



## MAREDAT: towards a World Ocean Atlas of MARine Ecosystem DATa

E. Buitenhuis, M. Vogt, R. Moriarty, N. Bednaršek, S. Doney, Karine Leblanc, C. Le Quéré, Y.-W. Luo, C. O'Brien, T. O'Brien, et al.

### ► To cite this version:

E. Buitenhuis, M. Vogt, R. Moriarty, N. Bednaršek, S. Doney, et al.. MAREDAT: towards a World Ocean Atlas of MARine Ecosystem DATa. *Earth System Science Data: Papers in open discussion*, 2012, 5 (2), pp.1077-1106. 10.5194/essdd-5-1077-2012 . hal-03278277

**HAL Id: hal-03278277**

**<https://univ-angers.hal.science/hal-03278277>**

Submitted on 17 Jul 2021

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Received: 13 November 2012 – Accepted: 14 November 2012  
– Published: 23 November 2012

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Published by Copernicus Publications.

## ESSDD

5, 1077–1106, 2012

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## Abstract

We present a summary of biomass data for 11 Plankton Functional Types (PFTs) plus phytoplankton pigment data, compiled as part of the MARine Ecosystem biomass DATA (MAREDAT) initiative. The goal of the MAREDAT initiative is to provide global gridded data products with coverage of all biological components of the global ocean ecosystem. This special issue is the first step towards achieving this. The PFTs presented here include picophytoplankton, diazotrophs, coccolithophores, *Phaeocystis*, diatoms, picoheterotrophs, microzooplankton, foraminifers, mesozooplankton, pteropods and macrozooplankton. All variables have been gridded onto a World Ocean Atlas (WOA) grid ( $1^\circ \times 1^\circ \times 33$  vertical levels  $\times$  monthly climatologies). The data show that (1) the global total heterotrophic biomass (2.0–6.4 Pg C) is at least as high as the total autotrophic biomass (0.5–2.6 Pg C excluding nanophytoplankton and autotrophic dinoflagellates), (2) the biomass of zooplankton calcifiers (0.9–2.3 Pg C) is substantially higher than that of coccolithophores (0.01–0.14 Pg C), (3) patchiness of biomass distribution increases with organism size, and (4) although zooplankton biomass measurements below 200 m are rare, the limited measurements available suggest that *Bacteria* and *Archaea* are not the only heterotrophs in the deep sea. More data will be needed to characterize ocean ecosystem functioning and associated biogeochemistry in the Southern Hemisphere and below 200 m.

Microzooplankton database: doi:10.1594/PANGAEA.779970.

## 1 Introduction

The MARine Ecosystem Model Intercomparison Project (MAREMIP) was initiated in 2007 to facilitate communication, collaboration and the sharing of data and procedures, such as model evaluation techniques, between research groups developing Dynamic Green Ocean Models (DGOMs; Le Quéré et al., 2005). DGOMs are global ocean biogeochemical models that represent more than two Plankton Functional Types

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(PFTs), thus including more ecological interactions than the unidirectional flow represented in Nutrient Phytoplankton Zooplankton Detritus (NPZD) models. After an exploratory phase, a kick-off meeting was held in 2009 (Le Quéré and Pésant, 2009). At this meeting it was decided to collectively synthesize existing biomass concentration measurements for “key plankton functional types that need to be simulated explicitly to capture important biogeochemical processes in the ocean” (Le Quere et al., 2005). This MARine Ecosystem biomass DATA (MAREDAT) special issue in Earth System Science Data is the result, with 11 papers on 11 PFTs and 1 paper describing a database of phytoplankton pigments ([http://www.earth-syst-sci-data.net/special\\_issue7.html](http://www.earth-syst-sci-data.net/special_issue7.html)). There are six papers relating to autotrophic groups: picophytoplankton (Buitenhuis et al., 2012a), diazotrophs (Luo et al., 2012), coccolithophores (O'Brien et al., 2012), *Phaeocystis* (Vogt et al., 2012), diatoms (Leblanc et al., 2012), and the HPLC-based phytoplankton pigment database (Peloquin et al., 2012). There are six papers relating to heterotrophic groups: picoheterotrophs (*Bacteria* and *Archaea*, Buitenhuis et al., 2012b), microzooplankton (here, we briefly reiterate and correct the microzooplankton biomass database that was recently published by Buitenhuis et al., 2010), planktic foraminifers (Schiebel and Movellan, 2012), mesozooplankton (Moriarty and O'Brien, 2012), pteropods (Bednaršek et al., 2012), and macrozooplankton (Moriarty et al., 2012). By this collaborative effort we are able to provide global databases for 9 out of the 10 PFTs that were proposed by Le Quéré et al. (2005).

The missing PFT is mixed phytoplankton, which is mostly made up of autotrophic dinoflagellates and nanophytoplankton other than coccolithophores and *Phaeocystis*. Nanophytoplankton are a taxonomically diverse group of algae, including prymnesiophytes, chlorophytes, and cryptophytes, which are not consistently treated as a distinct group in the literature. We excluded this PFT from the current collection of data because where the term is used in the literature it often includes members of PFTs that have been included in the data products in this special issue. Nanophytoplankton represent a significant part of the phytoplankton biomass. Demarcation issues between nanophytoplankton and the other PFTs will need to be resolved in order to improve

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our ability to describe the global ocean ecosystem, both directly and through models. Chemotaxonomic interpretation of the HPLC-based phytoplankton pigment database described in this special issue (Peloquin et al., 2012) offers one pathway toward resolving mixed phytoplankton biomass distribution. However, the most reliable way to prevent double counting and achieve a consistent dataset would be to measure the biomass of all phytoplankton groups in the same samples in transects that cross all ocean basins.

A similar demarcation issue occurs for the zooplankton. The sum of micro-, meso-, and macrozooplankton should represent the total zooplankton population. However, although small foraminifers are microzooplankton, they tend not to be included in microscopic counts. Likewise, pteropods fall partly in both meso- and macrozooplankton size-classes. In macrozooplankton studies, the focus is usually taxon specific, at a variety of levels between phylum and species. The sum of all relevant phyla is rarely accounted for, making an accurate assessment of the total biomass difficult.

In addition to the 9 PFTs mentioned above, we include data on two groups of zooplankton calcifiers, the calcite producing planktic foraminifers (Schiebel and Movelan, 2012) and the pteropods (Bednaršek et al., 2012), which include both shelled aragonite producing species and naked species. These data should be valuable in complementing research into phytoplankton calcifiers, i.e. coccolithophores, and in addressing the biogeochemical cycling of alkalinity, and thus of atmospheric CO<sub>2</sub>. The diazotroph dataset contains both biomass estimates and nitrogen fixation rate data, which are useful to evaluate the ecological roles of diazotrophs.

Since 1994, the World Ocean Atlas (WOA) has been synthesizing interpolated global gridded climatological datasets of physical and chemical parameters (temperature, oxygen, nutrients etc.). Initially, these datasets were annual averages, but increasingly they cover seasonal variations on a monthly basis in the surface ocean. WOA provides datasets that are filled by interpolation. These data products are used extensively by global ocean modelers for initialization and/or evaluation (e.g. Doney et al., 2009), in combination with biogeochemical datasets such as dissolved inorganic

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carbon, alkalinity,  $p\text{CO}_2$ , and DMS, which have been synthesized through initiatives like MAREDAT. The goal of MAREDAT is to provide similar data products and coverage for all biological components of the global ocean ecosystem, and this special issue is the first step towards achieving this. For ease of use we have gridded the biological variables onto the same grid as used for the WOA ( $1^\circ \times 1^\circ \times 33$  vertical levels  $\times$  monthly climatologies). Because of the large seasonal variability in biological components over most of the ocean, we have chosen to provide monthly files from the start. We accept that using a 4D grid will not yet provide enough information to furnish filled (interpolated) datasets. Hence, we did not interpolate the data but produced datasets with missing values. Our aim in bringing together these data has been to (1) stimulate research on observation-based improvements in our knowledge of the ecological and biogeochemical functioning of the ocean and (2) provide in situ-based data constraints for numerical models and satellite algorithms that distinguish multiple plankton groups.

## 2 Data

Both the raw data files and the gridded files that were compiled for the 11 PFTs and the phytoplankton pigments are publicly available from the PANGAEA World Data Centre (<http://www.pangaea.de/search?q=maredat>) and the MAREMIP website (<http://maremip.uea.ac.uk/.maredat.html>). The raw data include longitude, latitude, depth, date, abundance, biomass conversion factors, biomass, references and quality control flags. The pigment database contains pigment concentrations instead of abundance, biomass and biomass conversion factors. In order to arrive at a consistent collection of gridded data products for all abundance based PFTs, they were all gridded with the same program, and include the number of observations, average abundance, average biomass, median abundance, median biomass, standard deviation of abundance, and standard deviation of biomass, both for the total datasets and for the non-zero observations. In some datasets, some of this information was excluded for methodological reasons: there is no abundance for diazotrophs or mesozooplankton, and the databases for

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picoheterotrophs, diatom and mesozooplankton contain no zero observations. Although abundance is available for all the diazotroph sub-taxa, the total abundance was not included in the gridded file, since the cell volumes of these sub-taxa differ by more than 3 orders of magnitude. The *Phaeocystis* database contains the above biomass information with and without an estimate of the gelatinous mucus surrounding colonial cells. The diazotroph database includes biomass information based on cell counts and on *nifH* gene counts. The biomass concentrations of foraminifers are organic carbon only, while the coccolithophore and pteropod biomasses include both organic and inorganic carbon. In this paper, we only use the *Phaeocystis* biomass without mucus, and the diazotroph biomass based on cell counts.

Furthermore, we provide a database of microzooplankton distribution that was recently published by Buitenhuis et al. (2010). Some errors in the previous version (C. Stock, personal communication, 2011) have been corrected, and we also took this opportunity to grid this dataset in the same way as the others (<http://doi.pangaea.de/10.1594/PANGAEA.779970>).

## 2.1 Quality control by Chauvenet's criterion

In all contributing PFT papers Chauvenet's criterion has been used to exclude very high values from the gridded databases (Glover et al., 2011). While all collated data had already been quality controlled by the contributing researchers, there was still a risk of overrepresentation of high values from studies that (1) specifically targeted the occurrence/bloom of the relevant PFT, (2) high productivity coastal sites or (3) from errors in the reported units. Chauvenet's criterion assumes that the data has a normal distribution and rejects data on the presumption that if a set of  $n$  measurements was carried out twice, outliers would be excluded at  $1/(2n)$  probability of occurrence, thus preventing any bias between the outlier rejection in the two sets of measurements. The critical value occurs at  $p = 1 - 1/2n$ . Only the diatom data were normally distributed. All the other datasets were log-transformed. Log-transformation of biomass values meant the exclusion of zero values. Zero and very low values for biomass are a true reflection

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of the ecology of the oceans. Zero abundance/biomass is often treated as a lack of measurement even though it supplies useful information about the absence of an organism or PFT. This means that zero values are usually underrepresented, especially in the deep sea. Therefore, a one-sided Chauvenet's criterion was applied to identify only the high value outliers. For the smallest dataset (foraminifers,  $n = 1087$  non-zero observations) the critical value was 3.50 times the standard deviation from the average, while for the largest dataset (mesozooplankton,  $n = 153\,163$ ) it was 4.65 times the standard deviation. The pigment database was subjected to a different set of quality control procedures as described by Peloquin et al. (2012).

## 2.2 Gridding

All PFT and pigment data were gridded on a  $1^\circ \times 1^\circ$  horizontal grid, with gridbox centres from  $179.5^\circ$  W to  $179.5^\circ$  E and  $89.5^\circ$  S to  $89.5^\circ$  N. The vertical axis also follows the WOA spacing, centred on the 33 depths: 0, 10, 20, 30, 50, 75, 100, 125, 150, 200, 250, 300, 400, 500, 600, 700, 800, 900, 1000, 1100, 1200, 1300, 1400, 1500, 1750, 2000, 2500, 3000, 3500, 4000, 4500, 5000, and 5500 m. The time axis uses a climatological year with 12 months. By using a climatological year we implicitly ignore any temporal trend in the datasets, some of which span several decades, but at the present coverage this seemed justified.

## 2.3 Patchiness

We use the following formula as a mathematical representation of the patchiness of the horizontal distribution of the PFTs summed over all depths:

$$P = \bar{B} \times \sqrt{(\Sigma((L - B)^2)/(n - 1))} \quad (1)$$

where  $P$  is patchiness,  $\bar{B}$  is mean biomass,  $L$  is the average within  $10^\circ$  longitude and latitude of the individual observations  $B$ , and  $n$  is the number of observations.

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## 3 Results

### 3.1 Microzooplankton biomass database

The microzooplankton biomass database contains 4044 georeferenced data points. The gridded database contains 2029 data points (Fig. 1, Table 1). Data from the Northern Hemisphere makes up 64 % of the database, data from the top 225 m makes up 96 % of the database, and data from the spring and summer months makes up 63 % of the data. The average biomass is  $7.0 \pm 15.3 \mu\text{g C L}^{-1}$  with a median of  $1.8 \mu\text{g C L}^{-1}$ . Biomass is considerably lower in the tropics ( $3.4 \pm 7.5 \mu\text{g C L}^{-1}$ ) than in the Northern temperate ( $23\text{--}67^\circ\text{N}$ ,  $7.9 \pm 18.7 \mu\text{g C L}^{-1}$ ) and Southern temperate regions ( $8.4 \pm 13.2 \mu\text{g C L}^{-1}$ ), and increases further towards the Arctic ( $9.7 \pm 9.9 \mu\text{g C L}^{-1}$ ) and Antarctic ( $16.1 \pm 25.5 \mu\text{g C L}^{-1}$ ).

Compared to the microzooplankton database published by Buitenhuis et al. (2010), the corrected database contains both lower and higher values. Both the mean and the median of the whole dataset have decreased.

### 3.2 Comparison of PFT biomasses

The number of data points that are available for each PFT differs by two orders of magnitude (Table 2). The larger databases have been built on earlier data synthesis efforts (O'Brien et al., 2002; Vaultot et al., unpublished data; Gosselin et al., unpublished data). We intend to maintain this group effort and extend the databases in future. By making both the raw and gridded databases publicly available we also hope to encourage other researchers to publish extended versions. The horizontal distribution of each PFT at selected depths is presented in the contributing papers. Here, we compare the global average vertical profiles of the 11 PFTs and phytoplankton pigments (Fig. 2) and the zonal average sections (depth versus latitude) of the 11 PFTs in the top 200 m (Fig. 3, for the zonal average sections of pigments see Fig. 8 in Peloquin et al., 2012).

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### 3.2.1 Patchiness

We calculated the horizontal patchiness of each PFT. There is a clear increase in patchiness with organism size (Fig. 4), though the relationship is different for autotrophs (patchiness =  $2.14 \times \log(\text{size}) + 0.98$ ,  $n = 5$ ,  $p = 0.04$ ) and heterotrophs ( $\log(\text{patchiness}) = 0.25 \times \log(\text{size}) - 0.35$ ,  $n = 6$ ,  $p = 0.04$ ). This increased patchiness may reflect a change from small K-selected organisms, which tend to form a constant background biomass, to large r-selected organisms (Mac Arthur and Wilson, 1967), which go through bloom and bust cycles. For the zooplankton it may in addition reflect a tendency for larger organisms to swarm.

### 3.2.2 Autotrophic biomass

The highest phytoplankton biomass recorded in our data sets is found for *Phaeocystis* (Fig. 2a). As can be seen in Fig. 7 of Vogt et al. (2012), there is considerable sampling bias towards coastal waters, where dense *Phaeocystis* blooms can be a regular occurrence, and under which conditions often a mix of colonial and single cells are found. Under non-bloom conditions, *Phaeocystis* is mostly found as single cells, which cannot be distinguished from other nanophytoplankton with standard microscopic protocols, and therefore such measurements of background numbers of single *Phaeocystis* cells are almost absent from the database.

The next most abundant phytoplankton PFTs are picophytoplankton and diatoms (Fig. 2a). Except for a likely sampling bias of high diatom biomasses at 125 m depth, this is consistent with accepted wisdom about the importance of these two groups. However, dominance of picophytoplankton in the low latitudes and diatoms in the temperate latitudes has been suggested (Alvain et al., 2005; Uitz et al., 2006), while our plots of zonal average biomass show very little latitudinal differences in these groups (Fig. 3a, e). Dominance of picophytoplankton in low latitudes can be consistent with a homogenous latitudinal distribution, because of the increase in biomass from low to temperature latitudes (Fig. 3f), but for diatoms there is a real discrepancy.

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The average biomass of coccolithophores is surprisingly low (Fig. 2a), though it is almost constant down to 150 m, which is consistent with previous studies which showed the importance of coccolithophores in the lower euphotic layer (Cortés et al., 2001; Haidar and Thierstein, 2001). Coccolithophore biomass in the upper 70 m is lower even than diazotroph biomass, though the latter have hardly been measured at high latitudes (Fig. 3b), where they are thought not to occur (Carpenter, 1983).

### 3.2.3 Comparison of autotrophic biomass with pigment distributions

Recent syntheses suggest that virtually no pigment can be unequivocally assigned to quantify one marine algal type or species, since most of these pigments are shared across multiple phytoplankton taxa (Higgins et al., 2011). For this reason, statistical methods employing multiple pigment to chlorophyll ratios are required to adequately resolve the algal community composition (e.g., Mackey et al., 1995; Van den Meersche et al., 2008). Nonetheless, a preliminary analysis of the basin-scale distribution of a few key diagnostic pigments from the global phytoplankton pigment database (Peloquin et al., 2012) permits a rough comparison with some of the autotrophic biomass distributions from the abundance databases (Fig. 3). For example, zeaxanthin, roughly indicative of the presence of cyanobacteria, exhibited maximum concentration around the equatorial region (Figs. 8l and 9l in Peloquin et al., 2012). This is consistent with the biomass data of *Prochlorococcus* and *Synechococcus* (Fig. 6a, b in Buitenhuis et al., 2012a) and the observed lack of diazotroph biomass at high latitudes (Fig. 3b, Luo et al., 2012). In addition, divinyl chlorophyll *a* is a strong biomarker for the presence of *Prochlorococcus*. Concentration of this pigment in the subtropics occurs at slightly deeper depths in the Southern Hemisphere than in the Northern Hemisphere (Fig. 9f in Peloquin et al., 2012) mirroring those patterns observed in the *Prochlorococcus* biomass distribution (Fig. 6a in Buitenhuis et al., 2012a). Fucoxanthin, a widely prevalent pigment among diatom species, exhibits maxima at high latitudes, particularly in the Southern Hemisphere (Fig. 9g in Peloquin et al., 2012). However, Fig. 3e indicates much less meridional variability in diatom abundance, which further highlights the need

for incorporating the complexity of multiple pigment ratios when assessing phytoplankton distributions.

5 In order to also compare the depth profiles of biomass from the abundance and pigment databases, we first use pigment concentrations to calculate the contribution of different size classes of the phytoplankton to the overall chlorophyll concentration using the conversion factors of Uitz et al. (2006), and then convert chlorophyll to biomass using the C : Chl ratios of the PlankTOM5.3 model (Buitenhuis et al., 2012c), which uses photosynthetic parameters synthesised by Geider et al. (1997). Because the C : Chl ratio of diatoms is about a third of the other two phytoplankton groups in the model,  
10 we use one profile of C : Chl ratios as a function of depth for diatoms and another profile for all other phytoplankton. The resulting pigment based biomasses for diatoms and prokaryotes agree quite well with the abundance based biomasses (Fig. 2a, c). The pigment based biomass for nanophytoplankton is close to the abundance based biomass of coccolithophores plus picoeukaryotes. This is rather surprising given the  
15 taxonomic diversity of larger eukaryotes that have not been included in the biomass from abundance, and the exclusion of *Phaeocystis* biomass. The biomass of dinoflagellates is estimated at roughly a third of the diatom biomass.

A thorough chemotaxonomic analysis of the global pigment database will reveal patterns in phytoplankton community structure on finer scales, as well as potentially contribute missing information on autotrophic dinoflagellates and nanophytoplankton. In  
20 concert with MAREDAT biomass development and analysis, analysis of global pigment distributions will help further guide the representation of all PFTs in ecosystem models.

### 3.2.4 Heterotrophs

The largest zooplankton biomass is found for macrozooplankton, up to  $59 \mu\text{g C L}^{-1}$  at  
25 20 m depth (Fig. 2b). Macrozooplankton include many species that vertically migrate, so this sharp biomass peak at shallow depth could well be realistic, although as noted above, the biomass distribution of all PFTs tends to become more patchy with increasing organism size (Fig. 4), thus increasing the errors around the means. The biomass

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of planktic foraminifers is also quite large, up to  $44 \mu\text{g C L}^{-1}$  at 10 m depth, and decreases more gradually with depth than the biomass of macrozooplankton (Fig. 2b). At present, the database of foraminifers is limited to the Northern Hemisphere (Fig. 3i). The biomass of picoheterotrophs, mesozooplankton, microzooplankton and pteropods is fairly similar in the top 100 m, around  $6 \mu\text{g C L}^{-1}$  (Fig. 2b), while below 100 m the microzooplankton biomass is about half that of the picoheterotrophs and mesozooplankton, and pteropod biomass about a tenth, although there are no mesozooplankton data below 500 m.

The numbers of observations drop dramatically below 1000 m for the zooplankton. Picoheterotrophs are the only PFT for which there are still around 100 observations at each level down to 3000 m. It is difficult to make definite statements about the ecology of the deep sea with so little information, but the data suggest that there are non-negligible concentrations of zooplankton in the deep sea: up to  $6 \mu\text{g C L}^{-1}$  macrozooplankton in the mesopelagic and  $0.19 \mu\text{g C L}^{-1}$  microzooplankton below 2750 m, compared to  $0.36 \mu\text{g L}^{-1}$  picoheterotrophs. These biomass concentrations could make substantial contributions to global ocean biogeochemical cycles because of the large volume of the deep sea, and could be quite different from assuming that all deep sea activity is from picoheterotrophs.

### 3.2.5 Global PFT biomasses

The integrated global biomasses of the 11 PFTs are presented in Table 1. A low estimate was calculated by multiplying the median biomass at each depth by the volume of water at that depth, and a high estimate by using the mean concentrations at each depth. We interpolated biomass between depths without observations. The main uncertainties in the biomass estimates are the uncertainties around conversion from abundances to biomasses, and also the tendency to sample near the coast or where a PFT is thought to occur or even bloom. Because of the latter sampling bias, the maximum global biomasses are likely to be overestimates.

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We compare our phytoplankton biomass concentrations to the WOA 2005 total chlorophyll measurements. Without conversion to carbon this equates to 18 to 30 Tg Chl. We calculated the total phytoplankton biomass by multiplying the WOA 2005 chlorophyll concentration by the C : Chl ratio profile of the PlankTOM5.3 model (Buitenhuis et al., 2012c). The sum of our phytoplankton PFT biomasses is between 0.7 and 1.6 times the total phytoplankton derived from WOA chlorophyll down to 250 m (Fig. 2d), despite the fact that we did not include a large part of the nanophytoplankton nor the autotrophic dinoflagellates. One of the reasons for the overestimate at the surface is probably a strong sampling bias in the *Phaeocystis* dataset towards high values, as suggested above. Dividing our phytoplankton carbon without *Phaeocystis* by WOA chlorophyll results in C : Chl ratios of between 44 and 99 down to 250 m, except at 125 m where diatom biomass is unexpectedly high. While these are reasonable C : Chl ratios, they probably represent a spuriously close agreement by a combination of an underestimation due to not including dinoflagellates and some nanophytoplankton and an overestimation due to an overrepresentation of coastal samples. The coastal ocean represents 5 % of the ocean area, but phytoplankton biomass in the coastal ocean represents between 10 % (diazotrophs) and 44 % (*Phaeocystis* and diatoms) of the respective databases.

For the phytoplankton both the biomass and the number of observations decrease rapidly below 225 m. For diatoms, and in particular for *Phaeocystis*, we suspect an additional possible bias, because there are a few high values at depth, which show a considerable departure from the expected decrease of biomass with depth. These high concentrations below the euphotic zone are likely to be sinking cells after a bloom in the upper ocean rather than viable populations. However, recent samples from a depth range of 2000–4000 m that were taken during the Malaspina 2010 expedition confirm the ubiquitous presence of morphologically well-preserved, living phytoplankton cells of different taxa in the deep ocean (Agusti et al., ASLO conference presentation, 2012). The latter results suggest the existence of a far more efficient biological pump than previously thought, or the presence of physiological mechanisms that preserve cells at

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high pressures and low temperatures. We have integrated *Phaeocystis* biomass only to 225 m, and diatoms to 550 m.

For the picoheterotrophs, estimating global biomass from the depth profile seems to give reasonable results, since there are still a fair number of observations and the biomass in the deep sea is fairly homogenous. However, the uncertainty about abundance to biomass conversion applies to picoheterotrophs as well. For the mesozooplankton the biomass has only been integrated where there was data down to 500 m, and for the pteropods the biomass has only been integrated down to 1050 m (with only 4 observations between 1050 and 2000 m).

### 3.2.6 Comparison of autotrophic and heterotrophic PFT biomass

In order to place PFT biomass in a wider context, total heterotrophic biomass is examined in relation to total autotrophic biomass in the open ocean (Fig. 5). The median concentration for each group is considered. Lower biomass in the autotrophic component of the ecosystem reflects the higher turnover and metabolic costs of these small organisms (Odum, 1971). With higher turnover and metabolic costs a low standing crop with high productivity can supply higher trophic levels with the energy that is then stored in their biomass because of lower turnover and metabolic costs. As the data for each plankton group presented in Fig. 5 are mainly representative of the open ocean environment it is not surprising that an inverted pyramid is found with a high H : A (heterotroph : autotroph) ratio, as predicted by Gasol et al. (1997). Judging from the standard deviation associated with many of the PFTs (see Table 1) much work needs to be carried out before a more precise representation of both the autotrophic and heterotrophic plankton may be presented.

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## 4 Discussion

At a time when we, the human species, are subjecting the biosphere to unprecedented rates of change, we know very little at the global scale of the baseline functioning of the biosphere. There is a large gap between the detailed but anecdotal information that is available about the physiology of individual species under particular in situ or controlled laboratory conditions, and what we can say about the functioning of the biosphere as a whole. In ocean ecosystem modeling this gap only began to be addressed in the last decade. The present effort at synthesizing data on the global biomass distribution of most of the PFTs representing the lower trophic levels of the ocean ecosystem is the first attempt at comprehensively addressing this gap. It is necessarily crude and raises more questions than it answers. These questions indicate that despite the scarcity of data for most groups we still know much more about the abundance of organisms than about their carbon content/elemental composition, and much more about places where organisms are abundant than about the much larger volumes where biomass is relatively low.

Information becomes even more anecdotal, and understanding more scarce, when looking at time scales longer than a few seasons. For large regions of the global ocean systematic changes at an interannual scale, or longer, are largely unknown for most PFTs. Extending our perspective to the longer term and geological time scales, MAREDAT data may lead to a better understanding of both environmental and climate change, and the rate of CO<sub>2</sub> increase experienced over not only glacial-interglacial cycles but also since the beginning of industrialization. Over time intervals of millions of years, distribution and size of planktic foraminifers (Schmidt et al., 2004) and coccolithophores (Henderiks and Pagani, 2007) have been affected by climate change, and this might also be true for other PFTs. The MAREDAT approach is a step towards a more complete, qualitative and quantitative understanding of PFTs and associated feedbacks with past and future environmental and, in particular, climate change at a global scale and over long intervals of time.

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Currently, at least two large-scale programs are collecting plankton samples that will increase our knowledge on plankton community composition and species diversity in the global oceans. The Tara Oceans expedition (<http://oceans.taraexpeditions.org>) is collecting plankton samples during 2012–2014 for a depth range of 0 to 200 m, including samples from all the major ocean basins. The Malaspina 2010 expedition (<http://www.expedicionmalaspina.es>) completed its journey in 2011, and collected samples from the deep oceans, at depths down to several thousand metres (Laursen, 2011). The latter expedition will furnish us with new data to increase our understanding of deep ocean ecosystems, while the former will increase data coverage in the upper layers of the ocean.

The ranges of global biomass inventories we calculated from the profiles of median and mean biomass in several cases span more than an order of magnitude. Despite this uncertainty they indicate that heterotrophic PFTs are at least as abundant as autotrophic PFTs (Table 1, Fig. 2c), even if we account for the risk of double counting foraminifers as microzooplankton and pteropods as macrozooplankton in the sum of the zooplankton biomasses. Within the uncertainty in the data this is in agreement with Gasol et al. (1997), who estimated that the open ocean biomass of phytoplankton, total zooplankton and picoheterotrophs is roughly the same. We have compared our estimates of the sum of the available total phytoplankton biomass estimates with in situ chlorophyll. We find the sum of phytoplankton biomass is higher than biomass estimated from chlorophyll. This is likely due to a bias towards high values, because of more frequent sampling in the coast and in blooms. In future updates of the databases we intend to diminish this bias by including additional observational data and improving the cell to carbon conversion algorithms, in particular for those PFTs with a large range of morphotypes and cell sizes. This will allow a better determination of total phytoplankton biomass in the global ocean.

Plankton are governed by physical, chemical and biological processes that occur on a vast variety of temporal and spatial scales. This is one reason why quite large datasets are needed to reliably estimate the global biomass distribution of any PFT.

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Physical processes can drive patchiness in PFTs on scales from millimeters to thousands of kilometers (Pinel-Alloul, 1993; Folt and Burns, 1999). Over fine scales, millimeters to tens of meters, biological processes are often more important. For the picoheterotrophs, the estimated global biomass using the median and mean concentrations is very similar, indicating that the horizontal variation in biomass makes only a small contribution to the uncertainty in the estimated global biomass. This range does not include the uncertainty from the respective conversion factors from abundance to biomass. For the autotrophic PFTs, horizontal variability is larger (Fig. 4), and the difference between the median and the mean is more than an order of magnitude for three PFTs (Table 1). For diazotrophs this variability is compounded by lack of spatial coverage, but for coccolithophores and pteropods there is also large variability despite a better spatial coverage (Table 2, Fig. 3). For the zooplankton PFTs, individual behaviour, e.g. mating, predator avoidance and searching for food (Folt and Burns, 1999), and variables such as food concentration, swimming behavior (Pinel-Alloul, 1993) and species interactions (Mackas et al., 1985) are important examples of small scale biological processes that affect patchiness. Growth rates for a number of groups within the macrozooplankton, particularly the gelatinous members, salps, ctenophores, cnidarians and appendicularians are higher than those of mesozooplankton copepods (Hirst et al., 2003). The ability of these groups to “bloom” or swarm, through a combination of high grazing rates, growth rates and life history, when food concentration or other environmental factors are favourable, means that macrozooplankton may reach high biomass concentrations in areas where they amass resulting in a spatially heterogeneous distribution.

We show that the patchiness of PFT biomass increases with size. In terms of database synthesis, this means that more data would be needed for larger organisms before we can reliably generate interpolated datasets of biomass. In terms of model representation, it suggests that it will be more difficult to accurately represent individual data points, and that it will only be possible to represent the mean state or to build stochastic representations. It should be noted that by using point measurements (usually

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representative of  $< 1 \text{ m}^2$ ) and binning these into a horizontal grid spacing of  $1^\circ$ , there is potential for distorting the results. On the one hand, using gridded data means that the calculation cannot detect variations in patchiness that are smaller than  $1^\circ$ . On the other hand, there are not enough data points in each grid point to obtain a true reflection of the average biomass in that grid cell, and therefore fine scale variability could potentially be ascribed to a larger scale. There is no indication that the latter invalidates the increase in patchiness with size that we find, since if it did then patchiness should be significantly higher for smaller datasets, which is not the case ( $p = 0.5$ ,  $n = 11$ ).

Overall, this special issue has brought together abundance and biomass data for most of the PFTs in the lower trophic levels of the ocean ecosystem, as well as a global database of HPLC-based phytoplankton pigments. Qualitative information on the presence or absence of specific autotrophic groups from MAREDAT may help guide the a priori selection of pigment ratios that is essential for quantifying algal type abundance through Bayesian-type analyses (Mackey et al., 1996; Van der Meersche et al., 2008). Conversely, the biomass databases from MAREDAT will be instrumental in evaluating those quantitative results, which may help bridge some of the information gaps in phytoplankton distributions. In several cases the biomass databases represent the first of their kind to cover all ocean basins, and in the remaining cases they are substantially larger than what has been available so far. We hope to update the databases in future publications, and would welcome data submissions to the existing databases, and of new researchers to provide databases for the missing taxonomic groups. The gridded data products have been provided for the ocean ecosystem modeling community, but the raw data with references and metadata are also publicly available at <http://www.pangaea.de/search?&q=maredat>.

**Acknowledgements.** We thank Marie-Pierre Gosselin for collecting the first versions of several PFT databases, funded by EUR-OCEANS. We thank the guest editors Stéphane Pesant and Walker O. Smith, the ESSD editorial team Dave Carlson and Hans Pfeiffenberger, and the PAN-GAEA team. We acknowledge funding from the EU (to ETB, CarboChange, contract 264879,

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**Table 1.** PFT characteristics.

		Approximate diameter [ $\mu\text{m}$ ]		PFT biomass ( $\mu\text{g C L}^{-1}$ ) in top 200 m <sup>b</sup>					PFT global biomass [ $\text{Pg C}$ ] <sup>c</sup>	
		min	max	min	max	mean	median	std	min	max
autotrophs	picophytoplankton	0.6	3	0	575.00	13.51	5.72	23.58	0.28	0.64
	diazotrophs	0.6	2000 <sup>a</sup>	0	1890.00	8.00	0.03	60.92	0.008	0.12
	coccolithophores	5	20	0	501.74	2.99	0.12	17.89	0.010	0.14
	<i>Phaeocystis</i>	5	2000 <sup>a</sup>	0	5449.28	33.69	0.51	192.60	0.11	0.71
	diatoms	10	200	5e–6	9600.71	15.50	0.41	137.64	0.10	0.94
heterotrophs	picoheterotrophs	0.4	0.6	0	44.97	5.24	4.36	3.71	1.00	1.10
	microzooplankton	5	200	0	361.20	9.93	2.08	21.32	0.48	0.73
	foraminifers	100	1000	0	413.48	42.70	10.31	75.45	0.87	2.26
	mesozooplankton	200	2000	0.006	630.38	8.00	3.19	13.61	0.33	0.59
	pteropods	1000	3000	0	5045.09	4.93	0.01	64.99	0.026	0.67
	macrozooplankton	2000	10 000	0	7368.58	10.61	0.10	87.36	0.22	1.52

<sup>a</sup> Lower end of size range is for individual cells, higher end for colonies.<sup>b</sup> Calculated from gridded databases.<sup>c</sup> Lower estimate using median depth profiles, higher estimate using mean depth profiles, see Sect. 3.2.5 for details.

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**Table 2.** Database characteristics.

	doi:10.1594/PANGAEA	Raw data		Chauvenet's criteria		Number of data on WOA grid	Number of 10° boxes with data
		Total number	Excluded outliers	Standard deviation	Critical value (zc)		
autotrophs	picophytoplankton	777 385	40 946	0	0.79	4.36	10 747
	diazotrophs	774 851	3849	1 <sup>a</sup>	1.59 <sup>a</sup>	3.66 <sup>a</sup>	2280
	coccolithophores	785 092	11 703	1	1.24	4.05	5222
	<i>Phaeocystis</i>	779 101	3526	0	1.28	3.72	392
	diatoms	777 384	91 704	151 <sup>b</sup>	1.15 <sup>b</sup>	4.54	3852
heterotrophs	picoheterotrophs	779 142	39 766	0	0.44	4.37	9284
	microzooplankton	779 970	4282	0	0.91	3.67	2029
	foraminifers	777 386	1128	0	1.05	3.49	745
	mesozooplankton	785 501	153 163	0	1.13	4.65	42 245
	pteropods	777 387	15 134	0	1.52	4.13	7151
	macrozooplankton	777 398	36 237	32	1.93	4.29	8147

<sup>a</sup> The Chauvenet's criterion for the diazotroph database was calculated separately for the different data sources, but here we calculate one value for the standard deviation and zc for comparison to the other databases.

<sup>b</sup> The Chauvenet's criterion for the diatom database was calculated without log transformation, but here we calculate the logarithmic standard deviation for comparison to the other databases.

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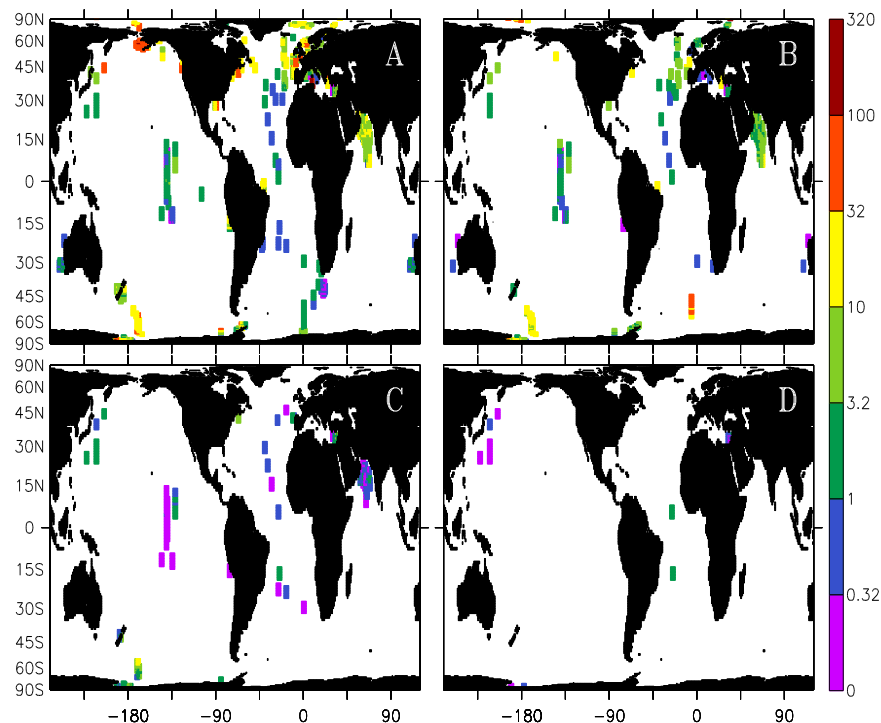
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**Fig. 1.** Microzooplankton biomass [ $\mu\text{g C L}^{-1}$ ]. (A) 0–40 m, (B) 40–112.5 m, (C) 112.5–225 m, (D) > 225 m.

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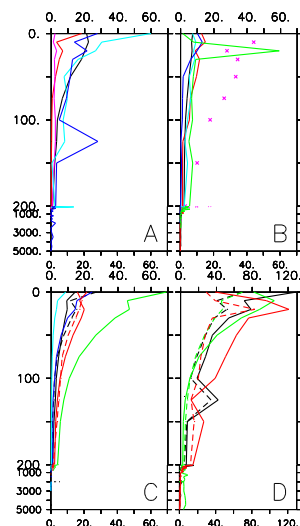
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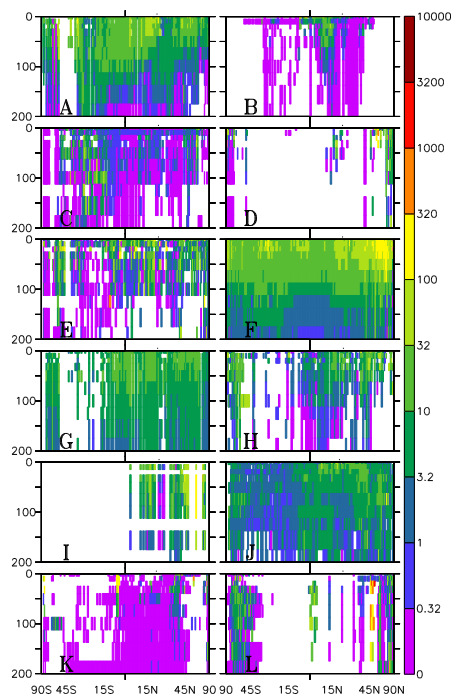
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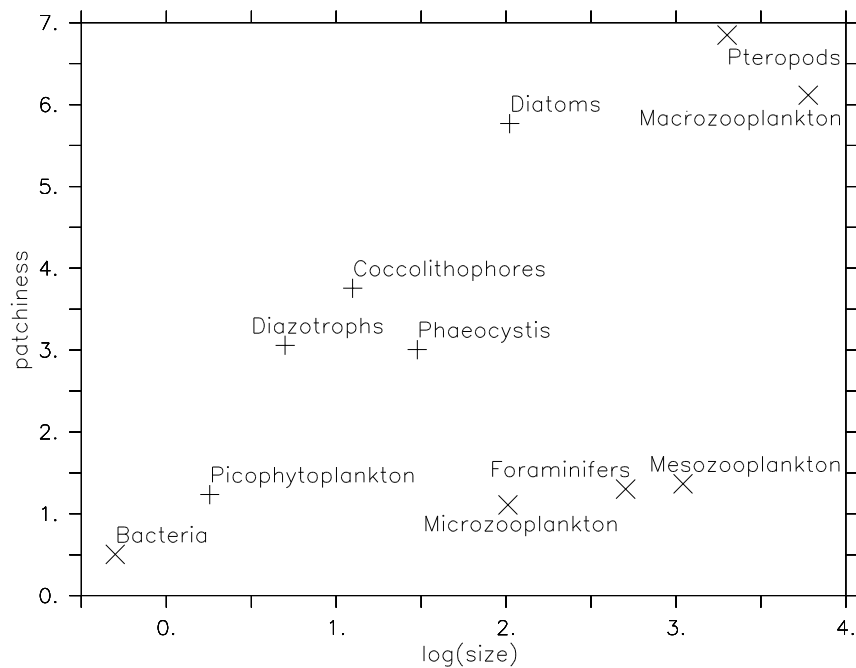
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**Fig. 2.** Depth profiles of average PFT biomass [ $\mu\text{gCL}^{-1}$ ]. **(A)** Autotrophs from abundance. Black: picophytoplankton, Red: diazotrophs, Magenta: coccolithophores, Cyan: *Phaeocystis*, Dark blue: diatoms. **(B)** Heterotrophs from abundance. Black: picoheterotrophs, Red: microzooplankton, Magenta crosses: foraminifers, Cyan: mesozooplankton, Dark blue: pteropods, Green: macrozooplankton. **(C)** Autotrophs from pigments. Black: prokaryotes from chlorophyll-b and zeaxanthin, Red: nanophytoplankton from 19'-hexanoyloxyfucoxanthin, 19'-butanoyloxyfucoxanthin, and alloxanthin, Dark blue: diatoms from fucoxanthin, Cyan: dinoflagellates from peridinin, Green: total, Dashed black: prokaryotes from sum of abundance based diazotroph and cyanobacteria, Dashed red: sum of abundance based biomass of coccolithophores and picoeukaryotes. **(D)** Dashed black: sum of available phytoplankton without and Solid black: with *Phaeocystis*, Dashed green: total phytoplankton from pigments, Solid green: WOA 2005 chlorophyll  $\times$  model C : Chl ratio, Dashed red: sum of heterotrophs without and Solid red: with foraminifers and pteropods. See text for details.



**Fig. 3.** Zonal average PFT biomass [ $\mu\text{g C L}^{-1}$ ]. **(A)** Picophytoplankton, **(B)** diazotrophs, **(C)** coccolithophores, **(D)** *Phaeocystis*, **(E)** diatoms, **(F)** WOA 2005 chlorophyll \* PlankTOM5.3 C : Chl ratio, **(G)** picoheterotrophs, **(H)** microzooplankton, **(I)** foraminifers, **(J)** mesozooplankton, **(K)** pteropods, **(L)** macrozooplankton.



**Fig. 4.** Patchiness (see Sect. 2.3) as a function of log (nominal organism size in  $\mu\text{m}$ ). Plusses: autotrophs, crosses: heterotrophs.

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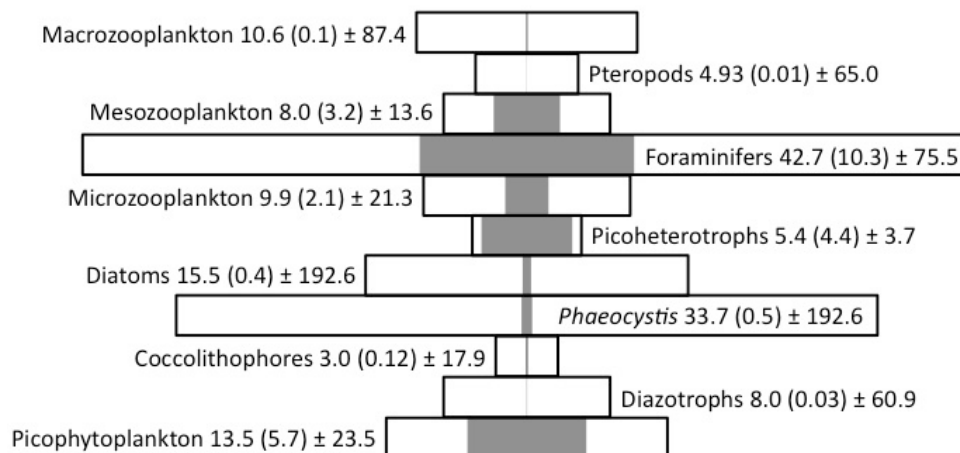
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**Fig. 5.** Trophic pyramid of autotrophic and heterotrophic PFTs. Mean (black outline) and median (grey fill, values in brackets) biomass ( $\mu\text{g C L}^{-1}$ ) in the top 200 m for each of the PFTs presented in the MAREDAT special issue. Standard deviation is not shown. For full details see Table 1.