



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, and at least some data in all other basins. The average picophytoplankton biomass is $12 \pm 22 \mu\text{g C l}^{-1}$ or 1.9 g C m^{-2} . We estimate a total global picophytoplankton biomass of 0.53–1.32 Pg C (17–39 % *Prochlorococcus*, 12–15 % *Synechococcus* and 49–69 % picoeukaryotes), with an intermediate/best estimate of 0.74 Pg C. Future efforts in this area of research should focus on reporting calibrated cell size and collecting data in undersampled regions.

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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 includes 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* ($\sim 0.6 \mu\text{m}$) and *Synechococcus* ($\sim 1 \mu\text{m}$), 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 (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, with warming of the temperate to subpolar North Atlantic and the Canadian high Arctic, 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://maremip.uea.ac.uk/maredat.html>).

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

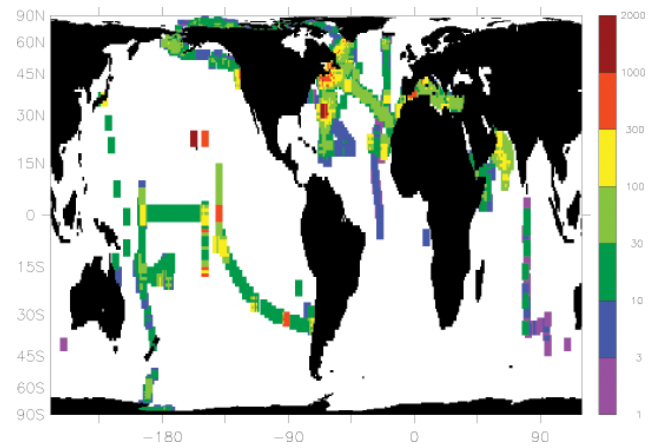


Figure 1. Horizontal distribution of the number of observations. Data points have been enlarged to $5^\circ \times 5^\circ$.

indirect measures were derived from cell sizes that were estimated from average forward-angle light scatter (FALS) multiplied 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., 2012b) 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 $575 \mu\text{g C l}^{-1}$, measured near the coast of Oman (Indian Ocean).

3 Results

The database contains 40 946 data points (Fig. 1). 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. For further details on the gridding, see Buitenhuis et al. (2012b). To limit

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	Caribbean Sea	McManus and Dawson (1994)
Li91001	Apr 1991	North Atlantic	Li (unpublished data)
BOFS	Jul 1991	North Atlantic	BODC (British Oceanographic Data Centre)
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)
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 Pacific	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)
AZOMP	1995–2009	North Atlantic	Li (2002, 2009); Li et al. (2009)

Table 1. Continued.

Cruise	Date	Area	Reference/Investigator
OMEX/D1221	Jun 1996	North Atlantic	BODC
AZMP	1997–2009	North Atlantic	Li (2002, 2009); Li et al. (2009)
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)
JOIS	2002–2009	North Atlantic, Arctic	Li (2002, 2009); Li et al. (2009)
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)
C3O	2007–2008	North Atlantic, Arctic	Li (2002, 2009); Li et al. (2009)
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)

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

	<i>Prochlorococcus</i>	<i>Synechococcus</i>	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 \times 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), $324 \text{ fg C cell}^{-1}$ including Verity et al. (1992).

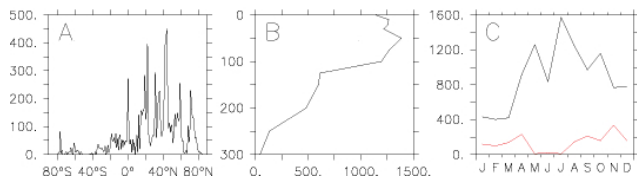


Figure 2. Number of grid points with data, as a function of (A) latitude, (B) Depth. Observations below 300 m are not shown (1.4 % of the data). The deepest observation is at 3000 m and the deepest non-zero observation at 1100 m. (C) Time. Red: Southern Hemisphere, black: total.

the overrepresentation of well sampled locations, we present results of the gridded data. Only 15 % of the data are from the Southern Hemisphere (Fig. 2a), 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 upper 112.5 m make up 81 % of the data (Fig. 2b), but the number of observations decreases more slowly than biomass (Fig. 3), and there are still 480 observations at 200 m depth (Fig. 2b), thus defining the vertical biomass profile fairly well. Zero values make up 1.6 % 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. 2c).

The average picophytoplankton biomass is $12 \pm 22 \mu\text{g C l}^{-1}$ (Fig. 4) or 1.9 g C m^{-2} . Of the vertically integrated biomass, 54 % occurs in the upper 40 m and 93 % in the upper 112.5 m (Fig. 2). *Synechococcus* is found at the most shallow depths (97 % above 112.5 m, Fig. 5), followed by picoeukaryotes (92 % above 112.5 m), while *Prochlorococcus* biomass decreases more slowly with depth (87 % above 112.5 m).

The average biomass is slightly higher in the tropics and considerably lower in the Arctic (Figs. 4, 6), but the standard deviation within latitudinal bands is high, so that none of the differences are significant. Antarctica: $11 \pm 8 \mu\text{g C l}^{-1}$ or 1.2 g C m^{-2} , south temperate zone ($67\text{--}23^\circ \text{S}$): $13 \pm 23 \mu\text{g C l}^{-1}$ or 2.2 g C m^{-2} , tropics: $15 \pm 24 \mu\text{g C l}^{-1}$ or 2.2 g C m^{-2} , north temperate zone: $12 \pm 22 \mu\text{g C l}^{-1}$ or 1.9 g C m^{-2} , and Arctic: $6 \pm 8 \mu\text{g C l}^{-1}$ 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. 6) 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).

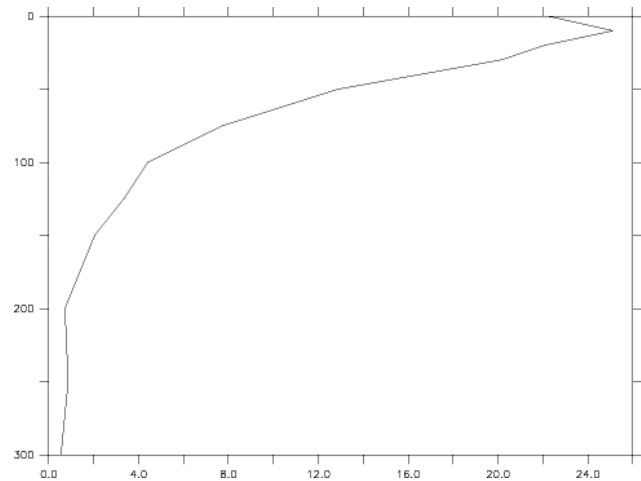


Figure 3. Average picophytoplankton biomass [$\mu\text{g C l}^{-1}$] as a function of depth [m].

Picoeukaryotes tend to dominate by $>75\%$ poleward of 40° , and dominate below 62.5 m depth in the tropics and below 225 m everywhere (Fig. 7). *Prochlorococcus* tends to dominate above 225 m between $20\text{--}40^\circ \text{N}$ and shares dominance with picoeukaryotes between $10\text{--}30^\circ \text{S}$ and at the surface in the tropics. *Synechococcus* only dominates around 50°S and is relatively abundant above 62.5 m between $10\text{--}40^\circ \text{N}$. This is consistent with the community structure of picophytoplankton that has been analysed by Bouman et al. (2011).

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 varies between 96 and 104 % of the value for the whole dataset, while the averages from the Southern and Northern Hemispheres are 119 % and 96 %, 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.

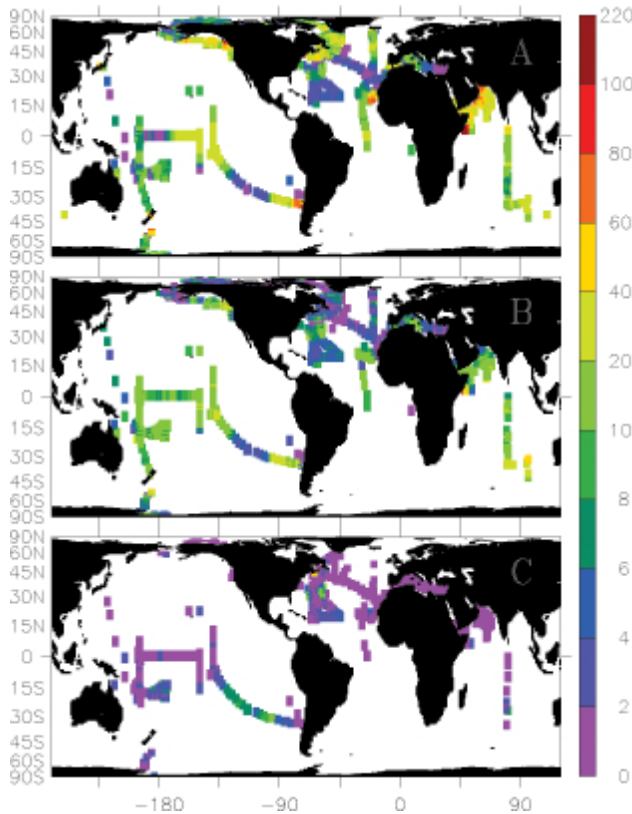


Figure 4. Picophytoplankton biomass [$\mu\text{g C l}^{-1}$]. (A) 0–40 m, (B) 40–112.5 m, (C) 112.5–225 m.

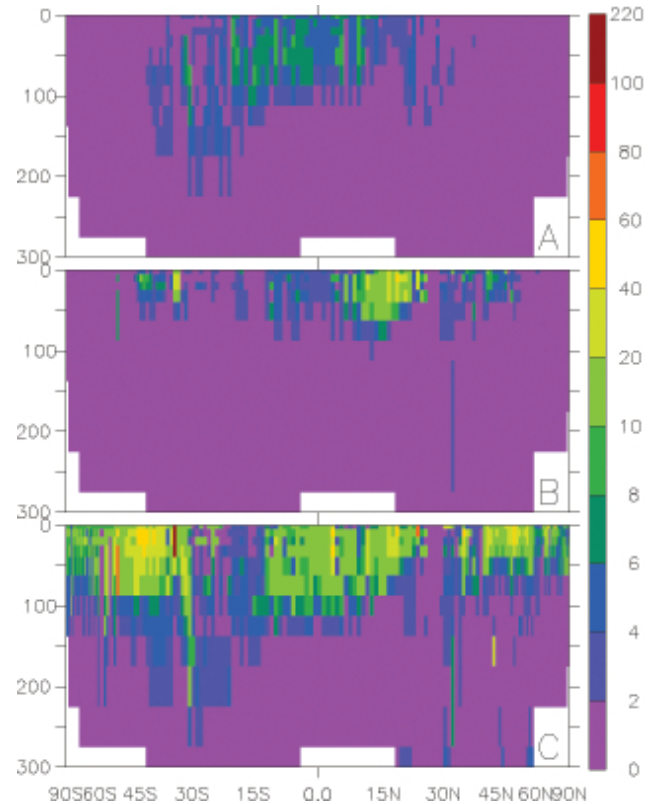


Figure 6. Zonal and time-averaged biomass [$\mu\text{g C l}^{-1}$] of (A) *Prochlorococcus*, (B) *Synechococcus*, (C) picoeukaryotes. Data have been filled by latitudinal interpolation of up to 22° .

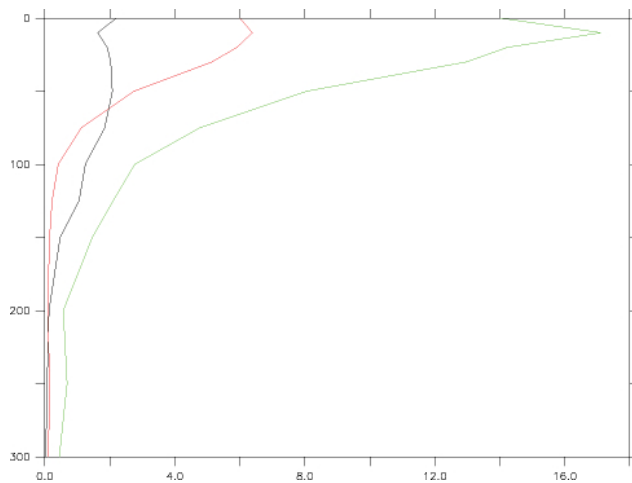


Figure 5. Average depth profiles of *Prochlorococcus* (black), *Synechococcus* (red) and picoeukaryotes (green) biomass [$\mu\text{g C l}^{-1}$].

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 flow cytometers (Dusenberry and Frankel, 1994).

It has been repeatedly shown that *Prochlorococcus* and *Synechococcus* increase in cell size with depth up to ~ 150 m. In contrast, previously published results for picoeukaryotes showed little variation in size as a function of depth (Li et al., 1993; DuRand et al., 2001; Grob et al., 2007). We compared the increase in size for the three groups at two locations. At BATS (Bermuda Atlantic Timeseries Station; which includes the data of DuRand et al., 2001), we also find an increase in cell size of *Prochlorococcus* and *Synechococcus* but not picoeukaryotes (Fig. 8a). However, in the Western Mediterranean (Almo-1 and -2, Jacquet et al., 2010), we find a similar increase in cell size of *Prochlorococcus* and *Synechococcus*, but a much larger increase of picoeukaryotes (Fig. 8b). The difference this could make to the global picophytoplankton biomass is large. If we use the standard conversion factors in the surface and increase these linearly up to a factor 3 below 150 m depth (blue lines in Fig. 8), then the global biomass becomes 1.32 Pg C (+78 %), or if we only apply this increasing conversion factor to *Prochlorococcus* and *Synechococcus*, we estimate a global biomass of 0.93 Pg C (+25 %). Our standard conversion factors are taken from laboratory studies. Conversion factors for heterotrophic bacteria

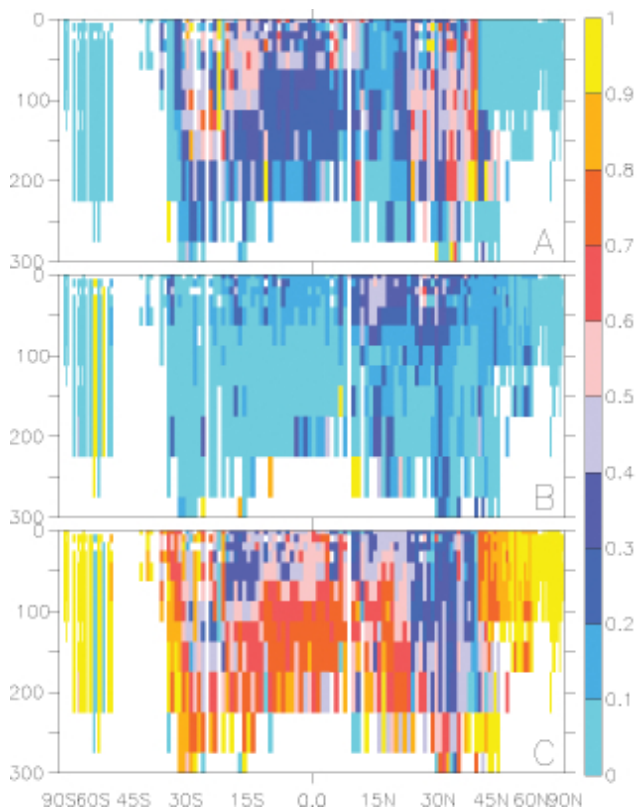


Figure 7. Zonal and time-averaged fraction of total picophytoplankton (A) *Prochlorococcus*, (B) *Synechococcus*, (C) picoeukaryotes.

from laboratory studies tend to be higher than from in situ measurements (Buitenhuis et al., 2012a). Indeed, even if we do not account for an increase of cell size with depth, the laboratory conversion factors lead to a higher biomass estimate than the indirect conversion factors. Other sources of variability are seasonal variations of cell size (DuRand et al., 2001) of all picophytoplankton and increasing cell size of *Prochlorococcus* with latitude towards the equator (Viviani et al., 2011). Thus, it is clear that there is considerable uncertainty in the conversion factors, but in the absence of general trends for the cell size variability of each group under all conditions, our estimate of 0.74 Pg C represents our best estimate of the global picophytoplankton biomass.

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 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) suggested that a third of global phytoplankton biomass is in the pico size class. Therefore, a 2–3-fold difference in the estimated picophytoplankton biomass would not only be important for calculating the relative contribution that picophytoplankton make to the phytoplankton

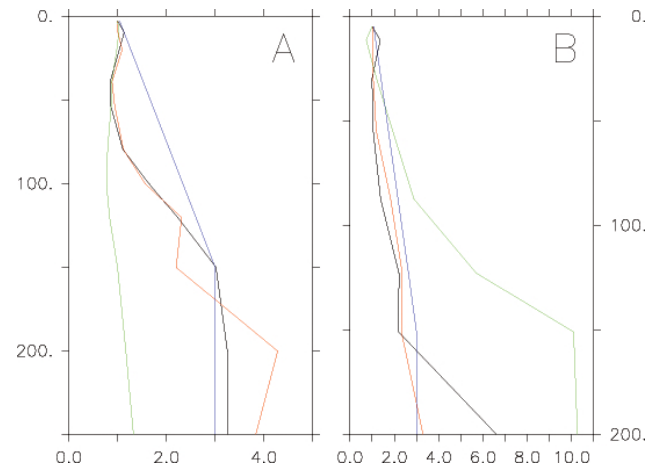


Figure 8. Cell size as a function of depth, normalised to cell size at the surface, (black) *Prochlorococcus*, (red) *Synechococcus*, (green) picoeukaryotes, (blue) exploratory conversion factor that increases up to a factor 3 below 150 m depth. (A) At BATS, (B) in the Western Mediterranean (Almo-1 and -2).

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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References

- Alvain, S., Moulin, C., Dandonneau, Y., and Breon, F. M.: Remote sensing of phytoplankton groups in case 1 waters from global SeaWiFS imagery, *Deep-Sea Res. Pt. I*, 52, 1989–2004, 2005.
- Bertilsson, S., Berglund, O., Karl, D. M., and Chisholm, S. W.: Elemental composition of marine *Prochlorococcus* and *Synechococcus*: Implications for the ecological stoichiometry of the sea, *Limnol. Oceanogr.*, 48, 1721–1731, 2003.
- Binder, B. J., Chisholm, S. W., Olson, R. J., Frankel, S. L., and Worden, A. Z.: Dynamics of picophytoplankton, ultraphytoplankton and bacteria in the central equatorial Pacific, *Deep-Sea Res. Pt. II*, 43, 907–931, 1996.
- Blanchot, J. and Rodier, M.: Picophytoplankton abundance and biomass in the western tropical Pacific Ocean during the 1992 El Niño year: Results from flow cytometry, *Deep-Sea Res. Pt. I*, 43, 877–895, 1996.
- Blanchot, J., Andre, J. M., Navarette, C., Neveux, J., and Radenac, M. H.: Picophytoplankton in the equatorial Pacific: vertical distributions in the warm pool and in the high nutrient low chlorophyll conditions, *Deep-Sea Res. Pt. I*, 48, 297–314, 2001.
- Bouman, H. A., Ulloa, O., Barlow, R., Li, W. K. W., Platt, T., Zwirgmaier, K., Scanlan, D. J., and Sathyendranath, S.: Water-column stratification governs the community structure of subtropical marine picophytoplankton, *Environmental Microbiology Reports*, 3, 473–482, 2011.
- Buck, K. R., Chavez, F. P., and Campbell, L.: Basin-wide distributions of living carbon components and the inverted trophic pyramid of the central gyre of the North Atlantic Ocean, summer 1993, *Aquat. Microb. Ecol.*, 10, 283–298, 1996.
- Buitenhuis, E. T., Li, W. K. W., Lomas, M. W., Karl, D. M., Landry, M. R., and Jacquet, S.: Bacterial biomass distribution in the global ocean, *Earth Syst. Sci. Data Discuss.*, 5, 301–315, doi:10.5194/essdd-5-301-2012, 2012a.
- Buitenhuis, E. T., Vogt, M., Bednarsek, N., Doney, S. C., Leblanc, K., Le Quééré, C., Luo, Y.-W., Moriarty, R., O'Brien, C., O'Brien, T., Peloquin, J., and Schiebel, R.: MAREDAT: Towards a World Ocean Atlas of MARine Ecosystem DATA, *Earth Syst. Sci. Data Discuss.*, in preparation, 2012b.
- Cailliau, C., Claustre, H., Vidussi, F., Marie, D., and Vaultot, D.: Carbon biomass, and gross growth rates as estimated from C-14 pigment labelling, during photoacclimation in *Prochlorococcus* CCMP 1378, *Mar. Ecol.-Prog. Ser.*, 145, 209–221, 1996.
- Campbell, L., Nolla, H. A., and Vaultot, D.: The Importance of *Prochlorococcus* to Community Structure in the Central North Pacific-Ocean, *Limnol. Oceanogr.*, 39, 954–961, 1994.
- Campbell, L., Liu, H. B., Nolla, H. A., and Vaultot, D.: Annual variability of phytoplankton and bacteria in the subtropical North Pacific Ocean at Station ALOHA during the 1991–1994 ENSO event, *Deep-Sea Res. Pt. I*, 44, 167–192, 1997.
- Campbell, L., Landry, M. R., Constantinou, J., Nolla, H. A., Brown, S. L., Liu, H., and Caron, D. A.: Response of microbial community structure to environmental forcing in the Arabian Sea, *Deep-Sea Res. Pt. II*, 45, 2301–2325, 1998.
- Campbell, L., Carpenter, E. J., Montoya, J. P., Kustka, A. B., and Capone, D. G.: Picoplankton community structure within and outside a *Trichodesmium* bloom in the southwestern Pacific Ocean, *Vie et Milieu*, 55, 185–195, 2005.
- Cavender-Bares, K. K., Rinaldo, A., and Chisholm, S. W.: Microbial size spectra from natural and nutrient enriched ecosystems, *Limnol. Oceanogr.*, 46, 778–789, 2001.
- Claustre, H., Bricaud, A., Babin, M., Bruyant, F., Guillou, L., Le Gall, F., Marie, D., and Partensky, F.: Diel variations in *Prochlorococcus* optical properties, *Limnol. Oceanogr.*, 47, 1637–1647, 2002.
- DuRand, M. D. and Olson, R. J.: Contributions of phytoplankton light scattering and cell concentration changes to diel variations in beam attenuation in the equatorial Pacific from flow cytometric measurements of pico-, ultra- and nanoplankton, *Deep-Sea Res. Pt. II*, 43, 891–906, 1996.
- DuRand, M. D., Olson, R. J., and Chisholm, S. W.: Phytoplankton population dynamics at the Bermuda Atlantic Time-series station in the Sargasso Sea, *Deep-Sea Res. Pt. II*, 48, 1983–2003, 2001.
- DuRand, M. D., Green, R. E., Sosik, H. M., and Olson, R. J.: Diel variations in optical properties of *Micromonas pusilla* (Prasinophyceae), *J. Phycol.*, 38, 1132–1142, 2002.
- Dusenberry, J. A. and Frankel, S. L.: Increasing the Sensitivity of a Facscan Flow Cytometer to Study Oceanic Picoplankton, *Limnol. Oceanogr.*, 39, 206–209, 1994.
- Echevarría, F., Zabala, L., Corzo, A., Navarro, G., Prieto, L., and Macias, D.: Spatial distribution of autotrophic picoplankton in relation to physical forcings: the Gulf of Cadiz, Strait of Gibraltar and Alboran Sea case study, *J. Plankton Res.*, 31, 1339–1351, 2009.
- Fu, F.-X., Warner, M. E., Zhang, Y., Feng, Y., and Hutchins, D. A.: Effects of increased temperature and CO₂ on photosynthesis, growth, and elemental ratios in marine *Synechococcus* and *Prochlorococcus* (Cyanobacteria), *J. Phycol.*, 43, 485–496, 2007.
- Garcia, C. M., Jimenez-Gomez, F., Rodriguez, J., Bautista, B., Estrada, M., Garcia Braun, J., Gasol, J. M., Figueiras, F. G., and Guerrero, F.: The size structure and functional composition of ultraplankton and nanoplankton at a frontal station in the Alboran Sea. Working groups 2 and 3 report, *Sci. Mar.*, 58, 43–52, 1994.
- Grob, C., Ulloa, O., Claustre, H., Huot, Y., Alarcón, G., and Marie, D.: Contribution of picoplankton to the total particulate organic carbon concentration in the eastern South Pacific, *Biogeochemistry*, 4, 837–852, doi:10.5194/bg-4-837-2007, 2007.
- Jacquet, S., Prieur, L., Nival, P., and Vaultot, D.: Structure and variability of the microbial community associated to the Alboran Sea frontal system (Western Mediterranean) in winter, *J. Oceanogr. Research and Data*, 3, 47–75, 2010.
- Johnson, Z. I., Zinser, E. R., Coe, A., McNulty, N. P., Woodward, E. M. S., and Chisholm, S. W.: Niche partitioning among *Prochlorococcus* ecotypes along ocean-scale environmental gradients, *Science*, 311, 1737–1740, 2006.
- Kana, T. M. and Glibert, P. M.: Effect of Irradiances up to 2000 $\mu\text{E m}^{-2} \text{s}^{-1}$ on Marine *Synechococcus* WH7803. 1. Growth, Pigmentation, and Cell Composition, *Deep-Sea Res.*, 34, 479–495, 1987.
- Landry, M. R., Kirshtein, J., and Constantinou, J.: Abundances and distributions of picoplankton populations in the central equatorial Pacific from 12° N to 12° S, 140° W, *Deep-Sea Res. Pt. II*, 43, 871–890, 1996.
- Le Quééré, C., Harrison, S. P., Prentice, I. C., Buitenhuis, E. T., Aumont, O., Bopp, L., Claustre, H., Da Cunha, L. C., Geider, R., Giraud, X., Klaas, C., Kohfeld, K. E., Legendre, L., Manizza, M., Platt, T., Rivkin, R. B., Sathyendranath, S., Uitz, J., Watson, A.

- J., and Wolf-Gladrow, D.: Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models, *Glob. Change Biol.*, 11, 2016–2040, 2005.
- Li, W. K. W.: Phytoplankton biomass and chlorophyll concentration across the North Atlantic, *Sci. Mar.*, 58, 67–79, 1994.
- Li, W. K. W.: Composition of Ultraphytoplankton in the Central North-Atlantic, *Mar. Ecol.-Prog. Ser.*, 122, 1–8, 1995.
- Li, W. K. W.: Cytometric diversity in marine ultraphytoplankton, *Limnol. Oceanogr.*, 42, 874–880, 1997.
- Li, W. K. W.: Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean, *Nature*, 419, 154–157, 2002.
- Li, W. K. W.: From cytometry to macroecology: a quarter century quest in microbial oceanography, *Aquat. Microb. Ecol.*, 57, 239–251, 2009.
- Li, W. K. W. and Harrison, W. G.: Chlorophyll, bacteria and picophytoplankton in ecological provinces of the North Atlantic, *Deep-Sea Res. Pt. II*, 48, 2271–2293, 2001.
- Li, W. K. W. and Wood, A. M.: Vertical Distribution of North-Atlantic Ultraphytoplankton – Analysis by Flow-Cytometry and Epifluorescence Microscopy, *Deep-Sea Res.*, 35, 1615–1638, 1988.
- Li, W. K. W., Dickie, P. M., Irwin, B. D., and Wood, A. M.: Biomass of Bacteria, Cyanobacteria, Prochlorophytes and Photosynthetic Eukaryotes in the Sargasso Sea, *Deep-Sea Res.*, 39, 501–519, 1992.
- Li, W. K. W., Zohary, T., Yacobi, Y. Z., and Wood, A. M.: Ultraphytoplankton in the Eastern Mediterranean-Sea – Towards Deriving Phytoplankton Biomass from Flow Cytometric Measurements of Abundance, Fluorescence and Light Scatter, *Mar. Ecol.-Prog. Ser.*, 102, 79–87, 1993.
- Li, W. K. W., McLaughlin, F. A., Lovejoy, C., and Carmack, E. C.: Smallest Algae Thrive As the Arctic Ocean Freshens, *Science*, 326, 539–539, 2009.
- Lindell, D. and Post, A. F.: Ultraphytoplankton Succession Is Triggered by Deep Winter Mixing in the Gulf-of-Aqaba (Eilat), Red-Sea, *Limnol. Oceanogr.*, 40, 1130–1141, 1995.
- Liu, H. B., Bidigare, R. R., Laws, E., Landry, M. R., and Campbell, L.: Cell cycle and physiological characteristics of *Synechococcus* (WH7803) in chemostat culture, *Mar. Ecol.-Prog. Ser.*, 189, 17–25, 1999.
- Llewellyn, C. A. and Gibb, S. W.: Intra-class variability in the carbon, pigment and biomineral content of prymnesiophytes and diatoms, *Mar. Ecol.-Prog. Ser.*, 193, 33–44, 2000.
- Lomas, M. W., Roberts, N., Lipschultz, F., Krause, J. W., Nelson, D. M., and Bates, N. R.: Biogeochemical responses to late-winter storms in the Sargasso Sea. IV. Rapid succession of major phytoplankton groups, *Deep-Sea Res. Pt. I*, 56, 892–908, 2009.
- Lomas, M. W., Steinberg, D. K., Dickey, T., Carlson, C. A., Nelson, N. B., Condon, R. H., and Bates, N. R.: Increased ocean carbon export in the Sargasso Sea linked to climate variability is countered by its enhanced mesopelagic attenuation, *Biogeosciences*, 7, 57–70, doi:10.5194/bg-7-57-2010, 2010.
- Marie, D., Zhu, F., Balague, V., Ras, J., and Vaultot, D.: Eukaryotic picoplankton communities of the Mediterranean Sea in summer assessed by molecular approaches (DGGE, TTGE, QPCR), *FEMS Microb. Ecol.*, 55, 403–415, 2006.
- McManus, G. B. and Dawson, R.: Phytoplankton Pigments in the Deep Chlorophyll Maximum of the Caribbean Sea and the Western Tropical Atlantic-Ocean, *Mar. Ecol.-Prog. Ser.*, 113, 199–206, 1994.
- Montagnes, D. J. S., Berges, J. A., Harrison, P. J., and Taylor, F. J. R.: Estimating Carbon, Nitrogen, Protein, and Chlorophyll-a from Volume in Marine-Phytoplankton, *Limnol. Oceanogr.*, 39, 1044–1060, 1994.
- Moran, S. B., Lomas, M. W., Kelly, R. P., Gradinger, R., Iken, K., and Mathis, J. T.: Seasonal succession of net primary productivity, particulate organic carbon export, and autotrophic community composition in the eastern Bering Sea, *Deep-Sea Res. Pt. II*, 65–70, 84–97, 2012.
- Moran, X. A. G., Lopez-Urrutia, A., Calvo-Diaz, A., and Li, W. K. W.: Increasing importance of small phytoplankton in a warmer ocean, *Glob. Change Biol.*, 16, 1137–1144, 2010.
- Neveux, J., Vaultot, D., Courties, C., and Fukai, E.: Green Photosynthetic Bacteria Associated with the Deep Chlorophyll Maximum of the Sargasso Sea, *CR. Acad. Sci. III-Vie.*, 308, 9–14, 1989.
- Neveux, J., Lantoine, F., Vaultot, D., Marie, D., and Blanchot, J.: Phycoerythrins in the southern tropical and equatorial Pacific Ocean: Evidence for new cyanobacterial types, *J. Geophys. Res.-Oceans*, 104, 3311–3321, 1999.
- Olson, R. J., Chisholm, S. W., Zettler, E. R., Altabet, M. A., and Dusenberry, J. A.: Spatial and Temporal Distributions of Prochlorophyte Picoplankton in the North-Atlantic Ocean, *Deep-Sea Res.*, 37, 1033–1051, 1990.
- Partensky, F., Blanchot, J., Lantoine, F., Neveux, J., and Marie, D.: Vertical structure of picophytoplankton at different trophic sites of the tropical northeastern Atlantic Ocean, *Deep-Sea Res. Pt. I*, 43, 1191–1213, 1996.
- Raven, J. A.: The twelfth Tansley Lecture. Small is beautiful: the picophytoplankton, *Funct. Ecol.*, 12, 503–513, 1998.
- Sherr, E. B., Sherr, B. F., and Wheeler, P. A.: Distribution of coccoid cyanobacteria and small eukaryotic phytoplankton in the upwelling ecosystem off the Oregon coast during 2001 and 2002, *Deep-Sea Res. Pt. II*, 52, 317–330, 2005.
- Shimada, A., Hasegawa, T., Umeda, I., Kadoya, N., and Maruyama, T.: Spatial Mesoscale Patterns of West Pacific Picophytoplankton as Analyzed by Flow-Cytometry – Their Contribution to Subsurface Chlorophyll Maxima, *Mar. Biol.*, 115, 209–215, 1993.
- Shimada, A., Nishijima, M., and Maruyama, T.: Seasonal appearance of *Prochlorococcus* in Suruga Bay, Japan in 1992–1993, *J. Oceanogr.*, 51, 289–300, 1995.
- Sieburth, J. M., Smetacek, V., and Lenz, J.: Pelagic Ecosystem Structure – Heterotrophic Compartments of Plankton and Their Relationship to Plankton Size Fractions – Comment, *Limnol. Oceanogr.*, 23, 1256–1263, 1978.
- Simon, N., Barlow, R. G., Marie, D., Partensky, F., and Vaultot, D.: Characterization of Oceanic Photosynthetic Picoeukaryotes by Flow-Cytometry, *J. Phycol.*, 30, 922–935, 1994.
- Takahashi, M. and Hori, T.: Abundance of Picophytoplankton in the Subsurface Chlorophyll Maximum Layer in Sub-Tropical and Tropical Waters, *Mar. Biol.*, 79, 177–186, 1984.
- Tremblay, G., Belzile, C., Gosselin, M., Poulin, M., Roy, S., and Tremblay, J.-E.: Late summer phytoplankton distribution along a 3500 km transect in Canadian Arctic waters: strong numerical dominance by picoeukaryotes, *Aquat. Microb. Ecol.*, 54, 55–70, 2009.
- Vaultot, D., Partensky, F., Neveux, J., Mantoura, R. F. C., and Llewellyn, C. A.: Winter Presence of Prochlorophytes in Surface Waters of the Northwestern Mediterranean-Sea, *Limnol.*

- Oceanogr., 35, 1156–1164, 1990.
- Vaulot, D., Eikrem, W., Viprey, M., and Moreau, H.: The diversity of small eukaryotic phytoplankton ($\leq 3 \mu\text{m}$) in marine ecosystems, *FEMS Microb. Rev.*, 32, 795–820, 2008.
- Veldhuis, M. J. W. and Kraay, G. W.: Vertical-Distribution and Pigment Composition of a Picoplanktonic Prochlorophyte in the Subtropical North-Atlantic – a Combined Study of Hplc-Analysis of Pigments and Flow-Cytometry, *Mar. Ecol.-Prog. Ser.*, 68, 121–127, 1990.
- Veldhuis, M. J. W. and Kraay, G. W.: Cell Abundance and Fluorescence of Picoplankton in Relation to Growth Irradiance and Nitrogen Availability in the Red-Sea, *Neth. J. Sea Res.*, 31, 135–145, 1993.
- Veldhuis, M. J. W., Kraay, G. W., and Gieskes, W. W. C.: Growth and Fluorescence Characteristics of Ultraplankton on a North South Transect in the Eastern North-Atlantic, *Deep-Sea Res. Pt. II*, 40, 609–626, 1993.
- Veldhuis, M. J. W., Kraay, G. W., VanBleijswijk, J. D. L., and Baars, M. A.: Seasonal and spatial variability in phytoplankton biomass, productivity and growth in the northwestern Indian Ocean: The southwest and northeast monsoon, 1992–1993, *Deep-Sea Res. Pt. I*, 44, 425–449, 1997.
- Verity, P. G., Robertson, C. Y., 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.
- Viviani, D. A., Bjoerkman, K. M., Karl, D. M., and Church, M. J.: Plankton metabolism in surface waters of the tropical and subtropical Pacific Ocean, *Aquat. Microb. Ecol.*, 62, 1–12, 2011.
- Worden, A. Z., Nolan, J. K., and Palenik, B.: Assessing the dynamics and ecology of marine picophytoplankton: The importance of the eukaryotic component, *Limnol. Oceanogr.*, 49, 168–179, 2004.
- Yacobi, Y. Z., Zohary, T., Kress, N., Hecht, A., Robarts, R. D., Waiser, M., and Wood, A. M.: Chlorophyll Distribution Throughout the Southeastern Mediterranean in Relation to the Physical Structure of the Water Mass, *J. Marine Syst.*, 6, 179–190, 1995.