Use of coccolith based proxies for palaeoceanographic reconstructions

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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. 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. 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 (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 and engage in the abiding increase of atmospheric oxygen.

In the geological record, coccolithophores appeared in the Late Triassic about ~230 Myr ago. 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.

Biology of coccolithophores

Coccolithophores are grouped under the division Haptophyta and class Prymnesiophyceae. 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. 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. 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. 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, suggesting the evolution of coccolithophores occurred from heterotrophs/mixotrophs to autotrophs.

Other cell structures and organelles such as cell membrane and Golgi bodies form coccoliths. 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
phase’ (Figure 2)\(^1\). The haploid phase bearing holococcoliths are made up of only one type of numerous crystalites 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\(^23\).

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\textsuperscript{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 \textit{E. huxleyi}), and third is the Polar Frontal Zone which is comprised of monospecific \textit{E. huxleyi} assemblage\textsuperscript{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\textsuperscript{32}.

\textbf{Preservation of coccoliths in the sediment and their palaeoceanographic implications}

Coccolithophores, during their life cycle, respond to the \textit{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\textsuperscript{33}, where they become a part of the sediment preserving imprints as fossil archives of the environment they lived in\textsuperscript{34}. Today, these tiny fossil remains are responsible for calcareous ooze covering 35% of the world ocean floor\textsuperscript{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 paleocirculation\textsuperscript{35–38}. Coccolith assemblages in the sediments were used to determine the shifts in the latitudinal positions of the ocean fronts\textsuperscript{39–41}. Alkenones\textsuperscript{42–44} and \textit{Gephyrocapsa} spp. morphological changes\textsuperscript{48} were used to reconstruct palaeotemperature whereas, morphological variability of \textit{E. huxleyi} was used to reconstruct palaeosalinity\textsuperscript{45}.

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

\textbf{Applications of coccolithophores}

\textbf{Palaeotemperature estimates}

Various methods have been established to reconstruct palaeotemperature by using coccoliths which include statistical analysis of the nanofossil assemblages, morphometric measurement of \textit{Gephyrocapsa} spp., relative abundances of the different \textit{Gephyrocapsa} spp., Mg/Ca of bulk coccoliths, and by studies on unsaturated alkenones\textsuperscript{47}.

Coccolithophore species show clear latitudinal distribution with respect to the specific tolerance and affinity towards different temperature gradients\textsuperscript{49}. Bollmann\textsuperscript{45} displayed significant correlation between morphologies of \textit{Gephyrocapsa} spp. and environmental gradients which show close relationship of \textit{Gephyrocapsa} spp. size with temperature. Based on the relative abundance of the different morphotypes within the genus \textit{Gephyrocapsa} in the Holocene sediments of Atlantic, Pacific and Indian Ocean, Bollmann \textit{et al.}\textsuperscript{38} proposed the global sea surface temperature (SST) calibration. They showed the potential use of \textit{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 foraminiferal transfer function. Saavedra-Pellitero \textit{et al.}\textsuperscript{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 \textit{et al.}\textsuperscript{37}).

Alkenones are the long chain di-unsaturated, triunsaturated ketones produced by coccolithophores of the genus \textit{Gephyrocapsa} and \textit{E. huxleyi}\textsuperscript{49}. Brassell \textit{et al.}\textsuperscript{43} showed the correlation between unsaturated alkenones and glacial–interglacial cycles in the late Quaternary, which was recorded using planktic foraminiferal δ\textsuperscript{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 \textit{et al.}\textsuperscript{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\textsuperscript{51}. The relationship $U37K = 0.033T + 0.044$, $R^2 = 0.958$ is identical within the error limits to the temperature estimates of radiolaria and dinoflagellates (see figure 6 in Saavedra-Pellitero \textit{et al.}\textsuperscript{37}).

$\delta$
for various time scale of the global ocean, with the brief
time period of inter-annual changes \(^\text{53}\) and long time scale
ranging from the Pliocene \(^\text{51}\) to the Pleistocene \(^\text{55}\). Rostek \(\text{et al.}\) \(^\text{56}\) 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 sig-
nificant error in palaeosalinity estimates \(^\text{57}\). 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 tempera-
ture and productivity \(^\text{58}\). Yet, it is evident from studies that
different organisms are tolerant to variable range of sali-
ity which is reflected in the abundance changes \(^\text{59}\). In the
culture studies, morphological variations in \(E.\ huxleyi\)
with respect to changing salinity have been demonstrat-
ed \(^\text{60}\). Bollmann and Herrle \(^\text{61}\) 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 signifi-
cantly within the salinity range of 33–38 psu with a stan-
ard 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 \(^\text{62}\).
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 experi-
ments were carried out to assess applicability of \(E.\ hux-
leyi\) coccolith morphology as a palaeosalinity proxy \(^\text{60}\).
The relationship between the salinity and the morphologic-
ical response is vaguely understood but probably is re-
lated to the regulation of turgor pressure which affects the
size of the cell \(^\text{63}\) 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 \(^\text{62}\). Ausín \(\text{et al.}\) \(^\text{54}\) used multivariate statistic-
al 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 ap-
plied these models to reconstruct SSS in the Alboran Sea
at high resolution for the last 25 kyr, emphasizing the re-
liability 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 iso-
topes 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 \(^\text{65}\). The monospecific cul-
ture studies have revealed positive linear correlation be-
tween salinity and hydrological isotopic composition of
the long chain alkenones, synthesized by \(E.\ huxleyi\) and
\(G.\ oceanica\) \(^\text{66}\). Meer \(\text{et al.}\) \(^\text{67}\) reconstructed past variation
in the SSS using alkenones and combined with the rela-
tive 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 sali-
nity 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 multi-
proxy approach \(^\text{68}\).

**Palaeoproductivity**

Kinkel \(\text{et al.}\) \(^\text{36}\) 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 \(^\text{69,70}\). Thus, the transfer function based on
deep photic zone taxa (e.g. \(F.\ profunda\), \(Gladiolithus flab-
bellatus\) and other coccoliths in the sediment provide
information about ocean stratification and palaeoproduct-
vity \(^\text{69,70}\). However, in high latitudes, the absence of
\(F.\ profunda\) excludes the use of some of these methods
where, siliceous organisms are commonly used to recon-
struct palaeoproductivity \(^\text{71}\). 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 \(\text{et al.}\) \(^\text{71}\)
reported that changes in the abundance of coccolitho-
phore reflect variation in the palaeoproductivity. In the
modern oceans, species like \(Gephyrocapsa\) spp., \(C.\ pelagicus\)
subsp. \(braarudi\) and \(G.\ oceanica\) tend to be abun-
dant in the high productive areas with high nutrient
availability \(^\text{25,72}\), which are usually considered as reliable
proxies for productivity estimates in the high nutrient
regions \(^\text{73}\). Amore \(\text{et al.}\) \(^\text{73}\) indicated small \(Gephyrocapsa\)

spp., and \(C.\ pelagicus\) subsp. \(braarudi\) as vital proxies to
indicate the prevailing influence of Portugal current and
conditions of high nutrient and increased productivity.
Whereas, the dominance of \(G.\ caribbeanica\), \(Syracos-
phaera\) spp., \(Rhodosphaera\) spp. and \(Umbilicosphaera-
sibogae\) denote periods of Iberian poleward current.
Schwab \(\text{et al.}\) \(^\text{74}\) 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. profunda84.

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 (CaCO₃) sediment deposits46. 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 – ¹⁶O/¹⁸O, ¹²C/¹³C75,76. 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 conditions77 and, (ii) studies in the sediments to explicate the methods to segregate fractions of single species46. 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 Schrag80 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 dissolution80. 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 calcite82. 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 proxy83 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/Ca84,85. Through culture based experiments on G. oceanica and E. huxleyi, Kongtai 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 processes85. 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 acidification87 or can over calcify as observed in the past88.

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 CO₂ during the glacial periods and possibly out gassing during the interglacial periods89. In the future world scenario, the SO is projected to absorb excess anthropogenic CO₂ 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 Oceans90. Due to their huge abundance and good preservation in the marine sediments with the signals of the surface water conditions14, the late Quaternary coccolithophores records are extensively used to decipher palaeoenvironmental conditions which include positions of oceanic fronts and current systems15,39,40. In the past decades coccoliths have been used as the indicators of
palaeoceanographic conditions of the SO. Boeckel et al.\textsuperscript{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.\textsuperscript{91} reconstructed late Quaternary surface waters of Atlantic Ocean conditions using coccolithophore assemblages. Getzner\text{a}u\text{e}r\textsuperscript{92} exhibited \textit{U. leptopora} and \textit{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\textsuperscript{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\textsuperscript{93}. Villa et al.\textsuperscript{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\textsuperscript{10}. Patil et al.\textsuperscript{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 \textit{E. huxleyi} in the Indian sector of the Southern Ocean\textsuperscript{30}. Fincham and Winter\textsuperscript{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.\textsuperscript{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.

\textbf{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\textsuperscript{96}. Baumann and Matthiessen\textsuperscript{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.\textsuperscript{98} 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. Girardeau et al.\textsuperscript{98} recorded changes in the long term trend in the coccolith abundance in the cores retrieved from Norway and Northern Iceland and indicated Millenial-scale modulation in Atlantic water advection to the Nordic Seas.

\textbf{Interpretation of geological history using coccoliths}

In the geological record since the coccolithophores inception (about \textasciitilde230 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.

\textbf{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\textsuperscript{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.


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