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

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Abstract

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 (Andrueliet al., 2003, 2004, 2005; Schiebel et al., 2004; Andrulieut, 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.

Introduction

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 cellulose 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 petriplates (Millipore). For
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.

- E. huxleyi is most abundant in some samples.
- G. oceanica is most abundant in other samples.
- U. irregularis is most abundant in most samples.

Legend:
- Others
- Michaelsarsia spp.
- Coronosphaera mediterranea
- Helicosphaera spp.
- Oolithotus antillarum (+fragilis)
- Umbilicosphaera hulburtiana
- Umbilicosphaera foliosa
- Umbilicosphaera sibogae
- Calcidiscus leptoporus
- Algiosphaera robusta
- Acanthoica quattrospina
- Rhabdosphaera clavigera
- Discosphaera tubifera
- Ceratolithus cristatus
- Umbellopsphaera irregularis
- Gephyrocapsa oceanica
- Emiliania huxleyi
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 Ooliolithus antillarum. Algirospaera 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 cristasus (heterococcolith and cera-tolith 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), Umbililosphaera tanis (all specimens seen in the SEM were Type I), Poricypridina magnaghi (identified in all SEM samples examined), Syracosphaera exigua (identified in all SEM samples examined), and Syracosphaera halldali (identified in all SEM samples examined).

Superimposed on this pattern of general uniformity is some apparent variation 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
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.
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).
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 south-east 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. exiguus*, and *P. maguaghii*. 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 Maldives are broadly similar to those 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 neoehlis*, *Pleoechrysis*, *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.

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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
Calciosolenia murrayi (Gran, 1912) Hay and Mohler in Hay et al., 1967 Type B/C
Calciosolenia murrayi (Gran, 1912) Hay and Mohler in Hay et al., 1967 Type A
Calciopappus rigidus Heimdal in Heimdal and Gaarder, 1981
Calciopappus rigidus (Heimdal in Heimdal and Gaarder, 1980) Norris, 1985
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
Michaeelsaria adriatica (Schiller, 1914) Manton et al., 1984
Oolithotus antillarum (Cohen, 1964) Reinhardt in Cohen and Reinhardt, 1968
Ophiaster hydroideus (Lohmann, 1903) Lohmann, 1913
Palusphaera vandeli Lecal, 1965
Polycrater galapagensis Manton and Oates, 1980
Portitectolithus maximus Kleijne, 1991
Rhabdosphaera clavigera var. stylifera (Lohmann, 1902) Kleijne and Jordan, 1990
Rhabdosphaera xiphos (Deflandre and Fert, 1954) Norris, 1984
Scyphosphaera apsteini 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 histricala 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 orbicularis Okada and McIntyre, 1977
Syracosphaera osca (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
Umbellophaera irregularis Paasche in Markali and Paasche, 1955
Umbellophaera tenuis (Kamptner, 1937) Paasche in Markali and Paasche, 1955 Type I
Umbilicosphaera foliosa (Kamptner, 1963) Geisen in Sáez et al., 2003
Umbilicosphaera hubertiiana Gaarder, 1970
Umbilicosphaera sibogae (Weber-van Bosse, 1901) Gaarder, 1970
Zygosphaera amoena Kamptner, 1937