Coccolithophore assemblages and a new species of *Alisphaera* from the Faafu Atoll, Maldives, Indian Ocean

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Abstract

Coccolithophore assemblages were investigated from the Faafu Atoll in November 2018. The surface waters were sampled around the islands of Magoodhoo and Adanga, from the coast to the open water towards both the lagoon and the ocean, as well as waters up to 40 m depth at selected stations. Coccolithophores were scarce close to the coast (0.1-4 x 10^3 coccospheres/litre) and increased in abundance towards both the lagoon and the open ocean (20-44 x 10^3 coccospheres/litre) and showed no clear depth trend. The assemblages were dominated by *Gephyrocapsa oceanica* and with a large contribution by species that are typically reported from the mid- to lower-photic zone, i.e., primarily *Oolithotus antillarum*, followed by *Calciosolenia* spp., *Michaelsarsia adriaticus*, *Calciopappus rigidus*, *Ophiaster* spp. and *Algirosphaera robusta*. As for other tropical settings, *Emiliania huxleyi* made a minor contribution. Taxa that are common in the upper layers of oligotrophic stratified settings like *Umbellosphaera* spp., *Discosphaera tubifera* and *Rhabdosphaera clavigera* were scarce. Overall, such assemblages displayed the characteristics of neritic settings, with high trophic resources and elevated water turbidity, even though the measured chlorophyll-*a* concentration was low throughout the investigated area.

Keywords

Coccolithophores; Indian Ocean; biogeography; *Alisphaera*; Magoodhoo Island.

1. Introduction

Coccolithophores are marine planktonic calcifying algae that play a major role in the ocean carbon cycle: as planktonic autotrophs they contribute to the drawdown of CO_2 from the surface ocean, while as calcifiers, since their first occurrence in the late Triassic (Westbroek et al., 1993), they affect the CO_2 equilibrium in surface waters and contribute to the sinking flux of calcium carbonate to the ocean bottom. Coccolithophores thus play an important role in climate regulation, also through the production of dimethyl sulphide (Malin and Steinke, 2004), a gas that promotes cloud condensation.

Knowledge of the response of coccolithophores to ecological forcing is fundamental to understand their response to and their feedback on climate change. Furthermore, biogeographic studies on coccolithophores in the present ocean (e.g., Jordan and Chamberlain, 1997) provide the key to interpreting the coccolith record of the past, thus allowing accurate reconstructions of past oceanographic changes.

The Indian Ocean is a key area influenced by the monsoon system, with a seasonal reversal of wind direction, precipitation regime and surface ocean currents (Schott and McCreary, 2001). Coastal areas dominated by the monsoons are characterised by seasonal upwelling of nutrient-rich waters that cause an increase of primary productivity (Rixen et al., 2000; Wyrtki, 1973), resulting in high export fluxes of organic matter and the development of an oxygen minimum zone at depth (Schulz et al., 1996; Von Rad et al., 1990).

Upwelling areas close to oligotrophic settings in the Indian Ocean have been often used as key areas to compare and contrast the distribution of phytoplankton and in particular of coccolithophores (Andruleit and Rogalla, 2002; Andruleit et al., 2003; Schiebel et al., 2004), the forcing of the monsoon system on calcification rates (Balch et al., 2000; Liu et al., 2020) and related geochemical proxies (Stoll et al., 2007a; Stoll et al., 2007b). In upwelling-dominated areas, coccolith fluxes define a seasonal pattern of monsoon and inter-monsoon variations (Broerse et al., 2000; Mergulhao et al., 2013) and several studies used calcareous nannofossils as proxies to understand the functioning of the monsoon system in the Quaternary (Andruleit et al., 2008; Carbacos et al., 2014; Rogalla and Andruleit, 2005; Tangunan et al., 2020; Tangunan et al., 2017).

Many plankton studies of coccolithophores (Norris, 1971; Norris, 1983; Norris, 1984; Norris, 1985), along longitudinal transects in the tropical-equatorial Indian Ocean (Kleijne, 1993; Kleijne et al., 1989; Young et al., 2017), in the Arabian Sea (Andruleit et al., 2005; Andruleit et al., 2003; Guptha, 1985; Guptha et al., 2005; Guptha et al., 1995), eastern Indian Ocean (Guptha et al., 2005; Hallegraeff, 1984; Takahashi and Okada, 2000) and along meridional transects in the Indian sector of the Southern Ocean (Mohan et al., 2008; Patil et al., 2014; Patil et al., 2020) revealed a distinct biogeography and a high biodiversity, often resulting in the description of new species (Andruleit et al., 2016; Andruleit and Jordan, 2017; Aubry and Kahn, 2007; Kahn and Aubry, 2012; Kleijne and Cros, 2009; Patil et al., 2019; Young and Andruleit, 2006). Coccolithophore populations have been studied from water samples during drilling operations of the International Ocean Discovery Program at different locations in the Inner Sea in the central Maldives (Young et al., 2017) but only in surface ocean waters and not in the lagoons.

The purpose of this study is to assess the distribution and species composition of coccolithophores from the Faafu Atoll in the Maldives. The sampling strategy aimed at comparing and contrasting the presence and biodiversity of coccolithophores from key areas of atoll, such as: a) from the reef flat to the fore reef; b) from the lagoon through the pass to the open ocean; c) from surface water to mid-photic depth.

2. Oceanographic setting

The Maldives archipelago in the central Equatorial Indian Ocean is an isolated carbonate platform that has grown on a lower Paleogene (60–50 Ma) volcanic basement since the Eocene (Betzler et al., 2017). A north-south–oriented double row of 1200 reef-rimmed atolls encloses the Inner Sea of the Maldives, up to 550 m deep. The atolls are separated by channels that allow the transport of equatorial waters and enclose 50-60 m deep lagoons, connected to the open ocean by passes.

The climate and ocean circulation of the tropical Indian Ocean is driven by the seasonally reversing winds of the South Asian Monsoon (Tomczak and Godfrey, 2003; Wyrtki, 1973), due to the differential heating of land and ocean that causes the seasonal migration of the Intertropical Convergence Zone (Gadgil, 2003).

In the northern Indian Ocean, during the summer monsoon (SM, June to October), SW winds drive the northward flowing East African Coastal Current close to the African coast, the southward flowing West India Coastal Current along the western coast of India and the eastward flowing Summer Monsoon Current in the central Indian Ocean. During the winter monsoon (WM, December-April), NE winds drive the southward flowing Somali current close to the African coast, the northward flowing West India Coastal Current along the western coast of India and the westward flowing Winter Monsoon Current in the central Indian Ocean (Schott and McCreary, 2001; Shankar et al., 2002). Intermonsoon periods occur in May and November and equatorial westerly winds dominate, inducing strong and deep-reaching (up to 200 m) surface currents (Tomczak and Godfrey, 2003).

Primary productivity is highly variable in both space and time in the Indian Ocean, with the highest sea surface chlorophyll-*a* values observed in the upwelling regions of the western coast of the Arabian Sea during the summer monsoon. In the equatorial region, chlorophyll-*a* values are below 0.1 mg/m^3 in the intermonsoon periods and below 0.5 mg/m^3 during the SW monsoon. The Maldives are crossed by the Monsoon Current, whose transport affects at least the upper 60 m of the water column (Schott and McCreary, 2001) and reverses seasonally, causing a plume of upwelling and higher chlorophyll concentration (>0.5 mg/m^3) in the down-current side offshore, i.e., eastward during the SM and westward during the WM (de Vos et al., 2014; Strutton et al., 2015). Chlorophyll-*a* concentration shows seasonal variations but is generally low in the atolls of the Maldives, as observed from satellite (Sasamal, 2007) and our Supplementary Fig. A.1.

3. Methods

Three sets of water samples were collected from the lagoon and open ocean in the south-eastern part of the Faafu Atoll from November 2nd to 6th, 2018: surface, deep and reef-flat samples. Sample position was measured with a Garmin etreck 30 hand GPS and the main parameters (temperature, oxygen concentration) of the water column were measured with a multiparametric probe WTW ® Multi 3430 (Fig. 1, Table 1).

Surface water samples (labelled MF) were collected with a bucket from the boat, or from the coast; vertical water samples (labelled MV) were collected at 0 m with a bucket and at 10, 25, 40 m depth with a hand held 5-litre Niskin bottle connected to a 50 m rope and triggered with a manual release; reef-flat samples (M 1 to 3 and Ad) were collected with a 2-litre water bottle while walking from the coast across the reef-flat.

For each sample type, 2 litres of water were filtered on cellulose acetate filters (0.45 μm pore size, 47 mm diameter) through a vacuum system in the laboratory at the MAHRE facility on Magoodhoo Island. All filters were oven-dried and stored in plastic petri dishes. A portion of filter was cut and fixed with microscope immersion oil between a glass slide and a cover slip. All samples thus prepared were analysed under an Olympus BX50 polarised light microscope at the University of Milano-Bicocca at 1000X. A total of 55-434 (1-280) coccospheres were counted on the filter for each open-water (reef-flat) sample over an area of 4-11 mm^2. These counts thus resulted in a detectability of 55-155 coccospheres/litre.

Selected samples were also observed with a Zeiss FEG Gemini 500 Scanning Electron Microscope (SEM), by attaching a small piece of filter to an aluminium stub with a graphite tape and Cr-coating. SEM observations focused on assessing the full range of species composition, focusing in particular on lightly-calcified species.

MV samples were also filtered with a vacuum filtration system using glass-fibre filters and these were analysed for chlorophyll concentration using spectrophotometric analysis (Leoni et al., 2007).

MODIS-Aqua chlorophyll-*a* concentration data at 4 km resolution were plotted as a time-averaged map and as a time series for year 2018 from NASA Giovanni (https://giovanni.gsfc.nasa.gov/giovanni) and are shown in Supplementary Fig. 1.

4. Results

4. 1 Coccolithophore distribution and species composition

Coccolithophore density in the surface waters is typically around 0.1-4 x 10^3 coccospheres/litre in 1-2 m depth coastal waters and increases with increasing bottom depth, towards both the lagoon and the open ocean. In these settings, coccolithophores are in the range of 10-44 x 10^3 coccospheres/litre, with no significant trend between the lagoon and the open ocean, but typically showing higher values close to the passes (Fig. 2).

At vertical stations, ~1°C decrease in temperature is observed from the surface to 40 m depth in the lagoon and is accompanied by a decrease in oxygen concentration and saturation. Sea surface temperature is ~0.5°C lower in the open ocean stations, resulting in a less pronounced temperature decrease with depth.

Chlorophyll concentration is low in the range of 0.13-0.65 μg/litre at all stations, showing a slightly-increasing trend with depth (Fig. 3). Low-resolution (4kmx4km) monthly satellite data over the area in November 2018 show values of 0.18 mg/m^3 (= 0.18 μg/litre), indicating the overall pattern of low chlorophyll concentration of the region of the atoll. No diatoms were observed in the filter samples, and only a few specimens of silicoflagellates were recovered, indicating that coccolithophores are the major mineralized phytoplankton group in the study area, at least in the investigated period.

The vertical trend in coccolithophore density is not consistent among stations, showing either an increase (MV3, MV5, V2), a decrease (MV1) or constant values (MV6) with increasing water depth. In the open water, the coccolithophore assemblage composition is dominated by two main species, *Gephyrocapsa oceanica* (34-64%) and *Oolithotus antillarum* (6-33%), followed by several minor species, that represent on average 27% of the open water and coastal assemblages, dropping to zero where coccolithophore density is below 100 coccospheres/litre. In coastal waters close to the Magoodhoo coast, coccolithophore density is close to the detection limit and the assemblage is usually represented by the two major species only.

Minor species are represented, in order of abundance (as detected by light microscopy, Plate 1) by *Calciosolenia* spp., *Calciopappus rigidus*, *Emiliania huxleyi*, *Umbilicosphaera* spp., *Umbellosphaera* spp., *Ophiaster* spp., *Michaelsarsia adriaticus*, *Algirosphaera robusta*, and rare *Syracosphaera* spp., *Discosphaera tubifera*, *Acanthoica quattrospina, Rhabdosphaera clavigera*, *Calcidiscus leptoporus*, *O. fragilis*, *Alisphaera* spp., and holococcolithophores. *Emiliania huxleyi*, the most common species in the global ocean, represents on average 5% (range 1.3-13%) of the total assemblage. *Florisphaera profunda* was detected in two deeper samples. Only one specimen of *H. carteri* was recovered in one sample. SEM observations documented the different species (Plate 2, 3), allowed detecting rare small species like *Palusphaera vandelii* and *Solisphaera galbula* and detailing the species of *Syracosphaera*, *Alisphaera* and holococcolithophores (Plate 4).

At some stations and/or depths, in both the lagoon and the ocean, minor species make a higher contribution, up to 56% of the total assemblage (where *G. oceanica* has low abundances): minor species are represented in these cases mostly by *Calciosolenia murrayi*, *C. rigidus* and *Ophiaster* spp.

4.2 Horizontal and vertical trends in coccolithophore assemblages

In surface water samples collected away from the coast, no significant trend in species assemblage composition was observed (Fig. 2), as all species are present both in the lagoon and open sea. The only exception is represented by *C. brasiliensis*, that shows a preference for the open ocean.

Along the vertical (0-40 m) transects, the contribution of major species to the total assemblage composition changes slightly, with an increase in the relative abundance of *O. antillarum* with depth but no clear trend for *G. oceanica*. As for the minor species, *C. murrayi, C. rigidus*, *U. irregularis*, *U. tenuis* and *D. tubifera* show higher relative abundances in the upper 10 m, decreasing with depth; holococcolithophores follow the same trend, as well as *U. hulburtiana* and *R. clavigera*, whose presence is however scattered.

In contrast, *A. robusta*, *M. adriaticus* and *Ophiaster* spp., show increasing relative abundances with depth and a similar trend is followed by *U. foliosa*, although its presence is scattered; *F. profunda* was only detected below 25 m depth at two stations. No vertical trend was detected for the other species.

4.3 A new *Alisphaera* species

The genus *Alisphaera* was rare in the analysed samples, with only a few coccospheres identified both in light and electron microscope observations from a few samples (MF08, MV1-10m, MV5-25). It was represented by rare specimens of *A. gaudii* and a species showing ultrastructural characters that were not common to any known species. The latter is therefore described here as a new species.

Family Alisphaeraceae

Genus: *Alisphaera*

Species: *Alisphaera bidentata* sp. nov. Malinverno

HOLOTYPE: Plate 3, fig. 9-10. SEM stub, stored at the Museum of Natural Sciences of Milan (MSNM No. 51417)

TYPE LOCALITY: Faafu Atoll, Maldives, sample MV1 - 10 m

ETYMOLOGY: from the Latin *bidentatus*, bearing two teeth

Monothecate dimorphic coccosphere. Coccoliths elliptical in outline, proximal and distal flange slightly more extended towards the apical pole of the coccosphere. A pointed protrusion is present on the wide longer side of the distal flange in some coccoliths located at the antapical pole and sparse in other parts of the coccosphere. Coccolith central area with a fissure; nodules along the inner margin of the narrow longer side of the distal flange are the result of an asymmetrical protrusion from each of the radial elements making the distal flange; a prominent tooth occurs at each shorter side of the inner margin as a result of a protrusion from the radial element at that position: such teeth are the most characteristic feature of this species.

Dimensions: coccosphere about 10 μm (but both observed specimens were collapsed); coccoliths 1.3-2.0 μm long, 0.8-1.1 μm wide; nodules up to 0.1 μm long, teeth 1.5 μm long.

Remarks: the two illustrated specimens were recovered from two distinct samples but display very consistent ultrastructural features. They show strong similarity to *A. pinnigera*, but the protrusion of the distal flange resembles more a hook rather than a right-angle triangle. Furthermore, some of the specimens of *A. pinnigera* illustrated on nannotax (JRSEM-193-44.JPG and 46.JPG; Young_etal_2003_177-61.JPG) have a smaller central area and larger (and fewer) elements making the wide longer side of the distal flange.

The presence of the two teeth on the shorter side of the inner margin has never been illustrated in *Alisphaera* and is a typical character that allows the distinction of this species. Indeed, small nodules in this position are illustrated from a few specimens of *A. gaudii* (Fig. 32 of Kleijne et al., 2002; Fig. 76D of Cros and Fortuno, 2002; unpublished JRYSEM_126_58alisph of nannotax), *A. quadrilatera* (fig. 75D of Cros and Fortuno, 2002) and *A. pinnigera* (fig. 75B of Cros and Fortuno, 2002), but they are small and only occur on a few coccoliths, while the teeth of *A. bidentata* occur on all coccoliths of the coccosphere.

4.4 Malformed coccolithophores

A few specimens of *G. oceanica* showed evidences of malformation, consisting of: incompletely-formed coccoliths lacking a bridge and central area, unconnected crystal elements, unconnected portions of coccoliths, collapsed shields, or incompletely-formed elements.
Such specimens are rare and were only recovered in a few surface water samples from the lagoon (MV3, MF08). Under the light microscope, they appear as irregular calcite spheres with no diagnostic characters for the identification. SEM observations allowed attribution to *G. oceanica* (Plate 3, fig. 23-24).

5. Discussion

5.1 Coccolithophore trends in the tropical-equatorial Indian Ocean and in the Maldives

Many studies focused on coccolithophores of the tropical equatorial Indian Ocean through water sampling from extensive surveys (Kleijne, 1993; Kleijne et al., 1989; Liu et al., 2018; Schiebel et al., 2004; Young et al., 2017) and/or specific locations (Andruleit et al., 2005; Andruleit et al., 2003; Guptha et al., 2005; Guptha et al., 1995; Hallegraeff, 1984; Painter et al., 2021; Stolz et al., 2015; Takahashi and Okada, 2000), and investigated their taxonomy (Kleijne, 1991; Kleijne, 1992; Norris, 1983; Norris, 1984; Norris, 1985), abundance, distribution and ecology of single species. These studies show an overall consistent pattern of major species abundances. Upwelling areas and/or periods are dominated by *G. oceanica*, with minor contribution by *E. huxleyi*, *Umbilicosphaera* spp. and some species of the Syracosphaerales, notably *A. robusta*, *C. rigidus*, *Calciosolenia* spp. and *M. adriaticus*. In contrast, stratified oligotrophic settings are dominated by *U. irregularis*, with minor contribution by *U. tenuis* and other oligotrophic species like *D. tubifera* and some holococcolithophores. Total coccosphere concentration in the Indian Ocean ranges from low (0-10x10^3 coccospheres/litre) to moderate concentrations (20-100x10^3 coccospheres/litre) moving from oligotrophic towards eutrophic settings (Kleijne et al., 1989; Young et al., 2017) even though the opposite correlation is also documented (Schiebel et al., 2004).

Coccolithophore assemblages in the Faafu Atoll lagoon and surrounding ocean waters show abundances in the range of 4-44x10^3 coccosphere/litre (much lower concentrations in samples collected in 1-2 m deep stations), comparable to other settings of the region, and are dominated by *G. oceanica* followed by a high number of species typical of the equatorial-tropical Indian Ocean, as also observed from the Inner Sea around Maalhosmadulu and Goidhoo atolls further north, which were sampled in the same season of a different year (Young et al., 2017).
Some differences can however be observed from the coccolithophores of the Inner Sea and will be discussed in the context of the Indian Ocean coccolithophore ecology. In the Inner Sea, *D. tubifera* was abundant but it is rare here, *C. cristatus* and *H. hyalina* made significant contributions there but are notably absent from our samples. In contrast, *O. antillarum* was rare in the Inner Sea but is

the second most abundant species in the Faafu Atoll. Among *Syracosphaera*, *S. exigua* is the most abundant species found by Young et al. (2017), but was not recorded here, where the most abundant species of the genus, as identified by SEM observations, were *S. halldalii*, *S. ossa* and *S. prolongata*. Among holococcolithophores, *P. magnaghii* and *C. diconstricta* were present in both surveys, and *P. maximus* was likely identified in one of our samples.

As in Young et al. (2017), typical shallow water taxa like genera *Cruciplacolithus*, *Pleurochrysis*, *Braarudosphaera*, were not observed, even from coastal samples in 1-2 m water depth.

5.2 Ecological implications of the main and upper photic zone (UPZ) species

Gephyrocapsa oceanica is the most abundant coccolithophore species in the Indian Ocean and makes a significant contribution in present-day fluxes (Andruleit et al., 2000; Broerse et al., 2000; Mergulhao et al., 2006) from the upwelling-dominated settings of the Arabian Sea and the Bay of Bengal. It is the dominant species in bottom sediments of the Arabian Sea (Andruleit and Rogalla, 2002; Dmitrenko, 1985; Guptha, 1985; Guptha, 1986; Houghton and Guptha, 1991; Martini and Muller, 1972; Mojtahein et al., 2015; Stolz et al., 2015) showing a clear positive response to increased nutrient conditions in monsoon-dominated settings.

In our samples, *G. oceanica* typically occurs in clusters (Plate 2 fig. 1) and is often bilayered (Plate 2 fig. 2). Its coccoliths show high (>56°) bridge angle, as typical in the tropics (Bollmann, 1997; Bollmann and Klaas, 2008) and variable size, corresponding to *G. oceanica* Equatorial and *G. oceanica* Larger of Bollmann (1997) as measured in Holocene coccoliths. In plankton samples, these two morphotypes are correlated with open ocean warm conditions and upwelling-neritic settings, respectively (Schiebel et al., 2004) and with warmer and colder SST, respectively (Bollmann and Klaas, 2008). We did not make morphometric measurements to assess the proportions, but qualitative microscope observations indicate a predominance of the larger morphotype (Plate 2 fig. 1, 2) which is well explained by the neritic setting.

Our *G. oceanica* specimens have a large central area, similar to Type 1 of Hagino et al. (2000) that is typical of high SST (>20°C) and low nutrients. However, only a few of our specimens (Plate 2, fig. 3) can be assigned to Type 1, while the majority of specimens (Plate 2, fig. 1, 2) differ from Type 1 in having a well developed inner tube cycle that forms a distinct collar, like in the specimens from upwelling settings (e.g. Andruleit et al., 2007, Fig. 5f).

A few individuals were malformed, showing incomplete crystals and coccoliths, but these were very rare among the individuals of the species and occurred in samples where no malformation was observed in other species. Although malformed specimens are reported from other surveys (Kleijne, 1990), these could also be interpreted as the result of partial corrosion, as the morphological evidences are uncertain.

Emiliania huxleyi is a ubiquitous species (McIntyre and Bé, 1967; Winter et al., 1994) and usually dominates in upwelling settings of tropical to arctic waters, but it is outnumbered by *G. oceanica* in tropical waters (Hagino, 2000). Data from the Indian Ocean indicate that *E. huxleyi* is abundant in the western Arabian Sea and Suez Gulf (Kleijne et al., 1989) as well as in the eastern Indian Ocean (Liu et al., 2021; Liu et al., 2018; Takahashi and Okada, 2000), while *G. oceanica* dominates in the area South of India at higher temperature and lower salinity. Such trend is also observed by Young et al. (2017) who found that *E. huxleyi* was more abundant than *G. oceanica* in the eastern Indian Ocean and decreased significantly towards the central Indian Ocean. In the Maldives, *E. huxleyi* was present in the Inner Sea only during part of their survey but was always present during our sampling in the area of Magoodhoo. Although we did not analyse specifically the morphotypes, all the observed *E. huxleyi* specimens belonged to type A, as also observed for the

Inner Sea further north (Young et al., 2017), while type C is reported as the dominant type in the equatorial upwelling as well as in the southern Indian sector of the southern Ocean.

Umbellosphaera irregularis is a typical upper photic zone species of tropical-subtropical stratified oligotrophic settings (Hagino et al., 2000; Haidar and Thierstein, 2001; McIntyre and Bé, 1967; Okada and Honjo, 1973; Okada and McIntyre, 1977; Reid, 1980). In the NE Indian Ocean it is the dominant species along with *U. tenuis* in oligotrophic environments (Takahashi and Okada, 2000), it is common in open ocean stratified waters off Tanzania (Stolz et al., 2015), the dominant species in the eastern equatorial Indian Ocean under stratified conditions (Guptha et al., 2005) and it is typically associated with warm stratified oligotrophic areas in the Indian Ocean (Andruleit et al., 2004; Guptha et al., 1995; Kleijne, 1993; Kleijne et al., 1989; Liu et al., 2018; Schiebel et al., 2004). In our samples, *U. irregularis* is always present as a minor species, pointing to a rather eutrophic setting.

Umbellosphaera tenuis is also a minor species in the assemblages of the Faafu Atoll and is represented by types I and O. These two types are always found in association and typically in combination with *U. irregularis* (Kleijne, 1993) in samples from the Indian Ocean (NE Indian Ocean, eastern Arabian Sea, northern Red Sea) and are indicated as typical of tropical areas. Other records of type O come in fact from tropical sites such as Palau (Pacific Ocean, 7°N, Konno and Jordan, 2006), western Pacific (Nishida, 1979), equatorial Pacific (Hagino and Okada, 2006), Atlantic Ocean (1.6 and 13.99°S, unpublished photos by JRY on Nannotax3), northern Gulf of Elat, 29.5°N (Winter et al., 1979 as *U. irregularis*) and Australian waters (Hallegraeff, 1984).

Other common UPZ species of the tropical and temperate settings are represented by *D. tubifera* and *R. clavigera* (Kleijne, 1992; McIntyre and Bé, 1967; Okada and McIntyre, 1977) which are typically present in the Indian Ocean but are rare or scattered in our survey, indicating unsuitable conditions.

Among the species of *Umbilicosphaera*, the most represented in our samples was *U. sibogae*, a temperate-subtropical species (Okada and McIntyre, 1979; Winter, 1985) typical of oligotrophic settings (Ziveri et al., 2004) and associated with oligotrophic stable waters in plankton and fluxes of the equatorial Pacific (Broerse, 2000; Hagino and Okada, 2006). *Umbilicosphaera sibogae* is reported as the third abundant species in the eastern equatorial Indian Ocean (Guptha et al., 2005), but showed low abundances throughout the Indian Ocean surface waters, decreasing in upwelling areas (Kleijne, 1993). It is the second most abundant species in fluxes of the Bay of Bengal (Mergulhao et al., 2013) and is reported to increase in settling fluxes off Pakistan during the NE monsoon (Andruleit et al., 2000). Although it is reported as a LPZ species in other oceans (McIntyre and Bé, 1967; Reid, 1980) as well as in the Arabian Sea off Tanzania (Stolz et al., 2015) and in the eastern Indian Ocean (Liu et al., 2018), it did not show any depth trend in our samples. *Umbilicosphaera foliosa*, a mesotrophic to eutrophic species in different oceans (Andruleit et al., 2005; Broerse, 2000; Hagino and Okada, 2006; Okada and McIntyre, 1979; Ziveri and Thunell, 2000) was less frequent here, as reported from other locations of the Indian ocean (Kleijne, 1993). Finally, *U. hulburtiana* was scattered in our samples and mostly restricted to the surface samples. Usually considered as an upper photic zone species typical of warm waters (Okada and McIntyre, 1977) it was found in surface waters only in the northeast Indian Ocean and Arabian Sea (Kleijne, 1993), but in the MPZ in open ocean non-upwelling settings off Tanzania (Stolz et al., 2015).

5.3 Middle photic zone (MPZ) coccolithophores in surface waters of the Faafu Atoll

Apart from the dominant role of *G. oceanica*, the majority of the species found in the Faafu Atoll are typical of the MPZ to LPZ assemblages of tropical to temperate settings.

The second most abundant species in all samples of the Faafu Atoll is in fact represented by *O. antillarum*, which is indicated as a Lower Photic Zone (LPZ) (Hagino et al., 2000; Takahashi and Okada, 2000) or MPZ species (Winter et al., 1994). In the plankton, *O. antillarum* is reported as an important component in the eastern equatorial Indian Ocean (Guptha et al., 2005), at mid-depth in the eastern Indian Ocean (Liu et al., 2021), in LPZ waters off Australia (Takahashi and Okada, 2000), in deep waters >60 m of the open ocean of the western equatorial Indian Ocean off Tanzania (Stolz et al., 2015), at 40-60 m in the northern and western Arabian Sea (Andruleit et al., 2005; Andruleit et al., 2003) and at the thermocline in the Java upwelling area (Andruleit, 2007). Increased abundances of *O. antillarum* are observed in upwelling areas of the Indian Ocean and in the surface waters of the western Arabian Sea, along with *A. robusta* (Kleijne, 1993), as well as south of Java, along with increasing total coccolithophores, *E. huxleyi* and *G. oceanica* (Young et al., 2017). A similar increase of *O. antillarum* in the upper water column in and around the upwelling front was observed in the equatorial Pacific Ocean (Hagino et al., 2000). In sinking fluxes from the Bay of Bengal, *O. antillarum* increases along with *F. profunda* during periods associated with oligotrophic conditions (Mergulhao et al., 2013).

Algirosphaera robusta is commonly indicated as a LPZ species (Hagino et al., 2000; Kleijne, 1993; Knappertsbusch, 1993; Okada and Honjo, 1973; Okada and McIntyre, 1979; Reid, 1980; Takahashi and Okada, 2000) or MPZ species (Dimiza et al., 2008; Jordan and Winter, 2000; Malinverno et al., 2003) and makes an important contribution to the fluxes in a coastal setting of the eastern Mediterranean (Malinverno et al., 2009). In the Indian Ocean, it occurs at the thermocline in the Java upwelling area (Andruleit, 2007), in the LPZ of the eastern Indian Ocean off Australia (Takahashi and Okada, 2000), but increases in abundance in surface waters of the upwelling areas off Somalia and south of India, thus indicating lower temperatures and eutrophic conditions (Kleijne et al., 2002). In our samples, *A. robusta* is present throughout the investigated water column depth, but is comparably more abundant in the deeper samples, confirming its preference for lower layers.

Another significant component of the typical MPZ community of coastal and pelagic subtropical settings is represented by species of *Calciosolenia*, *Michaelsarsia*, *Ophiaster* and *Calciopappus* (Cerino et al., 2017; Jordan and Chamberlain, 1997; Jordan and Winter, 2000; Malinverno et al., 2003) that make an important contribution in most samples of the Faafu Atoll.

Calciosolenia is represented by *C. murrayi*, *C. corsellii* and *C. brasiliensis*, but the former is the most abundant species, as in other coastal locations of the Indian Ocean, where it shows a preference for restricted local conditions in coastal surface waters and high turbidity (Andruleit and Rogalla, 2002; Andruleit et al., 2003; Painter et al., 2021; Reid et al., 1978).

Michaelsarsia is only represented by *M. adriaticus*, as reported for the northern Inner Sea of the Maldives (Young et al., 2017) as well as the eastern Arabian Sea and NE Indian Ocean (Kleijne, 1993). *Ophiaster* is frequent in Arabian Sea, NE Indian Ocean and South of India (Kleijne, 1993) as well as in coastal NW Arabian Sea (Painter et al., 2021) and is represented here by *O. hydroideus* and *O. reductus*. *Calciopappus* is represented by *C. rigidus*, which is common to abundant in the Arabian Sea (Andruleit et al., 2003) and South of India (Kleijne, 1993). The common presence of these typical MPZ species throughout the upper water column probably indicates high turbidity and/or elevated nutrient concentrations, as also observed at a coastal setting of the Mediterranean during the fall season (Cerino et al., 2017).

6. Conclusions

Coccolithophores are the main mineralised group of phytoplankton detected in the study area of the Faafu Atoll, as analysed from surface samples along the Magoodhoo and Adanga coast, from the lagoon and the open ocean as well as from 40 m deep profiles. Coccolithophore abundance is lowest (100-1000 coccospheres/litre) at shallow coastal locations and increases offshore in both the lagoon and the open ocean up to $44x10^3$ coccospheres/litre. The assemblage is dominated by *G. oceanica*, with a significant community of middle-lower photic zone taxa, mainly *O. antillarum* followed by *Calciosolenia* spp., *M. adriaticus*, *C. rigidus, Ophaster* spp. and *A. robusta*. Taxa that are typically found in stratified oligotrophic settings are present but not abundant, such as *U. irregularis*, *U. tenuis*, *D. tubifera* or even rare, like *Rhabdosphaera* spp. Finally, *E. huxleyi*, the most abundant and widespread species in the world's oceans is present here with low abundances, as testified from other surveys of the tropical Indian Ocean. Overall the assemblage is typical of neritic settings, with taxa that indicate eutrophic conditions accompanied by high turbidity, which possibly explain the high contribution of middle- and lower-photic zone taxa at the surface and the lack of other more competitive phytoplankton groups like e.g., diatoms, as testified by overall low chlorophyll-*a* concentrations detected in water samples.

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Figure captions

Figure 1: Map of the investigated area

Figure 2: Coccolithophore density in surface waters of a) the whole investigated area of the Faafu Atoll, b) the area around the island of Magoodhoo, c) the area around the island of Adanga. Grey area = land; light grey = reef; white = water. Coccolithophore assemblage composition and abundance in open water samples shows d) all species e) minor species across the transect drawn as dashed line in a.

Figure 3: vertical (0-40 m) distribution and assemblage composition of coccolithophores and main water properties along the MV stations. Left panels = temperature, chlorophyll concentration, oxygen concentration; central panels = abundance of all coccolithophore species; right panels = abundance of minor coccolithophore species.

Plate 1. Light microscope images of coccolithophores. 1-4, *E. huxleyi* in low and high focus: 1, 2 crossed nicols; 3, 4 parallel nicols; 5-8, *G. oceanica* in low and high focus: 5-6 crossed nicols, 7-8 parallel nicols; 9-11, *U. sibogae* low, medium and high focus; 12-14, *U. foliosa* low, medium and high focus; 15, 16 *U. irregularis*, 15 crossed nicols, 16 parallel nicols; 17 *U. tenuis* crossed nicols; 18-20, *O. antillarum*, 18, crossed nicols, 19, 20 parallel nicols low and high focus, 21-26, *A. robusta* in low, medium and high focus, 21-23 crossed nicols, 24-26 parallel nicols; 27-29, *U. hulburtiana*,

27, 28 crossed nicols low and high focus, 29 parallel nicols; 30, 31, *C. rigidus* crossed nicols, 30 circumpolar view, 31 lateral view; 32-34, *M. adriaticus*, 32 crossed nicols, 33 parallel nicols low and high focus; 35, *C. murrayi* crossed nicols; 36, 37, *C. brasiliensis*, 36 crossed nicols, 37 parallel nicols; 38-40, *S. pulchra*, 38 crossed nicols, 39, 40 parallel nicols low and high focus; 41-43, *D. tubifera* crossed nicols low, medium and high focus; 44-47, *C. leptoporus*, 44, 45 crossed nicols low and high focus, 46, 47 parallel nicols low and high focus.

Plate 2: SEM images of coccolithophores. 1, coccospheres of *Gephyrocapsa oceanica* with well-developed inner tube cycle; 2, bilayered coccosphere of *G. oceanica* with well-developed inner tube cycle; 3, bilayered coccosphere of *G. oceanica* with poorly-developed inner tube cycle; 4, *Emiliania huxleyi* type A; 5, *Umbilicosphaera sibogae*; 6, *U. foliosa*; 7, *U. hulburtiana*; 8, Tintinnid lorica, showing agglutinated coccoliths, mostly of *G. oceanica*; 9, *Calcidiscus leptoporus* subsp. *quadriperforatus*; 10, 11, *Oolithotus antillarum*: 11, collapsed coccosphere showing the proximal side of the coccoliths; 12, *O. fragilis*; 13, 14, 15, 16, *Calciopappus rigidus*: 13, with CFC in normal position, 14, with CFC enclosing the coccosphere; 15, 16, focus on the CFCs; 17, 18, 19, *Ophiaster reductus*, 17 whole coccosphere; 18, 19, focus on the CFCs and the antapical BCs with open central area; 20, 21, 22, *O. hydroideus*, 20 whole coccosphere, 21 focus on CFCs, 22 coccosphere surrounded by link coccoliths; 23, 24, *Michaelsarsia adriaticus*, 23 whole coccosphere, 24 detail on BCs. BC = body coccolith; CFC = circumflagellar coccolith.

Plate 3: SEM images of coccolithophores. 1, *Acanthoica quattrospina*; 2, *Discosphaera tubifera*, 3, *Rhabdosphaera clavigera* var. *stylifera*; 4, *Palusphaera vandelii*; 5, *Umbellosphaera irregularis*; 6, *U. tenuis* type O; 7, *U. tenuis* type I; 8, 9,10, 11, 12 *Alisphaera bidentata* sp. nov.: 9, 10: holotype; 11, 12: collapsed coccosphere; 13, 14, 15, *Calciosolenia brasiliensis*: 13 whole coccosphere, 14

focus on BC and a-apical coccoliths, 15 focus on a- and b-apical coccoliths; 16, *Alisphaera gaudii*; 17, 18, 19, *Calciosolenia murrayi*: 17 whole coccosphere, 18 focus on BC and apical coccoliths from one side, 19 focus on BC and apical coccoliths on the elongated side; 20, *Florisphaera profunda* var. *elongata*; 21, 22, *Algirosphaera robusta*, 22 partly collapsed coccosphere, showing the proximal side of BCs; 23, 24, partly dissolved coccospheres of *G. oceanica*, with separated coccolith elements collapsed on the sphere.

Plate 4: SEM images of coccolithophores. 1, *Solisphaera galbula*; 2, *Syracosphaera dilatata*; 3, *S, corolla*; 4, *S. noroitica*; 5, *S. florida*; 6, *S. prolongata*; 7, 8, *S. halldalii*; 9, *S. ossa* type I; 10, *S. rotula*, 11, *S. tumularis*; 12, *S. bannockii*, 13, *S. orbiculus*; 14, *S. mediterranea*, 15, *Syracosphaera* sp.; 16, *S. pulchra* HOL *oblonga* type; 17, *Calyptrolithina divergens*; 18, *Corisphaera gracilis*; 19, *Helladosphaera cornifera*; 20, partly dissolved and collapsed holococcolithophore, cf. *Helladosphaera vavilovii*; 21, *Poricalyptra magnaghii*; 22, *Calicasphaera diconstricta*; 23, *Poritectolithus* cf. *maximus*; 24, Unidentified holococcolithophore.

Table 1: Location of the samples and main hydrological parameters measured at each station.

Supplementary Figure 1: left, yearly sea surface Chlorophyll-*a* map from MODIS aqua during 2018; right: montly Chlorophyll-*a* values in the area indicated on the left panel. Data extracted and plotted from https://giovanni.gsfc.nasa.gov/giovanni.

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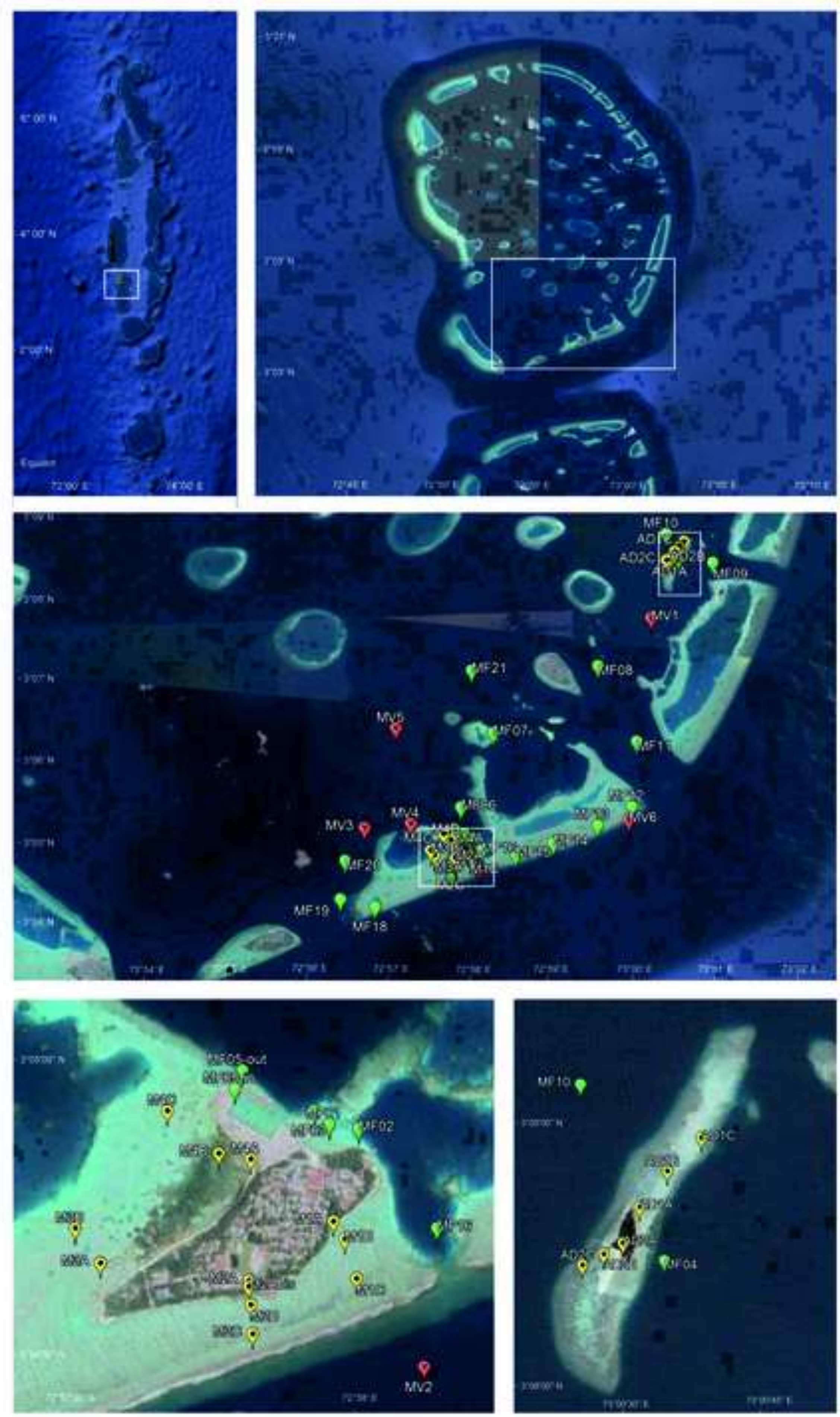
Figure 1


6°00' N
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Equator
MF10
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AD2C
AD2B
AD1A
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AD2
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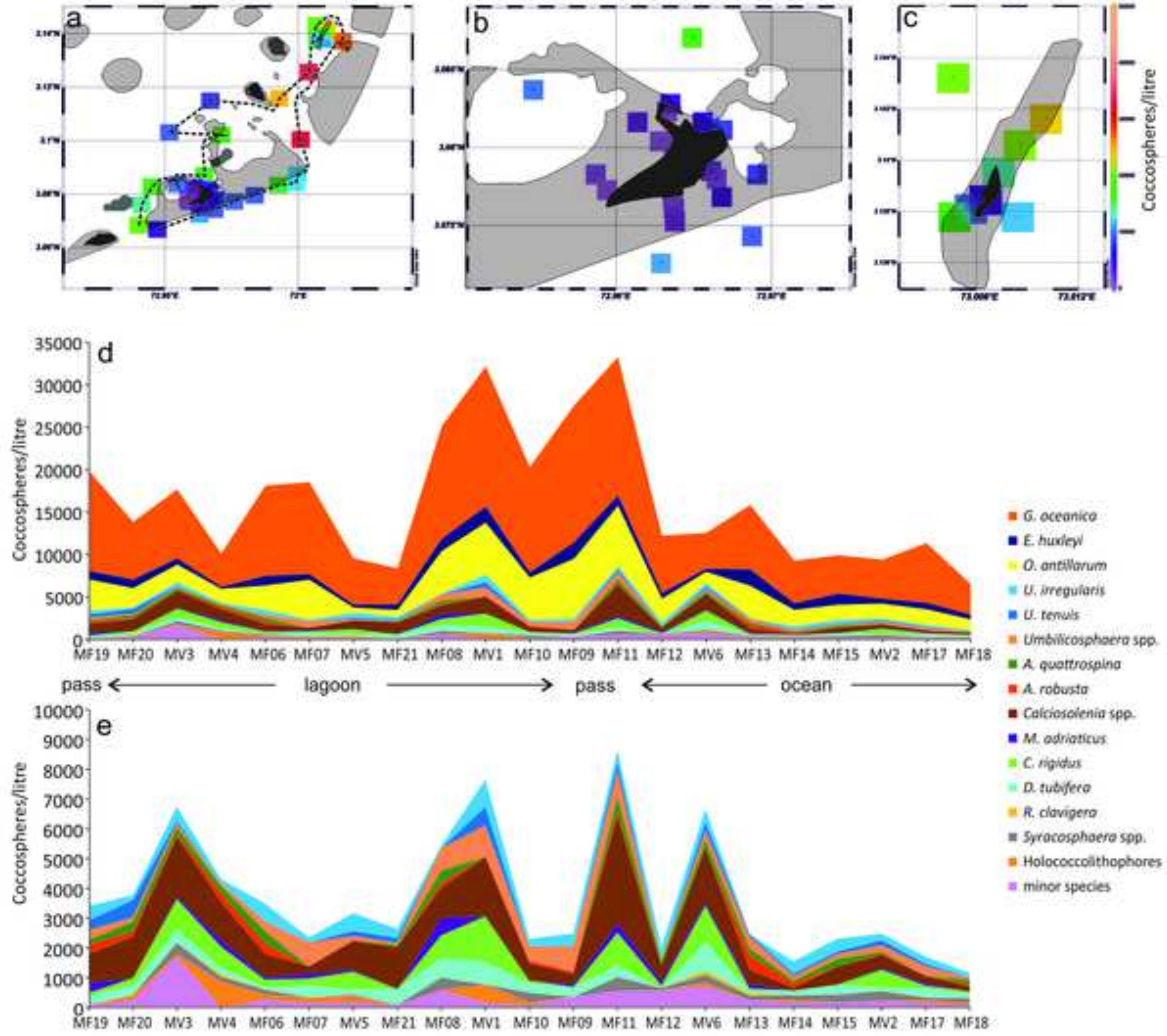
Figure 2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Coccospheres/litre
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Coccospheres/litre
MF19 MF20 MV3 MV4 MF06 MF07 MV5 MF21 MF08 MV1 MF10 MF09 MF11 MF12 MV6 MF13 MF14 MF15 MV2 MF17 MF18
G. oceanica
E. huxleyi
O. antillarum
U. irregularis
U. tenuis
Umbilicosphaera spp.
A. quattrospina
A. robusta
Calciosolenia spp.
M. adriaticus
C. rigidus
D. tubifera
R. clavigera
Syracosphaera spp.
Holococcolithophores
minor species

Figure 3a

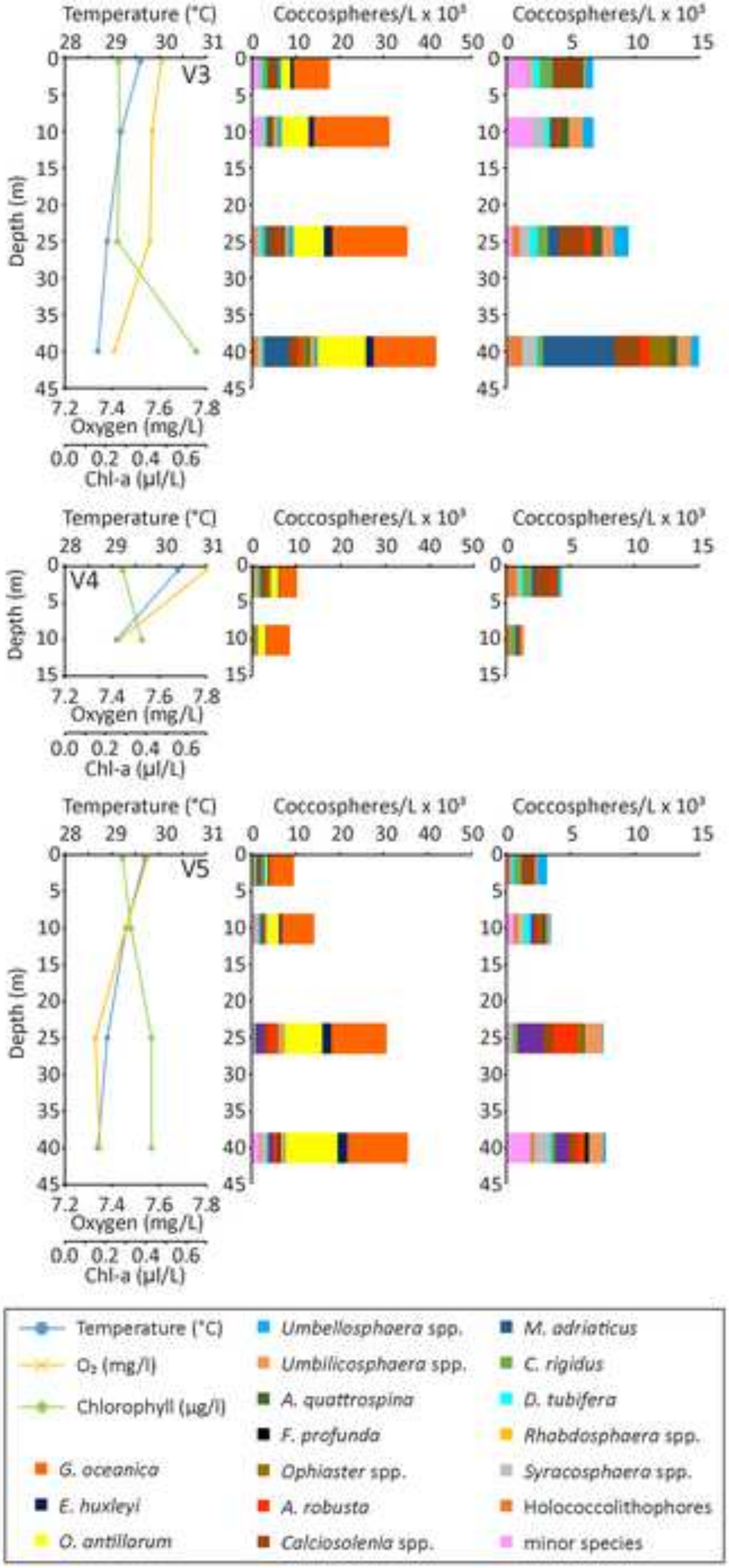
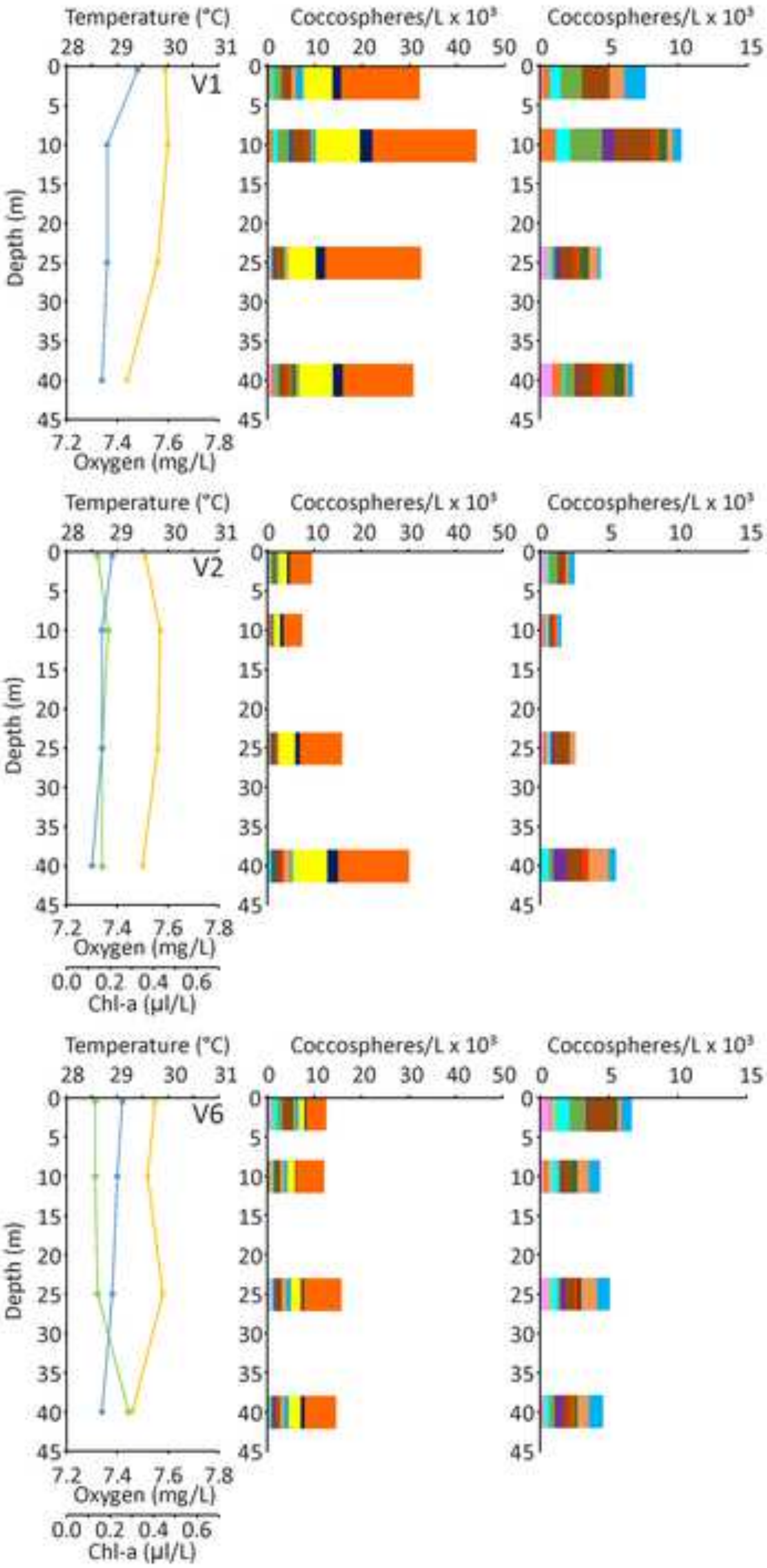

Temperature (°C)
28 29 30 31
Coccospheres/L x 10³
0 10 20 30 40 50
Coccospheres/L x 10³
0 5 10 15
V3
Depth (m)
0 5 10 15 20 25 30 35 40 45
7.2 7.4 7.6 7.8
Oxygen (mg/L)
0.0 0.2 0.4 0.6
Chl-a (µl/L)
V4
0 5 10 15
V5
Temperature (°C)
O₂ (mg/l)
Chlorophyll (µg/l)
G. oceanica
E. huxleyi
O. antillarum
Umbellosphaera spp.
Umbilicosphaera spp.
A. quattrospina
F. profunda
Ophiaster spp.
A. robusta
Calciosolenia spp.
M. adriaticus
C. rigidus
D. tubifera
Rhabdosphaera spp.
Syracosphaera spp.
Holococcolithophores
minor species

Figure 3b


Temperature (°C)
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Coccospheres/L x 10³
0 10 20 30 40 50
Coccospheres/L x 10³
0 5 10 15
V1
Depth (m)
0 5 10 15 20 25 30 35 40 45
7.2 7.4 7.6 7.8
Oxygen (mg/L)
Temperature (°C)
28 29 30 31
Coccospheres/L x 10³
0 10 20 30 40 50
Coccospheres/L x 10³
0 5 10 15
V2
Depth (m)
0 5 10 15 20 25 30 35 40 45
7.2 7.4 7.6 7.8
Oxygen (mg/L)
0.0 0.2 0.4 0.6
Chl-a (µl/L)
Temperature (°C)
28 29 30 31
Coccospheres/L x 10³
0 10 20 30 40 50
Coccospheres/L x 10³
0 5 10 15
V6
Depth (m)
0 5 10 15 20 25 30 35 40 45
7.2 7.4 7.6 7.8
Oxygen (mg/L)
0.0 0.2 0.4 0.6
Chl-a (µl/L)

Plate 1

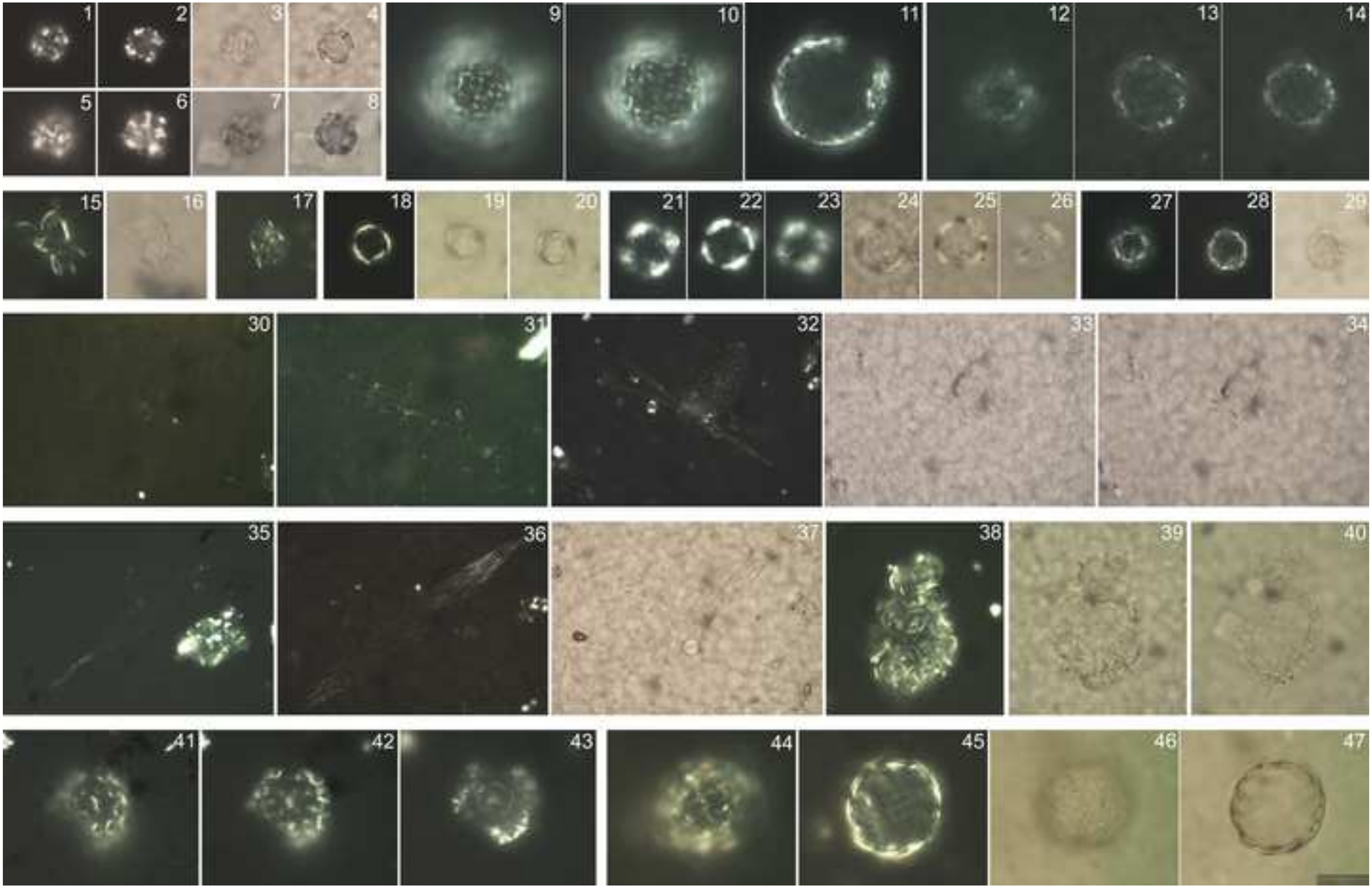
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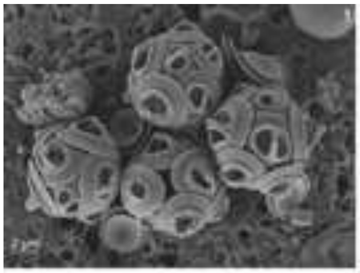
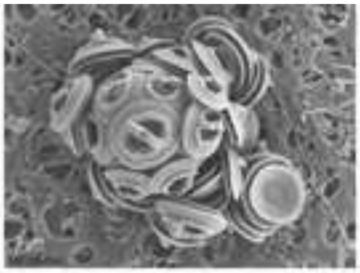
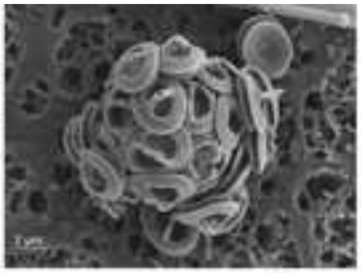
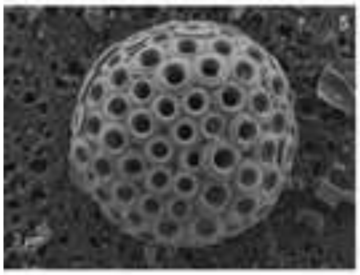
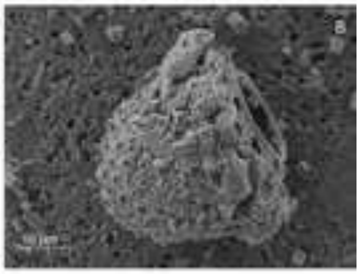
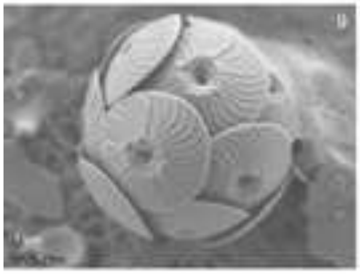
Plate 2

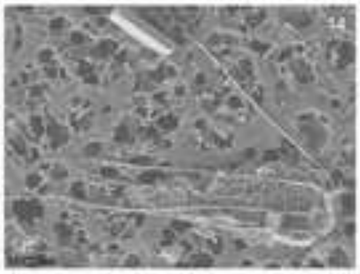


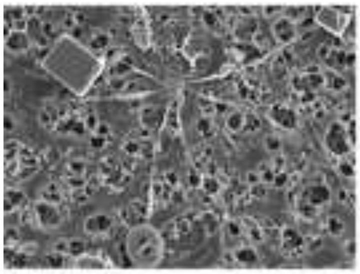
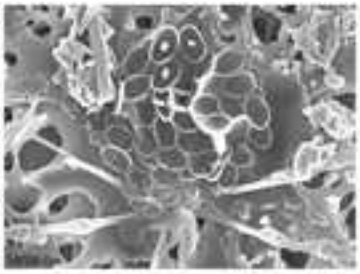
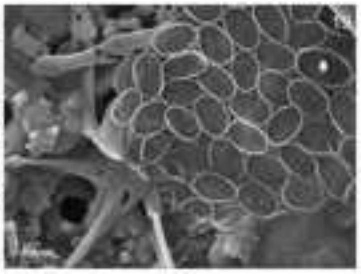



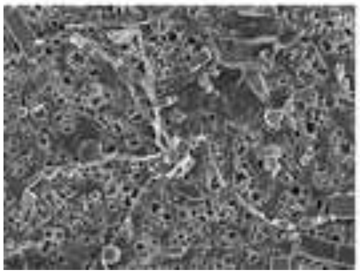



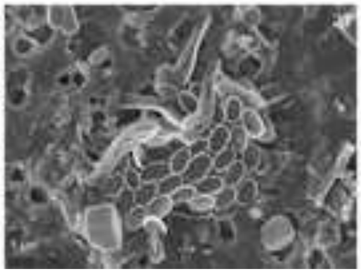
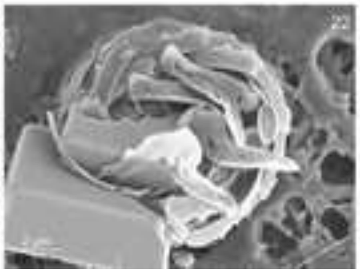




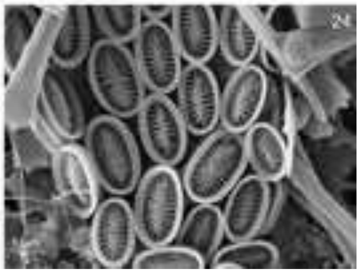
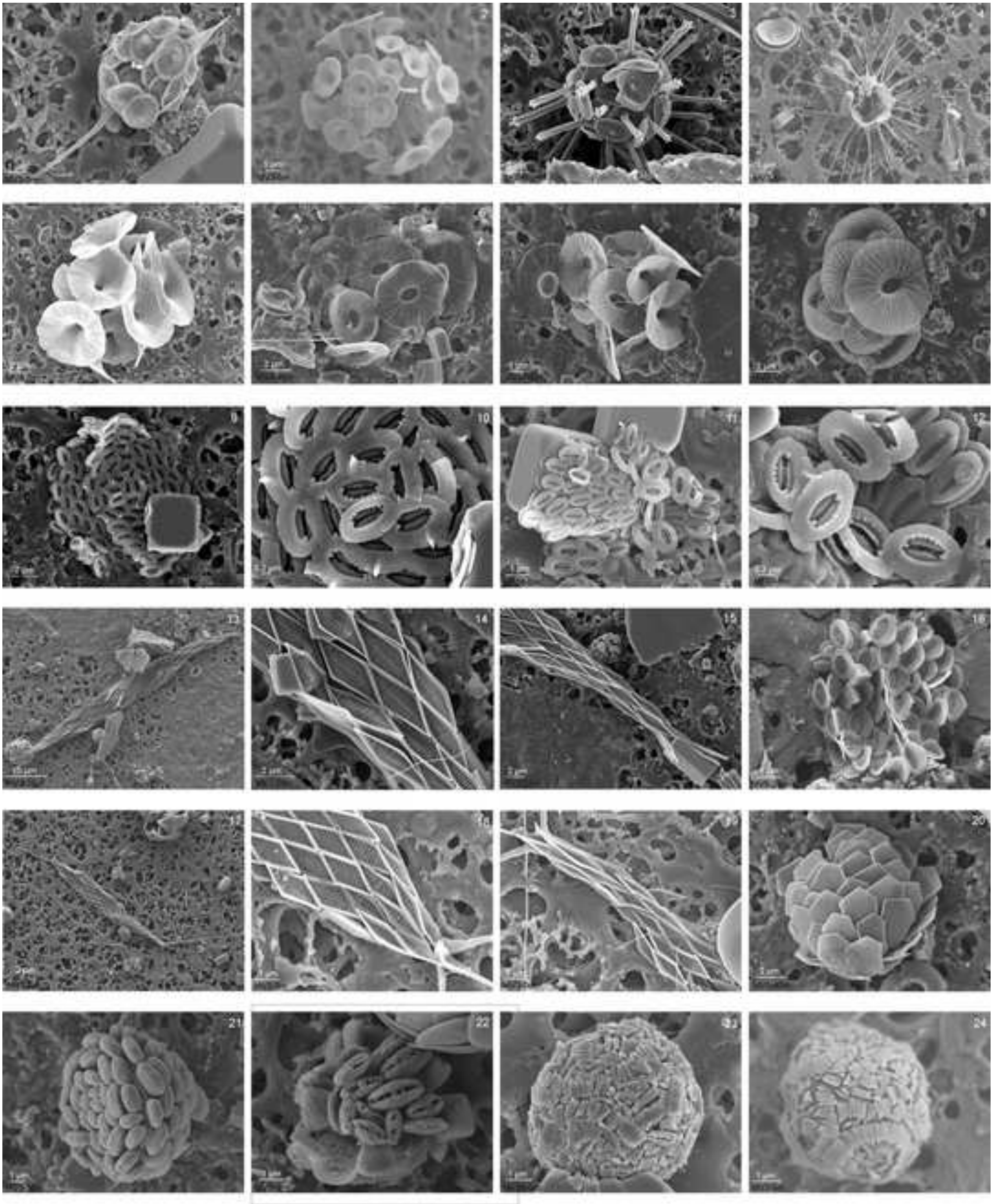


Plate 3



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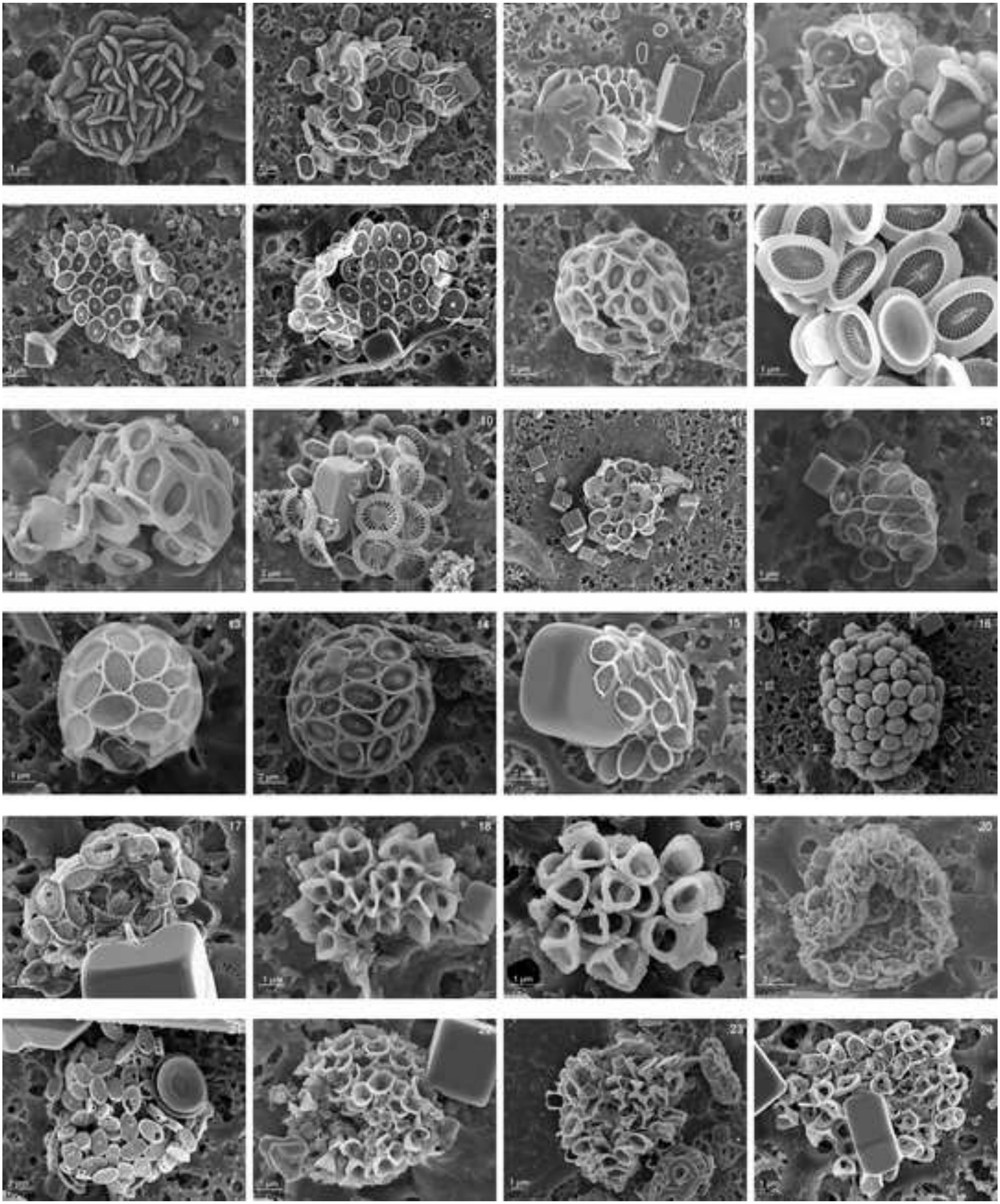

SAMPLE	LOCATION	DEPTH	COORDINATES N	COORDINATES E
M1A	Magoodhoo Island	0	3° 04' 42.6"	72° 57' 58.1"
M1B	Magoodhoo Island	0	3° 04' 40.8"	72° 57' 59.3"
M1C	Magoodhoo Island	0	3° 04' 36.7"	72° 58' 00.5"
M2A	Magoodhoo Island	0	3° 04' 36.5"	72° 57' 49.4"
M2B	Magoodhoo Island	0	3° 04' 34.0"	72° 57' 49.6"
M2C	Magoodhoo Island	0	3° 04' 31.0"	72° 57' 49.8"
M3A	Magoodhoo Island	0	3° 04' 38.3"	72° 57' 34.1"
M3B	Magoodhoo Island	0	3° 04' 41.9"	72° 57' 31.5"
M4A	Magoodhoo Island	0	3° 04' 49.0"	72° 57' 49.6"
M4B	Magoodhoo Island	0	3° 04' 49.6"	72° 57' 46.3"
M4C	Magoodhoo Island	0	3° 04' 54.0"	72° 57' 41.0"
Ad1A	Adanga Island	0	3° 08' 22.3"	73° 00' 32.0"
Ad1B	Adanga Island	0	3° 08' 26.2"	73° 00' 35.0"
Ad1C	Adanga Island	0	3° 08' 29.8"	73° 00' 38.7"
Ad2A	Adanga Island	0	3° 08' 18.4"	73° 00' 30.2"
Ad2B	Adanga Island	0	3° 08' 17.2"	73° 00' 28.1"
Ad2C	Adanga Island	0	3° 08' 16.0"	73° 00' 25.8"
V1	lagoon	0	3° 07' 33.22"	73° 00' 14.3"
V1	lagoon	10	3° 07' 33.22"	73° 00' 14.3"
V1	lagoon	25	3° 07' 33.22"	73° 00' 14.3"
V1	lagoon	40	3° 07' 33.22"	73° 00' 14.3"
V2	ocean	0	3° 04' 27.6"	72° 58' 07.5"
V2	ocean	10	3° 04' 27.6"	72° 58' 07.5"
V2	ocean	25	3° 04' 27.6"	72° 58' 07.5"
V2	ocean	40	3° 04' 27.6"	72° 58' 07.5"
V3	lagoon	0	3° 04' 58.4"	72° 56' 42.9"
V3	lagoon	10	3° 04' 58.4"	72° 56' 42.9"
V3	lagoon	25	3° 04' 58.4"	72° 56' 42.9"
V3	lagoon	40	3° 04' 58.4"	72° 56' 42.9"
V4	small lagoon	0	3° 05' 01.4"	72° 57' 16.9"
V4	small lagoon	10	3° 05' 01.4"	72° 57' 16.9"
V5	lagoon	0	3° 06' 11.8"	72° 57' 05.8"
V5	lagoon	10	3° 06' 11.8"	72° 57' 05.8"
V5	lagoon	25	3° 06' 11.8"	72° 57' 05.8"
V5	lagoon	40	3° 06' 11.8"	72° 57' 05.8"
V6	ocean	0	3° 05' 04.3"	72° 59' 57.4"
V6	ocean	10	3° 05' 04.3"	72° 59' 57.4"
V6	ocean	25	3° 05' 04.3"	72° 59' 57.4"
V6	ocean	40	3° 05' 04.3"	72° 59' 57.4"
MF01	enclosed bay Maghoodoo Island	0	3° 4' 52.61"	72° 57' 57.69"
MF02	enclosed bay Maghoodoo Island	0	3° 4' 52.14"	72° 58' 0.72"
MF03	shallow Magoodhoo lagoon	0	3° 4' 54.00"	72° 57' 56.17"
MF04	shallow close to Adanga Island	0	3° 8' 16.50	73° 0' 34.70"
MF05-in	Port of Maghoodoo Island	0	3° 4' 56.29"	72° 57' 47.95"
MF05-out	Out of the port of Maghoodoo Island	0	3° 4' 58.19"	72° 57' 48.74"
MF06	Lagoon	0	3° 5' 13.50"	72° 57' 53.80"
MF07	Lagoon	0	3° 6' 8.20"	72° 58' 17.40"
MF08	Lagoon in front of the pass	0	3° 6' 57.80"	72° 59' 34.80"
MF09	Pass	0	3° 8' 14.30"	73° 0' 60.00"

MF10	Lagoon behind Adanga Island	0	3° 8' 35.60"	73° 0' 25.60"
MF11	Pass	0	3° 6' 1.90"	73° 0' 3.40"
MF12	Ocean	0	3° 5' 14.10"	72° 59' 59.50"
MF13	Ocean	0	3° 5' 0.40"	72° 59' 34.40
MF14	Ocean	0	3° 4' 47.10"	72° 59' 1.50"
MF15	Ocean	0	3° 4' 38.70"	72° 58' 34.10"
MF16	Small pass	0	3° 4' 41.90"	72° 58' 8.80"
MF17	Ocean	0	3° 4' 21.40"	72° 57' 46.60"
MF18	Ocean	0	3° 4' 0.40"	72° 56' 50.80"
MF19	Pass	0	3° 4' 5.90"	72° 56' 25.10"
MF20	Lagoon	0	3° 4' 34.20"	72° 56' 28.50"
MF21	Lagoon	0	3° 6' 54.40"	72° 58' 1.80"

DATE	TIME	WEATHER	TEMPERATURE	CONDUCTIVITY	pH	O2	O2 %SAT
11/02/18	15:30	CLOUDY	29.1	53.4	8.225	9.51	125.6
11/02/18	15:30	CLOUDY	28.8	53.7	8.183	7.91	103.2
11/02/18	17:00	CLOUDY	28.8	53.7	8.162	7.36	95.7
11/03/18	15:30	SUNNY	32.1	52.9	8.27	10.65	149.3
11/03/18	15:30	SUNNY	29.5	53.7	8.232	8.89	116.1
11/03/18	15:30	SUNNY	29.1	53.8	8.199	7.9	103.7
11/05/18	16:00	SUNNY	30	53.8	8.246	10.97	142.3
11/05/18	16:00	SUNNY	29.6	53.8	8.267	10.1	133.3
11/04/18	15:30	SUNNY	34.1	52	8.209	11.44	167.2
11/04/18	15:30	SUNNY	32.5	53.5	8.445	15.12	>200
11/04/18	15:30	SUNNY	32	53.8	8.419	14.33	197.6
11/03/18	9:00	SUNNY	29.2	53.7	8.189	8.29	108.3
11/03/18	9:00	SUNNY	29.2	53.7	8.188	7.97	104.8
11/03/18	9:00	SUNNY	29.2	53.7	8.187	8.08	105.6
11/03/18	10:15	SUNNY	30	53.7	8.183	8.04	106.9
11/03/18	10:15	SUNNY	29.7	53.7	8.117	8.94	117.7
11/03/18	10:15	SUNNY	29.4	53.7	8.182	8.14	106.9
11/03/18	12:00	SUNNY	29.4	53.8	8.144	7.59	99.7
11/03/18	12:00	SUNNY	28.8	53.7	8.156	7.6	99
11/03/18	12:00	SUNNY	28.8	53.7	8.163	7.56	98.3
11/03/18	12:00	SUNNY	28.7	53.7	8.128	7.44	96.7
11/05/18	9:30	SUNNY	28.9	53.9	8.17	7.51	97.5
11/05/18	9:30	SUNNY	28.7	53.9	8.156	7.57	98
11/05/18	9:30	SUNNY	28.7	53.9	8.179	7.56	97.7
11/05/18	9:30	SUNNY	28.5	54	8.173	7.5	96.6
11/05/18	11:00	SUNNY	29.6	53.9	8.178	7.61	100.7
11/05/18	11:00	SUNNY	29.2	53.9	8.168	7.57	99.1
11/05/18	11:00	SUNNY	28.9	53.9	8.174	7.56	98.1
11/05/18	11:00	SUNNY	28.7	53.9	8.175	7.41	96.1
11/05/18	12:00	SUNNY	30.4	53.9	8.202	7.8	103.7
11/05/18	12:00	SUNNY	29.1	54	8.157	7.43	96.7
11/06/18	10:00	WET	29.7	53.9	8.181	7.55	99.1
11/06/18	10:00	WET	29.3	53.9	8.159	7.46	97.8
11/06/18	10:00	WET	28.9	53.9	8.166	7.33	85.2
11/06/18	10:00	WET	28.7	53.9	8.161	7.35	95.2
11/06/18	11:30	SUNNY	29.1	53.9	8.182	7.55	98.9
11/06/18	11:30	SUNNY	29	53.9	8.169	7.52	98.1
11/06/18	11:30	SUNNY	28.9	53.9	8.179	7.58	98.5
11/06/18	11:30	SUNNY	28.7	53.9	8.188	7.46	96.9
11/03/18	0:00						
11/03/18	6:10						
11/03/18	6:12						
11/03/18	11:30						
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11/06/18	16:05

Declaration of interests

☒ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Author statement

EM: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Software; Supervision; Validation; Visualization; Writing - original draft; Writing - review & editing.

BL: Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Writing - review & editing.

PG: Funding acquisition; Resources; Writing - review & editing.

Supplementary Figure 1