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29 Abstract

The smallest marine phytoplankton, collectively termed picophytoplankton, have been 30 routinely enumerated by flow cytometry since the late 1980s, during cruises throughout most of 31

- 32 the world ocean. We compiled a database of 40,946 data points, with separate abundance entries
- 33 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° 34
- spacing, the database covers 2.4% of the ocean surface area, with the best data coverage in the 35
- North Atlantic, the South Pacific and North Indian basins, and at least some data in all other 36
- basins. The average picophytoplankton biomass is $12 \pm 22 \ \mu g \ C \ L^{-1}$ or $1.9 \ g \ C \ m^{-2}$. We estimate a 37
- total global picophytoplankton biomass of 0.53 1.32 Pg C (17 39 % Prochlorococcus, 12 15 38
- 39 % Synechococcus and 49 - 69 % picoeukaryotes), with an intermediate / best estimate of 0.74 Pg
- 40 C. Future efforts in this area of research should focus on reporting calibrated cell size, and
- collecting data in undersampled regions. 41
- http://doi.pangaea.de/10.1594/PANGAEA.777385 42

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1 Introduction 44

Picophytoplankton are usually defined as phytoplankton less than 2 or 3 µm diameter (e.g. 45

- 46 Sieburth et al., 1978; Takahashi and Hori, 1984; Vaulot et al., 2008). They are the smallest class
- 47 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 48
- 49 Chlorophyta, Haptophyta, Cryptophyta and Heterokontophyta (Vaulot et al., 2008). The
- 50 prokaryotes belong to the phylum Cyanobacteria, and are subdivided into the genera
- Prochlorococcus (~0.6 µm) and Synechococcus (~1 µm), with each group having many ecotypes 51
- 52 that dominate in different ocean regions (Johnson et al. 2006).

- 53 Picophytoplankton tend to dominate the phytoplankton biomass under oligotrophic
- 54 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).
- 56 The abundance of the prokaryotes is often inversely related with the eukaryotes, which are
- 57 favoured by more physically active mixed layers (e.g., Boumann et al., 2011). Furthermore, with
- 58 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).
- 61 As part of the marine ecology data synthesis effort (MAREDAT, this special issue), we
- 62 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
- taxonomic groups in the marine ecosystem. It addresses both autotrophs and heterotrophs a
 covers the size range from bacteria to macrozooplankton.
- 65 66
- 67 **2 Data**
- 68 We compiled data for picophytoplankton abundance in three taxonomic groups:
- 69 *Prochlorococcus*, *Synechococcus*, and picoeukaryotes (Table 1). We used the size range of
- 70 picoeukaryotes as defined by the contributing researchers. The size range has a large impact on
- 71 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
- 73 (http://doi.pangaea.de/10.1594/PANGAEA.777385) and the MAREDAT webpage
- 74 (http://lgmacweb.env.uea.ac.uk/maremip/data/essd.shtml).75

76 2.2.1 Conversion factors

- 77 Conversion factors from cell abundance to carbon biomass for the three picophytoplankton
- 78 groups were compiled from the literature (Table 2). Conversion factors were either measured
- 79 directly on unialgal cultures in the laboratory, or derived from indirect methods on *in situ*
- 80 samples. Most of the indirect measures were derived from cell sizes that were estimated from
- 81 average forward angle light scatter (FALS) multiplied by a carbon content per biovolume. The
- 82 conversion factors of Veldhuis et al. (1997) were based on nitrate uptake in incubated *in situ*
- 83 samples and assuming a C:N ratio of 6. Since the biggest source of variability in the other indirect 84 measures is the carbon content per biovolume, which was measured on laboratory cultures, the
- 84 measures is the carbon content per biovolume, which was measured on laboratory cultures, the 85 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
- 87 factors as the standard.
- 88

89 2.2.2 Quality control

- 90
- 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
- 93 (Buitenhuis et al. 2012b) to the total carbon data. The data were not normally distributed, so we
- 94 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
- 96 Oman (Indian Ocean).
- 97

98 **3 Results**

- 99 The database contains 40,946 data points (Fig. 1). Data are included from a number of stations
- 100 that have been sampled repeatedly over many years, or programs where measurements have been
- 101 made on a fine resolution grid. Therefore, after gridding, we obtained 10,747 data points on the
- 102 World Ocean Atlas grid $(1^{\circ} \times 1^{\circ} \times 33 \text{ vertical layers} \times 12 \text{ months})$, representing a coverage of
- 103 vertically integrated and annually averaged biomass for 2.4% of the ocean surface. For further
- 104 details on the gridding, see Buitenhuis et al. (2012b). To limit the overrepresentation of well

105 sampled locations, we present results of the gridded data. Only 15% of the data are from the 106 Southern Hemisphere (Fig. 2A), 33% are from the tropics (43% of the ocean surface), while 13% 107 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 108 109 (Fig. 3), and there are still 480 observations at 200 m depth (Fig. 2B), thus defining the vertical 110 biomass profile fairly well. Zero values make up 1.6% of the data, and 95% of those are from 111 below 62.5 m depth. There is some sampling bias towards the growing season, with 67% of the 112 data sampled in the spring and summer months (Fig. 2C).

113 The average picophytoplankton biomass is $12 \pm 22 \ \mu g \ C \ L^{-1}$ (Fig. 4) or 1.9 g C m⁻². Of the 114 vertically integrated biomass 54% occurs in the upper 40 m, and 93% in the upper 112.5 m (Fig. 115 2). *Synechococcus* is found at the most shallow depths (97% above 112.5 m, Fig. 5), followed by 116 picoeukaryotes (92% above 112.5 m), while *Prochlorococcus* biomass decreases more slowly 117 with depth (87% above 112.5 m).

118 The average biomass is slightly higher in the tropics and considerably lower in the Arctic 119 (Fig. 4, 6), but the standard deviation within latitudinal 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 °S - 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: 120 121 $12 \pm 22 \ \mu g \ C \ L^{-1} \ or \ 1.9 \ g \ C \ m^{-2}$, and Arctic: $6 \pm 8 \ \mu g \ C \ L^{-1} \ or \ 0.6 \ g \ C \ m^{-2}$. We calculate the global 122 picophytoplankton biomass from the zonal and time averaged concentration filled by 123 interpolation across up to 22° latitude (Fig. 6) multiplied by the volume at each latitude and 124 125 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% 126 127 picoeukaryotes). Interpolation across up to 10° latitude only leaves a few missing values, and 128 estimates 0.73 Pg C. If we use the indirect *in situ* conversion factors for each of the three groups 129 (Table 2), the total biomass (with up to 22° interpolation) is 0.53 Pg C (39% *Prochlorococcus*, 130 12% Synechococcus, 49% picoeukaryotes).

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 - 40°N and shares dominance with picoeukaryotes between 10 - 30°S and at the surface in the tropics. *Synechococcus* only dominates around 50°S, and is relatively abundant above 62.5 m between 10 - 40°N. This is consistent with the community structure of picophytoplankton that has been analysed by Bouman et al. (2011).

138 **4 Discussion**

139 Although data coverage, at 2.4% of the ocean surface, is by no means complete, if we 140 randomly select half of the depth profiles in 10 random samples, the average integrated biomass 141 varied between 96 and 104% of the value for the whole dataset, while the averages from the 142 Southern and Northern Hemispheres are 119% and 96%, respectively. On the other hand, the 143 average using the indirect in situ conversion factors is 72% of the value estimated using the direct 144 conversion factors. Thus, the main uncertainty in determining the global picophytoplankton 145 biomass in this analysis is the conversion from cell abundance to carbon biomass. There is a 146 fairly tight relationship between forward angle light scatter (FALS; Cavender-Bares et al. 2001, 147 DuRand et al. 2002) or right angle light scatter (RALS; Simon et al. 1994; Worden et al. 2004), 148 as measured by flow cytometry, and cell size, which is probably the main source of uncertainty in 149 the conversion factor. Only about a third of our data came with FALS or RALS data, and even in 150 those cases these were in arbitrary units. We recommend the routine measurement of calibrated 151 size as the additional measurement that would do most to improve our knowledge of global 152 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 flow cytometers (Dusenberry and Frankel, 157 1999).

158 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 159 little variation in size as a function of depth (Li et al., 1993; DuRand et al., 2001; Grob et al. 160 2007). We compared the increase in size for the three groups at two locations. At BATS (which 161 includes the data of DuRand et al., 2001), we also find an increase in cell size of Prochlorococcus 162 and Synechococcus but not picoeukaryotes (Fig. 8A). However, in the Western Mediterranean 163 (Almo 1 and 2, Jacquet et al., 2010), we find a similar increase in cell size of Prochlorococcus 164 and Synechococcus, but a much larger increase of picoeukaryotes (Fig. 8B). The difference this 165 166 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 167 168 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 0.93 169 Pg C (+25%). Our standard conversion factors are taken from laboratory studies. Conversion 170 171 factors for heterotrophic bacteria from laboratory studies tend to be higher than from in situ 172 measurements (Buitenhuis et al., 2012a). Indeed, even if we do not account for an increase of cell 173 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 174 175 (DuRand et al., 2001) of all picophytoplankton and increaseing cell size of Prochlorococcus with latitude towards the equator (Viviani et al., 2011). Thus, it is clear that there is considerable 176 uncertainty in the conversion factors, but in the absence of general trends for the cell size 177 178 variability of each group under all conditions, our estimate of 0.74 Pg C represents our best 179 estimate of the global picophytoplankton biomass.

180 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 181 0.74 Pg C, and even our estimate using the indirect conversion factors is still almost double at 182 183 0.53 Pg C. Le Quéré et al. (2005) suggested that a third of global phytoplankton biomass is in the 184 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 185 to the phytoplankton, but also for calculating the total biomass of phytoplankton as the base of 186 the ocean ecosystem. 187

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

193 picoeukaryotes constitute 69% of global picophytoplankton biomass critically depends on the 194 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.

199

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Tables.

395 _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 (unpubl.)
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 (unpubl.)
Australia	Nov-Dec 1990	Tropical Pacific West	Shimada et al., 1993
HOT	1990-2008	Tropical Pacific	Campbell et al., 1997;
			Karl (unpubl.)
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 (unpubl.)
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 (unpubl.)
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,
	4 0 1000	E 115.17	1996
EQPACITOII	Aug - Sep 1992	Equatorial Pacific	Landry et al., 1996
L192037	Sep 1992	North Atlantic	Li, 1994; Li, 1995
EQPACIT012	Sep - Oct 1992	Equatorial Pacific	DuRand and Olson,
	D 1000		1996 Det 1 1000
EUMELIS	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
L193002	May 1993	North Atlantic	Li, 1994; Li, 1995
EROSDISCO93	Jul 1993	Mediterranean Sea	Simon, Barlow, Marie
	L 1 A 1000		(unpubl.)
INUAA93	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 - April 1995	Arabian Sea	Campbell et al., 1998	
Delaware95	Apr 1995	North Atlantic	Li, 1997	
MINOS	Jun 1995	Mediterranean Sea	Vaulot, Marie, Partensky	
			(unpubl.)	
Chile95	Jun 1995	South Pacific	Li (unpubl.)	
Lopez96	Jun 1995	Sargasso Sea	Li (unpubl.)	
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 (unpubl.)	
ArabianTTN050	Aug - Sep 1995	Aug - Sep 1995 Arabian Sea		
NOAA95	Sep - Oct 1995	Indian Ocean	Buck (unpubl.)	
ArabianTTN053	Nov 1995	Arabian Sea	Olson (unpubl.)	
ArabianTTN054	Dec 1995	Arabian Sea	Campbell et al., 1998	
AZOMP	1995-2009	North Atlantic	Li, 2002; Li, 2009; Li et	
			al., 2009	
OMEX / D1221	Jun 1996	North Atlantic	BODC	
AZMP	1997-2009	North Atlantic	Li, 2002; Li, 2009; Li et	
			al., 2009	
Kiwi6	Oct-Nov 1997	Antarctica	Landry (unpubl.)	
Kiwi7	Dec 1997	Antarctica	Landry (unpubl.)	
Almo-1	Dec 1997	Mediterranean Sea	Jacquet, Marie	
			(unpubl.)	
AESOPS/NBP97-1	1997	Ross Sea	Olson, Sosik (unpubl.)	
Almo-2	Jan 1998	Mediterranean Sea	Jacquet et al., 2010	
Kiwi8	Jan-Feb 1998	Antarctica	Landry (unpubl.)	
Kiwi9	Feb-Mar 1998	Antarctica	Landry (unpubl.)	
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; Li, 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 (unpubl.)	
C30	2007-2008	North Atlantic, Arctic	Li, 2002; Li, 2009; Li et	
			al., 2009	
Bering Sea	Mar 2008 - May 2010	North Pacific	Moran et al., in press	
Line P	Aug 2010 - Jun 2011	North Pacific	Lomas (unpubl.)	
FOODWEB	Feb - Aug 2011	North Atlantic	Lomas (unpubl.)	

Table 2. Cell abundance to carbon biomass conversion factors [fg C cell⁻¹]. 398

Tuble 2. Con abundance to earbon biomass conversion factors [15 C con].							
	Prochlorococcus	Synechococcus	picoeukaryotes	reference			
Direct from		250		Kana and Glibert			
cultures				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,	92	175		Veldhuis et al. 1997			
mostly from							
culture C per							
volume * in							
situ volume							
	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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Figures and captions 401



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Figure 1. Horizontal distribution of the number of observations. Data points have been enlarged to $5^{\circ}*5^{\circ}$. 404









90S60S 45S 30S 15S 0.0 15N 30N 45N 60N90N Figure 6. Zonal and time averaged biomass [μ g C L⁻¹] of A) *Prochlorococcus*, B) *Synechococcus*, C) picoeukaryotes. Data have been filled by latitudinal interpolation of up to 22°. 418





Synechococcus, C) picoeukaryotes.



