Earth Syst. Sci. Data, 4, 101–106, 2012
www.earth-syst-sci-data.net/4/101/2012/
doi:10.5194/essd-4-101-2012

Open Access Earth System Science Data

Picoheterotroph (*Bacteria* and *Archaea*) biomass distribution in the global ocean

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Received: 12 April 2012 – Published in Earth Syst. Sci. Data Discuss.: 8 May 2012
Revised: 10 August 2012 – Accepted: 14 August 2012 – Published: 10 September 2012

Abstract. We compiled a database of 39 766 data points consisting of flow cytometric and microscopical measurements of picoheterotroph abundance, including both *Bacteria* and *Archaea*. After gridding with 1° spacing, the database covers 1.3 % of the ocean surface. There are data covering all ocean basins and depths except the Southern Hemisphere below 350 m or from April until June. The average picoheterotroph biomass is $3.9 \pm 3.6\,\mu g\,C\,l^{-1}$ with a 20-fold decrease between the surface and the deep sea. We estimate a total ocean inventory of about 1.3×10^{29} picoheterotroph cells. Surprisingly, the abundance in the coastal regions is the same as at the same depths in the open ocean. Using an average of published open ocean measurements for the conversion from abundance to carbon biomass of $9.1\,fg\,cell^{-1}$, we calculate a picoheterotroph carbon inventory of about 1.2 Pg C. The main source of uncertainty in this inventory is the conversion factor from abundance to biomass. Picoheterotroph biomass is ~ 2 times higher in the tropics than in the polar oceans.

doi:10.1594/PANGAEA.779142

1 Introduction

Picoheterotrophs are the main degraders of detritus in the ocean (Azam and Malfatti, 2007). The term picoheterotrophs was introduced by Le Quéré et al. (2005) to include heterotrophic *Bacteria* and *Archaea*, and exclude cyanobacteria. Most picoheterotrophs (> 95 %, Cho and Azam, 1988; Turley and Stutt, 2000) live on dissolved organic matter (DOM) as suspended/detached organisms, though in the deep sea the contribution from other energy sources such as reduced nitrogen could be significant (Herndl et al., 2005). Attached picoheterotrophs living in and on particulate detritus, although less abundant, have a higher specific activity (up to 12 % of picoheterotroph production, Turley and Stutt, 2000). Picoheterotrophs that spend part of their time attached to particles both attach and detach from particles on a timescale of hours (Kiørboe et al., 2002). They also produce ectoenzymes that solubilize POC to DOC that can be subsequently used by detached picoheterotrophs (Thor et al., 2003; Azam and Malfatti, 2007). Thus, the relative importance of attached picoheterotrophs may be higher still than their contribution to picoheterotroph production suggests.

Picoheterotrophs have a higher biomass than the metabolic theory of ecology would predict based on their small size (Brown et al., 2004). This may be due in part to the fact that they respire organic matter that is formed as losses at all trophic levels, i.e. that their trophic status is unrelated to their size. Furthermore, not all picoheterotrophs show the same activity, ranging from ghost cells with cell membranes but no internal structures, dead cells containing nucleic acids but

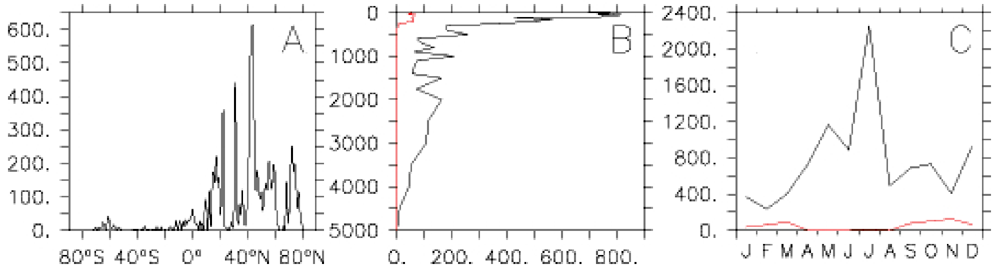

Figure 1. Number of grid points with data, as a function of **(A)** latitude, **(B)** depth, and **(C)** time. Red: Southern Hemisphere, black: total.

with compromised cell membranes, low nucleic acid cells with a lower specific activity and high nucleic acid cells (Gasol et al., 1999; Longnecker et al., 2006; Ortega-Retuerta et al., 2008; Morán et al., 2011). These dead or less active picoheterotrophs would contribute to a higher picoheterotroph biomass than the metabolic theory would predict.

Here, we present a database of picoheterotroph abundance and biomass in the global ocean. This is a contribution towards a world ocean atlas of plankton functional types (MAREDAT, this special issue), which we hope will help resolve some of the important issues on ecosystem functioning and its representation in models.

2 Data

Table 1 summarises the data that were compiled for this synthesis. Most of the data were obtained by flow cytometry. Cells were stained with nucleic acid stains, and therefore include (presumably recently) dead cells with compromised cell membranes, but not ghost cells. The data at BATS were stained with DAPI and counted microscopically, and could therefore include ghost cells. We treat *Bacteria* and *Archaea* as one group. Neither the DAPI stain used in microscopy nor the nucleic acid stains used in flow cytometry discriminate the two domains. *Archaea* make up about 5 % of picoheterotrophs in the surface, and typically about 50 % of the population that can be distinguished by domain-specific rRNA probes below 2000 m (Robinson et al., 2010 and references therein). In some cases, cyanobacteria will also have been included, especially *Prochlorococcus* near the surface, which have low red fluorescence and are therefore difficult to distinguish from picoheterotrophs. The data are available from PANGAEA (doi:10.1594/PANGAEA.779142) and the MAREDAT webpage (http://maremip.uea.ac.uk/.maredat.html).

2.1 Conversion factors

Table 2 gives abundance to carbon conversion factors from the literature. Picoheterotrophs have been shown to increase in size during incubation (Lee and Fuhrman, 1987). We therefore excluded measurements from cultures or incubated in situ samples. We also excluded conversion factor measurements from coastal waters. These have been shown to be higher than open ocean samples (Fukuda et al., 1998, Table 2), but not enough data are available to define the controlling factors for this increase or how it graduates to the open ocean value with distance from the coast. We are also unaware of measurements showing how the carbon content of picoheterotrophs varies with growth conditions. We therefore use a single conversion factor for the whole database. We calculated the conversion factor at BATS from the geometric mean cell volume and the relationship between cell volume and carbon content ($n = 164$) from Gundersen et al. (2002). We calculated the conversion factor as the average of the three studies in Table 2. The conservative conversion factor for incubated *Archaea* of 8.4 fg C cell^{-1} in Herndl et al. (2005) is similar to our conversion factor of 9.1 fg cell^{-1} for picoheterotrophs in the upper ocean, where the population is dominated by *Bacteria*.

2.2 Quality control

As a statistical filter for outliers, we applied the Chauvenet criterion (Glover et al., 2011; Buitenhuis et al., 2012) to the total carbon data. The data were not normally distributed, so we log transformed them, excluding 51 zero values. No high outliers were found by this criterion. The highest picoheterotroph biomass in the database is 74 µg C l^{-1}, measured near the coast of Oman.

3 Results

The database contains 39 766 data points. After gridding, we obtained 9284 points on the World Ocean Atlas grid (1° × 1° × 33 vertical layers × 12 months), i.e. we obtain a coverage of vertically integrated and annually averaged biomass for 1.3 % of the ocean surface. Only 6 % of the data are from the Southern Hemisphere (58 % of the ocean surface; Fig. 1a); 24 % are from the tropics (43 % of the ocean surface), while 15 % are from the polar oceans (5 % of the ocean surface). Observations from the coast (bottom depth < 225 m) make up 12 % of the data (4.9 % of the ocean area, 0.13 % of the ocean volume). Observations in the upper 112.5 m make up 57 % of the data (Fig. 1b), while observations below 950 m make up 13 % of the data. There are no

Table 1. Data sources.

Cruise	Date	Area	Reference/Investigator
Li89003	Apr 1989	North Atlantic	Li et al. (2004)
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)
Li91001	Apr 1991	North Atlantic	Li et al. (2004)
EQPACTT007	Feb–Mar 1992	Equatorial Pacific	Landry et al. (1996)
EQPACTT008	Mar–Apr 1992	Equatorial Pacific	Binder et al. (1996)
EQPACTT011	Aug–Sep 1992	Equatorial Pacific	Landry et al. (1996)
Li92037	Sep 1992	North Atlantic	Li et al. (2004)
Li93002	May 1993	North Atlantic	Li et al. (2004)
NOAA93	Jul–Aug 1993	North Atlantic	Buck et al. (1996)
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 (unpublished data)
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)
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)
ArabianTTN054	Dec 1995	Arabian Sea	Campbell et al. (1998)
AZOMP	1995–2009	Labrador Sea	Li et al. (2004); Li (2009)
AZMP	1997–2009	North Atlantic	Li et al. (2004); Li (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)
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)
PROSOPE99	Sep 1999	Mediterranean Sea	Marie et al. (2006)
GLOBEC LTOP	Mar 2001–Sep 2003	North Pacific	Sherr et al. (2006)
JOIS	2002–2009	Arctic	Li et al. (2009)
C3O	2007–2008	Arctic	Li et al. (2009)

observations below 350 m in the Southern Hemisphere. Although there are some zero values in the raw database, presumably because of a detection limit in small samples, there are no zero values in the gridded dataset. There is some sampling bias towards the growing season, with 72 % of the data sampled during the spring and summer months (Fig. 1c).

The average abundance is $4.3\times10^8 \pm 3.9\times10^8$ picoheterotrophs l^{-1} with a median of 3.1×10^8 picoheterotrophs l^{-1}. The average biomass is $3.9 \pm 3.6\,\mu\mathrm{g\,C\,l}^{-1}$ (Fig. 2) with a median of $2.8\,\mu\mathrm{g\,C\,l}^{-1}$. The biomass decreases with depth, from $7.3 \pm 4.3\,\mu\mathrm{g\,C\,l}^{-1}$ at the surface to $0.36 \pm 0.19\,\mu\mathrm{g\,C\,l}^{-1}$ at 2750–4750 m depth (Fig. 3). The average biomass in the top 225 m is slightly higher in the northern temperate region (23–67° N, $5.5 \pm 3.7\,\mu\mathrm{g\,C\,l}^{-1}$; Figs. 2, 3, 4) and tropics ($5.5 \pm 3.6\,\mu\mathrm{g\,C\,l}^{-1}$) than in Antarctica ($3.2 \pm 1.9\,\mu\mathrm{g\,C\,l}^{-1}$), the Arctic ($2.4 \pm 2.1\,\mu\mathrm{g\,C\,l}^{-1}$) and southern temperate region ($3.1 \pm 1.9\,\mu\mathrm{g\,C\,l}^{-1}$). The differences between most of these regions are significant (one-way ANOVA with violated homogeneity of variances, Games Howell post-hoc test, $p < 0.001$), except for Antarctica, for which there are only 23 measurements in the upper 225 m, and which was only significantly different from the tropics ($p = 0.014$). There is no significant difference between abundance in coastal waters and in the upper 225 m of the open ocean (Fig. 3, t-test, $p = 0.86$).

If we calculate a total ocean picoheterotroph biomass based on the average profile with depth (Fig. 3) and multiply by the volume of ocean water at each depth, we calculate an inventory of 1.1 Pg C, of which 0.28 Pg C is found in the upper 225 m, 0.51 Pg C below 950 m, and only 0.0079 Pg C in the coastal ocean. If we calculate the inventory separately in the top 225 m for the 5 regions mentioned above, the inventory is higher at 0.35 Pg C due to the larger ocean volume at low latitudes. Since we do not have enough data to calculate regional differences in the deep sea, this would increase the total ocean picoheterotroph inventory to 1.2 Pg C.

Table 2. Conversion factors.

fg C cell^{-1}	reference
7.7 (5.5, 9.8)	oceanic, Antarctica Carlson et al. (1999)
12.4 ± 6.3 ($n = 6$)	oceanic, Pacific Fukuda et al. (1998)
30.2 ± 12.3 ($n = 5$)	coastal, Japan Fukuda et al. (1998)
7.1	oceanic, Atlantic, BATS Gundersen et al. (2002)
9.1	average (oceanic only)

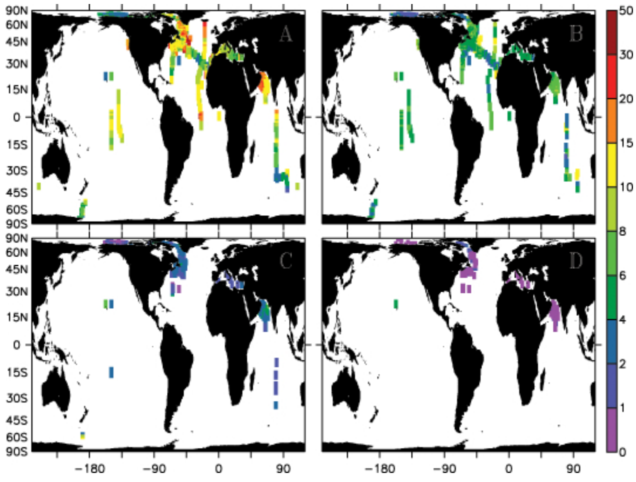

Figure 2. Picoheterotroph biomass (µg C l^{-1}) averaged over all available months. **(A)** 0–40 m, **(B)** 40–225 m, **(C)** 225–950 m, **(D)** ≥ 950 m.

4 Discussion

We could find only few measurements of carbon content of picoheterotrophs that were measured directly after collection, i.e. without incubation, from open ocean waters (Table 2). The range in these measurements is considerable, from 5.5 to 23.5 fg C cell^{-1}. Thus, there is a corresponding uncertainty in our conversion from cell abundance to carbon biomass.

In addition, a higher conversion factor has been found in coastal waters (Fukuda et al., 1998). However, it has not been established how far this higher conversion factor extends between the coastal bay waters and the open ocean. If we assume the higher conversion factor is valid up to a water depth to the bottom of 225 m (i.e. the continental shelf), then, based on the average profile of picoheterotroph biomass (Fig. 3), increasing the conversion factor from 9.1 to 30.2 fg cell^{-1} would only add 0.02 Pg C to the global inventory. Thus, at present the main sources of uncertainty in picoheterotroph biomass appear to be the open ocean conversion factor and lack of spatial coverage, and not the increase in the conversion factor near the coast. All of the open ocean conversion factors in Table 1 were measured on samples from the upper 250 m, so whether the conversion factor changes with depth is yet to be resolved.

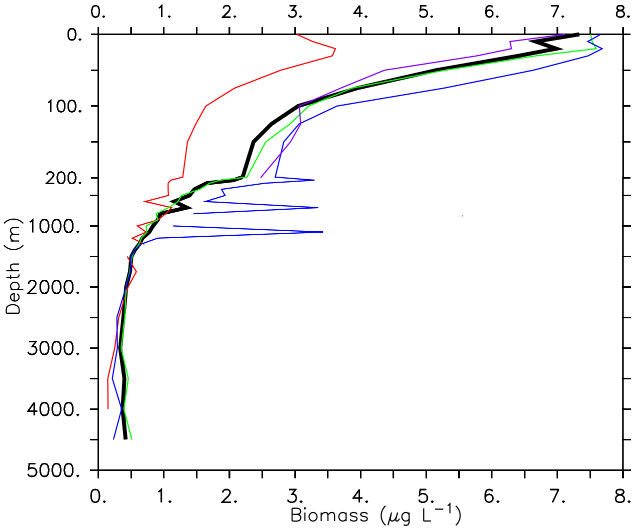

Figure 3. Picoheterotroph biomass averaged over all available longitudes, latitudes and months, as a function of depth, (black line) global average, (blue line) tropical oceans, (green line) temperate regions, (red line) polar oceans, (purple line) coastal ocean abundance × open ocean conversion factor.

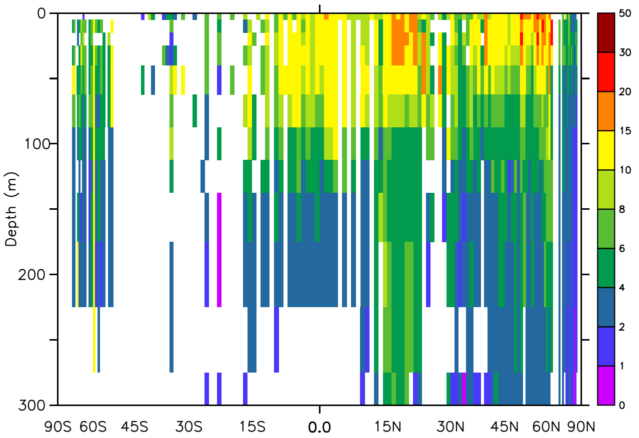

Figure 4. Picoheterotroph biomass (µg C l^{-1}) averaged over all available longitudes and months in the top 300 m.

Whitman et al. (1998) estimated the global ocean picoheterotroph inventory at 2.0 Pg C. This higher estimate is entirely due to their use of a higher conversion factor of 20 fg C cell^{-1}. In fact, the present database gives a 20 % higher inventory of global picoheterotroph abundance of 1.2×10^{29} cells based on an averaged depth profile, or 30 % higher, 1.3×10^{29} cells, based on regional inventories in the upper 225 m, but a considerably lower biomass inventory of 1.1–1.2 Pg C. Despite the uncertainties that we discuss above, we judge that the direct measurements of cellular carbon contents for open ocean picoheterotrophs that we have used here are the most precise conversion factors. For applications where biomass rather than abundance of picoheterotrophs is relevant (most notably in biogeochemical models), the database that is presented here has the largest coverage and the best estimates that are available at present.

Acknowledgements. We thank Liam Aspin for help with the statistics, and NERC for funding (NE/G006725/1) to ETB. We thank the three reviewers for their helpful comments.

Edited by: S. Pesant

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