COCCOLITHOPHORES 2014

INA Workshop
on Extant Coccolithophores research
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coccolithophore biocalcification and Ocean Acidification
paleontological agenda for extant research
phylogeny, species-concepts and molecular genetics
life-cycles, ecology and biogeography

organized by
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INA Workshop on Extant Coccolithophores research

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October 5th-10th, 2014
Abstracts of presentations to be given at the workshop

The following pages give the abstracts for the Coccolithophores 2014 conference. They are arranged in alphabetical order of the first authors surname. Abstracts are for talks unless the title is followed by [POSTER].
Evolutionary origin of the living coccolithophores: A tango in two keys.

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Molecular biology has been a major determinant in unravelling the main clades among living coccolithophorids (classified as taxonomic orders and families), thereby helping to delineate the roots of living genera deep in the Cenozoic. A little acknowledged, although implicit, benefit of molecular studies is to have validated the method of morphostructural analysis, which describes coccoliths in terms of margin and central opening, each with its characteristic mono- or polycyclic structural units. This method consistently reconstructs the evolutionary history of extinct taxa of higher taxonomic ranks and their relationship with taxa of the same ranks that have living representatives. Whereas molecular biology proceeds backwards (from Present through Deep Time), morphostructural analysis applied to evolutionary history, proceeds forward, i.e., from Deep Time to Present. In principle, both approaches—or keys—should lead to convergent results. If they do not, evolutionary histories using the present as a key must be reconsidered. I will discuss here the Cretaceous origin of the living Family Rhabdosphaeraceae, the biphyletic nature of the Order Zygodiscales, which justifies the introduction of the Order Pontosphaerales for the living taxa, and the lack of a phylogenetic root for the Order Isochrysidales beyond 52 Ma; the living genera of this order cannot be rooted in the Paleocene to middle Eocene genus Toweius, which is itself a descendant of the Genus Biscutum. Finally I will speculate on the origin of highly derived coccoliths such as those of Florisphaera and Picarola, and compare the potential for diversification associated with different morphostructures.

Coccolithophore distribution from seawater column samples along the western Iberian margin during a late summer situation

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The western Iberian margin, where wind-driven coastal upwelling usually occurs from May to late September, was the study area of EUROFLEETS cruise Iberia-Forams, carried out between September 10th and 16th, 2012. Here we present results from seawater samples collected at 11 stations in a north-south transect along the Iberian margin. Seawater samples at defined depths across the upper 300 meters were filtered in order to perform qualitative and quantitative analysis of extant coccolithophores. The aim of this work is studying the composition of the coccolithophore assemblages along the western Iberian margin as well as across the water column at each station. The influence of environmental variables such as temperature, salinity, fluorescence, oxygen content, and turbidity on coccolithophore horizontal and vertical distribution has been examined by comparing our results with the CTD profiles recorded during the cruise. During the cruise no upwelling occurred along the margin and the hydrographic conditions revealed a strong influence of subtropical waters.

Approximately 15 species were identified. Two vertical zones, separated by a seasonal or a permanent thermocline, can be distinguished in the photic zone: the upper part, counting on more diversity and dominated by small placoliths; and the lower part, mainly inhabited by Florisphaera profunda. Minor changes are encountered with regard to the horizontal distribution, where temperature is likely the dominant environmental variable.

Acknowledgement
The research leading to these results has received funding from the European Union Seventh Framework Programme (FP7/2007-2013) under grant agreement n° [228344], [EUROFLEETS]°.
Distribution of extant coccolithophore populations in a meridional transect in the North Atlantic

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The distribution of living coccolithophores in the surface water of the North Atlantic was investigated along a broad meridional transect from 33°N to 77°N conducted during early summer 1992. The transect sampled the North Atlantic subtropical gyre, crossed the Azores Front and sampled North Atlantic Transitional waters as well as sub-polar waters of the Norwegian Sea. Satellite-based data together with in-situ CTD measurements were used to constrain the physico-chemical characteristics of the surface water. All countings were performed with a Scanning Electron Microscope.

Maximum numbers of > 500·10^3 coccospheres/l were reached in the northern North Atlantic (at 55°N) as well as in the southern Norwegian Sea (at around 62-67°N) whereas lowest bulk coccolithophore standing stocks of mostly < 25·10^3 coccospheres/l were observed between 40° and 52°N. The maximum coccosphere densities were essentially due to high numbers of *Emiliania huxleyi* (types A, C and B/C) which dominate the assemblages north of 52°N. In addition, *Coccolithus pelagicus* (both holo- and heterococcolith-bearing phases), *Calciopappus caudatus*, and *Syracosphaera* spp. were also found in this area of increased primary productivity. The low bulk coccolithophore standing stocks in the North Atlantic Transitional waters south of 52°N were mainly dominated by holococcolithophores (i.e., *Corisphaera gracilis*, *Syracosphaera* spp., *Alisphaera* spp., and *Gephyrocapsa muelleriae*). In the subtropical gyre further to the south, *G. ericsonii* and *E. huxleyi* (type A) became the predominant members of the population. Although the observed populations only represents a snap-shot of the assemblage distribution in the region, its relation to the different water masses of the North Atlantic provide valuable information for potential future paleoceanographic reconstructions.

Biogeography and ecology of *Calcidiscus* and *Umbilicosphaera* in the South Atlantic [POSTER]

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Research based on genetic divergences, life cycles, and morphometries has indicated that some former, apparently globally distributed coccolithophore species are composed of two or more discrete species with subtle morphological differences. However, their discrete ecological adaptations and distributions are still only known in part. Thus, we present here the biogeographical distribution patterns and ecological information of five coccolithophorid species (*Calcidiscus leptoporus*, *C. leptoporus* small, *C. quadriperforatus*, *Umbilicosphaera foliosa* and *U. sibogae*). The mapping is solely based on surface sediments from the South Atlantic whereas sediment trap data from this region is added for morphometrical evaluation of the species.

The three *Calcidiscus* species can easily been distinguished by a combination of size and qualitative characters of the distal shield. Mostly encountered in the temperate to sub-polar regions *Calcidiscus leptoporus* exhibits a negative correlation to temperature and to salinity. However, a positive response to nitrate and phosphate concentrations is detected. Its strong preference for highly dynamic environments therefore emphasised by the CCA. In contrast, the *C. leptoporus* small and the large *C. quadriperforatus* both are mainly found in the warm, more oligotrophic South Atlantic.

Two round *Umbilicosphaera* species are distinguished largely based on coccosphere characters. However, the two species exhibit significant differences in coccolith morphology and show only little overlap in size. Highest numbers in the South Atlantic are encountered in sub-tropical latitudes and basically come from *U. sibogae*. In contrast, abundances of *U. foliosa* only increased in the cold and nutrient-enriched Benguela upwelling. The distribution patterns of *U. foliosa* confirm results of earlier studies with a weak trend towards higher proportions in environments with a greater nutrient availability. In contrast, the more common *U. sibogae* mostly occurs under rather oligotrophic conditions.
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Coccolithophores in late Glacial to Holocene sediments of the Norwegian Sea and their paleoceanographic implications [POSTER]

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A coccolith-based micropalaeontological investigation of a 8.5 m long late Glacial to Holocene sediment core (GIK 23312-1), recovered from 977 m water depth in the Gamlenbanken area off western Norway (66°56’N, 7°44’E), was conducted in order to document the pattern and timing of surface circulation changes in the study area. Comparison of the coccolithophore records with other proxy records (TOC, carbonate, isotopes) from the same site as well as from other cores were carried out in order to assess the sensitivity of coccolithophores to short-term climatic changes.

In general, the coccolith assemblage is of low diversity and was dominated by *Emiliania huxleyi*. Other species, such as *Coccolithus pelagicus*, *Gephyrocapsa muellerae*, and *Calcidiscus leptoporus* contributed considerably to the assemblage. Long-term trends in changes of both coccolith numbers and %-abundance of the species reflect major steps in Atlantic Water influx to the Norwegian Sea at orbital scale. Absolute total coccolith numbers are relatively low before about 10.8 ka, indicating relatively harsh environmental conditions with the influence of meltwater and a rather small inflow of Atlantic surface water. However, maxima of *G. muellerae*, *G. ericsonii*, and *C. leptoporus* suggest a first warming due to an increased influence of Atlantic surface water already during the Bølling-Allerød at around 14 ka. After a short return to more pronounced cool conditions, an early Holocene maximum in coccolith productivity, which is mainly due to elevated numbers of *E. huxleyi*, illustrates another step in the inflow of relatively warm Atlantic water. Nevertheless, coccolithophore productivity did not increase significantly before the middle Holocene at about 5.8 ka at the studied site. This is later than previously observed and may be attributed to the fact that the main core of the Atlantic water intrusion was located further to the west and, thus, may not have drastically influenced the studied site at the upper continental margin. After the observed coccolithophore production maximum between 4.2 and 2.5 ka, indicated by changes in the numbers and relative abundances of the dominant coccolith species, cooling of the surface waters took place after 2.5ka.
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A coccolith-based micropalaeontological investigation of a 8.5 m long late Glacial to Holocene sediment core (GIK 23312-1), recovered from 977 m water depth in the Gamlenbanken area off western Norway (66°56’N, 7°44’E), was conducted in order to document the pattern and timing of surface circulation changes in the study area. Comparison of the coccolithophore records with other proxy records (TOC, carbonate, isotopes) from the same site as well as from other cores were carried out in order to assess the sensitivity of coccolithophores to short-term climatic changes.

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Change in calcification state of *Emiliania huxleyi* in the Western Mediterranean Sea during the last century

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A study of sediment trap located in the Gulf of Lion (Western Mediterranean Sea) has recently revealed a progressive decrease of the coccolith mass of *E. huxleyi* between 1994 and 2006 (Meier et al., 2014). We tested the results of this study by using other types of samples collected at the same location: a sediment core covering the last century and several water samples collected and filtered at different seasons and depths in the euphotic zone in 1993, 1997, 2013 and 2014. Decrease in coccolith mass is observed in these two types of sample, confirming the results of the sediment trap study. The observed rates of decrease are however smaller: we recorded a 0.015 pg/year decrease in the core for the last century, and 0.035 pg/year in the water samples, when Meier et al., 2014 found 0.1 pg/year in their sediment trap study (about half of that decrease is due to the last years of the records, and the decrease is about 0.05 pg/year between 1994 and 2004). Interannual dynamics is therefore recorded differently in these types of samples. Depth and seasonal distribution of morphotypes as well as short and pronounced oceanographic events imprint strongly the record of *E. huxleyi* coccolith mass. That complexity is due to the changes in morphotype composition of the assemblages. This result emerges from numerous biometric measurements and from a large collection of SEM photography. Yet it is difficult to express the shift of coccolith mass has only due to a shift in the relative abundance of morphotypes exhibiting difference in coccolith mass: a decrease of calcification in each of the morphotypes is also a possible explanation but not yet demonstrated.

Morphogenetic characterization of new *Gephyrocapsa* isolates suggests introgressive hybridization in the *Emiliania/Gephyrocapsa* complex (Haptophyta)

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The coccolithophore genus *Gephyrocapsa* contains a cosmopolitan assemblage of pelagic species, including the bloom forming *Gephyrocapsa oceanica*, a sister taxon of the emblematic coccolithophore *Emiliania huxleyi*. These two species have been extensively studied and are well represented in culture collections, whereas cultures of other species of this complex are lacking. We report on three new strains of *Gephyrocapsa* isolated into culture from samples from the Chilean coastal upwelling zone using a novel flow cytometric single-cell sorting technique. The strains were morpho-genetically characterized by scanning electron microscopy and phylogenetic analysis of 6 genes (nuclear *18S* and *28S* rDNA, plastidial *16S* and *tufA*, and mitochondrial *cox1* and *cox3* genes). Morphometric features of the coccoliths indicate that these isolates are distinct from *G. oceanica* and correspond to *G. mullerae*. Surprisingly, nuclear, plastidial, and mitochondrial gene phylogenies placed these strains within the *E. huxleyi* clade and well separated from *G. oceanica* isolates, making *E. huxleyi* a polyphyletic group. Specifically, the *G. mullerae* morphotype strains clustered with the mitochondrial beta clade of *E. huxleyi*, which, like *G. mullerae*, has been associated with cold (temperate and sub-polar) waters. We discuss putative evolutionary explanations, focusing on the possibility that these results might reflect past hybridization and introgression between *E. huxleyi* clade beta and *G. mullerae*, while the inability of *tufA* phylogenies to separate *G. oceanica* and *E. huxleyi* clade alpha might indicate a similar history of early hybridization between these two types that are both associated with warmer waters. These results have important implications for understanding the role of hybridization in adaptation and speciation in vast ocean meta-populations of phytoplankton and for relating morphological species concepts to ecological and evolutionary units of diversity.
Morphologic studies of living coccolithophores present opportunities to understand the intensely complex physiology of modern marine protists, including morphological plasticity (intra-specific variability) and survival strategies; all of which are crucial for the proper understanding of evolutionary patterns in the fossil record.

The spirothecate coccospheres in living Gaarderia and Umbellosphaera species are of an unusual construction, consisting of coccoliths whose size and shape change from the inner side of the coccosphere to the outer side, with internal microliths and external macroliths. Microliths are small (~2-4 µm) cup-like coccoliths closer to the cell surface. The external macroliths are considerably larger (>5 µm) with a narrow central depression. Microliths and macroliths differ by exhibiting different proportions between the margin and central area. The central area of the microliths is large and generally occupied by a grill, whereas the margin is very narrow. The macroliths show opposite characters, with a narrow central area and a flaring margin. The non-overlapping microliths are densely packed, forming an inner layer of saucer-like coccoliths open to the outside. In contrast, the macroliths are imbricate, with the margins of adjacent coccoliths overlapping to form a continuous, regular exotheca. This construction has been proposed to represent adaptative morphology to mixotrophic behavior (Aubry, 2009).

The early Paleocene Ellipsolithus macellus (63.25 to ~54 Ma) is known only from its coccoliths that are strongly reminiscent of the coccoliths secreted by the two aforementioned living genera, although there are no phylogenetic relationships between them and Ellipsolithus (as the former belong to the Order Syracosphaerales). Ellipsolithus macellus is distinctive in being elliptical to long-elliptical, with a central area that occupies half of the coccolith. Intraspecific variability involving size and general shape is noticeable but no previous attempt has been made at characterizing E. macellus through morphometric analysis, possibly because the taxon is generally uncommon. We report two morphotypes of Ellipsolithus macellus in the Early Paleocene (Danian) assemblages recovered from the Qreiya section in Upper Egypt, differing by their ellipticity and size. We refer to these two morphologies, occasionally illustrated in the literature, as morphotype A (the holotype) and morphotype B. Morphotype B exhibits lesser ellipticity than morphotype A, which is also a marked difference between the microliths and the macroliths in both Gaarderia and Umbellosphaera.

Through quantitative analysis we conducted a comparative morphometric analysis of the coccoliths of E. macellus, Gaarderia corolla and Umbellosphaera spp. Our objective was to test whether these two E. macellus morphotypes are akin to the differentiated coccoliths that occur on the coccospheres of the living taxa. If so, they may represent an early adaptation to mixotrophic behavior in the middle Danian Ocean, roughly 1 Myr prior to widespread adaptation to increasing oligotrophy by the calcareous plankton. However the differences between the latter are much greater than between the two morphotypes of Ellipsolithus, which renders our data inconclusive. An alternate interpretation is that the two morphotypes represent pseudo-cryptic species, which would imply that cryptic speciation would have occurred shortly after the evolutionary appearance of the genus Ellipsolithus. The two morphotypes, however, differ only by their ellipticity, without much difference in size as commonly reported between well-documented pseudo-cryptic species. This study shows the difficulty in interpreting taxonomic differences in extinct taxa, and offers an alternative to cryptic speciation. Our study is inconclusive with regard to one explanation or the other concerning E. macellus, but it has enabled us to demonstrate that the microliths and macroliths of Gaarderia and Umbellosphaera are functionally adapted to mixotrophy, and that the two genera have followed slightly different adaptive morphologies.
The coccolithophore family tree: tracking modern groups back through time using exceptionally preserved fossil records

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Nannopaleontologists routinely examine tens of thousands of fossil specimens in samples from a near-continuous 220-million-year evolutionary history of coccolithophores. This huge volume of data and the rather uniform preservation in most marine calcareous sediments, have together been considered evidence of a reasonably complete fossil record. However, the recent discovery of extraordinary nannofossil preservation from Tanzania (Cretaceous-Paleogene) together with revised estimates of modern coccolithophore diversity, which is far higher than the preserved Holocene record, suggests our understanding of the taphonomy of these plankton is incomplete. The Tanzanian Kilwa Group and other clay-rich hemipelagic sedimentary successions contain nannofossil assemblages with very high species diversities, distinct taxic compositions, and conserved small and fragile coccoliths, many of which are new to science. These fossils are best viewed by electron microscopy of broken, untreated rock surfaces, where they occur in unaltered concentrations, which most likely represent zooplanktonic fecal pellets or organic aggregates, representing snapshot samples of life assemblages, rather than the time-averaged and preservation-modified assemblages typical of more normal preservation states. The assemblages provide a benchmark against which to compare other biodiversity data, but also provide valuable insights into the evolution and origination of the modern coccolithophore groups, in particular, those that have little or no previous fossils record, such as the deep photic zone *Gladiolithus* and the most diverse modern group, the Syracosphaerales. Here we will review the major palaeobiological discoveries from these exceptionally preserved fossil localities and demonstrate that much of the modern coccolithophore diversity was established by at least Eocene times, with several groups originating prior to this in the Mesozoic.
Recent studies on ocean acidification due to the increase of carbon dioxide in the atmosphere have provided evidence on a possible impact on coccolithophore calcification. In the framework of the MedSeA (Mediterranean Sea Acidification in a changing climate, EU-FP7) project, we collected data from May 2011 to February 2013 to deepen knowledge on coccolithophore associations at a coastal site in the Gulf of Trieste, for which a long-term time series of plankton data is available (C1-LTER 1986-present).

The main aims of this study were to assess the contribution of coccolithophores to the phytoplankton community, also in relation with the available time series for the site, to identify the seasonal distribution of different species, to evaluate the relationships with high quality measurements of the carbonate system and other environmental parameters, and to compare the results of the coccolithophore analyses obtained by different methods (phase contrast versus polarized light microscopy and scanning electron microscopy).

Coccolithophores showed a high interannual variability and a typical seasonal pattern, with maxima in the autumn-winter and minima in summer. The seasonal pattern was mainly linked to [HCO₃⁻], which is the preferential form used by coccolithophores for calcification. During the analysed period, the coccolithophore community was characterized by species adapted to a variety of environmental conditions: in autumn-winter, *Emiliania huxleyi* dominated, followed by *Acanthoica quattrospina*, *Syracosphaera pulchra* and some minor species (only present in autumn, e.g. *Ophiaster hydroideus*, *Calcio-pappus rigidus*, *Michaelsarsia adriaticus*); in spring, the association was dominated by holococcolithophores and minor *E. huxleyi*; in summer, low overall abundances coincide with low *E. huxleyi* concentration and the dominance of small *Syracosphaera* species, *Rhabdosphaera clavigera* and holococcolithophores. The comparison between the total coccolithophore abundances obtained by phase contrast microscope with the Utermöhl method and those obtained by polarized light microscope revealed good correspondence in winter and autumn, and less in spring. In fact, the polarized light microscope counting, coupled with scanning electron microscope observations on selected samples, allowed us to recognize species with very small and/or less calcified coccoliths, that would be probably lumped with other flagellates with the Utermöhl method, improving the assessment of coccolithophore species diversity and their contribution to the total phytoplankton.
Exploring the complexity of life cycles. The case of *Rhabdosphaera clavigera*

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Nowadays, the formerly *Sphaerocalyptra quadridentata* (Schiller 1913) Deflandre 1952 is considered as the holococcolithophore phase of *Algirosphaera robusta* (Lohmann 1902) Norris 1984. Several, non ambiguous, Scanning Electron Microscopy (SEM) images of *Algirosphaera robusta* Het-Hol combination coccospheres have been discovered during the last years (Triantaphyllou and Dimiza 2003; Dimiza *et al.* 2008), which corroborated the combinations with the same species observed by Kamptner (1941).

Nevertheless a SEM image, with a *Rhabdosphaera clavigera* Murray and Blackman 1898 partially embracing a specimen of the formerly *Sphaerocalyptra quadridentata*, shows a notable HET-HOL combination coccosphere (Cros and Fortuño 2002).

From calcareous nannoplankton community data of Mediterranean waters it is possible to realize that the three before mentioned taxa (*S. quadridentata*, *A. robusta* and *R. clavigera*) usually share the same waters. But, whilst the formerly *Sphaerocalyptra quadridentata* and *Rhabdosphaera clavigera* are found in shallow waters, the heterococcolithophore *Algirosphaera robusta* generally resides in deeper layers.

All these findings might lead to consider the three above referred taxa as different steps of a highly complex *Rhabdosphaera clavigera* life cycle.


Species-specific calcite production in the Arctic Ocean reveals *Coccolithus pelagicus* as a key calcifier.

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The phytoplankton community of the Arctic Ocean may potentially be sensitive to ocean acidification, with coccolithophores generally expected to suffer, although culture studies have shown conflicting results. This is partly attributable to species-specific and strain-specific responses. A key unknown is the role of different species of coccolithophores in oceanic calcite production. Here we present results from a survey of calcite production (through $^{14}$C uptake), coccolithophore composition and species-specific calcite production, derived from partitioning the calcite budget of the community, in the Arctic Ocean and Iceland Basin. We will examine our data in the context of the in situ environment, including the carbonate chemistry. Distinct differences were observed in the community composition, with *Emiliania huxleyi* numerically dominating the Barents and Norwegian Seas, and *Calciopappus* sp and *Coccolithus pelagicus* HOL predominant in the Greenland Sea. However, species-specific calcite production shows that, except for the Barents Sea where *Emiliania huxleyi* was the main calcifier, *Coccolithus pelagicus* was the major calcite producer in the Arctic Ocean, and may therefore be a key coccolithophore species for considering in future predictions of Arctic communities.
The composition and distribution of living coccolithophores in the northeastern Mediterranean Sea

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A study on living coccolithophores from the euphotic zone in the north-eastern Mediterranean Sea was used to determine the species spatial and temporal variations. A total of 98 plankton samples from 24 stations in the North Aegean (Athos, Skyros and Limnos basins), Central Aegean (Cyclades Islands, Saroni and Evoikos gulfs), South Aegean (Antikythira straits, Cretan Sea, Rhodos gyre) and south-eastern Ionian Sea, have been collected during several sampling periods between 2001 and 2014. These stations fall along some established N-S trophic gradients from mesotrophic to ultra-oligotrophic regions. The former involve the NE Aegean Sea east off Limnos island (under the direct influence of the Black Sea waters inflowing into the Aegean through the Dardanelles Straits), the Saroni and Evoikos gulfs and the Rhodes cyclonic gyre. All the rest, represent oligotrophic to ultra-oligotrophic environments, where annual mean chlorophyll a concentrations hardly pass 0.2 μg l⁻¹ and picophytoplankton cells (cyanobacteria, picoeukaryotes) dominate (45 - 80%) both autotrophic biomass and production.

The coccolithophore distribution was quantitatively documented through Scanning Electron Microscopy in terms of density, diversity and community structure. A total of 86 coccolithophore species were identified. *Emiliania huxleyi* is the most abundant species with early spring concentrations up to 27 x 10³ cells l⁻¹, typi- cally constituting more than 40% of the coccolithophore assemblages. Other characteristic species like *Syracosphaera molischii, Algirosphaera robusta, Syracosphaera pulchra, Gephyrocapsa ericsonii, Syracosphaera protrudens, Rhabdosphaera clavigera, Umbellosphaera tenuis, Helicosphaera carteri* often exceed 10⁵ cells l⁻¹. Holococcolithophores are well represented, with *Syracosphaera pulchra* HOL oblonga, *Coronosphaera mediterranea* HOL wettsteinii, *Helladosphaera cornifera* and *Algirosphaera robusta* HOL being the most abundant species. The studied coccolithophore communities indicate a close relationship between coccospheρhe densities and surface water circulation, with the sea temperature gradient affecting species composition. High species diversities associated with dominance of K-selected taxa Rhabdosphaeraceae and holococcolithophores were recorded during summer, whereas low diversities coupled with maximum cell concentrations were observed during late autumn-early spring and typically associated with dominant *Emiliania huxleyi*. In general, cell numbers are usually higher in the upper and middle photic zone (~60 m water depth). In the lower photic zone, the presence of *Florisphaera profunda, Algirosphaera robusta* and *Syracosphaera anthonis* becomes important, making up the typical deep assemblages.

*Emiliania huxleyi* in the Eastern Mediterranean Sea provided strong evidence for seasonal variation in cocco- sphere and coccolith size, morphology and calcification. Biometric analysis showed a consistent relation of increase in the size of coccoliths and coccospheres, including the thickness of the inner tube elements (INT), with low sea surface temperatures and moderate productivity, during winter and early spring season. A better assessment of this relationship will be obtained from a current study in the NE Aegean Sea, within which a seasonal sampling of coccolithophore assemblages is coupled with biogeo- chemical and productivity measurements, also involving CO₂ concentrations, bio-optical studies and remote sensing of the study area.

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Monitoring coccolithophore assemblages variability, calcification and carbonate production in Subantarctic sediment traps

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Coccolithophores recorded in material retrieved from two sediment traps located south of Australia (140°E- 47°S, Subantarctic Zone) at 1000, 2000 and 3800 m, were studied in order to monitor monthly and seasonal evolution of the assemblages along 2 years.

Additionally, the use of circular polarized light, adding to a computer application, permit the measurement of some features in coccoliths as well as the calculation of the amount of calcite produced by the most significant species. Particularly significant is the evaluation of the degree of calcification of selected taxa and morphotypes, and the relationship with environmental and oceanographic parameters.

The Subantarctic zone represents more than half the areal extent of the Southern Ocean and serves as an interface between the warm and nutrient-depleted waters of the subtropical gyres north of the Subtropical Front, and the cold and macronutrient-rich waters south of the Polar Front. The euphotic zone in the study region is dominated by nanophytoplankton and picophytoplankton, including abundant number of coccolithophores and other prymnesiophytes.

Coccosphere geometry as a proxy for cellular behaviour: linking modern and palaeo observations

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The geological record contains a rich archive of exported coccolithophore populations that can inform our predictions of their response to current and near-future environmental change. However, these fossilised remains represent integrated populations of millions of individuals recording reproductive success over daily timescales, with each cell responding to its own microenvironment. Therefore, to maximise the application of coccolithophore fossil records we shift away from the traditional viewpoint of these fossils as time-integrated assemblages, towards a cellular-level focus that allows closer comparison with living populations. Our research explores the link between the individual cell and the success of the species, by developing frameworks for understanding cellular skeletal architecture and how plankton populations are impacted by, and in turn, impact their environment. We combine culturing of living coccolithophores with analysis of naturally occurring populations in the ocean and with exquisitely preserved fossils. Finding these fossils is challenging, but there are exceptional situations where the usual preservation bias is greatly reduced and we find complete coccospheres that allow the direct comparison with modern cells. These coccospheres preserve invaluable information about the original living cell including its size, levels of particulate organic carbon and inorganic carbon, ontogeny, and growth phase.
Coccolithophores are unicellular calcifying eukaryotes and important primary producers in the world oceans. However, little is known about their roles in the coastal ecosystems. Main objective of this study was to determine coccolithophore diversity and species succession in the coastal waters of Rovinj. Coccolithophore flora of Rovinj and the northern Adriatic was well studied in the early 20th century by Schiller (1913, 1925) and Kamptner (1941), in those taxonomic studies they described about 50 coccolithophore species. Afterwards, species lists were produced by Relevante (1985/1986) and Viličić (2002), both of which were only based on literature data, and contained many synonyms and taxonomic inaccuracies. Moreover, there are only scarce records of diversity and ecology of coccolithophores in the Adriatic. Thus, this study also considers coccolithophore dynamics in relation to variable environmental conditions. This is particularly important in marginal seas such as the Adriatic where the small water body, with at times restricted circulation, can result in amplified responses to external changes.

The research was completed over a one year period (Oct/2008–Nov/2009) every ten days in the coastal area 1 nm (1.8 km) in front of Rovinj (45°4’40”N, 13°36’29”E) using microscopic examination, both light and electron scanning, as well as pigment analysis with high-performance liquid chromatography.

A total of 60 coccolithophore morphospecies were recorded during the study. Dominating genus was Syracosphaera, represented by 20 species. Coccolithophores of both HET and HOL phases were present throughout the investigated period, while seasonality in HET/HOL phases was observed only for Coronosphaera mediterranea HET (autumn)/Coronosphaera mediterranea HOL wettsteini type (spring).

Pigment analysis pointed to a clear domination of haptophytes in the investigated area. High concentrations of 19’-hexanoyloxyfucoxanthin were recorded throughout the year with a distinct peak in the late spring. This late spring period (March- June) was characterised by a high species diversity and higher contribution of coccolithophorids to the total phytoplankton assemblage (>60%). The typical summer coccolithophores, Rhodosphaera clavigera and Syracosphaera pulchra, were related to high temperatures and low nitrate concentrations. Calciosolenia murrayi and C. brasiliensis was related to elevated nutrient concentrations, and were characteristic for the autumn assemblage. They were able to find favourable living conditions despite the abundant occurrence of diatoms and low light transmission values. Highest abundances of the species Emiliania huxleyi (10⁶ cells L⁻¹) were recorded in January during a monospecific bloom (92% of whole phytoplankton community). E. huxleyi was the most frequently recognised species and was related to low temperature and nutrient rich waters, present in high numbers both during winter and summer.

These results indicate that a change in the perception of the importance of coccolithophores in the coastal waters is inevitable and diatoms and dinoflagellates are joined by coccolithophores as the most important phytoplankton groups in the northern Adriatic.


It has recently been proposed that coccolithophore species were differentially affected by environmental changes over the Palaeocene-Eocene Thermal Maximum (PETM). Based on coccolithophore cell geometry, Gibbs et al. (2013) concluded *C. pelagicus* showed indications of slower reproduction during this period of rapid ocean warming and acidification. It is suggested that this is indicative of its limited physiological ability to adapt. In light of anthropogenically induced changes in the future ocean, a deeper understanding of the variability underlying coccolithophore responses is important. At present, the sensitivity of calcification processes to changing seawater carbonate chemistry has only been well characterized for the Isochrysidales species *E. huxleyi*. In this study we present results on calcification rates as well as changes in coccolith morphology in the Coccolithales species *Coccolithus pelagicus ssp. braarudii* (strain PLY182g) over a broad pCO$_2$ range (55 to 4500 µatm). Calcification rates reached a narrow optimum around 300-400 µatm. Coccolith morphology varied accordingly. We observed the incomplete formation of coccoliths at low pCO$_2$, while elevated pCO$_2$ resulted in malformed laths with blocky crystal units. From 500 µatm upwards coccoliths became malformed, starting with an increase in malformed bridges between 500 and 1000 µatm. From 1375 to 2250 µatm, all coccoliths were malformed, and above 3000 µatm no coccolith structures were present in the cells. Our results differ from previous studies in that we present (1) a significant negative influence of realistic CO$_2$ levels (200-1000 µatm) on calcification processes in *C. pelagicus ssp. braarudii* as opposed to Langer et al. (2006), and (2) a stronger response in *C. pelagicus ssp. braarudii* than that presented for *E. huxleyi* by Bach et al. (2012). Taken together these findings are in line with the conclusion of Gibbs et al. (2013). Evidence now exists from both the paleorecord, as well as from physiological studies, that a restructuring of coccolithophore communities can be expected in the future due to the differential sensitivity of key species to rapid environmental change.

Seasonal change in living coccolithophores in the coastal waters of Japan

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Seasonal changes in coccolithophores were studied in the surface waters of the following three coastal stations in Japan; Tomari Port, Tottori from July 2008 to June 2014, Usa Bay, Kochi from March to November 1995, and Futami Bay, Chichi-jima Island from December 2012 to March 2014. The former two stations are located on the shelf of the Japanese archipelago whereas the latter station is in the coastal water of an isolated island in the North Pacific Subtropical Gyre.

Coccolithophore floras of Tomari Port and of Usa Bay resembled each other, and differed from that of Futami Bay in seasonal trend of standing crop and of major taxa. In Tomari Port and Usa Bay, the standing crop was relatively high in spring and autumn, and low in winter and summer. In Futami Bay, the standing crop was relatively high in winter through early spring, and low from mid spring through autumn. Emiliania huxleyi and Gephyrocapsa oceanica occurred in most samples, throughout the year, in all stations. They increased in abundance in spring and autumn in Tomari Port and in Usa Bay, and from winter through early spring in Futami Bay. Discosphaera tubifera, Rhabdosphaera spp. Umbilicosphaera spp. Algirosphaera oryza, Oolithotus antillarum, and/or Floripsaera profunda, appeared in the sea surface water of the Tomari Port and in the Usa Bay in autumn, but occurred in the Futami Bay from winter through early spring.

Frequent sampling in Tomari Port (≥ twice a week in June) revealed that B. bigelowii and Tergestiella adriatica occurred synchronously every mid June within short period (5-15 days). Fragments of B. bigelowii were observed but intact cells of B. bigelowii were not found from the June samples from Futami and Usa Bays, where the sampling was conducted with 1-month interval. We consider that we missed the occurrence of B. bigelowii in Futami and Usa Bays due to too coarse sampling interval.

Composition, abundance and distribution of coccolithophores of the Mexican Pacific and the southern Gulf of Mexico

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Despite coccolithophores form a very distinctive, conspicuous and important group of the marine phytoplankton, in México the study of this group is fairly recent. This is a modern review of the composition, abundance and distribution of coccolithophores and their assemblages found along the Mexican Pacific (including the Gulf of California) and the southern Gulf of Mexico, in recent years (2000-2013), with special focus on the influence of oceanographic and climatic conditions. Several oceanographic cruises have been carried out in both regions, and sampling and protocols have been followed to collect and study the coccolithophores species and their ecology. Additional data such as temperature, salinity, dissolved oxygen and fluorescence have been measured in situ, whereas samples for analysing discrete chlorophyll a, nutrients and phytoplankton have been taken. About 50 coccolithophores species have been recognized in both regions, where Emiliania huxleyi and Gephyrocapsa oceanica are the most frequent and very often the most abundant species. Other species with high densities are Calcidiscus leptoporus, Oolithotus antillarum, Reticulofenestra sessilis, Syracosphaera pulchra, Umbilicosphaera hulburtiana in the Mexican Pacific and Umbellosphaera tenuis in the Gulf of Mexico. Highest coccolithophore densities (e.g. Emiliania huxleyi alone or with Gephyrocapsa oceanica) reached to 1.1 x 10^5 cells L^-1 in coasts off Baja California, the Mexican Pacific, and 1.2 x 10^5 cells L^-1, in a coastal location from the southern Gulf of Mexico. In vertical profiles, the peaks of highest coccolithophore densities often coincide with the chlorophyll a maxima layers. Oligotrophic and more oceanic waters and haline fronts in coastal waters of the southern Gulf of Mexico, and oceanographic eddies, upwellings, eutrophication and “El Niño” events in the Mexican Pacific, are among the main processes detected that affect the composition, abundance and distribution of coccolithophores.
Investigation of kinetic variation in ribulose-1, 5-biosphosphate carboxylate/oxygenase (RuBisCO) in marine Haptophytes

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While small in biomass, marine phytoplankton constitute approximately 50% of global primary production. Due to their ability to simultaneously fix carbon and biomineralise calcium carbonate and biogenic silica, marine coccolithophores and diatoms are major players in the global carbon cycle and drivers of carbon export from the surface ocean. Understanding the mechanisms by which these organisms handle and fix carbon and the relative diversity between species in each phylum is essential to elucidate their environmental preferences and potential to adapt to future environmental change.

In this study we measure variability in the half-saturation constant of carboxylation for RuBisCO across the Haptophyte and Heterokontophyta phylum. We find a large spread in this kinetic parameter in the Haptophytes versus a small range and larger values in the diatoms. This suggests variation in the carbon requirements and ability to concentrate carbon across the Haptophytes, and even between two *Emiliania huxleyi* strains. We suggest a few explanations for this variation and also explore how Haptophytes and Heterokontophyta differ in RuBisCO and carbon handling function.

Coastal coccolithophorid assemblages from tropical islands

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Coccolithophorid assemblages from lagoonal and/or coastal settings around various tropical islands (Puerto Rico, Ogasawara Islands, Guam and Palau) were investigated to ascertain which species may be diagnostic for shallow waters. The data were compared to determine if there were any regional differences or whether a cosmopolitan assemblage exists.

Results obtained thus far suggest that *Cruciplacolithus neohelis* could be viewed as endemic to coastal environments, since it does not occur in offshore assemblages, but is present at most of our sampling sites. The presence of *Reticulofenestra* spp. have been linked previously with coastal upwelling areas, while others like *Gephyrocapsa* spp., *Helicosphaera* spp., *Coronosphaera* spp., *Syracosphaera* spp. and *Umbellosphaera* spp. are commonly found at most sites. The finding of holococcolithophorids in just one set of samples, suggests that seasonal differences may occur at tropical localities, and highlights the need for taking samples at different times of the year. For some species, we cannot determine yet if they are part of the tychoplankton or belong to local populations. These findings suggest that previous published biogeographic and depth zonations should not be used so rigidly, when reconstructing palaeoenvironments, since we still have a lot to learn about coccolithophorid ecology.
Unlike the majority of biomineralisation, which is mediated via proteins, the coccolithophores employ acidic polysaccharides as the template for a multitude of intricate calcium carbonate liths which are precipitated inside their cells and expelled to form an external spherical armour. Massive accumulations of these calcium carbonate coccoliths (we estimate a flux of ~ 6x10^{25} liths/year) form sediments on the deep seafloor, a dominant sink of carbon from the atmosphere over geological timescales, and a buffer for seawater chemistry. This acidic, coccolith-associated polysaccharide (CAP) plays a dual role, likely determined by the calcifying vesicle chemistry, promoting and limiting precipitation. We have developed novel techniques for the extraction and characterisation of these biomineral-mediating molecules from both cultures and sediments. The composition of the acidic polysaccharide is distinctive for different species suggestive that interactions with galacturonic acid residues are key to dictating the architecture of the liths, and the contrasting polysaccharide chemistry between species is likely reflective of coccolith vesicle conditions. The observation of this unique species-specific CAP is not only restricted to different clades of coccolithophores. We can now also demonstrate a distinct/signature-like CAP variation between strains of *Emiliania huxleyi*, offering an alternative mode of fingerprinting morphotypes which can be extended into palaeoreconstructions of assemblages.

Distribution of extant coccolithophores in the China Seas and their response to environments

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Distribution of extant coccolithophores of the South China Sea and the East China Sea have been studied based on sea surface water samples taken from three cruises. In the South China Sea, sea surface water (5 m in depth) samples were obtained during cruise in August 2008 (62 stations) and in April 2010 (79 stations). Twenty-four species were counted and identified with scanning electron microscope and polarizing microscope. In spring, the common species were *Florisphaera profunda*, *Emiliania huxleyi*, *Gephyrocapsa oceanica*, *Umbellosphaera tenuis*, and *Palusphaera vandelli*. The absolute abundance of coccoliths in spring ranged from 5.13x10^{3} coccoliths/L to 1.89x10^{6} coccoliths/L, while those of coccospheres ranged from 0.79x10^{3} cells/L to 2.96x10^{5} cells/L. In summer, the common species were *Emiliania huxleyi*, *Gephyrocapsa oceanica*, *Florisphaera profunda*, *Umbellosphaera irregularis*, *Gephyrocapsa ericsonii*, *Umbellosphaera tenuis*, *Discosphaera tubifera*. The absolute abundance of coccoliths in summer ranged from 6.03x10^{3} coccoliths/L to 0.74x10^{6} coccoliths/L, while those of coccospheres ranged from 1.24x10^{5} cells/L to 2.57x10^{5} cells/L. The Shannon-Wiener index of living cell in spring and summer ranged from 0.48 to 1.79 and 0.39 to 2.18 respectively. The results showed that the living coccolithophores in spring were main distributed in the adjacent area between the Pearl River estuary and the continental shelf of the northern SCS, the Kuroshio area of the NE Taiwan Island, the Luzon Strait where the upper stream of the Kuroshio intruded into the SCS basin, the upwelling area off the east coast of Vietnam and Hainan island. The abundance is greater in spring than in summer. Coccolithophore abundance is negatively correlated with temperature, salinity and nutrient concentration.

In the East China Sea, sea surface water samples were collected in June 2011. 64 water samples are analyzed, but only nine samples have coccolithophores, most of which located over the Changjiang River plume area. The sporadic occurrence of coccolithophorid flora is in agreement with previous studies. *Gephyrocapsa oceanica* dominated in the coccolithophore community and developed a bloom that was not reported before in the ECS. The cells density reached to as much as 620,000 cells/l. Various degrees of coccolithophore deformation were identified in the surface water of ESC, which we attribute as malformation, stunted growth of coccolith element. High rate and severely malformation was found in shelf waters of ESC, while normal cells occurred round the Changjiang River plume area. It is suggested that the occurrence and distribution of malformation in ESC was possibly cause by the carbonate chemistry in ambient water.
Pleistocene changes in nannofossil size and extinction of deep-sea benthic foraminifera: coincidence or causal relationship? [POSTER]

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This research provides new evidences of a possible link between the decreasing size trend recorded by some nannofossil taxa and the Last Global Extinction suffered by the elongate deep-sea benthic foraminifera during the last 1.07 Ma. Since the early Cenozoic to the Holocene a generalized decreasing size pattern of the nannofossil assemblages has been documented in deep-sea sediments from different latitudes and oceanographic settings (e.g. Herrmann and Thierstein 2012 and reference therein). Previous taxonomic and biometric investigations indicated that Cenozoic extinction of large-sized species occurred in different nannofossil lineages, such as Calcidiscus, Coccolithus, Helicosphaera, and Reticulofenestra associated with the development of modern small-coccolith producing taxa, such as Emiliania, Gephyrocapsa, Reticulofenestra haqii, R. minutula and Umbilicosphaeraeaceae in the following Neogene.

The high resolution micropaleontological and geochemical dataset of the site MD 97-2114 (Lupi et al., 2008; Lupi, 2009; Cobianchi et al., 2012; Mancini et al., 2013) permitted to observe, in terms of absolute and relative abundances, species richness and diversity, the evolutionary turnover of calcareous nannofossils and foraminiferal Extinction Group (Ext. Gp) throughout the Pleistocene documenting a surprising causal correlation between the decrease in abundance and size of the genus Reticulofenestra and the LGE of the elongate deep-sea benthic foraminifera in the SW Pacific Ocean. The area around New Zealand has been extensively studied in the foraminifera content during the past 15 years (see for example data from ODP Leg 181) but less data have been collected about the nannofossil content and the performed studies have regarded either one site or a very short time interval (Fenner and Di Stefano, 2005; Lupi et al., 2008; Lupi, 2009; Cobianchi et al., 2012). At the best of our knowledge, this is the first study which reports the integrated nannofossil and benthic foraminiferal data furnishing new idea evidences about the hypothesis that lowered pCO$_2$ during increasingly severe MPT glacial, may have caused the decline and possible loss of the Ext. Gp’s phytoplankton food source.

This hypothesis is particularly intriguing because the declining pCO$_2$ during Neogene cooling is coeval with the declining relative abundance of reticulofenestrids thus indicating that a common paleoclimate forcing was probably at the origin of this important global change in the food chain.

In the studied site MD 97-2114, the final demise of the reticulofenestrid group occurred slightly later than the last global extinction of the elongate deep-sea benthic foraminifera during the MPT interval. However, we argue that new data provided by the study of calcareous nannofossils from well calibrated sites collected near the MD 97-2114 (ODP site 1123; 1125) could be used to better constrain the possible lag time occurring between foraminiferal and nannofossil response to this common paleoclimate forcing. Only with more case-studies we could point out any possible relationships between deep-sea benthic foraminifera and calcareous nannofossils excluding a simple coincidence.
A coccolithophore PIC:POC proxy: Investigating algal biology in the sedimentary laboratory

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Coccolithophores are the ocean’s dominant calcifying phytoplankton; they play an important, but currently poorly understood, role in long-term biogeochemical climatic feedbacks. Most calcite producing marine organisms are likely to calcify less in a future world where higher carbon dioxide concentrations will lead to ocean acidification (OA), but this may not be true for coccolithophores. In coccolithophores, calcification occurs in an intra-cellular vesicle, where the site of calcite precipitation is buffered from the external environment and is subject to a uniquely high degree of biological control. Culture manipulation experiments mimicking the effects of OA in the laboratory have yielded empirical evidence for phenotypic plasticity, competition and evolutionary adaptation in asexual populations. However, the extent to which these results are representative of natural populations, and of the response over timescales of greater than a few hundred generations, is unclear. Here we present a new sediment-based proxy for the PIC:POC (particulate inorganic to particulate organic carbon ratio) of coccolithophore biomass, equivalent to the fractional energy contribution to calcification, and a biologically meaningful measure of the organism’s tendency to calcify. Employing the geological record as a laboratory, we apply this proxy to sedimentary material from the south Pacific to investigate the integrated response of real ancient coccolithophore populations to environmental change over many thousands of years. We show that the phenotypic response is species-specific, is controlled by carbonate chemistry, and is of a greater magnitude than expected based on laboratory experiments. We suggest that the mechanism of phenotypic change is evolutionary adaptation, and driven by sex, is elusive to laboratory experiments. Our results provide a new perspective on phenotypic change in real populations over long timescales.
Coccolithophore assemblage distribution along a temperate to polar gradient in the Southern Ocean

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In recent years, several studies in different areas of the world oceans focused on the biogeography, ecology and fine-scale taxonomy of coccolithophores. Besides, coccolithophores are known to play an important role in the production of particulate inorganic carbon in the Southern Ocean within the so-called “great calcite belt”, a circum-polar region between 30°- 60° latitude South (Balch et al., 2011). The Southern Ocean is characterized by the eastward flow of the Antarctic Circumpolar Current (ACC), driven by the westerly winds which flow between 45-55°S (Orsi et al., 1995). Different fronts within the ACC are identified as bands of enhanced lateral property gradients in surface waters and by pronounced isopycnal tilt throughout the deep water column. These fronts, namely the Subantarctic Front (SAF) and the Polar Front (PF), carry out most of the transport of the ACC and are associated with strong surface currents. The ACC fronts separate water masses with similar physical characteristics: the Subantarctic Zone (SAZ) between the STF and the SAF, the Polar Frontal Zone (PFZ) between the SAF and the PF and the Antarctic Zone (AZ) south of the PF.

In the high-latitude Southern Ocean, Emiliania huxleyi is the dominant coccolithophore species, but different coccolithophore assemblages are found in different water masses, as already observed from different sectors of the Southern Ocean (Böckel and Bauman, 2008; Cubillos et al., 2007; Findlay and Giraud, 2000; Gravolosa et al., 2008; Hiramatsu and De Dekker, 1996; Mohan et al., 2008).

Besides, within E. huxleyi different morphotypes are recognised: A (Young and Westbroek, 1991), B/C (Young et al., 2003) and O (Hagino et al., 2005) and their distribution is also related to the position of the oceanographic fronts.

The main goals of this work are:
- to provide further data on coccolithophore diversity in the New Zealand sector of the SO;
- to describe the correlation between coccolithophore species distribution and the location of the main ACC fronts;
- to provide new data on the distribution and size of the different E. huxleyi morphotypes along the latitudinal transect.


Adaptation of coccolithophores to high pCO$_2$ in the Kiel Fjord (SW Baltic Sea)?

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The Kiel Fjord has been demonstrated to be a site of naturally elevated pCO$_2$ due to upwelling of CO$_2$ rich waters throughout large parts of the year (Thomsen et al. 2010). Coccolithophores are a common member of the autumn phytoplankton bloom in Kiel Bay (Meier et al., in press). During exceptional years coccolithophore cell numbers can reach bloom strength (>10$^6$ cells/l in September 2009). This bloom in the surface layer co-occurred with high pCO$_2$ and CaCO$_3$ undersaturation in bottom waters (~18 m water depth). We here present coccolithophore cell counts, morphometric analyses and environmental data over the years 2009-2013 in order to investigate whether an adaptation of coccolithophores to elevated pCO$_2$ is likely.


Coccolithophores growing conditions in the deep ecological niche of the South Pacific Gyre.

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The distribution of coccolithophores in the global ocean can be deduced from satellite imagery due to the high reflectance of coccoliths. This method can detect coccoliths in the upper few meters to few tens of meters of the water column, while no signal is received from deeper in the photic zone. There is growing field evidence, however, that the deeper part of the photic zone could harbor significant populations of coccolithophores. One such deep ecological niche occurs at the depth (150-200m) nutricline of the South Pacific Gyre that was investigated during the BIOSOPE cruise (2004). In situ chlorophyll a measurements indicate the presence of deep chlorophyll maximum at the nutricline, and coccolithophore cell counts show maximum cell abundance at the same depth. Conditions at this deep ecological niche include low irradiance (< 15 μmol.m$^{-2}$.s$^{-1}$), low nutrient concentrations (1 μmol.L$^{-1}$ for the nitrate and 0.2 μmol.L$^{-1}$ for the phosphate) and elevated pCO$_2$ (600 μatm). We observed that even at the lowest nitrate and phosphate concentrations attained in our experiments (1.57±0.44 μmol.L$^{-1}$ and 0.09±0.02 μmol.L$^{-1}$ respectively), the cells were still fit and did not suffer nutrient limitation. The same nutrient concentrations occur between 150m and 200m in the South Pacific Gyre, which corresponds to the depth of the deep ecological niche of coccolithophores. Low irradiance (30 μmol.m$^{-2}$.s$^{-1}$), instead, significantly reduced growth rates. These results suggest that coccolithophores are limited by light, rather than by nutrients, in this deep ecological niche. The lowest nutrient concentrations we observed in our experiment are comparable to those that result in nutrient limitation in other, published, experiments carried out with Emiliania huxleyi. We are designing additional experiments that will help us understand if the strain isolated from the BIOSOPE transect is adapted to growth in low nutrient conditions. Furthermore, our experiments will be relevant to coccolithophore growth in the future ocean that will likely be more acidic and nutrient-depleted than the modern ocean. Our preliminary experimental results, in fact, suggest reduced calcification rates in the deep ecological niche of the South Pacific Gyre.
Pelagic calcite production: cellular calcification, growth rates and ecophysiological factors

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While coccolithophores represent a small fraction of the organic biomass and primary production in marine ecosystems (<10%), coccolithophores have a key role in pelagic calcite production and export to the deep sea. Hence, coccolithophores play an important part in the oceans carbonate pump, which is estimated to export ~1.5 Gt of carbon to the deep-sea each year, in contrast to the 10 Gt of carbon per year that marine ecosystems export via the biological carbon pump. On a cellular scale, calcite is formed through the production of coccoliths, with the amount of calcification per cell determined by the number of coccoliths, their calcite content, and how fast the coccoliths are produced. Coccolith production is intrinsically linked to growth rates, while the number of coccoliths and their calcite content differ between species. At the community level, calcite production is a function of the amount of calcification per cell and the number of cells present, and hence pelagic calcite production is determined by the species composition of the community and the level of growth (and death) of the population – clearly the carbonate pump is a function of species-specific interactions of ecology and physiology.

In this talk I will present recent research into comparative levels of coccolith production in different coccolithophore communities, estimates of coccolithophore growth (and mortality) rates for natural populations, and attempts to elucidate the ecophysiological factors driving pelagic calcite production. This will look at scales from individual cells to diverse communities, from blooms to non-blooms and from the subtropics to the poles.

Have coccolithophore abundances increased in the North Atlantic over the last 50 years? Evidence from the Continuous Plankton Recorder

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Little is known about long-term variability of extant coccolithophores. We used data from the Continuous Plankton Recorder (CPR) sampling program - the largest ongoing plankton survey in the World- to produce the most detailed study on 45 years (1965-2010) of coccolithophore variability in the North Atlantic with respect to four climate indices, seven environmental parameters and five phytoplankton groups (diatoms, dinoflagellates, *Trichodesmium*, chlorophytes, silicoflagellates). Results show that coccolithophores are increasing in frequency and quantity regionally and basin-wise. Explanations for these trends are discussed combining statistical inference, physiological, remote sensing, and sedimentary evidence. A 3-10 fold increase in coccolithophores cannot be explained by simple changes in methodology, nutrient availability, climate modes, global warming or ocean acidification alone. More importantly, results also suggest that this trend might not be limited to the North Atlantic.
This study provides an analysis of the present-day coccolithophore (living) assemblages and recent (fossil) assemblages from Pacific sector of the Southern Ocean (SO) along a latitudinal transect. The southernmost station is located in the seasonal sea ice covered zone at ~68°S (Ross Sea) and the northernmost one in the New Zealand Margin at ~44°S. Plankton samples and surface sediment samples were collected during austral summer in the course of R/V Polarstern cruise ANT-XXVI/2 (Punta Arenas, Chile-Wellington, New Zealand; from 27th November 2009 to 27th January 2010).

For the study of living coccolithophores, 2-3 litre water column samples were collected using the membrane pump and CTD casts (4-6 samples from the upper 200 m) and were filtered through cellulose membranes, with 0.45 μm pore size on board R/V Polarstern. For the study of recent fossil coccolithophores, the uppermost undisturbed centimetre was sampled from surface sediment samples recovered with multicorer at the same locations as the CTD stations. Sediment samples were prepared using a combined technique of dilution and filtering. Coccolithophore assemblages were examined under Scanning Electron Microscope (SEM) in the University of Bremen (Germany).

The maximum abundances of cells per litre were reached close to the Subtropical Front and increases in the numbers of coccospheres and coccoliths were observed both at the Subantarctic Front and the Polar Front (PF). However, numbers decrease southward until almost a monospecific and sporadic record of E. huxleyi (types B/C and C) south of the PF. Different coccolithophore assemblages were established coincident with areas bounded by the major surface oceanographic fronts, i.e. the Polar Front Zone and for the Subantarctic Zone. The present-day coccolithophore numbers and assemblage distribution in relation to the surface frontal dynamics of the SO and its preservation in the recent sedimentary record provide relevant information for potential future palaeoceanographic reconstructions.

This work aims to provide new insights into the late Pleistocene interglacial Marine Isotope Stage 11 (MIS 11) in the Pacific sector of the Southern Ocean, where little information is available. MIS 11, between ca. 424 and 374 kyr, is a unique exceptionally long interglacial period often regarded as an analogue of what the Holocene would have been without any anthropogenic interference. Thick white layers with high carbonate content have been observed at high southern latitudes during this time interval.

We generated a multi-parameter record of coccolithophore data on MIS 11 sediments from core PS75/059-2. This core was retrieved west of the East Pacific Rise crest at 54°12.90’S and 125°25.53’W (3613 m water depth) during R/V Polarstern ANT XXVI/2 expedition in the polar South Pacific. In order to characterize the coccolithophore palaeoproductivity during MIS 11 two independent proxies were chosen: the Nannofossil Accumulation Rate (NAR) and the coccolith Sr/Ca ratio measured in the <20μm (coccolith) size fraction. Nannofossil assemblage counts under a scanning electron microscope indicated that in the fine coccolith fraction almost all the carbonate comes from Gephyrocapsa caribbeanica. Coccolith Sr/Ca results vary from 1.58 mmol/mol to 2.47 mmol/mol during the interval selected for this study, which extends from MIS 12 to the onset of MIS 10 (i.e. ~469.3 to ~364.7 kyr). NAR and Sr/Ca show a steep increase in productivity during MIS 11, with values always above 2.12 mmol/mol. This pattern remains the same after applying a correction for the temperature effect. All the information retrieved, together with the ongoing research, will allow us to evaluate if the coccolithophores modified the equilibrium of the inorganic carbon system during MIS 11 in the Pacific sector of the Southern Ocean.
Ancient coccolithophore cells: life in both greenhouse and icehouse worlds

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Cell size is a key trait of phytoplankton physiology, which is captured in the geometry (coccolith length, number of coccoliths per cell and coccosphere size) of individual coccolithophore coccospheres. We use the coccosphere geometry of modern coccolithophores as a ‘framework’ to interpret the physiology of exceptionally preserved fossil cells from the last 66 million years during an interval when climate shifted from the warm ‘greenhouse’ background state of the early Cenozoic to the ‘icehouse’ state of the last ~34 million years. Our fossil coccosphere data reveal cell size trends in the dominant taxa during the Paleogene, to the Eocene-Oligocene boundary. These cell size trends combine both variability within species populations and major patterns of species turnover, which is particularly characteristic of the dominant reticulofenestrids. We have a continuous record of cell size for Coccolithus pelagicus extending back to the late Paleocene, which demonstrates the variability in cellular geometry of this remarkable, long-lived taxon, a key component of both greenhouse and icehouse coccolithophore communities. With additional coccosphere geometry data from the subordinate taxa, we also reconstruct the relative cellular abundance of taxa in fossil communities based on the number of coccoliths per cell of each species. This allows us to explore shifts in mean community cell size through time and, uniquely, to reconstruct relative cellular calcite contributions. Cellular geometry is therefore a valuable archive of palaeobiological information that can be used to explore trends in community structure through time. We emphasize the crucial link between the physiology of individual cells and the population-wide success of different species during this long-term global trend towards cooler and more nutrient rich ‘icehouse’ oceans.

Living coccolithophores in the western equatorial Indian Ocean off Tanzania [POSTER]

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This study was conducted to provide information about the upper water column distribution of living coccolithophores in the western equatorial Indian Ocean off Tanzania. In total, 49 plankton samples, collected in February 2008 from 8 stations, were analysed. Since some of the analysed samples contained hardly any coccospheres, single coccoliths were also counted where present. Usually, the coccolithophore standing stock was below 10000 cells/ litre. Exceptions are the northern Pemba Channel, where cell concentrations reached nearly 23000 cells/ litre in the upper and intermediate water column, and one offshore station with a peak of 15000 cells/ litre at intermediate water depth. Lowest coccolithophore standing stocks with <500 cells/ litre were observed in the intermediate and lower photic zone of the most offshore open ocean stations and in the southern Pemba Channel stations. The distribution of the coccolithophore species is rather patchy. The coccolithophore assemblages comprised 37 different taxa of which Gephyrocapsa oceanica, Emiliania huxleyi, LPZ species (F. profunda, G. flabellatus, A. robusta), taxa of the genus Syracosphaera, and U. irregularis were the dominating species. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found. At most profiles a vertical succession of species was found.
Dominance of holococcolithophores in an estuarine winter coccolithophore community

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The coccolithophore life cycle commonly involves the alternation between holococcolith (haploid) and heterococcolith (diploid) phase (Young et al., 2005). It is thought that coccolithophore life phases represent an adaptation to environmental forcing, notably nutrient availability and UV irradiance (Houdan et al., 2006; Quintero-Torres et al., 2006; Cros and Estrada, 2013). In the Mediterranean Sea, the holococcolith phase prefers shallow oligotrophic environments, while the heterococcolith phase dominates in deeper and nutrient enriched waters (Dimiza et al., 2008; Cros and Estrada, 2013). However, the adaptational benefits and ecological preferences of the two life phases are still unclear, and more observations are needed.

We investigated the distribution of coccolithophores along the oligotrophic Krka River estuary (Eastern Adriatic Sea). The sampling was conducted on 25-26 February 2013, at six stations, following a deep-to-shallow water transect, from the coastal area to the lower reach of the estuary. Up to six depths were sampled at each station and subsamples were collected for biological and chemical analysis. Qualitative SEM analysis of the coccolithophore community was conducted following the protocol of Bollmann et al. (2002). Distribution of the haploid holococcolith phase was described using the holococcolithophore prevalence index (HOLP), introduced by Cros and Estrada (2013). The index expresses the contribution of the holococcolith phase to the total abundance of species with a heterococcolith-holococcolith life cycle.

The analysis of temperature, salinity, chlorophyll a fluorescence and nutrient levels indicated that the investigated area was divided in two distinct systems. Coastal stations were oligotrophic and phosphorus limited, with uniform vertical profiles of temperature and salinity. On the other hand, estuarine stations were characterized by higher nutrient availability and the presence of a sharp halocline. Coccolithophores were present throughout the investigated area, dominating the phytoplankton community along with diatoms and cryptophytes. A total of 56 coccolithophore taxa was detected, 16 of which (29%) were holococcolithophores and 38 heterococcolithophores (68%). The highest coccolithophore cell counts were detected in the estuary, below the halocline (up to 3.4 x 105 cells/l). At the coastal stations, maximum values of up to 4.8 x 104 cells/l were found in a deeper layer (20-40m). The distribution of the HOLP index showed high contribution of holococcolithophores at the halocline of the estuarine stations, whereas the coastal stations were dominated by heterococcolith phase. We argue that the holococcolith phase is tolerant to low salinity, and is capable of exploiting high bacterial abundance and high concentrations of organic matter found at the halocline by mixotrophic nutrition. Finally, environmental drivers other than nutrient availability and irradiance, such as salinity, are proved to be of great importance for shaping coccolithophore community.


The genus *Papposphaera* comprises at present 7 more or less well defined taxa. Four of these are from the polar regions (*P. sagittifera*, *P. sarion*, *P. obpyramidalis* and *P. simplicissima*) while three species have non-polar type localities, i.e. the generic type species *P. lepida*, *P. thomsenii* and *P. bourrellii*. Additional undescribed forms have been reported from the Indian Ocean (3) by Østergaard (2001) and from the Mediterranean (6) by Cros and Fortuno (2002). A recent re-examination of material from Arctic sampling sites has unveiled the existence of at least three additional polar species. While dealing with species diversity within *Papposphaera* it is also critical to examine in particular the exact circumscription of the much related genus *Pappomonas* (type species: *P. flabellifera*). The two genera remain fairly easy to distinguish when comparing only features of the generic type species. However, when taking into account the entire range of *Papposphaera/Pappomonas* diversity known to us, the picture becomes much more blurred with respect to referring a specific form to one or the other genus. Based exclusively on morphological evidence it appears that in particular the genus *Papposphaera* is currently encompassing a range of forms that can most likely not in the future be retained within the genus. It similarly applies to a group of undescribed forms of *Pappomonas* that their generic affiliation must be critically re-evaluated. A possible taxonomic framework for managing the morphological diversity encountered will be presented for discussion. Irrespective of efforts made here to handle species diversity based on morphological features and scattered life history facts, molecular evidence will be needed in order to establish a more robust future taxonomic framework for these forms.


Coccolithophore evidence for the direct influence of Black Sea waters inflow into the NE Aegean Sea [POSTER]

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A study on living coccolithophores from the euphotic zone is conducted off Limnos Island in the NE Aegean Sea, an area under the direct influence of the Black Sea waters inflowing into the Aegean through the Dardanelles Straits, during January 2011, May 2011, October 2013 and March 2014. The north Aegean basin can be described as a continental margin ecosystem, characterized by a generally cyclonic circulation (Lykousis et al., 2002) and the dual flow circulation between the NE Mediterranean and Black Seas through the Dardanelles and the Bosporus Straits. The low saline and cooler surface (0-40 m) Black Sea Water (BSW) is characterized by coccolithophore assemblages entirely dominated by Emiliania huxleyi; max. fluxes reach 3.2 x10^6 coccospheres m^-2 day^-1 during May, June and September (Triantaphyllou et al., 2013). BSW flows along the eastern coast of Greece on a generally cyclonic motion until it reaches the south western Aegean, and enhances the productivity in the north eastern Aegean Sea. During winter, BSW tends to flow northwest of Limnos Island filling the northernmost part of the Aegean before moving westwards. During summer, the strong northerly winds (Etesians) blowing over the Aegean Sea, deflect some BSW south of Limnos, which then are directed to the southwest. In addition, these winds trigger the upwelling of colder, nutrient-rich masses from deeper layers, along the eastern Aegean margin as evidenced by a low SST signal. BSW inflow rates show strong seasonal and interannual variability, reaching its maximum during mid to late summer and its minimum during winter (Zervakis et al., 2000). BSW spreading during winter may affect the stratification of the water column thus influencing dense water formation activity; the existence of the low density BSW surface layer acts as an insulating lid that impedes air–sea interactions thus hindering dense water formation over the area it covers (Zervakis et al., 2000; Velaoras et al., 2013).

The NE Aegean Sea represents a mesotrophic region, with annual mean chlorophyll a concentrations exceeding (Ignatiades et al., 2002; Zervoudaki et al., 2011) to > 1 μg l^-1 (Psarra, unpubl.), while remotely sensed surface chlorophyll a values largely exceed 1 μg l^-1, for the same period. On the other hand, during fall, values are lower, approximately 0.2 μg l^-1, characteristic of oligotrophic conditions, despite the presence of the surface BSW layer (Ignatiades et al., 2002; Lagaria et al., 2013).

The coccolithophore distribution was quantitatively documented through Scanning Electron Microscopy and a total of approx. 30 coccolithophore species were identified. E. huxleyi is the most abundant species, with late spring concentrations more than 4 x10^3 cells l^-1 in the surface waters (0-10 m), coming from the northern branch of BSW; in contrast to typical spring Aegean E. huxleyi values that normally range up to 30 x10^3 cells l^-1. Other characteristic species like Syracosphaera protrudens and S. molischii are present with up to 2 x10^3 cells l^-1. A second peak is observed deeper in the water column (up to 60 m), where E. huxleyi does not exceed 5 x10^4 cells l^-1. The southern branch of BSW, south of Limnos Island, presents much lower E. huxleyi values (approx. 20-35 x10^3 cells l^-1) during late spring. During the warm late summer-autumn period, E. huxleyi is generally presented with very low cell densities in the surface layer (up to 3.5 x10^3 cells l^-1), peaking at 50 m depth up to 7.5 x10^3 cells l^-1. However, concentrations of 12 x10^3 cells l^-1 restricted only at the surface waters south of Limnos Island, are indicative of a light inflow of the southern BSW branch. Impressively, E. huxleyi is dramatically reduced towards the mid photic zone (values < 10^3 cells l^-1), marking the presence of totally different water mass; the Levantine Intermediate Water (LIW) masses that flow northward along the eastern Aegean Sea (e.g., Zervakis et al., 2004).

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Coccolithophore biogeographic trends and export production in the Eastern Mediterranean and Black Seas

[POSTER]

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The export production of coccolithophores has been measured from Black Sea, North Aegean Sea, Cretan Sea, South Cretan margin and Ionian Sea, and compared in order to define the spatial and seasonal variability in their assemblage composition.

A sediment trap mooring has been deployed for one year (10/2007- 9/2008) at 1000 m water depth, in western Black Sea. The maximum coccosphere fluxes, with almost monospecific assemblage of Emiliania huxleyi, have been recorded during May, June and September (max. 3.2 x 10^8 coccospheres m^2 day^-1). The seasonally controlled coccolithophore patterns are strongly related to those of sea surface temperature and accumulated rainfall in the area, triggering riverine nutrient input.

Coccosphere fluxes in North Aegean Sea have been calculated from a sediment trap deployment at 500 m (1/2011-12/2011). E. huxleyi is the dominant species, followed by Rhabdosphaera spp., Syracosphaera spp. and Florisphaera profunda as minor assemblage components. Maximum fluxes have been observed in February and June (max. summer 2.9 x 10^6 coccospheres m^2 day^-1).

A single mooring with two sediment traps (500 and 1700 m) was deployed at the southern margin of the Cretan Sea (Triantaphyllou et al., 2004). The results obtained from 500 m depth show that the highest flux values were observed between late March to late June (max. 9.4 x 10^5 coccospheres m^2 day^-1). The pattern was characterized by three main phases that correlate well with the gradual increase in SST from January till September. Coccosphere sinking assemblages were characterized by high abundances of E. huxleyi, followed by F. profunda, Rhabdosphaera spp. and Syracosphaera spp.

Six moorings have been deployed at different sites along the south–west margin of Crete, providing a total of eight sediment-trap time series (6/2005-5/2006), (Malinverno et al., 2009). Maximum coccosphere fluxes were recorded in between March to June (4.3 x 10^5–3.4 x10^6 coccospheres m^2 day^-1), featured by dominance of E. huxleyi and subordinate Helicosphaera carteri, Umbilicosphaera spp. and Syracosphaera pulchra; intermediate fluxes from June to November, with high abundance of the deep photic zone species Algirosphaera robusta, F. profunda, Gladiolithus flavellatus; low fluxes from November to February, with high flux of A. robusta, S. pulchra and Syracosphaera spp. These three periods correspond to the seasonal changes in sea surface temperature and surface mixed layer depth.

Coccolithophore fluxes from the central part of the Ionian Sea have been studied from a sediment trap mooring (9/1999-6/2001) at 500 m water depth (Malin-
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Peak coccolithophore export production is observed in May (3.5 x 10^5 coccospheres m^-2 day^-1), a secondary peak is observed in September-October. The assemblage is dominated year-round by the cosmopolitan species *E. huxleyi*, followed by the deep-dwelling *F. profunda* and by several minor species (*Syracosphaera* spp., *Rhabdosphaera* spp., *A. robusta*, *G. flabellatus*) which are most abundant during the summer period of upper water column stratification.

NESTOR mooring line (4500m depth) was deployed at the deepest basin of the SE Ionian Sea (36° 2.96 N, 21° 28.93 E). The mooring line was instrumented with five pairs of sediment traps, set at 700, 1200, 2000, 3200, and 4300m depth. The Ionian Sea displays high seasonal variability with maximum productivity rates observed during the late winter/spring convective mixing period (Stavrakakis *et al.*, 2013). Our coccolithophore flux study from the shallower trap (700 m) for an overall interval between 6/2010 and 8/2012, reveals a peak during late spring- early summer (max. May 2012; 1.43 x 10^6 coccospheres m^-2 day^-1) that is in accordance with the peak of total mass flux. The assemblage is dominated by *E. huxleyi*, followed by *A. robusta*, *Syracosphaera* spp., *H. carteri*, *Umbilicosphaera sibogae*.

A high seasonal pattern characterizes the assemblages; the export production and fluxes are strongly dependent on the nutrient influx, the vertical mixing/ and or intermediate waters upwelling, SST of the water column and the influence of episodic dust input events leading to enhanced fluxes of lithogenic matter, in a north - south and east - west transient.


The Nannotax website was initially primarily a site for documenting calcareous nannofossils but in its current incarnation - Nannotax3 (http://ina.tmsoc.org/Nanotax3) it also has rather comprehensive coverage of extant nannoplankton. Coverage of these is primarily based on the Young et al. (2003) guide to extant coccolithophore taxonomy and includes all the images from the guide and the taxon descriptions. Most taxa described since then have also been included and many additional images. There are now about 1600 images of extant coccolithophores in the system (vs. 700 in the guide) and 523 extant taxa (including genera and higher taxa). Complementing this content the Farinacci catalog pages provide the original descriptions of most taxa and these are now linked to and from the main taxon pages.

There is also now skeletal coverage of some of the other microplankton groups of obvious interest to coccolithophore specialists, including calcareous dinoflagellates (Thoracosphaeraceae), Parmales, and non-calcifying haptophytes (Pavlovales, Phaeocystales and Prymnesiales). These are covered in a separate ‘non-coccolithophores’ module currently with outline taxonomy of about 500, mostly extant, taxa. Data here is basic nomenclature derived from standard compilations (Jordan et al. 2004, Konno et al. 2007, Edvardsen et al. 2011, Streng et al. 2004) with a scattering of images (ca 250 so far), but no descriptions or diagnoses.

There are several ways in which the site could be developed, including: (1) Linkages to external data sources for DNA sequences, cultures, etc; (2) Improvement of description and illustration of coccolithophores; (3) Inclusion of occurrence data for coccolithophores; (4) Broadening of scope, bringing the non-coccolithophore component up to similar level to the coccolithophores in terms of illustrations and descriptive content, possibly with the aim to allow identification of any nannoplankton <20µm? This talk will review such possibilities with the aim to stimulate discussion on priorities and possibilities, including ways of involving a broader community of contributors.


In their seminal review of coccolithophore biogeography Winter et al. (1994) argued that in tropical and subtropical water three depth zones of coccolithophores could be recognised - Upper Photic, Middle Photic and Lower Photic. Of these the upper and lower photic are well established in terms of both typical composition and basic ecology. The upper photic zone is characterised by taxa such as Umbellosphaera and Discosphaera and is the surface mixed layer assemblage, inhabiting an environment of high light but low nutrients. Similarly the deep photic zone is characterised by taxa such as Florisphaera and Gladiolithus and is a genuine shade flora occurring at light levels <1% of surface in the lower part of the thermocline and below where nutrient levels are consistently high. The mid-photic zone assemblage by contrast is less well established and more variable. I will argue that it typically corresponds to the deep chlorophyll maximum which is also the upper part of thermocline and nutricline. This is not usually a zone in which coccolithophores are especially abundant, they appear to be outcompeted by other phytoplankton. Nonetheless many coccolithophore species seem to occur characteristically in this zone including Oolithotus, Calciopappus, Michaelsarsia, Algirosphaera, Papposphaera many Syracosphaera species, Emiliania huxleyi type C and Gephyrocapsa oligotrophic (sensu Bollmann 1997). Many of these taxa also occur at the surface in Arctic waters suggesting a rather intriguing ecology. Arguably better characterisation of this mid photic assemblage and clearer separation of it from the deep photic assemblage should be a priority for understanding coccolithophore biogeography and interpreting assemblage data from sediment traps and ultimately the fossil record.