Use of coccolith based proxies for palaeoceanographic reconstructions

Pallavi P. Choudhari[1,2], Shramik M. Patil[1] and Rahul Mohan[1,*]

[1]National Centre for Polar and Ocean Research, Ministry of Earth Sciences, Headland Sada, Vasco-da-Gama, Goa 403 804, India
[2]Goa University, School of Earth, Ocean and Atmospheric Sciences, Taleigao Plateau, Goa 403 206, India

Coccolithophores are one of the major groups of marine carbonate producers and are the most important pelagic unicellular calcifying organisms which play a pivotal role in the marine biogeochemical cycles. Since past few decades, coccolithophores have gained attention due to their unique role in the global carbon cycle and particularly due to their combined effects on the biological carbon and carbonate counter pumps. Owing to their high diversity, better preservation, fast turnover rate and significant role in the marine biogeochemical cycles, coccolithophores are identified as a potential proxy to reconstruct palaeoceanographic changes. In this review, a broad introduction of the biology and biogeography of extant coccolithophores is discussed with a brief overview on the preservation of the coccoliths and their applications. This includes how coccolith abundance, diversity and morphometric studies are used to reconstruct palaeotemperature, palaeosalinity, palaeoproductivity and palaeocirculation. In addition, implications of coccolithophores in the isotopic studies for the estimation of palaeotemperature and palaeoproductivity are also discussed.

Keywords: Coccolithophores, nannoplankton, palaeoceanography, palaeoclimate, Southern Ocean.

Introduction

MAJORITY of marine life relies on photosynthetic microorganisms living in the photic zone of the World Oceans. These photosynthetic groups account for about 50% of the total global primary production which influences the global carbon cycle[1]. Major photosynthetic groups in the oceans that make up this production are cyanobacteria, diatoms, silicoflagellates, and the most interesting ones are the calcareous nannoplankton, the coccolithophores. Coccolithophores are motile or non-motile widely distributed algae; these are covered with calcite plates (coccoliths) during at least one phase of their life cycle[2,3]. Coccolithophores play a vital role in the biological and carbonate counter pumps through photosynthesis and calcification respectively and thus can affect the biogeochemical cycle to a larger extent[4,5] (Figure 1). Over the past ~230 million years, coccolithophores have changed the organic and inorganic carbon composition of the Earth system, globally decreasing the carbonate saturation state of sea water[6] and engage in the abiding increase of atmospheric oxygen[7].

In the geological record, coccolithophores appeared in the Late Triassic about ~230 Myr ago[8,9]. Today more than 250 coccolithophore species are flourishing in the global oceans highlighting their presence from coastal to open ocean waters and indicating dominance in the subtropical and subpolar regions[10,11].

Biology of coccolithophores

Coccolithophores are grouped under the division Haptophyta and class Prymnesiophyceae[12]. They are recognized by the organelle similar to the flagellar apparatus known as haptonema, present along with a pair of flagellum. In most coccolithophores species, haptonema is rudimentary and unlike other haptophyte groups, where haptonema serves the purpose of adhering and predation, in coccolithophores it appears to serve more of an obstacle sensing device[13]. However, certain coccolithophores that live in the extreme oligotrophic conditions and prolonged darkness, show indications of potential mixotrophy and phagotrophy and consist of distinct coiled haptonema[13]. Coccolithophores photosynthesize through pigments such as chlorophyll *a*+*c* in their paired golden brown chloroplasts. In certain members like Pavlovphyceae, holococcolithophores of *Calyptrosphaera* spp. and in particular species of Prymnesiophytes, a solitary chloroplast is observed[13]. According to the hypothesis of endosymbiotic evolution, the arrangement of the thylakoids and the absence of a girdle or peripheral lamella reflect the secondary origin of coccolithophore chloroplast[13], suggesting the evolution of coccolithophores occurred from heterotrophs/mixotrophs to autotrophs[14].

Other cell structures and organelles such as cell membrane and Golgi bodies form coccoliths[15]. In the single coccosphere (which mineralize during both stages of the life cycle), the type of coccolith is defined by the distinct phases of the life cycle. Generally, coccolithophores reproduce asexually by mitotic division followed by meiotic division with redistribution of coccoliths to the daughter cells. However, many species possess complicated life cycle with two stages, viz. ‘haploid phase’ and ‘diploid

---

*For correspondence. (e-mail: rahulmohan@ncpor.res.in)

phase' (Figure 2)[3]. The haploid phase bearing holococcoliths are made up of only one type of numerous crystallites of equal shape and size, whereas diploid phase bearing heterococcoliths are made up of crystal units of variable shapes and size[16].

Ecology and biogeography of coccolithophores

The distribution of coccolithophores exhibit patterns along latitudinal belts or water masses separated by oceanic frontal systems, which are defined by their specific temperature, salinity and nutrient profiles[17]. Most prevailing coccolithophore species have narrow temperature range[18]. This partly explains control and role of temperature in large scale distribution of coccolithophore species in latitudinal defined different biogeographical zones[19]. Highest coccolithophore diversity was reported in the subtropical oceanic gyres, low diversity in the temperate oceanic and subpolar waters[20] and lowest diversity in the coastal and inland waters. Some coastal species of coccolithophores such as *Pleurochrysis carterae* exhibit wider salinity tolerance and can grow well in salinities from 15 to 45 psu[21]. Other species such as *Coccolithus pelagicus* documented in the salinity as high as 250 psu in the Dead Sea and *Emiliania huxleyi* in the salinity as low as 11 psu in the Black Sea[22]. Coccolithophores are exclusively marine dwelling protists with only one freshwater species – *Hymenomonas roseola* reported so far[23].

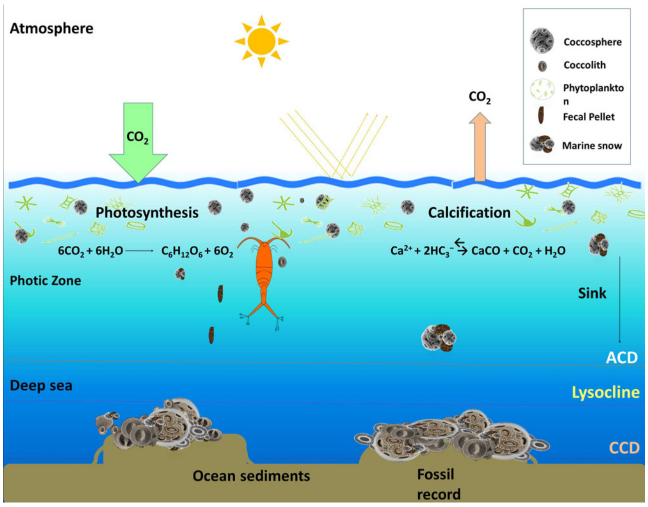

Figure 1. Role of coccolithophores in the biogeochemical cycles. (ACD, Aragonite compensation depth; CCD, Calcite compensation depth) (image modified after Rost and Riebesell[4]).

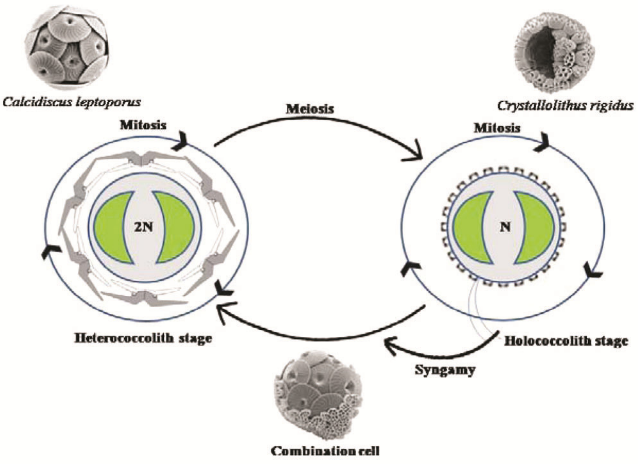

Figure 2. Life cycle of coccolithophore (e.g. *Calcidiscus leptoporus* modified after Geisen *et al.*[3]).

Species assemblages dominate in the specific environments and can be marked by the type of coccoliths and coccosphere morphology they possess[17]. For instance, placolith-bearing coccolithophores occur in the mesotrophic to eutrophic environments where waters are well mixed. Umbelliform coccolithophores (which form large flaring coccoliths and double layered coccospheres) dominate in oligotrophic environments. In the stable water column, floriform coccolithophores (flower shaped and possess asymmetrical coccospheres) dominate in the deep photic zone whereas, motile groups observed in different environments but in low abundance[24].

McIntyre and Bé[25], and Winter and Siesser[26] vaguely outlined coccolithophore floral zones as Subarctic, Temperate, Subtropical, Tropical and Subantarctic. In the past few decades detailed distribution pattern of coccolithophores in the different sectors of the Southern Ocean was studied. Eynaud *et al.*[27] reported high cell density areas in the Atlantic sector of the Southern Ocean; continental shelf region of South Africa; the area between the Subtropical Convergence and the Subantarctic Front; and the southern border of the Antarctic Polar Front. Boeckel *et al.*[28] assessed quantitative distribution pattern of coccolithophore groups in the surface sediments collected from the South Atlantic and Southern Ocean covering latitudes between 29°N and 55°S and longitudes between 41°E and 62°W.

Boeckel *et al.*[28] reported high abundance of lower photic taxa – *Florisphaera profunda* in the sediments below warmer stratified surface waters with deep nutricline and presence of *E. huxleyi* and *Calcidiscus leptoporus* in the high nutrient colder environments. In the same study, they showed presence of *Gephyrocapsa* spp. *Helicosphaera* spp. and *C. pelagicus* in the moderate to high nutrient, well mixed upper water column. In the Pacific sector of the Southern Ocean biogeographic distribution of coccolithophores was studied by Saavedra-Pellitero and Baumann[29]. They showed maximum number of coccoliths in the sediments near East Pacific rise and close to the Subtropical Front. The dominant taxa reported in this region were, *E. huxleyi*, *C. leptoporus*, *Gephyrocapsa* spp., *Umbellosphaera tenuis* and *C. pelagicus* subsp. *braarudii.* They reported decrease in the number of coccolithophore species poleward and presence of monospecific occurrence of *E. huxleyi* and occasional occurrence of *C. leptoporus* at south of the Polar Front. In the Indian sector of the Southern Ocean, three major oceanographic zones associated with different coccolithophore assemblages were recognized[10,11]. First is the Agulhas Retroflection and Subtropical Zone (ARFZ, STZ) which is characterized by high coccolithophore diversity. Second is the Subantarctic Zone (SAZ) which is characterized by low coccolithophore diversity and high coccolithophore abundance (mainly comprising of *E. huxelyi*), and third is the Polar Frontal Zone which is comprised of monospecific *E. huxleyi* assemblage[10,11,30,31].

Owing to the affinity of different coccolithophore species to the different oceanographic settings, their morphological alterations in these different geographical regions, and due to their crucial role in the marine biogeochemistry, coccolithophores have turn out to be an important proxy to understand palaeoceanographic and palaeoclimatic changes[32].

Preservation of coccoliths in the sediment and their palaeoceanographic implications

Coccolithophores, during their life cycle, respond to the *in situ* environmental conditions. These environmental changes can alter coccolithophores abundance, diversity, morphology as well as their elemental composition. Coccolithophores gets transported to the ocean floor in the form of marine snow with a sinking speed of 150–570 m/day[33], where they become a part of the sediment preserving imprints as fossil archives of the environment they lived in[34]. Today, these tiny fossil remains are responsible for calcareous ooze covering 35% of the world ocean floor[14]. In recent years, extensive work has been carried out to understand late Quaternary palaeoceanographic and palaeoclimatic changes using coccolith archives. The absolute/relative abundance of coccoliths, their morphological changes and elemental composition have been used to reconstruct palaeotemperature, palaeosalinity, palaeoproductivity and palaeocirculation[35–38]. Coccolith assemblages in the sediments were used to determine the shifts in the latitudinal positions of the oceanic fronts[39–41]. Alkenones[42–44] and *Gephyrocapsa* spp. morphological changes[38] were used to reconstruct palaeotemperature whereas, morphological variability of *E. huxleyi* was used to reconstruct palaeosalinity[45].

This article is based on the review of Baumann[19], and Stoll and Ziveri[46] to provide a brief review on the implications of coccolithophores as proxy for palaeoceanographic settings.

Applications of coccolithophores

Palaeotemperature estimates

Various methods have been established to reconstruct palaeotemperature by using coccoliths which include statistical analysis of the nannofossil assemblages, morphometric measurement of *Gephyrocapsa* spp., relative abundances of the different *Gephrocapsa* spp., Mg/Ca of bulk coccoliths, and by studies on unsaturated alkenone[47].

Coccolithophore species show clear latitudinal distribution with respect to the specific tolerance and affinity towards different temperature gradients[48]. Bollmann[45] displayed significant correlation between morphologies of *Gephyrocapsa* spp. and environmental gradients which show close relationship of *Gephyrocapsa* spp. size with temperature. Based on the relative abundance of the different morphotypes within the genus *Gephyrocapsa* in the Holocene sediments of Atlantic, Pacific and Indian Ocean, Bollmann *et al.*[38] proposed the global sea surface temperature (SST) calibration. They showed the potential use of *Gephyrocapsa* spp. to reconstruct palaeotemperature in the range 14°–29.4°C, with standard error of 1.78°C which is comparable to the temperature estimates of planktic foraminifera transfer function. Saavedra-Pellitero *et al.*[37] reconstructed palaeotemperature using Multivariate Statistical Analysis of modern coccolithophores utilizing down core coccolith assemblages in offshore Chile. They showed simple linear correlation ($r = 0.81$) between the estimated SST by coccolithophores assemblages and Alkenones, validating SST reconstruction for the time frame of ~27 kyr to 10 kyr BP. In this study, coccolithophore based temperature reconstruction defined Last Glacial Maximum vaguely, but fluctuations observed between 19 kyr and 25 kyr BP. broadly coordinated with the fluctuation in the alkenone SST records, Byrd ice core data and also comparable with SST estimates of radiolaria and dinoflagellates (see figure 6 in Saavedra-Pellitero *et al.*[37]).

Alkenones are the long chain di-unsaturated, tri-unsaturated ketones produced by coccolithophores of the genus *Gephyrocapsa* and *E. huxleyi*[49]. Brassell *et al.*[43] showed the correlation between unsaturated alkenones and glacial–interglacial cycles in the late Quaternary, which was recorded using planktic foraminiferal δ^{18}O values. Thus, the abundance data of unsaturated index of long chain alkenones can give constant palaeoclimatic curve even in the events of barren foraminiferal dissolution. The first systematic study on alkenones in the core top sediments was carried out by Sikes *et al.*[50], which was later validated by core top calibration using large globally distributed datasets from 60°N to 60°S of Atlantic, Pacific and Indian Ocean with mean SST between 0°C and 29°C[51]. The relationship $U37K = 0.033T + 0.044$, $R^2 = 0.958$ is identical within the error limits to the *E. huxleyi* calibrations of Prahl and Wakeham[52]. The effective use of alkenones is based on the factors such as, ecology, genetics, physiology and digenesis of the coccolithophores which cause alkenone unsaturation index to deviate from the unique relation with the SST. However these biomarkers over the years have exhibited to be one of the robust SST proxies[44] and enabled the descriptions of SST for various time scale of the global ocean, with the brief time period of inter-annual changes[53] and long time scale ranging from the Pliocene[54] to the Pleistocene[55]. Rostek *et al.*[56] used a combination of foraminiferal oxygen isotope records and palaeotemperature records derived from abundance ratio of unsaturated alkenones in the deep sea core from the junction of Arabian Sea and Bay of Bengal to extract salinity signals.

Palaeosalinity estimates

Unlike palaeotemperature, palaeosalinity is difficult to reconstruct using geological archives with the same accuracy and dependency as temperature, which leads to significant error in palaeosalinity estimates[57]. Previously the use of transfer function based on the relative abundance of microfossil to reconstruct palaeosalinity was not accepted as the composition of assemblages is apparently determined mainly by the other parameters like temperature and productivity[58]. Yet, it is evident from studies that different organisms are tolerant to variable range of salinity which is reflected in the abundance changes[59]. In the culture studies, morphological variations in *E. huxleyi* with respect to changing salinity have been demonstrated[60]. Bollmann and Herrle[61] investigated the relationship between size of *E. huxleyi* coccoliths and sea surface salinity (SSS) in the culture based investigations. They showed that, the *E. huxleyi* coccolith size varies significantly within the salinity range of 33–38 psu with a standard error of 0.49 psu. In addition, *in situ* studies in the Atlantic, Pacific, and Southern Ocean showed significant relationship between SSS and *E. huxleyi* placolith size[62]. Their plankton-derived multiple regression models for *in situ* salinity varied from that of the previous studies of the Holocene sediment samples. Similar culture-based experiments were carried out to assess applicability of *E. huxleyi* coccolith morphology as a palaeosalinity proxy[60]. The relationship between the salinity and the morphological response is vaguely understood but probably is related to the regulation of turgor pressure which affects the size of the cell[63] and thus the size of a single coccolith. This hypothesis also explains the morphological variation in *E. huxleyi* between the open ocean dataset and the coastal dataset[62]. Ausín *et al.*[64] used multivariate statistical analyses and showed that the distribution of modern coccolithophores in the Atlantic Ocean, in the Western Mediterranean, and west of the Strait of Gibraltar was primarily influenced by annual average salinity at 10 m depth. They observed similar outcomes in the Modern Analog Technique and Weighted-Averaging Partial Least Square (WA-PLS) regression calibration models and applied these models to reconstruct SSS in the Alboran Sea at high resolution for the last 25 kyr, emphasizing the reliability of both models to drive coccolithophore-based transfer function for reconstruction of SSS. In the past few decades, owing to the firm response of hydrogen isotopes of long-chain alkenones fractionation to salinity for different environments, hydrogen isotopes of long-chain alkenones have gained attention as a promising proxy for reconstruction of palaeosalinity[65]. The monospecific culture studies have revealed positive linear correlation between salinity and hydrological isotopic composition of the long chain alkenones, synthesized by *E. huxleyi* and *G. oceanica*[66]. Meer *et al.*[67] reconstructed past variation in the SSS using alkenones and combined with the relative past SSS generated using organic walled dinocyst distribution in the same core from the Black sea. This combined result signifies the freshening of the Black sea surface waters in the last 3 kyr, suggesting that past salinity was ~18 times higher than the present day salinity. Similarly, alkenones have gained fame for their potential use in reconstruction of past salinity especially in multiproxy approach[68].

Palaeoproductivity

Kinkel *et al.*[36] described the significance of coccoliths in the sediments for estimation of palaeoproductivity. High abundance of the deep photic zone flora (e.g. *Florisphaera profunda*) is associated with deep thermocline and nutricline which indicates low productivity whereas, low abundance of the deep photic zone flora is associated with shallow thermocline and nutricline indicating high productivity[69,70]. Thus, the transfer function based on deep photic zone taxa (e.g. *F. profunda*, *Gladiolithus flabellatus*) and other coccoliths in the sediment provide information about ocean stratification and palaeoproductivity[40,69,70]. However, in high latitudes, the absence of *F. profunda* excludes the use of some of these methods where, siliceous organisms are commonly used to reconstruct palaeoproductivity[71]. By correlating accumulation records of coccolithophores with P/Ti, Sr/Ti, and other palaeoproductivity records in Subantarctic region of the Atlantic sector of the Southern Ocean, Flores *et al.*[71] reported that changes in the abundance of coccolithophore reflect variation in the palaeoproductivity. In the modern oceans, species like *Gephyrocapsa* spp., *C. pelagicus* subsp. *braarudii* and *G. oceanica* tend to be abundant in the high productive areas with high nutrient availability[45,72], which are usually considered as reliable proxies for productivity estimates in the high nutrient regions[73].Amore *et al.*[73] indicated small *Gephyrocapsa* spp., and *C. pelagicus* subsp. *braarudii* as vital proxies to indicate the prevailing influence of Portugal current and conditions of high nutrient and increased productivity. Whereas, the dominance of *G. caribbeanica*, *Syracosphaera* spp., *Rhabdosphaera* spp. and *Umbilicosphaerasibogae* denote periods of Iberian poleward current. Schwab *et al.*[74] studied two sediment cores from the south of Azores Islands, North of the Atlantic Subtropical gyre and proposed reduced Atlantic Meridional Overturning Circulation indicative of strong increase in productivity. This is represented by high abundance and accumulation rates of coccoliths, alkenones, Ba/Ti ratios, high abundance of diatoms, and low abundance of *F. profunda*[74].

Geochemical applications of coccolithophores

Recent developments in methodologies and instrumentation to extract and analyse coccoliths from the sediments have increased understanding of coccolith geochemical composition and its use to study palaeoclimatic and palaeoceanographic changes. Coccolithophores are the only organism in the ocean which provide indicators of past oceanographic and climate condition from organic (biomarkers/molecular fossil) as well as inorganic ($CaCO_3$) sediment deposits[46]. Applications of isotopic proxies depend on the comparison of isotopic composition of calcite in coccolith and sea water or in the culture medium. The isotopic composition of calcite is the reflection of the relative abundance of two isotopes, commonly the more abundant and light isotope over a rare, and heavier for example – $^{16}O/^{18}O$, $^{12}C/^{13}C$[75,76]. Isotope-based reconstruction is largely explored using foraminifera, but where foraminifera are rare and/or sediment is limited, coccolith carbonate can be a good alternative for isotopic studies. But, considering the difficulty to segregate coccoliths belongs to single coccolithophore species and vital effects of different species the isotopic investigations are subjected to deviate. To obtain a reliable coccolith based isotopic proxy two things are essential, viz. (i) lab drawn culture experiments on coccolithophores to obtain strong relationship with environmental conditions[77] and, (ii) studies in the sediments to explicate the methods to segregate fractions of single species[46]. Ziveri *et al.*[78] postulated correction factors of specific species coccoliths for carbon isotopic vital effects. In the recent core top study, Hermoso *et al.*[79] demonstrated that, the isotopic composition of coccolith is governed to the fundamental level by environmental factors which regulate the growth rate and not only by the temperature and isotopic composition of the sea water.

Apart from isotopic ratios, extensive work has been carried out on the elemental ratios of coccoliths. In coccoliths, largely explored elements are Sr/Ca and Mg/Ca ratios. Stoll and Schrag[80] were pioneered in the analysis of Sr/Ca ratios of coccoliths who described its potential use in palaeoproductivity reconstruction. Coccolith Sr/Ca ratio derived data has the advantage as it may not rely on sedimentation rate and also comparatively unaffected by partial dissolution[80]. Mejía *et al.*[81] reconstructed palaeoproductivity records from the Agulhas bank slope using coccolith Sr/Ca ratio along the second last glacial and interglacial cycles.

In coccolithophores, temperature has prominent control on Mg fractionation in the coccolith calcite[82]. There are competing views on the use of Mg/Ca coccolith derived temperature. On the one hand, Mg/Ca coccolith temperature indicator will assist in further enhancing the alkenone under saturation proxy[83] whereas on the other hand owing to their small size and extremely low Mg/Ca ratio (0.1 to 0.2 mmol/mol), it is complicated to obtain robust data on variations in the coccolith Mg/Ca[46,82]. Through culture based experiments on *G. oceanica* and *E. huxleyi*, Kongtae *et al.*[84] showed potential use of coccolith Mg/Ca as a temperature proxy. In this study, Mg isotope in both species showed positive relation to temperature at some growth phases, whereas Mg isotope in *G. oceanica* showed weak correlation with temperature during late exponential growth phase thus hindering the coccolith temperature signals.

Coccolithophores are sensitive to the changes in the pH/carbonate mineral saturation of the sea water and it affects the intracellular biomineralization processes[85]. Stoll *et al.*[86] showed that boron isotopes and B/Ca composition of the calcite could differentiate between modulations of pH or dissolved inorganic carbon in the coccolith vesicle. If biogenic carbonates recorded extracellular pH passively, B/Ca signal in the fossils can be a helpful tool to reconstruct variation in pH of the environment they lived. Also, it would help understand the mechanism by which the cells respond to changing carbonate chemistry of the ocean as most of the calcifying organisms may be disturbed as a result of future ocean acidification[87] or can over calcify as observed in the past[88].

Coccolithophore studies in the Southern Ocean

The Southern Ocean (SO) influences earth's climate by storing and transporting large amount of heat and carbon dioxide between atmosphere and oceans. The SO is documented to have influenced past climate by sequestering CO_2 during the glacial periods and possibly out gassing during the interglacial periods[89]. In the future world scenario, the SO is projected to absorb excess anthropogenic CO_2, thereby decreasing pH of its water mass thus affecting the aragonite-calcite saturation levels. The recent studies indicate SO's role in modulating present and past climate, however what runs the glacial–interglacial carbon dynamics in SO are not well documented.

Coccolithophores are thought to be responsible for the seasonal Great Calcite belt in the SO – a vast region of elevated albedo covering approximately 16% of the World Oceans[90]. Due to their huge abundance and good preservation in the marine sediments with the signals of the surface water conditions[34], the late Quaternary coccolithophores records are extensively used to decipher palaeoenvironmental conditions which include positions of oceanic fronts and current systems[35,39,40]. In the past decades coccoliths have been used as the indicators of palaeoceanographic conditions of the SO. Boeckel *et al.*[28] identified six surface sediment assemblages, which exhibit distribution pattern as a function of positions of nutricline and thermocline and characteristics of overlying surface waters. Flores *et al.*[91] reconstructed late Quaternary surface waters of Atlantic Ocean conditions using coccolithophore assemblages. Geitzenauer[92] exhibited *U. leptopora* and *C. pelagicus* as a useful palaeoclimatic indicator in late Quaternary sediments of the Subantarctic Pacific Ocean.

Fluctuation in the subtropical front for 130 kyr and marine isotope stages 1–5 are identified through changes in calcareous nannoplankton assemblage at South of Australia[41]. Surface sediment coccolithophore assemblages were studied in order to define oceanic frontal boundaries and water masses for the last 10 kyr in the Australian sector of the Southern Ocean[93]. Villa *et al.*[94] extracted 15 cores from the SO and correlated calcareous nannofossils with interglacial intervals with warmer SST showing signs of high productive and an open-ocean environment, and with occurrence of coccolithophores in the Western Antarctic Basin and nearly absence of coccolithophore in the Eastern Antarctic Basin shows signs of more variable SST near the west Antarctic ice sheet.

The Southern Indian Ocean, for various reasons, remained relatively less explored with few studies on the ecology and biogeography of the extant coccolithophores. Three coccolithophore assemblages were identified and the demarcating areas between the assemblages coincide with the position of the Subtropical, Subantarctic and Polar front[10]. Patil *et al.*[11] reported three assemblages and revealed that, regions with elevated temperatures and low nutrient concentration exhibit high diversity, whereas regions with low temperature, high nutrient concentration show much less diversity. Increase in temperature in coming decades is assumed to shift oceanic frontal regions southward. This could possibly alter the biogeographic distribution patterns of the planktic (free floaters) organisms including coccolithophores. Evidence for this is the poleward expansion of the coccolithophore species *E. huxleyi* in the Indian sector of the Southern Ocean[30]. Fincham and Winter[95] obtained isotopic ratios and nannoplankton counts showing that majority of samples are recent and not older than 85 kyr, in the South West Indian Ocean describing the influence of Agulhas current on the sedimentation at this region. Patil *et al.*[31] reported silicifying haptophytes, xenospheres and anomalous coccospheres from the Southern Indian Ocean highlighting new occurrences of haptophytes to the Southern Indian Ocean and their adaptation to the changing environment.

Coccolithophore studies in the Arctic seas

The Arctic Ocean is the shallowest and smallest ocean; yet it is a critical component in the interconnected system that regulates Earth's climate. Encircled by continents, the Arctic Ocean is largely covered by sea ice. The necessity to understand the importance of geologic history of the Arctic Ocean and its impact on global climate and ocean circulation has been recognized since 1981 by the international palaeoceanographic community[96]. Baumann and Matthiessen[97] studied coccolith and dinoflagellate cyst assemblages in five sediment cores from the Norwegian Sea and Fram Strait. Considerable change in both the assemblages corresponds approximately to the onset of the Holocene climatic optimum. They indicated that reorganization of the hydrographic properties in the North Atlantic realm after the ice sheets had vanished was most probably connected to this change. Backman *et al.*[96] studied late Pleistocene and Holocene stratigraphic distributions of calcareous nannofossils in seven short cores from the Arctic Basin and in one core from the Norwegian Sea. The influence of Atlantic shallow waters was mostly represented in the Arctic Ocean cores by the assemblages. Giraudeau *et al.*[98] recorded changes in the long term trend in the coccolith abundance in the cores retrieved from Norway and Northern Iceland and indicated Millennial-scale modulation in Atlantic water advection to the Nordic Seas.

Interpretation of geological history using coccoliths

In the geological record since the coccolithophores inception (about ~230 myr), coccolithophores have evolved rapidly and dominated making sharp zonation between Triassic and Holocene which makes them important proxy for delineating ancient oceanic to hemipelagic realms and also in petroleum exploration. These zonations helped biostratigraphers to study major extinction events, determination of the age of the ODP/DSDP/IODP cores, past climatic changes, glacial–interglacial climatic fluctuations, etc. Owing to their high diversity and rapid evolution since 20 Myr, coccoliths preserved in the sediment are also widely being used in scientific and oil drilling as zonal markers.

Conclusion and future perspectives

Coccoliths in the sediment samples provide information on condition of water masses, palaeoecology and palaeoceanography. In the past few decades, coccoliths have been used as a potential tool to reconstruct palaeoceanographic settings. Though these methods are validated to an extent through culture studies and transfer function, the need for extensive research to determine coccolith as a robust proxy still exists. Species morphology can be stable, if it is tested under different ecological parameters, and under strong genetic control[99]. Sediment trap data for coccolith flux to the deep sediment is scarcely established and more information is needed for better understanding of transformation of planktonic coccolithophores to the ocean sediments. The use of geochemical composition of coccoliths as a proxy has shown promise for palaeoceanographic reconstruction in the sediment that lack foraminifera. But their small size and difficulty in segregating single species has hindered the potential of coccolith-based isotopic studies. In general, foraminifera are widely studied and used to reconstruct palaeoceanographic conditions whereas coccolithophores have gained attention recently as a potential proxy for palaeoceanographic reconstruction, thus leaving extensive scope for further research in this field.

---

1. Field, C. B., Behrenfeld, M. J., Randerson, J. T. and Falkowski, P., Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, 1998, **281**(5374), 237–240.
2. Green, J. C., Course, P. A. and Tarran, G. A., The life-cycle of *Emiliania huxleyi*: a brief review and a study of relative ploidy levels analysed by flow cytometry. *J. Mar. Syst*., 1996, **9**(1–2), 33–44.
3. Geisen, M., Billard, C., Broerse, A. T., Cros, L., Probert, I. and Young, J. R., Life-cycle associations involving pairs of holococcolithophorid species: intraspecific variation or cryptic speciation? *Eur. J. Phycol*., 2002, **37**(4), 531–550.
4. Rost, B. and Riebesell, U., Coccolithophores and the biological pump: responses to environmental changes. In *Coccolithophores* (eds Thierstein, H. R. and Young, J. R.), Springer, Berlin, Heidelberg, 2004, pp. 99–125.
5. Young, J. R., Geisen, M. and Probert, I., A review of selected aspects of coccolithophore biology with implications for paleobiodiversity estimation. *Micropaleontology*, 2005, **51**(4), 267–288.
6. Ridgwell, A., A Mid-Mesozoic revolution in the regulation of ocean chemistry. *Mar. Geol*., 2005, **217**(3–4), 339–357.
7. Falkowski, P. G. *et al*., The rise of oxygen over the past 205 million years and the evolution of large placental mammals. *Science*, 2005, **309**(5744), 2202–2204.
8. Jafar, S. A., Significance of Late Triassic calcareous nannoplankton from Austria and Southern Germany. *Neues. Jahrb. Geol. Paläontol*., 1983, **166**(2), 218–259.
9. Bralower, T. J., Bown, P. R. and Siesser, W. G., Significance of upper Triassic nannofossils from the southern hemisphere (ODP Leg 122, Wombat Plateau, NW Australia). *Mar. Micropaleontol*., 1991, **17**(1–2), 119–154.
10. Mohan, R. *et al*., Ecology of coccolithophores in the Indian sector of the Southern Ocean. *Mar. Micropaleontol*., 2008, **67**(1–2), 30–45.
11. Patil, S. M., Mohan, R., Shetye, S. S., Gazi, S., Baumann, K.-H. and Jafar, S., Biogeographic distribution of extant Coccolithophores in the Indian sector of the Southern Ocean. *Mar. Micropaleontol*., 2017, **137**, 16–30.
12. Edvardsen, B., Eikrem, W., Green, J. C., Andersen, R., Moon-van der Staay, S. Y. and Medlin, L., Phylogenetic reconstructions of the Haptophyta inferred from 18S ribosomal DNA sequences and available morphological data. *Phycologia*, 2000, **39**(1), 19–35.
13. Billard, C. and Inouye, I., What is new in coccolithophore biology? In *Coccolithophores* (eds Thierstein, H. R. and Young, J. R.), Springer, Berlin, Heidelber, 2004, pp. 1–29.
14. DeVargas, C., Aubry, M. P., Probert, I. and Young, J., Origin and evolution of coccolithophores: from coastal hunters to oceanic farmers. In *Evolution of Primary Producers in the Sea* (eds Falkowski, P. G. and Knoll, A. H.), Academic Press, 2007, pp. 251–285.
15. Brownlee, C. and Taylor, A., Calcification in coccolithophores: a cellular perspective. In *Coccolithophores* (eds Thierstein, H. R. and Young, J. R.), Springer, Berlin, Heidelberg, 2004, pp. 31–49.
16. Young, J. R. *et al*., Guidelines for coccolith and calcareous nannofossil terminology. *Palaeontology*, 1997, **40**, 875–912.
17. Winter, A., Jordan, R. W. and Roth, P. H., Biogeography of living coccolithophores in ocean waters. In *Coccolithophores* (eds Winter, A. and Siesser, W. S.), Cambridge University Press, 1994, pp. 161–177.
18. McIntyre, A. and Bé, A. W., Modern coccolithophoridae of the Atlantic Ocean – I. Placoliths and cyrtoliths. *Deep Sea Res*., 1967, **14**(5), 561–597.
19. Baumann, K.-H., Andruleit, H., Boeckel, B., Geisen, M. and Kinkel, H., The significance of extant coccolithophores as indicators of ocean water masses, surface water temperature, and palaeoproductivity: a review. *Paläont. Z. (ZDB)*, 2005, **79**(1), 93–112.
20. Hulburt, E. M., The diversity of phytoplanktonic populations in oceanic, coastal, and estuarine regions. *J. Mar. Res*., 1963, **21**(2), 81–93.
21. Brand, L. E., The salinity tolerance of forty-six marine phytoplankton isolates. *Estuar. Coast. Shelf Sci*., 1984, **18**(5), 543–556.
22. Bukry, D., Coccoliths as paleosalinity indicators; evidence from Black Sea. In *The Black Sea-Geology, Chemistry and Biology* (eds Degens, E. and Ross, D. A.), 1974, pp. 353–363.
23. Braarud, T., Coccolith morphology and taxonomic position of *Hymenomonas roseola* Stein and *Syracosphaera carterae* Braarud and Fagerland. *Nytt. Mag. Bot*., 1954, **3**, 1–4.
24. Young, J. R., Possible functional interpretations of coccolith morphology. *Abh. Geol. B-A*, 1987, **39**, 305–313.
25. McIntyre, A. and Bé, A. W., Modern coccolithophoridae of the Atlantic Ocean – I. Placoliths and cyrtoliths. *Deep Sea Res. A*, Elsevier, 1967, **14**(5), 561–597.
26. Winter, A. and Siesser, W. G., *Coccolithophores*, Cambridge University Press, 1994, p. 242.
27. Eynaud, F., Giraudeau, J., Pichon, J. J. and Pudsey, C. J., Sea-surface distribution of coccolithophores, diatoms, silicoflagellates and dinoflagellates in the South Atlantic Ocean during the late austral summer 1995. *Deep Sea Res. I*, 1999, **46**(3), 451–482.
28. Boeckel, B., Baumann, K.-H., Henrich, R. and Kinkel, H., Coccolith distribution patterns in South Atlantic and Southern Ocean surface sediments in relation to environmental gradients. *Deep Sea Res. I*, 2006, **53**(6), 1073–1099.
29. Saavedra-Pellitero, M. and Baumann, K.-H., Comparison of living and surface sediment coccolithophore assemblages in the Pacific sector of the Southern Ocean. *Micropaleontology*, 2015, **61**(6), 507–520.
30. Patil, S. M., Mohan, R., Shetye, S. and Gazi, S., Phytoplankton abundance and community structure in the Antarctic polar frontal region during austral summer of 2009. *Chin. J. Oceanol. Limn*., 2013, **31**(1), 21–30.
31. Patil, S. M., Mohan, R., Shetye, S., Gazi, S. and Jafar, S., Morphological variability of *Emiliania huxleyi* in the Indian sector of the Southern Ocean during the austral summer of 2010. *Mar. Micropaleontol*., 2014, **107**, 44–58.
32. Roth, P. H., Mullin, M. M. and Berger, W. H., Coccolith sedimentation by fecal pellets: laboratory experiments and field observations. *Geol. Soc. Am. Bull*., 1975, **86**(8), 1079–1084.
33. Honjo, S., Coccoliths: production, transportation and sedimentation. *Mar. Micropaleontol*., 1976, **1**, 65–79.
34. Baumann, K.-H., Andruleit, H. and Samtleben, C., Coccolithophores in the Nordic Seas: comparison of living communities with surface sediment assemblages. *Deep Sea Res. II*, 2000, **47**(9–11), 1743–1772.
35. McIntyre, A., Ruddiman, W. F. and Jantzen, R., Southward penetrations of the North Atlantic Polar Front: faunal and floral evidence of large-scale surface water mass movements over the last 225,000 years. *Deep Sea Res. I*, 1972, **19**(1), 61–77.
36. Kinkel, H., Baumann, K.-H. and Cepek, M., Coccolithophores in the equatorial Atlantic Ocean: response to seasonal and Late

Quaternary surface water variability. *Mar. Micropaleontol.*, 2000, **39**(1–4), 87–112.

37. Saavedra-Pellitero, M., Flores, J. A., Lamy, F., Sierro, F. J. and Cortina, A., Coccolithophore estimates of paleotemperature and paleoproductivity changes in the southeast Pacific over the past ~27 kyr. *Paleoceanography*, 2011, **26**, PA1201.
38. Bollmann, J., Henderiks, J. and Brabec, B., Global calibration of Gephyrocapsa coccolith abundance in Holocene sediments for paleotemperature assessment. *Paleoceanogr., Paleoclimatol.*, 2002, **17**(3), 1035.
39. Winter, A. and Martin, K., Late Quaternary history of the Agulhas current. *Paleoceanography*, 1990, **5**(4), 479–486.
40. Flores, J. A., Gersonde, R. and Sierro, F. J., Pleistocene fluctuations in the Agulhas Current Retroflection based on the calcareous plankton record. *Mar. Micropaleontol.*, 1999, **37**(1), 1–22.
41. Findlay, C. S. and Flores, J. A., Subtropical front fluctuations south of Australia (45°09′S, 146°17′E) for the last 130 ka years based on calcareous nannoplankton. *Mar. Micropaleontol.*, 2000, **40**(4), 403–416.
42. Marlowe, I. T., Green, J. C., Neal, A. C., Brassell, S. C., Eglinton, G. and Course, P. A., Long chain (n-C37–C39) alkenones in the Prymnesiophyceae. Distribution of alkenones and other lipids and their taxonomic significance. *Eur. J. Phycol.*, 1984, **19**(3), 203–216.
43. Brassell, S. C. *et al.*, Palaeoclimatic signals recognized by chemometric treatment of molecular stratigraphic data. *Org. Geochem.*, 1986, **10**(4–6), 649–660.
44. Herbert, T. D., Heinrich, D. H. and Karl, K. T., Alkenone paleotemperature determinations. In *Treatise on Geochemistry* (eds Elderfield, H., Hollard, H. D. and Turekian, K. K.), Elsevier, 2003, vol. 6, pp. 391–432.
45. Bollmann, J., Morphology and biogeography of *Gephyrocapsa* coccoliths in Holocene sediments. *Mar. Micropaleontol.*, 1997, **29**(3–4), 319–350.
46. Stoll, H. M. and Ziveri, P., Coccolithophorid-based geochemical paleoproxies. In *Coccolithophores* (eds Thierstein, H. R. and Young, J. R.), Springer, Berlin, Heidelberg, 2004, pp. 529–562.
47. Mix, A. C., Bard, E. and Schneider, R., Environmental processes of the ice age: land, oceans, glaciers (EPILOG). *Quat. Sci. Rev.*, 2001, **20**(4), 627–657.
48. Melinte, M. C., Calcareous nannoplankton, a tool to assign environmental changes. *Geo-Eco-Marina*, 2004, 9–10.
49. Volkman, J. K., Eglinton, G., Corner, E. D. and Forsberg, T. E. V., Long-chain alkenes and alkenones in the marine coccolithophorid *Emiliania huxleyi*. *Phytochemistry*, 1980, **19**(12), 2619–2622.
50. Sikes, E. L., Farrington, J. T. and Keigwin, L. D., Use of the alkenone unsaturation ratio U37K to determine past sea surface temperatures: core-top SST calibrations and methodology considerations. *Earth Planet. Sci. Lett.*, 1991, **104**(1), 36–47.
51. Müller, P. J., Kirst, G., Ruhland, G., Von Storch, I. and Rosell-Melé, A., Calibration of the alkenone paleotemperature index U37K′ based on core-tops from the eastern South Atlantic and the global ocean (60°N–60°S). *Geochim. Cosmochim. Acta*, 1998, **62**(10), 1757–1772.
52. Prahl, F. G. and Wakeham, S. G., Calibration of unsaturation patterns in long-chain ketone compositions for palaeotemperature assessment. *Nature*, 1987, **330**(6146), 367.
53. Kennedy, J. A. and Brassell, S. C., Molecular records of twentieth-century El Niño events in laminated sediments from the Santa Barbara basin. *Nature*, 1992, **357**(6373), 62.
54. Lawrence, K. T., Liu, Z. and Herbert, T. D., Evolution of the eastern tropical Pacific through Plio-Pleistocene glaciation. *Science*, 2006, **312**(5770), 79–83.
55. Martínez-Garcia, A., Rosell-Melé, A., Geibert, W., Gersonde, R., Masqué, P., Gaspari, V. and Barbante, C., Links between iron supply, marine productivity, sea surface temperature, and CO_2 over the last 1.1 Ma. *Paleoceanography*, 2009, **24**(1), PA1207.
56. Rostek, F., Ruhlandt, G., Bassinot, F. C., Muller, P. J., Labeyrie, L. D., Lancelot, Y. and Bard, E., Reconstructing sea surface temperature and salinity using δ^{18}O and alkenone records. *Nature*, 1993, **364**(6435), 319.
57. Rohling, E. J. and Bigg, G. R., Paleosalinity and δ^{18}O: a critical assessment. *J. Geophys. Res.*, 1998, **103**(C1), 1307–1318.
58. Duplessy, J. C., Labeyrie, L., Juillet-Leclerc, A., Maitre, F., Duprat, J. and Sarnthein, M., Surface salinity reconstruction of the North Atlantic Ocean during the last glacial maximum. *Oceanol. Acta*, 1991, **14**(4), 311–324.
59. Wolff, T., Grieger, B., Hale, W., Dürkoop, A., Mulitza, S., Pätzold, J. and Wefer, G., On the reconstruction of paleosalinities. In *Use of Proxies in Paleoceanography* (eds Fischer, G. and Wefer, G.), Springer, Berlin, Heidelberg, 1999, pp. 207–228.
60. Fielding, S. R., Herrle, J. O., Bollmann, J., Worden, R. H. and Montagnesd, D. J., Assessing the applicability of *Emiliania huxleyi* coccolith morphology as a sea-surface salinity proxy. *Limnol. Oceanogr.*, 2009, **54**(5), 1475–1480.
61. Bollmann, J. and Herrle, J. O., Morphological variation of *Emiliania huxleyi* and sea surface salinity. *Earth Planet. Sci. Lett.*, 2007, **255**(3–4), 273–288.
62. Bollmann, J., Herrle, J. O., Cortés, M. Y. and Fielding, S. R., The effect of sea water salinity on the morphology of *Emiliania huxleyi* in plankton and sediment samples. *Earth Planet. Sci. Lett.*, 2009, **284**(3–4), 320–328.
63. Kirst, G. O., Salinity tolerance of eukaryotic marine algae. *Annu. Rev. Plant Biol.*, 1990, **41**(1), 21–53.
64. Ausín, B. *et al.*, Coccolithophore productivity and surface water dynamics in the Alboran Sea during the last 25 kyr. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 2015, **418**, 126–140.
65. Weiss, G. M., Pfannerstill, E. Y., Schouten, S., Sinninghe Damsté, J. S. and van der Meer, M. T., Effects of alkalinity and salinity at low and high light intensity on hydrogen isotope fractionation of long-chain alkenones produced by *Emiliania huxleyi*. *Biogeosciences*, 2017, **14**(24), 5693–5704.
66. Schouten, S., Ossebaar, J., Schreiber, K., Kienhuis, M. V. M., Langer, G. and Bijma, J., The effect of temperature and salinity on the stable hydrogen isotopic composition of longchain alkenones produced by *Emiliania huxleyi* and *Gephyrocapsa oceanica*. *Biogeosciences*, 2005, **2**(6), 1681–1616.
67. Van der Meer, M. T., Baas, M., Rijpstra, W. I. C., Marino, G., Rohling, E. J., Damsté, J. S. S. and Schouten, S., Hydrogen isotopic compositions of long-chain alkenones record freshwater flooding of the Eastern Mediterranean at the onset of sapropel deposition. *Earth Planet. Sci. Lett.*, 2007, **262**(3–4), 594–600.
68. Van der Meer, M. T., Sangiorgi, F., Baas, M., Brinkhuis, H., Damsté, J. S. S. and Schouten, S., Molecular isotopic and dinoflagellate evidence for Late Holocene freshening of the Black Sea. *Earth Planet. Sci. Lett.*, 2008, **267**(3–4), 426–434.
69. Beaufort, L., Lancelot, Y., Camberlin, P., Cayre, O., Vincent, E., Bassinot, F. and Labeyrie, L., Insolation cycles as a major control of equatorial Indian Ocean primary production. *Science*, 1997, **278**(5342), 1451–1454.
70. Molfino, B. and McIntyre, A., Precessional forcing of nutricline dynamics in the equatorial Atlantic. *Science*, 1990, **249**(4970), 766–769.
71. Flores, J. A., Filippelli, G. M., Sierro, F. J. and Latimer, J. C., The White Oceanhypothesis: a late Pleistocene Southern Ocean governed by coccolithophores and driven by phosphorus. *Front Microbiol.*, 2012, **3**, 233.
72. Cachao, M. and Moita, M. T., *Coccolithus pelagicus*, a productivity proxy related to moderate fronts off Western Iberia. *Mar. Micropaleontol.*, 2000, **39**(1–4), 131–155.
73. Amore, F. O., Flores, J. A., Voelker, A. H. L., Lebreiro, S. M., Palumbo, E. and Sierro, F. J., A Middle Pleistocene Northeast

Atlantic coccolithophore record: Paleoclimatology and paleoproductivity aspects. *Mar. Micropaleontol.*, 2012, **90**, 44–59.
74. Schwab, C., Kinkel, H., Weinelt, M. and Repschläger, J., Coccolithophore paleoproductivity and ecology response to deglacial and Holocene changes in the Azores Current System. *Paleoceanogr., Paleoclimatol.*, 2012, **27**(3), PA3210.
75. Hermoso, M., Coccolith-derived isotopic proxies in palaeoceanography: where geologists need biologists. *Cryptogamie Algol.*, 2014, **35**(4), 323–352.
76. Bains, S., Corfield, R. M. and Norris, R. D., Mechanisms of climate warming at the end of the Paleocene. *Science*, 1999, **285**(5428), 724–727.
77. Dudley, W. C. and Goodney, D. E., Oxygen isotope content of coccoliths grown in culture. *Deep Sea Res.*, 1979, **26**(5), 495–503.
78. Ziveri, P., Stoll, H., Probert, I., Klaas, C., Geisen, M., Ganssen, G. and Young, J., Stable isotope vital effects incoccolith calcite. *Earth Planet. Sci. Lett.*, 2003, **210**(1–2), 137–149.
79. Hermoso, M., Candelier, Y., Browning, T. J. and Minoletti, F., Environmental control of the isotopic composition of subfossil coccolith calcite: are laboratory culture data transferable to the natural environment? *Geol. Res. J.*, 2015, **7**, 35–42.
80. Stoll, H. M. and Schrag, D. P., Coccolith Sr/Ca as a new indicator of coccolithophorid calcification and growth rate. *Geochem. Geophys.*, 2000, **1**(5), 1–24.
81. Mejía, L. M. *et al.*, Effects of mid latitude westerlies on the paleoproductivity at the Agulhas Bank slope during the penultimate glacial cycle: evidence from coccolith Sr/Ca ratios. *Paleoceanogr., Paleoclimatol.*, 2014, **29**(7), 697–714.
82. Stoll, H. M., Ruiz Encinar, J., Ignacio Garcia Alonso, J., Rosenthal, Y., Probert, I. and Klaas, C., A first look at paleo temperature prospects from Mg in coccolith carbonate: cleaning techniques and culture measurements. *Paleoceanogr., Paleoclimatol.*, 2001, **2**(5).
83. Conte, M. H., Thompson, A., Lesley, D. and Harris, R. P., Genetic and physiological influences on the alkenone/alkenoate versus growth temperature relationship in *Emiliania huxleyi* and *Gephyrocapsa oceanica*. *Geochim. Cosmochim. Acta*, 1998, **62**(1), 51–68.
84. Kongtae, R., Kitagawa, H. and Shiraiwa, Y., Mg isotopes and Mg/Ca values of coccoliths from cultured specimens of the species *Emiliania huxleyi* and *Gephyrocapsa oceanica*. *Mar. Micropaleontol.*, 2010, **77**(3–4), 119–124.
85. Riebesell, U., Zondervan, I., Rost, B., Tortell, P. D., Zeebe, R. E. and Morel, F. M., Reduced calcification of marine plankton in response to increased atmospheric CO_2. *Nature*, 2000, **407**(6802), 364.
86. Stoll, H., Langer, G., Shimizu, N. and Kanamaru, K., B/Ca in coccoliths and relationship to calcification vesicle pH and dissolved inorganic carbon concentrations. *Geochim. Cosmochim. Acta*, 2012, **80**, 143–157.
87. Orr, J. C. *et al.*, Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, 2005, **437**(7059), 681.
88. Beaufort, L. *et al.*, Sensitivity of coccolithophores to carbonate chemistry and ocean acidification. *Nature*, 2011, **476**(7358), 80.
89. Sigman, D. M. and Boyle, E. A., Glacial/interglacial variations in atmospheric carbon dioxide. *Nature*, 2000, **407**(6806), 859.
90. Balch, W. M. *et al.*, Factors regulating the Great Calcite Belt in the Southern Ocean and its biogeochemical significance. *Global Biogeochem. Cycles*, 2016, **30**(8), 1124–1144.
91. Flores, J. A. and Marino, M., Pleistocene calcareous nannofossil stratigraphy for ODP Leg 177 (Atlantic sector of the Southern Ocean). *Mar. Micropaleontol.*, 2002, **45**(3–4), 191–224.
92. Geitzenauer, K. R., Roche, M. B. and McIntyre, A., Modern Pacific coccolith assemblages: Derivation and application to Late Pleistocene analysis. *Geol. Sot. Am. Mem.*, 1976, **45**, 423–448.
93. Findlay, C. S. and Giraudeau, J., Movement of oceanic fronts south of Australia during the last 10 ka: interpretation of calcareous nannoplankton in surface sediments from the Southern Ocean. *Mar. Micropaleontol.*, 2002, **46**(3–4), 431–444.
94. Villa, G., Palandri, S. and Wise, S. W., Quaternary calcareous nannofossils from Periantarctic basins: paleoecological and paleoclimatic implications. *Mar. Micropaleontol.*, 2005, **56**(3–4), 103–121.
95. Fincham, M. J. and Winter, A., Paleoceanographic interpretations of coccoliths and oxygen-isotopes from the sediment surface of the southwest Indian Ocean. *Mar. Micropaleontol.*, 1989, **13**(4), 325–351.
96. Backman, J., Fornaciari, E. and Rio, D., Biochronology and paleoceanography of late Pleistocene and Holocene calcareous nannofossil abundances across the Arctic Basin. *Mar. Micropaleontol.*, 2009, **72**(1–2), 86–98.
97. Baumann, K.-H. and Matthiessen, J., Variations in surface water mass conditions in the Norwegian Sea: evidence from Holocene coccolith and dinoflagellate cyst assemblages. *Mar. Micropaleontol.*, 1992, **20**(2), 129–146.
98. Giraudeau, J., Grelaud, M., Solignac, S., Andrews, J. T., Moros, M. and Jansen, E., Millennial-scale variability in Atlantic water advection to the Nordic Seas derived from Holocene coccolith concentration records. *Quat. Sci. Rev.*, 2010, **29**(9–10), 1276–1287.
99. Geisen, M. *et al.*, Species level variation in coccolithophores. In *Coccolithophores* (eds Thierstein, H. R. and Young, J. R.), Springer, 2004, pp. 327–366.

ACKNOWLEDGEMENTS. We thank the Secretary of the Ministry of Earth Sciences (MoES), Government of India and the Director of the ESSO-National Centre for Polar and Ocean Research for supporting the Polar Micropalaeontology and Past Climate project. S. M. Patil thanks DST INSPIRE for providing funding (DST/INSPIRE/04/2015/001969). This is NCPOR Contribution No. J-24/2020-21.

doi: 10.18520/cs/v119/i2/307-315