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Data report: surface seawater plankton sampling for coccolithophores undertaken during IODP Expedition 359[1]

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Keywords: International Ocean Discovery Program, IODP, *JOIDES Resolution*, Expedition 359, Indian Ocean transect, Maldives, coccolithophores

Contents

Abstract

Data on extant coccolithophore assemblages from plankton samples collected during International Ocean Discovery Program Expedition 359 to the Maldives is presented. Samples include 12 collected during passage across the Indian Ocean from Darwin, Australia, to the Maldives and 40 collected in the Maldives. Assemblages were analyzed by light and scanning electron microscopy, and detailed assemblage data are presented. Comparison with previous data from the region suggests that there are consistent distinctive aspects to Indian Ocean assemblages.

Introduction

Knowledge of coccolithophore biogeography is an essential basis for paleoecological interpretation of coccolithophore assemblages and for investigation of evolutionary patterns (e.g., Winter et al., 1994; Knappertsbusch et al., 1997; Baumann et al., 2005). However, there have been relatively few large-scale surveys of coccolithophores, and their biogeography is poorly known in many areas, notably the Indian Ocean. There have been some useful studies of Indian Ocean coccolithophores, including a transect from Java to Aden (Kleijne et al., 1989; Kleijne, 1993), a study of the southeast Indian Ocean (Takahashi and Okada 2000), studies of coccolithophores in various upwelling areas (Andruleit et al., 2003, 2004, 2005; Schiebel et al., 2004; Andruleit, 2007), and a short north–south transect study in the equatorial Indian Ocean (Guptha et al., 2005). However, this sampling has been patchy, there has been little resampling of areas studied, and the data have not been synthesized. Consequently, the coccolithophore assemblages of the Indian Ocean are poorly characterized, and in particular it is difficult to determine how they differ from those in the Atlantic and Pacific Oceans, even though it is becoming increasingly clear that there are significant differences between Pacific and Atlantic Ocean assemblages (Hagino and Young, 2015).

International Ocean Discovery Program (IODP) Expedition 359 commenced with a transit across the equatorial Indian Ocean from Darwin, Australia, to the Maldives (Figure **F1A**). This transit presented a valuable opportunity to sample the equatorial assemblages to determine broad patterns of coccolithophore distribution and compare them with those recorded previously, notably by Kleijne et al. (1989). Sampling continued within the Maldives drilling area to (1) determine whether assemblages within the Maldives show evidence of ecological restriction or modified assemblages related to the particular environment of the atoll chain, (2) investigate reproducibility of assemblage data by repeat sampling within a limited area over an extended period, and (3) investigate the potential of the Maldives for coccolithophore research.

This report provides a concise overview of the sampling undertaken and the preliminary results. Fuller documentation and analysis will be published later, in conjunction with other data.

Materials and methods

Seawater samples for plankton study were collected in two ways. While the ship was under way, samples were collected from the sea surface using a bucket and rope from the starboard main deck. While the ship was stationary at drill sites, a plankton sampling bottle (WildCo Beta 8.3 L van Dorn style in situ sample bottle, shipboard equipment) was deployed to collect water from ~15 m below the water's surface. Using a plankton sampling bottle to sample from depth is preferable for obtaining cleaner samples and to avoid the possibility of sampling water from which the plankton has settled out, but in practice, both sampling techniques yielded good assemblages. After sampling, 1 or 2 L of seawater were vacuum filtered onto microfilter discs using 25 mm filtration funnels (Pall Laboratory #4203) on a stainless steel filter ramp (shipboard equipment). Prefiltration through a brass 38 µm test sieve was used to remove larger zooplankton and contaminants (this was more important for the bucket-collected samples). Two filter disc types were used: 0.8 µm pore cellulosic filters (Sartorius Stedim Cellulose Nitrate) and 0.8 µm pore polycarbonate track-etched filters (Whatman Nuclepore). After collection, the filters were oven dried (at 40°–60°C) and stored in 47 mm plastic petrislides (Millipore). For

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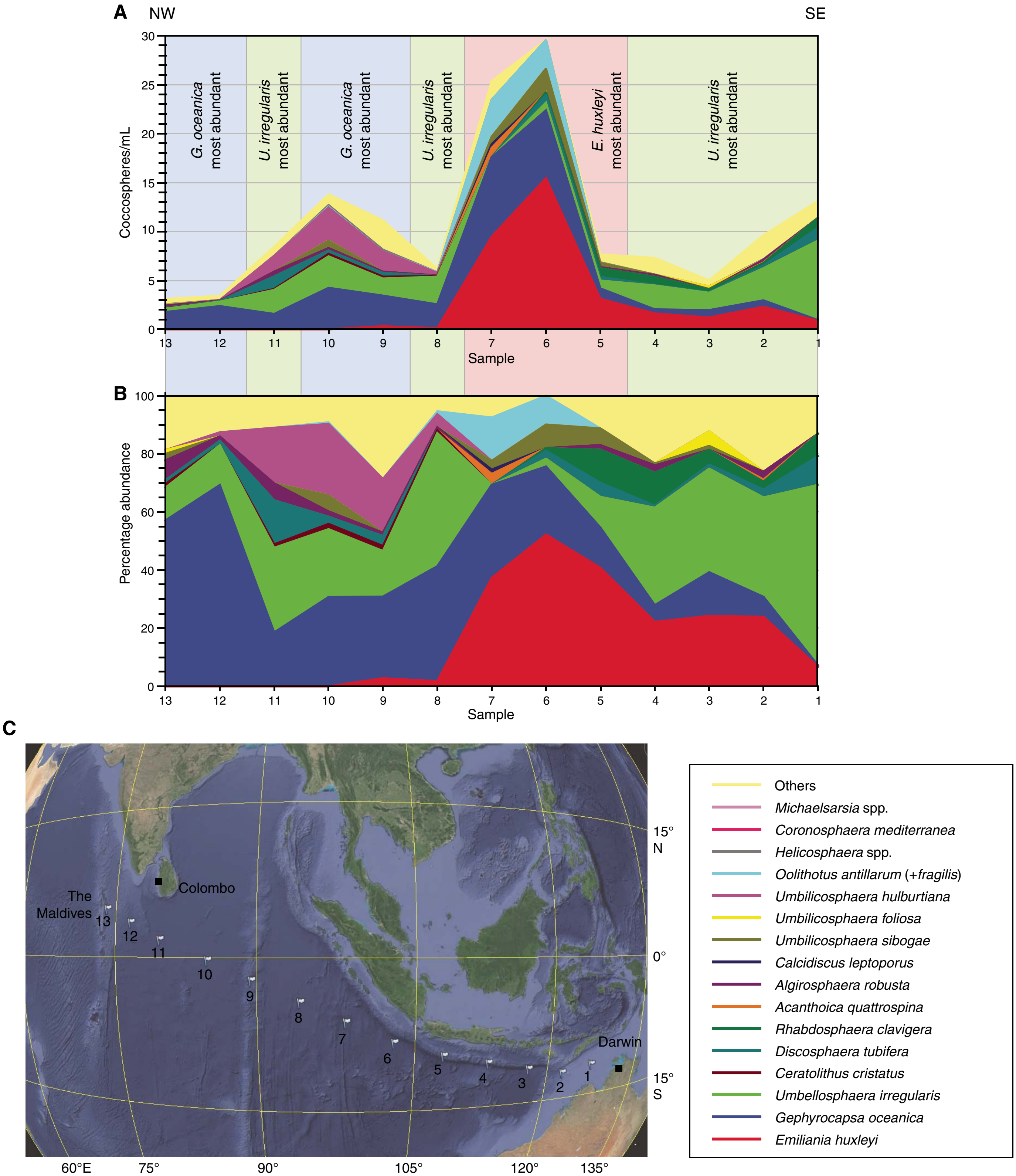
Figure F1. Coccolithophore assemblages along the transect across the Indian Ocean between Darwin and the Maldives. A. Absolute abundances (1000 cells/L) of the coccolithophore species as counted by light microscopy. Some categories in Table T1 are combined here; in particular the Others category includes all holococcoliths and *Syracosphaera* species. B. Same data as A, plotted as percentage abundances. C. Map of the Indian Ocean showing sampling localities.



light microscopy, a portion of cellulosic filter was cut out and mounted on a microscope slide using Norland optical adhesive (NOA) 74, a low-viscosity version of the standard NOA61 adhesive that penetrates better into the filter mesh. For electron microscopy, portions of the polycarbonate filters were cut out and mounted on aluminum stubs using carbon tabs and sputter coated with gold-palladium using a Leitz EM ACE2000 sputter coater.

Samples were examined and assemblages counted at 1000× magnification using a Zeiss Axioplan microscope with cross-polarized illumination (Tables **T1**, **T2**). About 150 coccospheres were counted and identified, mostly to species level. For taxonomy, the syntheses of Young et al. (2003, 2014) and Jordan et al. (2004) were followed. Counts were converted into cell densities per liter by recording the area counted and calculating the proportion of the filter surface this represented. Selected samples were examined by electron microscopy using the shipboard Hitachi TM3000 scanning electron microscope (SEM) to confirm identification and identify smaller species that cannot be recognized using light microscopy (Table **T3**).

Results

Indian Ocean transect

Thirteen surface water samples (Plkt-1 to Plkt-13) were collected during the passage across the Indian Ocean from Darwin, Australia, to the Maldives (Figure **F1A**). The assemblages counted by light microscopy in these samples are listed in Table **T1**. The assemblage data are illustrated as cell concentrations of the principal taxa (Figure **F1B**) and as percentage abundance (Figure **F1C**) along the route. All samples were also examined by scanning electron microscopy, and the species observed are listed in Table **T3**, although it should be noted that the time spent per sample was highly variable. Figure **F2** illustrates several of the most common species.

The data can be divided into three parts. There are low abundance assemblages (<15,000 coccospheres/L) at the beginning and end of the transect separated by higher abundance samples (>25,000 coccospheres/L) from two stations, Plkt-6 and Plkt-7 (Figure **F1B**).

The first five samples (Plkt-1 to Plkt-5), from the eastern part of the transect, are characterized by high relative abundances of *Umbellosphaera irregularis* and *Emiliania huxleyi* with subsidiary *Rhabdosphaera clavigera* var. *stylifer*, *Discosphaera tubifera*, and *Gephyrocapsa oceanica*.

The next two samples (Plkt-6 and Plkt-7), from southwest of Java, have higher abundances (>25,000 coccospheres/L) and are characterized by high relative abundances of *E. huxleyi*, *G. oceanica,* and *Oolithotus antillarum*. *Algirosphaera robusta* and *Umbilicosphaera sibogae* are also notably common. *Umbellosphaera* and *Rhabdosphaera* are almost absent from these two samples.

The final six samples (Plkt-8 to Plkt-13) again have low abundances (<15,000 coccospheres/L) and are dominated by *G. oceanica*, *U. irregularis*, and *Umbilicosphaera hulburtiana*. *D. tubifera* is also common, and *Michaelsarsia adriaticus* noticeably abundant in one sample (Plkt-9). Conversely, *E. huxleyi* is unusually rare, and *R. clavigera* is absent.

Maldives assemblages

Forty water samples (Plkt-14 to Plkt-53) were collected, approximately daily, during the drilling operations within the Maldives. Water temperature and salinity were measured on several occasions, and they remained constant with salinities of 35 and temperatures of 27°–28°C. The assemblages counted by light microscopy in these samples are listed in Table **T2**. The assemblage data are illustrated as cell concentrations of the principal taxa (Figure **F2A**) and as percentage abundance (Figure **F2B**) along the route. Several samples were also observed by scanning electron microscopy, and all species observed were imaged as summarized in Table **T3**. Figure **F3** illustrates several of the most common species.

All assemblages have low-abundance coccolithophore populations, with between 4,000 and 12,000 cells/L, and in all samples the dominant species is *Gephyrocapsa*. The rest of the assemblage is also broadly constant throughout the sampling period. The second and third most abundant species are usually *U. irregularis* and *D. tubifera*, although this ranking becomes more variable in the last six samples counted (Plkt-36 to Plkt-41) (Table **T2**). Other consistently present species are *Ceratolithus cristatus* (heterococcolith and ceratolith phase), *E. huxleyi* (all specimens seen in the SEM were Type A), *Helicosphaera hyalina*, *Coronosphaera mediterranea*, *Michaelsarsia* (all specimens seen in SEM were *Michaelsarsia adriatica*), *Umbellosphaera tenuis* (all specimens seen in the SEM were Type I), *Poricalyptra magnaghii* (identified in all SEM samples examined), *Syracosphaera exigua* (identified in all SEM samples examined), and *Syracosphaera halldallii* (identified in all SEM samples examined).

Superimposed on this pattern of general uniformity is some apparently random variability and some evidence of change through time. Random variability is most obviously seen in *Gephyrocapsa* abundance and in total cell numbers (Figure **F4**; Table **T2**). Samples from the sites at the mouth of the Kardiva Channel (Sites U1465, U1467, and U1469) showed more variability than those further into the Inner Sea (Sites U1467 and U1468).

Apparent secular change through the sampling interval includes a general increase in the proportion of *G. oceanica* accompanied by

Table T1. Assemblage data for the Indian Ocean transect. **Download table in .csv format.**

Table T2. Assemblage data for the Maldives sites. **Download table in .csv format.**

Table T3. Scanning electron microscopy occurrence data. **Download table in .csv format.**

Figure F2. Coccolithophore assemblages sampled within the Maldives during drilling. A. Absolute abundances (1000 cells/L) of the coccolithophore species as counted by light microscopy. Some categories in Table T1 are combined here; in particular the Others category includes all holococcoliths and *Syracosphaera* species. B. Same data as A, plotted as percentage abundances. C. Location map.

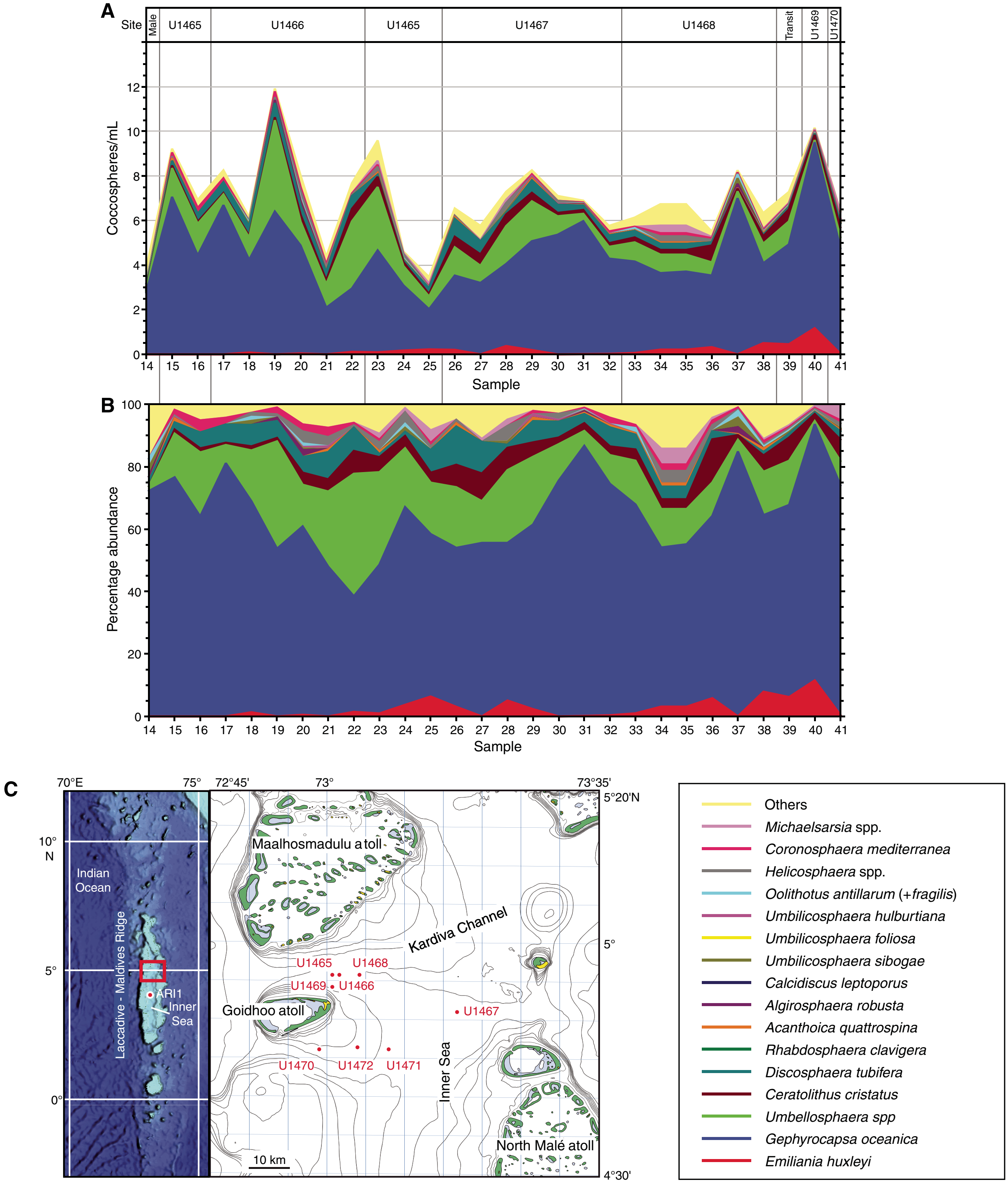


Figure F3. SEM images of common coccolithophores from samples collected within the Maldives. A. *Gephyrocapsa oceanica* (Sample Plkt-29). B. *Emiliania huxleyi* Type A (sensu Young and Westbroek, 1991) (Sample Plkt-26). C. *Umbellosphaera tenuis* Type I (sensu Kleijne, 1993) (Sample Plkt-41). D. *Umbellosphaera irregularis* (Sample Plkt-38). E. *Poricalyptra magnaghii* (Sample Plkt-38). F. *Helicosphaera hyalina* (Sample Plkt-38). G. *Syracosphaera exigua* (Sample Plkt-28). H. *Syracosphaera prolongata* (Sample Plkt-38). I. *Ceratolithus cristatus*-ceratolith stage, plain view (Sample Plkt-26). J. *Ceratolithus cristatus*-ceratolith stage, side view (Sample Plkt-32). K. *Ceratolithus cristatus*-heterococcolith stage (Sample Plkt-41).

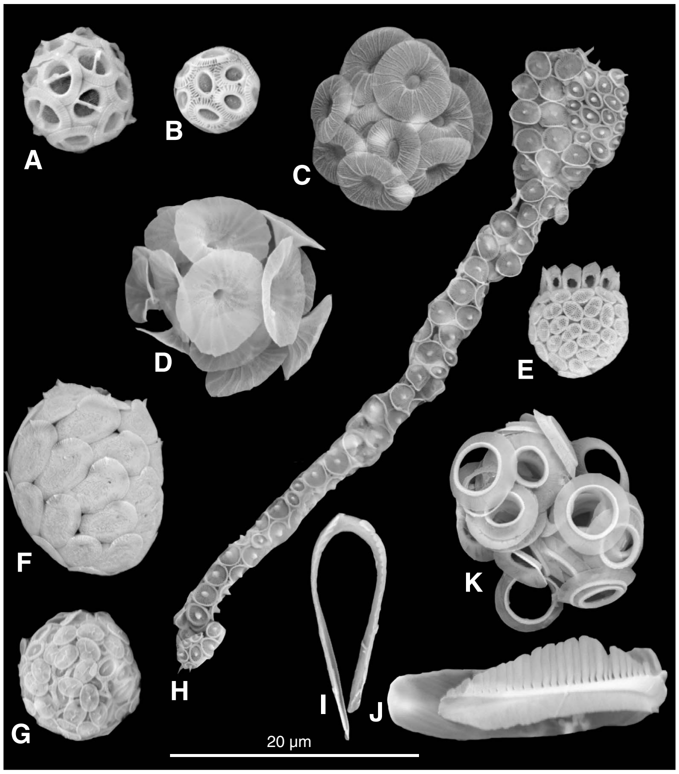
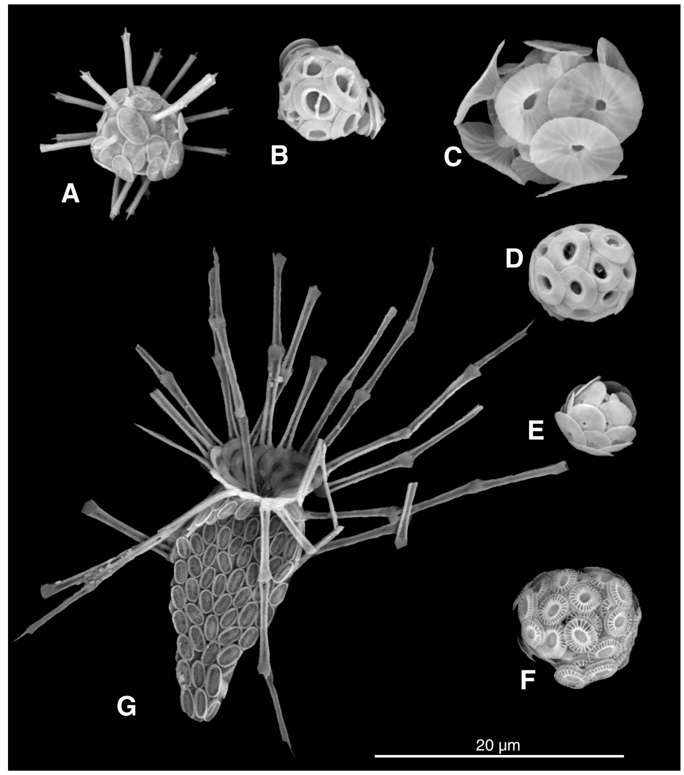


Figure F4. SEM images of common coccolithophores from the transect across the Indian Ocean. A. *Rhabdosphaera clavigera* var. *stylifera* (Sample Plkt-01). B. *Gephyrocapsa oceanica* (Sample Plkt-10). C. *Umbellosphaera irregularis* (Sample Plkt-01). D. *Umbilicosphaera hulburtiana* (Sample Plkt-10). E. *Oolithotus antillarum* (Sample Plkt-07). F. *Emiliania huxleyi* Type C (sensu Young and Westbroek, 1991) (Sample Plkt-03). G. *Michaelsarsia adriatica* (Sample Plkt-09).



appearance and increase in abundance of *E. huxleyi*. In parallel, *U. irregularis* and *D. tubifera* decline in abundance.

One of the most conspicuous aspects of the assemblages is the consistent presence of *Ceratolithus* in multiple phases. This includes loose ceratoliths, ceratoliths surrounded by hoop coccoliths, numerous loose heterococcoliths, and frequent coccospheres of the heterococcolith phase. The heterococcolith coccospheres often include hoop coccoliths and coccoliths intermediate in morphology between fully formed heterococcoliths and hoop coccoliths. All observed ceratoliths were of the *Ceratolithus cristatus* var. *telesmus* type, and all complete heterococcoliths were of the *Ceratolithus cristatus* var. *coccolithomorpha* type. *Ceratolithus* was evidently thriving in this environment during the sampling. Ceratoliths were, however, rare in the "mudline" Holocene samples collected during the expedition and virtually absent in the Pleistocene and Pliocene sediments.

Biogeography

The basic pattern shown in the transect data of an upwelling community dominated by placolith coccoliths (*Emiliania*, *Gephyrocapsa*, and *Umbilicosphaera*) contrasted with oligotrophic assemblages dominated by *Umbellosphaera* and *Discosphaera* is exactly as has often been described (e.g., Young, 1994; Winter et al., 1994). The details, however, are distinctive and are reinforced by the results from the Maldives. These include

- The dominant *Umbellosphaera* species is *U. irregularis*, and *U. tenuis*, when present, is represented by the lightly calcified but ornamented Type I of Kleijne (1993). This classification applies to all 40 samples studied.
- *Rhabdosphaera stylifera* is common in the southeast Indian Ocean but absent from the rest of the transect and all the Maldives samples.
- *E. huxleyi* is present in the southeast Indian Ocean and in the Java upwelling but absent from the rest of the transect. *E. huxleyi* did appear in the Maldives in the later part of the survey, but all specimens are Type A, whereas in the equatorial upwelling they are primarily Type C.
- *Gephyrocapsa ericsonii* and *Reticulofenestra parvula* are notably absent.
- *S. exigua*, which is only very sporadically recorded elsewhere, is a common member of these assemblages, especially in the Maldives. Other unusual species encountered repeatedly include *P. magnaghii* (present in nearly every sample examined by SEM, but no other *Poricalyptra* species were observed), *Calicasphaera diconstricta* (a species which has almost never been recorded since its original description by Kleijne [1993]), and *Poritectolithus maximus*.
- *Ceratolithus* assemblages are exclusively composed of the *telesmus* type ceratoliths and *coccolithomorpha* type heterococcoliths.

These aspects have not previously been mentioned as features of Indian Ocean assemblages, but intriguingly, comparison with the available literature suggests that they are all consistent features. The most relevant comparisons are with Kleijne (1993) for the northern Indian Ocean and with Takahashi and Okada (2000) for the southeast Indian Ocean. Kleijne (1993) recognized four assemblages in the northern Indian:

1. Ocean-A-1: *E. huxleyi* dominated with *G. oceanica*,
2. B: *G. oceanica* dominated,
3. C-1: *U. irregularis* dominated, and
4. D: Syracosphaeraceae and *G. oceanica* dominated.

Our assemblages could mostly be characterized as a mixture of the B and C-1 groups of Kleijne (1993). This includes both the dominant species, *G. oceanica*, *U. irregularis*, and *U. tenuis* Type I and the more distinctive minor species *C. cristatus* var. *telesmus*, *S. exigua*, and *P. magnaghii*. It is also noticeable that *R. clavigera*, normally an almost ubiquitous species in oligotrophic warm-water assemblages, is absent. Similarly, the assemblages recorded from the southeast Indian Ocean by Takahashi and Okada (2000) are similar to those we encountered in that area, with an assemblage dominated by *U. irregularis* and *E. huxleyi* with common *D. tubifera* and *R. clavigera*.

Overall, there is intriguing evidence that the Indian Ocean equatorial and subtropical coccolithophore assemblages have stable characteristic features that distinguish them from the equivalent assemblages in both the Atlantic and Pacific Oceans. Further characterization of these patterns and of the interplay of ecological and molecular genetic controls causing them would be useful to study.

The assemblages from the Maldives are broadly similar to those from the open waters of the north Indian Ocean and the Arabian Sea as sampled during this expedition and recorded in previous studies. The most distinctive element of the assemblage was the high abundance of *Ceratolithus* throughout the sampling period. However, this abundance was not reflected in the surface sediment samples, and it may have been an unusual event. Distinctive inner neritic elements such as *Cruciplacolithus neohelis*, *Pleurochrysis*, *Braarudosphaera*, or *Tergestiella* were not observed, but it was not possible to sample from shallow water or lagoonal locations. Overall, the sampling was very productive in terms of recovery of diverse assemblages, and this clearly would be a good field area for coccolithophore research.

See the **Appendix** for a list of all taxa recorded.

Acknowledgments

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Appendix

Full citations are given here for all taxa recorded. Bibliographic references can be found in Young et al. (2003) or on the Nannotax website (Young et al., 2014).

Acanthoica quattrospina Lohmann, 1903
Algirosphaera robusta (Lohmann, 1902) Norris, 1984
Alisphaera gaudii Kleijne et al., 2002
Alisphaera unicornis Okada and McIntyre, 1977
Anthosphaera fragaria Kamptner, 1937
Calcidiscus leptoporus subsp. *quadriperforatus* (Kamptner, 1937) Geisen et al., 2002 HOL
Calciosolenia murrayi Gran, 1912
Calciopappus rigidus Heimdal in Heimdal and Gaarder, 1981
Calicasphaera diconstricta Kleijne, 1991
Calyptrolithina multipora (Gaarder in Heimdal and Gaarder, 1980) Norris, 1985
Calyptrosphaera galea Lecal-Schlauder, 1951
Calyptrosphaera sphaeroidea Schiller, 1913
Ceratolithus cristatus Norris, 1965 CER *telesmus* type, *sensu* Young et al., 2003
Ceratolithus cristatus Norris, 1965 HET *coccolithomorpha* type, *sensu* Young et al., 2003
Ceratolithus cristatus Norris, 1965 HET hoops type, *sensu* Young et al., 2003
Corisphaera gracilis Kamptner, 1937
Corisphaera sp.
Coronosphaera mediterranea (Lohmann, 1902) Gaarder in Gaarder and Heimdal, 1977
Cyrtosphaera aculeata (Kamptner, 1941) Kleijne, 1992
Discosphaera tubifera (Murray and Blackman, 1898) Ostenfeld, 1900
Emiliania huxleyi (Lohmann, 1902) Hay and Mohler in Hay et al., 1967 Type B/C
Emiliania huxleyi (Lohmann, 1902) Hay and Mohler in Hay et al., 1967 Type A
Gephyrocapsa oceanica Kamptner, 1943
Helicosphaera hyalina Gaarder, 1970
Helicosphaera carteri (Wallich, 1877) Kamptner, 1954
Helladosphaera cornifera (Schiller, 1913) Kamptner, 1937
Helladosphaera pienaarii Norris, 1985
Homozygosphaera arethusae (Kamptner, 1941) Kleijne, 1991 HOL
Homozygosphaera spinosa (Kamptner, 1941) Deflandre, 1952
Homozygosphaera triarcha Halldal and Markali, 1955
Homozygosphaera vercellii Borsetti and Cati, 1979
Michaelsarsia adriaticus (Schiller, 1914) Manton et al., 1984
Oolithotus antillarum (Cohen, 1964) Reinhardt in Cohen and Reinhardt, 1968
Ophiaster hydroideus (Lohmann, 1903) Lohmann, 1913
Palusphaera vandelii Lecal, 1965
Polycrater galapagensis Manton and Oates, 1980
Poricalyptra magnaghii (Borsetti and Cati, 1976) Kleijne, 1991
Poritectolithus maximus Kleijne, 1991
Rhabdosphaera clavigera var. *stylifera* (Lohmann, 1902) Kleijne and Jordan, 1990
Rhabdosphaera xiphos (Deflandre and Fert, 1954) Norris, 1984
Scyphosphaera apsteinii Lohmann, 1902
Syracosphaera bannockii HOL (Borsetti and Cati, 1976) Cros et al., 2000
Syracosphaera corolla Lecal, 1966
Syracosphaera exigua Okada and McIntyre, 1977
Syracosphaera halldalii Gaarder in Gaarder and Hasle, 1971 ex Jordan, 1994
Syracosphaera halldalii Gaarder in Gaarder and Hasle 1971, ex Jordan, 1994 HOL
Syracosphaera hastata Kleijne and Cros, 2009
Syracosphaera histrica Kamptner, 1941 HOL
Syracosphaera leptolepis Kleijne and Cros, 2009
Syracosphaera molischii Schiller, 1925
Syracosphaera nana (Kamptner, 1941) Okada and McIntyre, 1977
Syracosphaera nodosa Kamptner, 1941
Syracosphaera noroitica Knappertsbusch, 1993
Syracosphaera orbiculus Okada and McIntyre, 1977
Syracosphaera ossa (Lecal, 1966) Loeblich and Tappan, 1968
Syracosphaera prolongata Gran, 1912 ex Lohmann, 1913
Syracosphaera pulchra Lohmann, 1902
Syracosphaera pulchra Lohmann, 1902 HOL *oblonga* type
Syracosphaera rotula Okada and McIntyre, 1977
Umbellosphaera irregularis Paasche in Markali and Paasche, 1955
Umbellosphaera tenuis (Kamptner, 1937) Paasche in Markali and Paasche, 1955 Type I
Umbilicosphaera foliosa (Kamptner, 1963) Geisen in Sáez et al., 2003
Umbilicosphaera hulburtiana Gaarder, 1970
Umbilicosphaera sibogae (Weber-van Bosse, 1901) Gaarder, 1970
Zygosphaera amoena Kamptner, 1937