



## Full Length Article

## Spatial and vertical variability of summer coccolithophores in relation to water column stratification and nutrient gradients in the Gulf of Aqaba

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## ABSTRACT

Coccolithophore abundance and diversity were examined across five stations and depths in the Gulf of Aqaba during late summer (18–24 September 2016). Temperature varied mainly with depth, nutrients were largely uniform except nitrate and chlorophyll-*a* showed little spatial variation. Abundance peaked at the deep chlorophyll maximum, averaging  $38.4 \pm 20.2$  cells  $\text{ml}^{-1}$ , with *Gephyrocapsa huxleyi* dominating and *Umbellosphaera tenuis* as a key contributor constituting 40.2% and 8.5% of the total density, respectively. A total of 64 species (36 genera) were identified, including eight new Red Sea records, with Syracosphaeraceae as the most diverse family (23 species). Clear vertical zonation patterns were observed, with four species—*G. huxleyi*, *Syracosphaera pulchra*, *U. irregularis* and *U. tenuis*—occurring ubiquitously across depths and stations. Coccolithophore density showed significant correlations with ammonia (positive) and salinity (negative) highlight strong environmental control of coccolithophore communities in these oligotrophic waters. In general, the results indicate the high diversity, vertical zonation and environmental interaction of coccolithophore community in the oligotrophic waters of the study area.

## Introduction

Coccolithophores are unicellular marine microalgae within the class Prymnesiophyceae, distinguished by the formation of calcite plates called coccoliths (Hagino and Young, 2015; Young et al., 2003). These structures are synthesized intracellularly through a process of biomineralization and subsequently secreted to the cell surface (Young et al., 2003). They have two morphologically different stages. During the diploid phase, species typically produce heterococcoliths (HET), which are made of radially intergrown calcite crystals, whereas during the haploid phase, they produce holococcoliths (HOL), which are composed of small, equidimensional crystals (de Vargas et al., 2007; Monteiro et al., 2016). Coccolithophores play a crucial role in both inorganic and organic carbon pumping in oceans, as they have a dual role of being photosynthetic and calcifying organisms (Han et al., 2025; Vuković and Godrijan, 2025). Although in oligotrophic waters they often represent a small fraction of phytoplankton biomass, these organisms play a key role in atmospheric carbon and sulphur exchange, as well as in the vertical flux and sedimentation of biogenic matter (Balch, 2018). They are also well adapted ecologically to the stratified, nutrient-deficient waters of

tropical and subtropical regions, where they often dominate open-ocean phytoplankton communities (Iglesias-Rodríguez et al., 2002). Although present worldwide in the photic zone, their distribution tends to favour warm low-productivity environments (Cortés et al., 2001). Community composition is also affected by depth and hydrographic conditions: HOL inhabit the nutrient-deficient surface layers, whereas HET dominate in deeper, more nutrient-rich and less illuminated waters (Winter et al., 1979). Recent studies have further emphasized the remarkable diversity and ecological importance of coccolithophores, particularly members of the family Syracosphaeraceae, highlighting their widespread occurrence in oligotrophic tropical and subtropical oceans and their sensitivity to variations in temperature, nutrient availability, light intensity and water-column stratification (Vuković and Godrijan, 2025). Furthermore, recent investigations from different marine environments have demonstrated pronounced spatial and vertical variability in coccolithophore assemblages in response to hydrodynamic conditions, water-mass characteristics and nutrient gradients (Dimiza et al., 2023, 2026; González-Martín et al., 2024). The Gulf of Aqaba (GoA) is a 180-km-long, semi-enclosed basin, shares many of the major hydrographic and climatic features of the Red Sea. It is characterized by extremely

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saline waters, a hot and arid climate, and very little rainfall, which together contribute to a very strong regime of evaporation (Plaehn et al., 2002). The GoA undergoes a distinct seasonal pattern, with thermal stratification starting in spring and continuing throughout the summer, followed by deep vertical mixing during winter (Manasrah et al., 2007), while mixing is usually initiated at the end of September (Biton and Gildor, 2011). Due to spatial variations, the southern part of the gulf experiences more pronounced and prolonged stratification than the northern region (Berman and Gildor, 2022). During the stratified summer period, elevated solar irradiance and low concentrations of depleted inorganic nutrients result in low surface primary productivity. This, in turn, promotes the formation of a subsurface chlorophyll maximum layer, where productivity is enhanced under more favourable light and nutrients (Manasrah et al., 2018). Late summer represents the final stage of seasonal stratification in the GoA, when surface waters experience their strongest nutrient depletion before the onset of autumn and winter mixing. Consequently, this period provides an ideal natural setting for investigating the response of coccolithophore communities to maximum oligotrophic conditions, allowing the influence of water-column stratification and nutrient limitation on their spatial and vertical distribution to be clearly evaluated (Berman and Gildor, 2022; Biton and Gildor, 2011). Although traditionally classified as an oligotrophic water body (El-Sherbiny et al., 2025), the seasonal fluctuations in the GoA enable it to sustain relatively higher productivity than other oligotrophic systems. During the stratified summer period, the ultraphytoplankton ( $<8\ \mu\text{m}$ ) predominates in the water column, and is highly adapted to nutrient-depleted conditions (Lindell and Post, 1995). Conversely, with the onset of winter mixing and the replenishment of nutrients, larger phytoplankton groups such as diatoms and dinoflagellates become dominant, reflecting a pronounced shift in community structure (Lindell and Post, 1995). Stratification periods have a significant influence on the spatial and vertical patterns of microphytoplankton across the GoA region (El-Sherbiny et al., 2019). In response to these dynamic hydrographic conditions, coccolithophores play a vital role within the phytoplankton community of the GoA. Their population dynamics are strongly influenced by seasonal water column processes. In the course of winter mixing, when nutrient replenishment from deeper layers occurs, coccolithophores achieve comparatively higher cell densities, reflecting favourable growth conditions. In contrast, during the summer stratification period, overall abundances decline as nutrient limitation intensifies; however, species diversity reaches its maximum, accompanied by a distinct vertical stratification in community structure (Keuter et al., 2023; Winter et al., 1979). Research on coccolithophore diversity and community structure in both the GoA and the Red Sea remains scarce, despite their ecological significance as primary producers and indicators of marine environmental change. The first study of coccolithophore diversity in the GoA was conducted by Winter et al. (1979), who investigated two stations, one in the extreme north and the other near the Straits of Tiran. Recently, Keuter et al. (2023) studied the seasonal dynamics of coccolithophores at a single station in the northern part of the GoA for 2 years. Whereas, Alqudah et al. (2024) assessed surface sediments adjacent to the Jordanian coastal waters, providing insights into sedimentary species composition. In the broader Red Sea region, Okada and Honjo (1975) included the central Red Sea in their comparative analysis of coccolithophore diversity across multiple seas. Kleijne (1991) carried out a comprehensive survey in both the Red Sea and the Gulf of Suez, sampling numerous stations during an expedition that also encompassed the Indian Ocean, North Atlantic Ocean, and Mediterranean Sea. Additionally, McIntyre (1969) focused on sediments collected from the southern and central Red Sea regions, whereas Aljahdali (2021) investigated northern Red Sea hot brine sites.

This study presents the first comprehensive assessment of coccolithophore communities throughout the Saudi Arabian sector of the GoA during the late summer stratification period. Specifically, the study aimed to (i) characterize the spatial and vertical distribution of coccolithophore abundance, diversity and community composition; (ii)

examine the influence of water-column stratification and physico-chemical variables, including temperature, salinity, nutrients and chlorophyll-*a*, on coccolithophore distribution; (iii) identify dominant and depth-specific coccolithophore taxa; and (iv) document new coccolithophore records for the GoA and the Red Sea. The findings provide an important baseline for understanding coccolithophore ecology and biodiversity in this oligotrophic ecosystem and for assessing future environmental change.

## Materials and methods

### Study area

Five stations were selected along the Saudi Arabian coastline of the GoA for the present study (Fig. 1). Station 1 was located near the Jordanian border towards the north, whereas station 5 was positioned close to the Straits of Tiran. All stations were located in deep-water areas, with bottom depths ranging between 700 and 1000 m.

### Sampling and analysis

Sampling at all study stations was conducted between 10:00 and 12:00 h onboard RV *Al-Azizi* during 18–24 September 2016. To measure water column physical properties such as salinity, temperature and dissolved oxygen (DO), a pre-calibrated CTD (Seabird Electronics, SBE 25 plus) was deployed. Water samples were collected from five depths (surface, 10 m, 50 m, 70 m and 100 m) using a Niskin rosette sampler (Fig. 2). The deep chlorophyll maximum (DCM) was determined in situ from CTD fluorescence profiles prior to water sampling at each station. Water samples for coccolithophore and environmental analyses were collected directly from the DCM, which consistently occurred at approximately 70 m throughout the study area during the sampling period (Fig. 2). For chlorophyll-*a* determination, 3–4 L of seawater from each depth was filtered onto 0.7  $\mu\text{m}$  Whatman GF/F filters, which were then kept at  $-20\ ^\circ\text{C}$  until analysis. For inorganic nutrient analysis, 500 mL of seawater was filtered through 0.2  $\mu\text{m}$  polycarbonate filters, and the filtrates were preserved at  $-20\ ^\circ\text{C}$  until analysis. Chlorophyll-*a* and nutrient concentrations were later determined based on Parsons et al. (1984). To assess coccolithophore community composition, seawater samples (250–500 mL) were collected from the five previously described depths. The filtered volume varied between samples depending on the particulate load and the extent of filter clogging during filtration. This approach ensured efficient filtration while retaining sufficient coccolithophore material for accurate identification and quantitative analysis using scanning electron microscopy (SEM). Samples were filtered through 0.8  $\mu\text{m}$  pore-size polycarbonate track-etched filters (25 mm diameter, Whatman Nucleopore) using a filtration unit connected to a low-pressure vacuum system ( $\sim 5\ \text{psi}$ ). Care was taken to ensure that the material was evenly distributed on the filters. Following filtration, filters were rinsed in 2 mL of deionized water (pH 7) to get residual salts off, then air-dried and kept in Petri dishes. Each filter had an effective filtration area that was proportional to 23 mm diameter. For identification and enumeration, filter sections were mounted onto sputter-coated copper SEM stubs using double-sided adhesive tape and coated with approximately 20 nm of gold. Observations were made with a Hitachi S-3500 N scanning electron microscope. All coccolithophore cells (coccospheres) and detached coccoliths present on the analysed filter portions were identified and counted. Depending on abundance, between 150 and 650 fields of view per sample were examined at 1000 $\times$  magnification, ensuring a minimum count of 150 coccospheres per sample. In samples with low abundances, additional fields were examined. Absolute abundances of coccolithophores (cells  $\text{mL}^{-1}$ ) were calculated following Jordan and Winter (2000), by scaling raw counts from the known scanned area using the standard conversion equation:

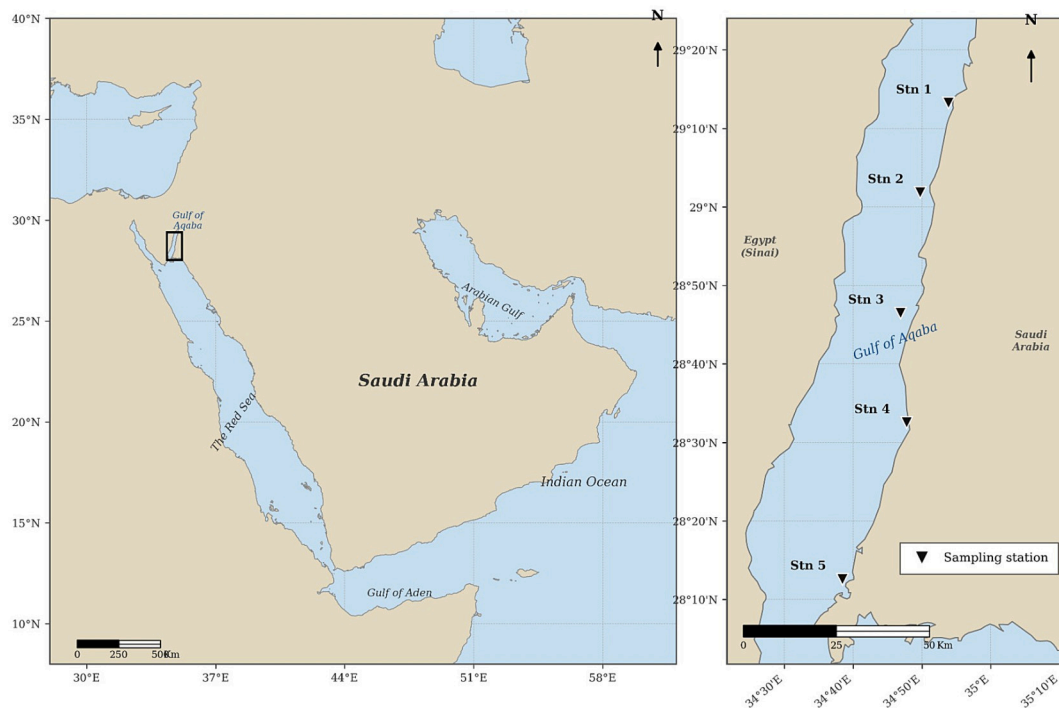


Fig. 1. Map showing the study stations (Stn) along the Gulf of Aqaba.

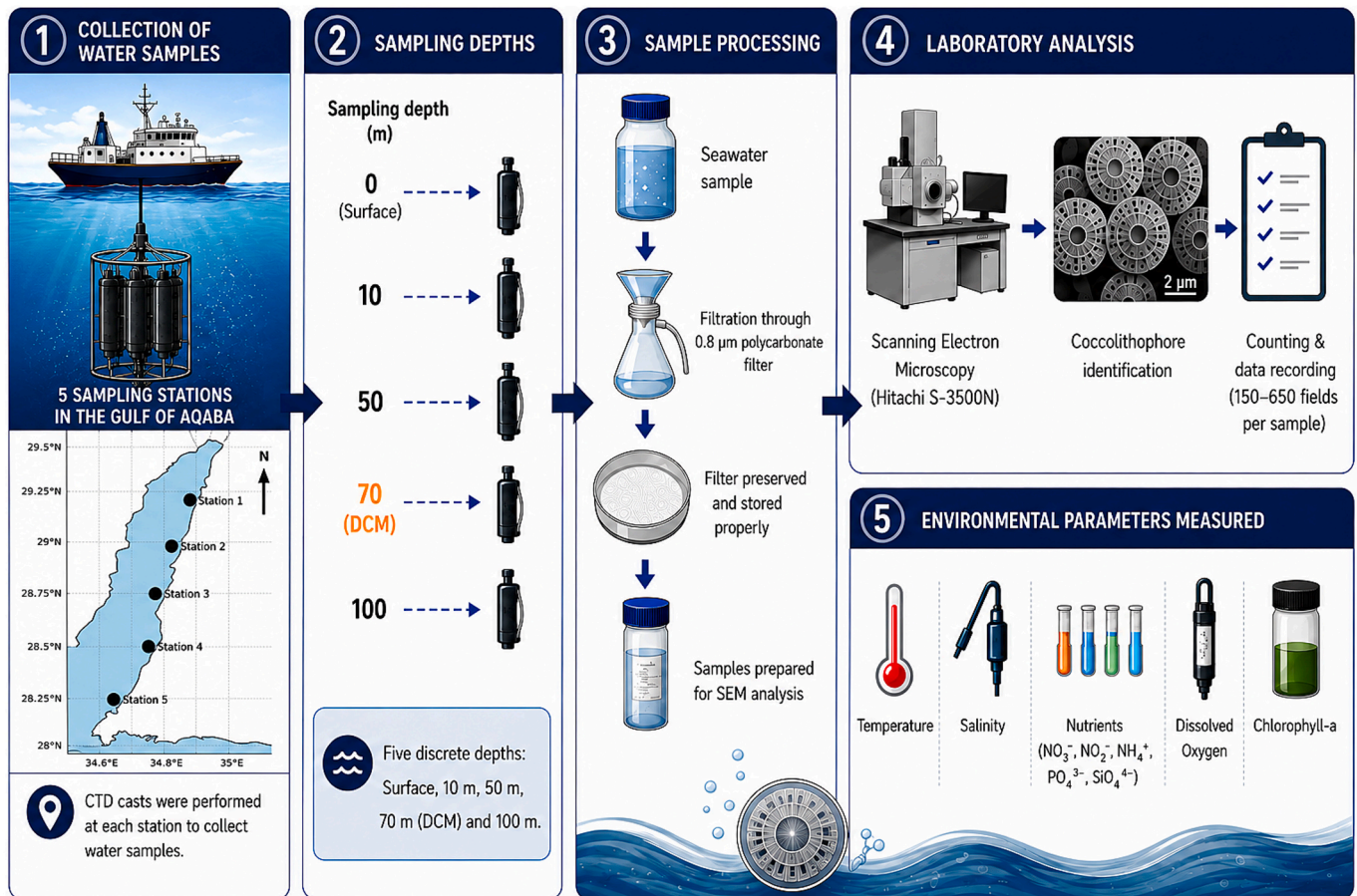


Fig. 2. Schematic overview of the sampling design and analytical procedures employed for coccolithophore investigations in the Gulf of Aqaba.

$$A = \frac{N \times S}{V}$$

where  $A$  represents the absolute abundance of coccospheeres or detached coccoliths ( $\text{ml}^{-1}$  seawater),  $N$  is the number of coccospheeres or detached coccoliths recorded on the filter,  $S$  is scaling factor (total filter area divided by the scanned filter area) and  $V$  is volume of seawater filtered (ml). Coccolithophore species identification followed the taxonomic references of Cros and Fortuño (2002), Young et al. (2003) and Tomas (2012) together with the Nannotax3 database (<http://ina.tmsoc.org/Nannotax3/>). Species names were verified against the most up-to-date taxonomic nomenclature available through the World Register of Marine Species (<https://www.marinespecies.org>) and AlgaeBase (<https://www.algaebase.org>).

#### Data processing and statistical evaluation

Pearson correlation was applied to explore associations between biotic and abiotic variables, whereas one-way ANOVA was used to assess spatial and vertical variations across stations and depths. All statistical analyses were performed using SPSS (v. 23). The relationship between environmental variables and coccolithophore total density was explored using redundancy analysis (RDA). Prior to analysis, physico-chemical parameters and chlorophyll- $a$  were standardized. Ordination was constrained to the environmental matrix, and the significance of the canonical axes was tested using 999 random permutations. These analyses were performed in PAST version 4.3. In addition, species composition, distribution patterns and diversity indices were analysed using PRIMER (v. 6).

## Results

### Physico-chemical parameters and phytoplankton biomass (chlorophyll- $a$ )

Temperature exhibited insignificant spatial variation but differed significantly with depth ( $F = 21.27$ ,  $P < 0.01$ ). Spatially, station 5 had the highest mean temperature ( $25.90 \pm 1.06$  °C), whereas station 1 the lowest ( $24.71 \pm 0.99$  °C). Regarding depth, the highest mean temperature occurred at the surface ( $26.29 \pm 0.38$  °C), whereas the lowest ( $23.18 \pm 0.53$  °C) was recorded at 100 m (Fig. 3A). Salinity showed slight spatial variation with a clear north–south decreasing trend ( $F = 26.09$ ,  $P < 0.01$ ), ranging from  $41.06 \pm 0.03$  at station 1 to  $40.73 \pm 0.07$  at station 4. Vertical differences were minimal, with slightly higher surface values (40.92) compared to deeper layers (70–100 m:  $\sim 40.81$ ) (Fig. 3B). DO remained relatively uniform across stations and depths, ranging from  $2.91 \pm 0.34$  at station 5 to  $4.01 \pm 1.59$  mg L $^{-1}$  at station 4, with only a slight increase towards the surface (Fig. 3C). Nitrate did not exhibit significant spatial or vertical variations among stations or depths (Supplementary material Table 1). However, a slight spatial trend was observed, with mean concentrations increasing southwards from  $2.24 \pm 1.86$   $\mu\text{mol L}^{-1}$  at station 1 to a maximum of  $5.08 \pm 2.01$   $\mu\text{mol L}^{-1}$  at station 4. Vertically, lower mean values were recorded at 10 m depth ( $2.33 \pm 0.89$   $\mu\text{mol L}^{-1}$ ), whereas the highest concentrations were detected at 100 m ( $4.84 \pm 2.28$   $\mu\text{mol L}^{-1}$ ) (Fig. 4A). Nitrite and ammonia displayed uniform distributions (Figs. 4B–C) with narrow mean concentration ranges ( $0.18$ – $0.23$   $\mu\text{mol L}^{-1}$  and  $0.02$ – $0.09$   $\mu\text{mol L}^{-1}$ , respectively) and no significant spatial or vertical variation. Inorganic phosphate and silicate varied significantly among stations ( $F = 23.84$  and  $8.36$ ,  $P < 0.01$ ) but not with depth. Lowest mean of phosphate was recorded at station 4 ( $0.21 \pm 0.01$   $\mu\text{mol L}^{-1}$ ) and the highest at station 3 ( $0.61 \pm 0.29$   $\mu\text{mol L}^{-1}$ ), whereas vertically its values ranged from  $0.31 \pm 0.20$   $\mu\text{mol L}^{-1}$  at 10 m to  $0.39 \pm 0.31$   $\mu\text{mol L}^{-1}$  at 100 m (Fig. 4D). Lowest mean value of silicate was observed at station 2 (2.67

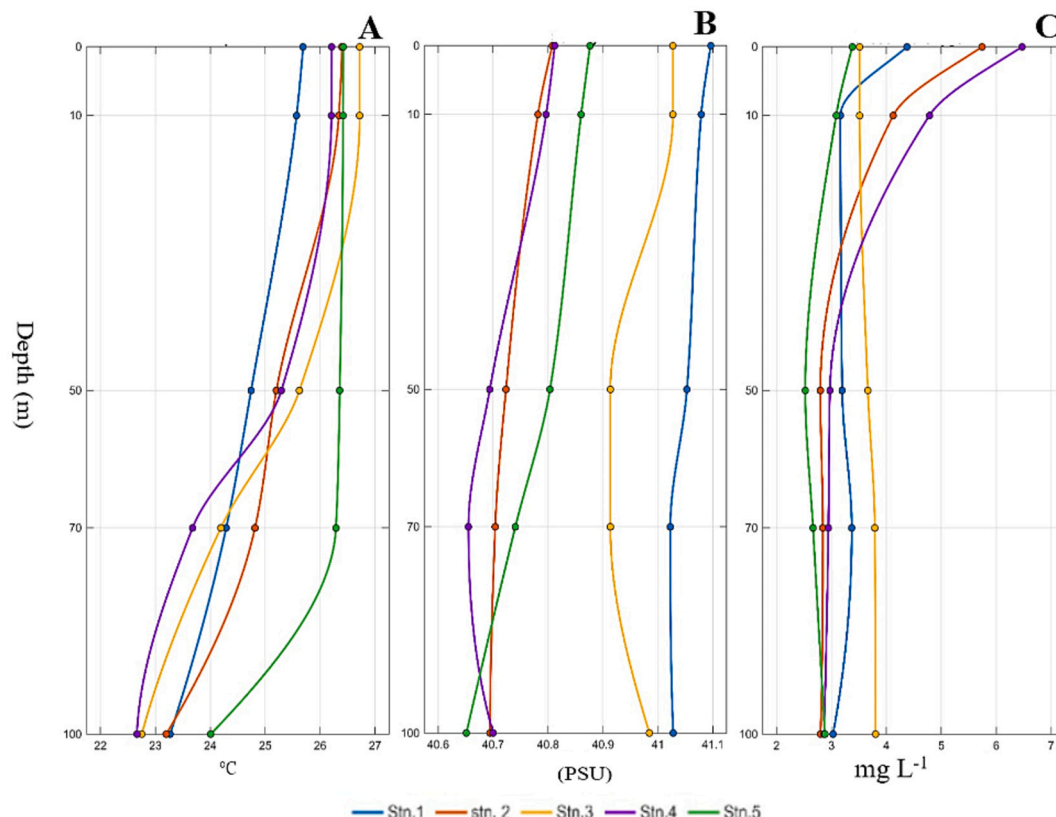


Fig. 3. Vertical distribution of physical parameters observed in the present study. A: Temperature (°C), B: Salinity (PSU), and C: Dissolved oxygen (mg L $^{-1}$ ).

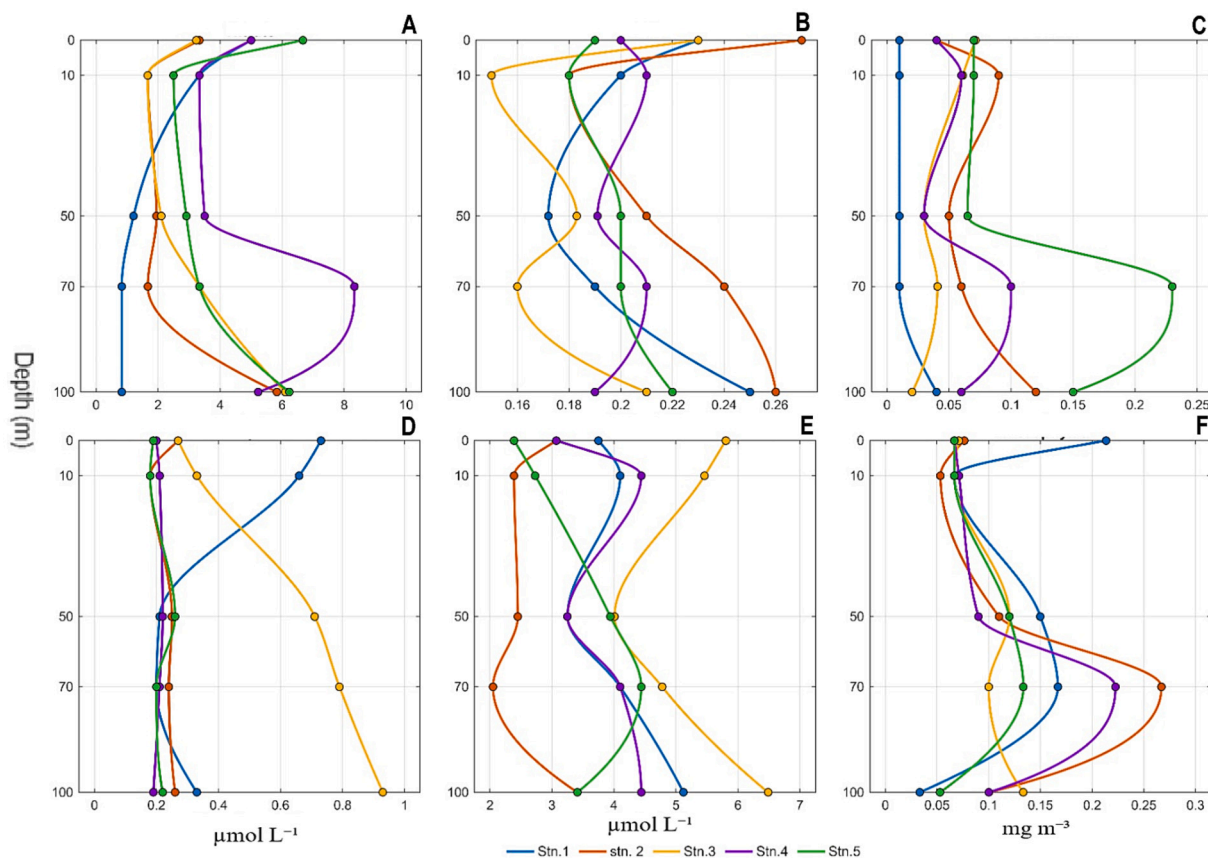


**Fig. 4.** Vertical distribution of inorganic nutrients ( $\mu\text{mol L}^{-1}$ ) and chlorophyll-*a* ( $\text{mg m}^{-3}$ ) observed in the present study. A: Nitrate, B: Nitrite, C: Ammonia, D: Phosphate, E: Silicate, and F: Chlorophyll-*a*.

$\pm 0.55 \mu\text{mol L}^{-1}$ ), and the highest at station 3 ( $5.31 \pm 0.95 \mu\text{mol L}^{-1}$ ). Vertically, concentrations ranged from a minimum of  $3.38 \pm 0.63 \mu\text{mol L}^{-1}$  at 50 m depth to a maximum of  $4.57 \pm 1.29 \mu\text{mol L}^{-1}$  at 100 m depth (Fig. 4E). Phytoplankton biomass revealed no significant spatial or vertical variation. Spatially, mean values ranged from  $0.09 \pm 0.04 \text{ mg m}^{-3}$  at station 5 to  $0.13 \pm 0.07 \text{ mg m}^{-3}$  at station 1. Vertically, the lowest average biomass occurred at 10 m ( $0.06 \pm 0.01 \text{ mg m}^{-3}$ ), whereas the highest was recorded at DCM layer (70 m:  $0.18 \pm 0.07 \text{ mg m}^{-3}$ ) (Fig. 4F).

#### Coccolithophore total abundance

Coccolithophore abundances ranged between  $12.8 \text{ cells ml}^{-1}$  at surface water of station 3 and  $80.1 \text{ cells ml}^{-1}$  at 70 m at station 2 with an average of  $38.4 \pm 20.2 \text{ cells ml}^{-1}$  (Fig. 5). Their abundances showed pronounced depth-wise variation ( $F = 6.70$ ,  $P < 0.01$ ) than its spatial differences (Supplementary material Table 1). The mean abundances were the lowest from the northernmost station, station 1 ( $25.66 \pm 8.79 \text{ cells ml}^{-1}$ ), and the highest was reported from station 4 ( $43.50 \pm 17.50 \text{ cells ml}^{-1}$ ) (Fig. 5). The vertical mean abundances were the least from the surface waters ( $20.51 \pm 6.15 \text{ cells ml}^{-1}$ ), whereas the DCM layer (i. e., 70 m depth) reported the highest mean abundance ( $64.33 \pm 18.03 \text{ cells ml}^{-1}$ ), which was followed by the 100 m depth ( $44.13 \pm 21.22 \text{ cells ml}^{-1}$ ).

#### Dominant contributors to total coccolithophore abundance

The study recorded the dominance of 11 coccolithophore species, which contributed the most to total abundance among the various species observed (Fig. 6). *Gephyrocapsa huxleyi* (Lohmann) P. Reinhardt,

1972 (formerly known as *E. huxleyi*) was the most dominant species observed in the current study. It also played a major role in the overall abundance of coccolithophores over the course of the study. Spatially, mean abundances ranged from  $8.21 \pm 2.64 \text{ cells ml}^{-1}$  at the northernmost station (station 1) and increased gradually towards the south, reaching a maximum of  $19.54 \pm 13.69 \text{ cells ml}^{-1}$  at station 5 (Fig. 6). Vertically, abundances increased towards deeper waters, with the lowest mean value recorded in surface waters ( $8.32 \pm 2.19 \text{ cells ml}^{-1}$ ) and the highest at the DCM layer ( $20.51 \pm 7.56 \text{ cells ml}^{-1}$ ), closely followed by the 100 m depth ( $20.25 \pm 13.40 \text{ cells ml}^{-1}$ ). For the entire study period, the lowest abundance ( $4.3 \text{ cells ml}^{-1}$ ) was recorded at 50 m depth in station 1, whereas the highest individual abundance ( $38.9 \text{ cells ml}^{-1}$ ) was observed at 100 m depth in station 5. The percentage contribution of this species to total abundance was also important. At station 3, the DCM layer had the lowest contribution (22%), whereas the 50 m depth had the most (68%). It is worth noting that its contribution was continuously significant at all depths at station 5, ranging from 36% at the DCM layer to 60% at 100 m depth (Fig. 7). *U. tenuis* (Kamptner) Paasche, 1955, was the next significant species that contributed significantly to the total abundance (ranging from 2% to 19% across various depths and stations). It is clear that this species was more prominent in the northern stations, contributing 8–19% at station 1 and 8–18% at station 2 (Fig. 7). In contrast, it showed the least dominance in the southernmost station (station 5). Across stations, the lowest mean density was recorded at station 5 ( $1.27 \pm 1.37 \text{ cells ml}^{-1}$ ) and the highest at station 2 ( $5.43 \pm 2.60 \text{ cells ml}^{-1}$ ). The 100 m layer exhibited the lowest mean density in the water column ( $2.31 \pm 1.17 \text{ cells ml}^{-1}$ ), whereas the DCM layer exhibited the highest ( $5.13 \pm 2.16 \text{ cells ml}^{-1}$ ). For this species, the maximum individual density was  $8.4 \text{ cells ml}^{-1}$ , whereas the lowest was  $0.5 \text{ cells ml}^{-1}$  (Fig. 6). *Calciopappus rigidus* Heimdal, 1981, had another significant individual density in this study where  $10.5 \text{ cells ml}^{-1}$

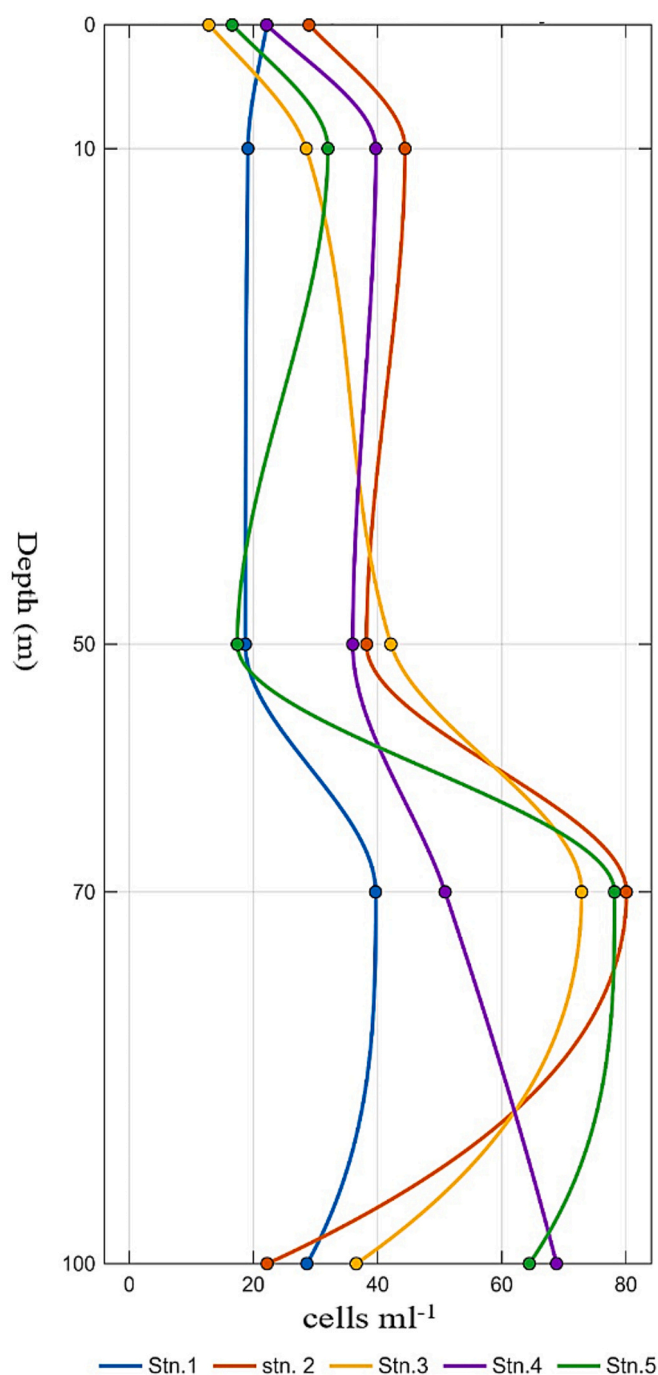


Fig. 5. Vertical distribution of total coccolithophore abundances (cells ml<sup>-1</sup>) from various stations during the study period.

ml<sup>-1</sup> were observed at the DCM layer at both stations 2 and 3. The contributions of eight other dominant species (*Algirosphaera robusta* (Lohmann) R.E.Norris, 1984, *Discosphaera tubifera* (Murray & Blackman) Ostenfeld, 1900, *Gephyrocapsa ericsonii* McIntyre & Bé, 1967, *G. oceanica* Kamptner, 1943, *Ophiaster hydroideus* (Lohmann) Lohmann, 1913, *Rhabdosphaera clavigera* var. *stylifera* (Lohmann) Kleijne & R.W.Jordan, *Syracosphaera pulchra* Lohmann, 1902 and *U. irregularis* Paasche, 1955) are presented in Fig. 6.

#### Coccolithophore community structure

The recorded species in the current study under the phylum Haptophyta can be divided into two main classes: Coccolithophyceae and

Haptophyta incertae sedis. Within Coccolithophyceae, the dominant subclass Prymnesiophyceae comprises four orders Coccolithales, Isochrysidales, Syracosphaerales and Zygodisciales. Collectively, these four orders include nine families. This class also contains another order, Coccolithophyceae incertae sedis. The second class, Haptophyta incertae sedis, consists of three families. The family Syracosphaeraceae showed the highest species richness in the present study, with 23 coccolithophore species, followed by Rhabdosphaeraceae (9 species), Calyptosphaeraceae (7 species), Calcidiscaceae (4 species), Helicosphaeraceae and Noelaerhabdaceae (3 species each), Calciosoleniaceae and Pontosphaeraceae (2 species each), and Coccolithaceae (1 species). A total of 64 species, belonging to 36 different genera, were identified in the current study (Supplementary material Table 2 and see also Figs. 8 and 9). The most species-rich genus was *Syracosphaera*, represented by 18 species, followed by *Alisphaera* (5 species) and *Gephyrocapsa* and *Helicosphaera* (3 species each). Among the species recorded, the majority (72.2%) were HET-type, including species characterized by complex calcified coccoliths. HOL-type species accounted for 22.8%, composed of small, uniformly calcified coccoliths. Nannolith-forming species represented 5% of the assemblage, consisting of species that produce non-motile, plate-like calcareous structures.

#### Spatial and vertical distribution of coccolithophores

In the present study, clear zonation patterns were observed for the different coccolithophore species. Among them, four species—*G. huxleyi*; *S. pulchra*; *U. irregularis* and *U. tenuis*—were ubiquitous, occurring throughout the study region and at all sampling depths. Whereas, *Florisphaera profunda* His. Okada & Honjo, 1973, was recorded only in the deeper layers (70 and 100 m), *Alisphaera extenta* Kleijne, R.W. Jordan, Heimdal, Samtleben, A.H.L. Chamberlain & Cros, 2002, occurred exclusively at the DCM depth. Among identified taxa, 28 were found in the surface waters, accounting for nearly 35% of the total assemblage and 18 species (23%) were present across all sampling stations, although not necessarily at all depths. In contrast, another set of 18 species occurred only at the northern stations (stations 1 and 2) and were completely absent from the southern stations (Supplementary material Table 2).

#### Species diversity and new records from the Red Sea

In this study, 64 coccolithophore species representing 36 genera were identified. A comparative account of previous investigations from both the GoA and the Red Sea is provided in Supplementary material Table 3, encompassing records from both water column as well as sediment samples. In the present study, eight species are reported for the first time in the GoA and the Red Sea. These species are *Calicasphaera concava* A.Kleijne, 1991, *Calyptrolithophora papillifera* (Halldal) Heimdal, 1980, *Ceratolithus cristatus* Kamptner, 1954, *Cyrtosphaera lecaliae* A. Kleijne 1992, *Palusphaera vandellii* Lecal-Schlauder, 1967, *Syracosphaera delicata* Cros et al., 2000, *S. didyma* Kleijne & Cros, 2009 and *Zygospaera amoena* Kamptner, 1937. Concerning the global distribution of the recorded species in the area of study, 16 species exhibited a worldwide distribution and are considered pioneer species that dominate coccolithophore assemblages in the world's oceans. *Gephyrocapsa huxleyi* was the predominant and most abundant species recorded in this study. Nineteen species exhibited a broad distribution pattern extending across tropical, subtropical and temperate zones, whereas 13 species were restricted to tropical and subtropical regions. Species such as *Calcipappus rigidus* Heimdal, 1981, *Poricalyptra magnaghii* (Borsetti & Cati) Kleijne, 1991, *Syracosphaera halldalii* Gaarder ex R.W.Jordan & J.C. Green, 1994, and *Syracosphaera ossa* Lecal-Schlauder, 1968, observed in this study, are previously known to occur only in the tropical zone, whereas *Alisphaera gaudii* Kleijne, Jordan, Heimdal, Samtleben, Chamberlain & Cros, 2002, *Calyptrolithina divergens* var. *tuberosa* (Heimdal) Jordan, Kleijne & Heimdal, 1993, and *Helicosphaera pavementum* Okada

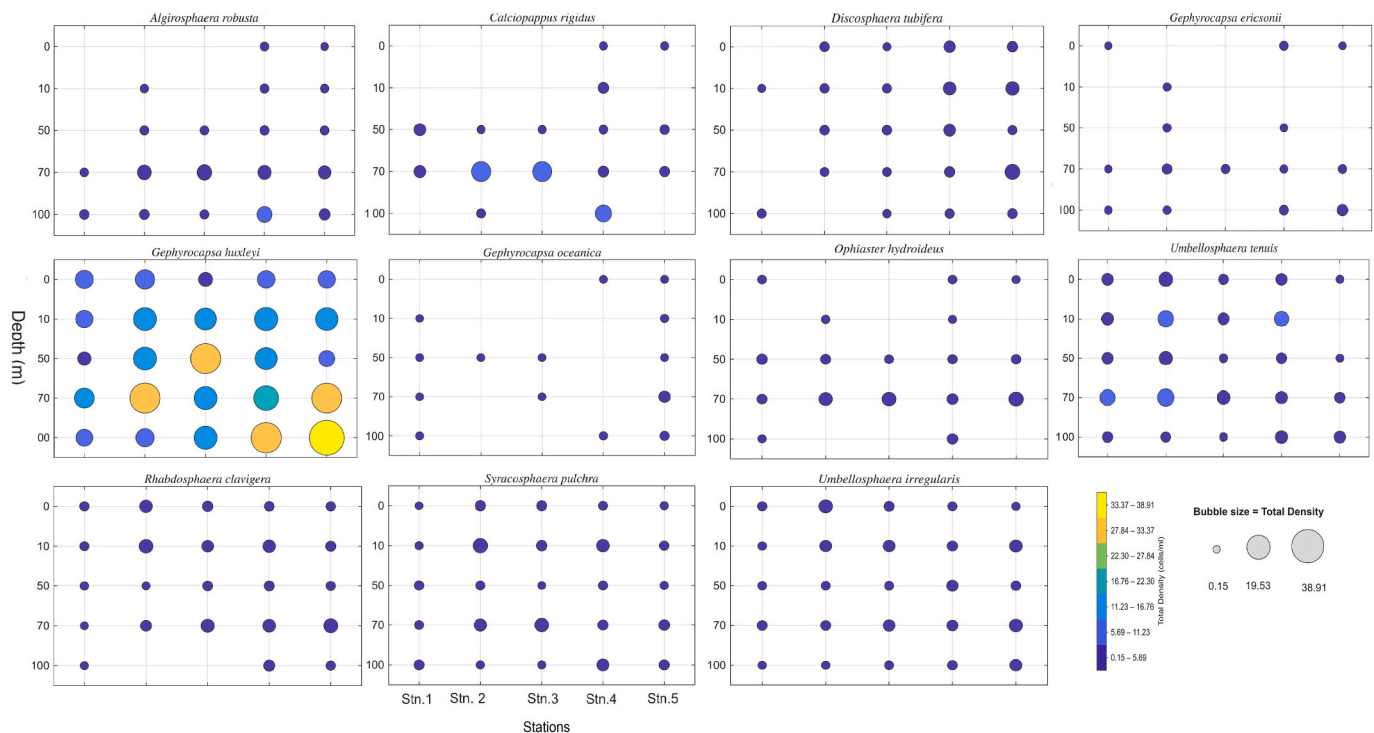


Fig. 6. Vertical distribution of individual abundances of dominant coccolithophore species (cells ml<sup>-1</sup>) observed in the present study from various stations.

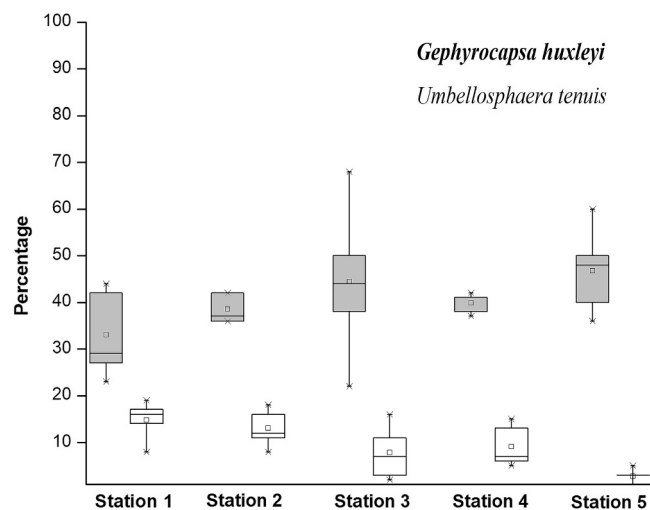


Fig. 7. Boxplots showing the percentage contribution of *Gephyrocapsa huxleyi* (grey) and *Umbellosphaera tenuis* (white) at different depths across various stations during the study period. The boxplots represent the interquartile range (25th–75th percentiles), with the median shown as a horizontal line and the mean indicated by a square. Whiskers extend to the minimum and maximum values within each sector, and error bars represent variability across stations.

& McIntyre, 1977 are known to occur only in subtropical zone. *Coccolithus pelagicus* subsp. *braarudii* (K.R.Gaardner) M.Geisen, C.Billard, A.T. C.Broerse, L.Cros, I.Probert & J.C.Young, 2002, *Sphaerocalyptra quadridentata* (Schiller) Deflandre, 1952 and *Syracosphaera corolla* J.Lecal, 1966, recorded in the current study, are primarily distributed in subtropical/temperate regions, whereas species such as *Syracosphaera delicata* Cros et al., 2000, *Syracosphaera didyma* Kleijne & Cros, 2009, *Zygospheera amoena* Kamptner, 1937 and *Zygospheera marsilii* (Borsetti & Cati) Heimdal, 1982 have been previously reported only from temperate zones.

#### Statistical interpretations

Pearson correlation analysis revealed a significant positive association between coccolithophore total density and ammonia ( $r = 0.46$ ,  $P < 0.05$ ), whereas a significant negative correlation was observed with salinity ( $r = -0.52$ ,  $P < 0.01$ ) (Fig. 10). The RDA indicated that coccolithophore distribution was strongly associated with environmental gradients across depths and stations in the GoA (Fig. 11). The first canonical axis (RDA1) explained 98.16% of the total constrained variance, whereas the second axis (RDA2) accounted for only 1.54%, indicating that the primary environmental gradients represented by RDA1 overwhelmingly governed the observed patterns in coccolithophore community composition. RDA1 clearly separated nutrient-enriched from nutrient-poor conditions and reflected the combined influence of temperature, salinity and macronutrient availability on species distribution. The vectors for nitrate, nitrite, phosphate, silicate and DO were closely grouped and oriented opposite to total coccolithophore density (TD) and *G. huxleyi*, indicating greater coccolithophore abundance and the dominance of *G. huxleyi* under warm, oligotrophic surface-water conditions. In contrast, *U. tenuis*, located near the centre of the ordination plot, exhibited a weaker association with the measured environmental gradients, suggesting a broader ecological tolerance.

Overall, the RDA demonstrates that the combined effects of water-column stratification, temperature, salinity and nutrient availability are the principal drivers of coccolithophore distribution in the GoA, with *G. huxleyi* serving as a characteristic indicator of oligotrophic surface waters. Concerning the different biodiversity indices, species number (*S*) varied among stations and depths, with the highest average richness observed at 70 m ( $29 \pm 3.6$ ), reflecting peak diversity at mid-depths (Fig. 12). Whereas, surface waters showed high variability ( $19 \pm 9.1$ ), with station 5 recording the highest richness (32 species) and station 3 the lowest (9 species). Moderate richness occurred at 50 m ( $24.2 \pm 7.0$ ), whereas 100 m showed a general decline ( $18.2 \pm 5.5$ ). Margalef's richness index (*d*) followed a similar pattern, where the maximum appeared at 70 m ( $2.55 \pm 0.28$ ). Surface waters exhibited the greatest variability ( $1.83 \pm 1.04$ ), with station 5 showing the highest value (3.20) and station 3 the lowest (0.85). Moderate richness was observed

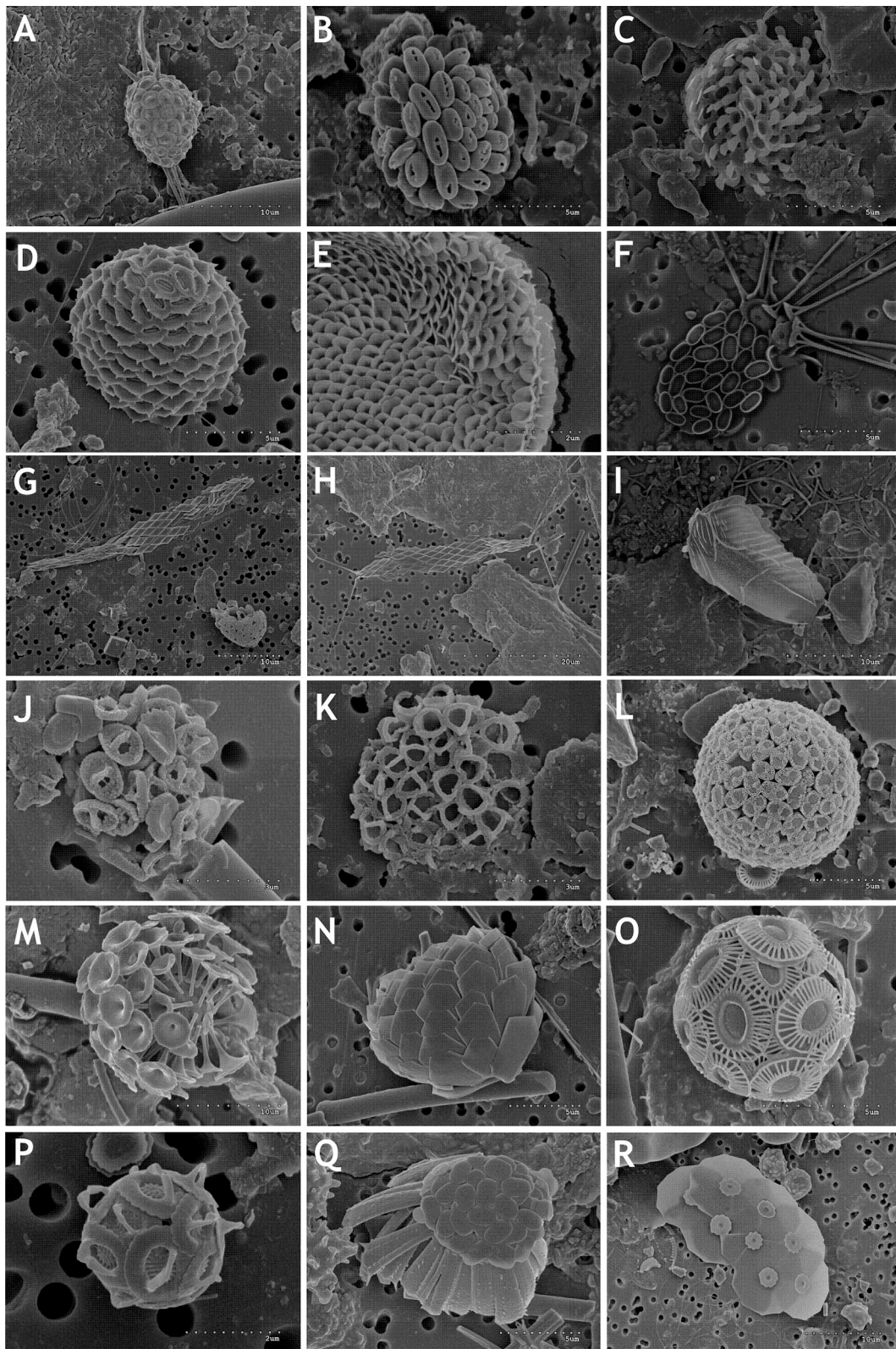


**Fig. 8.** SEM images of coccolithophores collected from Gulf of Aqaba. A: *Acanthoica quattropsina*, B: *Algirosphaera robusta*, C: *Alisphaera capulata*, D: *Alisphaera gaudii*, E: *Alisphaera unicornis*, F: *Calciopappus rigidus*, G: *Calciosolenia brasiliensis*, H: *Calciosolenia murrayi*, I: *Ceratolithus cristatus*, J: *Corisphaera gracilis*, K: *Corisphaera* type B, L: *Coronosphaera mediterranea*, M: *Discosphaera tubifera*, N: *Florisphaera profunda*, O: *Gephyrocapsa huxleyi*, P: *Gephyrocapsa oceanica*, Q: *Gladiolithus flabellatus*, R: *Hayaster perplexus*.

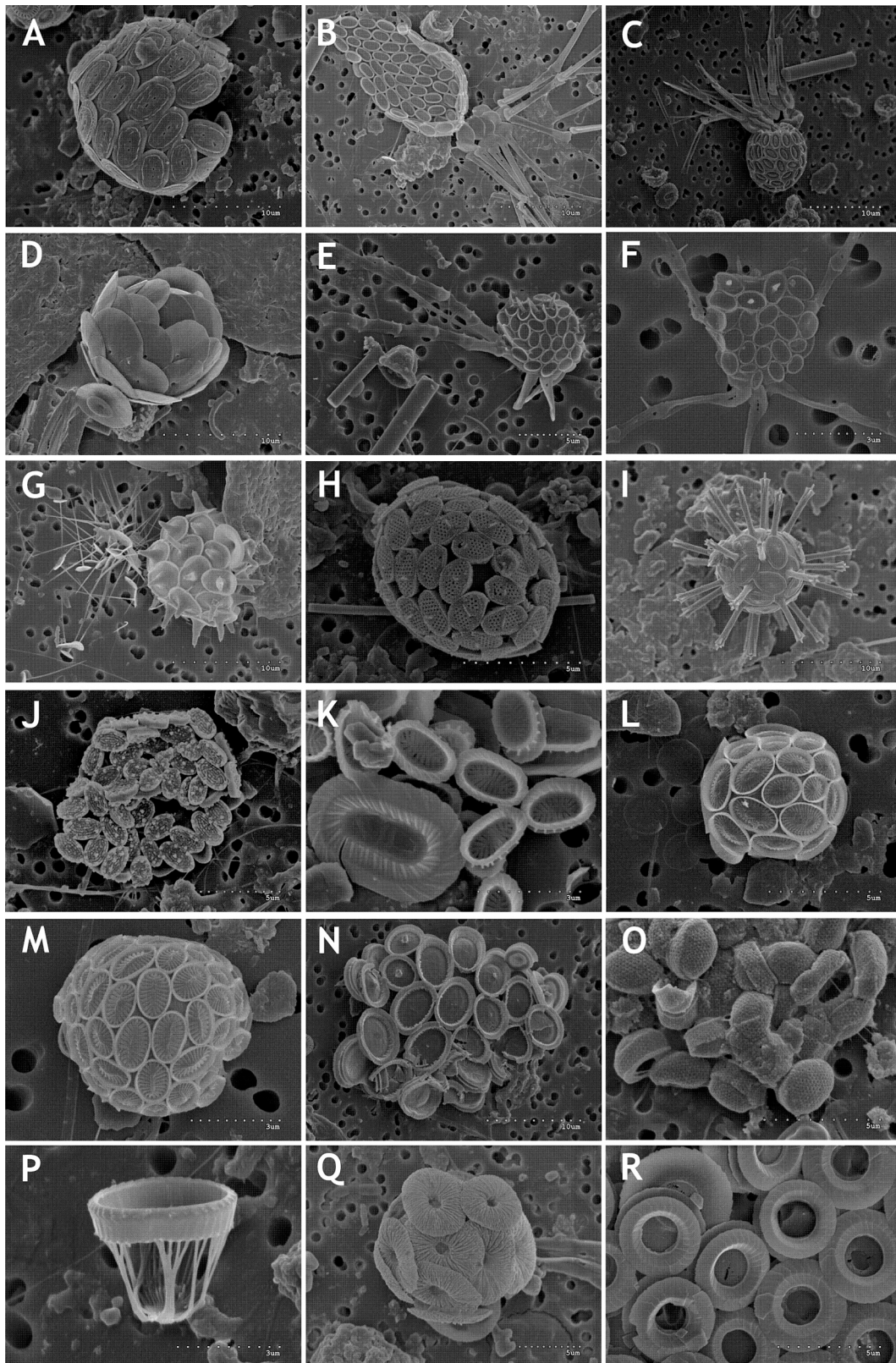


**Fig. 9.** SEM images of coccolithophores collected from Gulf of Aqaba. A: *Helicosphaera pavimentum*, B: *Michaelsarsia adriatica*, C: *Michaelsarsia elegans*, D: *Oolithotus antillarum*, E: *Ophiaster hydroideus*, F: *Ophiaster reductus*, G: *Palusphaera vandellii* and *Cyrtosphaera aculeata*, H: *Poricalyptra magnaghii*, I: *Rhabdosphaera clavigera*, J: *Syracolithus* sp. type A, K: *Syracosphaera azureaplaneta*, L: *Syracosphaera leptolepis*, M: *Syracosphaera nana*, N: *Syracosphaera pulchra*, O: *Syracosphaera pulchra* HOL galea type, P: *Syracosphaera winteri*, Q: *Umbellosphaera tenuis*, R: *Umbilicosphaera sibogae*.

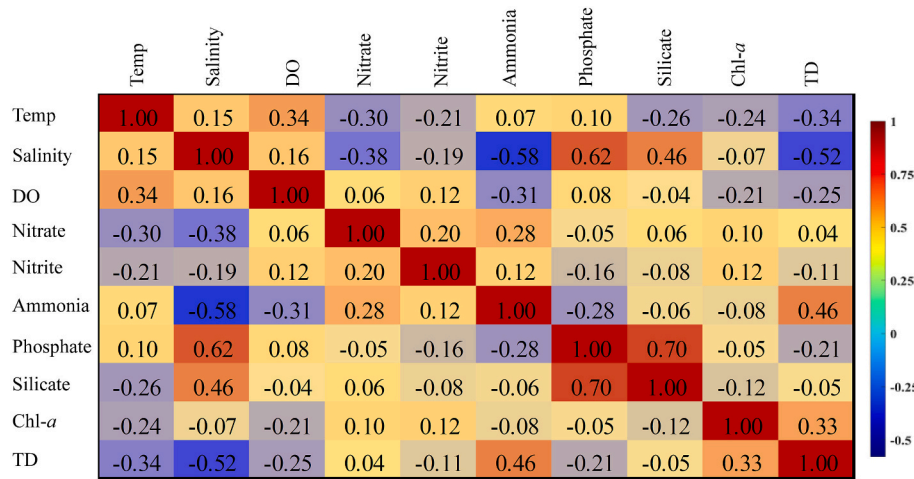


Fig. 10. Pearson correlation analysis between various biotic and abiotic parameters obtained in the present study.

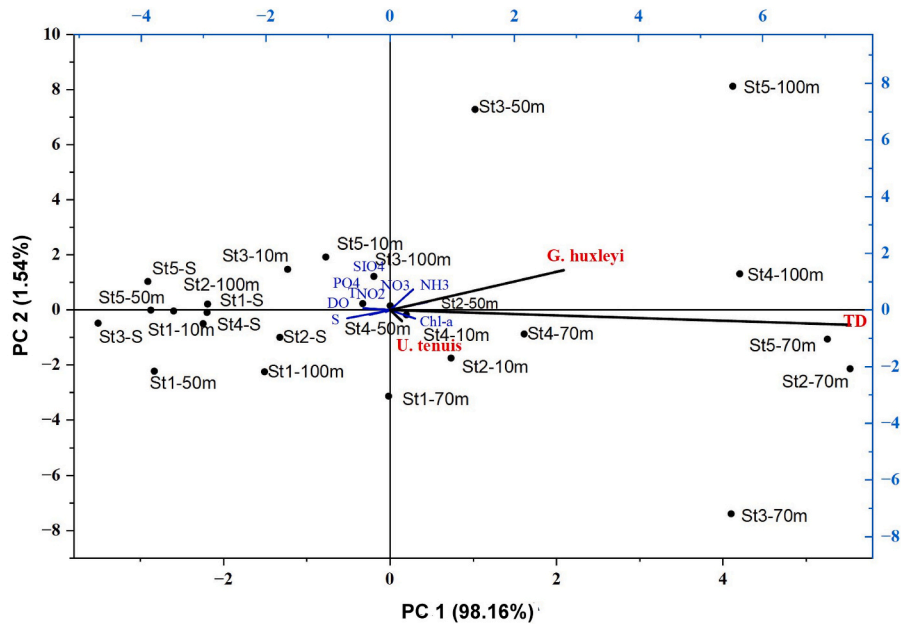


Fig. 11. Redundancy analysis (RDA) showing the influence of environmental variables on total coccolithophore abundances.

at 50 m ( $2.45 \pm 0.63$ ), whereas the lowest values occurred at 10 m ( $1.53 \pm 0.33$ ) and 100 m ( $1.62 \pm 0.48$ ). Pielou's evenness ( $J'$ ) indicated generally well-distributed species across stations and depths, with the highest mean evenness at 70 m ( $0.75 \pm 0.03$ ). Surface waters had moderate evenness ( $0.72 \pm 0.08$ ), whereas 50 m showed greater variability ( $0.71 \pm 0.13$ ) due to lower evenness at station 3 (0.48). Evenness at 10 m ( $0.69 \pm 0.03$ ) and 100 m ( $0.71 \pm 0.09$ ) reflected relatively balanced species distributions. Shannon–Wiener diversity showed highest mean diversity at 70 m ( $2.53 \pm 0.17$ ), whereas surface, 50 m and 100 m depths showed moderate but more variable diversity ( $2.00 \pm 0.18$ ,  $2.20 \pm 0.38$  and  $2.04 \pm 0.41$ , respectively). Diversity at 10 m was relatively homogeneous ( $1.95 \pm 0.14$ ), indicating more balanced species composition in shallow waters (Fig. 12).

## Discussion

The present study conducted in mid-September, represents the concluding phase of the summer stratification period in the GoA as reported by Biton and Gildor (2011). Despite being close to the onset of seasonal mixing, clear signatures of stratification were still evident in

our results, as reflected by the vertical distribution of temperature and salinity. There were strong vertical gradients in temperature, which implies the persistence of a stratified water column, whereas salinity remained relatively stable with depth and showed minimal variability among the different stations. In the GoA, the transition from stratification to winter mixing typically begins in early October, when surface cooling and convective processes gradually break down the thermocline and lead to the development of a well-mixed water column.

Our observations of the physical parameters are consistent with those reported in previous studies carried out in the summer period (Berman et al., 2023). It is well established that the southern part of the GoA experiences stronger and more persistent stratification than the northern region. This spatial distinction has been reported in several earlier studies (Berman and Gildor, 2022; Levanon-Spanier et al., 1979) and is further supported by our present findings. The present results verify the fact that stratification signals were stronger in the southern stations, whereas the northern stations exhibited relatively weaker vertical gradients. Such spatial variability underscores the influence of regional hydrographic conditions on the intensity and duration of stratification within the GoA. The distribution of inorganic nutrients

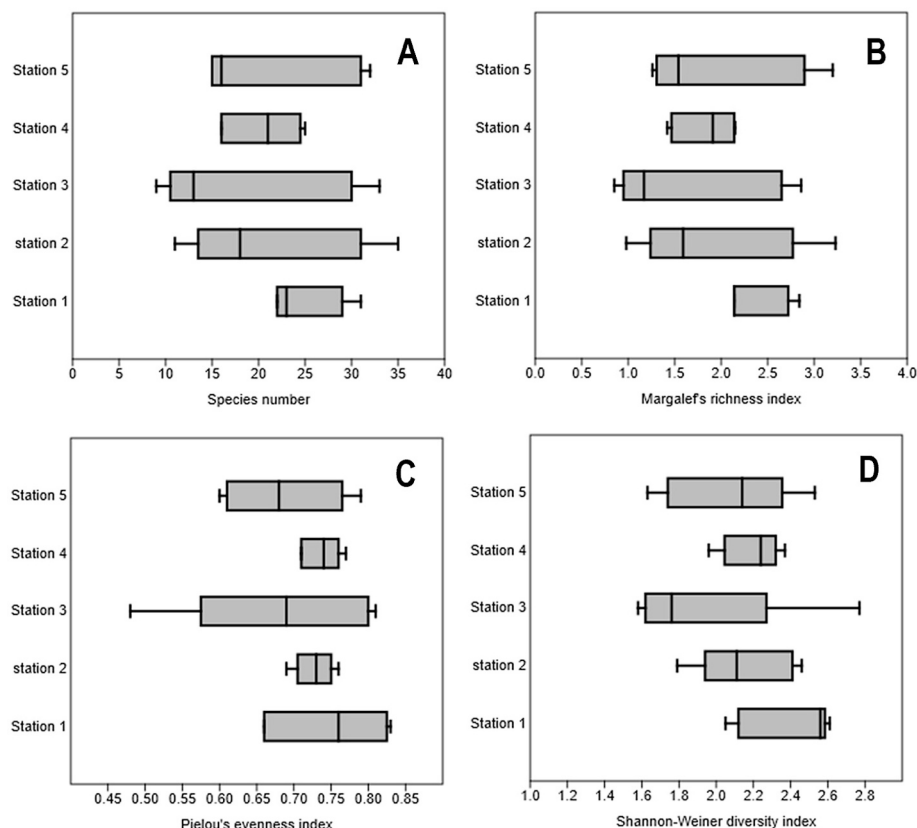


**Fig. 12.** Boxplots showing the various biodiversity indices obtained in the present study. The boxes represent the interquartile range (25th–75th percentiles), the mean is shown as a horizontal line. Whiskers extend to the minimum and maximum values, while error bars represent variability across stations.

other than nitrates further indicated the continuation of summer stratification in the GoA (Fuller et al., 2005; Mackey et al., 2007). The surface waters were mostly nutrient-depleted, consistent with the absence of external inputs and the region's minimal precipitation (Acker et al., 2008; Manasrah et al., 2007). An exception was observed in the case of nitrates, which were present in measurable amounts at the surface and increased markedly with depth. This vertical pattern is characteristic of the stratified period, yet the elevated nitrate signal near the surface may also be indicative of the imminent breakdown of stratification, as the onset of winter mixing approaches. In the GoA, primary productivity is strongly regulated by the seasonal mixing regime. The deep convective mixing that develops during winter entrains nutrient-rich waters into the euphotic zone, replenishing the depleted surface layer and fuelling phytoplankton growth (Fuller et al., 2005; Post et al., 2011). Therefore, the nutrient profiles observed in this study not only confirm the late-summer stratification but also provide an early indication of the shift into the highly productive winter. According to previous studies, the timing of the present investigation would generally fall within the summer stratification period. However, the detection of considerable nitrate concentrations throughout the water column suggests that the system was already undergoing a transition from stratified to mixed conditions. This transitional phase, occurring between late summer stratification and the onset of winter mixing, is further supported by several indicators observed in the present study. It is well established that subsurface nitrate concentrations in the GoA increase during summer stratification, as reported in previous studies of Mackey et al. (2007), El-Sherbiny et al. (2019), Berman and Gildor (2022) and Berman et al. (2023), reflecting the isolation of nutrient-rich deep layers from the nutrient-depleted surface. Nonetheless, the detectable nitrate concentrations in the surface waters suggest that vertical transport processes may already have influenced the upper water column during the late summer period. Although these observations are consistent with

the early stages of seasonal mixing described by Biton and Gildor (2011), other hydrodynamic processes, including localized upwelling, internal wave activity, or episodic wind-driven mixing, may also have contributed to the upward transport of nutrients into the surface layer. Therefore, the observed nutrient distribution likely reflects the combined influence of these physical processes during the transition from late summer stratification towards winter mixing. This underscores the fact that winter mixing has an inter-annual variability depending on regional hydrographic conditions and wind patterns (Berman et al., 2023). This variability explains why the present study, conducted in mid-September, revealed both persistent signals of stratification and early signs of mixing within the water column. Despite the considerable presence of nitrates in the water column, phytoplankton biomass, estimated as chlorophyll-*a*, was significantly lower both spatially and vertically, indicating the presence stratification in the region (Acker et al., 2008). Previous studies suggest that nutrients, particularly phosphates, may serve as a limiting factor in the GoA (Suggett et al., 2009), which could explain the observed lower phytoplankton biomass in this study. It is well known that during the summer stratification period, the GoA becomes highly oligotrophic, exhibiting much lower phytoplankton biomass compared to other seasons (Lindell and Post, 1995). The values obtained in the current study are well comparable with previous findings in the area during this period (Berman and Gildor, 2022; El-Sherbiny et al., 2019; Mackey et al., 2007). During the summer period in the GoA, ultraphytoplankton groups (<8  $\mu\text{m}$ ) dominate, as they are well known to thrive under nutrient-limited conditions (Lindell and Post, 1995). Once winter mixing becomes well established, conditions in the Gulf change drastically. With the influx of nitrates and other essential nutrients, along with more favourable environmental conditions, primary productivity increases, as documented by previous studies of Levanon-Spanier et al. (1979), Fuller et al. (2005) and Post et al. (2011).

In the current study, the average coccolithophore abundance was fairly low that are comparable to nutrient-poor gyres as well as oligotrophic waters (Winter et al., 2002). Moreover, its total densities indicated greater vertical than spatial variation, a pattern that is usually observed in oligotrophic waters during stratified periods in the eastern Mediterranean Sea and GoA (Keuter et al., 2022, 2023, respectively). Stratification depletes surface waters of nutrients, creating unfavourable conditions for the growth of most marine phytoplankton; consequently, only pico- and nano-phytoplankton thrive under these nutrient-limited conditions (Fenchel, 1988). During summer stratification, the GoA becomes highly oligotrophic, favouring the dominance of ultra-phytoplankton such as picoeukaryotes, which thrive under nutrient-depleted conditions (Lindell and Post, 1995). Compared with other larger phytoplankton groups, the occurrence of coccolithophores is rather favourable; however, their abundance still remains lower than that of ultraphytoplankton. Although their abundance may appear lower compared with other phytoplankton groups, coccolithophores in oligotrophic waters like GoA play a crucial role in driving the downward transport of biogenic material and facilitate the movement of carbon and sulphur between the atmosphere and surface waters (de Vargas et al., 2007). In the present study, coccolithophores showed their highest abundances at deeper layers, at DCM (~70 m) and at 100 m depth. This vertical distribution pattern is a characteristic feature commonly observed during the summer stratification period in both tropical and subtropical areas, as well as in other oligotrophic waters (Haidar and Thierstein, 2001; Keuter et al., 2022; Oviedo et al., 2015; Winter et al., 2002). According to Winter et al. (1979), temperature, nutrient availability and light penetration are the major factors regulating the distribution and abundance of coccolithophores in the GoA. Earlier studies in the region, including that of Frada et al. (2022) and Keuter et al. (2023), who studied one station in the northernmost GoA, reported similar vertical differences in coccolithophore abundance, with higher abundances occurring in deeper layers during the summer stratification period. Similarly, Winter et al. (1979) observed comparable distribution patterns at both the northernmost and southernmost stations of the gulf, with densities close to those recorded in the present study. Based on these results, our findings show that such vertical patterns, including deeper maxima and comparable densities during stratification, are consistent throughout the GoA, as this is the first investigation to comprehensively cover the entire region. Although spatial differences were minimal, a clear trend of increasing coccolithophore abundance was observed towards the southern GoA near the Tiran Strait. This pattern may be attributed to the stronger stratification in the southern region than in the northern part of the Gulf during the summer period (Berman and Gildor, 2022; Levanon-Spanier et al., 1979). No statistically significant correlation was found between coccolithophore abundance and the major abiotic factors, suggesting that their distribution and abundance in the GoA are influenced collectively by multiple environmental parameters (competition, grazing, etc.) rather than by a single dominant factor. The lack of significant correlations is a common feature reported in other studies as well (Cortés et al., 2001; Haidar and Thierstein, 2001). For instance, although availability of nitrates in the water column was relatively high, no significant relationship was observed between coccolithophore density and this nutrient. Although coccolithophores are generally expected to thrive in nitrogen-rich waters (Vuković and Godrijan, 2025), their growth in the GoA may be constrained by other limiting factors of primary productivity, which likely inhibit their response to nitrate availability.

*Gephyrocapsa huxleyi* was the dominant species contributing to the total coccolithophore abundance in the current study. Its distribution was similar to that of the vertical distributions of the total coccolithophore community, with highest abundance in deeper waters, whereas surface occurrences, though lower, remained ecologically significant. This species is well known for its ubiquitous distribution throughout the water column in oceans worldwide and plays a major role in marine

productivity (Haidar and Thierstein, 2001; Kinkel et al., 2000; Winter et al., 2002). The densities of this species observed in the current study are comparable to those documented in previous investigations from the GoA (Frada et al., 2022; Keuter et al., 2023; Winter et al., 1979), as well as in other oligotrophic marine systems (Ausín et al., 2018; Keuter et al., 2022; Oviedo et al., 2015). This species is known for its preference for elevated nitrate concentrations. In the present study, higher nitrate levels were observed, creating favourable conditions for this species, which often competes with larger phytoplankton, such as diatoms, and frequently dominates over them under these conditions. Furthermore, they are known to thrive under intense light conditions (Nanninga and Tyrrell, 1996), which makes them particularly well suited to dominate the highly illuminated waters of the GoA. *Umbellosphaera tenuis* also contributed significantly to the density of total coccolithophore and was predominantly occurred at the northern stations, suggesting a preference for conditions in the northern GoA. Similar patterns have been previously reported in the GoA by Winter et al. (1979) and Keuter et al. (2023). Many studies in tropical and subtropical regions have reported the co-dominance of *U. tenuis* and *G. huxleyi*, with *U. tenuis* identified as a characteristic coccolithophore species of oligotrophic waters (Boeckel and Baumann, 2008; Cortés et al., 2001; Keuter et al., 2022; Kinkel et al., 2000; Kleijne, 1993). Species within the genus *Umbellosphaera* are known to dominate in oligotrophic surface waters (0–100 m) in subtropical latitudes (10–30°N) as documented by Okada and Honjo (1973), whereas they are generally absent at higher latitudes. Other major species, such as *S. pulchra* and *U. irregularis*, which contributed significantly to total abundances or were dominant throughout the area of study, are also recognized as key constituents of coccolithophore communities in both tropical and subtropical waters. These species are also significant in the biogenic calcite production and contribute to nutrient cycling within oligotrophic ecosystems (Dimiza et al., 2015; Kinkel et al., 2000). The deep-dwelling coccolithophore species *F. profunda* showed strong vertical preferences in this study, predominantly occurring at depths of 70–100 m. This distribution likely reflects its adaptation to low-light, nutrient-enriched conditions found in the deeper euphotic zone, which are typical of oligotrophic tropical and subtropical waters (Ausín et al., 2018; Boeckel and Baumann, 2008; Keuter et al., 2022, 2023; Kinkel et al., 2000; Oviedo et al., 2015; Winter et al., 1979, 2002). Moreover, *A. extenta* was only detected at DCM, suggesting a preference for deeper waters in oligotrophic environment. The present study also revealed a clear zonation in species distribution, with some taxa preferring the warm surface waters, others restricted to the northern stations and a few occurring throughout the region. This pattern underscores that coccolithophore distribution in the GoA during the stratification period is a complex process, warranting further detailed investigations to fully understand the underlying distribution patterns. Similar relationships between hydrodynamic conditions and living coccolithophore assemblages have recently been reported from the eastern Mediterranean, where hydrodynamic regime strongly influenced species composition and vertical distribution (Dimiza et al., 2026). The different biodiversity indices obtained in the present study further support this conclusion. Comparable vertical changes in coccolithophore diversity and community composition have also been documented in the western Black Sea during summer, demonstrating the importance of environmental gradients in structuring coccolithophore assemblages (Dimiza et al., 2023).

Among the different life cycle phases of coccolithophores, the present study recorded a dominance of species in the HET stage compared to the HOL stage. However, in terms of abundance, HOL outnumbered HET, consistent with their ability to thrive under nutrient-depleted conditions (Oviedo et al., 2015). The community structure of coccolithophore showed the dominance of the family Syracosphaeraceae, represented by 23 species, indicating the preference of its members for nutrient-depleted, stratified waters. Although none of these species dominated in terms of abundance, they are considered ecologically important due to their widespread distribution. The family

Syracosphaeraceae is one of the most diverse and widely distributed groups of coccolithophores, typically associated with warm, oligotrophic and stratified waters of tropical and subtropical oceans (Ausín et al., 2018; Dimiza et al., 2015; Keuter et al., 2019, 2022). The dominance of Syracosphaeraceae observed in the present study agrees with recent global syntheses that recognize this family as one of the most diverse and ecologically important coccolithophore groups inhabiting oligotrophic tropical and subtropical oceans (Vuković and Godrijan, 2025). The present study reports 8 new records, increasing the total number of documented coccolithophore species to 64 (Supplementary material Table 2). These newly recorded species most likely reflect the comprehensive spatial and vertical sampling strategy employed in the present study, together with detailed species identification using SEM, rather than recent changes in species distributions. Previous investigations in the GoA and the Red Sea were generally restricted to fewer stations, limited depth coverage or localized surveys, which may have underestimated the regional diversity of coccolithophores. These new records therefore expand the known biodiversity of the Red Sea and highlight the importance of systematic, high-resolution surveys for documenting the full extent of coccolithophore diversity in oligotrophic marine ecosystems. Typically, coccolithophore diversity increases during the summer stratification period than during other seasons, as stratified conditions create stable light and nutrient gradients that favour a wider range of species (Dimiza et al., 2015; Haidar and Thierstein, 2001; Keuter et al., 2023; Winter et al., 1979). This increase in species richness not only reflects the seasonal peak in diversity but also highlights the benefits of extensive spatial coverage, which was not observed in previous studies in the GoA (Keuter et al., 2023; Winter et al., 1979) and the Red Sea (Kleijne, 1991; Okada and Honjo, 1975). These new records substantially improve our understanding of coccolithophore biodiversity in the region and establish important baseline information for future ecological and biogeographical studies. Overall, these findings underscore that coccolithophore distribution in the GoA during the stratification period is a complex process, influenced by both seasonal dynamics and spatial heterogeneity, and warrant further detailed investigations to fully resolve the patterns and drivers of their distribution.

## Conclusion

This study provides the first comprehensive assessment of coccolithophore communities across the Saudi Arabian sector of the GoA during the late summer stratification period. The results demonstrated pronounced vertical variation in coccolithophore abundance, diversity and community composition, with maximum abundance and species richness occurring near the DCM ( $\approx 70$  m), highlighting the importance of water-column stratification in shaping community structure. The observed spatial differences were comparatively minor, indicating that vertical environmental gradients exert a stronger influence than horizontal variability during the stratified season. The study further demonstrated that coccolithophore distribution is closely associated with key environmental variables, particularly water-column stratification, nutrient availability and salinity. *Gephyrocapsa huxleyi* was the dominant species throughout the study area, whereas *U. tenuis* and several other taxa displayed distinct depth and spatial preferences, reflecting species-specific ecological adaptations to oligotrophic conditions. A total of 64 coccolithophore species belonging to 36 genera were identified, including eight species recorded for the first time from the GoA and the Red Sea, substantially expanding the known regional diversity. These findings provide an important taxonomic and ecological baseline for future studies on coccolithophore biodiversity, biogeography and environmental change in the Red Sea. Overall, this study advances our understanding of the spatial and vertical ecology of coccolithophores in one of the world's most oligotrophic marine ecosystems and provides valuable baseline information for assessing the impacts of future environmental and climatic changes on coccolithophore

communities in the GoA.

## CRedit authorship contribution statement

**Mohsen M. El-Sherbiny:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Faisal M. Alsaq:** Writing – review & editing, Visualization, Software, Formal analysis.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ejar.2026.08.004>.

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