Coastal Coccolithophores (Guest Ed. R.W. Jordan)
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Coccolithophorids from the Marquesas Islands and atolls in the Tuamotu and Society Archipelagos (South Pacific Ocean)

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Abstract Coccospheres and loose coccoliths were found on solid substrates (intertidal sediments and macroalgae) collected from the Marquesas Islands and atolls in the Tuamotu and Society Archipelagos, South Pacific Ocean. Visual observations suggest that the species diversity (11 taxa) and abundances were both low; however, the presence of *Braarudosphaera bigelowii*, *Cruciplacolithus neohelis* and *Gephyrocapsa oceanica* coccospheres provided evidence of a coastal assemblage. The association among the two species, *B. bigelowii* and *C. neohelis*, and living oyster shells was unusual, given that *B. bigelowii* is normally found in the plankton and *C. neohelis* on sand or coral fragments.

Keywords Atolls, coastal coccolithophores, South Pacific Ocean

1. Introduction

Unlike their open-ocean counterparts, coastal coccolithophorid assemblages have not been studied in great detail. Taxonomic studies during the second half of the last century revealed that genera such as *Hymenomonas* and *Pleurochrysis* resided in coastal waters, and had a benthic phase in their life-cycles (see review in Billard, 1994); however, these genera are almost never reported in modern distribution studies or from surface sediments of coastal areas (although, see Marshall & Cohn, 1982; Nikolaides & Moustaka-Gouni, 1990). In contrast, surveys of coastal waters have encountered two other groups of coccolithophorids, one including *Braarudosphaera* and *Cruciplacolithus*, which may be considered to be refugia taxa (Bown, 2005), and another including genera such as *Gephyrocapsa*, *Reticulofenestra* and *Helicosphaera* that are common in coastal waters, but may be found in open-ocean waters, too. More recently, another possible refugia taxon, *Tergestiella* (= *Cyclagelosphaera*), has been added to this community list (Hagino et al., 2015). Early studies of coastal waters and sediments did not record many of these taxa, however, presumably because they were rare or treated as reworked.

Perhaps due to logistical reasons, phytoplankton studies are extremely uncommon around atolls, many of which are situated in the middle of the Pacific Ocean; however, the islands in French Polynesia have attracted quite a lot of attention – particularly Takapoto and Nuku Hiva. The phytoplankton composition of Takapoto Atoll has been investigated, with diatoms found to be the most diverse, and dinoflagellates the dominant group (Ricard et al., 1979; Delesalle et al., 2001). Although one unpublished dataset has recorded the presence of the prymnesiophytes *Chrysochromulina* and *Phaeocystis* (Delesalle & Chrétiennot-Dinet *in* Delesalle et al., 2001), the taxonomic identification of the coccolithophorids in other studies has been undetermined (Ricard et al., 1979; Delesalle et al., 2001). In contrast, the diatom *Aulacodiscus kittonii* var. *africanus* (Cottam) Rattray has been observed producing a red tide in the bay of Tai O Hae, Nuku Hiva (Sournia & Plessis, 1974), while phytoplankton blooms (identified by high chlorophyll *a* concentrations) have been detected around the Marquesas Islands (Signorini et al., 1999; Martinez & Maamaatuaiahutapu, 2004). The lagoons of the French Polynesian atolls are very sensitive to environmental change, and have often been subjected to mass mortality of the benthos and coral/clam bleaching events (Adessi, 2001; Andréfouët et al., 2014).

During expeditions to French Polynesia, CR-G collected samples from various substrates, primarily with the intention of studying attached marine diatoms (Riaux-Gobin et al., 2014, 2015; Riaux-Gobin & Witkowski, 2015). Thus, traditional water samples were not procured; however, some coastal coccolithophorids have benthic

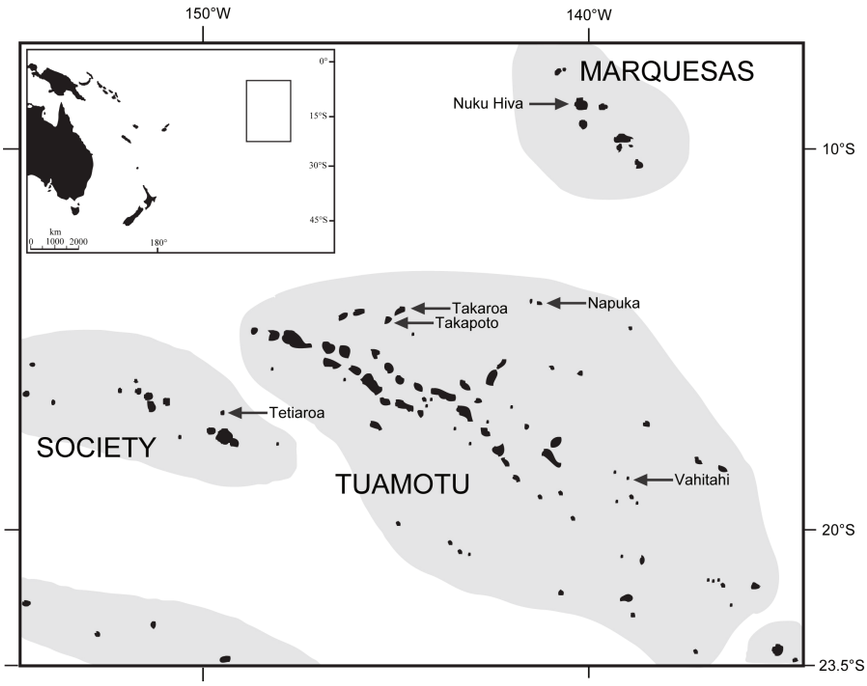


Figure 1: Location of sampling sites in the Marquesas, and the Tuamotu and Society Archipelagos. Inset shows sampling area (box) to the east of Australasia

life-stages, and others live on sandy surfaces, so, in hindsight, the samples from these expeditions provided a good opportunity to use a different approach in looking for calcareous nannoplankton. Herein, we report on the coccolithophorid assemblages from the Marquesas Islands and atolls in the Tuamotu and Society Archipelagos (Fig. 1).

2. Materials and methods

Samples of intertidal coral sands, detrital sediments from lagoonal and oceanic areas, short algal turfs, macroalgal debris and scrapes (a few millilitres) of the external shell surfaces of the black-lipped pearl-oyster, *Pinctada margaritifera* (Linnaeus), and from a smaller bivalve (probably a winged oyster) were collected in 2010–2013 (as part of the CORDIA Project) from four South Pacific atolls – Napuka (14°10.046'S, 141°16.106'W), Takaroa (14°25.219'S, 144°58.697'W) and Takapoto (14°42.438'S, 145°15.128'W), in the Tuamotu Archipelago, and Tetiaroa (17°01.405'S, 149°35.500'W) from the Society Archipelago. Samples were also collected, in 2015, from Nuku Hiva (8°56.022'S, 140°06.921'W), in the Marquesas Archipelago, and in 2017 from Vahitahi (18°47'S, 138°50'W), in the Tuamotu Archipelago, as part of the Tara Pacific 2016–2018 Expedition. All samples were preserved in filtered, buffered (neutralised) formalin (10% final concentration). For scanning electron microscope (SEM) examination, 2 to 3 drops of each sample were filtered through a 1μm Nuclepore filter (Analytic Lab, St Mathieu de Treviers, France) and rinsed twice with deionised (milliQ Gradient, Millipore, New York, USA) water to remove salts. The filters were air dried, then mounted onto aluminium stubs (Hitachi Ltd Instrument Division, Ichige, Japan), before being coated with gold-palladium alloy with an EMSCOPE SC500 sputter-coater (Emscope Laboratories Ltd, Ashford, England) and examined with a Hitachi FEG S-4500 SEM (Hitachi), which was operated at 5kV (in the C2M Laboratory, Perpignan University, Via Domitia, France).

3. Results

Diatoms were very scarce, but diverse, in the samples, whilst dinoflagellates were more abundant (data not shown here). Coccolithophorids (and loose coccoliths) were also rare in the macroalgal samples, but were more numerous in the lagoon coral sands and oyster-shell scrapes. It should be noted that the wild oysters were benthic, but the farmed oysters were attached to ropes in the water-column. Apart from one wild oyster from Takapoto, all the other shell scrapes were from living individuals. The coccolithophorid taxa encountered in this study, and their distributions, are shown in Plate 1 and Table 1, respectively.

Emiliania huxleyi Hay & Mohler var. *huxleyi*
(= morphotype A)
Pl. 1, figs 1, 2

Loose coccoliths were rare at Nuku Hiva (macroalga and bivalve scrape) and Tetiaroa (lagoon coral sand). The coccoliths were assigned to morphotype A (= var. *huxleyi*).

Gephyrocapsa oceanica Kamptner
Pl. 1, figs 3–8

Coccospheres were relatively common at Takaroa (lagoon sediment and scrape of farmed pearl-oyster shell) and

	MARQUESAS		TUAMOTU					SOCIETY
	Nuku Hiva		Napuka	Takaroa		Takapoto	Vahitahi	Tetiaroa
	macroalga	bivalve scrape	lagoon coral sand	lagoon sediment	lagoon farmed pearl -oyster scrape	wild pearl -oyster scrape	macroalga	lagoon coral sand
Emiliania huxleyi	c	c						c
Gephyrocapsa oceanica		c	●	●	●			c
Cruciplacolithus neohelis				c		●		
Calcidiscus leptoporus	c	c	c					
Umbilicosphaera sibogae				c				c
Syracosphaera mediterranea						c+		
Syracosphaera rotula								c
Syracosphaera sp. 1						c		
Syracosphaera sp. 2					c			
Umbellosphaera irregularis							c	c
Braarudosphaera bigelowii					●			

c:coccolith(s) ●:coccosphere +: from shell of dead pearl-oyster

Table 1: Distribution of coccospheres and coccoliths in each sample and at each sampling site

Napuka (lagoon coral sand), with loose coccoliths at Nuku Hiva (scrape of bivalve shell), Napuka (lagoon coral sand) and Tetiaroa (lagoon coral sand). Specimens were encountered both with and without a distinct collar around the central area.

Calcidiscus leptoporus (Murray & Blackman) Loeblich & Tappan

Pl. 1, figs 9, 10

Loose coccoliths were found at Nuku Hiva (macroalga and scrape of bivalve shell) and Napuka (lagoon coral sand).

Cruciplacolithus neohelis (McIntyre & Bé) Reinhardt

P. 1, figs 11–13

Coccospheres and loose coccoliths were observed at Takapoto (scrape of wild pearl-oyster shell). Loose coccoliths were also found at Takaroa (lagoon sediments).

Umbilicosphaera sibogae (Weber-Van Bosse) Gaarder

Pl. 1, fig. 14

Loose coccoliths were encountered at Takaroa (lagoon sediments) and Tetiaroa (lagoon coral sand).

Syracosphaera mediterranea Lohmann

Pl. 1, fig. 15

One loose coccolith was found at Takapoto (scrape of dead wild pearl-oyster shell).

Syracosphaera rotula Okada & McIntyre

Pl. 1, fig. 16

One loose coccolith was observed at Tetiaroa (lagoon coral sand).

Syracosphaera sp. 1

Pl. 1, fig. 17

One loose coccolith was found at Takapoto (scrape of wild pearl-oyster shell). Bears some resemblance to *Michaelsarsia elegans,* but cannot be identified with certainty.

Syracosphaera sp. 2

Pl. 1, fig. 18

One loose coccolith was encountered at Takaroa (scrape of farmed pearl-oyster shell from the lagoon). It resembles *S. hirsuta* and *S. borealis* in having a groove on the proximal surface of the laths, with the former species being a more likely candidate, given the tropical location of Takaroa.

Umbellosphaera irregularis Paasche

Pl. 1, fig. 19

Only a few loose coccoliths were encountered, one from Vahitahi (macroalga), the other from Tetiaroa (coral sand).

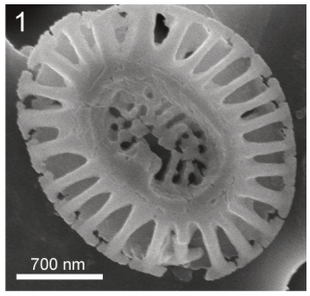
Braarudosphaera bigelowii (Gran & Braarud) Deflandre

Pl. 1, fig. 20

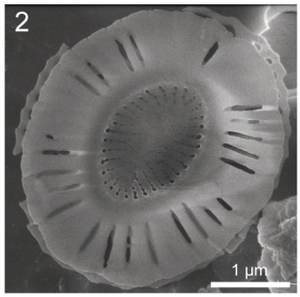
Coccospheres were relatively common at Takaroa Atoll (scrape from farmed live pearl-oyster shell from the la-

Plate 1

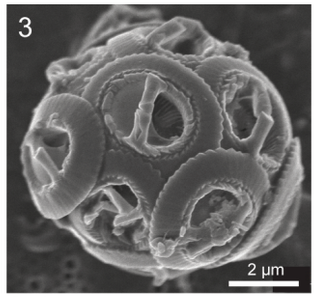
SEM images of all taxa found in the study



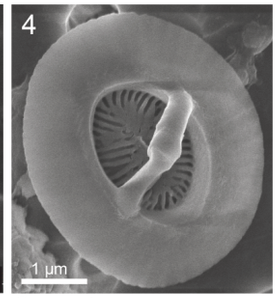
Emiliania huxleyi var. *huxleyi*
Nuku Hiva, 24 Nov 2015



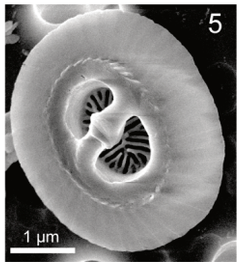
E. huxleyi var. *huxleyi*
Tetiaroa, 19 Oct 2012



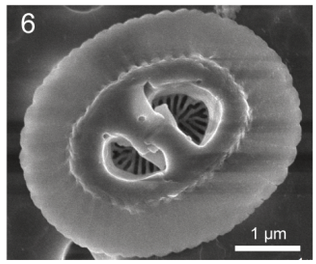
Gephyrocapsa oceanica
Takaroa 12 Oct 2013



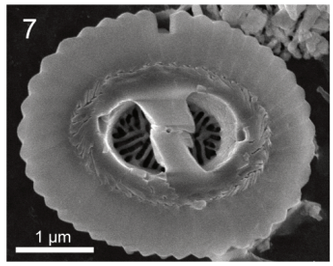
G. oceanica
Nuku Hiva, 24 Nov 2015



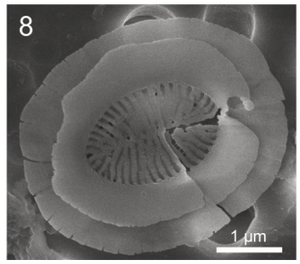
G. oceanica
Napuka, 25 Sept 2012



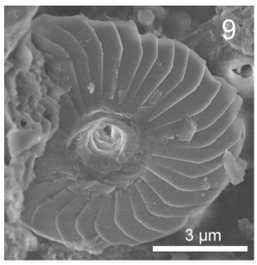
G. oceanica
Napuka, 25 Sept 2012



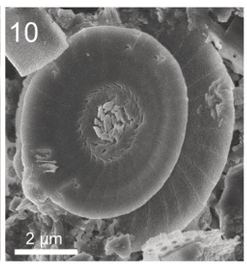
G. oceanica
Napuka, 25 Sept 2012



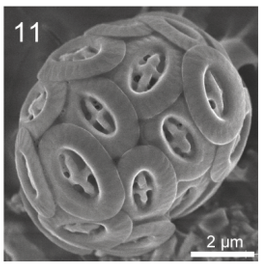
G. oceanica
Tetiaroa, 19 Oct 2012



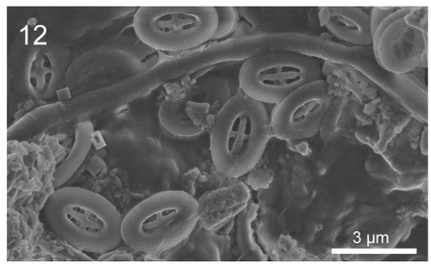
Calcidiscus leptoporus
Nuku Hiva, 24 Nov 2015



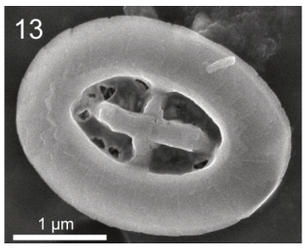
C. leptoporus
Nuku Hiva, 24 Nov 2015



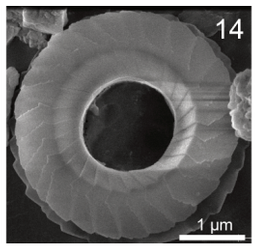
Cruciplacolithus neohelis
Takapoto, 8 Oct 2013



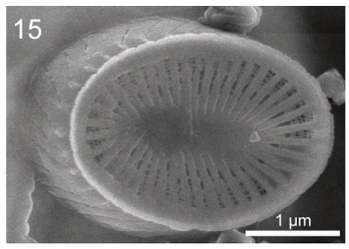
C. neohelis
Takapoto, 8 Oct 2013



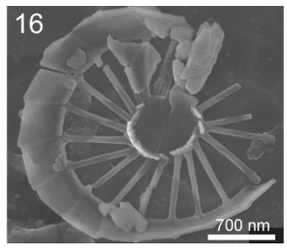
Cruciplacolithus neohelis
Takapoto, 8 Oct 2013



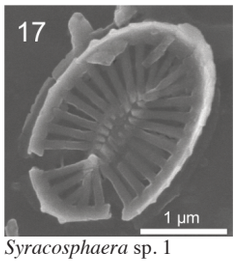
Umbilicosphaera sibogae
Tetiaroa, 19 Oct 2012



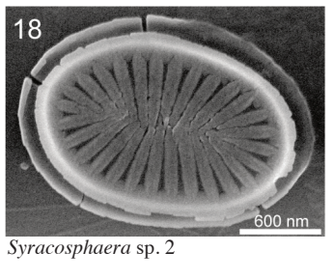
Syracosphaera mediterranea
Takapoto, 8 Oct 2013



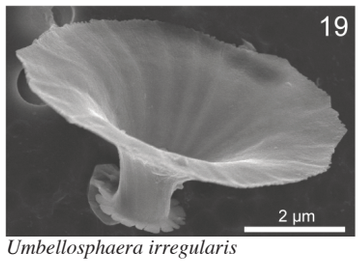
Syracosphaera rotula
Tetiaroa, 19 Oct 2012



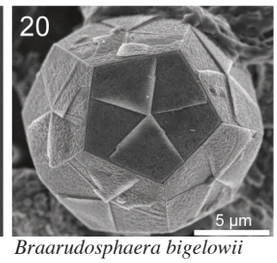
Syracosphaera sp. 1
Takapoto, 8 Oct 2013



Syracosphaera sp. 2
Takaroa, 12 Oct 2013



Umbellosphaera irregularis
Vahitahi, 22 Oct–3 Nov, 2016
collected by V. Parravicini



Braarudosphaera bigelowii
Takaroa, 12 Oct 2013

goon). Measurement of the pentalith side length (about 5.7μm) showed that the specimen belonged to intermediate form B (Takano et al., 2006; Konno et al., 2007). Only coccospheres with a flat pentalith face were observed (cf. Konno et al., 2007).

4. Discussion

Despite the paucity of the data, this is the first detailed study on living coccolithophorids from atolls, and it at least allows us to make a comparison with other studies. The somewhat low diversity (11 taxa) is perhaps a reflection of the fact that water samples were not collected. Other studies, utilising water samples, have reported more than 20 taxa (e.g. Konno & Jordan, 2006; Konno et al., 2019 [this issue]; Tsutsui et al., unpub. obs., 2017), although some of these sites were offshore. Unfortunately, quantitative counts could not be made in the present study due to the sample acquisition method (using lagoon coral sands and oyster and bivalve scrapes); however, our observations revealed that coccospheres of *G. oceanica* (at Napuka and Takaroa), *B. bigelowii* (at Takaroa) and *C. neohelis* (at Takapoto) were relatively common, with other taxa represented only by loose coccoliths. The latter two species are representative of coastal coccolithophorid assemblages, and are often considered to be refugia taxa (Bown, 2005). Although *G. oceanica* is planktonic, *C. neohelis* is known to live on coral fragments (West, 1969; Kawachi & Inouye, 1994) and beach sand (Fresnel, 1986; Malin & Steinke, 2004; Konno & Jordan, 2006) in shallow waters. The preferred habitat of *B. bigelowii* is uncertain; however, it is usually found in coastal water samples (Konno et al., 2007; Hagino et al., 2016). So, it was quite surprising that, in this study, *B. bigelowii* and *C. neohelis* were associated with living pearl-oyster shells.

The oysters are filter feeders, obtaining most of their carbon from nanoflagellates in the >2μm size range (Fournier et al., 2012), notably from cryptophytes (Loret et al., 2000). According to pigment analyses, prymnesiophytes (including '*Cricosphaera* sp.') have also made a major contribution to the gut contents of such oysters (Loret et al., 2000). Thus, there is a possibility that *B. bigelowii* and *C. neohelis* are consumed by the oysters. Clearly more observations are needed to confirm this, and to expand on the current dataset.

The coccospheres and coccoliths found in this study were presumed to be living, or recently so, specimens, as opposed to the much older nannofossils found in the foregut of a sea cucumber from Nuku Hiva, Marquesas Archipelago (Tsutsui et al., 2019 [this issue]).

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