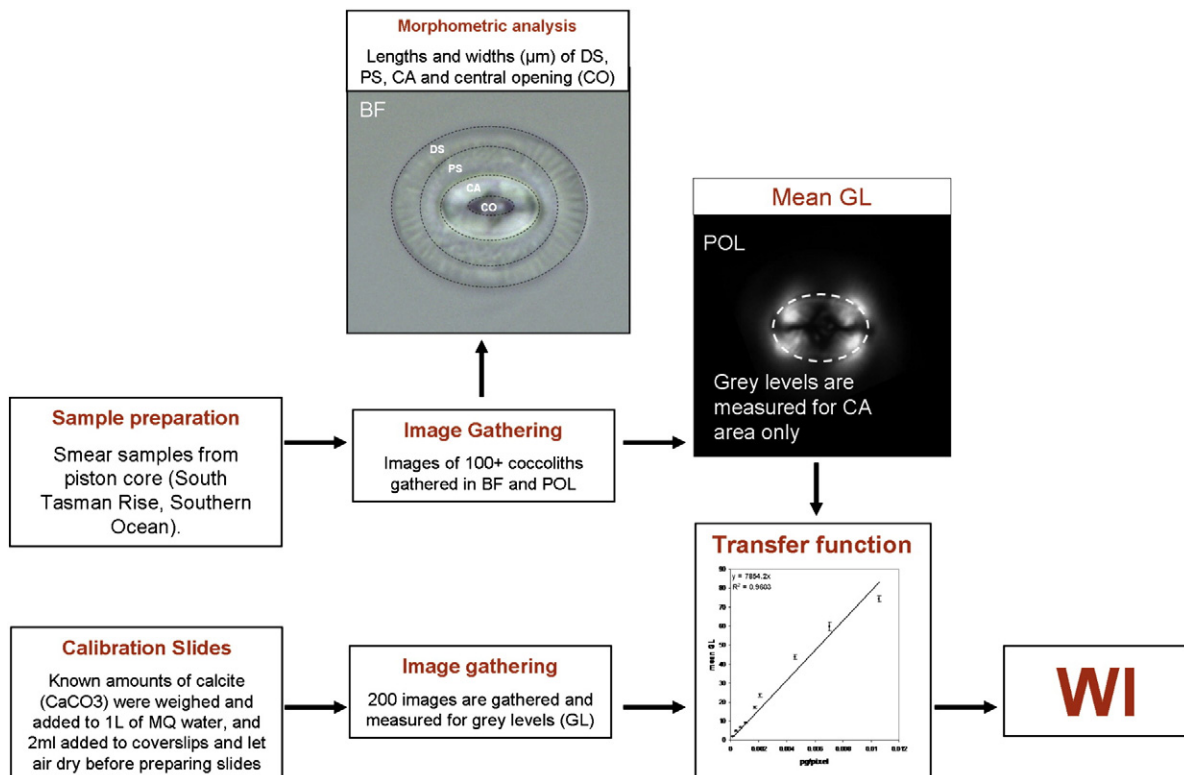


Fig. 1. Diagram summarizing all steps of image gathering, calibration and morphometric analysis of the coccoliths.

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