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Global marine plankton functional type biomass distributions: coccolithophores

C. J. O'Brien[1], J. A. Peloquin[1], M. Vogt[1], M. Heinle[2], N. Gruber[1], P. Ajani[3], H. Andruleit[4], J. Arístegui[5], L. Beaufort[6], M. Estrada[7], D. Karentz[8], E. Kopczyńska[9], R. Lee[10], A. J. Poulton[11], T. Pritchard[12], and C. Widdicombe[13]

[1]Environmental Physics Group, Institute for Biogeochemistry and Pollutant Dynamics, ETH Zürich, Universitätsstrasse 16, 8092 Zurich, Switzerland
[2]Laboratory for Global Marine and Atmospheric Chemistry, School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK
[3]Department of Biological Sciences, Macquarie University, North Ryde, NSW, 2109, Australia
[4]Bundesanstalt für Geowissenschaften und Rohstoffe (BGR), Geozentrum Hannover, Stilleweg 2, 30655 Hannover, Germany
[5]Instituto de Oceanografía y Cambio Global (IOCAG), Universidad de Las Palmas de Gran Canaria, 35017, Las Palmas de Gran Canaria, Spain
[6]Centre Européen de Recherche et d'Enseignement des Géosciences de l'Environnement (CEREGE), CNRS/Aix-Marseille Univ., Ave. Louis Philibert, 13545 Aix en Provence, France
[7]Institut de Ciencies del MAR (CSIC), Passeig Maritim de la Barceloneta, 3749, 08003 Barcelona, Catalunya, Spain
[8]University of San Francisco, College of Arts and Sciences, 2130 Fulton Street, San Francisco, CA 94117, USA
[9]Institute of Biochemistry and Biophysics, Department of Antarctic Biology, Polish Academy of Sciences, Ustrzycka 10/12, 02-141 Warsaw, Poland
[10]Centre for Environmental Science, EPA Victoria, Ernest Jones Drive, Macleod VIC 3085, Australia
[11]National Oceanography Centre Southampton, University of Southampton, UK
[12]Waters and Coastal Science Section, Office of Environment and Heritage, P.O. Box A290, Sydney South NSW 1232, Australia
[13]Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, UK

Correspondence to: C. J. O'Brien (colleen.obrien@env.ethz.ch)

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Abstract. Coccolithophores are calcifying marine phytoplankton of the class Prymnesiophyceae. They are considered to play an import role in the global carbon cycle through the production and export of organic carbon and calcite. We have compiled observations of global coccolithophore abundance from several existing databases as well as individual contributions of published and unpublished datasets. We make conservative estimates of carbon biomass using standardised conversion methods and provide estimates of uncertainty associated with these values. The quality-controlled database contains 57 321 individual observations at various taxonomic levels. This corresponds to 11 503 observations of total coccolithophore abundance and biomass. The data span a time period of 1929–2008, with observations from all ocean basins and all seasons, and at depths ranging from the surface to 500 m. Highest biomass values are reported in the North Atlantic, with a maximum of 127.2 $\mu g C L^{-1}$. Lower values are reported for the Pacific (maximum of 20.0 $\mu g C L^{-1}$) and Indian Ocean (up to 45.2 $\mu g C L^{-1}$). Maximum biomass values show peaks around 60° N and between 40 and 20° S, with declines towards both the equator and the poles. Biomass estimates between the equator and 40° N are below 5 $\mu g C L^{-1}$. Biomass values show a clear seasonal cycle in the Northern Hemisphere, reaching a maximum in the summer months (June–July). In the Southern Hemisphere the seasonal cycle is less evident, possibly due to a greater proportion of low-latitude data. The original and gridded datasets can be downloaded from Pangaea (doi:10.1594/PANGAEA.785092).

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1 Introduction

Marine plankton are the main driver for the global marine cycling of elements such as carbon, nitrogen and phosphorus, primarily through the process of carbon fixation and nutrient uptake during primary production and subsequent export of organic matter to the deep ocean. Modern marine ecosystem models seek to represent the functional diversity of marine plankton using the concept of plankton functional types (PFTs; Iglesias-Rodríguez, 2002; Le Quéré et al., 2005). PFTs are groups of plankton with defined biogeochemical functions, for example calcification, DMS-production or nitrogen fixation. The inclusion of these groups in marine ecosystem models provides great potential for improving our understanding of marine processes (see for example Dutkiewicz et al., 2012; Marinov et al., 2010; Vogt et al., 2010; Manizza et al., 2010), but has also highlighted a need for extensive observational datasets for model parameterisation and validation (Hood et al., 2006; Le Quéré et al., 2005; Anderson, 2005).

The MARine Ecosystem DATa (MAREDAT) project (as part of the MARine Ecosystem Model Intercomparison Project – MAREMIP) seeks to compile global biomass data for PFTs commonly represented in marine ecosystem models: silicifiers, calcifiers (including coccolithophores, pteropods and foraminifera), DMS-producers, pico-phytoplankton, diazotrophs, bacteria, and three zooplankton sizeclasses (micro-, meso- and macrozooplankton). A summary of the findings for all groups is presented in Buitenhuis et al. (2013).

This paper presents a database of global coccolithophore biomass distributions compiled as part of the MAREDAT effort. The coccolithophores are a globally occurring group of calcifying phytoplankton of the class Prymnesiophyceae (Jordan et al., 2004; Winter and Siesser, 1994; Thierstein and Young, 2004). They are thought to play an important role in the global carbon cycle due to their contribution to primary production and export as well as through calcite production (Iglesias-Rodríguez, 2002; Hay, 2004; Jin et al., 2006), with blooms of over 100 000 km^2 observed in some ocean regions (Brown and Yoder, 1994; Holligan et al., 1993). The coccolithophores have received considerable attention in recent years due to their potential sensitivity to climate change and particularly ocean acidification (Doney et al., 2009). The decrease in carbonate saturation state in the oceans caused by rising atmospheric CO_2 is generally expected to have negative effects on calcifying marine organisms due to the increasing energetic cost of calcification (Hofmann et al., 2010). There have, however, been mixed results from experimental and field studies of coccolithophores, with some showing a negative effect of ocean acidification (e.g. Beaufort et al., 2011; Riebesell and Zondervan, 2000) whereas others show no change or even increased calcification and production (Langer et al., 2006; Iglesias-Rodríguez et al., 2008). Changes in ocean temperature, stratification and nutrient supply are also expected to affect coccolithophore distributions, although again the direction of this change is unclear (Hood et al., 2006; Iglesias-Rodríguez, 2002). Given these uncertainties, it is more important than ever to understand the current distribution of coccolithophores in the global oceans.

Remote sensing approaches are frequently used to study the distribution of coccolithophore blooms (e.g. Smyth, 2004; Brown and Yoder, 1994; Iglesias-Rodríguez, 2002; Hirata et al., 2011). The reflective properties of the calcite-based coccoliths allow blooms to be observed in satellite images (Holligan et al., 1983), providing great potential for improving our understanding of coccolithophore distributions on a global scale. There are, however, several limitations to this approach. Firstly, satellite images pick up the optical properties of the calcite-based coccoliths themselves and do not distinguish between living cells and detached coccoliths (Tyrell and Merico, 2004). Secondly, satellite data are limited to waters within the optical depth of the satellite and provide no information as to the vertical structure of cells within the water column or cells occurring below this depth. Finally, more detailed taxonomic information cannot yet be obtained from satellite images. There is, therefore, a continuing need for in situ observations of coccolithophores in order to better understand their distribution, ecology and contribution to global plankton biomass.

This database compiles existing published and unpublished coccolithophore abundance data and provides standardised biomass estimates using species-specific conversion factors. We also provide a detailed discussion of our conversion methods and quality control procedures and discuss the uncertainties associated with the biomass values. Although this dataset was born from the needs of the modelling community, we anticipate that it will be of use to scientists from a range of fields including biological oceanography, marine ecology, biogeochemistry and remote sensing.

2 Data

2.1 Origin of data

Our data consists of abundance measurements obtained from several existing databases (NMFS-COPEPOD, BODC, OBIS, OCB DMO, Pangaea, WOD09, OOV)[1], as well as published and unpublished data from a number of contributing authors (P. Ajani, H. Andruleit, J. Arístegui, L. Beaufort, M. Estrada, D. Karentz, E. Kopczyńska, R. Lee, T. Pritchard and C. Widdicombe). Table 1 summarises the origin of all

[1]NMFS-COPEPOD: National Marine and Fisheries Service – The Coastal & Oceanic Plankton Ecology, Production, & Observation Database; BODC: British Oceanographic Data Centre; OBIS: the Ocean Biogeographic Information System; OCB DMO: Ocean Carbon and Biogeochemistry Coordination and Data Management Office; Pangaea: Data Publisher for Earth and Environmental Science; WOD09: World Ocean Database 2009; OOV: Observatoire Océanologique de Villefrance-sur-Mer.

Table 1. List of data contributions, sorted in temporal order.

Investigator/Institute	Year(s)	Region	Data points	Flagged	Reference
Meteor	1929–1930	N Atlantic	66	–	NMFS-COPEPOD
Murmansk Marine Biological Institute, Russia	1954–1973	Barents Sea	267	–	WOD09
H. Marshall	1965	NW Sargasso Sea	32	32	Marshall (1969)
ORSTOM	1965	Tropical Pacific	161	–	WOD09
Instituto del Mar del Peru	1966–2005	Peruvian coastal zone	2668	92	WOD09
NOAA/University of Alaska (OCSEAP)	1969–1978	Gulf of Alaska	293	265	WOD09
J. Throndsen	1970	Tropical Pacific/Caribbean	105	–	NMFS-COPEPOD
SAHFOS	1970–1999	N Atlantic	391	–	WOD09
Institute of Biology of the Southern Seas, Ukraine	1972–1990	Indian Ocean	558	–	NMFS-COPEPOD
Tokyo University Ocean Research Institute, Japan	1975	W Pacific	68	–	WOD09
National Institute for Environmental Studies, Japan	1976–1985	W Pacific	120	44	WOD09
NOAA	1976–1977	Puget Sound, WA, US	18	–	WOD09
Japan Meteorological Agency	1977–1986	W Pacific	1963	29	WOD09
Institute of Ocean Sciences, Sidney, Canada	1979	US Coast (Oregon)	29	–	WOD09
E. Baldina et al.	1979–1986	Tropical Atlantic	941	–	NMFS-COPEPOD
Aomori Prefectural Fisheries Experimental Station, Japan	1980	West Pacific	2	–	WOD09
TPFS	1983	West Pacific	1	–	WOD09
AtlantNIRO	1984–1991	Atlantic	365	–	NMFS-COPEPOD
M. Estrada	1985	Mediterranean Sea	260	–	Estrada (1991), Estrada (unpublished data)
M. Estrada	1985	Weddell Sea	126	–	Estrada and Delgado (1990), Estrada (unpublished data)
Osaka Prefectural Fisheries Experimental Station, Japan	1985	W Pacific	8	8	WOD09
P. Tett	1988–1989	North Sea	50	–	BODC
D. Harbour	1989	North Atlantic	33	–	BODC
B. Zeitzschel	1989	North Atlantic	205	205	Zeitzschel et al. (2002)
D. Harbour	1990	North Atlantic	68	–	BODC
D. Harbour	1991	North Atlantic	78	–	BODC
AESOPS	1992	Southern Ocean	31	–	WOD09
G. Fryxell	1992	Equatorial Pacific	186	–	Fryxell (2003)
K. Takahashi and H. Okada	1992	SE Indian Ocean	114	–	Takahashi and Okada (2000)
M. Fiala	1992–1995	Southern Ocean	73	–	OOV
E. Ramos	1992–2005	Peruvian Coastal Zone	229	–	Ramos (2006)
C. Widdicombe	1992–2008	English Channel	625	–	Widdicombe et al. (2010)
H. Andruleit	1993	Arabian Sea	71	–	Andruleit (2003)
R. Uncles	1993–1995	North Sea	20	–	BODC
P. Wassmann and T. Ratkova	1993–2003	Arctic/Sub-Arctic	108	–	Ratkova (2012)
D. Harbour	1994	Arabian Sea	65	–	BODC
OMEX I project members; P. Wassmann	1994	NE Atlantic	186	–	Omex I project members and Wassmann (2004)
C. Grados	1995	Peruvian Coastal Zone	12	–	Grados et al. (2007)
R. Schiebel	1995–1997	Arabian Sea	49	–	Schiebel (2004a,b)
J. Aiken, T. Bale, P. Holligan, A. Poulton and D. Robins	1995–2000	Atlantic	408	–	BODC
G. Tarran	1996	North Atlantic	199	–	BODC
P. Ajani, R. Lee and T. Pritchard	1997–1998	SE Australia	45	45	Ajani et al. (2001)
H. Andruleit	1999	E Indian Ocean	45	–	Andruleit (2007)
K. Pagou and G. Assimakopoulou	1999–2000	Aegean Sea	52	–	Pagou and Assimakopoulou (2008)
H. Andruleit	2000	Arabian Sea	22	–	Andruleit (2005)
D. Karentz	2000	E Pacific	7	–	Karentz (unpublished data)
E. Kopczyńska	2001	Southern Ocean	13	–	Kopczyńska et al. (2007)
H. Andruleit	2001–2002	E Pacific	49	–	Andruleit (unpublished data)
J. Arístegui	2003–2004	N Atlantic	152	–	Arístegui (unpublished data)
P. Assmy	2004	Southern Ocean	28	–	Assmy (2007)
L. Beaufort	2004	Pacific	99	–	Beaufort (unpublished data)
R. Mohan	2004	Southern Ocean	131	–	Mohan et al. (2008)
M. Silver	2004	Hawaii	13	–	Silver (2009)

datasets, sorted in temporal order. The database contains 58 384 data points when all counts of individual taxa are considered separately, which equates to 11 503 samples of total coccolithophore abundance collected from 6741 depth-resolved stations. Abundance data were standardised to units of cells per litre, and ancillary data such as temperature, salinity, chlorophyll and nutrients were retained where available.

2.2 Biomass conversion

To convert the abundance data (cell counts per unit volume) to biomass estimates (expressed as the concentration of organic carbon per unit water volume), we first needed to multiply the abundance data by the average biovolume for each species, and then multiplied the resulting biovolume concentration with the average organic carbon content per biovolume.

We determined cell biovolumes for each of the taxonomic groups reported in the database based on an extensive literature survey. Coccolithophore taxonomy has been subject to numerous revisions over the time span of the dataset, making it challenging to match historical data to current species names and descriptions. For consistency, data entries were matched to currently accepted species names following the taxonomic scheme of Jordan et al. (2004) wherever possible. Where full taxonomic information was not provided, data were matched to the lowest taxonomic group possible. Data that could not be assigned to a particular taxonomic group were categorised as unidentified coccolithophores. We identified a total of 195 taxonomic groups for this dataset (Table A3), ranging from identifications at the sub-species to the family level. Morphotype information is reported for *Emiliania huxleyi* in only one dataset, and we have therefore chosen to use a single biomass conversion factor for all occurrences of this species. Additionally, 2258 samples consisted of combined counts of coccolithophores without further size or taxonomic information, and 1988 samples contained at least some counts of unidentified or partially identified coccolithophores. For our biomass conversions, we began by converting only cell counts for which full species or sub-species identifications were provided. Each species/sub-species was assigned an idealised shape (e.g. sphere, prolate sphere, cone) based on the work of Hillebrand et al. (1999) and Sun (2003) as well as species descriptions in the literature. We then estimated cell dimensions (e.g. diameter, length, width) for each taxonomic group in order to calculate cell biovolumes (units: μm^3).

Cytoplasm dimensions have been published for very few coccolithophore species, with species descriptions usually providing the more easily observed coccosphere dimensions only. Observations of 16 species of coccolithophore from laboratory and field studies show cytoplasm diameter varying from 30 to 90 % of the total coccosphere diameter, depending on the species and level of calcification (Table 2); naked coccolithophores have also been observed for some species, although they are relatively rare in field samples (Frada et al., 2012). While these 16 species represent only a small fraction (10 %) of the species represented in the database, they include some of the more dominant coccolithophores in terms of both abundance and frequency of observation: these 16 species together account for an average of 75 ± 32 % of coccolithophore abundance per sample (median = 92 %), and we therefore consider them to be reasonably representative for the purposes of estimating coccolithophore biomass.

Given the lack of data and the lack of consistency among the few available cytoplasm measurements, we chose to estimate coccolithophore biovolumes by assuming cytoplasm dimensions to be 60 % of the mean coccosphere dimensions for all species – this value represents the midpoint of observed ratios of cytoplasm to total coccosphere diameter. These calculations can be expected to overestimate organic biomass for species with a higher ratio of coccosphere to cytoplasm volume, and underestimate biomass for species with a lower ratio. Biovolumes are calculated based on the mid-point of coccosphere dimensions. Uncertainty ranges are provided using biovolumes and biomasses calculated from $0.6 \times$ minimum coccosphere dimensions and $0.6 \times$ maximum coccosphere dimensions.

The range of coccosphere dimensions (e.g. diameter, length, width) for each species or sub-species in the database was determined based on a literature survey (Table A3). For some datapoints, coccosphere dimensions were provided alongside abundance data. In these cases the provided measurements were used in preference to our literature-based values. Biovolume estimates were then further converted to carbon biomass (units: $\mu g C L^{-1}$) using the prymnesiophyte-specific conversion factor developed by Menden-Deuer and Lessard (2000). Biovolume and biomass values based on the mid-point are hereafter referred to as "mean" biovolume and biomass. We assess the likely over- or under-estimation of our mean biomass estimates for different species of coccolithophore through a comparison with direct biomass measurements as well as biomass values calculated from measured cytoplasm dimensions for 16 species (Table 2).

For 23 species only a single set of dimensions or a single biovolume value was reported in the literature. In these cases, we have assumed the reported values to be the mean estimates. Minimum and maximum biovolume values were estimated for these species based on the ratios of minimum and maximum biovolume to mean biovolume observed for all other species in the database. These ratios were found to be 0.5 ($\pm$ standard deviation of 0.2) for minimum biovolume/mean biovolume, and 2.1 ($\pm$0.8) for maximum biovolume/mean biovolume. For cell counts with identifications only to the level of genus or family, or for combined counts of multiple species, we calculate minimum and maximum biomass values per cell based on the absolute minimum and maximum of all species reported for that taxonomic group. Mean biomass values per cell were calculated by taking the

Table 2. Comparison of coccolithophore biomass estimates from coccosphere dimensions (assuming cytoplasm diameter = 0.6 × coccosphere diameter) with biomass estimates from observed cytoplasm diameters for 16 species. Cytoplasm dimensions are from Stoll et al. (2002) as well as previously unpublished measurements from the datasets presented in Franklin et al. (2009) and Poulton et al. (2010).

Species	Coccosphere			Cytoplasm	
	Diameter (μm)	Estimated cell diameter (μm)	Biomass estimate (pg C cell^{-1})	Diameter (corresponding coccosphere) (μm)	Biomass estimate (pg C cell^{-1})
Algirosphaera robusta	6.5–16	6.75	22	5.29 (16.9)	11.4
Calcidiscus leptoporus	5–28	9.9	61.8	9.6–11.3 (16.25–30.75)	57.2–89.1
Calcidiscus quadriperforatus	10–15	7.5	29.2	10.2 (32.5)	66.4
Coccolithus pelagicus	8–22	9.0	47.8	14.1 (16.3)	160.6
Discosphaera tubifera	4.5–14	6.0	16.0	4.7 (15.0)	8.3
Emiliania huxleyi	3.5–15	5.6	13.0	3.4–3.5 (5.4–11.0)	3.5–3.7
Florisphaera profunda	4–12	4.8	8.8	3.9 (12.4)	4.9
Gephyrocapsa oceanica	5–15	6.0	16.0	5.0 (16.1)	9.9
Oolithotus antillarum	10–13	6.9	23.3	4.7 (15.1)	8.3
Oolithotus fragilis	4–30	10.2	66.9	13.8 (27.5)	149.8
Rhabdosphaera clavigera	7.9–12	6.0	15.8	6.3 (20.0)	18.2
Syracosphaera tumularis	10–20	9.0	47.8	15.7 (50.3)	215.2
Umbellosphaera irregularis	10–15	7.5	29.2	6.3 (20.0)	17.9
Umbellosphaera tenuis	9.2–16	7.6	29.8	5.7 (18.3)	14.1
Umbilicosphaera sibogae	8.5–43	15.5	205.1	7.1–30 (25–60)	25.3–1227.9
Umbilicosphaera foliosa	10–18	8.4	39.6	8.8–9.4 (12.6–30)	44.3–53.5

mean of all reported biomass values for species within the taxonomic group. Taking the mean of the biomass values avoided weighting mean biomass values towards a single large species. For some genera, however, insufficient species-level data were available to calculate biomass using this approach. In these cases we were able to obtain a range of coccosphere dimensions from the literature, and calculated biovolumes and biomasses based on the mid-point of these values as detailed above for the species-specific cell counts.

For cell counts of unidentified coccolithophores, we have chosen to use a spherical coccosphere with diameter of 10 μm (cell diameter of 6 μm) to calculate our mean biovolume and biomass estimates. This value was selected based on the diameters of species most commonly occurring in the database. The large uncertainty associated with this value is taken into account by providing minimum and maximum biovolume and biomass estimates based on the absolute minimum and maximum values across all species in the database. Following the biomass conversions, data were compiled to total coccolithophore biomass per sample for the purposes of further analyses. Further taxonomic information is reported in the attached dataset (doi:10.1594/PANGAEA.785092) and coccolithophore biodiversity patterns will be discussed in O'Brien et al. (2013).

2.3 Quality control

Our quality control procedure flagged data based on a number of criteria, with flag values (1–4) provided in the data table. Flag 1 was applied to 33 samples that included observations of the species *Thoracosphaera heimii* – this species was originally thought to be a coccolithophore, but further investigations have shown it to be a calcified dinoflagellate cyst (Tangen et al., 1982). Flag 2 was applied to 205 samples for which only biomass values were provided, without corresponding cell counts; and flag 3 is applied to 482 samples with integrated water column values rather than discrete depth measurements, or to samples for which no depth information was provided. Flag 4 was assigned to outliers identified by the statistical analyses to be outlined below.

For the next stage of the quality control process, we removed samples with flags 2 and 3 and corrected samples with flag 1 to remove counts of *T. heimii*. For the remaining 9194 non-zero samples, we used Chauvenet's criterion to identify statistical outliers in the log-normalized biomass data (Buitenhuis et al., 2013; Glover et al., 2011). Based on this analysis, we identified one sample with a biomass value with probability of deviation from the mean greater than $1/2n$, with $n = 8997$ being the number of non-zero samples (two-sided z score: $|zc| = 4.03$). This sample is denoted by a flag value of 4.

An additional flag column denotes the quantification method used for determining coccolithophore abundance. Of the 9193 non-zero samples included in the database, 4209 are known to have been analysed using light microscopy, 500 using SEM and 197 with flow cytometry. For the remaining 4287 the method is unknown. Coccolithophore counts from SEM are consistently higher than those obtained using light microscopy due to the better identification of smaller and more fragile species. For example, Bollmann

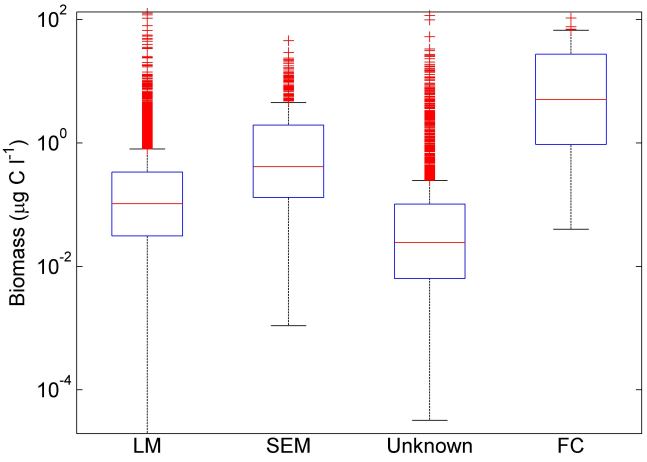

Figure 1. Boxplots depicting distributions of non-zero biomass estimates for different quantification methods: light microscopy (LM), scanning electron microscopy (SEM), unknown method and flow cytometry (FC). Horizontal lines depict the median, boxes depict the interquartile range (25th to 75th percentiles) and points marked beyond the whiskers of the plot are outliers (points falling greater than 1.5 times the interquartile range below the 25th percentile or above the 75th percentile).

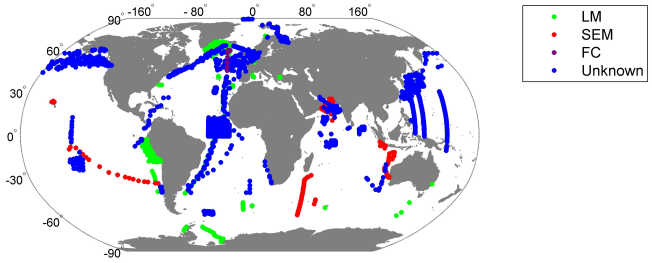

Figure 2. Global distribution of coccolithophore observations included in the dataset. Marker colour denotes the quantification method used: light microscopy (green), SEM (red), flow cytometry (cyan) and unknown (blue)

Table 3. Biomass estimates ($\mu g C L^{-1}$) for four analysis methods: light microscopy (LM), scanning electron microscopy (SEM), flow cytometry (FC) and unreported analysis method (unknown). All values are reported for non-zero biomass estimates only.

Method	*n*	Median	Mean	St. Dev.	Max
LM	4209	0.10	0.72	4.38	126.5
SEM	500	0.41	2.25	4.41	45.2
FC	197	5.04	14.66	18.29	105.5
Unknown	4287	0.024	0.39	2.96	116.0

et al. (2002) found that species such as syracosphaerids, small reticulofenestrids, small gephyrocapsids and holococcolithophores are likely to be missed in light microscopy analyses. Cell density has been shown to differ up to 23 % between the two methods when analysing samples with large numbers of small species such as *E. huxleyi*, *Gephyrocapsa ericsonii* and *G. protohuxleyi*.

We have made a statistical comparison of abundance and biomass values to determine whether a systematic bias can be associated with the enumeration method for samples in our database (Table 3, Fig. 1). Our comparison of coccolithophore abundance and biomass shows greater differences between methods than would be expected from previous comparisons of enumeration methods, but we suggest that these differences are likely to be at least partially explained by real differences in coccolithophore abundance and community composition. For example, we expect that SEM is more likely to be used for samples with a known portion of small coccolithophores which are difficult to identify or enumerate using light microscopy alone. Although median biomass from SEM studies is higher by a factor of four than the median for light microscopy studies, the highest values reported in the dataset are from light microscopy studies. Since the quantification method is unknown for nearly 50 % of samples, we have chosen to retain SEM data in the gridded dataset and all analyses, though users may access a subset of this data from the raw file. In contrast, we have excluded 199 datapoints collected using flow cytometry from the gridded dataset. These values are significantly higher again than those collected using either SEM or light microscopy.

Based on our full quality control procedure we removed a total of 888 flagged samples for the purposes of our analyses, and a further 32 samples were corrected to remove the contribution of *T. heimii* to total coccolithophore biomass (note: one sample contained data for *T. heimii* only). All data are included in the published raw dataset in the event that a user has different requirements for the quality control procedure, while the gridded dataset contains the unflagged datapoints only.

An additional column in the raw dataset denotes the taxonomic level to which coccolithophores are identified, as this has a major influence on the level of uncertainty associated with our biomass calculations. Coccolithophores identified to species level are denoted by the flag value 0, those identified to genus or family level as flag value 1, and unidentified coccolithophores as flag value 3. If coccosphere dimensions are known, cells identified to genus or family level receive flag value 2, and unidentified coccolithophores receive flag value 4. All samples of unidentified or partially identified coccolithophores have been included in our analyses and in the gridded file.

Several datasets report biomass values in addition to abundance data. While we have chosen to use our own conversion methods for consistency, it is likely that the original biomass values are based on more accurate estimates of cell size. All original biomass values are included in the submitted database and can be substituted for our estimates if desired.

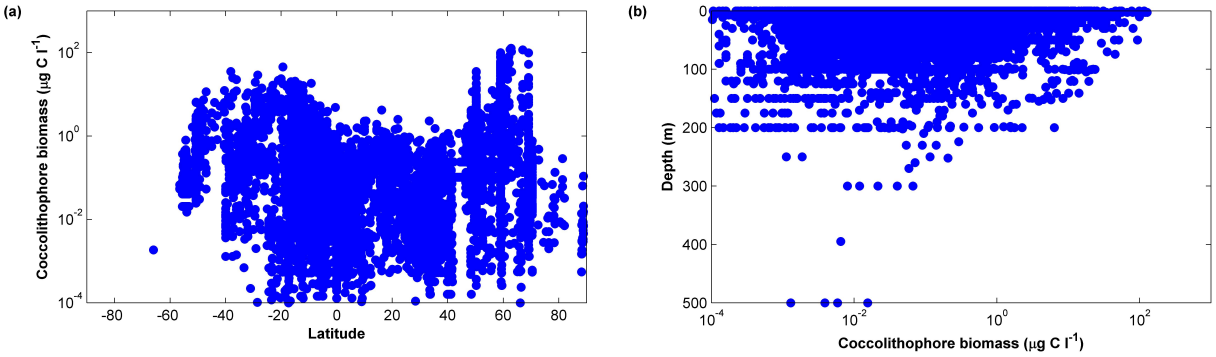

Figure 3. Distribution of coccolithophore biomass ($\mu g\,C\,L^{-1}$) **(a)** as a function of latitude and **(b)** as a function of depth.

3 Results

Excluding flagged data, the database contains coccolithophore biomass observations for 11 503 samples, collected from 6741 depth-resolved stations (Fig. 2). Highest coccolithophore abundance is 9.8×10^6 cells L^{-1}. 2507, or 21.8 % of samples, were found to be zero values. These data were retained in the dataset, since confirmed zero values hold valuable information for the study of plankton distributions. There is, however, inconsistency in the reporting of zero values in plankton datasets: often abundance data are reported only for a limited range of target groups that are expected to be present. There is also likely to be a bias due to sampling focusing on areas where coccolithophores are expected to occur. Values reported in the subsequent sections are therefore calculated based on non-zero data only. Where zero-datapoints are included, this value follows in parentheses. Arithmetic mean values are reported plus or minus one standard deviation. We also provide median biomass values, as these are less influenced by high values and provide a better representation of the central tendency of the data.

3.1 Spatial and temporal coverage

The database includes non-zero coccolithophore observations from the surface to a depth of 500 m (Fig. 3b, with 83.9 % of observations (84.1 % with zero values included) from the upper 50 m and 61.5 % (63.3 %) from the upper 10 m of the water column. Mean depth is 27.0 (±40.5) m and median depth is 10.0 m. Data are reported from all ocean basins, with 54.4 % of samples (58.9 % with zero values included) from the Northern Hemisphere and 45.4 % (40.9 %) from the Southern Hemisphere (Table 4). 31.6 % of non-zero data are from the Atlantic Ocean, 40.2 % from the Pacific Ocean and 10.4 % from the Indian Ocean. Despite the high number of observations reported from the Pacific compared to the Atlantic, the spatial coverage of this ocean basin is relatively poor, with many observations limited to intensively studied regions in Peruvian and Japanese coastal waters. 9.9 % of non-zero observations are from the polar regions, with 5.1 % from the Southern Ocean and 4.8 % from Arctic waters. Coccolithophores are reported to be present in only one sample below 60° S (Table 5, Fig. 4). In contrast, the database contains non-zero observations of coccolithophores in Arctic waters up to a maximum of 88.92° N. 46.3 % of data are from tropical waters between 20° S and 20° N.

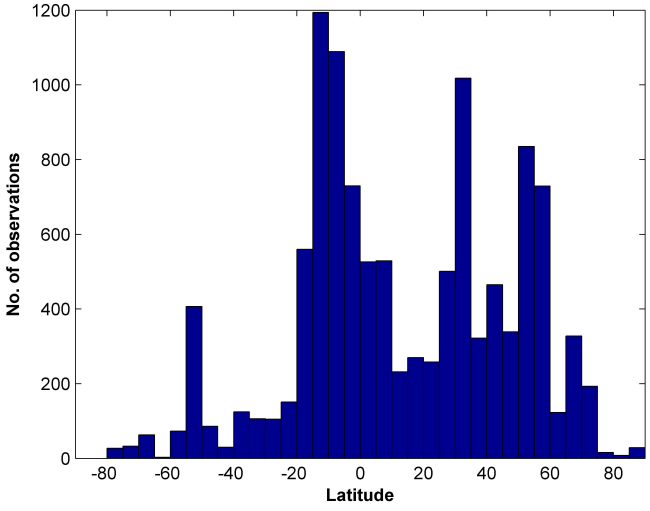

Figure 4. Frequency distribution of coccolithophore observations as a function of latitude for the period 1929–2008.

Data are reported from the years 1929 to 2008 (Fig. 5). A total of 66 non-zero observations are reported for 1929–1930, with no further observations until 1954. 78.7 % of observations were collected between 1980 and 2008, and 51.8 % between 1990 and 2008. Data are reported from all months of the year in both hemispheres, although relatively few data were collected during the winter months (13.6 % of all NH data, 15.6 % of SH data, Table 4). Northern Hemisphere data are strongly biased towards summer observations (38.4 % of all data).

Table 4. Seasonal distribution of abundance data for the Northern and Southern Hemisphere. Number of data points for each month. All: all data, non-zero: data with non-zero carbon biomass.

Month	Globe all	Globe non-zero	NH all	NH non-zero	SH all	SH non-zero
Jan	737	367	489	177	247	189
Feb	1271	922	389	260	881	662
Mar	872	729	489	367	383	362
Apr	942	793	433	317	500	467
May	1095	935	634	534	461	401
Jun	944	607	694	394	246	213
Jul	1203	859	1056	734	146	125
Aug	1053	942	697	607	356	335
Sep	1111	1005	810	728	290	266
Oct	1304	975	699	441	605	534
Nov	752	671	245	196	507	475
Dec	219	191	59	50	160	141
Spring	–	–	1556	1218	1402	1275
Summer	–	–	2447	1735	1288	992
Autumn	–	–	1754	1365	1344	1230
Winter	–	–	937	487	748	673
Total	11 503	8996	6694	4805	4782	4170

3.2 Biomass distribution

3.2.1 Geographical distribution

Coccolithophore biomass values range from 2.0×10^{-5} to 127.2 $\mu g C L^{-1}$. The global mean is 0.88 $\mu g C L^{-1}$ ± 4.8 $\mu g C L^{-1}$ and median biomass is 0.072 $\mu g C L^{-1}$. Highest median biomass values were recorded in the Southern Hemisphere between 40 and 50° S (0.77, Figs. 3, 6, Table 5), and in the Northern Hemisphere between 50 and 60 ° N. Maximum biomass values show peaks around 60° N and between 40 and 20° S, with declines towards both the equator and the poles. Biomass estimates between the equator and 40° N are below 5 $\mu g C L^{-1}$. The highest biomass estimate of 127.2 $\mu g C L^{-1}$ is for a sample off the Icelandic coast (62.8° N, 20.0° W).

Strong differences can be observed between the Atlantic and Pacific Ocean, with Atlantic biomass values reaching 127.2 $\mu g C L^{-1}$ (mean 1.7 ± 7.5, median 0.12 $\mu g C L^{-1}$) compared to just 20.0 $\mu g C L^{-1}$ in the Pacific (mean 0.3 ± 0.9, median 0.04 $\mu g C L^{-1}$). The relatively poor spatio-temporal coverage of Pacific Ocean observations, however, may contribute to this discrepancy. Indian Ocean biomass values reach a maximum of 45.2 $\mu g C L^{-1}$, with a mean of 1.1 ± 3.4 and median of 0.03 $\mu g C L^{-1}$.

In the Southern Ocean, the maximum biomass value reported is 6.5 $\mu g C L^{-1}$, mean biomass is 0.19 ± 0.58 $\mu g C L^{-1}$ and median biomass is 0.04 $\mu g C L^{-1}$. Higher values are recorded in the Arctic Ocean, with a maximum of 98.9 $\mu g C L^{-1}$, mean of 0.78 ± 5.7 $\mu g C L^{-1}$ and median of 0.05 $\mu g C L^{-1}$.

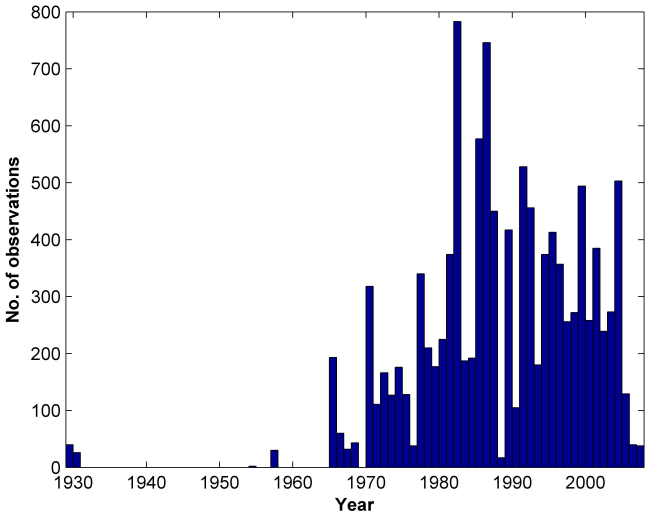

Figure 5. Frequency distribution of coccolithophore observations by year, for the period 1929–2008.

3.2.2 Depth distribution

Highest biomass values are reported in surface waters and decline with depth (Figs. 3b, 6), although biomass values of up to 23 $\mu g C L^{-1}$ are still reported at 100 m depth. Mean biomass for the surface layer (0–10 m) is 0.9 ± 5.2 $\mu g C L^{-1}$ and median biomass is 0.09 $\mu g C L^{-1}$. Biomass values below 200 m reach a maximum of 0.01 $\mu g C L^{-1}$. The deepest observations of coccolithophores are at 500 m depth, with biomasses reaching a maximum of just 0.004 $\mu g C L^{-1}$.

3.2.3 Seasonal distribution

The data show a clear seasonal cycle in the Northern Hemisphere, with biomass values reaching just 1.1 $\mu g C L^{-1}$ in December and over 100 $\mu g C L^{-1}$ in the summer months (June–July, Fig. 7). In the Southern Hemisphere the seasonal cycle is less evident, possibly due to the greater contribution of data from low latitudes where seasonal changes are less pronounced.

3.2.4 Uncertainty

The expected uncertainty associated with our conversions of cell abundance to carbon biomass due to varying cell size is depicted in Fig. 8. Biomass estimates are best constrained where detailed taxonomic information is available, and for samples containing species for which a limited size range has been reported. Very high uncertainty (range of biomass values greater than 5000 % of the mean biomass) is associated with counts of unidentified coccolithophores. This is to be expected given the large range of sizes reported for the approximately 200 known coccolithophore species (see Appendix Table A3).

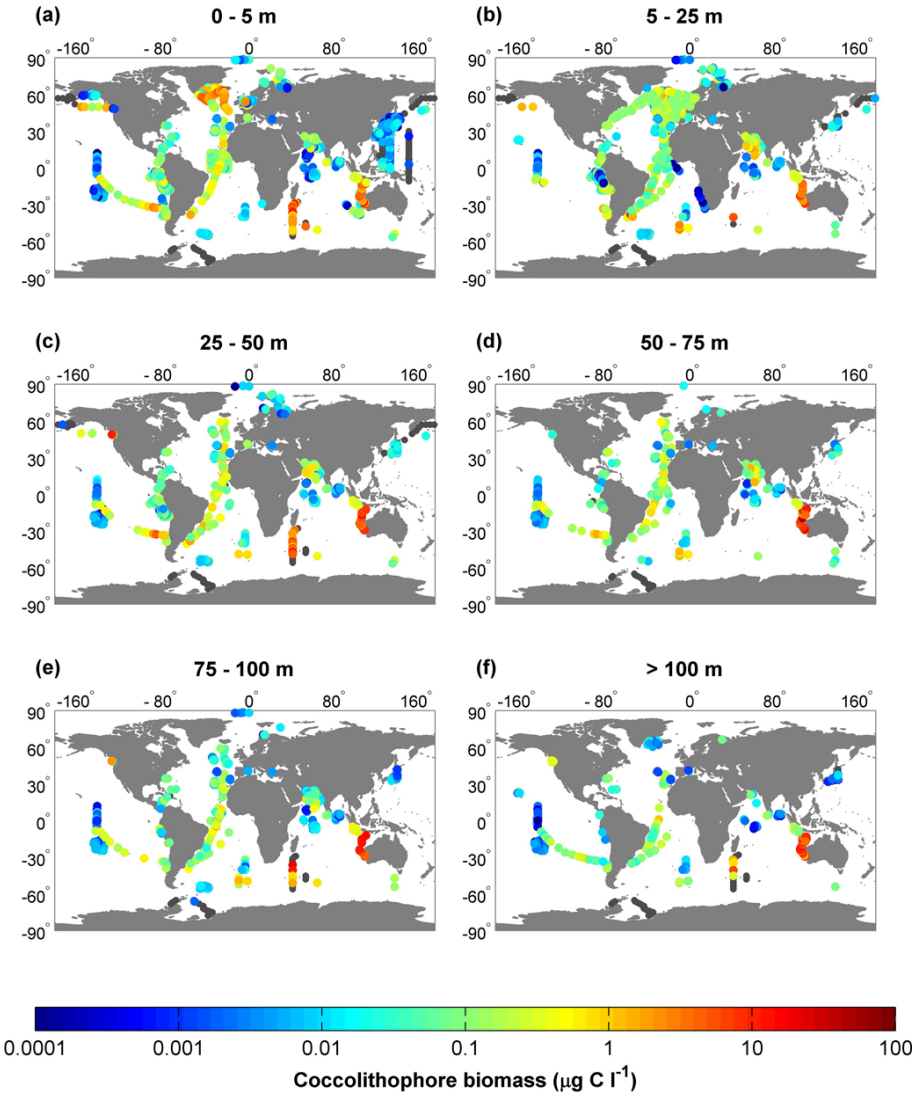

Figure 6. Mean coccolithophore carbon biomass ($\mu g\,C\,L^{-1}$) for six depth bands **(a)** 0–5 m **(b)** 5–25 m **(c)** 25–50 m **(d)** 50–75 m **(e)** 75–100 m and **(f)** > 100 m depth.

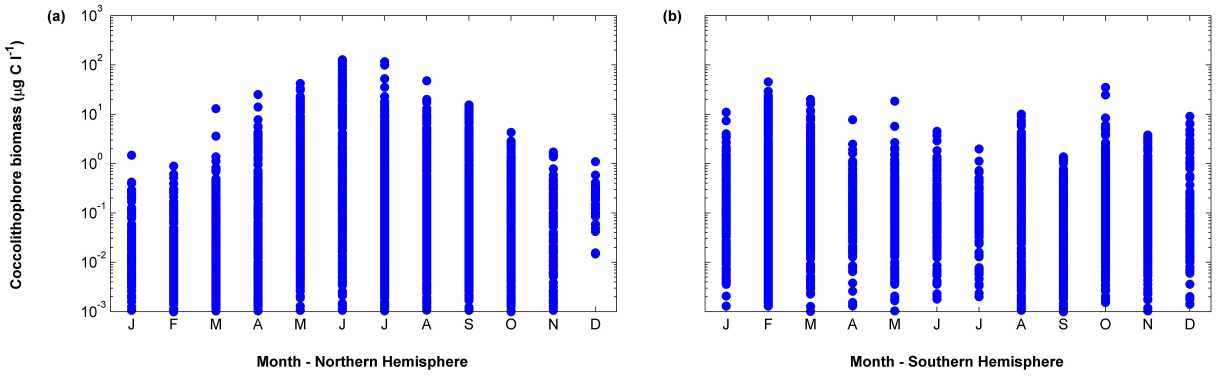

Figure 7. Seasonal distribution of coccolithophore biomass data for **(a)** Northern Hemisphere and **(b)** Southern Hemisphere.

Table 5. Latitudinal distribution of quality-controlled data in ten degree latitudinal bands (−90 to 90°). All data: total number of data points; non-zero data: number of non-zero biomass values; mean, standard deviation, median and maximum biomass values calculated from non-zero data only.

Latitudinal band	All data	Non-zero data	Mean	S.D.	Median	Max
−90–−80°	0	0	–	–	–	–
−80–−70°	60	0	–	–	–	–
−70–−60°	66	1	0.002	–	0.002	0.002
−60–−50°	480	456	0.2	0.5	0.04	6.5
−50–−40°	116	77	1.8	2.4	0.77	12.3
−40–−30°	231	207	1.1	3.7	0.19	35.1
−30–−20°	256	247	2.0	4.0	0.16	29.1
−20–−10°	1754	1467	0.7	2.2	0.09	45.2
−10–0°	1819	1715	0.2	0.7	0.05	18.4
0–10°	1055	860	0.1	0.2	0.03	2.3
10–20°	502	315	0.2	0.4	0.09	4.2
20–30°	759	420	0.1	0.2	0.02	2.5
30–40°	1340	773	0.1	0.1	0.01	2.3
40–50°	804	505	0.3	0.7	0.10	11.5
50–60°	1564	1319	2.7	7.8	0.32	99.3
60–70°	451	451	3.7	14.7	0.10	127.2
70–80°	209	146	0.1	0.1	0.05	0.8
80–90°	37	37	0.02	0.05	0.007	0.3

An additional source of uncertainty, however, is the estimation of cell biovolumes from coccosphere dimensions, and is more difficult to quantify. A comparison of our biomass estimates based on coccosphere dimensions with estimates from available cytoplasm dimensions suggests that we may be underestimating coccolithophore biomass values by a factor of up to 5 for some species (Table 2). It is worth noting, however, that the cytoplasm dimensions considered here are based on either culture specimens (Stoll et al., 2002) or a small number of field samples from the Icelandic Basin (Poulton et al., 2010) and the Mauritanian Upwelling (Franklin et al., 2009). For one of the best-studied species, *E. huxleyi*, our mean biomass estimate of 13 pg C cell^{-1} falls within the range of published carbon measurements of 7.8 to 27.9 pg C cell^{-1} (Fernandez et al., 1993; van Bleijswijk et al., 1994; Verity et al., 1992), while our estimates from the cytoplasm measurements in Table 2 show much lower values of 3.5–3.7 pg C cell^{-1}.

4 Discussion

There are many sources of uncertainty associated with our calculations. We have attempted to quantify the uncertainty associated with variable cell dimensions by providing minimum and maximum biomass values for each datapoint, but this does not represent the full range of uncertainty associated with our biomass values.

The estimation of cell biovolumes from coccosphere dimensions is likely to result in additional errors which are at present difficult to quantify. A more accurate estimation of coccolithophore biomass will only be possible with improved understanding of coccolithophore cytoplasm dimensions (e.g. Stoll et al., 2002), and we highlight this as a key data requirement for improved estimates of coccolithophore biomass from abundance data. While the routine measurement of coccolithophore cell dimensions is a time-consuming process, there also appears to be potential to estimate cell size from coccolith length (Henderiks and Pagani, 2007; Henderiks, 2008).

Few observations of coccosphere dimensions are reported in the literature for most species, and the number of cells that have been studied to derive the given ranges is rarely reported. Measurements are often from a single geographical location, meaning that size variation between strains is not accounted for. There is additionally inconsistency as to whether the range of coccosphere sizes reported is the full range of sizes that occurs or only those most commonly observed. A further source of uncertainty is the generalisation of at times complex geometry to fit a particular geometric form.

The uncertainty ranges provided around our biomass estimates are intended to reflect the influence of cell size on coccolithophore biomass. Since these are based on cytoplasm dimensions estimated from total coccosphere size, it is unclear whether biomass values towards the high end of our uncertainty range are biologically realistic. We may expect larger coccospheres to be characterised by a greater proportion of inorganic carbon rather than reflecting a constant ratio of cytoplasm : coccosphere dimensions.

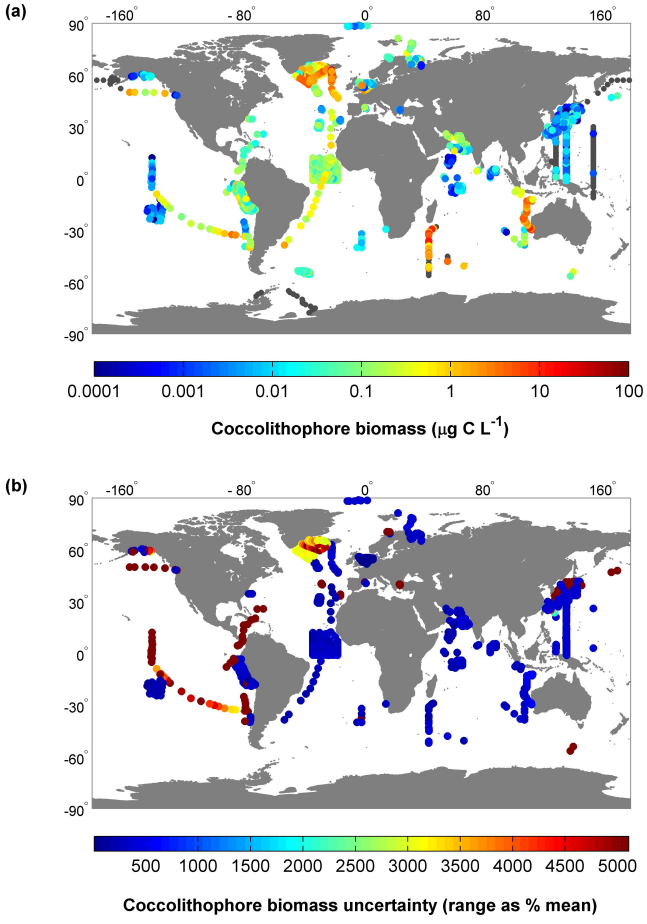

Figure 8. **(a)** Surface (0–5 m) mean coccolithophore biomass ($\mu g C L^{-1}$) and **(b)** range of uncertainty in cell biomass estimates (% of the mean) due to uncertainty in cell size.

While our uncertainty ranges are very high, a comparison of our mean biomass estimates to previously published coccolithophore biomass values shows strong consistency: our highest mean biomass estimates (i.e., those associated with large *E. huxleyi* blooms: maximum of 127 $\mu g C L^{-1}$) are similar to past estimates from light microscopy-based cell counts (e.g. Holligan et al., 1993: 130 $\mu g C L^{-1}$), but slightly lower than coccolithophore biomass estimates from fatty acid biomarkers in mesocosm experiments (de Kluijver et al., 2010: 190 $\mu g C L^{-1}$).

In addition to the errors introduced by the biomass conversion process, a considerable degree of uncertainty is already associated with the cell abundance data. Coccolithophores can be quantified using several techniques, including visual or automated identification from scanning electron microscopy, regular light microscopy and light microscopy using cross-polarised light. Additionally, samples can be prepared for light microscopy either by filtration or by using the Utermöhl sedimentation method (Utermöhl, 1958). Reid (1980) and Bollmann et al. (2002) both concluded that inverted light microscopy is unreliable for determining cell densities of small coccolithophores.

Despite these limitations, the Utermöhl method of sedimentation and inverted light microscopy remains widely used in studies investigating phytoplankton assemblages, and any compilation of global coccolithophore distributions would be incomplete without these data. Cell counts from SEM can additionally be unreliable at high cell densities, where shedded coccoliths can lead to difficulties in distinguishing individual coccospheres (A. Poulton, personal observation). The synthesis of datasets obtained from these different methods would be greatly improved by further comparative studies similar to those carried out by Bollmann et al. (2002), as it is currently unclear to what extent small and rare species are being overlooked in different ocean regions as a result of these methodological differences.

Users of the gridded data file should also take into consideration the sparse nature of the original data. Often monthly mean gridded values have been derived from relatively few individual datapoints that do not represent the full range of values that occur in a given location. We expect to see a bias toward higher biomass values, given that studies are often conducted in locations and times of year when blooms are expected to occur.

We have not included estimates of inorganic carbon content in the database, as we do not feel that useful estimates of coccolithophore calcite can currently be provided from the abundance data. The ratio of inorganic : organic carbon has been shown to vary considerably with environmental and growth conditions (Zondervan, 2007), with ratios for the species *E. huxleyi* alone ranging from 0.26 to 2.3 (van Bleijswijk et al., 1994; Paasche, 2002). While some estimates have been made of the relationship between inorganic and organic carbon for *E. huxleyi*-dominated communities (e.g. Fernández et al., 1993; Poulton et al., 2010), the relationship of calcite content to biomass for other coccolithophore communities remains less well understood.

The biomass estimates presented here represent a first attempt to assess global coccolithophore biomass distributions. While we recognise that the uncertainties associated with these biomass estimates are significant, we nevertheless feel that they provide a more informative dataset than would a compilation of abundance data alone given the large size variation among coccolithophore species. The coccolithophores present particular challenges for the compilation and synthesis of diverse datasets due to the wide range of methods used for their quantification as well as the limited understanding of cell dimensions. The strong biases associated with the different methods highlight the need for coccolithophore abundance data to be published alongside appropriate metadata to allow users to assess data quality.

5 Conclusions

This database represents the largest effort to date to compile coccolithophore abundance observations and provide standardised biomass estimates to the scientific community. We report our biovolume and biomass conversion procedures in detail and discuss the associated uncertainties. We anticipate that this dataset, together with others from the MAREDAT special issue, will be a valuable resource for studies of plankton distributions and ecology and in particular for the evaluation and development of marine ecosystem models. While data are clearly lacking for certain regions, the dataset nevertheless represents the largest available compilation of global coccolithophore abundance and biomass. We hope to improve the spatial and temporal coverage of the dataset as well as the accuracy of biomass conversions as additional data become available in the future.

Appendix A

A1 Data table

A full data table containing all biomass data points can be downloaded from the data archive PANGAEA (doi:10.1594/PANGAEA.785092). The data file contains longitude, latitude, depth, sampling time, abundance counts and biomass concentrations, as well as the full data references.

A2 Gridded netcdf biomass product

Monthly mean biomass data have been gridded onto a $360 \times 180^\circ$ grid, with a vertical resolution of 33 depth levels (equivalent to World Ocean Atlas depths) and a temporal resolution of 12 months (climatological monthly means). This dataset is provided in netcdf format for easy use in model evaluation exercises. The netcdf file can be downloaded from PANGAEA (doi:10.1594/PANGAEA.785092). This file contains total and non-zero abundance and biomass values. For all fields, the means, medians and standard deviations resulting from multiple observations in each of the 1° pixels are given. The ranges in biomass values due to uncertainties in cell size are not included as variables in the netcdf product, but are given as ranges (minimum cell biomass, maximum cell biomass) in the data table.

A3 Biomass conversion details

Table A3. Biomass conversion details for coccolithophore taxa reported in the database: biovolume category (best available taxonomic description, species names corrected where possible); number of datapoints (*n*, flagged and unflagged data); coccosphere shape (S = sphere, PS = prolate spheroid, C = cone, CY = cylinder, DC = double cone, V = various shapes, L = species dimensions unknown, cell biovolume estimate from literature); minimum, maximum and mean coccosphere dimensions (μm), cell biovolume (μm^3) and cell biomass ($pg\,C\,L^{-1}$).

Biovolume Category	*n*	Shape	Diameter (μm)			Length (μm)			Width (μm)			Biovolume (μm^3)			Biomass ($pg\,C\,cell^{-1}$)			References
			Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	
Acanthoica sp.	199	PS										61	126	85	9	18	12	
Acanthoica acanthifera	130	PS				6.0	7.0	6.5	5.0	5.0	5.0	17	20	18	3	3	3	4, 16
Acanthoica janchenii	5	PS						7.0			6.5	17	70	33	3	10	5	16
Acanthoica ornata	4	PS				14.0	16.0	15.0	11.0	12.0	11.5	192	261	224	26	34	30	26
Acanthoica quattrospina	1446	PS				7.0	15.0	11.0	5.0	9.5	7.3	20	153	65	3	21	10	4, 9, 10, 11, 12, 16
Algirosphaera cucullata	25	S	8.0	11.0	9.5							58	151	97	9	21	14	4, 16
Algirosphaera robusta	448	S	6.5	16.0	11.3							31	463	161	5	57	22	4, 9, 10, 11, 12, 16, 25
Alisphaera sp.	60	S										75	211	125	11	28	18	
Alisphaera extenta	45	S	6.5	10.0	8.3							31	113	64	5	16	10	17
Alisphaera gaudii	45	S	11.0	12.0	11.5							151	195	172	21	26	23	17
Alisphaera ordinata	67	S	10.0	12.0	11.0							113	195	151	16	26	21	17
Alisphaera pinnigera	70	S	7.0	13.0	10.0							39	248	113	6	32	16	4, 17
Alisphaera spatula	25	S			11.0							75	316	151	11	40	21	5
Alisphaera unicornis	165	S	7.3	12.0	9.7							44	195	102	7	26	15	4, 9, 10, 22
Alveosphaera bimurata	67	DC						18.0			8.0	33	137	65	5	19	10	22
Anacanthoica acanthos	50	PS				8.0	12.5	10.3	7.0	7.0	7.0	44	69	57	7	10	9	4, 11, 16, 26
Anacanthoica cidaris	25	S			13.0							124	522	248	17	63	32	16
Anthosphaera sp.	305	S	4.5	16.0	10.3							10	463	122	2	57	17	4, 10, 18
Anthosphaera fragaria	141	S	4.5	7.0	5.8							10	39	22	2	6	4	4, 10, 18
Braarudosphaera sp.	6	S	5.0	16.0	10.5							14	463	131	2	57	18	
Braarudosphaera bigelowii	1034	S	5.0	16.0	10.5							14	463	131	2	57	18	8, 10
Calcidiscus sp.	83	S	5.0	28.0	16.5							64	1432	364	10	157	46	
Calcidiscus leptoporus	967	S	5.0	28.0	16.5							14	2483	508	2	257	62	4, 9, 10, 11, 15
Calcidiscus quadriperforatus	67	S	10.0	15.0	12.5							113	382	221	16	48	29	4, 10, 11
Calcioconus sp.	7	C				15.0	18.0	16.5	10.0	12.0	11.0	85	147	113	12	20	16	
Calcioconus vitreus	17	C				15.0	18.0	16.5	10.0	12.0	11.0	85	147	113	12	20	16	26
Calciopappus sp.	122	C										18	44	29	3	7	5	
Calciopappus caudatus	49	C				26.0	36.0	31.0	3.5	4.0	3.8	18	33	25	3	5	4	10
Calciopappus rigidus	181	C				9.0	12.0	10.5	6.0	9.0	7.5	18	55	33	3	8	5	4, 10, 12
Calciosolenia sp.	61	V										31	817	240	5	95	31	
Calciosolenia brasiliensis	1394	DC				33.0	100.0	66.5	4.0	8.0	6.0	30	362	135	5	46	19	1, 4, 9, 10, 12, 19
Calciosolenia murrayi	1311	CY	3.0	10.0	6.5	21.0	75.0	48.0				32	1272	344	5	141	43	1, 4, 9, 10, 11, 12
Calicasphaera blokii	45	S	6.5	7.7	7.1							31	52	40	5	8	6	15
Calicasphaera concava	45	S	7.0	11.0	9.0							39	151	82	6	21	12	15
Calicasphaera diconstricta	25	S	6.2	8.5	7.4							27	69	45	4	10	7	15
Calyptrolithina divergens	67	PS				5.5	8.0	6.8	5.5	6.0	5.8	19	33	25	3	5	4	10
Calyptrolithina multipora	92	S	13.9	22.5	18.2							304	1288	682	39	143	80	10, 15
Calyptrolithina wettsteinii	45	PS				12.5	15.8	14.2	10.7	13.0	11.9	162	302	225	22	39	30	11, 15
Calyptrolithophora gracillima	1	PS				9.5	18.0	13.8	9.0	16.0	12.5	87	521	243	13	63	32	4, 10
Calyptrolithophora papillifera	141	S	9.0	20.0	14.5							82	905	345	12	104	44	4, 10, 11
Calyptrosphaera sp.	820	S	5.0	22.0	13.5							254	484	350	33	59	44	
Calyptrosphaera globosa	4	S	17.0	20.0	18.5							556	905	716	67	104	84	26
Calyptrosphaera incisa	1	S			10.0							57	238	113	9	31	16	26
Calyptrosphaera insignis	8	S	11.0	14.0	12.5							151	310	221	21	40	29	26
Caneosphaera sp.	15	S	4.5	18.0	11.3							10	660	161	2	78	22	4, 9, 10, 11, 22
Canistrolithus sp.	74	S	14.3	23.8	19.0							327	1515	776	42	165	90	4
Ceratolithus sp.	6	S	7.0	18.9	13.0							39	764	246	6	89	32	
Ceratolithus cristatus	107	S	7.0	18.9	13.0							39	764	246	6	89	32	4, 10, 22
Coccolithus sp.	1191	S	8.0	22.0	15.0							58	1204	382	9	134	48	
Coccolithus pelagicus	1108	S	8.0	22.0	15.0							58	1204	382	9	134	48	9, 10, 11
Coccolithus pelagicus holo	625	S	8.0	18.0	13.0							58	660	248	9	78	32	10
Corisphaera sp.	40	S	4.5	9.2	6.9							15	52	28	3	8	5	
Corisphaera gracilis	93	S			6.5							16	65	31	3	10	5	10
Corisphaera strigilis	49	S	5.0	7.0	6.0							14	39	24	2	6	4	4
Coronosphaera sp.	626	S	12.0	53.0	32.5							222	509	345	29	62	44	
Coronosphaera binodata	4	S	13.0	16.0	14.5							248	463	345	32	57	44	4, 26
Coronosphaera mediterranea	544	S	12.0	17.0	14.5							195	556	345	26	67	44	4, 9, 10
Cribrosphaera sp.	15	S			8.3							32	136	65	5	19	10	23
Cribrosphaera ehrenbergii	5	S			8.3							32	136	65	5	19	10	23
Crystallolithus sp.	11	S	8.0	20.0	14.0							58	905	310	9	104	40	10
Cyrtosphaera aculeata	93	S			7.0							19	81	39	3	12	6	4, 10, 16
Cyrtosphaera lecaliae	45	S			9.0							41	173	82	6	23	12	16
Discosphaera sp.	152	S	4.5	14.0	10.0							10	310	113	2	40	16	
Discosphaera tubifera	1312	S	4.5	14.0	10.0							10	310	113	2	40	16	1, 4, 9, 10, 11, 12, 16
Emiliania huxleyi	5651	S	3.5	15.0	9.3							5	382	90	1	48	13	1, 4, 9, 10, 11, 12, 14, 22
Florisphaera profunda var. elongata	49	S			12.0							98	410	195	14	51	26	4, 10, 12, 24, 25
Florisphaera profunda var. profunda	536	S	4.0	12.0	8.0							7	195	58	1	26	9	25
Gephyrocapsa sp.	909	S	2.6	15.0	8.8							22	121	50	4	17	8	
Gephyrocapsa ericsonii	254	S	3.0	5.0	4.0							3	14	7	1	2	1	4, 9, 10, 25
Gephyrocapsa muellerae	49	S	7.0	8.0	7.5							39	58	48	6	9	7	4
Gephyrocapsa oceanica	933	S	5.0	15.0	10.0							14	382	113	2	48	16	4, 6, 9, 10, 11, 12
Gephyrocapsa ornata	422	S	3.3	4.5	3.9							31	31	31	5	5	5	4, 10
Gephyrocapsids	9	S	2.6	15.0	8.8							19	165	56	3	22	9	
Gladiolithus flabellatus	245	S	8.0	12.0	10.0							58	195	113	9	26	16	4

Table A3. Continued.

Biovolume Category	*n*	Shape	Diameter (μm)			Length (μm)			Width (μm)			Biovolume ($μm^3$)			Biomass (pg C $cell^{-1}$)			References
			Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	
Halopappus sp.	582	V										65	273	132	10	35	18	
Halopappus quadribrachiatus	6	S	5.0	8.0	6.5							14	58	31	2	9	5	26
Halopappus vahseli	8	C						21.0			14.0	116	489	233	16	60	31	26
Heimiella excentrica	18	S	18.0	24.0	21.0							660	1563	1047	78	170	118	26
Helicosphaera sp.	398	V										150	672	340	21	79	43	
Helicosphaera carteri	553	PS				10.0	28.0	19.0	13.0	20.0	16.5	191	1267	585	26	140	70	1, 4, 9, 10, 11, 12
Helicosphaera carteri (holo)	67	S	10.0	15.5	12.8							113	421	234	16	52	31	4, 11
Helicosphaera hyalina	109	PS				12.0	22.0	17.0	11.0	18.0	14.5	164	806	404	22	94	50	4, 10, 12
Helicosphaera pavimentum	131	PS				10.5	13.5	12.0	10.5	12.5	11.5	131	239	179	18	31	24	4, 22
Helicosphaera wallichii	49	S						14.7			13.4	149	627	299	21	75	38	4, 22
Helladosphaera sp.	60	PS				4.9	9.0	7.0	4.0	6.4	5.2	9	42	21	2	7	4	
Helladosphaera cornifera	158	PS				4.9	9.0	7.0	4.0	6.4	5.2	9	42	21	2	7	4	4, 10, 11
Holococcolithophora sphaeroidea	100	S	6.0	12.0	9.0							24	195	82	4	26	12	4, 10
Homozygosphaera sp.	45	S	6.0	15.0	10.5							41	315	131	6	40	18	
Homozygosphaera arethusae	45	S	6.0	15.0	10.5							24	382	131	4	48	18	4
Homozygosphaera triarcha	92	S	8.0	13.0	10.5							58	248	131	9	32	18	4, 10
Lohmannosphaera sp.	4	S	6.0	12.0	9.0							24	195	82	4	26	12	1, 9, 10, 11, 12, 25, 26
Lohmannosphaera adriatica	32	S	10.0	12.0	11.0							113	195	151	16	26	21	1, 9, 10, 11, 12, 25, 26
Lohmannosphaera paucoscyphos	18	S			8.0							29	122	58	5	17	9	26
Michaelsarsia sp.	18	V										77	573	247	11	69	32	
Michaelsarsia adriaticus	270	PS				10.0	30.0	20.0	8.0	15.0	11.5	72	763	299	11	89	38	1, 9, 10, 11, 12, 25, 26
Michaelsarsia elegans	200	S	9.0	15.0	12.0							82	382	195	12	48	26	4, 9, 10
Michaelsarsia splendens	32	S			12.0							98	410	195	14	51	26	25, 26
Navilithus altivelum	45	S	5.0	8.0	6.5							14	58	31	2	9	5	28
Oolithotus sp.	39	S										60	1651	364	9	178	46	
Oolithotus antillarum	301	S	10.0	13.0	11.5							113	248	172	16	32	23	4
Oolithotus fragilis	579	S	4.0	30.0	17.0							7	3054	556	1	310	67	4, 9, 10, 22
Ophiaster sp.	101	S	3.5	10.5	7.0							5	131	39	1	18	6	1, 4, 10, 11, 12
Ophiaster hydroideus	1748	S	3.5	8.0	5.8							5	58	22	1	9	4	1, 4, 10, 11, 12
Palusphaera vandelii	145	S	4.0	8.7	6.4							7	74	29	1	11	5	4, 10, 22
Pappomonas sp.	294	V										21	894	1331	4	103	147	
Pappomonas flabellifera	25	PS				4.5	7.5	6.0	3.0	5.0	4.0	5	21	11	1	4	2	20, 29
Papposphaera sp.	192	S	4.0	16.0	10.0							9	48	23	2	7	4	
Papposphaera borealis	67	S			7.0							7	58	24	1	9	4	21
Papposphaera lepida	165	S	4.5	16.0	10.3							10	39	22	2	6	4	4, 10, 29
Picarola margalefii	94	S	6.0	12.0	9.0							24	195	82	4	26	12	4
Pleurochrysis carterae	32	S	12.0	17.0	14.5							195	556	345	26	67	44	3, 10
Pleurochrysis roscoffensis	8	S	12.0	20.0	16.0							195	905	463	26	104	57	7
Polycrater galapagensis	141	S	9.8	15.8	12.8							106	446	237	15	55	31	4
Pontosphaera sp.	114	V										261	1056	551	34	119	66	
Pontosphaera discopora	2	S	17.0	28.0	22.5							556	2483	1288	67	257	143	9, 10
Pontosphaera echinofera	5	PS						16.0			12.0	195	821	391	26	95	49	26
Pontosphaera haeckelli	2	S	11.0	15.0	13.0							151	382	248	21	48	32	26
Pontosphaera inermis	1	S	7.0	9.0	8.0							39	82	58	6	12	9	26
Pontosphaera nigra	42	PS				20.0	24.0	22.0	14.0	16.0	15.0	443	695	560	55	82	67	26
Pontosphaera ovalis	1	S	5.0	6.0	5.5							14	24	19	2	4	3	26
Pontosphaera stagnicola	1	S	14.0	20.0	17.0							310	905	556	40	104	67	26
Pontosphaera syracusana	555	S	15.0	30.0	22.5							382	3054	1288	48	310	143	1, 10
Poricalyptra sp.	45	V										43	200	103	7	27	15	
Poricalyptra aurisinae	67	S	7.0	12.0	9.5							39	195	97	6	26	14	4
Poricalyptra magnaghii	92	PS				10.0	13.5	11.8	6.5	11.6	9.1	48	205	109	7	27	15	22
Poritectolithus sp.	70	S	6.8	14.0	10.4							35	310	126	6	40	18	4, 5
Poritectolithus poritectus	70	S			9.0							41	173	82	6	23	12	4
Reticulofenestra parvula	159	S	3.0	3.8	3.4							3	6	4	1	1	1	4, 10
Reticulofenestra sessilis	284	S	6.0	10.5	8.3							24	131	64	4	18	10	9, 22, 25
Rhabdosphaera sp.	295	S	4.0	12.0	8.0							202	252	223	27	33	29	
Rhabdosphaera ampullacea	1	S	6.8	7.3	7.1							36	44	40	6	7	6	25
Rhabdosphaera clavigera	1641	S	7.9	12.0	10.0							56	195	111	8	26	16	1, 4, 9, 10, 11, 12, 16
Rhabdosphaera hispida	46	S	10.0	12.0	11.0							113	195	151	16	26	21	26
Rhabdosphaera tignifer	2	L										800	800	800	93	93	93	27
Rhabdosphaera xiphos	212	S	4.0	6.0	5.0							7	24	14	1	4	2	4
Scyphosphaera apsteinii	414	S	18.0	25.0	21.5							660	1767	1124	78	189	126	1, 4, 9, 10, 11, 25
Solisphaera sp.	45	S	5.0	9.4	7.2							17	76	39	3	11	6	
Solisphaera blagnacensis	45	S	5.6	9.4	7.5							20	93	48	3	13	7	2
Solisphaera emidasius	45	S	5.0	8.0	6.5							14	58	31	2	9	5	2
Sphaerocalyptra sp.	45	S	5.0	22.0	13.5							14	1204	278	2	134	36	4, 10, 11
Sphaerocalyptra adenensis	71	S	5.5	8.5	7.0							19	69	39	3	10	6	4
Sphaerocalyptra quadridentata	68	S	5.0	9.0	7.0							14	82	39	2	12	6	4, 10, 11
Syracolithus sp.	47	S	10.0	19.0	14.5							113	776	345	16	90	44	
Syracolithus dalmaticus	29	S	10.0	19.0	14.5							113	776	345	16	90	44	4, 10
Syracosphaera sp.	1249	S										92	598	246	13	72	32	
Syracosphaera ampliora	25	S	5.6	10.2	7.9							20	120	56	3	17	8	4, 22
Syracosphaera anthos	183	S	7.0	13.0	10.0							39	248	113	6	32	16	4, 9, 10
Syracosphaera anthos holo	2	S			15.0							191	802	382	26	93	48	26
Syracosphaera bannockii	112	S	5.0	7.0	6.0							14	39	24	2	6	4	4
Syracosphaera borealis	49	S	6.5	8.2	7.4							31	62	45	5	9	7	22
Syracosphaera brandtii	43	S	12.0	15.0	13.5							195	382	278	26	48	36	26
Syracosphaera corolla	141	S	9.8	11.6	10.7							641	641	641	76	76	76	22
Syracosphaera cupulifera	3	S			10.0							57	238	113	9	31	16	26
Syracosphaera delicata	45	S	6.5	7.5	7.0							31	48	39	5	7	6	4
Syracosphaera dentata	19	S	5.0	17.0	11.0							14	556	151	2	67	21	26
Syracosphaera dilatata	117	S	9.0	14.0	11.5							82	310	172	12	40	23	5

Table A3. Continued.

Biovolume Category	*n*	Shape	Diameter (μm)			Length (μm)			Width (μm)			Biovolume ($μm^3$)			Biomass (pg C $cell^{-1}$)			References
			Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	
Syracosphaera epigrosa	117	S	8.0	13.0	10.5							58	248	131	9	32	18	22
Syracosphaera exigua	94	S	7.5	11.7	9.6							48	181	100	7	24	14	22
Syracosphaera grundii	38	S	8.0	10.0	9.0							58	113	82	9	16	12	26
Syracosphaera halldalii	116	S	6.0	18.0	12.0							24	660	195	4	78	26	4, 9, 10, 22
Syracosphaera histrica	273	PS				10.8	20.0	15.4	9.0	14.0	11.5	99	443	230	14	55	30	10, 22
Syracosphaera lamina	165	PS				12.0	47.0	29.5	12.5	23.5	18.0	212	2936	1081	28	299	122	9, 11, 22
Syracosphaera marginaporata	165	S	3.0	6.0	4.5							3	24	10	1	4	2	5
Syracosphaera molischii	1083	S	4.5	11.3	7.9							10	163	56	2	22	8	4, 9, 10, 11, 22
Syracosphaera nana	106	S	5.5	8.2	6.9							19	62	36	3	9	6	4, 22
Syracosphaera nodosa	248	S	6.5	20.0	13.3							31	905	263	5	104	34	4, 10, 22
Syracosphaera noroitica	70	S	9.0	11.0	10.0							82	151	113	12	21	16	22
Syracosphaera orbiculus	165	S	6.0	9.3	7.7							24	91	51	4	13	8	22
Syracosphaera ossa	141	S	6.0	8.3	7.2							24	65	41	4	10	6	4, 22
Syracosphaera pirus	240	PS				6.0	18.0	12.0	6.0	10.0	8.0	24	204	87	4	27	13	9, 10, 12, 22
Syracosphaera prolongata	511	C				10.0	70.0	40.0	7.0	8.0	7.5	55	507	254	8	62	33	4, 10, 11, 22
Syracosphaera pulchra	1531	PS				5.0	70.0	37.5	10.0	23.0	16.5	57	4188	1155	9	411	129	1, 4, 9, 10, 11, 12
Syracosphaera pulchra (holo)	257	S	8.0	28.0	18.0							58	2483	660	9	257	78	10, 11
Syracosphaera rotula	116	S	5.0	7.2	6.1							14	42	26	2	7	4	4, 10, 22
Syracosphaera schilleri	1	S			15.0							191	802	382	26	93	48	26
Syracosphaera spinosa	2	S	8.0	9.5	8.8							58	97	76	9	14	11	26
Syracosphaera subsalsa	5	PS				20.0	28.0	24.0	14.0	18.0	16.0	443	1026	695	55	116	82	26
Syracosphaera tumularis	94	S	10.0	20.0	15.0							113	905	382	16	104	48	4
Thoracosphaera heimii	33	S	12.0	12.6	12.3							195	226	210	26	30	28	25
Turrilithus latericioides	206	S	8.0	11.0	9.5							58	151	97	9	21	14	4
Umbellosphaera sp.	690	S	9.2	16.0	12.6							101	422	224	14	52	30	
Umbellosphaera irregularis	1079	S	10.0	15.0	12.5							113	382	221	16	48	29	9
Umbellosphaera tenuis	420	S	9.2	16.0	12.6							88	463	226	13	57	30	4, 10, 11
Umbilicosphaera sp.	1968	S	8.5	43.0	25.8							84	3825	929	12	379	106	
Umbilicosphaera foliosa	46	S	10.0	18.0	14.0							113	660	310	16	78	40	4, 10, 13, 22, 25
Umbilicosphaera hulburtiana	289	PS				8.5	28.0	18.3	8.5	24.0	16.3	69	1824	545	10	195	66	4, 10
Umbilicosphaera sibogae	1601	S	8.5	43.0	25.8							69	8992	1931	10	818	205	1, 4, 9, 10, 11, 12, 22
Zygosphaera sp.	1	S	6.0	15.0	10.5							32	163	80	5	22	12	
Zygosphaera amoena	45	S	5.0	7.0	6.0							14	39	24	2	6	4	4
Zygosphaera hellenica	120	S	8.0	15.0	11.5							58	382	172	9	48	23	4, 10, 11, 12, 15, 25
Zygosphaera marsilii	27	S	6.0	8.5	7.3							24	69	43	4	10	7	4, 10

References: (1) Avancini et al. (2006), (2) Bollmann et al. (2006), (3) Bottino (1978), (4) Cros and Fortuño (2002), (5) Cros i Miguel (2002), (6) Doan-Nhu and Larsen (2010), (7) Gayral and Fresnel (1976), (8) Hagino et al. (2000), (9) Hallegraeff (1984), (10) Heimdal (1997), (11) Heimdal and Saugestad (2002), (12) Hernandez-Becerril and Bravo-Sierra (2001), (13) Inouye and Pienaar (1984), (14) Klaveness (1972), (15) Kleijne (1991), (16) Kleijne (1992), (17) Kleijne et al. (2002), (18) Lecal (1967), (19) Malinverno (2004), (20) Manton and Oates (1975), (21) Manton et al. (1976), (22) Okada and McIntyre (1977), (23) Priewalder (1973), (24) Quinn et al. (2005), (25) Reid (1980), (26) Schiller (1930), (27) Vilicic (1985), (28) Young and Andruleit (2006), (29) Young et al. (2003)

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References

Ajani, P., Lee, R., Pritchard, T., and Krogh, M.: Phytoplankton dynamics at a long-term coastal station off Sydney, Australia, J. Coastal Res., 34, 60–73, 2001.

Aktan, Y., Luglie, A., Aykulu, G., and Sechi, N.: Species composition, density and biomass of coccolithophorids in the Istanbul Strait, Turkey, Pak. J. Bot., 35, 45–52, 2003.

Anderson, T. R.: Plankton functional type modelling: running before we can walk?, J. Plankton Res., 27, 1073–1081, doi:10.1093/plankt/fbi076, 2005.

Andruleit, H.: Living coccolithophores recorded during the onset of upwelling conditions off Oman in the western Arabian Sea, J. Nannoplankton Res., 27, 1–14, 2005.

Andruleit, H.: Status of the Java upwelling area (Indian Ocean) during the oligotrophic Northern Hemisphere winter monsoon season as revealed by coccolithophores, Mar. Micropaleontol., 64, 36–51, doi:10.1016/j.marmicro.2007.02.001, 2007.

Andruleit, H., Stäger, S., Rogalla, U., and Cepek, P.: Living coccolithophores in the northern Arabian Sea: ecological tolerances and environmental control, Mar. Micropaleontol., Supplement, 49, 157–181, doi:10.1016/S0377-8398(03)00049-5, 2003.

Assmy, P.: Phytoplankton abundance measured on water bottle samples at stations PS65/424-3, 514-2, 570-4 & 587-1, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, doi:10.1594/PANGAEA.603388, doi:10.1594/PANGAEA.603393, doi:10.1594/PANGAEA.603398 and doi:10.1594/PANGAEA.603400, 2007.

Avancini, M., Cicero, A. M., Di Girolamo, I., Innamorati, M., Magaletti, E., and Sertorio Zunini, T. (Eds.): Guida al riconoscimento del plancton dei mari italiani, Vol. I – Fitoplancton, Ministero dell'Ambiente della Tutela del Territorio e del Mare, ICRAM, 2006.

Beaufort, L., Probert, I., de Garidel-Thoron, T., Bendif, E. M., Ruiz-Pino, D., Metzl, N., Goyet, C., Buchet, N., Coupel, P., Grelaud, M., Rost, B., Rickaby, R. E. M., and de Vargas, C.: Sensitivity of coccolithophores to carbonate chemistry and ocean acidification, Nature, 476, 80–83, doi:10.1038/nature10295, 2011.

Bollmann, J., Cortés, M. Y., Haidar, A. T., Brabec, B., Close, A., Hofmann, R., Palma, S., Tupas, L., and Thierstein, H. R.: Techniques for quantitative analyses of calcareous marine phytoplankton, Mar. Micropaleontol., 44, 163–185, doi:10.1016/S0377-8398(01)00040-8, 2002.

Bollmann, J., Cortés, M. Y., Kleijne, A., Ø stergaard, J. B., and Young, J. R.: Solisphaera gen. nov. (Prymnesiophyceae), a new coccolithophore genus from the lower photic zone, Phycologia, 45, 465–477, doi:10.2216/05-14.1, 2006.

Bottino, N.: The effects of arsenate and arsenite on the growth and morphology of the marine unicellular algae Tetraselmis chui (Chlorophyta) and Hymenomonas carterae (Chrysophyta), J. Exp. Mar. Biol. Ecol., 33, 153–168, doi:10.1016/0022-0981(78)90005-9, 1978.

Brown, C. and Yoder, J.: Coccolithophorid blooms in the global ocean, J. Geophys. Res., 99, 7467–7482, 1994.

Buitenhuis, E. T., Vogt, M., Moriarty, R., Bednaršek, N., Doney, S. C., Leblanc, K., Le Quéré, C., Luo, Y.-W., O'Brien, C., O'Brien, T., Peloquin, J., Schiebel, R., and Swan, C.: MAREDAT: towards a world atlas of MARine Ecosystem DATa, Earth Syst. Sci. Data, Earth Syst. Sci. Data, 5, 227–239, doi:10.5194/essd-5-227-2013, 2013.

Cros, L. and Fortuño, J.: Atlas of northwestern Mediterranean coccolithophores, Sci. Mar., 66 (Suppl. 1), 7–182, 2002.

Cros i Miguel, L.: Planktonic coccolithophores of the NW Mediterranean, Ph.D. thesis, University of Barcelona, 2002.

Doan-Nhu, H. and Larsen, J.: Haptophyte algae of Vietnamese waters. The orders Phaeocystales, Prymnesiales and Isochrysidales (Prymnesiophyceae), Nova Hedwigia, 91, 193–222, doi:10.1127/0029-5035/2010/0091-0193, 2010.

Doney, S. C., Fabry, V. J., Feely, R. A., and Kleypas, J. A.: Ocean acidification: the other CO_2 problem, Annual Review of Marine Science, 1, 169–192, doi:10.1146/annurev.marine.010908.163834, 2009.

Dutkiewicz, S., Ward, B. A., Monteiro, F., and Follows, M. J.: Interconnection of nitrogen fixers and iron in the Pacific Ocean: theory and numerical simulations, Global Biogeochem. Cy., 26, 1–16, doi:10.1029/2011GB004039, 2012.

Estrada, M.: Phytoplankton assemblages across a NW Mediterranean front: changes from winter mixing to spring stratification, Oecologia Aquatica, 10, 157–185, 1991.

Estrada, M. and Delgado, M.: Summer phytoplankton distributions in the Weddell Sea, Polar Biol., 10, 441–449, 1990.

Fernández, E., Boyd, P., Holligan, P. M., and Harbour, D. S.: Production of organic and inorganic carbon within a large-scale coccolithophore bloom in the northeast Atlantic Ocean, Mar. Ecol.-Prog. Ser., 97, 271–285, 1993.

Frada, M. J., Bidle, K. D., Probert, I., and de Vargas, C.: *In situ* survey of life cycle phases of the coccolithophore *Emiliania huxleyi (Haptophyta)*, Environ. Microbiol., 14, 1558–1569, doi:10.1111/j.1462-2920.2012.02745.x, 2012.

Franklin, D. J., Poulton, A. J., Steinke, M., Young, J., Peeken, I., and Malin, G.: Dimethylsulphide, DMSP-lyase activity and microplankton community structure inside and outside of the Mauritanian upwelling, Prog. Oceanogr., 83, 134–142, doi:10.1016/j.pocean.2009.07.011, 2009.

Fryxell, G.: Abundance and carbon biomass of phytoplankton at station TT0X_X-CTDX, doi:10.1594/PANGAEA.122734 to doi:10.1594/PANGAEA.122756, 2003.

Gayral, P. and Fresnel, J.: Nouvelles observations sur deux Coccolithophoracées marines: *Cricosphaera roscoffensis* (P. Dangeard) comb. nov. et *Hymenomonas globosa* (F. Magne) comb. nov., Phycologia, 15, 339–355, 1976.

Glover, D. M., Jenkins, W. J., and Doney, S. C.: Modeling Methods for Marine Science, Cambridge University Press, 2011.

Grados, C., Flores, G., Villanueva, P., Chang, F., and Ayón, P.: Phytoplankton abundance at stations off Paita in August 1995, Piura, Peru, Instituto del Mar del Peru, doi:10.1594/PANGAEA.603265 and doi:10.1594/PANGAEA.603267, 2007.

Hagino, K., Okada, H., and Matsuoka, H.: Spatial dynamics of coccolithophore assemblages in the Equatorial Western-Central Pacific Ocean, Mar. Micropaleontol., 39, 53–72, doi:10.1016/S0377-8398(00)00014-1, 2000.

Hallegraeff, G. M.: Coccolithophorids (Calcareous Nanoplankton) from Australian Waters, Bot. Mar., 27, 229–248, doi:10.1515/botm.1984.27.6.229, 1984.

Hay, W. W.: Carbonate fluxes and calcareous nannoplankton, in: Coccolithophores: from Molecular Processes to Global Impact, edited by: Thierstein, H. and Young, J., Springer, 509–528, 2004.

Heimdal, B.: Coccolithophores, in: Identifying marine phytoplankton, edited by: Tomas, C. R., Academic Press, San Diego, 1997.

Heimdal, B. R. and Saugestad, A.: Light microscope studies on coccolithophorids from the western Mediterranean Sea, with notes on combination cells of *Daktylethra pirus* and *Syracosphaera pulchra*, Plant Biosyst., 136, 3–27, doi:10.1080/11263500212331358491, 2002.

Hernandez-Becerril, D. and Bravo-Sierra, E.: Coccolithophorids from the west coast of Baja California, Mexico, Hydrobiologia, 452, 31–45, 2001.

Hillebrand, H., Dürselen, C., Kirschtel, D., Pollingher, U., and Zohary, T.: Biovolume calculation for pelagic and benthic microalgae, J. Phycol., 424, 403–424, 1999.

Hirata, T., Hardman-Mountford, N. J., Brewin, R. J. W., Aiken, J., Barlow, R., Suzuki, K., Isada, T., Howell, E., Hashioka, T., Noguchi-Aita, M., and Yamanaka, Y.: Synoptic relationships between surface Chlorophyll-*a* and diagnostic pigments specific to phytoplankton functional types, Biogeosciences, 8, 311–327, doi:10.5194/bg-8-311-2011, 2011.

Hofmann, G. E., Barry, J. P., Edmunds, P. J., Gates, R. D., Hutchins, D. A., Klinger, T., and Sewell, M. A.: The effect of Ocean acidification on calcifying organisms in marine ecosystems: an organism-to-ecosystem perspective, Annu. Rev. Ecol. Evol. S., 41, 127–147, doi:10.1146/annurev.ecolsys.110308.120227, 2010.

Holligan, P., Viollier, M., Harbour, D., Camus, P., and Champagne-Philippe, M.: Satellite and ship studies of coccolithophore production along a continental shelf edge, Nature, 304, 339–342,

1983.
Holligan, P. M., Fernández, E., Aiken, J., Balch, W. M., Boyd, P., Burkill, P. H., Finch, M., Groom, S. B., Malin, G., Muller, K., Purdie, D. A., Robinson, C., Trees, C. C., Turner, S. M., and van der Wal, P.:A biogeochemical study of the coccolithophore, *Emiliania huxleyi*, in the North Atlantic, Global Biogeochem. Cy., 7, 879–900, 1993.
Hood, R., Laws, E., Armstrong, R., Bates, N., Brown, C., Carlson, C., Chai, F., Doney, S., Falkowski, P., and Feely, R.: Pelagic functional group modeling: progress, challenges and prospects, Deep-Sea Res. Pt. II, 53, 459–512, doi:10.1016/j.dsr2.2006.01.025, 2006.
Iglesias-Rodríguez, M. D.: Representing key phytoplankton functional groups in ocean carbon cycle models: coccolithophorids, Global Biogeochem. Cy., 16, 1–20, doi:10.1029/2001GB001454, 2002.
Iglesias-Rodríguez, M. D., Halloran, P. R., Rickaby, R. E. M., Hall, I. R., Colmenero-Hidalgo, E., Gittins, J. R., Green, D. R. H., Tyrrell, T., Gibbs, S. J., von Dassow, P., Rehm, E., Armbrust, E. V., and Boessenkool, K. P.: Phytoplankton calcification in a high-CO_2 world., Science, 320, 336–340, doi:10.1126/science.1154122, 2008.
Inouye, I. and Pienaar, R.: New observations on the Coccolithophorid Umbilicosphaera sibogae var. foliosa (Prymnesiophyceae) with reference to cell covering, cell structure and flagellar apparatus, Eur. J. Phycol., 19, 357–369, doi:10.1080/00071618400650401, 1984.
Jin, X., Gruber, N., Dunne, J. P., Sarmiento, J. L., and Armstrong, R. A.: Diagnosing the contribution of phytoplankton functional groups to the production and export of particulate organic carbon, $CaCO_3$, and opal from global nutrient and alkalinity distributions, Global Biogeochem. Cy., 20, 1–17, 2006.
Jordan, R., Cros, L., and Young, J.: A revised classification scheme for living haptophytes, Micropaleontology, 50, 55–79, 2004.
Klaveness, D.: Coccolithus huxleyi (Lohm.) Kamptn II. The flagellate cell, aberrant cell types, vegetative propagation and life cycles, Brit. Phycol. J., 3, 309–318, 1972.
Kleijne, A.: Holococcolithophorids from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean, Mar. Micropaleontol., 17, 1–76, doi:10.1016/0377-8398(91)90023-Y, 1991.
Kleijne, A.: Extant Rhabdosphaeraceae (coccolithophorids, class Prymnesiophyceae) from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean, Scripta Geologica, 100, 1–63, 1992.
Kleijne, A., Jordan, R. W., Heimdal, B. R., Samtleben, C., Chamberlain, A. H. L., and Cros, L.: Five new species of the coccolithophorid genus *Alisphaera* (Haptophyta), with notes on their distribution, coccolith structure and taxonomy, Phycologia, 40, 583–601, doi:10.2216/i0031-8884-40-6-583.1, 2002.
Kopczynska, E. E., Savoye, N., Dehairs, F., Cardinal, D., and Elskens, M.: Spring phytoplankton assemblages in the Southern Ocean between Australia and Antarctica, Polar Biol., 31, 77–88, doi:10.1007/s00300-007-0335-6, 2007.
Langer, G., Geisen, M., Baumann, K.-H., Kläs, J., Riebesell, U., Thoms, S., and Young, J. R.: Species-specific responses of calcifying algae to changing seawater carbonate chemistry, Geochem. Geophy. Geosy., 7, Q09006, doi:10.1029/2005GC001227, 2006.
Le Quéré, C., Harrison, S., Prentice, I., Buitenhuis, E., Aumont, O., Bopp, L., Claustre, H., Da Cunha, L., Geider, R., Giraud, X., Klaas, C., Kohfeld, K., Legendre, L., Manizza, M., Platt, T., Rivkin, R., Sathyendranath, S., Uitz, J., Watson, J., and Wolf-Gladrow, D.: Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models, Glob. Change Biol., 11, 2016–2040, doi:10.1111/j.1365-2486.2005.1004.x, 2005.
Lecal, J.: Le Nannoplancton des Côtes d'Israël, Hydrobiologia, 29, 305–387, doi:10.1007/BF00189902, 1967.
Malinverno, E.: Morphological variability within the genus Calciosolenia (coccolithophorids) from the eastern Mediterranean Sea, Micropaleontology, 50, 81–91, 2004.
Manizza, M., Buitenhuis, E. T., and Le Quéré, C.: Sensitivity of global ocean biogeochemical dynamics to ecosystem structure in a future climate, Geophys. Res. Lett., 37, 3–7, doi:10.1029/2010GL043360, 2010.
Manton, I. and Oates, K.: Fine-structural observations on Pappsphaera Tangen from the Southern Hemisphere and on Pappomonas gen. nov. from South Africa and Greenland, Brit. Phycol. J., 10, 93–109, doi:10.1080/00071617500650091, 1975.
Manton, I., Sutherland, J., and McCully, M.: Fine structural observations on coccolithophorids from South Alaska in the genera Papposphaera tangen and Pappomonas manton and oates, Eur. J. Phycol., 11, 225–238, doi:10.1080/00071617600650511, 1976.
Marinov, I., Doney, S. C., and Lima, I. D.: Response of ocean phytoplankton community structure to climate change over the 21st century: partitioning the effects of nutrients, temperature and light, Biogeosciences, 7, 3941–3959, doi:10.5194/bg-7-3941-2010, 2010.
Marshall, H. G.: Phytoplankton distribution off the North Carolina coast, Am. Midl. Nat., 82, 241–257, doi:10.2307/2423833, 1969.
Menden-Deuer, S. and Lessard, E. J.: Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton, Limnol. Oceanogr., 45, 569–579, 2000.
Mohan, R., Mergulhao, L. P., Guptha, M., Rajakumar, A., Thamban, M., AnilKumar, N., Sudhakar, M., and Ravindra, R.: Ecology of coccolithophores in the Indian sector of the Southern Ocean, Mar. Micropaleontol., 67, 30–45, doi:10.1016/j.marmicro.2007.08.005, 2008.
O'Brien, C. J., Vogt, M., and Gruber, N., et al.: in preparation, 2013.
Okada, H. and McIntyre, A.: Modern coccolithophores of the Pacific and North Atlantic oceans, Micropaleontology, 23, 1–55, 1977.
Omex I project members and Wassmann, P.: Phytoplankton abundance measured on water bottle samples at station JMX_XX, doi:10.1594/PANGAEA.202662 to doi:10.1594/PANGAEA.202700, 2004.
Paasche, E.: A review of the coccolithophorid *Emiliania huxleyi* (Prymnesiophyceae), with particular reference to growth, coccolith formation, and calcification-photosynthesis interactions, Phycologia, 40, 503–529, 2002.
Pagou, K. and Assimakopoulou, G.: Abundance of microplankton from bottles SEPT-1999-K1–APRIL-2000-K6, Hellenic Center of Marine Research, Institut of Oceanography, Greece, doi:10.1594/PANGAEA.687204 to doi:10.1594/PANGAEA.687209 and doi:10.1594/PANGAEA.688625 to doi:10.1594/PANGAEA.688633, 2008.

Poulton, A. J., Charalampopoulou, A., Young, J. R., Tarran, G. A., Lucas, M. I., and Quartly, G. D.: Coccolithophore dynamics in non-bloom conditions during late summer in the central Iceland Basin (July–August 2007), Limnol. Oceanogr., 55, 1601–1613, doi:10.4319/lo.2010.55.4.1601, 2010.

Priewalder, H.: Die Coccolithophoridenflora des Locus typicus von Pseudotextularia elegans (Rzehak), Reingruberhöhe, Niederösterreich; (Maastricht), Jahrbuch Geologischen Bundesanstalt, 116, 3–34, 1973.

Quinn, P. S., Cortés, M. Y., and Bollmann, J.: Morphological variation in the deep ocean-dwelling coccolithophore *Florisphaera profunda* (Haptophyta), Eur. J. Phycol., 40, 123–133, doi:10.1080/09670260400024667, 2005.

Ramos, E.: Phytoplankton abundance in surface water in 1992, Ancon, Peru, Universidad Nacional Mayor de San Marcos, doi:10.1594/PANGAEA.465179 to doi:10.1594/PANGAEA.465192, 2006.

Ratkova, T.: ArcOD – Phytoplankton from the White Sea, Barents Sea, Norwegian Sea and Arctic Basin 1993–2003, Ocean Biogeographic Information System, unpublished data, 2012.

Reid, F. M. H.: Coccolithophorids of the North Pacific central gyre with notes on their vertical and seasonal distribution, Micropaleontology, 26, 151–176, 1980.

Riebesell, U. and Zondervan, I.: Reduced calcification of marine plankton in response to increased atmospheric CO_2, Nature, 407, 364–367, 2000.

Schiebel, R.: Distribution of diatoms, coccolithophores and planktic foraminifers along a trophic gradient during SW monsoon in the Arabian Sea, Mar. Micropaleontol., 51, 345–371, doi:10.1016/j.marmicro.2004.02.001, 2004a.

Schiebel, R.: Distribution of diatoms, coccolithophores and planktic foraminifera in the Arabian Sea, doi:10.1594/PANGAEA.736805, 2004b.

Schiller, J.: Coccolithinae, in: Kryptogamen – flora von Deutschland, Österreich und der Schweiz, edited by Rabenhorst, L., Akademische Verlagsgesellschaft m. b. H., Leipzig, 1930.

Silver, M.: Vertigo KM0414 phytoplankton species data and biomass data: abundance and fluxes from CTDs, Ocean Carbon and Biogeochemistry Data System, OCB DMO, WHOI, 2009.

Smyth, T. J.: Time series of coccolithophore activity in the Barents Sea, from twenty years of satellite imagery, Geophys. Res. Lett., 31, 2–5, doi:10.1029/2004GL019735, 2004.

Stoll, H. M., Klaas, C. M., Probert, I., Ruiz Encinar, J., and Garcia Alonso, J. I.: Calcification rate and temperature effects on Sr partitioning in coccoliths of multiple species of coccolithophorids in culture, Global Planet. Change, 34, 153–171, 2002.

Sun, J.: Geometric models for calculating cell biovolume and surface area for phytoplankton, J. Plankton Res., 25, 1331–1346, doi:10.1093/plankt/fbg096, 2003.

Takahashi, K. and Okada, H.: Environmental control on the biogeography of modern coccolithophores in the Southeastern Indian Ocean offshore of Western Australia, Mar. Micropaleontol., 39, 73–86, 2000.

Tangen, K., Brand, L. E., Blackwelder, P. L., and Guillard, R. R. L.: *Thoracosphaera heimii* (Lohmann) Kamptner is a dinophyte: observations on its morphology and life cycle, Mar. Micropaleontol., 7, 193–212, 1982.

Thierstein, H. R. and Young, J. R. (Eds.): Coccolithophores: from Molecular Processes to Global Impact, Springer, 509–528, 2004.

Tyrell, T. and Merico, A.: *Emiliania huxleyi*: bloom observations and the conditions that induce them, in: Coccolithophores: from Molecular Processes to Global Impact, edited by: Thierstein, H. R. and Young, J., Springer, 75–97, 2004.

Utermöhl, H.: Zur Vervollkommnung der quantitativen Phytoplankton-Methodik, Ver. Theor. Angew. Limnol., 9, 1–38, 1958.

van Bleijswijk, J. D. L., Kempers, R. S., Veldhuis, M. J., and Westbroek, P.: Cell and growth characteristics of types A and B of *Emiliania huxleyi* (Prymnesiophyceae) as determined by flow cytometry and chemical analyses, J. Phycol., 30, 230–241, 1994.

Verity, P. G., Robertson, C. R., Tronzo, C. R., Andrews, M. G., Nelson, J. R., and Sieracki, M. E.: Relationships between cell volume and the carbon and nitrogen content of marine photosynthetic nanoplankton, Limnol. Oceanogr., 37, 1434–1446, 1992.

Vilicic, D.: An examination of cell volume in dominant phytoplankton species of the central and southern Adriatic Sea, Int. Revue Ges. Hydrobiol., 70, 829–843, 1985.

Vogt, M., Vallina, S. M., Buitenhuis, E. T., Bopp, L., and Le Quéré, C.: Simulating dimethylsulphide seasonality with the dynamic green ocean model PlankTOM5, J. Geophys. Res., 115, 1–21, doi:10.1029/2009JC005529, 2010.

Widdicombe, C. E., Eloire, D., Harbour, D., Harris, R. P., and Somerfield, P. J.: Long-term phytoplankton community dynamics in the Western English Channel, J. Plankton Res., 32, 643–655, doi:10.1093/plankt/fbp127, 2010.

Winter, A. and Siesser, W. G. (Eds.): Coccolithophores, Cambridge University Press, New York, 1994.

Young, J., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I., and Østergaard, J. B.: A guide to extant coccolithophore taxonomy, Journal of Nannoplankton Research Special Issue 1, 2003.

Young, J. R. and Andruleit, H.: *Navilithus altivelum*: a remarkable new genus and species of deep photic coccolithophores, J. Micropalaeontol., 25, 141–151, doi:10.1144/jm.25.2.141, 2006.

Zeitzschel, B., Deckers, M., Karrasch, B., Kremling, K., Podewski, S., Stienen, C., and Ullrich, S.: Hydrochemistry and biological data measured on water bottle samples during METEOR cruise M10/2, doi:10.1594/PANGAEA.66713, 2002.

Zondervan, I.: The effects of light, macronutrients, trace metals and CO_2 on the production of calcium carbonate and organic carbon in coccolithophores: a review, Deep-Sea Res. Pt. II, 54, 521–537, doi:10.1016/j.dsr2.2006.12.004, 2007.