

Author Version of : *Phycologia*, vol.61(3); 2022; 284-298

Distribution of extant coccolithophores from the northwest continental shelf of India during the summer monsoon

Mintu Chowdhury^{1,2}, Haimanti Biswas^{1,3}, Diksha Sharma^{1,4}, Saumya Silori^{1,3} And Amos Winter⁵

¹National Institute of Oceanography, Biological Oceanography Division, Dona Paula, Goa 403004

²School of Oceanographic Studies, Jadavpur University, 188 Raja S.C. Mallick Rd, Kolkata 700032

³Academy of Scientific and Innovative Research (AcSIR), Ghaziabad- 201002

⁴Bharathidasan University, Tiruchirappalli, TN, 620024

⁵Indiana State University, Department of Earth and Environmental Systems, Terre Haute, Indiana, USA 47809-1902

Corresponding author: Haimanti Biswas; Email: haimanti.biswas@nio.org

Abstract

Coccolithophores contribute substantially to marine primary production as well as to particulate inorganic carbon (PIC) flux to the deep sea; however, there is no literature available so far from the Indian continental shelf on this functional group. We present here the first study describing the spatial variability and species composition of living coccolithophore communities from the north-western continental shelf waters (northeastern Arabian Sea) of India (SW monsoon; August 2018). We found a total of 18 species from 11 genera with *Gephyrocapsa oceanica* as the dominant coccolithophore. *Florisphaera profunda*, *Calcidiscus leptoporus*, *Helicosphaera carteri* and *Umbilicosphaera sibogae* were also observed in significant quantities in most of the stations. Cell abundances ranged from $0.3\text{--}85.6 \times 10^3 \text{ l}^{-1}$ with the maximum occurrence at the northernmost station. Coccolithophore diversity was comparatively higher in the southernmost region, while high dominance was noticed in the north. Redundancy analysis (RDA) revealed that nutrient availability was an important factor to modulate the distribution and abundance of coccolithophores. *Gephyrocapsa oceanica* was recorded in each station and showed a positive association with $\text{NO}_2 + \text{NO}_3$ levels, whereas *F. profunda* and *U. sibogae* were confined mostly to deepwater. Our study shows that a substantial number of coccolithophores are present in the shelf water and could be important as primary producers as well as for the carbon export flux. Further research attention to broaden our knowledge of the role of this functional group is warranted.

Keywords

Arabian Sea; Coccolithophore diversity; *Florisphaera profunda*; *Gephyrocapsa oceanica*; SW Monsoon

Introduction

Coccolithophores (Prymnesiophyceae), ubiquitous calcifying unicellular nanophytoplankton (2–20 μm ; Taylor *et al.* 2017), are among the most abundant eukaryotic primary producers in contemporary oceans and have been playing an important role in the biogeochemical cycling of carbon since the Jurassic. They are usually found in diverse marine habitats (Winter *et al.* 1994; Thierstein & Young 2004; Godrijan *et al.* 2018), including upwelling waters (Mitchell-Innes & Winter 1987; Henderiks *et al.* 2012; Menschel *et al.* 2016). It has been estimated that almost 10% of global phytoplankton biomass is contributed by this group (Tyrrell & Young 2009), yet in many oceanic regions they contribute up to 70% of the vertical carbonate flux below 1000 m water depth owing to the precipitation of calcium carbonate liths within their short (1–2 d) life cycle (Balch 2018). Coccolithophores exhibit both haploid and diploid stages in their haplo-diplonic life cycle, with each stage having an environmental preference. This ability is thought to be advantageous for their ubiquitous distribution (Frada *et al.* 2019; de Vries *et al.* 2021).

The large-scale distribution pattern of different coccolithophorid species is controlled by environmental variables such as temperature, salinity (Winter *et al.* 2014), water column stability (Young 1994), and availability of micronutrients as well as trace nutrients (Balch *et al.* 2016; Perrin *et al.* 2016). Biological factors such as grazing (Harvey *et al.* 2015), competition with other phytoplankton (Boyd *et al.* 2010), viral infection (Brussaard 2004) and ongoing climate change (Meyer & Riebesell 2015) will play a crucial role in the overall distribution and physiology of coccolithophores. For example, studies have reported occurrences of coccolithophores in polar waters due to changes in physicochemical factors (Winter *et al.* 2014; Malinverno *et al.* 2015; Patil *et al.* 2020). Coccolithophorid abundance in the North Atlantic has increased by 2%–20% depending on the regional variability in the last 50 years, a time when atmospheric CO_2 concentrations have increased by 22% (Rivero-Calle *et al.* 2015; Krumhardt *et al.* 2016). The fossil remains of coccolithophores in the sediment are popularly used as proxies for the past environmental variability and paleoproductivity (Baumann *et al.* 2005). Moreover, lipids (alkenone) produced by coccolithophores, stored in marine sediments, have been extensively used as a valuable indicator of palaeoceanographic changes (Sicre *et al.* 2016).

The usual paradigm for the global distribution of coccolithophores is that they are outcompeted by diatoms in highly productive waters (Smayda 1989). During the southwest (SW) monsoon (June–September), in some parts of the Arabian sea (Oman and Somali coasts as well as the southwest coast of India), upwelling-induced high productivity occurs. In contrast, the onset of winter monsoon (northeast monsoon) (November–January) and successive cooling of the surface water generate

convective mixing, which leads to high productivity dominated by large diatoms in the northern Arabian Sea (Banse 1987; Madhupratap *et al.* 1996; Andruleit *et al.* 2003; Vijayan *et al.* 2021). During the SW monsoon, the shelf region of the southwestern Arabian Sea remains nutrient-enriched with high microphytoplankton biomass; conversely, low nutrient concentrations are seen in the northeastern Arabian sea when mostly nanophytoplankton and picophytoplankton prevail (Silori *et al.* 2021). This change in the trophic status could promote the growth of coccolithophores in the northern Arabian Sea (Andruleit *et al.* 2003, 2004). A prominent succession of diatom bloom followed by coccolithophores was noticed in response to nutrient pulses in an experimental continuous culture system (Cermeño *et al.* 2011). There are substantial reports available from the western Indian shelf area on phytoplankton community distribution by HPLC pigment analysis showing the dominance of picoplanktonic cyanobacteria along with Prymnesiophyceae (Roy *et al.* 2015; Vijayan *et al.* 2021). However, the distribution of extant coccolithophores, which comprise a major part of Prymnesiophyceae from the northwestern shelf water of India, has not been studied to date (Arundhathy *et al.* 2021).

There are only very few studies on living coccolithophore abundance from the north Indian ocean including the Arabian Sea (Liu *et al.* 2018). The available literature on coccolithophore assemblage is mostly from the surface sediments (Andruleit & Rogalla 2002; Rogalla & Andruleit 2005) or sediment trap samples (Andruleit *et al.* 2000; Broerse *et al.* 2000; Mergulhao *et al.* 2006). The living flora from water samples was studied mostly during 1994–1997 by the Joint Global Ocean flux Study (JGOFS) programme, mainly from the central and western Arabian Sea (Kleijne 1993; Guptha *et al.* 1995; Zeltner 2000; Balch *et al.* 2000; Andruleit *et al.* 2003; Schiebel *et al.* 2004; Andruleit *et al.* 2005). These previous studies showed that coccolithophore abundance and flux were directly linked to monsoon variability and that *Gephyrocapsa oceanica* Kamptner was a dominating species. In this study, for the first time, we present the distribution of extant coccolithophore from the northwestern shelf waters of India.

Material And Methods

Water sampling

Coccolithophore samples were collected 09–12 August 2018 onboard the RV Sindhu Sadhna (SSD 55) in the northwestern Indian shelf waters during the Indian SW monsoon (Fig. 1). The sampling covered five stations along the 200 m isobath (continental shelf break) from 17°N to 21°N at 1° intervals. Six depths were sampled at each station (surface, 05, 10, 20, 40 and 60 m) using a Seabird CTD (SeaCAT 19plus v2) fitted to a rosette system with twenty-four 10-litre Niskin bottles. At the same time, values of depth, salinity, temperature, dissolved oxygen (DO) and Chlorophyll *a* (Chl*a*)

were derived from pre-calibrated sensors fitted to the CTD. The Mixed Layer Depth (MLD) was calculated using the density difference (0.2 kg m^{-3}) from the surface (Levitus 1982).

Dissolved inorganic nutrient analysis

Nitrate + nitrite and dissolved silicate (DSi) were analysed manually onboard immediately after collection following standard spectrophotometric methods (UV-1800 UV-Vis Spectrophotometer, Shimadzu, Kyoto, Japan) by Grasshoff *et al.* (1992) against the standard reference solutions (KNO_3 and Na_2SiF_6 ; Sigma, St. Louis, Missouri, USA). Ammonium was not measured onboard due to technical difficulties. Dissolved inorganic phosphate (DIP) was analysed by following the UNESCO (1994) method using K_2HPO_4 as the reference solution (Merck, Darmstadt, Germany). All procedures were calibrated with available standard reference materials (Merck).

Coccolithophore analyses

For quantitative and qualitative analyses of coccolithophores, 3.0 litres of water were collected and filtered immediately through $0.8 \mu\text{m}$ (47 mm, PALL Supor® Membrane, Pall Corporation, Washington, USA) filters using a vacuum pump (Tarson, Kolkata, India) with a pressure of below 200 Mb. After filtration, alkaline distilled water was used to wash the remaining salts and the filter was then removed carefully from the filtration cups and oven-dried overnight at $40\text{--}50^\circ\text{C}$. The dried filters were kept in plastic Petri dishes in a dry container until further analysis. Coccolithophore samples were inspected with a JEOL-JSM IT300 scanning electron microscope (JEOL Ltd., Tokyo, Japan) in the central analytical facility at the CSIR-NIO, Goa. For SEM analysis, a small part (area 19.64 mm^2) of the dried filter was cut carefully, mounted on an SEM stub and sputtered with gold. For the standing crop, we have taken a minimum of 100 random fields (depending on cell abundance) at a fixed magnification ($1,000\times$). For the community composition, an average of 250 coccospheres were identified at varying magnification ($1,000\times$ to $10,000\times$) following the identification key provided by Young *et al.* (2003), as well as the available web taxonomy guide for coccolithophore identification, Nannotax3 (Young *et al.* 2017). Cell densities per litre of water are calculated as follows (Andrulleit *et al.* 2003):

$$\text{Coccolithophore abundance (cells l}^{-1}\text{)} = \frac{F \times C}{A \times V}$$

where F = effective filtration area (mm^2), C = number of coccospheres, V = filtered volume (litres) and A = investigated filter area (mm^2).

Univariate and multivariate analysis

A univariate technique was employed for coccolithophore assemblage data for deriving Shannon-Wiener diversity index H' , and Dominance index D' , using the software PAST v4.03 (Hammer *et al.* 2001). Coccolithophore species that contributed individually more than 1% to the total population are considered for statistical analysis. A cluster analysis (CA) was employed using PAST v4.03 (Hammer *et al.* 2001) using Bray-Curtis similarity to identify the coccolithophore species with similar environmental influences. A multivariate ordination technique was used to explore the interrelationships between major coccolithophore species and a suite of environmental variables using CANOCO version 4.5 (Braak & Smilauer 2002). The species data were square-root transformed before analysis. The data were tested with Detrended Correspondence Analysis (DCA) to choose a suitable ordination technique which revealed that axis gradient length <2 . Linear multivariate model, RDA, was used to delineate the relationship between environmental variables and biological variables (Leps & Smilauer 2003). Monte Carlo simulation was used in the RDA for testing the levels of significance of the environmental variables with coccolithophore abundance.

Results

Physical environment

During this study, the water column was weakly stratified, mostly due to the SW monsoon wind-driven surface circulation. MLD increased southward manifested by the noticeable deepening (from 40 m to 50 m) of the thermocline, halocline and oxycline within 18–20°N. However, the southernmost station showed comparatively shallower MLD (40 m) (Fig. 2). The northern, as well as southernmost stations, were distinct in terms of the vertical profile of temperature, salinity and DO (Fig. 3). Relatively warmer water prevailed down to 30 m depth in the northernmost station and down to 55 m in the southern counterpart. Slightly high salinity water (36.6 ± 0.15) was present in the northern stations whereas relatively low salinity water (36.4 ± 0.11) occurred in the southernmost station (Fig. 3). Within the MLDs, the oxygen concentration was 4.0 ml l^{-1} , and the level decreased to $<1.0 \text{ ml l}^{-1}$ below the MLD. Low oxygen concentration occurred below 60 m depth in the southernmost station and gradually increased towards the north. Chl a concentration in the study area ranged from 0.1–1.2 $\mu\text{g l}^{-1}$ ($0.56 \pm 0.25 \mu\text{g l}^{-1}$) (Fig. 3). The highest Chl a concentration was recorded at 18°N and 20°N (down to 50 m) whereas the lowest concentration was observed at 17°N throughout the water column.

Nutrient stoichiometry

The mixed layer (ML) was associated with low nutrient concentrations (Fig. 4). The nutricline was shallower at about 30 m at the northernmost station and was found consistently at greater depths (50

m) in the other stations. Nitrate + nitrite concentrations ranged from undetectable to $3.01 \mu\text{mol l}^{-1}$ ($0.47 \pm 0.59 \mu\text{mol l}^{-1}$) within the ML and 12.5 to $15.4 \mu\text{mol l}^{-1}$ ($13.9 \pm 1.12 \mu\text{mol l}^{-1}$) below the ML (Fig. 4). The lowest concentration occurred from 17°N down to 20 m. DIP and DSi concentrations ranged from $0.35\text{--}1.52 \mu\text{mol l}^{-1}$ ($0.80 \pm 0.26 \mu\text{mol l}^{-1}$) and $0.06\text{--}1.01 \mu\text{mol l}^{-1}$ ($0.46 \pm 0.2 \mu\text{mol l}^{-1}$) within the ML, respectively. The concentration of DIP was $0.70 \mu\text{mol l}^{-1}$ down to 40 m throughout the study area except at 19°N , where a higher concentration ($1.2 \mu\text{mol l}^{-1}$) was noticed.

Coccolithophore community structure and species distribution

The present study documented a total of 11 genera and 18 species of coccolithophores. The list and individual contribution of all the species is given in Table 1. Coccolithophore cell abundances from the major contributing groups ranged from $0.3\text{--}85.6 \times 10^3 \text{ cells l}^{-1}$ with the highest abundance recorded at the northernmost station (21°N , Fig. 5). The cell abundance of some coccolithophores was less than 1% of the total community and these were considered as minor contributors. Their abundance varied between $0\text{--}2.5 \times 10^3 \text{ cells l}^{-1}$ ($0.1 \pm 0.3 \times 10^3 \text{ cells l}^{-1}$).

Major contributors

Gephyrocapsa oceanica (67%) was the predominant species followed by *Florisphaera profunda* His. Okada & Honjo (11%), *Umbilicosphaera sibogae* (Weber Bosse) Gaarder (3.4%), *Helicosphaera carteri* (G.C. Wallich) Kamptner (3.2%), *Calcidiscus leptoporus* (G. Murray & V.H. Blackman) Loeblich & Tappan (2.6%), *Calciopappus rigidus* Heimdal (2.0%) and *Syracosphaera mediterranea* Lohmann (1.0%) (Fig. 6). *Gephyrocapsa oceanica* contributed to 46%–89% of the total population and the maximum contribution of this species was recorded at 21°N , whereas the minimum contribution was observed at 19°N where the contribution from *F. profunda* (40%) was nearly the same as *G. oceanica*. The abundance of *G. oceanica* ranged from $2.2\text{--}76.9 \times 10^3 \text{ cells l}^{-1}$, with a mean value of $19.8 \pm 21 \times 10^3 \text{ cells l}^{-1}$, and the species was present in all stations and depths (Fig. 5). Other major species such as *H. carteri*, *U. sibogae* and *C. rigidus* were observed nearly in every station; however, their contribution did not exceed 10% of the total community (Fig. 6). The most diverse coccolithophore community was observed at 17°N . Here *Michaelsarsia adriatica* (J. Schiller) Manton, G. Bremer & Oates contributed 10% of the population while 30% of the community was composed of minor species. Interestingly, *M. adriatica* was only recorded from this station. *Helicosphaera carteri*, *C. leptoporus*, *C. rigidus* and *S. mediterranea* were recorded mostly from the mixed layers, and their abundance was $0.0\text{--}5.6 \times 10^3 \text{ cells l}^{-1}$ ($0.8 \pm 1.5 \times 10^3 \text{ cells l}^{-1}$), $0.0\text{--}4.5 \times 10^3 \text{ cells l}^{-1}$ ($0.5 \pm 1.2 \times 10^3 \text{ cells l}^{-1}$), $0.0\text{--}1.8 \times 10^3 \text{ cells l}^{-1}$ ($0.3 \pm 0.5 \times 10^3 \text{ cells l}^{-1}$) and $0.0\text{--}3.0 \times 10^3 \text{ cells l}^{-1}$ ($0.3 \pm 0.6 \times 10^3 \text{ cells l}^{-1}$), respectively. Below the mixed layers, only minor variations in the community structure of

the coccolithophore were observed. *Florisphaera profunda*, usually a deep-dwelling species, dominated in this zone. Its abundance varied from 0.0 to 6.45×10^3 cells l^{-1} ($1.0 \pm 1.8 \times 10^3$ cells l^{-1}). The highest abundance of this species was recorded at 19°N from 60 m (31.9×10^3 cells l^{-1}). *Umblicosphaera sibogae* was also found mostly in the subsurface region and its abundance ranged from 0.0 to 2.6×10^3 cells l^{-1} ($0.6 \pm 0.6 \times 10^3$ cells l^{-1}).

Minor contributors

Three species of *Calciosolenia* in order of abundance, *Calciosolenia brasiliensis* (Lohmann) Jer.R. Young, *Calciosolenia murrayi* Gran and *C. corsellii* Malinverno were documented in this study. Similarly, *Helicosphaera hyalina* Gaarder, *H. princei* da Gama & O. Varol were also recorded. *Syracosphaera lamina* Lecal-Schlauder, was present mostly in the southern region (17–19°N), whereas *S. mediterranea* was found in the north (20–21°N). Five species of the minor group were found only at a particular location. For instance, *Michaelsarsia adriatica* and *Calciosolenia murrayi* were found only at the southernmost station. The globally dominating coccolithophore *Emiliania huxleyi* (Lohmann) W.W. Hay & H. Mohler was observed only at 20°N.

Statistical analysis

The Shannon-Wiener diversity index (Fig. 7) showed high spatial variability and ranged between 0.15 and 2.1 (0.84 ± 0.42). A similar distribution was manifested in the dominance index (Fig. 7), with values varying from 0.16 to 0.93 (0.58 ± 0.19). Maximum diversity (minimum dominance index) was observed at 17°N, consisting of 14 species, whereas the lowest diversity (high dominance index) was recorded at 21°N due to the high abundance of *G. oceanica*. To evaluate the relationship between major coccolithophore taxa and environmental variables, a redundancy analysis was carried out (Fig. 8). The first two axes contributed 86.8% of the dataset variability. Axis 1 of RDA displayed 72.1% of the total variance and was influenced by temperature, DO and $NO_2 + NO_3$. Axis 2 explained only 14.7% variation and was mainly characterized by salinity, DIP and DSi. Total coccolithophore abundance, *G. oceanica* and *H. carteri* were positively associated with $NO_2 + NO_3$, whereas a negative association with temperature, DO, DSi and DIP was noticed. *Florisphaera profunda* grouped with salinity and DIP concentration. Opposite to that, *C. rigidus* was associated with DSi.

Cluster analysis of the major species revealed that there were three groups (Fig. 9). Group 1 consisted solely of *G. oceanica*, which was the most abundant species that showed the unique status as it was distinct from the rest. Group 2 consisted of only two species, *H. carteri* and *F. profunda*, which showed 60% similarity in the Bray-Curtis similarity index (Fig. 9). Group 3 was comprised of

C. leptoporus, *U. sibogae*, *S. mediterranea* and *C. rigidus* due to similarity in their abundance, although the distributions of these species were distinct.

Discussion

The occurrence of high saline, warm water with low nutrient levels during the SW monsoon in the Indian northwestern shelf would be expected to favour mostly smaller phytoplankton (Silori *et al.* 2021). Our study confirmed that a considerable number of coccolithophores can be found under such hydrographic conditions. Coccolithophores are well known to dominate in warm oligotrophic waters like the Mediterranean Sea (Oviedo *et al.* 2015) as well as in nutrient-enriched upwelling waters (Menschel *et al.* 2016), although coccolithophore floristic composition varies with changing nutrient stoichiometry (Hagino *et al.* 2000). The non-diatom smaller phytoplankton come to prominence when the DSi levels decrease (Sieracki *et al.* 1993). Additionally, low nitrate + nitrite levels can be advantageous for smaller cells owing to their high surface area to volume ratio compared to large diatoms (Marañón 2015). This was observed in the present study where low DSi, as well as nitrate + nitrite levels, were probably advantageous for the high abundance of the nanoplanktonic coccolithophores. Andruleit *et al.* (2003) noticed that in the northeastern Arabian Sea (off Pakistan) during the late SW monsoon (September) coccolithophore distribution was more dependent on MLD and nutrient availability than on salinity and temperature. The authors concluded that the relative standing crop of coccolithophores was suppressed by the higher abundance of diatoms. During the winter monsoon-induced convective mixing, this area is usually dominated by large diatoms due to nutrient enrichment (Madhupratap *et al.* 1996). A recent study (Vijayan *et al.* 2021), revealed a high concentration of 19'-hexanoyloxyfucoxanthin (marker pigment of Prymnesiophyceae) indicating the probable presence of coccolithophores during the NE monsoon in this area. Andruleit *et al.* (2000) also observed high fluxes of coccolithophores from the eastern and northern Arabian Sea during the upwelling as well as winter convection mixing, suggesting a preference for high nutrient concentrations. In the present study, the highest abundance of coccolithophores was noticed from the northernmost station where nutrient concentrations were relatively higher than the rest.

The vertical distribution of various coccolithophores exhibited definite patterns with variable depths (Winter *et al.* 1994; Hagino *et al.* 2000; Takahashi & Okada 2000; Andruleit *et al.* 2003). Nutrient availability, temperature, the depth of the mixed layers and light intensity are the key factors in shaping the vertical distribution of coccolithophorid species in the marine environment (Oviedo *et al.* 2015 and references therein). However, within the lower photic zone, the available light for performing optimum photosynthesis can be limiting and species with low light adaptability will dominate. Certain species (*F. profunda*, *U. sibogae*) may be more adapted to minimum light intensities

than other species and may dominate in the shade zone. These species may also be mixotrophic as an ecological strategy for survival in the low light condition (Poulton *et al.* 2017). Furthermore, Godrijan *et al.* (2020) reported that coccolithophores uptake a variety of dissolved organic compounds (osmotrophy) present in the seawater, which may be a key survival strategy for those living in the lower euphotic zone. Kawachi & Inouye (1995) suggested that the haptonema functions as a food-gathering organelle or particle collector (Aubry 2009). Avrahami & Frada (2020) noticed that different species of coccolithophores ingested bacteria as prey under nutrient-replete and phosphorus-limited conditions suggesting their ability to adapt with mixotrophy and ingestion of prey. Although observational or experimental evidence of coccolithophorid mixotrophy is limited, recent studies supported this phenomenon (Poulton *et al.* 2017 and reference therein). Besides their wide adaptability to variable nutrient and light levels and trophic preferences, and their ability to divide during both haploid and diploid phases (haplo-diplontic life cycle), are advantageous for their niche expansion (de Vries *et al.* 2021).

In this study, *G. oceanica* was the most abundant species (group 1, based on the similarity index) and their high nutrient preference was evident from the positive correlation with nitrate + nitrite levels. This species usually dominates in high-nutrient environments, such as upwelling areas and continental shelves (Mitchell-Innes & Winter 1987; Houghton & Gupta 1991). *Gephyrocapsa oceanica* has been reported as a dominating species not only from the Arabian Sea but also from the entire North Indian Ocean (Andruleit & Rogalla 2002; Andruleit *et al.* 2004; Mergulhao *et al.* 2006; Liu *et al.* 2018). Mergulhao *et al.* (2006) reported the association of *G. oceanica* with nutrient availability in the Arabian Sea. Silva *et al.* (2008) noticed in Lisbon Bay that *G. oceanica* was a better-adapted species to nutrient-rich, highly productive coastal waters with high competitive efficiency. Guerreiro *et al.* (2013) observed in waters off Portugal that *G. oceanica* was indicative of high productivity associated with nutrient enrichment.

In addition to nutrients, temperature and light availability may play important roles in controlling the distribution of *G. oceanica* (Heinle 2013). The most common coccolithophore species recorded from the upwelling front is generally *G. oceanica* in tropical waters, whereas *E. huxleyi*, the dominant worldwide coccolithophore, is found in temperate to arctic waters (Mitchell-Innes & Winter 1987; Kleijne 1993; Giraudeau & Bailey 1995). The optimum temperature of *E. huxleyi* was shown to be around 20°C (Heinle 2013), whereas for *G. oceanica* this is above 25°C. The annual average SST in the Arabian Sea (usually >25°C, summer average >28°C; Reynolds & Smith 1994; Shenoi *et al.* 2002) is perhaps one of the reasons for such wide occurrence of *G. oceanica* over *E. huxleyi* (Kleijne 1993; Young 1994), even though both genera belong to the same family (Noelaerhabdaceae; Bendif & Young

2014). *Gephyrocapsa oceanica* was mostly confined to upper euphotic layers in most of our stations, suggesting that it may have a higher light preference, as has been suggested by other studies (Stolz *et al.* 2015; Jin *et al.* 2016). However, in open ocean regions like the eastern Indian Ocean (Liu *et al.* 2021) and eastern North Atlantic (Narciso *et al.* 2021) these species were also recorded in the mid-depth flora linked to nutrient availability. In our work, the surface solar light intensity (photosynthetically active radiation, PAR) was recorded from 18°N and was $300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ at the 0–2 m water depth (Fig. S1) and it decreased to <1% at nearly 40 m depth. Likewise, in a laboratory experiment, it was noticed that the optimum light intensity for the growth of *G. oceanica* was $350 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Heinle 2013).

In contrast to *G. oceanica*, *F. profunda* was found in depths of 10–80 m in the northern Arabian Sea (Andruleit *et al.* 2003) suggesting its low light preference. Consistent with this finding, our results showed a similar distribution pattern where the high abundance of *F. profunda* was frequently noticed between 20–60 m water depths and was perhaps influenced by the position of the thermo-halocline where light availability is considerably reduced (Oviedo *et al.* 2015; Bonomo *et al.* 2021; Narciso *et al.* 2021). The RDA ordination plot showed that *F. profunda* prefers high salinity and high DIP concentrations. The decreasing abundance of *F. profunda* towards the south may be attributed to a greater thermocline depth. Using sediment trap samples of the northeastern Arabian Sea, Andruleit & Rogalla (2002) showed that the relative abundance of *F. profunda* declined with the deepening of the MLD.

Another important observation in our study was that *F. profunda* was recorded from deeper water and had the highest abundance at 19°N below 40 m, where the oxygen level was lower than 3 ml l^{-1} . Importantly, this region is located in the northern part of the permanent Oxygen Minimum Zone (OMZ) of the Arabian Sea (Naqvi 1991). As the OMZ is increasing due to recent warming (Rixen *et al.* 2020) this species may be able to cope with low oxygenated water (also low pH) and may perhaps become an important part of the coccolithophore flora of this region. How this species successfully calcifies under such unusual conditions is of high research interest. *Florisphaera profunda* occurs primarily within the lower photic zone (75–100 m) in the South China Sea where light intensity is 1% of the surface solar light (Jin *et al.* 2016). The positive correlation between DIP and *F. profunda* in the RDA plot can be attributed to higher DIP levels ($>2.5 \mu\text{M}$) at the base of the euphotic depth where the maximum number of cells of *F. profunda* was found. From the above discussion, *G. oceanica* and *F. profunda* clearly occupy two contrasting niches mostly related to light and nutrient availability in the study area and that explains the negative correlation of their abundances in the RDA plot. Another species, *Algirosphaera robusta* (Lohmann) R.E. Norris, was identified from samples in the

southernmost station only at 60 m depth, which is indicative of its preference for low light regions and high nutrient levels (nitrate + nitrite *c.* 15 μ M). This species was also documented by Liu *et al.* (2021) from the lower euphotic zone of the Eastern Indian Ocean, where relatively lower temperatures and high nutrient levels (*c.* 15 μ M nitrate) prevail.

Along with *F. profunda*, *H. carteri* was found in cluster 2. The presence of this species was also reported earlier from the Arabian Sea (Andruleit & Rogalla 2002). A maximum flux of *F. profunda* and *H. carteri* was noticed in sediment traps in the northern Arabian Sea and was associated with nutrient enrichment during the winter monsoon (Andruleit *et al.* 2000). Like *G. oceanica*, the presence of *H. carteri* was also related to nitrite + nitrate concentrations in the RDA plot. Menschel *et al.* (2016) reported the occurrences of *H. carteri* in moderate to high nutrient enrichment in the upwelling region near concepción, Chile.

The third cluster comprised four species: *C. rigidus*, *C. leptoporus*, *S. mediterranea* and *U. sibogae*. *Calcidiscus leptoporus* did not show any clear association with any of the environmental variables in the RDA plot. The most likely reason is that their highest occurrence (at 11°N) was associated with moderate nutrient levels. Jin *et al.* (2016) also noticed the presence of this species in the mid-depth of the South China Sea, characterized by moderate nutrient concentrations. Schiebel *et al.* (2004) reported the presence of *C. leptoporus* (small morphotype; Kleijne 1993; Knappertsbusch *et al.* 1997) in the oligotrophic water of the Arabian Sea. The presence of *C. leptoporus* subsp. *quadriperforatus* (*C. leptoporus* large morphotype) in the Arabian Sea was also noticed, and was not related to nutrient levels (Andruleit *et al.* 2005). Although both morphotypes were detected in the Arabian Sea, the larger one was much more prevalent (Renaud *et al.* 2002). In the present study, both the small and the large morphotype of *C. leptoporus* were documented (data not shown). Although this is usually an oceanic species, it has previously been found associated with moderate to high nutrient levels (Andruleit *et al.* 2000).

The next two species described in the third cluster, *S. mediterranea* and *U. sibogae* were grouped in the RDA ordination plot probably because of their similar niche preferences. In a study of surface sediments, members of the family Syracosphaeraceae were mostly found on the shelf and coastal areas of the Arabian Sea (Andruleit & Rogalla 2002) and were associated with nutrient availability (Giraudeau 1992). In the present study, abundance of *S. mediterranea* was mostly confined between 20–21°N and could be attributed to relatively higher nutrient concentration within the mixed layers. An abundance of *S. mediterranea* was also noticed in the oligo-mesotrophic waters of the coastal Mediterranean Sea (Šupraha *et al.* 2016) and in the central Portuguese margin (Guerreiro *et al.* 2014). Godrijan *et al.* (2018) found that the abundance of *S. mediterranea* was positively correlated with

nitrite and silicate levels. Conversely, *S. lamina* Lecal-Schlauder, a minor contributing species (<1%) in this study, was found in the mid-depth of the southern region associated with relatively low nutrients, suggesting a difference in the trophic level preferences of these species. Narciso *et al.* (2021) found *S. lamina* below 80 m in the eastern North Atlantic ocean, and its overall contribution was <2%. In general, *Syracosphaera* is a genus with a high number of species (Godrijan *et al.* 2018) occupying diverse ecological niches and therefore they have been categorized as a ‘miscellaneous group’ (Young 1994).

The three species of *Calciosolenia* we identified (minor species) were confined within the mixed layers, with a few exceptions. *Calciosolenia murrayi* was present only in the southernmost station and nearly at all depths. Andruleit *et al.* (2003) found *C. murrayi* to be one of the abundant species in the surface waters of the northern Arabian Sea where diatoms were dominant primary producers. Such co-occurrence suggested the higher competitive efficiency of *C. murrayi* (Andruleit *et al.* 2003). *Michaelsarsia adriatica* was present in the southernmost station within the mixed layers, and was also reported from the northern Arabian Sea (Andruleit *et al.* 2004). Balch *et al.* (2019) found this species along with *C. murrayi* at nearly 100 m depth close to the nitracline from the Atlantic meridional transect. However, the same species was also found towards the upper photic zone in the same study but in a different transect (Balch *et al.* 2019). Nutrient availability is perhaps responsible for such vertical distribution.

The greater abundance of *U. sibogae* with increasing water depth could be due to the higher nutrient availability towards the nutricline (Mergulhao *et al.* 2006; Stolz *et al.* 2015). This placolith-bearing coccolithophore showed preference for high nutrient concentrations (Young 1994) and belongs to the mid-depth zone coccolithophore flora (Stolz *et al.* 2015). In contrast, Broerse *et al.* (2000) noticed a slightly enhanced flux of *U. sibogae* in the Somali upwelling region (Western Arabian Sea) related to the NE monsoon. However, they did not find any increase in *U. sibogae* flux concerning SW monsoon-related nutrient enrichment. This suggested that nutrient enrichment may not always impact *U. sibogae* abundance. This species was also recorded from the nutrient-poor region (Okada & McIntyre 1979; Kleijne 1993). Similar to *U. sibogae*, *U. hulburtiana* Gaarder, which is a common species in the Indian ocean (Andruleit *et al.* 2003; Liu *et al.* 2021), co-occurred in the study area. Stolz *et al.* (2015) also noticed *U. sibogae* and *U. hulburtiana* as part of the mid-depth flora in the western equatorial Indian Ocean (off Tanzania).

Calciopappus rigidus was present mainly in surface to subsurface waters of the northern region and was associated with temperature in the RDA plot, suggesting a close link with warm water. Andruleit *et al.* (2003) also reported the presence of *C. rigidus* within nutrient-rich water above the

thermocline from the northern Arabian Sea. The study by Godrijan *et al.* (2018) reported that temperature plays a major role in *C. rigidus* distribution. However, unlike their study (DSi was $> 2 \mu\text{M}$), we noticed that *C. rigidus* was also associated with DSi in the RDA plot, suggesting a possibility of its dependence on DSi for some essential physiological processes. Studies found that low DSi concentration hampers the process of calcification in some coccolithophores (Durak *et al.* 2016; Langer *et al.* 2021). On the contrary, the bloom-forming species *E. huxleyi* and *G. oceanica* did not show any DSi dependence, and that probably provides them with the advantages over other coccolithophores as well as diatoms to inhabit low silicate waters (Margalef 1978; Durak *et al.* 2016).

Conclusions

- The abundance and distribution pattern of coccolithophores has been documented for the first time from the northwestern Indian continental shelf water during the summer monsoon.
- The availability of nitrate + nitrite was positively correlated with coccolithophore total abundance and also seemed to play a role in species distribution within the mixed layers.
- The most abundant coccolithophore, *G. oceanica*, was found to be a surface-dwelling species and was directly linked to nitrate + nitrite availability.
- *Florisphaera profunda* and *U. sibogae* were dominant in the lower photic zone, where nutrient concentration was high.
- The maximum abundance of *F. profunda* coincided with low dissolved oxygen levels suggesting the possibility of higher tolerance of this species to low oxygen compared to other deep-dwelling species.
- The study area undergoes contrasting seasonal changes in physicochemical settings with the monsoonal reversal, when a different floristic composition of coccolithophores can be expected.

A Quantitative Estimation Of The Contribution Of Coccolithophores To Primary Production And Carbon Export Fluxes, Along With The Distribution Of Holo- And Heterococcoliths Need To Be Investigated In The Future.

Acknowledgements

We thank the Director, CSIR NIO, for his support. We thank Mr. Areef Sarder for his kind cooperation and technical help during the SEM analysis. We also acknowledge the active support from the captain,

scientists, technical staff, ship cell staff, crew members, deckhand and the students onboard RV Sindhu Sadhna (SSD 55).

Funding

This study was conducted under the CSIR funded project (MLP 1802). The financial supports provided by CSIR, UGC and DST for the first, third and fourth authors, respectively, are gratefully acknowledged. NIO contribution number for this paper is XXXX.

Running Title

Coccolithophores from Indian northwestern shelf waters

References

- Andrulleit H. & Rogalla U. 2002. Coccolithophores in surface sediments of the Arabian Sea in relation to environmental gradients in surface waters. *Marine Geology* 186: 505–526. [https://doi.org/10.1016/S0025-3227\(02\)00312-2](https://doi.org/10.1016/S0025-3227(02)00312-2).
- Andrulleit H.A., von Rad U., Brans A. & Ittekkot V. 2000. Coccolithophore fluxes from sediment traps in the northeastern Arabian Sea off Pakistan. *Marine Micropaleontology* 38: 285–308. [https://doi.org/10.1016/S0377-8398\(00\)00007-4](https://doi.org/10.1016/S0377-8398(00)00007-4).
- Andrulleit H., Stäger S., Rogalla U. & Čepeck P. 2003. Living coccolithophores in the northern Arabian Sea: ecological tolerances and environmental control. *Marine Micropaleontology* 49: 157–181. [https://doi.org/10.1016/S0377-8398\(03\)00049-5](https://doi.org/10.1016/S0377-8398(03)00049-5).
- Andrulleit H., Rogalla U. & Stäger S. 2004. From living communities to fossil assemblages: origin and fate of coccolithophores in the northern Arabian Sea. *Micropaleontology* 50: 5–21. https://doi.org/10.2113/50.Suppl_1.5.
- Andrulleit H., Rogalla U. & Stäger S. 2005. Living coccolithophores recorded during the onset of upwelling conditions off Oman in the western Arabian Sea. *Journal of Nanoplankton Research* 27: 1–14.
- Arundhathy M., Jyothibabu R., Santhikrishnan S., Albin K.J., Parthasarathi S. & Rashid C.P. 2021. Coccolithophores: an environmentally significant and understudied phytoplankton group in the Indian Ocean. *Environmental Monitoring and Assessment* 193: Article 144. <https://doi.org/10.1007/s10661-020-08794-1>.
- Aubry M.P. 2009. A sea of Lilliputians. *Palaeogeography, Palaeoclimatology, Palaeoecology* 284: 88–113. <https://doi.org/10.1016/j.palaeo.2009.08.020>.
- Avrahami Y. & Frada M.J. 2020. Detection of phagotrophy in the marine phytoplankton group of the coccolithophores (Calcihaptophycidae, Haptophyta) during nutrient-replete and phosphate-limited growth. *Journal of Phycology* 56: 1103–1108. <https://doi.org/10.1111/jpy.12997>.
- Balch W.M. 2018. The ecology, biogeochemistry, and optical properties of coccolithophores. *Annual Review of Marine Science* 10: 71–98. <https://doi.org/10.1146/annurev-marine-121916-063319>.

- Balch W.M., Drapeau D.T. & Fritz J.J. 2000. Monsoonal forcing of calcification in the Arabian Sea. *Deep Sea Research Part II* 47: 1301–1337. [https://doi.org/10.1016/S0967-0645\(99\)00145-9](https://doi.org/10.1016/S0967-0645(99)00145-9).
- Balch W.M., Bates N.R., Lam P.J., Twining B.S., Rosengard S.Z., Bowler B.C., Drapeau D.T., Garley R., Lubelczyk L.C., Mitchell C. & Rauschenberg S. 2016. Factors regulating the Great Calcite Belt in the Southern Ocean and its biogeochemical significance. *Global Biogeochemical Cycles* 30: 1124–1144. <https://doi.org/10.1002/2016GB005414>.
- Balch W.M., Bowler B.C., Drapeau D.T., Lubelczyk L.C., Lyczkowski E., Mitchell C. & Wyeth A. 2019. Coccolithophore distributions of the North and South Atlantic Ocean. *Deep Sea Research Part I: Oceanographic Research Papers* 151: Article 103066. <https://doi.org/10.1016/j.dsr.2019.06.012>.
- Banse K. 1987. Seasonality of phytoplankton chlorophyll in the central and northern Arabian Sea. *Deep Sea Research Part A: Oceanographic Research Papers* 34: 713–723. [https://doi.org/10.1016/0198-0149\(87\)90032-X](https://doi.org/10.1016/0198-0149(87)90032-X).
- Baumann K.H., Andrulleit H., Böckel B., Geisen M. & Kinkel H. 2005. The significance of extant coccolithophores as indicators of ocean water masses, surface water temperature, and palaeoproductivity: a review. *Paläontologische Zeitschrift* 79: 93–112. <https://doi.org/10.1007/BF03021756>.
- Bendif E.M. & Young J. 2014. On the ultrastructure of *Gephyrocapsa oceanica* (Haptophyta) life stages. *Cryptogamie Algologie* 35: 379–388. <https://doi.org/10.7872/crya.v35.iss4.2014.379>.
- Bonomo S., Schroeder K., Cascella A., Alberico I. & Lirer F. 2021. Living coccolithophore communities in the central Mediterranean Sea (Summer 2016): relations between ecology and oceanography. *Marine Micropaleontology* 165: Article 101995. <https://doi.org/10.1016/j.marmicro.2021.101995>.
- Boyd P.W., Strzepek R., Fu F. & Hutchins D.A. 2010. Environmental control of open-ocean phytoplankton groups: now and in the future. *Limnology and Oceanography* 55: 1353–1376. <https://doi.org/10.4319/lo.2010.55.3.1353>
- Braak T.C.J. & Smilauer P. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination, version 4.5. www.canoco.com.
- Broerse A.T.C., Brummer G.J. & Van Hinte J.E. 2000. Coccolithophore export production in response to monsoonal upwelling off Somalia (northwestern Indian Ocean). *Deep Sea Research Part II: Topical Studies in Oceanography* 47: 2179–2205. [https://doi.org/10.1016/S0967-0645\(00\)00021-7](https://doi.org/10.1016/S0967-0645(00)00021-7).
- Brussaard C.P.D. 2004. Viral control of phytoplankton populations—a review. *Journal of Eukaryotic Microbiology* 51: 125–138. <https://doi.org/10.1111/j.1550-7408.2004.tb00537.x>.
- Cermeño P., Lee J.B., Wyman K., Schofield O. & Falkowski P.G. 2011. Competitive dynamics in two species of marine phytoplankton under non-equilibrium conditions. *Marine Ecology Progress Series* 429: 19–28. <https://doi.org/10.3354/meps09088>.
- de Vries J., Monteiro F., Wheeler G., Poulton A., Godrijan J., Cerino F., Malinverno E., Langer G. & Brownlee C. 2021. Haplo-diplontic life cycle expands coccolithophore niche. *Biogeosciences* 18: 1161–1184. <https://doi.org/10.5194/bg-18-1161-2021>.

- Durak G.M., Taylor A.R., Walker C.E., Probert I., De Vargas C., Audic S., Schroeder D., Brownlee C. & Wheeler G.L. 2016. A role for diatom-like silicon transporters in calcifying coccolithophores. *Nature Communications* 7: Article 10543. <https://doi.org/10.1038/ncomms10543>.
- Frada M.J., Bendif E.M., Keuter S. & Probert I. 2019. The private life of coccolithophores. *Perspectives in Phycology* 6: 11–30. <https://doi.org/10.1127/pip/2018/0083>.
- Giraudeau J. & Bailey G.W. 1995. Spatial dynamics of coccolithophore communities during an upwelling event in the Southern Benguela system. *Continental Shelf Research* 15: 1825–1852. [https://doi.org/10.1016/0278-4343\(94\)00095-5](https://doi.org/10.1016/0278-4343(94)00095-5).
- Giraudeau J. 1992. Distribution of recent nannofossils beneath the Benguela system: southwest African continental margin. *Marine Geology* 108: 219–237. [https://doi.org/10.1016/0025-3227\(92\)90174-G](https://doi.org/10.1016/0025-3227(92)90174-G).
- Godrijan J., Young J.R., Pfannkuchen, D.M., Precali R. & Pfannkuchen M. 2018. Coastal zones as important habitats of coccolithophores: a study of species diversity, succession, and life-cycle phases. *Limnology and Oceanography* 63: 1692–1710. <https://doi.org/10.1002/lno.10801>.
- Godrijan J., Drapeau D. & Balch W.M. 2020. Mixotrophic uptake of organic compounds by coccolithophores. *Limnology and Oceanography* 65: 1410–1421. <https://doi.org/10.1002/lno.11396>.
- Grasshoff K., Kremling K. & Ehrhardt M. 1992. *Methods of seawater analysis*. John Wiley & Sons Ltd., New York, USA.
- Guerreiro C., Oliveira A., De Stigter H., Cachão M., Sá C., Borges C., Cros L., Santos A., Fortuño J.M. & Rodrigues A. 2013. Late winter coccolithophore bloom off central Portugal in response to river discharge and upwelling. *Continental Shelf Research* 59: 65–83. <https://doi.org/10.1016/j.csr.2013.04.016>.
- Guptha M.V.S., Mohan R. & Muralinath A.S. 1995. Living coccolithophorids from the Arabian Sea. *Oceanographic Literature Review* 42: 992.
- Hagino K., Okada H. & Matsuoka H. 2000. Spatial dynamics of coccolithophore assemblages in the Equatorial Western-Central Pacific Ocean. *Marine Micropaleontology* 39: 53–72. [https://doi.org/10.1016/S0377-8398\(00\)00014-1](https://doi.org/10.1016/S0377-8398(00)00014-1).
- Hammer Ø., Harper D.A.T. & Ryan P.D. 2001. PAST: Paleontological Statistics Software Package for education and data analysis. *Palaeontologia Electronica* 4: Article 9.
- Harvey E.L., Bidle K.D. & Johnson M.D. 2015. Consequences of strain variability and calcification in *Emiliana huxleyi* on microzooplankton grazing. *Journal of Plankton Research* 37: 1137–1148. <https://doi.org/10.1093/plankt/fbv081>.
- Heinle M. 2013. *The effects of light, temperature and nutrients on coccolithophores and implications for biogeochemical models*. PhD thesis. University of East Anglia, UK. 206 pp.
- Henderiks J., Winter A., Elbrächter M., Feistel R., Van der Plas A., Nausch G. & Barlow R. 2012. Environmental controls on *Emiliana huxleyi* morphotypes in the Benguela coastal upwelling system (SE Atlantic). *Marine Ecology Progress Series* 448: 51–66. <https://doi.org/10.3354/meps09535>.

- Houghton S.D. & Gupta M.S. 1991. Monsoonal and fertility controls on recent marginal sea and continental shelf coccolith assemblages from the western Pacific and northern Indian oceans. *Marine Geology* 97: 251–259. [https://doi.org/10.1016/0025-3227\(91\)90119-O](https://doi.org/10.1016/0025-3227(91)90119-O).
- Jin X., Liu C., Poulton A.J., Dai M. & Guo X. 2016. Coccolithophore responses to environmental variability in the South China Sea: species composition and calcite content. *Biogeosciences* 13: 4843–4861. <https://doi.org/10.5194/bg-13-4843-2016>.
- Kawachi M. & Inouye I. 1995. Functional roles of the haptonema and the spine scales in the feeding process of *Chrysochromulina spinifera* (Fournier) Pienaar et Norris (Haptophyta=Prymnesiophyta). *Phycologia* 34: 193–200. <https://doi.org/10.2216/i0031-8884-34-3-193.1>.
- Kleijne A. 1993. *Morphology, taxonomy and distribution of extant coccolithophorids (calcareous nannoplankton)*. PhD thesis. Amsterdam Free University, Netherlands. 321 pp.
- Knappertsbusch M., Cortes M.Y. & Thierstein H.R. 1997. Morphologic variability of the coccolithophorid *Calcidiscus leptoporus* in the plankton, surface sediments and from the Early Pleistocene. *Marine Micropaleontology* 30: 293–317. [https://doi.org/10.1016/S0377-8398\(96\)00053-9](https://doi.org/10.1016/S0377-8398(96)00053-9).
- Krumhardt K.M., Lovenduski N.S., Freeman N.M. & Bates N.R. 2016. Apparent increase in coccolithophore abundance in the subtropical North Atlantic from 1990 to 2014. *Biogeosciences* 13: 1163–1177. <https://doi.org/10.5194/bg-13-1163-2016>.
- Langer G., Taylor A.R., Walker C.E., Meyer E.M., Joseph O.B., Gal A., Harper G.M., Probert I., Brownlee C. & Wheeler G.L. 2021. Role of silicon in the development of complex crystal shapes in coccolithophores. *New Phytologist* 231: 1845–1857. <https://doi.org/10.1111/nph.17230>.
- Leps J. & Smilauer P. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge, UK. 282 pp.
- Levitus S. 1982. *Climatological atlas of the world ocean*, vol. 13. US Department of Commerce, National Oceanic and Atmospheric Administration, USA. 196 pp.
- Liu H., Sun J., Wang D., Zhang X., Zhang C., Song S. & Thangaraj S. 2018. Distribution of living coccolithophores in eastern Indian Ocean during spring intermonsoon. *Scientific Reports* 8: Article 12488. <https://doi.org/10.1038/s41598-018-29688-w>.
- Liu H., Wang D., Yun M., Zhang X., Zhang G., Thangaraj S. & Sun J. 2021. Vertical biogeography and realized niche traits of living coccolithophore community in the eastern Indian Ocean. *Journal of Geophysical Research: Biogeosciences* 126: Article e2020JG005922. <https://doi.org/10.1029/2020JG005922>.
- Madhupratap M., Kumar S.P., Bhattathiri P.M.A., Kumar M.D., Raghukumar S., Nair K.K.C. & Ramaiah N. 1996. Mechanism of the biological response to winter cooling in the northeastern Arabian Sea. *Nature* 384: 549–552. <https://doi.org/10.1038/384549a0>.
- Malinverno E., Triantaphyllou M.V. & Dimiza M.D. 2015. Coccolithophore assemblage distribution along a temperate to polar gradient in the West Pacific sector of the Southern Ocean (January 2005). *Micropaleontology* 61: 489–506.

- Marañón E. 2015. Cell size as a key determinant of phytoplankton metabolism and community structure. *Annual Review of Marine Science* 7: 241–264. <https://doi.org/10.1146/annurev-marine-010814-015955>.
- Margalef R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta* 1: 493–509.
- Menschel E., Gonzalez H.E. & Giesecke R. 2016. Coastal-oceanic distribution gradient of coccolithophores and their role in the carbonate flux of the upwelling system off Concepción, Chile (36 S). *Journal of Plankton Research* 38: 798–817. <https://doi.org/10.1093/plankt/fbw037>.
- Mergulhao L.P., Mohan R., Murty V.S.N., Guptha M.V.S. & Sinha D.K. 2006. Coccolithophores from the central Arabian Sea: sediment trap results. *Journal of Earth System Science* 115: 415–428. <https://doi.org/10.1007/BF02702870>.
- Meyer J. & Riebesell U. 2015. Reviews and syntheses: responses of coccolithophores to ocean acidification: a meta-analysis. *Biogeosciences* 12: 1671–1682. <https://doi.org/10.5194/bg-12-1671-2015>.
- Mitchell-Innes B.A. & Winter A. 1987. Coccolithophores: a major phytoplankton component in mature upwelled waters off the Cape Peninsula, South Africa in March, 1983. *Marine Biology* 95: 25–30. <https://doi.org/10.1007/BF00447481>.
- Naqvi W.A. 1991. Geographical extent of denitrification in the Arabian Sea in relation to some physical processes. *Oceanologica Acta* 14: 281–290. <https://archimer.ifremer.fr/doc/00101/21257/>.
- Narciso A., Javidpour J., Chi X., Cachão M. & Kaufmann M. 2021. Characterization of the coccolithophore community off Cabo Verde archipelago, including the Senghor Seamount (Eastern North Atlantic). *Estuarine, Coastal and Shelf Science* 250: Article 107146. <https://doi.org/10.1016/j.ecss.2020.107146>.
- Okada H. & McIntyre A. 1979. Seasonal distribution of modern coccolithophores in the Western North Atlantic Ocean. *Marine Biology* 54: 319–328. <https://doi.org/10.1007/BF00395438>.
- Oviedo A., Ziveri P., Álvarez M. & Tanhua T. 2015. Is coccolithophore distribution in the Mediterranean Sea related to seawater carbonate chemistry? *Ocean Science* 11: 13–32. <https://doi.org/10.5194/os-11-13-2015>.
- Patil S.M., Mohan R., Shetye S.S., Gazi S., Choudhari P. & Jafar S. 2020. Interannual changes of austral summer coccolithophore assemblages and southward expanse in the Southern Indian Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography* 178: Article 104765. <https://doi.org/10.1016/j.dsr2.2020.104765>.
- Perrin L., Probert I., Langer G. & Aloisi G. 2016. Growth of the coccolithophore *Emiliana huxleyi* in light- and nutrient-limited batch reactors: relevance for the BIOSOPE deep ecological niche of coccolithophores. *Biogeosciences* 13: 5983–6001. <https://doi.org/10.5194/bg-13-5983-2016>.
- Poulton A.J., Holligan P.M., Charalampopoulou A. & Adey T.R. 2017. Coccolithophore ecology in the tropical and subtropical Atlantic Ocean: new perspectives from the Atlantic Meridional Transect (AMT) programme. *Progress in Oceanography* 158: 150–170. <https://doi.org/10.1016/j.pcean.2017.01.003>.

- Renaud S., Ziveri P. & Broerse A.T. 2002. Geographical and seasonal differences in morphology and dynamics of the coccolithophore *Calcidiscus leptoporus*. *Marine Micropaleontology* 46: 363–385. [https://doi.org/10.1016/S0377-8398\(02\)00081-6](https://doi.org/10.1016/S0377-8398(02)00081-6).
- Reynolds R.W. & Smith T.M. 1994. Improved global sea surface temperature analyses using optimum interpolation. *Journal of Climate* 7: 929–948. [https://doi.org/10.1175/1520-0442\(1994\)007<0929:IGSSTA>2.0.CO;2](https://doi.org/10.1175/1520-0442(1994)007<0929:IGSSTA>2.0.CO;2).
- Rivero-Calle S., Gnanadesikan A., Del Castillo C.E., Balch W.M. & Guikema S.D. 2015. Multidecadal increase in North Atlantic coccolithophores and the potential role of rising CO₂. *Science* 350: 1533–1537. <https://doi.org/10.1126/science.aaa8026>.
- Rixen T., Cowie G., Gaye B., Goes J., do Rosário Gomes H., Hood R.R., Lachkar Z., Schmidt H., Segsneider J. & Singh A. 2020. Reviews and syntheses: present, past, and future of the oxygen minimum zone in the northern Indian Ocean. *Biogeosciences* 17: 6051–6080. <https://doi.org/10.5194/bg-17-6051-20>.
- Rogalla U. & Andruleit H. 2005. Precessional forcing of coccolithophore assemblages in the northern Arabian Sea: implications for monsoonal dynamics during the last 200,000 years. *Marine Geology* 217: 31–48. <https://doi.org/10.1016/j.margeo.2005.02.028>.
- Roy R., Chitari R., Kulkarni V., Krishna M.S., Sarma V.V.S.S. & Anil A.C. 2015. CHEMTAX-derived phytoplankton community structure associated with temperature fronts in the northeastern Arabian Sea. *Journal of Marine Systems* 144: 81–91. <https://doi.org/10.1016/j.jmarsys.2014.11.009>.
- Schiebel R., Zeltner A., Treppke U.F., Waniek J.J., Bollmann J., Rixen T. & Hemleben C. 2004. Distribution of diatoms, coccolithophores and planktic foraminifers along a trophic gradient during SW monsoon in the Arabian Sea. *Marine Micropaleontology* 51: 345–371. <https://doi.org/10.1016/j.marmicro.2004.02.001>.
- Shenoi S.S.C., Shankar D. & Shetye S.R. 2002. Differences in heat budgets of the near-surface Arabian Sea and Bay of Bengal: implications for the summer monsoon. *Journal of Geophysical Research: Oceans* 107 (C6): 5-1–5-14. <https://doi.org/10.1029/2000JC000679>.
- Sicre M.A., Jalali B., Martrat B., Schmidt S., Bassetti M.A. & Kallel N. 2016. Sea surface temperature variability in the North Western Mediterranean Sea (Gulf of Lion) during the Common Era. *Earth and Planetary Science Letters* 456: 124–133. <https://doi.org/10.1016/j.epsl.2016.09.032>.
- Sieracki M.E., Verity P.G. & Stoecker D.K. 1993. Plankton community response to sequential silicate and nitrate depletion during the 1989 North Atlantic spring bloom. *Deep Sea Research Part II: Topical Studies in Oceanography* 40: 213–225. [https://doi.org/10.1016/0967-0645\(93\)90014-E](https://doi.org/10.1016/0967-0645(93)90014-E).
- Silori S., Sharma D., Chowdhury M., Biswas H., Bandyopadhyay D., Shaik A.U.R., Cardinal D., Mandeng-Yogo M. & Narvekar J. 2021. Contrasting phytoplankton and biogeochemical functioning in the eastern Arabian Sea shelf waters recorded by carbon isotopes (SW monsoon). *Marine Chemistry* 232: Article 103962. <https://doi.org/10.1016/j.marchem.2021.103962>.
- Silva A., Palma S. & Moita M.T. 2008. Coccolithophores in the upwelling waters of Portugal: four years of weekly distribution in Lisbon bay. *Continental Shelf Research* 28: 2601–2613. <https://doi.org/10.1016/j.csr.2008.07.009>.

- Smayda T.J. 1989. Primary production and the global epidemic of phytoplankton blooms in the sea: a linkage? In: *Novel phytoplankton blooms. Coastal and estuarine studies* (Ed. by E.M. Cosper, V.M. Bricelj & E.J. Carpenter), pp 449–483. Springer, Berlin, Germany. https://doi.org/10.1007/978-3-642-75280-3_26.
- Stolz K., Baumann K.H. & Mersmeyer H. 2015. Extant coccolithophores from the western equatorial Indian Ocean off Tanzania and coccolith distribution in surface sediments. *Micropaleontology* 61: 473–488. <https://www.jstor.org/stable/44511371>.
- Šupraha L., Gerecht A.C., Probert I. & Henderiks J. 2015. Eco-physiological adaptation shapes the response of calcifying algae to nutrient limitation. *Scientific Reports* 5: Article 16499. <https://doi.org/10.1038/srep16499>.
- Takahashi K. & Okada H. 2000. Environmental control on the biogeography of modern coccolithophores in the southeastern Indian Ocean offshore of Western Australia. *Marine Micropaleontology* 39: 73–86. [https://doi.org/10.1016/S0377-8398\(00\)00015-3](https://doi.org/10.1016/S0377-8398(00)00015-3).
- Taylor A.R., Brownlee C. & Wheeler G. 2017. Coccolithophore cell biology: chalking up progress. *Annual Review of Marine Science* 9: 283–310. <https://doi.org/10.1146/annurev-marine-122414-034032>.
- Thierstein H.R. & Young J.R. [Eds] 2004. *Coccolithophores: from molecular processes to global impact*. Springer, Berlin, Germany. 565 pp.
- Tyrrell T. & Young J. R. 2009. Coccolithophores. In: *Encyclopedia of ocean sciences* (Ed. by J.H. Steele, K.K. Turekian & S.A. Thorpe), pp 3568 –3576. Academic Press, San Diego, USA.
- UNESCO 1994. *Protocols for the Joint Global Ocean Flux Study (JGOFS), core measurements*. IOC Manuals and Guides 29. UNESCO, Paris, France. 170 pp.
- Vijayan A.K., Reddy B.B., Sudheesh V., Marathe P.H., Nampoothiri V.N., Harikrishnachari N.V., Kavya P., Gupta G.V.M. & Ramanamurthy M.V. 2021. Phytoplankton community structure in a contrasting physico-chemical regime along the eastern Arabian Sea during the winter monsoon. *Journal of Marine Systems* 215: Article 103501. <https://doi.org/10.1016/j.jmarsys.2020.103501>.
- Winter A., Henderiks J., Beaufort L., Rickaby R.E. & Brown C.W. 2014. Poleward expansion of the coccolithophore *Emiliana huxleyi*. *Journal of Plankton Research* 36: 316–325. <https://doi.org/10.1093/plankt/fbt110>.
- Winter A., Jordan R. & Roth P.H. 1994. Biogeography of coccolithophores in oceanic waters. In: *Coccolithophores* (Ed. by A. Winter & W.G. Siesser), pp 161–177. Cambridge University Press, Cambridge, UK.
- Young J.R. 1994. Function of coccoliths. In: *Coccolithophores* (Ed. by A. Winter & W.G. Siesser), pp 63–82. Cambridge University Press, Cambridge, UK.
- Young J.R., Geisen M., Cros L., Kleijne A., Sprengel C., Probert I. & Østergaard J. 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research* 1: 1–132.
- Young J.R., Bown P.R. & Lees J.A. 2017. *Nannotax3 website*. *International Nannoplankton Association*. <https://www.mikrotax.org/Nannotax3>; searched on March, 2020.

Zeltner A. 2000. *Monsoonal influenced changes of coccolithophore communities in the northern Indian Ocean: alteration during sedimentation and record in surface sediments*. PhD thesis. Evolution - Paleontological Collection, University of Tübingen, Germany.

Legends For Figures

Fig. 1. Map showing sampling locations along the northwest continental shelf of India. A total of five stations have been sampled at one-degree intervals covering the 200-m isobaths.

Fig. 2. Latitudinal distribution of mixed layer depth (MLD) in the northwestern shelf water of India. The MLD was calculated using a 0.2 kg m^{-3} density difference from the surface (Levitus 1982).

Fig. 3. Vertical profiles of temperature, salinity, dissolved oxygen (DO) and Chlorophyll *a* for the five stations.

Fig. 4. Vertical profiles of dissolved inorganic nutrients ($\mu\text{mol l}^{-1}$): nitrate + nitrite; dissolved inorganic phosphate (DIP) and dissolved silicate (DSi).

Fig. 5. Vertical distribution of major coccolithophore species in the upper 60 m (unit: $\times 10^3 \text{ cells l}^{-1}$) along the northwestern shelf water of India.

Fig. 6. Coccolithophore community structure of the five locations along the northwestern shelf water of India.

Fig. 7. Cross-sectional profile of coccolithophore diversity index and dominance index in the northwestern shelf water of India.

Fig. 8. Redundancy analysis (RDA) ordination bi-plot showing the relationship between environmental parameters and major coccolithophore species. The black line and black dashed arrows denote environmental and biological parameters, respectively.

Fig. 9. Cluster analysis of the major coccolithophore species data combined from all the stations and depths using the Bray–Curtis similarity.

Figs 10–15. Coccolithophore species, SEM, recorded from the northwestern Arabian Sea shelf water during the summer monsoon 2018.

Fig. 10. *Algirosphaera robusta*. Scale bar = 2 μm .

Fig. 11. *Calcidiscus leptoporus* subsp. *quadriperforatus*. Scale bar = 5 μm .

Fig. 12. *Calciopappus rigidus*. Scale bar = 5 μm .

Fig. 13. *Emiliana huxleyi*. Scale bar = 2 μm .

Fig. 14. *Florisphaera profunda*. Scale bar = 2 μm .

Fig. 15. *Gephyrocapsa oceanica*. Scale bar = 2 μm .

Figs 16–21. Coccolithophore species, SEM, recorded from the northwestern Arabian Sea shelf water during the SW monsoon 2018.

Fig. 16. *Helicosphaera carteri*. Scale bar = 5 μm .

Fig. 17. *Helicosphaera hyaline*. Scale bar = 2 μm ;

Fig. 18. *Michaelsarsia adriatica*. Scale bar = 10 μm .

Fig. 19. *Syracosphaera mediterranea*. Scale bar = 5 μm .

Fig. 20. *Umbilicosphaera hulburtiana*. Scale bar = 5 μm .

Fig. 21. *Umbilicosphaera sibogae*. Scale bar = 10 μm .

Table 1. Coccolithophore species abundance ($\times 10^3$) cells l^{-1} in the north–western shelf water of India during the southwest monsoon.

Depth	21° N						20° N						19° N				18° N				17° N			
	0	5	10	20	40	60	0	5	10	20	40	60	5	10	40	60	0	5	20	60	0	5	20	40
<i>Algirosphaera robusta</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Calcidiscus leptoporus</i>	2.3	–	–	–	–	–	–	1.5	–	–	–	–	–	–	0.5	–	0.6	3.7	4.7	–	–	–	–	–
<i>Calciopappus caudatus</i>	–	–	–	–	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Calciopappus rigidus</i>	–	–	1.4	–	–	–	–	1.5	1.8	1.1	–	–	–	0.5	–	–	–	–	–	–	0.3	–	–	0
<i>Calciosolenia brasiliensis</i>	–	–	–	–	–	–	–	–	–	–	–	–	2.5	–	–	–	–	–	–	–	0.5	–	–	0
<i>Calciosolenia corsellii</i>	–	–	–	–	–	–	–	1.5	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Calciosolenia murrayi</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	0
<i>Emiliania huxleyi</i>	–	–	–	–	–	–	–	–	–	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Florisphaera profunda</i>	–	–	–	–	6.0	1.5	–	–	0.9	–	3.1	2.6	–	–	1.0	6.4	–	–	3.7	0.7	–	–	0.5	–
<i>Gephyrocapsa oceanica</i>	61.1	74.5	66.4	70.3	10.7	2.2	12.9	13.5	18.6	11.4	24.1	7.1	7.6	6.6	6.6	0.4	12.0	18.4	14.1	3.1	0.5	2.1	0.1	7
<i>Helicosphaera carteri</i>	–	5.0	2.8	5.6	–	–	–	1.5	0.9	0.6	2.7	0.6	–	0.5	0.5	–	0.3	–	–	–	–	–	–	0
<i>Helicosphaera hyalina</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	0.1	–	–	–
<i>Helicosphaera princei</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	1.3	–	–	–	–	–
<i>Michaelsarsia adriatica</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	–	–	1
<i>Syracosphaera lamina</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	0.3	–	–	–	0.1	–	–	–
<i>Syracosphaera mediterranea</i>	–	1.7	–	–	1.2	–	–	3.0	0.9	0.6	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–
<i>Umblicosphaera hulbertiana</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	0
<i>Umblicosphaera sibogae</i>	–	1.7	1.4	0.9	1.2	0.7	–	–	0.9	–	2.7	1.3	–	–	–	0.2	0.3	–	0.7	0.7	0.1	–	–	1

Figure 1

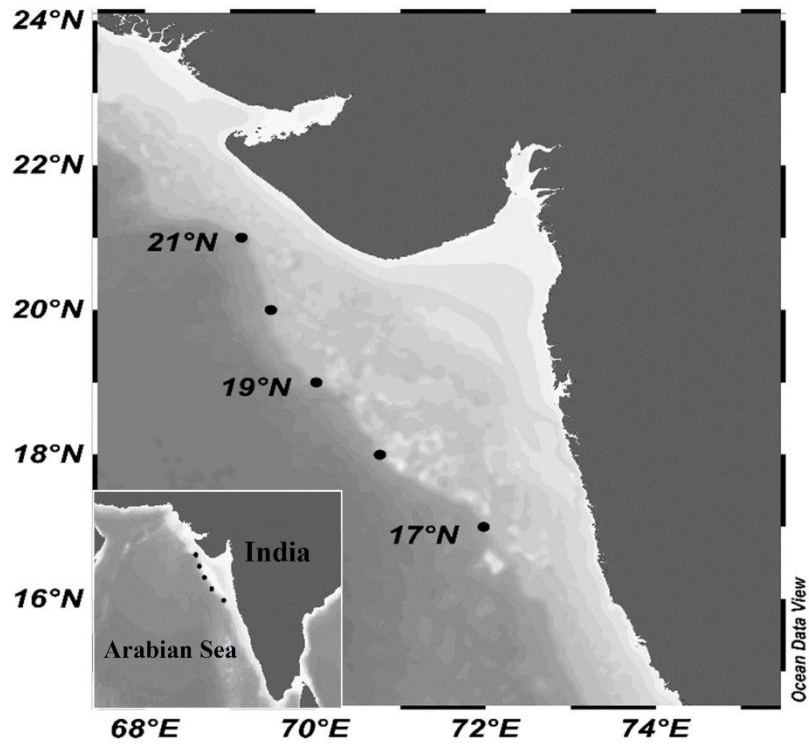


Figure 2

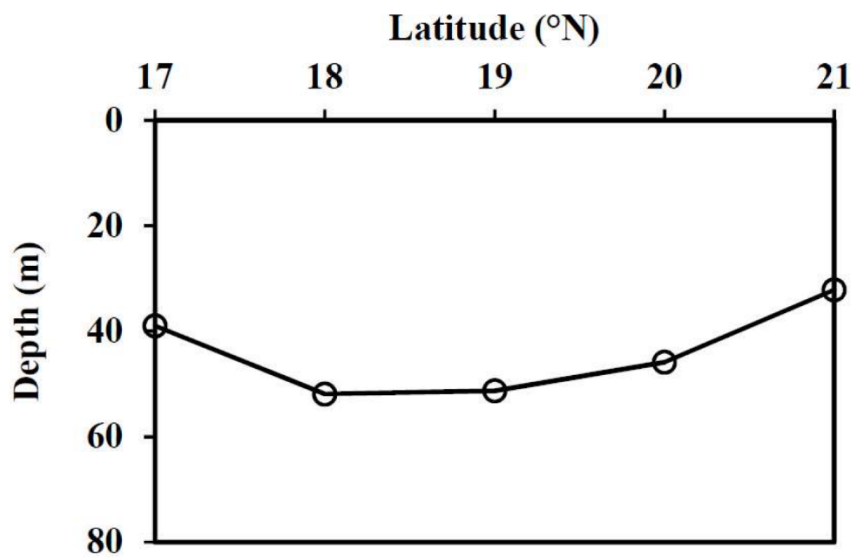


Figure 3

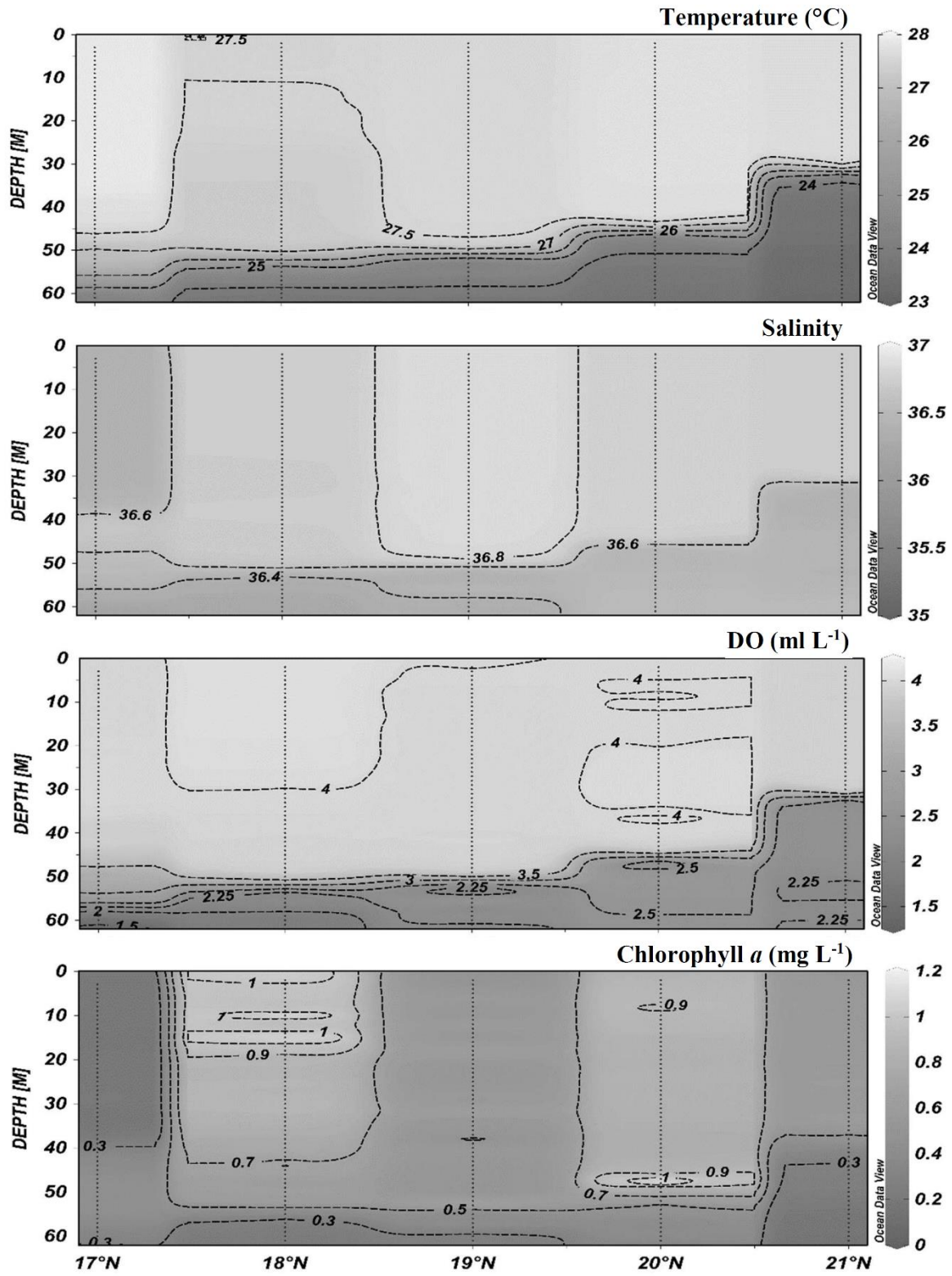


Figure 4

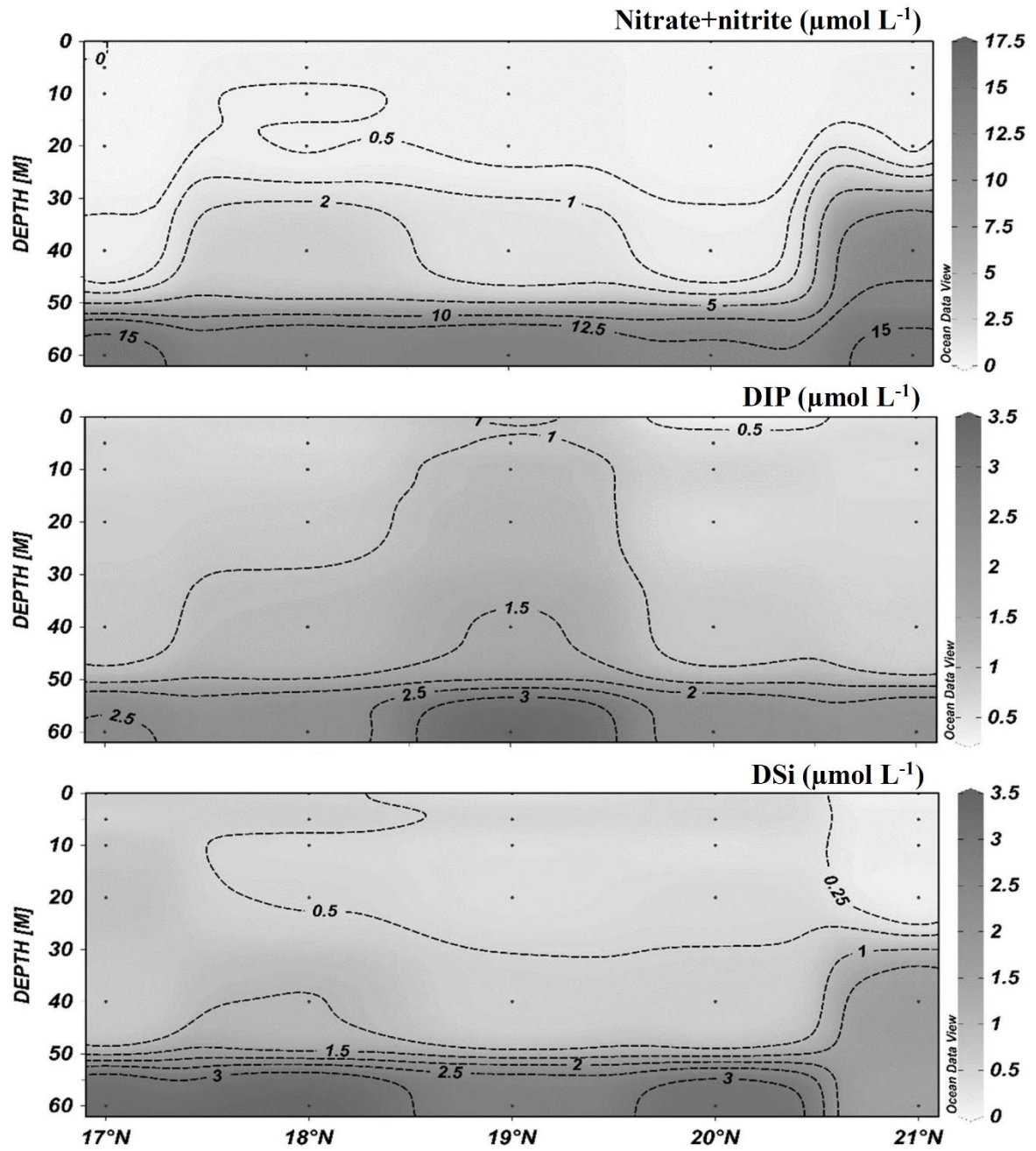


Figure 5

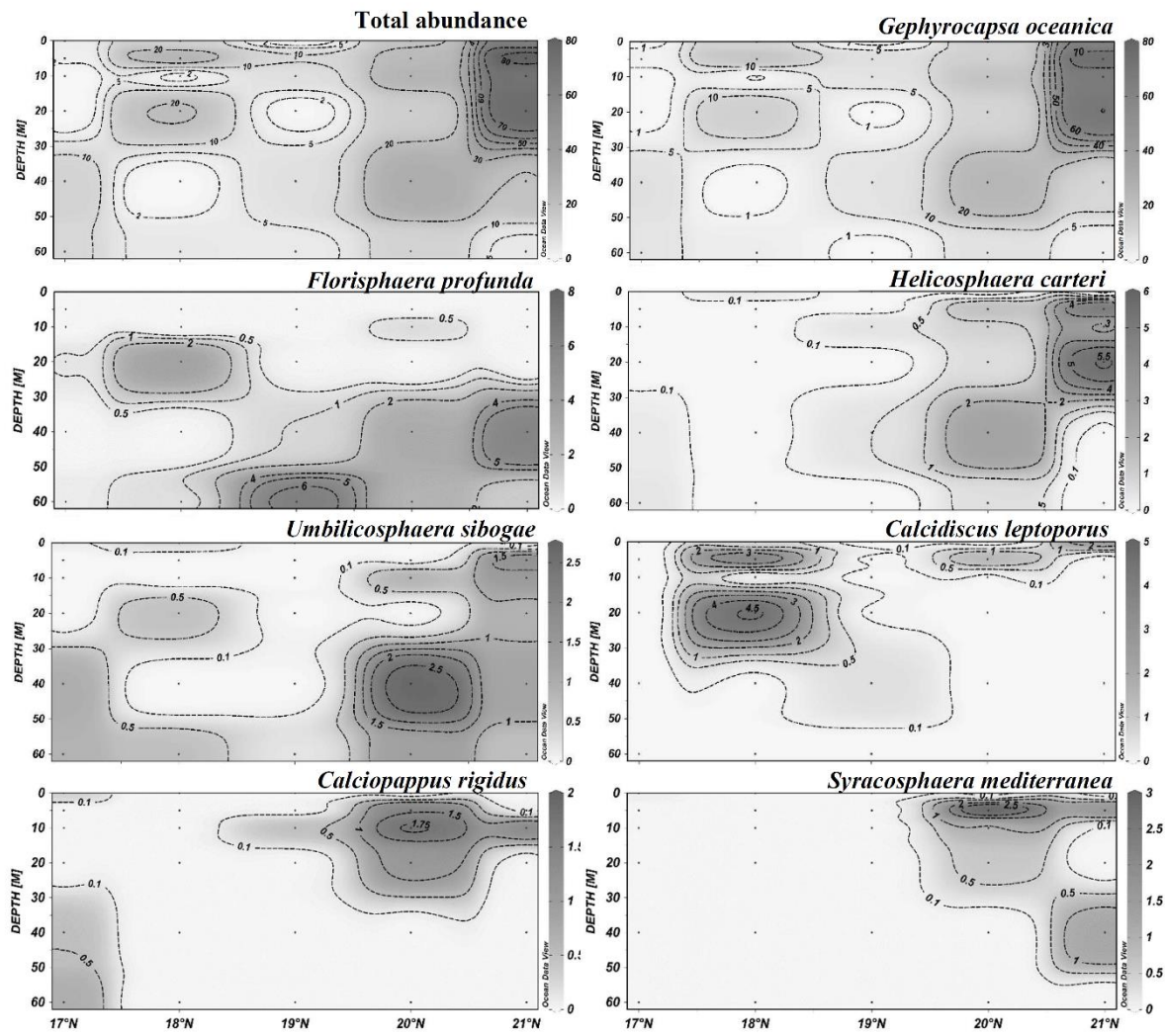


Figure 6

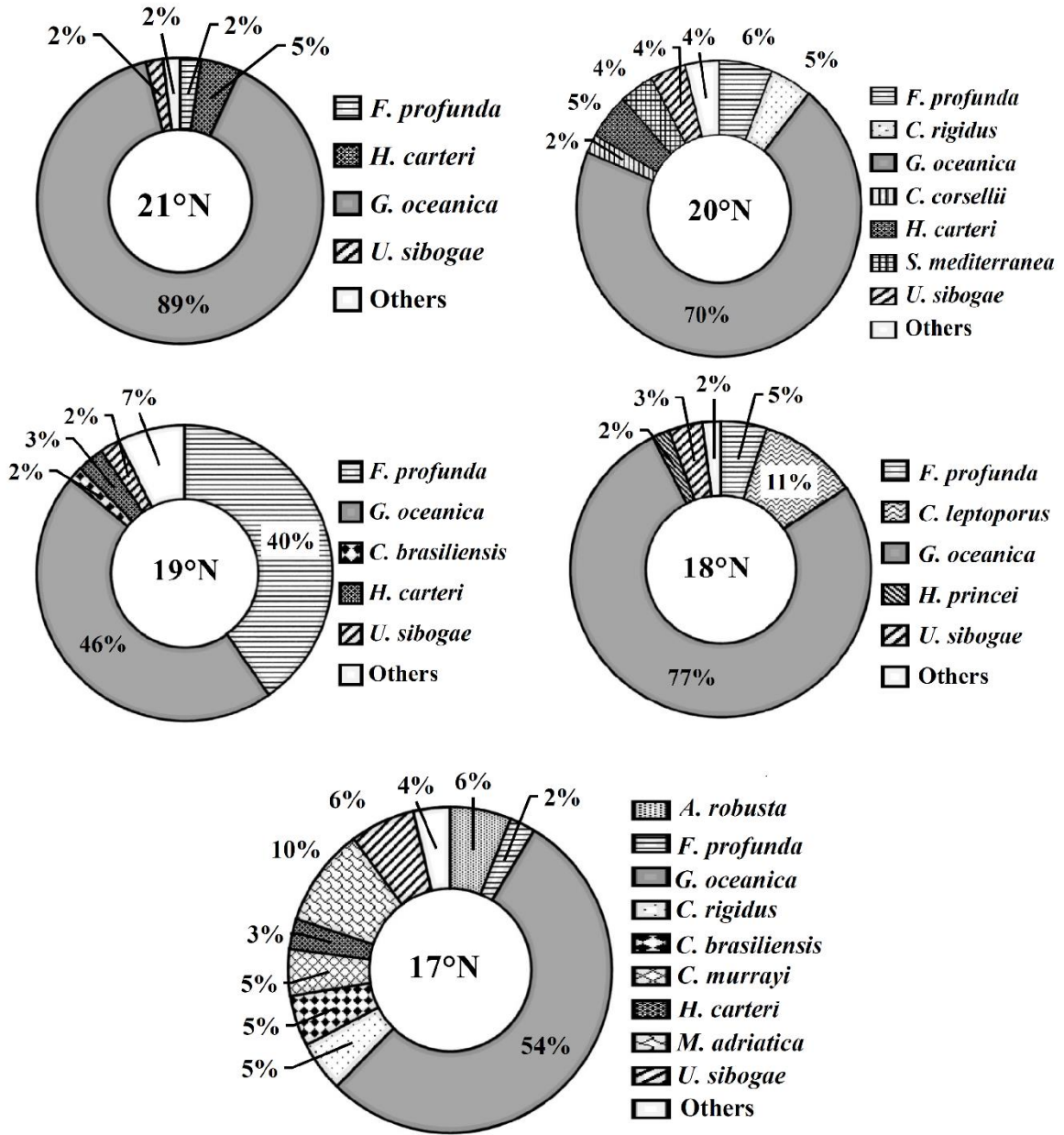


Figure 7

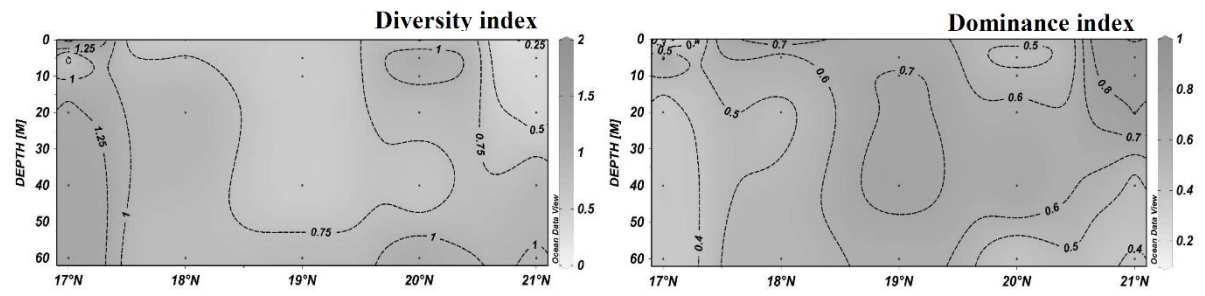


Figure 8

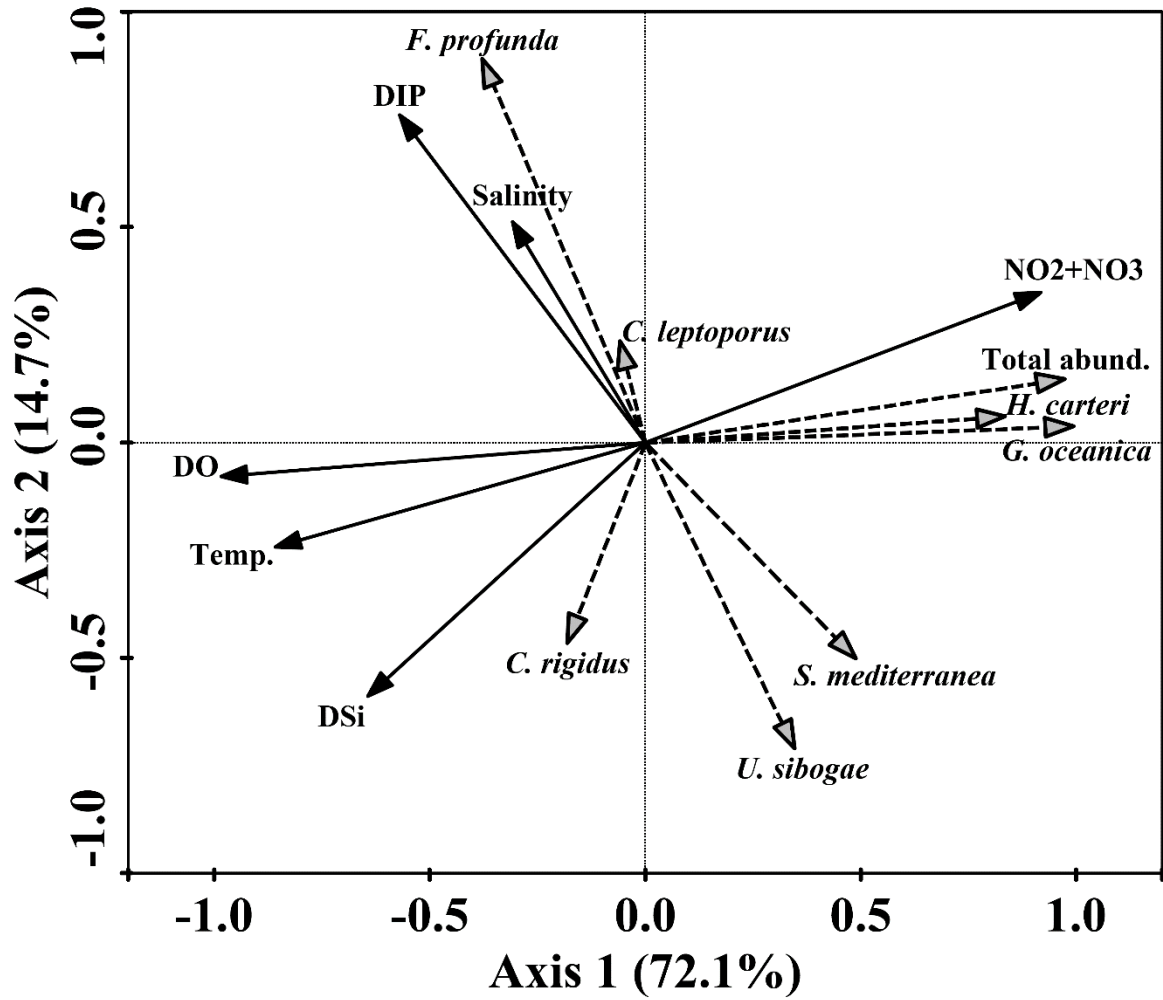


Figure 9

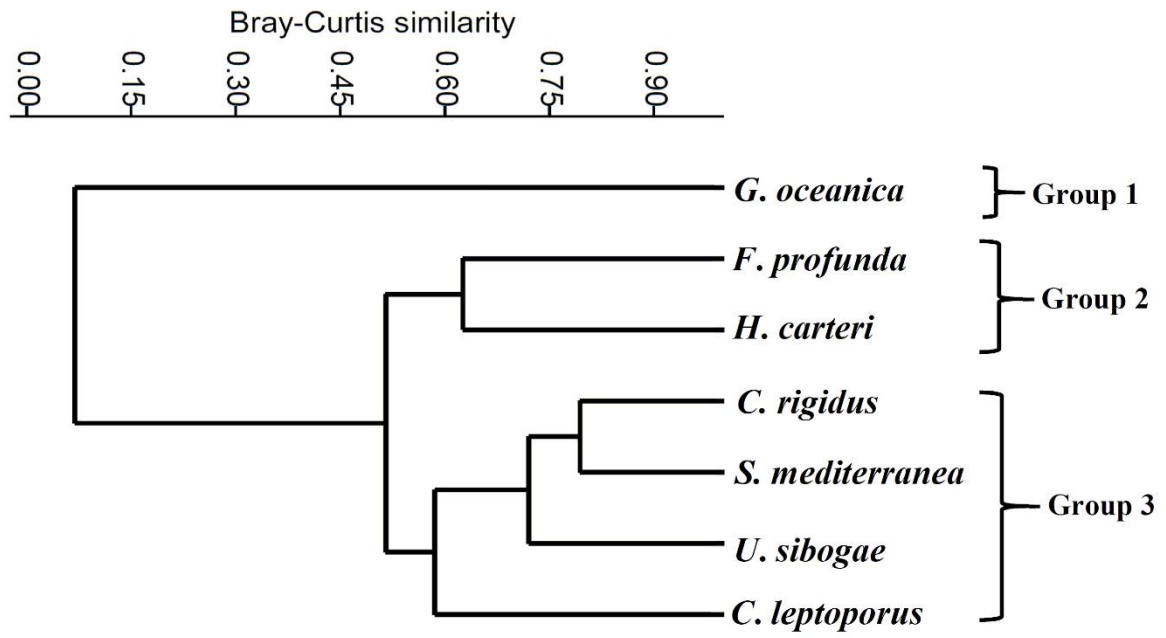


Figure 10 -15

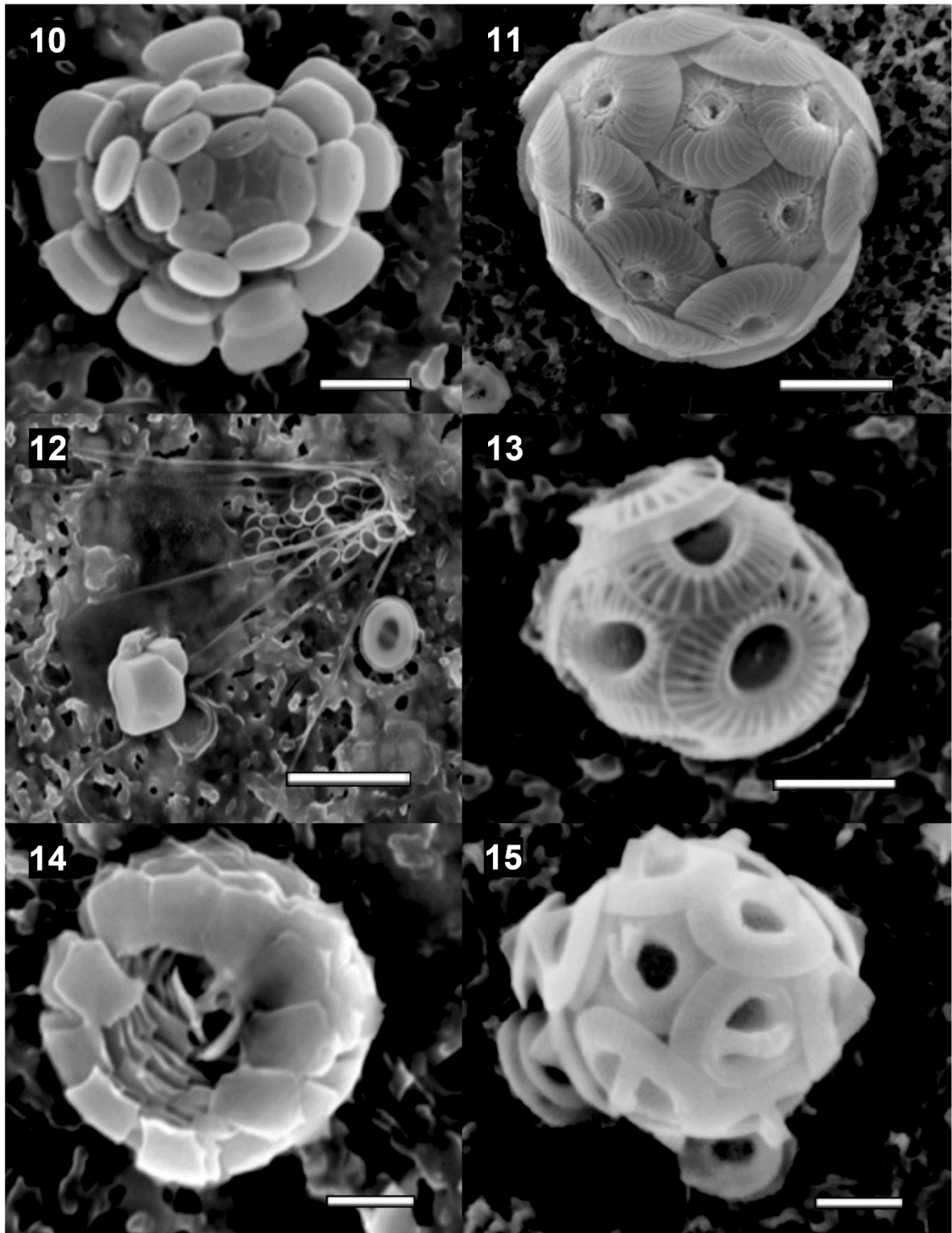
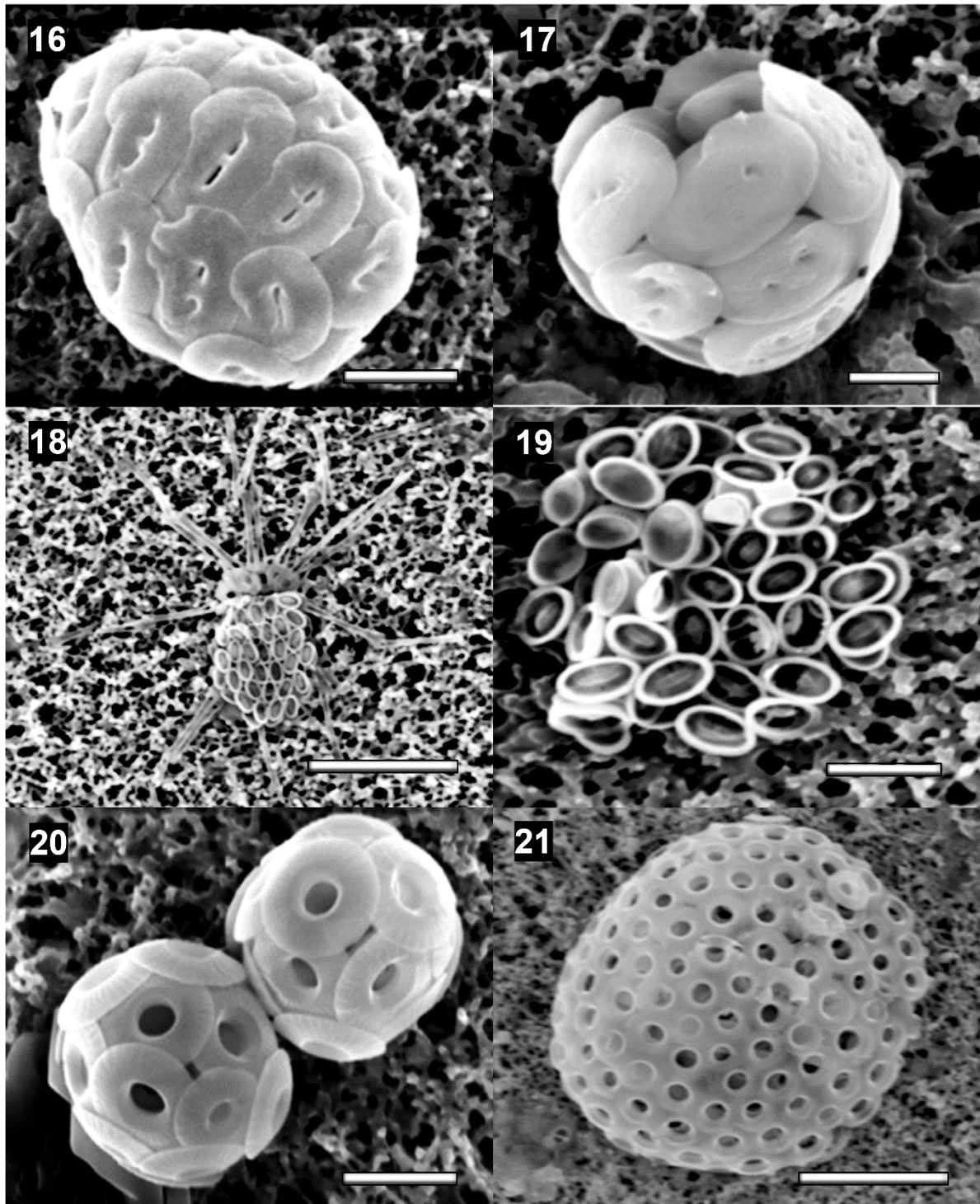


Figure 16 -21



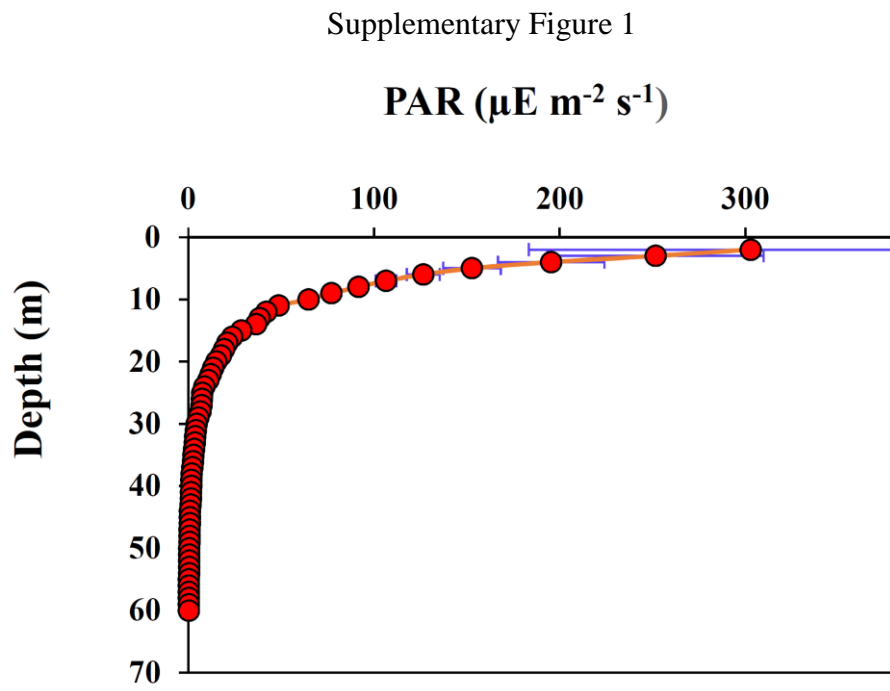


Fig. S1. Photosynthetically Available Radiation (PAR) recorded at 18°N.