Lagoon coccolithophorids from the Republic of Palau, NW Equatorial Pacific

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Abstract During an intensive study of the marine lakes and reefal lagoons of the Republic of Palau in the NW Equatorial Pacific, examination of filtered neuston net and bottle samples revealed that diatoms were the predominant microplankton group with mineralised cell coverings. However, a low-diversity coccolithophorid assemblage was also present, with *Gephyrocapsa oceanica* always being the most numerous species, while *Helicosphaera carteri*, *Coronosphaera mediterranea* and *Umbilicosphaera hulburtiana* were found at four or more sampling points. Although the diversities of the shallow and deeper lagoon waters were similar (15-16 spp.), the assemblage composition was different. Only *G. oceanica* and *H. carteri* were present in the two lake samples, while species seemingly restricted to very shallow lagoon-waters included *Anacanthoica cidaris*, *Calciopappus rigidus*, *Cruciplacolithus neohelis* and *Syracosphaera* sp.II cf. *S. epigrosa*. In addition, coccolith-covered tintinnids were present at two shallow lagoon sites, suggesting that these microzooplankton had a regular supply of locally-produced coccoliths to build up their exoskeletons, and that coccolithophorids may have an important ecological role to play in tropical coastal environments.

Keywords Coccolithophorids, marine lake, coastal lagoon, Republic of Palau, NW Pacific, tintinnids

1. Introduction

In general, studies of tropical coccolithophorid assemblages from shallow-water environments are rare. Despite this, it is known that the marginal seas of the western Pacific are dominated by Gephyrocapsa oceanica, which often represents about 90% or more of such low-diversity coccolithophorid assemblages, and that these assemblages are often associated with malformation and reduced cell-size (Okada & Honjo, 1970, 1975; Hallegraeff, 1984; Kleijne, 1990). In more localised studies, Marshall (1933) recorded five species of coccolithophorids from surface-waters overlying the Great Barrier Reef, but believed they were washed in from the open ocean, while an absence of coccolithophorids at certain times of the year correlated with salinities below 35% (= 35PSU). Yet, surprisingly, Emiliania huxleyi was not among those species recorded by Marshall (1933). Another report focussed on the microalgal assemblages of an Indonesian mangrove environment, recording 10 species of haptophyte from the mangrove area and four species from the open water (Inouye, 1988). Of the mineralised haptophyte taxa, species of Ochrosphaera, Hymenomonas, Jomonlithus and Pleurochrysis were present in the mangrove area, whilst Gephyrocapsa oceanica was present in the open-water area. Further afield, Kling (1975) identified 27 species from lagoonal waters over the southern shelf of British Honduras (Belize), with assemblages dominated by E. huxleyi. Like the plankton samples, the underlying sediments were dominated by E. huxleyi and G. oceanica, but also included Helicosphaera carteri, Ceratolithus cristatus and Braarudosphaera bigelowii, which were absent from the plankton (Scholle

& Kling, 1972). Sarno *et al.* (1993) reported a low abundance of coccolithophorids in a Mediterranean coastal lagoon (Fusaro Lagoon, maximum water-depth 6m), identifying only *E. huxleyi* and *Calciosolenia brasiliensis* (as *Anoplosolenia*), as well as recording two non-calcifying haptophyte species and undetermined coccolithophorid taxa. More recently, Guerreiro *et al.* (2005) found abundant coccoliths in sediments from the mouth of the Douro Estuary, NW Portugal, including a high percentage of *H. carteri* (up to 84.4%), which they related to local confinement (*i.e.*, a lagoon-like system).

2. Study area

The Republic of Palau consists of a group of islands, which are part of the Mariana Islands (or Western Caroline Islands) in the NW Equatorial Pacific, that were formed by regional tectonic uplift of coralline reefs during the Miocene. These limestone islands (Plate 1, Figure 1) have been continuously subjected to weathering and sea-level change (Plate 1, Figure 2), resulting in the formation of island basins. As sea-level rose after the last glaciation, the basins became filled with sea-water through cracks and channels (Plate 1, Figure 3) in the limestone to form marine lakes. There are now about 70 of these lakes in the Republic of Palau, and they exhibit great variation in size and water-depth. At least 12 of these lakes are permanently stratified (meromictic) and semi-isolated from the surrounding lagoonal waters, with either gentle mixing in the top 1m between high tidal waters, entering via surface channels, and the marine lake waters, or more regular mixing at deeper lake depths, often with great tidal force (Hamner & Hamner, 1998). A



Typical mushroom-shaped 'rock island' in Palau



Island showing erosion caused by constant wave-action. Limestone overhang makes it difficult to get onto at low tide



Channel entrance on the lagoon side leading to a marine lake



Typical blue lagoon



Small island of rock, trees and coralline sand, nicknamed 'Three Coconut Island', used as a lunch-time stop (but not sampled for nannoplankton)



Underwater shot of diver in Mecherchar Jellyfish Lake, noted for huge number of non-stinging jellyfish inhabiting its surface-waters



Pier and lagoon waters outside Jellyfish Lake



Tourist diving spot, Big Drop-Off



Turtle Cove, another divers' paradise



Low-ceilinged entrance to Milky Way Lake



Sampling shallow lagoon-waters off 'Fantasy Island', another lunch-time spot



Outdoor filtration at base-camp on Carp Island

monthly average precipitation of about 18cm ensures that these lake-waters have a brackish lens on top of them, and a vertical salinity gradient. The lakes are surrounded by mangrove trees, and humic acids generated by the partial breakdown of fallen mangrove leaves at the bottom of the lake ensure that the lake-waters remain neutral to slightly acidic. However, in the past, this may not have been the case, as benthic foraminifers were present in at least one lake about 100 years ago (Lipps & Langer, 1999; Kawagata *et al.*, 2005a, b), when mangrove-derived organic matter was negligible (Orem *et al.*, 1991).

In contrast to the marine lakes, the lagoon environments are fully connected to the sea (Plate 1, Figure 4), and are generally shallow (<5m water-depth), characterised by living reefal communities and coralline sands (Plate 1, Figure 5). Away from the lagoons, but still within the main reefal area, the water-depths increase to over 40m.

To date, only few papers on the algal flora in these lagoons or marine lakes have been published, but recent papers by our collaborative research group have documented some of the seaweed (Hara *et al.*, 2002; Hoshina *et al.*, 2004) and dinoflagellate (Higa *et al.*, 2004; Horiguchi & Sukigara, 2005; Tamura & Horiguchi, 2005; Tamura *et al.*, 2005) diversity. Here, we report on the coccolithophorid communities in various lagoons and in two marine lakes, and briefly mention other plankton groups we encountered during this survey.

3. Material and methods3.1 Sampling sites

Although samples have been collected over the last five years from numerous sites, especially the marine lakes, only those samples which contained coccolithophorids are listed here and indicated on the map (Figure 1). Many of the samples were taken in close proximity (here labelled as 'outside') to one of the islands, including Ngeteklou Island, Ngeruktabel Island (close to the locations of Ngeruktabel Island Lake 2 and Shrimp Lake), Ulong Island, Ongael Island, Inoki Island, Mecherchar Island (close to the location of Mecherchar Jellyfish Lake, JFL: Plate 1, Figures 6, 7), Bablomekang Island, Angaur Island, and lunch-time stops at beaches on smaller islands or along the coast of the larger islands (Plate 1, Figures 5, 11). Since most of the small islands used as lunch-time stops seemingly have no official name, either a nickname was given to it (e.g., 'Three Coconut Island' or 'Fantasy Island': Plate 1, Figures 5, 11, respectively), or it was simply named using the sampling date (e.g., Lunch (27-6-2005)). A red tide outside JFL, characterised by the dinoflagellate genus Ceratium, was also sampled in July, 2002. Other samples were taken at tourist diving sites, such as Big Drop-Off (Plate 1, Figure 8), German Drop-Off, Turtle Cove (Plate 1, Figure 9), and a site overlying the location of the shipwreck of the Iro, an Imperial Japanese Navy Fleet Tanker sunk during WWII. Numerous marine lakes were also sampled, of which two, Ngeruktabel Island Lake 3 (NIL3) and Milky Way Lake (MWL: Plate 1, Figure 10), were later found to contain nannoplankton. NIL3 is an enclosed lake with a rocky lake-bed, while MWL is much shallower (several metres deep), with abundant corals on the lake-bed, and is actually connected to the sea *via* a narrow opening, large enough for humans to swim through (Plate 1, Figure 10).

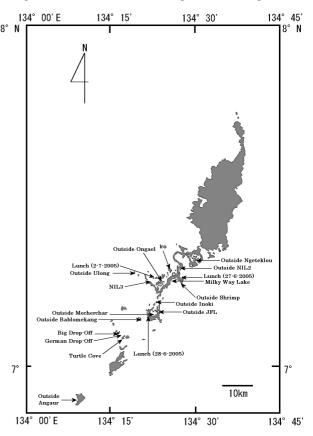


Figure 1: Map of the Republic of Palau, showing the location of the sampling sites used in this study

3.2 Physico-chemical data

Data from the 1st, 2nd and 4th expeditions (November, 2001, May, 2002 and May, 2003, respectively) were acquired with a multiple water-quality monitor (U-22, Horiba Co. Ltd.), which measured water temperature, salinity, pH, dissolved oxygen and turbidity at discrete depths in the top 10m. However, for the 3rd expedition, salinity measurements were acquired using a Shibuya S-10 salinometer, while temperature and pH were measured with a Piccolo Plus ATC Temp pH meter (Hanna Instruments). During the 6th expedition, conductivity and salinity were measured with a Horiba Cond Meter ES-51, pH with a pH ep5 meter (Hanna Instruments), and temperature and dissolved oxygen with a DO meter ID-100 (Iijima Electronics Corp.). No physico-chemical data is available from the 5th expedition.

Since most of our nannoplankton samples were collected from surface-waters, only the surface temperature, surface salinity and pH records from our database are presented here (Table 1). Konno, Jordan

	NIL3	Milky Way Lake	outside Ulong	outside Inoki	outside Shrimp Lake	Lunch (27-6-2005)	Lunch (28-6-2005)	Lunch (2-7-2005)	outside Ngeteklou	outside NIL2	outside Bablomekang	outside Jellyfish Lake, 2002	outside Jellyfish Lake, 2005	outside Ongael	Turtle Cove	German Drop-Off	Big Drop-Off	Iro	outside Angaur, 0 m	outside Angaur, 20 m Dive 1	outside Angaur, 20 m Dive 2
Sampling dat	e 27/7 2003		1/7 2005	29/6 2005	27/6 2005	27/6 2005	28/6 2005	2/7 2005	25/5 2002	24/5 2002	24/5 2002	23/5 2002	1/7 2005	2/7 2005	21/5 2002	27/5 2003	30/7 2002	24/5 2002	30/6 2005	30/6 2005	30/6 2005
Depth to sea-bed (n) -	-	1	1	1	1	1	1	4-5	4-5	4-5	4-5	4-5	4-5	>30	>30	40	40	>40	>40	>40
Temperature (°C	28.0	31.3	31.4	29.8	29.8	30.8	30.8	29.2	n/a	30.6	n/a	30.9	30.9	30.4	29.7	28.7	28.2	30.8	30.0	n/a	n/a
Salinity (%	3.	1 3.5	3.33	2.90	2.80	2.84	2.89	n/a	n/a	3.8	n/a	3.7	3.28	n/a	3.5	4.0	3.3	3.7	2.85	3.24	3.21
pl	H 7.79	9 8.50	8.21	8.43	8.31	8.32	8.46	8.28	n/a	8.08	n/a	8.09	8.21	8.32	8.14	8.03	8.05	8.07	8.22	n/a	n/a

Table 1: Sampling date, approximate depth to the sea-bed, and physico-chemical data recorded at each of the sampling sites. The samples and measurements were obtained from surface-waters unless stated otherwise. Vertical lines are used here to distinguish between the lake, very shallow (<1m), shallow (<5m) and deep (up to 40m) lagoon sites. n/a = data not available

3.3 Sample collection and preparation

During the first five expeditions, water samples were mainly collected by a Nytal-Swiss HD10 plankton net (with 10μ m mesh-openings), although 11 or 21 water bottles were occasionally used. Since the water volume and flow rate were not measured, the net samples could not be quantified. However, the samples were useful for providing presence/absence data (see Table 2).

During the 6th expedition, surface-water samples were collected quantitatively from a number of marine lakes and lagoons using 11 or 21 plastic water-bottles. Outside Angaur, water-samples were also obtained from 20m water-depth by a scuba diver, who twice flushed out the sea-water inside the open water-bottle, using air from the tank, before collecting the sea-water sample *in situ*

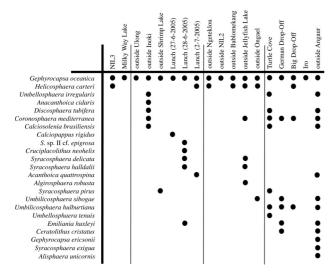


Table 2: Presence/absence of coccolithophorid species at each sampling site. The order of the species in the list was chosen to reflect their distribution, rather than their taxonomic affiliations. To simplify the table, data for outside Jellyfish Lake (including the 2002, 2005 and red tide samples), and the data from outside Angaur (including samples from 0m and two 20m dives), were combined to make two presence/absence records. The vertical lines are used here to distinguish between the lake, very shallow (<1m), shallow (<5m) and deep (up to 40m) lagoon sites

and screwing on the lid. Onshore, the water-samples were filtered using Millipore HA-type polycarbonate filters (47mm diameter, 0.45 μ m porosity) using an Eyela Aspirator A-3S (Tokyo Rikakikai Co., Ltd.) filtration apparatus, air dried and then stored in plastic petrislides (Plate 1, Figure 12).

In the case of the samples from the first five expeditions, an 8 x 8mm portion of each filter was cut out and mounted onto an aluminium stub, coated with platinum/palladium in an Eiko IB-3 ion sputtercoater and examined in a Hitachi S-2250N scanning electron microscope. Photographs were taken with

the camera attachment, using Fuji Neopan 120 SS black and white film. In the case of the 6th expedition samples, a 3 x 3mm portion of each filter was prepared and observed as above. All testate microplankton groups were counted on the filter piece (Table 3), while coccospheres were identified to species level (Table 4) using the pictorial guide of Young *et al.* (2003) and the most recent classification scheme of Jordan *et al.* (2004).

All of the samples and negatives used in this study are curated in the Department of Earth & Environmental Sciences, Faculty of Science, Yamagata University.

4. Results

4.1 Physico-chemical data

Although a variety of instruments were utilised over the five-year sampling period, and samples were collected at different times of the year and in different years, the range of daytime surface-water temperatures and pH in the lagoons seems to be relatively narrow: 28.0-31.5°C and 8.0-8.5, respectively. The lake-water pH of NIL3 was slightly lower (7.79) than the lagoon-waters and MWL, perhaps because the latter is semi-isolated from the sea and surrounded by mangrove trees. However, the surface salinity of the lagoons varied quite considerably, from 2.8-4.0%. This may be due to a precipitation effect, that is, if a heavy downpour occurred in the days prior to, or earlier on the same day as, our measurements, then one would expect the surface salinity to decrease. However, at this stage we cannot rule out the possibility that some of the values were due to instrument imprecision, by cheaper, less accurate instruments (i.e., after the U-22 Horiba instrument was broken).

4.2 Microplankton abundance

The counts of mineralised microplankton revealed that diatoms generally dominated the surface-water samples overlying both the shallow and deep lagoon areas. However, diatom abundance was still generally low, around 10⁴ cells/litre. At most sites, armoured dinoflagel-

	outside Ulong	outside Inoki	outside Shrimp Lake	Lunch (27-6-2005)	Lunch (28-6-2005)	outside Jellyfish Lake	outside Ongael	outside Angaur, 0 m	outside Angaur, 20 m Dive 1	outside Angaur, 20 m Dive 2	
Diatoms	10060	11400	20200	22020	15420	10260	2100	22.420	11760	0.120	
	18960			22020	15420	18360	2100	33420		9420	
Coccolithophorids	60	10320	1740	720	2880	5100	60	180	1560	2040	
Dinoflagellates	1020	5400	2400	5460	5340	4800		360	2220	3240	
Silicoflagellates										120	
Foraminifera	540	180	660	300	300	600		120		180	
Tintinnids (with coccoliths)		1380	240	60	540	780	60			120	
Tintinnids (without coccoliths)	60	1020	660	120	600	1080	60	240		240	

Table 3:Absolute abundances (in cells/litre) of some of the microplankton groups at each sampling site. Vertical lines are used here to distinguish between the lake, very shallow (<1m), shallow (<5m) and deep (up to 40m) lagoon sites

lates were the second most numerous group (with the exception of red-tide samples, which were not counted), although occasionally the coccolithophorids outnumbered them (*e.g.*, outside Inoki). Tintinnids with and without coccoliths attached to their tests tended to be more numerous in the shallow lagoons, as did the foraminifera.

Of the coccolithophorids, *Gephyrocapsa oceanica* was always the dominant species, although numbers were low, varying from 60-9420 cells/litre.

4.3 Coccolithophorid diversity

In this study, 23 coccolithophorid taxa were identified, representing a wide variety of families. However, somewhat surprisingly, no holococcolithophorids were present in our samples. In terms of distribution, two coccolithophorid species were found in the enclosed lake, NIL3, whereas only *Gephyrocapsa oceanica* was present in MWL. In the very shallow lagoon-waters (about 1m water-depth), a total of 15 taxa were identified. However, the highest diversity at any given very shallow lagoonal

20 m Dive 2 outside Angaur, 20 m Dive 1 outside Jellyfish Lake utside Shrimp Lake outside Angaur, 0 m unch (27-6-2005) unch (28-6-2005) outside Angaur, outside Ulong outside Inoki 9420 480 4140 1020 Gephyrocapsa oceanica 1680 2520 120 480 Umbellosphaera irregularis 60 180 Anacanthoica cidaris 180 Discosphaera tubifera Calciosolenia brasiliensis 60 240 Calciopappus rigidus Cruciplacolithus neohelis 180 Syracosphaera delicata 900 Syracosphaera halldalii 60 60 60 Syracosphaera pirus Umbilicosphaera sibogae 60 300 Umbilicosphaera hulburtiana 60 300 120 Ceratolithus cristatus 60 180 Emiliania huxlevi 60 120 360 Svracosphaera exigua 120 Alisphaera unicornis

Table 4: Absolute abundances (in cells/litre) of the coccolithophorid species at each sampling site (data from the 6th expedition, 2005). Vertical lines are used here to distinguish between the lake, very shallow (<1m), shallow (<5m) and deep (up to 40m) lagoon sites

location was only six taxa, which occurred outside Inoki and at Lunch (28-6-2005), with the other sampling sites being poorly represented. In the shallow lagoon-waters (about 5m waterdepth), the number of taxa at each site was generally much lower, only one or two taxa, although at one site it was six. At the deep lagoon sites (up to 40m water-depth), 16 taxa were identified, with 13 taxa outside Angaur. In summary, there was no clear trend in diversity, although four taxa (Anacanthoica cidaris, Calciopappus rigidus, Cruciplacolithus neohelis and Syracosphaera sp. II cf. S. epigrosa) were found only in shallow waters, and six taxa (Alisphaera unicornis, Ceratolithus cristatus, Gephyrocapsa ericsonii, Syracosphaera exigua,

Umbellosphaera tenuis and Umbilicosphaera hulburtiana) only at the deeper-water sites.

5. Microplankton taxonomy5.1 Coccolithophorids

Emiliania huxleyi (Lohmann) Hay & Mohler var. huxleyi Pl.2, Figs 1-3. Coccospheres were sometimes over-calcified, but in general possessed coccoliths with thick elements in the distal shield and grill elements covering the central-area, and so were assigned to var. huxleyi (= type A).

Gephyrocapsa ericsonii McIntyre & Bé Pl.2, Fig.4

Gephyrocapsa oceanica Kamptner sensu lato Pl.2, Figs 5-15. In this study, there was a wide variation in coccolith morphology, including specimens with or without collars, bridge-angles between 45° and 80°, variable

bridge thickness, central-area diameter and shield-element number, and occasionally with an extra bridge-strut. Whether all these morphologies belong to a single species, or a number of cryptic taxa, is uncertain at this time. Bollmann (1997) described a number of morphotypes based on bridge-angle, coccolith length and biogeographic distribution. Using these criteria, most of our specimens can be assigned to the large (GL) morphotype, however, examples of equatorial (GE) and oligotrophic (GO) morphotypes may be seen in Pl.2, Fig.6 and Pl.2, Fig.8, respectively.

Cruciplacolithus neohelis (McIntyre & Bé) Reinhardt

Pl.3, Figs 1-3. Specimens possessing coccoliths with the characteristic cross-shaped central-area structure were found at one of the lunch-time stops. Previous reports of this species have been restricted to Hawaii (West, 1969), France (Fresnel, 1986), Japan (Kawachi & Inouye,

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1994) and off Bermuda (McIntyre & Bé, 1967).

Umbilicosphaera hulburtiana Gaarder Pl.3, Figs 4-8. Generally the coccoliths are elliptical, however, some of our specimens clearly possess both enlarged globular-like forms and small circular forms (see Pl.3, Fig.8).

Umbilicosphaera sibogae (Weber-Van Bosse) Gaarder Pl.3, Figs 9-11

Helicosphaera carteri (Wallich) Kamptner Pl.4, Figs 1-13. Most coccospheres possess typical carteri-like coccoliths, however, occasionally the coccoliths on a single coccosphere exhibit a wide morphological variation, with some coccoliths being wallichii-like in appearance (see Pl.4, Figs 4, 6, 7). In addition, some coccoliths possess unaligned slits (i.e., one straight, one curved; see Pl.4, Figs 12, 13). Differences in flange-width also occur, while some specimens have a blunt, spine-like structure on the wing (see Pl.4, Figs 7-10).

Ceratolithus cristatus Kamptner Pl.5, Fig.1. Only the 'coccolithomorpha' type was encountered in this study.

Acanthoica quattrospina Lohmann
Pl.5, Figs 2, 3
Algirosphaera robusta (Lohmann) Norris
Pl.5, Figs 4, 5
Anacanthoica cidaris (Schlauder) Kleijne
Pl.5, Fig.6

Discosphaera tubifera (Murray & Blackman) Ostenfeld Pl.5, Figs 7-9

Calciosolenia brasiliensis (Lohmann) Young Pl.5, Figs 10-12

Syracosphaera delicata Cros et al.

Pl.6, Figs 8-10

Syracosphaera sp. II cf. S. epigrosa Okada & McIntyre sensu Kleijne

Pl.7, Figs 1, 2

Syracosphaera exigua Okada & McIntyre Pl.6, Figs 6, 7

Syracosphaera halldalii Gaarder ex Jordan & Green

Pl.6, Figs 1-5

Syracosphaera pirus Halldal & Markali

Pl.7, Figs 3, 4

Coronosphaera mediterranea (Lohmann) Gaarder

Pl.7, Figs 5-8

Calciopappus rigidus Heimdal

Pl.7, Figs 9, 10

Alisphaera unicornis Okada & McIntyre Pl.7, Figs 11, 12

Umbellosphaera irregularis Paasche Pl.8, Figs 1-8. Most coccospheres found in this study belong to the classic form of *U. irregularis*. However, a

rarer second type, originally referred to as *U. tenuis* Type 0 (Kleijne, 1993) and later as *U. irregularis* type 0 (Young *et al.*, 2003), was encountered at Turtle Cove and outside Angaur at 20m water-depth (Pl.8, Figs 7, 8). Kleijne (1993) suggested that Type 0 is characteristic of low latitudes.

Umbellosphaera tenuis (Kamptner) Paasche Pl.8, Figs 9-12. Apart from her Type 0, above, Kleijne (1993) described four other types of *U. tenuis* (Types I-IV). Recently, Young *et al.* (2003) separated her Type III into types IIIa and IIIb. In this study, only types I and IIIb were encountered at Turtle Cove, which Kleijne (1993) suggested were characteristic of low latitudes and latitudes higher than Type I, respectively.

5.2 Calcareous dinoflagellates

In this study, a number of calcareous dinoflagellate-like tests were observed, but only *Thoracosphaera heimii* could be identified with certainty and is illustrated here.

Thoracosphaera heimii (Lohmann) Kamptner Pl.9, Figs 1-4. Reports of calcareous dinoflagellates in shallow coastal waters appear to be rare, however, in one such paper, Sarno *et al.* (1993) recorded *T. heimii* in Fusaro Lagoon (<10m water-depth) in the Mediterranean.

5.3 Tintinnids

Given the apparent lack of taxonomic works on Palauan tintinnids, our specimens have been simply numbered, although some effort has been made to identify them to the generic level.

Tintinnid type 1

Pl.8, Fig.5. Bears some resemblance to species of *Tintinnopsis* Stein (see figures in Taniguchi, 1997, pl.6; Lynn & Small, 2002, fig.3C).

Tintinnid type 2

Pl.9, Figs 6, ?7. Bears some resemblance to species of *Tintinnopsis* Stein (see figures in Taniguchi, 1997, pl.7; Lynn & Small, 2002, figs 3A, B).

Tintinnid type 3

Pl.9, Fig.8. Bears some resemblance to species of *Stenosemella* Jörgensen (see figures in Taniguchi, 1997, pl.10; Lynn & Small, 2002, fig.7).

Tintinnid type 4 Pl.9, Fig.9

Tintinnid type 5

Pl.9, Fig.10. Bears some resemblance to species of *Tintinnopsis* Stein (see figures in Taniguchi, 1997, pl.6).

5.4 Radiolaria

Specimens were only encountered in the lagoonal sur-

face-waters overlying the wreck of the Iro. Although no attempt has been made to identify them, their presence was somewhat surprising, since they are usually considered to be open-ocean plankton.

Radiolarian sp.1 Pl.9, Fig.11 Radiolarian sp.2 Pl.9, Fig.12

5.5 Silicoflagellates

Specimens conforming to Dictyocha fibula Ehrenberg sensu lato were encountered in some of the more enclosed lagoons, as well as at Turtle Cove. Three types are separated here, but clearly more detailed taxonomic work needs to be done. Their presence in such shallow water was surprising to us. However, from culture experiments, the optimum growth of this species occurred at 10°C and 24‰ (van Valkenburg & Norris, 1970). A different species, Dictyocha speculum Ehrenberg, which occasionally blooms in its naked stage in the Baltic Sea, reached its maximum cell-division rate at 15°C and between 20-25% (Henriksen et al., 1993). Since the lagoon-waters in Palau are generally higher in both temperature and salinity than these optimum conditions, this may account for the low abundance of silicoflagellates recorded in the present study.

Dictyocha fibula Ehrenberg – type 1

Pl.9, Fig.13. Skeleton with a squarish basal ring, equal radial spines, smaller portals at the ends of the major axis, short pikes, struts arising from the basal ring, connected by an apical bar aligned along the major axis, bearing an apical spire in the middle.

Dictyocha fibula Ehrenberg – type 2

Pl.9, Fig.14. Skeleton with a diamond-shaped, but slightly lobed, basal ring covered by blunt protrusions, inequal radial spines (shorter in the minor axis), each terminating in a rosette of spinulae, smaller portals at the ends of the major axis, short pikes ending in a bulb of spinulae, struts arising from the indented part of the basal ring, connected by an apical bar aligned along the major axis.

Dictyocha fibula Ehrenberg – type 3

Pl.9, Fig.15. Skeleton with a diamond-shaped basal ring, inequal radial spines (shorter in the minor axis), smaller portals at the ends of the major axis, diagonally opposing struts arising either from the mid-point of each side of the basal ring or nearer to one end, resulting in asymmetry. Struts connected by an apical bar aligned along the major axis.

6. Discussion

This study reports, for the first time, the coccolithophorid assemblages inhabiting some of the marine lakes and lagoons of the Republic of Palau. Despite the relatively low diversity, this study has shown that species previously thought of as open-ocean plankton can also be found in shallow coastal waters. Some species, such as Cruciplacolithus neohelis and Anacanthoica cidaris, have been rarely reported elsewhere. This study also shows that some of the more common 'monomorphic' species (Gephyrocapsa oceanica, Helicosphaera carteri and Umbilicosphaera hulburtiana) exhibit wide morphological variability, sometimes in the same sample and even on the same coccosphere. Clearly these features (e.g., extra bridge-struts and variable slit orientation) need to be studied further to determine whether they are genetically or environmentally controlled. Malformation of coccoliths has been associated in the past with low salinity and nutrient depletion in the surface-waters (Kleijne, 1990), whilst morphological variability through fine-scale speciation has been recently documented (Geisen et al., 2004). The morphotypes of Umbellosphaera are also in need of further study, particularly their biogeographic, seasonal and vertical distributions on a worldwide scale. As Young et al. (2003) noted, no follow-up work has been carried out since Kleijne (1993) provided biogeographic data on the various types using her own dataset. Future genetic studies may show that these morphotypes are separate taxa, and so any distributional data that we can acquire in the meantime may prove useful. Although here we have only presented preliminary numerical data on the coccolithophorids, we hope that future work will include a more thorough investigation of their absolute abundance and distribution in both the inner and outer reefal lagoons. The existence of coccolith-covered tests is clear evidence that some of the tintinnids in the shallow waters are utilising this coccolithophorid resource. Perhaps this shows that coccolithophorids may be playing an important role in lagoon ecology.

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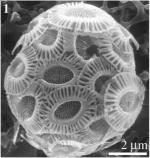
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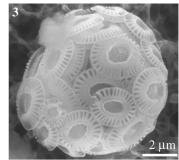
1-3: Emiliania huxleyi var. huxleyi (= type A)



Coccosphere bearing coccoliths with no overcalcification. Outside Angaur, 20m Dive 1

 $2 \mu m$

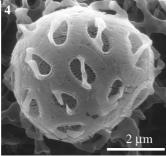
Sphere bearing liths with signs of overcalcification around CA. Outside Angaur, 20m Dive 2



Coccosphere bearing coccoliths with significantly thicker distal-shield elements. German Drop-Off

Gephyrocapsa ericsonii

5, 6: Gephyrocapsa oceanica



Sphere (larger form; GL) bearing liths showing characteristic col-lar, some with additional protrusions into CA. Lunch (28-6-2005) liths with narrow CA. Outside Ngeteklou Small sphere bearing liths with bridge angles of about 45°. Outside Angaur, 20m Dive 2

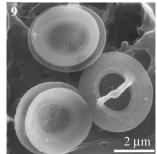
7-9: Gephyrocapsa oceanica



Sphere (larger form; GL) bearing liths with wide CA with bridge-elements not touching. Outside NIL2

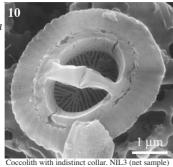


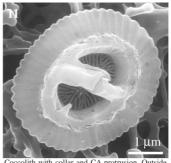
Coccosphere (oligotrophic form; GO) bearing coccoliths with fewer distal-shield elements. Iro



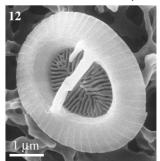
Liths (distal and proximal views) with wide shields and no collar. Outside JFL, May, 2002

10-12: Gephyrocapsa oceanica distal views



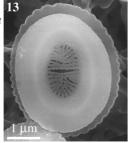


Coccolith with collar and CA protrusion. Outside JFL, May, 2002

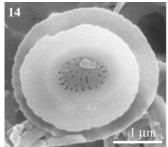


Coccolith with CA protrusion, no collar. Turtle Cove

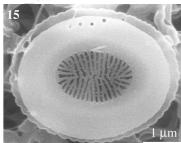
13-15: Gephyrocapsa oceanica proximal views



Coccolith with narrow CA. NIL3 (net sample)

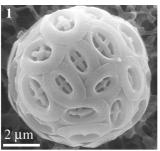


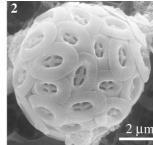
Coccolith with narrow CA and few grill elements. Outside Ngeteklou

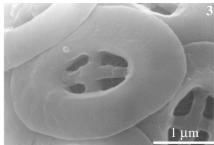


Coccolith with wider CA. Outside NIL2

1-3: Cruciplacolithus neohelis





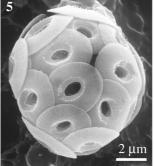


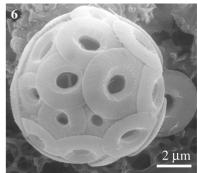
Coccospheres showing some coccolith size variation. Lunch (28-6-2005)

Close-up of one of the coccoliths in Fig.2

4-6: Umbilicos phaerahulburtiana Coccospheres bearing coccoliths exhibiting size and shape variation



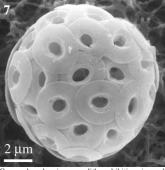


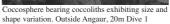


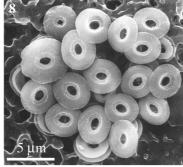
Outside Angaur, 20m Dive 2

7,8: Umbilicosphaera hulburtiana

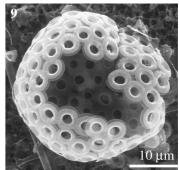
9: Umbilicosphaera sibogae



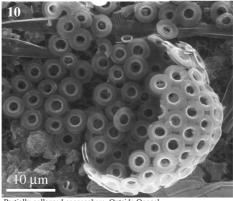


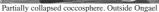


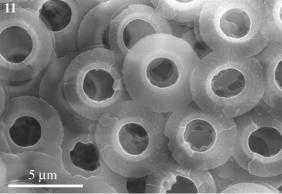
Collapsed coccosphere with large and small coccoliths, and elliptical and circular coccoliths. Turtle Cove



10, 11: Umbilicosphaerasibogae

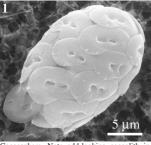




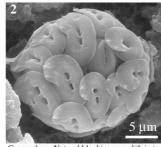


Close-up of coccoliths in distal and proximal view. German Drop-Off

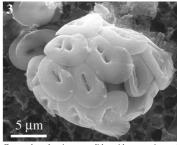
1-13: Helicosphaera carteri



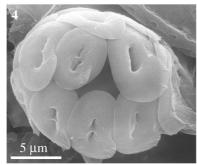
Coccosphere. Note odd-looking coccolith in bottom left corner. Red tide, outside JFL



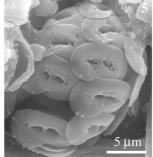
Coccosphere. Note odd-looking coccolith in top right corner. Red tide, outside JFL, July, 2002



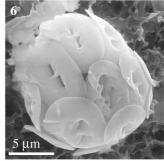
Coccosphere bearing coccoliths with some size and flange variation. Red tide, outside JFL, July, 2002



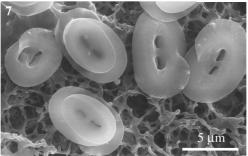
Coccosphere. Note coccolith with unaligned slits. Outside Ngeteklou



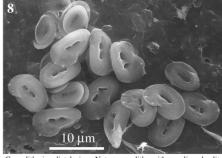
Coccosphere. Note coccolith with unaligned slits. NIL3 (net sample)



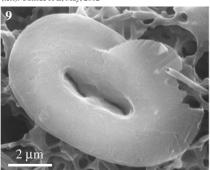
Coccosphere. Note coccolith with parallel slits. Big Drop-Off



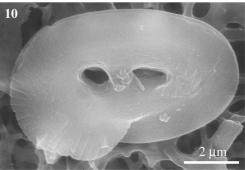
Coccoliths in distal and proximal views. Note coccolith with parallel slits (left). Outside JFL, May, 2002



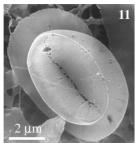
Coccoliths in distal view. Note coccolith with unaligned slits (centre). Outside JFL, May, 2002



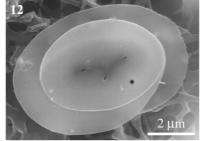
Coccolith, distal view. Outside Bablomekang



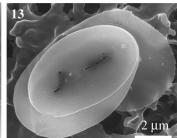
Coccolith, distal view. Outside Ongael



Coccolith, proximal view. NIL3 (net sample)



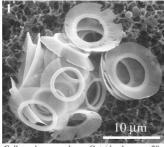
Coccolith, proximal view. Note unaligned slits. Outside JFL, May, 2002

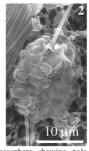


Coccolith, proximal view. Note unaligned slits and oddly-shaped flange. Outside JFL, May, 2002

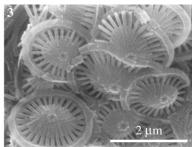
1: Ceratolithus cristatus `coccolithomorpha"type'

2, 3: A can thoicaquattrospina





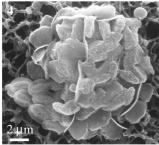
Coccosphere showing pole and body coccoliths. Lunch (2-7-2005)



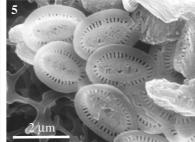
Close-up of body coccoliths. Lunch (2-7-2005)

4, 5: Algirosphaerarobusta

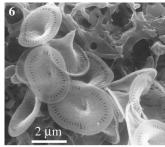
6: Anacanthoica cidaris



Collapsed coccosphere. Outside JFL, July, 2005

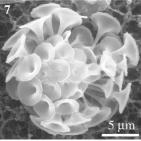


Close-up of coccoliths in proximal view. Outside JFL, July, 2005



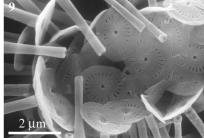
Coccoliths in both distal and proximal view. Outside Inoki

7-9: Discosphaera tubifera



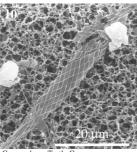


Coccosphere. Outside Angaur, 20m Dive 1

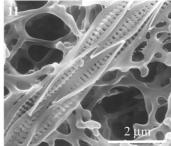


Close-up of coccoliths (same specimen as in Fig.8). Outside Angaur, 20m Dive 1

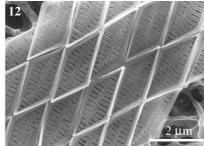
10-12: Calciosolenia brasiliensis



Coccosphere. Turtle Cove



Narrower coccoliths near the poles of the coccosphere. Turtle Cove

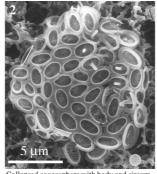


Wider body coccoliths. Turtle Cove

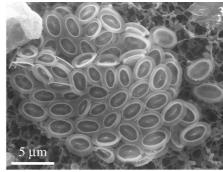
1-3: Syracosphaera halldalii



Sphere with body coccoliths and a circumflagellar coccolith. Outside JFL, July, 2005

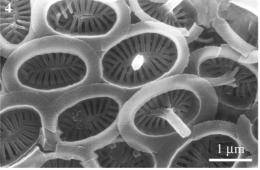


Collapsed coccosphere with body and circumflagellar coccoliths. Lunch (28-6-2005)

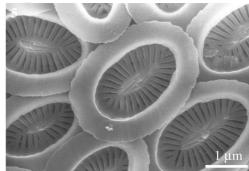


Collapsed coccosphere. Lunch (28-6-2005)

4,5: Syracosphaera halldalii

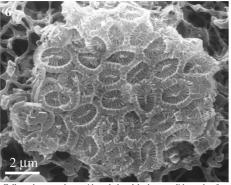


Close-up of circum-flagellar coccoliths (same specimen as Fig.2). Lunch (28-6-2005)

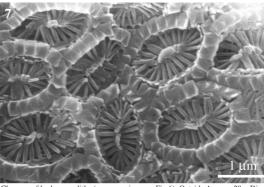


Close-up of body coccoliths (same specimen as Fig.3). Lunch (28-6-2005)

6,7: Syracosphaera exigua

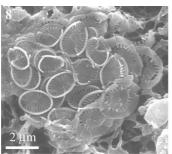


Collapsed coccosphere with endothecal body coccoliths and a few exothecal cyrtoliths. Outside Angaur, 20m Dive 2

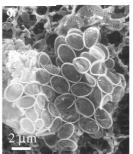


Close-up of body coccoliths (same specimen as Fig.6). Outside Angaur, 20m Dive 2

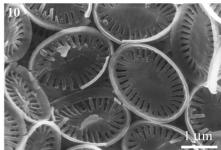
8-10: Syracosphaera delicata



Collapsed coccosphere with endothecal body coccoliths and a few exothecal cyrtoliths. Outside JFL, July, 2005

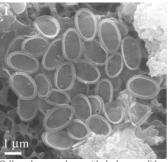


Collapsed coccosphere with endothecal body coccoliths and a few exothecal cyrtoliths. Lunch (28-6-2005)

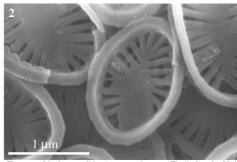


Close-up of body coccoliths (same specimen as Fig.9). Lunch (28-6-2005)

1, 2: Syracosphaera sp. II cf. S. epigrosa?



Collapsed coccosphere with body coccoliths. Lunch (28-6-2005)

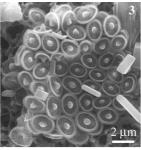


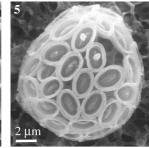
Close-up of body coccoliths (same specimen as Fig.1). Lunch (28-6-2005)

3, 4: Syracosphaera pirus

5:

Coronosphaera mediterranea



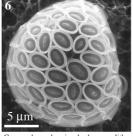


Collapsed sphere with endothecal body liths and a few exothecal cyrtoliths. Outside JFL, July, 2005 and a circum-flagellar coccolith. Turtle Cove

Coccosphere showing body and circum-flagellar coccoliths. Big Drop-Off

6-8:

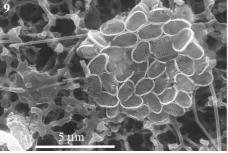
Coronosphaera mediterranea

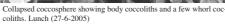


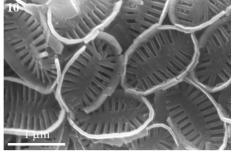
Coccosphere showing body coccoliths. Collapsed coccosphere. Outside JFL, Outside Inoki

Close-up of coccoliths (same specimen as Fig.7). Outside JFL, May, 2002

9, 10: Calciopappus rigidus

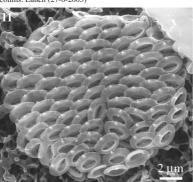




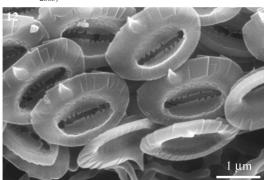


Close-up of body coccoliths (same specimen as Fig.9). Lunch (27-6-2005)

11, 12: Alisphaera unicornis

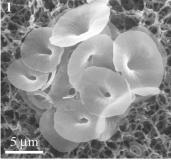


Collapsed coccosphere. Outside Angaur, 20m Dive 1

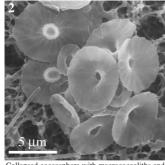


Close-up of coccoliths (same specimen as Fig.11). Outside Angaur, 20m Dive 1

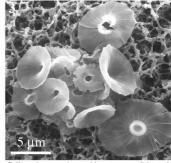
1-3: Umbellosphaera irregularis



Collapsed coccosphere with macrococcoliths and a micrococcolith. Turtle Cove

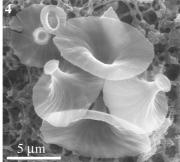


Collapsed coccosphere with macrococcoliths and a few micrococcoliths. Turtle Cove

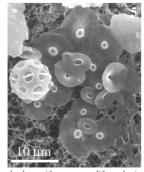


Collapsed coccosphere with macrococcoliths and a few micrococcoliths. Outside Angaur, 20m Dive 1

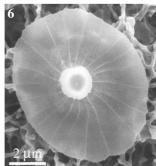
4-6: Umbellosphaera irregularis



Collapsed coccosphere with macrococcoliths and a micrococcolith. Outside Inoki



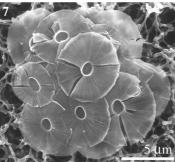
Collapsed sphere with macrococcoliths and micrococcoliths. Note size variation of macrococcoliths. Turtle Cove



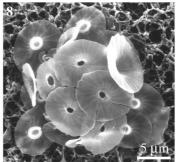
Proximal view of macrococcolith. Turtle Cove

7,8: *Umbellosphaera irregularis* type 0

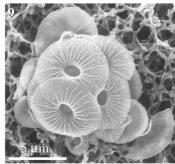
9: *Umbellosphaera tenuis* type I



Collapsed coccosphere. Turtle Cove



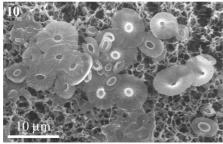
Collapsed coccosphere. Outside Angaur, 20m Dive



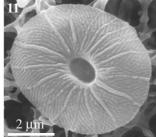
Collapsed coccosphere with macrococcoliths and a micrococcolith. Turtle Cove

10, 11: *Umbellosphaera tenuis* type I

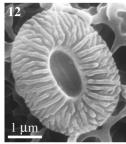
12: *Umbellosphaera tenuis* type IIIb



Collapsed coccosphere with one of U. irregularis on right. Turtle Cove

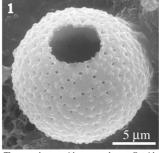


Close-up of macrococcolith. Turtle Cove

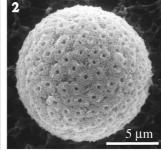


Close-up of micrococcolith. Turtle Cove

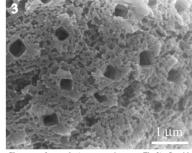
1-3: Thoracosphaera heimii



Thoracosphere with operculum. Outside Ngeteklou



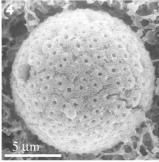
Partially corroded thoracosphere. Outside Angaur, 20m Dive 1



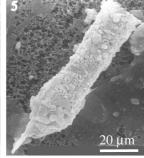
Close-up of crystals (same specimen as Fig.2). Outside Angaur, 20m Dive 1

4: Thoracosphaera heimii

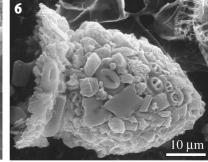
5, 6: Tintinnids



Thoracosphere with operculum. Outside Angaur, 20m Dive 1

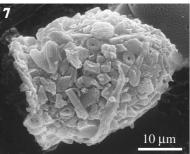


Tintinnid type 1. Test bearing coccoliths. Outside JFL, May, 2002

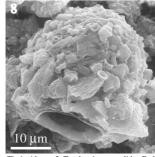


Tintinnid type 2. Test bearing coccoliths of *G. oceanica* an *H. carteri*. Outside Ongael

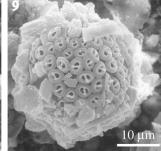
7-9: Tintinnids



Tintinnid type 2?. Test bearing coccoliths. Outside JFL May, 2002



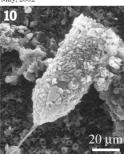
Tintinnid type 3. Test bearing coccoliths. Red tide, outside JFL, July, 2002



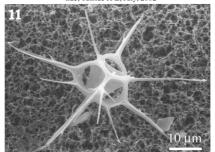
Tintinnid type 4. Test bearing coccoliths of *G. oceanica*. Red tide, outside JFL, July, 2002

10: Tintinnid

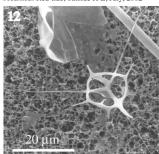
11, 12: Radiolarians



Tintinnid type 5. Test bearing coccoliths. Outside Ongael

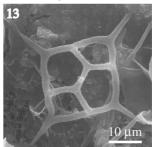


Radiolarian sp.1. Iro

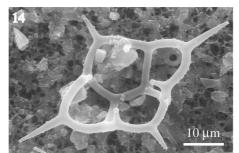


Radiolarian sp.2. Iro

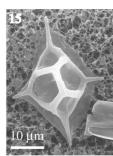
13-15: Silicoflagellates



Dictyocha fibula type 1. Outside Ngeteklou



Dictyocha fibula type 2. Outside Ongael



Dictyocha fibula type 3. Turtle Cove