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Earth System Science Data Discussions

Interactive comment on "Global marine plankton functional type biomass distributions: coccolithophores" *by* C. J. O'Brien et al.

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We wish to thank the reviewer for the detailed analysis of our paper and his/her thoughtful comments, which have greatly improved the quality of this manuscript and associated dataset. A detailed reply to each point follows below:

Reviewer Comment #1:

A major point is that no effort appears to have been made to engage the specialist scientists who have spent months or years at sea collecting such data. This will inevitably greatly reduce the amount of data included in the dataset and therefore its value (this compilation only scratches the surface of what is out there; there is vastly more data than has been assembled here). The recommended approach for these

compilation exercises, and the one most usually followed (for instance in similar compilations thathave been carried out for diatoms and diazotrophs), is to write to a wide range of the foremost scientists in the field to request them to send data. This appears not to have been done in this case. I wrote out a list of 15 experts that I would have expected to have been involved; only one is actually involved. Of the two multi-author edited books titled "Coccolithophores" that have been published in the last 20 years (the most recent was published in 2004), not a single chapter author is included in the author list of this paper. This is in stark contrast to Luo et al 2012, for instance, which appears to involve all of the acknowledged most active data collectors and has therefore been able to pull in the bulk of the data on nitrogen-fixers and nitrogen fixation.

Author Response #1:

We are well aware that our compilation includes just a fraction of the data that have been collected over the years, but it was not for the lack of trying: our data compilation effort began in 2010 with a joint data request together with the authors of the diatom and Phaeocystis papers in this special issue. As part of this process we contacted a total of 164 researchers who were identified as potential data contributors and who were offered co-authorship of the respective papers (full details can be provided to the reviewer on request). These included 14 chapter authors of the two books referred to above. Of these 164, unfortunately only 13 followed up by contributing data. Of these, 9 contributions included coccolithophore abundances which are included in the present dataset.

Despite the limited number of direct contributions, the coccolithophore dataset has the second best coverage of the MAREDAT phytoplankton datasets when considered on the WOA grid (after only the picophytoplankton), and the best coverage when considered on a ten degree grid. The coccolithophore dataset is also one of only four MAREDAT datasets to include species level taxonomic data. This information allows for more precise biomass estimates as well as potential value for investigation of species composition and diversity. It is the most extensive compilation currently available of global

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coccolithophore observations, and whilst we agree that the compilation is far from complete it nevertheless provides a valuable first insight into coccolithophore distributions at a global scale.

An update of the MAREDAT datasets is planned for 2015. We hope that the publication of these initial results will encourage further contributions in the future, as the benefits from the contribution of data to such a global product will emerge.

Reviewer Comment #2:

Some ill-advised decisions have been made, including to calculate cell biomass even when the species was not reported and so the conversion from cell number to cell mass is unknown.

Author Response #2:

One of the objectives of the MAREDAT effort was to calculate biomass estimates across all functional groups. This required us to take decisions about the conversion of cell counts to biomass even when not all possible information was available, i.e., when we only the genus and not the species was known. We are well aware that this increases the uncertainty in the final estimated biomass product, but the benefit of having biomass estimates available outweighs, in our opinion, the increased uncertainty.

Recognizing this source of uncertainty, particularly where only unidentified coccolithophores are reported for a sample, we have added an additional flag column to the database to allow users to more easily use their own judgement when deciding whether or not to use these datapoints for their analyses.

The number of critical cases is not that large: Of the 57 321 unflagged rows in the raw database, 39 368 are counts of coccolithophores identified to the species or subspecies level, 11 225 to a higher taxonomic level, and 6728 are unidentified coccolithophores. Of the unidentified counts, 1719 are accompanied by coccosphere dimensions which have been used for our biomass estimates, and 3264 are zero values and

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hence valuable datapoints reporting the absence of coccolithophores in a sample. Of the remaining 1745 unidentified counts, 555 are from samples also containing identified coccolithophores. For these samples, our options were to (a) exclude entire sample due to the unidentified cells, (b) remove unidentified cells from the total biomass estimate, or (c) include a biomass estimate for the unidentified cells in the total. We have chosen option (c), since many of these datasets contain otherwise high quality data from projects such as the AMT cruises and BIOSOPE, and the alternative option of estimating biomass from only the identified cells in samples is likely to introduce even greater uncertainty to our estimates.

This leaves a total of 1190 non-zero samples of unidentified coccolithophores only, without any information regarding cell dimensions. Many of these counts are from the under-sampled Pacific Ocean. We believe that the inclusion of these few datapoints is a useful addition to the database despite the high uncertainty associated with the biomass estimates.

In response, we have added the following paragraph to section 2.3 (Quality Control, p. 9):

"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 by flag value 1, and unidentified coccolithophores by 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."

Reviewer Comment #3:

It is also unfortunate and counter-productive to calculate biomass from the coccosphere size, i.e. the size including the coccoliths. Biomass is conventionally used

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to refer to the organic carbon only. The term is not used to refer to the sum of POC + PIC, and to do so in the dataset is misleading and would lead to confusion and even scientific errors in subsequent studies if they used the 'biomass' data without realising that in fact it represented both POC and PIC. It does seem sensible to me to include in the dataset estimates of both POC and PIC (as well as of cell concentrations), but not to lump the two of them together.

Author Response #3:

While we agree that cytoplasm dimensions would be the ideal measurement from which to calculate biomass estimates, unfortunately these measurements are not readily available for most species in the database. We have nevertheless made changes to our biomass estimates to better reflect the organic biomass component of coccolithophore cells. We have added a table of cytoplasm measurements for 16 species (Table 2; Sources: Stoll et al. 2002, Poulton et al. unpublished data). These data show cytoplasm diameters ranging from 30 to 90% of the total coccosphere diameter. Given the limited data availability and considerable discrepancies between the two data sources, we have chosen to use the mid-point of these values, with cytoplasm dimensions estimated as 60% of coccosphere dimensions for all species in the dataset. Our resulting biomass estimates are consistent with measured carbon content for Emiliania huxleyi, and our maximum biomass estimates per sample are comparable to literature estimates of coccolithophore biomass.

We have added the following paragraphs to section 2.2 (Biomass Conversions, p. 6):

"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

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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 %)."

"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 more heavily calcified cells, and underestimate biomass for more weakly calcified cells. Biovolumes are calculated based on the mid-point of coccosphere dimensions. Uncertainty ranges are provided using biovolumes and biomasses calculated from 0.6 * minimum coccosphere dimensions and 0.6 * maximum coccosphere dimensions."

"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)."

We have added the following paragraph to section 3.2.4 (Uncertainty, pp. 12-13): "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, Emiliania huxleyi, our mean biomass estimate of 13 pg C cell -1 falls within

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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."

We have added the following paragraph to section 4 (Discussion, p. 13):

"The estimation of cell biovolumes from coccosphere dimensions is likely to result in additional errors which are difficult to quantify at present. A more accurate estimation of coccolithophore biomass will be possible only with improved understanding of coccolithophore cytoplasm dimensions (e.g. Stoll et al. 2012), and we highlight this as a key data requirement for improved estimates of coccolithophore biomass from abundance data."

We have added the following paragraphs to section 4 (Discussion, p. 14):

"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."
"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 Emiliania huxleyi blooms: maximum of 127 μg C l -1) are similar to past estimates from light microscopy-based cell counts (e.g. Holligan et al. 1993: 130 μg C l -1) but slightly lower than coccolithophore biomass estimates from fatty acid biomarkers in mesocosm experiments (de Kluijver et al. 2010: 190 μg C l -1)."

We have added the following paragraph to section 4 (Discussion, p. 15):

"We have not included estimates of inorganic carbon content in the database, as we

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

Reviewer Comment #4:

The issue of morphotypes, and whether to include this information if available, is not mentioned.

Author Response #4:

We have addressed this issue by adding the following sentence to section 2.2 (Biomass Conversions, p. 5):

"Morphotype information is reported for E. huxleyi in only one dataset, and we have therefore chosen to use a single biomass conversion factor for all occurrences of this species."

Reviewer Comment #5:

The most widely used taxonomy guides, those produced by Jeremy Young and colleagues, should be mentioned.

Author Response #5:

We have added references to Young et al. (2003) to the supplementary table where appropriate. Many other taxonomy guides and species descriptions co-authored by Jeremy Young and colleagues are already referenced in the supplementary table of species dimensions and shapes.

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Reviewer Comment #6:

Most seriously, there is no mention of the different techniques used to quantify coccolithophore abundance. A key paper on the topic (Bollmann et al, 2002) is not even cited. This is important because there is quite a wide variety of different techniques with important differences in the information they yield. Some of the techniques are: (1) visual counting from scanning electron microscope images, (2) visual counting under a light microscope, (3) visual counting under a light microscope using cross-polarised light, (4) flow cytometry, and (5) automated identification using the SYRACO software. Depending on the technique used there is a great variation in the quality of the resulting information. Some methods yield robust estimates, others are not proven. Some can count small coccolithophores but not large. Other techniques can count large but not small coccolithophores. Some are more laborious tending to lead to smaller numbers of cells being counted and hence, potentially, errors associated with concentration estimates derived from small numbers. A cell or biomass concentration estimate that is derived from seeing just one cell on a microscope image and then scaling up has much greater uncertainty compared to caluculations from counting 100 cells in a sample. These issues are not even mentioned in the paper, much less dealt with. For instance, it is arguably better to exclude information from some sources in order to maintain a high overall standard to the data quality. At the very least a column should be added to the dataset to indicate the quantification method, so that subsequent users of the dataset can make their own decisions about which sorts of data to include and which not. Uncertainties associated with scaling up from counts of scarce species should be calculated and reported in the dataset.

Author Response #6:

We agree with the reviewer that the biases introduced by different quantification methods need to be better addressed. While the previous data sheet already included a column denoting the quantification method, we have now made this information more accessible by providing the same information in numerical form in an additional flag col-

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umn. We have also made additional attempts to determine the quantification method used where this information was not originally provided. The database contains 4209 non-zero counts analysed by light microscopy, 500 from SEM and 197 from flow cytometry. No datasets reported automated image analysis as the quantification method. The sampling method is not known for the remaining 4287 non-zero samples. We have added a quantitative comparison of data collected using the different methods to the supplementary materials. Based on this analysis, we have excluded the flow cytometry data from the gridded dataset and the analyses presented in the paper. All other data are retained in the database, although we note and discuss the likely biases introduced by comparing data analysed using light microscopy and SEM. We have also added color-coded symbols to figure 1 indicating the quantification method used for different datapoints.

We have added the following paragraphs to section 2.3 (Quality Control, pp. 8-9):

"An additional flag column denotes the quantification method used for determining coccolithophore abundance. Of the 9193 non-zero samples included in the database, 3822 are known to have been analysed using light microscopy, 452 using SEM and 197 with flow cytometry. For the remaining 4722 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 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, G. 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 (see supplementary material, Figure S1, Table S2). Our comparison of coccolithophore abundance and biomass shows larger differences between

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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 than the median for light microscopy studies by a factor of 4, the maximum values reported for each are similar. Since the quantification method is unknown for more than 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 197 samples collected using flow cytometry from the gridded dataset. These values are significantly higher again than those collected using either SEM or light microscopy."

We have added the following paragraphs to section 4 (Discussion, p. 14):

"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 sim-

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ilar 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."

Finally, we have added the following final paragraph to the discussion:

"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."

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