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# Picophytoplankton biomass distribution in the global ocean

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## Abstract

The smallest marine phytoplankton, collectively termed picophytoplankton, have been routinely enumerated by flow cytometry since the late 1980s, during cruises throughout most of the world ocean. We compiled a database of 40 946 data points, with separate abundance entries for *Prochlorococcus*, *Synechococcus* and picoeukaryotes. We use average conversion factors for each of the three groups to convert the abundance data to carbon biomass. After gridding with 1° spacing, the database covers 2.4 % of the ocean surface area, with the best data coverage in the North Atlantic, the South Pacific and North Indian basins. The average picophytoplankton biomass is $12 \pm 22\,\mu g\,C\,l^{-1}$ or $1.9\,g\,C\,m^{-2}$. We estimate a total global picophytoplankton biomass of 0.53–0.74 Pg C (17–39 % *Prochlorococcus*, 12–15 % *Synechococcus* and 49–69 % picoeukaryotes). Future efforts in this area of research should focus on reporting calibrated cell size, and collecting data in undersampled regions.

## 1 Introduction

Picophytoplankton are usually defined as phytoplankton less than 2 or 3 µm diameter (e.g. Sieburth et al., 1978; Takahashi and Hori, 1984; Vaulot et al., 2008). They are the smallest class of phytoplankton, and are composed of both prokaryotes and eukaryotes. The eukaryotes (0.8–3 µm) are a taxonomically diverse group that include representatives from four algal phyla: the Chlorophyta, Haptophyta, Cryptophyta and Heterokontophyta (Vaulot et al., 2008). The prokaryotes belong to the phylum Cyanobacteria, and are subdivided into the genera *Prochlorococcus* (~0.6 µm) and *Synechococcus* (~1 µm), although with each group having many ecotypes that dominate in different ocean regions (Johnson et al., 2006).

Picophytoplankton tend to dominate the phytoplankton biomass under oligotrophic conditions such as in the subtropical gyres (Alvain et al., 2005), where their high surface to volume ratio makes them the best competitors for low nutrient concentrations





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(Raven, 1998). The abundance of the prokaryotes is often inversely related with the eukaryotes, which are favoured by more physically active mixed layers (e.g. Boumann et al., 2011). Furthermore, as the temperate to subpolar North Atlantic and the Canadian high Arctic warm, picophytoplankton (specifically picoeukaryotes) have been found to become an increasingly large fraction of the total chlorophyll (Li et al., 2009; Moran et al., 2010).

As part of the marine ecology data synthesis effort (MAREDAT, this special issue), we compiled a database on picophytoplankton in the global ocean. MAREDAT is a community effort to synthesise abundance and carbon biomass data for the major lower trophic level taxonomic groups in the marine ecosystem. It addresses both autotrophs and heterotrophs and covers the size range from bacteria to macrozooplankton.

## 2 Data

We compiled data for picophytoplankton abundance in three taxonomic groups: *Prochlorococcus*, *Synechococcus*, and picoeukaryotes (Table 1). We used the size range of picoeukaryotes as defined by the contributing researchers. The size range has a large impact on the resulting biomass (see Discussion). All of the data were obtained by flow cytometry. Both the raw data and the gridded data are available from PANGAEA (http://doi.pangaea.de/10.1594/PANGAEA.777385) and the MAREDAT webpage (http://lgmacweb.env.uea.ac.uk/maremip/data/essd.shtml).

### 2.1 Conversion factors

Conversion factors from cell abundance to carbon biomass for the three picophytoplankton groups were compiled from the literature (Table 2). Conversion factors were either measured directly on unialgal cultures in the laboratory, or derived from indirect methods on in situ samples. Most of the indirect measures were derived from cell sizes that were estimated from average forward angle light scatter (FALS) multiplied





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by a carbon content per biovolume. The conversion factors of Veldhuis et al. (1997) were based on nitrate uptake in incubated in situ samples and assuming a C:N ratio of 6. Since the biggest source of variability in the other indirect measures is the carbon content per biovolume, which was measured on laboratory cultures, the advantage of using in situ biovolume to determine conversion factors does not seem to improve the local applicability of these data and we therefore used the directly measured conversion factors as the standard.

### 2.2 Quality control

Contributed data were assumed to have undergone the contributing researchers own internal quality control procedures. As a statistical filter for outliers, we applied the Chauvenet criterion (Buitenhuis et al., 2012) to the total carbon data. The data were not normally distributed, so we log transformed them, excluding zero values. No high outliers were found by this criterion. The highest picophytoplankton biomass in the database is 575 $\mu g\,C\,l^{-1}$, measured near the coast of Oman (Indian Ocean).

## 3 Results

The database contains 40 946 data points. Data are included from a number of stations that have been sampled repeatedly over many years, or programs where measurements have been made on a fine resolution grid. Therefore, after gridding, we obtained 10 747 data points on the World Ocean Atlas grid ($1^\circ \times 1^\circ \times 33$ vertical layers $\times$ 12 months), representing a coverage of vertically integrated and annually averaged biomass for 2.4 % of the ocean surface. To limit the overrepresentation of well sampled locations, we present results of the gridded data. Only 15 % of the data are from the Southern Hemisphere (Fig. 1a), 33 % are from the tropics (43 % of the ocean surface), while 13 % are from the polar oceans (5 % of the ocean surface). Observations in the top 112.5 m make up 81 % of the data (Fig. 1b). Zero values make up 1.6 %





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of the data, and 95 % of those are from below 62.5 m depth. There is some sampling bias towards the growing season, with 67 % of the data sampled in the spring and summer months (Fig. 1c).

The average picophytoplankton biomass is $12 \pm 22\,\mu g\,C\,l^{-1}$ (Fig. 2) or $1.9\,g\,C\,m^{-2}$. Of the vertically integrated biomass 54 % occurs in the top 40 m, and 93 % in the top 112.5 m (Fig. 3). *Synechococcus* is found at the most shallow depths (97 % in the top 112.5 m, Fig. 4), followed by picoeukaryotes (92 % in the top 112.5 m), while *Prochlorococcus* biomass decreases more slowly with depth (87 % in the top 112.5 m).

The average biomass is slightly higher in the tropics and considerably lower in the Arctic (Fig. 5), but the standard deviation within latitude bands is high, so that none of the differences are significant. Antarctica: $11 \pm 8\,\mu g\,C\,l^{-1}$ or $1.2\,g\,C\,m^{-2}$, South temperate (67–23° S): $13 \pm 23\,\mu g\,C\,l^{-1}$ or $2.2\,g\,C\,m^{-2}$, tropics: $15 \pm 24\,\mu g\,C\,l^{-1}$ or $2.2\,g\,C\,m^{-2}$, North temperate: $12 \pm 22\,\mu g\,C\,l^{-1}$ or $1.9\,g\,C\,m^{-2}$, and Arctic: $6 \pm 8\,\mu g\,C\,l^{-1}$ or $0.6\,g\,C\,m^{-2}$. We calculate the global picophytoplankton biomass from the zonal and time averaged concentration filled by interpolation across up to 22° latitude (Fig. 5) multiplied by the volume at each latitude and depth, integrating to the bottom, and counting missing values as 0. We thus estimate a total global picophytoplankton biomass of 0.74 Pg C (17 % *Prochlorococcus*, 15 % *Synechococcus* and 69 % picoeukaryotes). Interpolation across up to 10° latitude only leaves a few missing values, and estimates 0.73 Pg C. If we use the indirect in situ conversion factors for each of the three groups (Table 2), the total biomass (with up to 22° interpolation) is 0.53 Pg C (39 % *Prochlorococcus*, 12 % *Synechococcus*, 49 % picoeukaryotes).

## 4 Discussion

Although data coverage, at 2.4 % of the ocean surface, is by no means complete, if we randomly select half of the depth profiles, in 10 random samples the average integrated biomass varied between 96 and 104 % of the value for the whole dataset, while the averages from the Southern and Northern Hemispheres are 119 % and 96 %,





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respectively. On the other hand, the average using the indirect in situ conversion factors is 72 % of the value estimated using the direct conversion factors. Thus, the main uncertainty in determining the global picophytoplankton biomass in this analysis is the conversion from cell abundance to carbon biomass. There is a fairly tight relationship between forward angle light scatter (FALS; Cavender-Bares et al., 2001; DuRand et al., 2002) or right angle light scatter (RALS; Simon et al., 1994; Worden et al., 2004), as measured by flow cytometry, and cell size, which is probably the main source of uncertainty in the conversion factor. Only about a third of our data came with FALS or RALS data, and even in those cases these were in arbitrary units. We recommend the routine measurement of calibrated size as the additional measurement that would do most to improve our knowledge of global picophytoplankton biomass distribution.

In addition to the uncertainty in the carbon conversion factor, there is uncertainty about the abundance of *Prochlorococcus* in near surface oligotrophic waters, where the cellular chlorophyll content, and thus the ability to detect them as algae from their red fluorescence, is at its minimum, and near the detection limit of standard flowcytometers (Dusenberry and Frankel, 1999).

It has been repeatedly shown that *Prochorococcus* and *Synechococcus* increased in cell size with depth up to ~150 m. In contrast, picoeukaryotes showed little variation in size as a function of depth (Li et al., 1993; DuRand et al., 2001; Grob et al., 2007). Though we find that picoeukaryotes make the largest contribution to the picophytoplankton biomass (Fig. 4), we may have overestimated the decrease in carbon concentration with depth over the top 150 m for the prokaryotes and to a lesser extent for the total picophytoplankton. Viviani et al. (2011) showed that surface samples of *Prochorococcus* increased in cell size with latitude towards the equator.

Even so, the considerable depths to which picophytoplankton are found is an indication of their competitiveness under low light, due to the smaller chlorophyll package effect in these smallest phytoplankton (Partensky et al., 1993).

Le Quéré et al. (2005) estimated that the global picophytoplankton biomass, including nitrogen fixers, is 0.28 Pg C. Our estimate, excluding nitrogen fixers, is considerably





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higher at 0.74 Pg C, and even our estimate using the indirect conversion factors is still almost double at 0.53 Pg C. Le Quéré et al. (2005) suggest a third of global phytoplankton biomass is in the pico size class. Therefore, a 2.6-fold difference in the estimated picophytoplankton biomass would not only be important for calculating the relative contribution that picophytoplankton make to the phytoplankton, but also for calculating the total biomass of phytoplankton as the base of the ocean ecosystem.

For picoeukaryotes, the definition of the size range to be included is a major source of ambiguity. Whether phytoplankton between 2 and 3 µm diameter are included as picophytoplankton not only affects the abundance of the picoeukaryotes, but also which conversion factor is applicable. Here, we have included measurements of cells up to 3 µm diameter in the carbon conversion factor (Table 2). As a consequence, our conclusion that picoeukaryotes constitute 69 % of global picophytoplankton biomass critically depends on the definition of the size cut off.

In summary, thanks to the routine use of flow cytometry for measurement of picophytoplankton abundance, we obtained a global dataset with reasonable coverage. The two main issues that deserve future attention are better resolution of cell sizes and better sampling coverage in the Southern Hemisphere.

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**Table 1.** Data sources.

| Cruise | Date | Area | Reference/Investigator |
|---|---|---|---|
| Li87022 | Jun 1987 | North Atlantic | Li and Wood (1988); Li et al. (1992) |
| CHLOMAX | Sep–Oct 1987 | Sargasso Sea | Neveux et al. (1989) |
| Endeavour177 | May–Jun 1988 | Sargasso Sea | Olson et al. (1990) |
| Li88026 | Sep 1988 | North Atlantic | Li et al. (1992) |
| Bermuda | 1988–1989 | Sargasso Sea | Olson et al. (1990) |
| EROSDISCO89 | Jan 1989 | Mediterranean Sea | Vaulot et al. (1990) |
| Li89003 | Apr 1989 | North Atlantic | Li et al. (1992) |
| Oceanus206 | May 1989 | Sargasso Sea | Olson et al. (1990) |
| EROSBAN | Jul 1989 | Mediterranean Sea | Partensky (unpublished data) |
| NIOZNatl89 | Aug–Sep 1989 | North Atlantic | Veldhuis and Kraay (1990); Veldhuis et al. (1993) |
| Palau | Aug–Sep 1990 | Tropical Pacific West | Shimada et al. (1993) |
| NOPACCS | Aug–Oct 1990 | Pacific Ocean | Ishizaka (unpublished data) |
| Australia | Nov–Dec 1990 | Tropical Pacific West | Shimada et al. (1993) |
| HOT | 1990–2008 | Tropical Pacific | Campbell et al. (1997); Karl (unpublished data) |
| BATS | 1990–2010 | North Atlantic | DuRand et al. (2001); Lomas et al. (2010) |
| Iselin 9102 | Feb 1991 | Carribean Sea | McManus and Dawson (1994) |
| Li91001 | Apr 1991 | North Atlantic | Li (unpublished data) |
| BOFS | Jul 1991 | North Atlantic | BODC |
| POEM91 | Oct 1991 | Mediterranean Sea | Li et al. (1993) |
| EUMELI3 | Oct 1991 | Tropical Atlantic | Partensky et al. (1996) |
| EQPACTT007 | Feb–Mar 1992 | Equatorial Pacific | Landry et al. (1996) |
| Eddy92 | Mar 1992 | Mediterranean Sea | Yacobi et al. (1995) |
| EROSVALD | Mar 1992 | Mediterranean Sea | Vaulot, Marie (unpublished data) |
| EQPACTT008 | Mar–Apr 1992 | Equatorial Pacific | Binder et al. (1996) |
| EQPACTT008D | Mar–Apr 1992 | Equatorial Pacific | DuRand and Olson (1996) |
| NIOZIndian | May 1992–Feb 1993 | Indian Ocean/Red Sea | Veldhuis and Kraay (1993) |
| SurugaBay | May 1992–Oct 1993 | Japan | Shimada et al. (1995) |
| EUMELI4 | Jun 1992 | Tropical Atlantic | Partensky et al. (1996) |
| Surtropac17 | Aug 1992 | Equatorial Pacific | Blanchot and Rodier (1996) |
| EQPACTT011 | Aug–Sep 1992 | Equatorial Pacific | Landry et al. (1996) |
| Li92037 | Sep 1992 | North Atlantic | Li (1994, 1995) |
| EQPACTT012 | Sep–Oct 1992 | Equatorial Pacific | DuRand and Olson (1996) |
| EUMELI5 | Dec 1992 | Tropical Atlantic | Partensky et al. (1996) |
| Aquaba | 1992–1993 | Red Sea | Lindell and Post (1995) |
| Malaga93 | Jan 1993 | Mediterranean Sea | Garcia et al. (1994) |
| Li93002 | May 1993 | North Atlantic | Li (1994, 1995) |
| EROSDISCO93 | Jul 1993 | Mediterranean Sea | Simon, Barlow, Marie (unpublished data) |
| NOAA93 | Jul–Aug 1993 | North Atlantic | Buck et al. (1996) |
| Flupac | Sep–Oct 1994 | Equatorial Pacific | Blanchot et al. (2001) |
| OLIPAC | Nov 1994 | Equatorial Pacific | Neveux et al. (1999) |





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**Table 1.** Continued.

| Cruise | Date | Area | Reference/Investigator |
|---|---|---|---|
| ArabianTTN043 | Jan 1995 | Arabian Sea | Campbell et al. (1998) |
| ArabianTTN045 | Mar–Apr 1995 | Arabian Sea | Campbell et al. (1998) |
| Delaware95 | Apr 1995 | North Atlantic | Li (1997) |
| MINOS | Jun 1995 | Mediterranean Sea | Vaulot, Marie, Partensky (unpublished data) |
| Chile95 | Jun 1995 | South Atlantic | Li (unpublished data) |
| Lopez96 | Jun 1995 | Sargasso Sea | Li (unpublished data) |
| Li95016 | Jul 1995 | North Atlantic | Li and Harrison (2001) |
| Ictio-Alborán Cadiz 95 | Jul 1995 | North Atlantic | Echevarría et al. (2009) |
| ArabianTTN049 | Jul–Aug 1995 | Arabian Sea | Olson (unpublished data) |
| ArabianTTN050 | Aug–Sep 1995 | Arabian Sea | Campbell et al. (1998) |
| NOAA95 | Sep–Oct 1995 | Indian Ocean | Buck (unpublished data) |
| ArabianTTN053 | Nov 1995 | Arabian Sea | Olson (unpublished data) |
| ArabianTTN054 | Dec 1995 | Arabian Sea | Campbell et al. (1998) |
| | 1995–2009 | North Atlantic, Arctic | Li (2002, 2009); Li et al. (2009) |
| OMEX/D1221 | Jun 1996 | North Atlantic | BODC |
| Kiwi6 | Oct–Nov 1997 | Antarctica | Landry (unpublished data) |
| Kiwi7 | Dec 1997 | Antarctica | Landry (unpublished data) |
| Almo-1 | Dec 1997 | Mediterranean Sea | Jacquet, Marie (unpublished data) |
| AESOPS/NBP97-1 | 1997 | Ross Sea | Olson, Sosik (unpublished data) |
| Almo-2 | Jan 1998 | Mediterranean Sea | Jacquet et al. (2010) |
| Kiwi8 | Jan–Feb 1998 | Antarctica | Landry (unpublished data) |
| Kiwi9 | Feb–Mar 1998 | Antarctica | Landry (unpublished data) |
| Southwest Pacific | Mar–Apr 1998 | South Pacific | Campbell et al. (2005) |
| PROSOPE99 | Sept 1999 | Mediterranean Sea | Marie et al. (2006) |
| GLOBEC LTOP | Mar 2001–Sep 2003 | North Pacific | Sherr et al. (2005) |
| NP | Feb 2004–Mar 2005 | North Atlantic | Lomas et al. (2009) |
| BIOSOPE | Oct–Dec 2004 | South East Pacific | Grob et al. (2007) |
| ArcticNet2005 | Aug–Sep 2005 | Arctic, North Atlantic | Tremblay et al. (2009) |
| DOP | May 2006–May 2008 | North Atlantic | Lomas (unpublished data) |
| Bering Sea | Mar 2008–May 2010 | North Pacific | Moran et al. (2012) |
| Line P | Aug 2010–Jun 2011 | North Pacific | Lomas (unpublished data) |
| FOODWEB | Feb–Aug 2011 | North Atlantic | Lomas (unpublished data) |





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**Table 2.** Cell abundance to carbon biomass conversion factors [fg C cell$^{-1}$].

| | *Prochlorococcus* | *Synechococcus* | picoeukaryotes | reference |
|---|---|---|---|---|
| Direct from cultures | | 250 | | Kana and Glibert (1987) |
| | | 600 | 3800 ± 100 | Verity et al. (1992) |
| | | | 800, 1360 | Montagnes et al. (1994) |
| | 49 ± 9 | | | Cailliau et al. (1996) |
| | | 350 (200–500) | | Liu et al. (1999) |
| | | | 4400 | Llewellyn and Gibb (2000) |
| | 27 ± 6 | | | Claustre et al. (2002) |
| | 53 ± 9 | 170 ± 65 | | Bertilsson et al. (2003) |
| | 16 ± 1 | 249 ± 21 | | Fu et al. (2007) |
| average | 36 | 255* | 2590 | |
| Indirect, mostly from culture C per volume × in situ volume | 92 | 175 | | Veldhuis et al. (1997) |
| | 53 | 246 | 2108 | Campbell et al. (1994) |
| | 56 | 112 | | DuRand et al. (2001) |
| | 39 ± 1 | 82 ± 8 | 530 ± 185 | Worden et al. (2004) |
| average | 60 | 154 | 1319 | |

* excluding Verity et al. (1992), 324 fg C cell$^{-1}$ including Verity et al. (1992).





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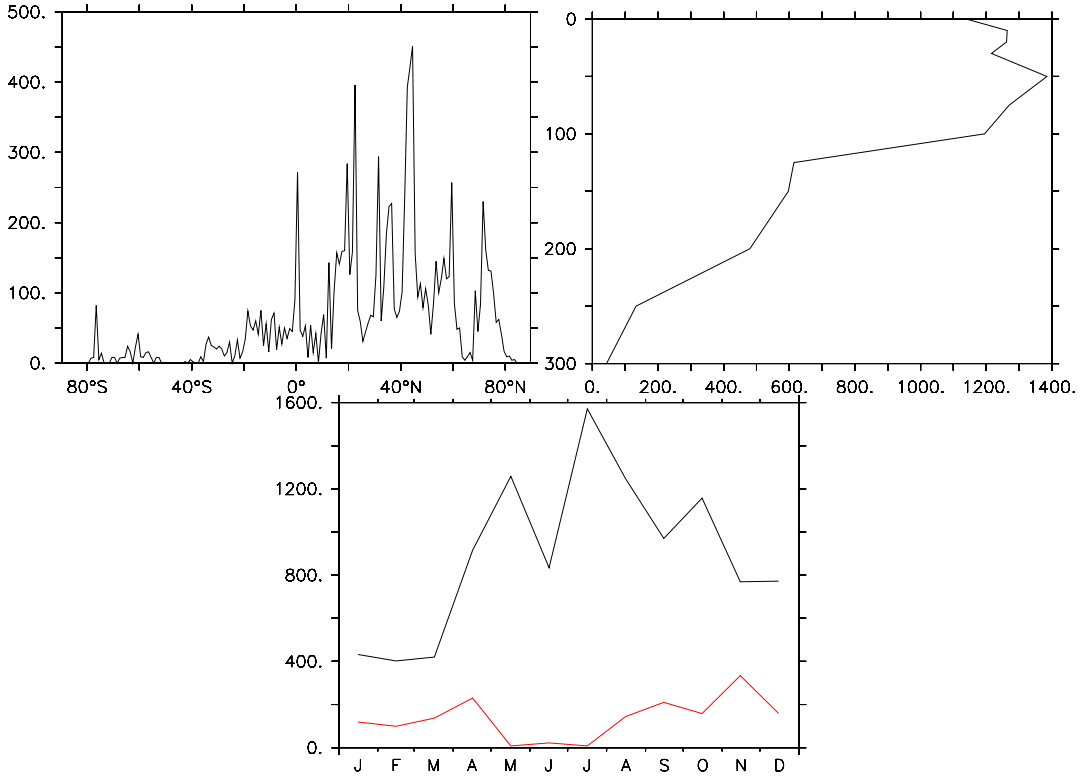


**Fig. 1.** Number of grid points with data, as a function of, Left) latitude. Middle) depth. Observations below 300 m are not shown (1.4 % of the data). The deepest observation is at 3000 m, and the deepest non-zero observation at 1100 m. Right) time. Red: Southern Hemisphere, Black: total.





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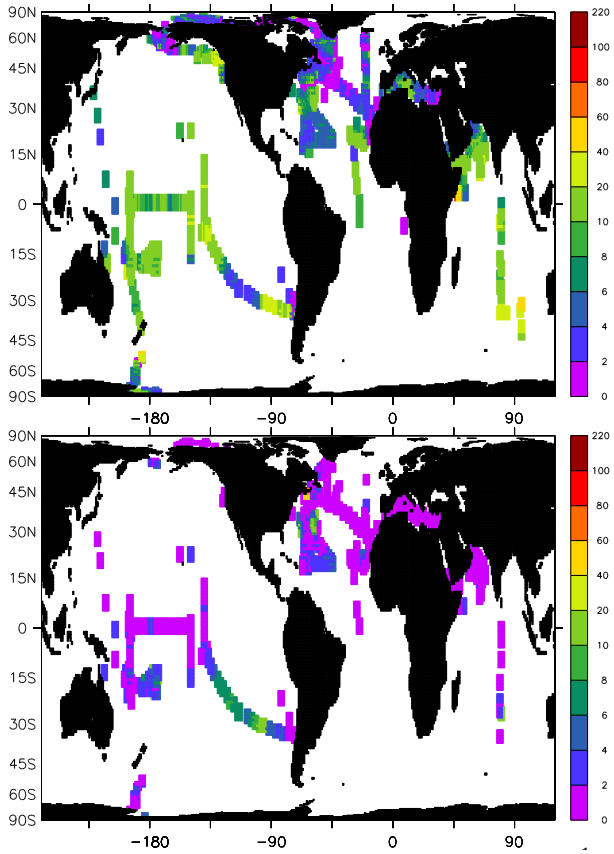


**Fig. 2.** Picophytoplankton biomass [µg C $l^{-1}$]. Top) 0–40 m, Middle) 40–112.5 m, Bottom) 112.5–225 m.





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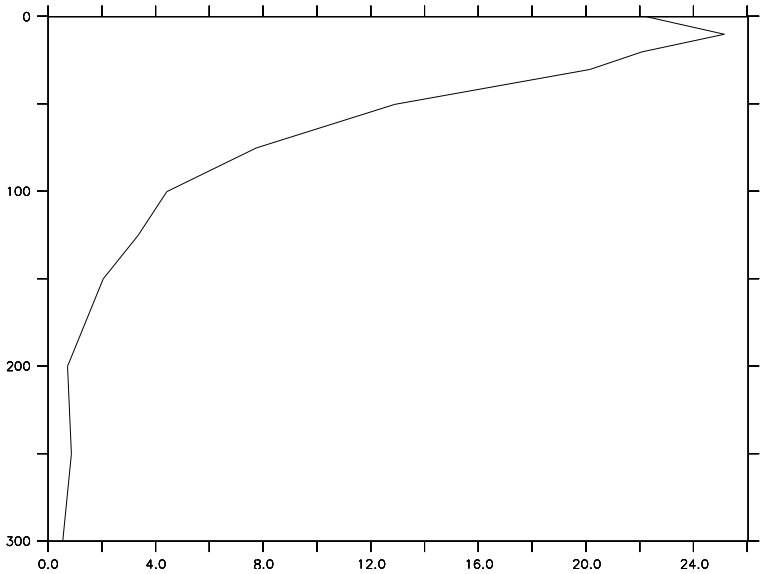


**Fig. 3.** Average picophytoplankton biomass [$\mu g\, C\, l^{-1}$] as a function of depth [m].





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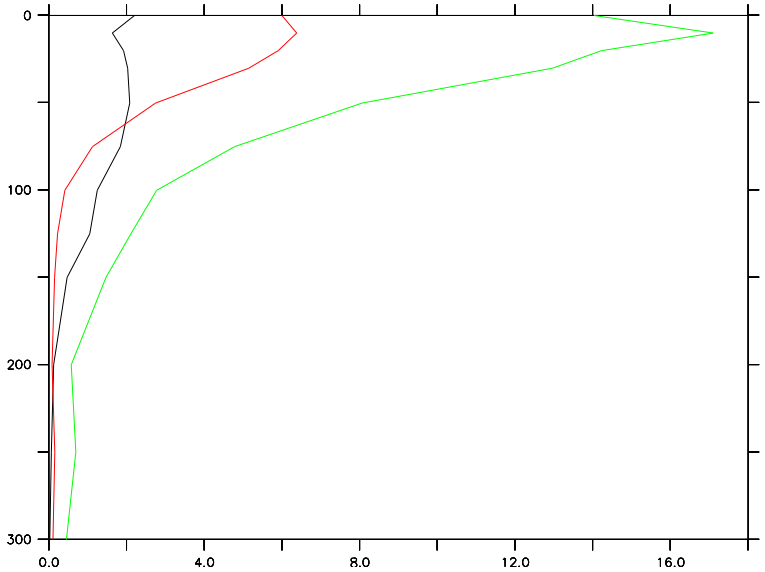


**Fig. 4.** Average depth profiles of *Prochlorococcus* (black) *Synechococcus* (red) and picoeukaryotes (green) biomass [$\mu g\,C\,l^{-1}$].





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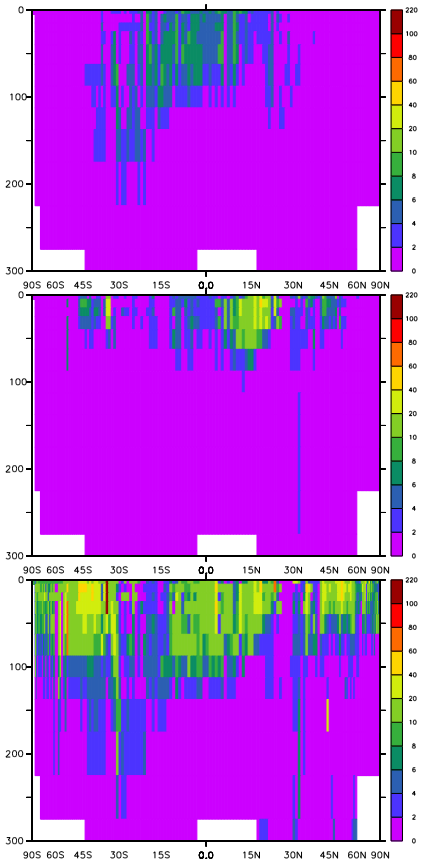


**Fig. 5.** Zonal and time averaged biomass [$\mu g\,C\,l^{-1}$] of Top) *Prochlorococcus*, Middle) *Synechococcus*, Bottom) picoeukaryotes. Data have been filled by latitudinal interpolation of up to 22°.





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