

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

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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 is data covering all ocean basins and depths except the southern hemisphere below 350 m or from April until June. The average picoheterotroph biomass is $3.9 \pm 3.6 \mu\text{g C L}^{-1}$ with a 20-fold decrease between the surface and the deep sea. We estimate a total ocean inventory of about $1.3 \cdot 10^{29}$ 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.

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1 Introduction

Picoheterotrophs are the main degraders of detritus in the ocean (Azam and Malfatti, 2007). The term picoheterotrophs was introduced by Le Quere 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 (Kjørboe 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 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

53 higher picoheterotroph biomass than the metabolic theory would predict.

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

58

59 **2 Data**

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

73

74 **2.1 Conversion factors**

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

89

90 **2.2 Quality control**

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

95

96 **3 Results**

97 The database contains 39,766 data points. After gridding, we obtained 9,284 points on the World
98 Ocean Atlas grid (1° × 1° × 33 vertical layers × 12 months), i.e. we obtain a coverage of
99 vertically integrated and annually averaged biomass for 1.3% of the ocean surface. Only 6% of
100 the data are from the southern hemisphere (58% of the ocean surface; Figure 1A), 24% are from
101 the tropics (43% of the ocean surface), while 15% are from the polar oceans (5% of the ocean
102 surface). Observations from the coast (bottom depth < 225 m) make up 12% of the data (4.9% of
103 the ocean area, 0.13% of the ocean volume). Observations in the upper 112.5 m make up 57% of
104 the data (Figure 1B), while observations below 950 m make up 13% of the data. There are no

105 observations below 350 m in the southern hemisphere. Although there are some zero values in the
106 raw database, presumably because of a detection limit in small samples, there are no zero values
107 in the gridded dataset. There is some sampling bias towards the growing season, with 72% of the
108 data sampled during the spring and summer months (Figure 1C).

109 The average abundance is $4.3 \cdot 10^8 \pm 3.9 \cdot 10^8$ picoheterotrophs L^{-1} with a median of $3.1 \cdot 10^8$
110 picoheterotrophs L^{-1} . The average biomass is $3.9 \pm 3.6 \mu g C L^{-1}$ (Figure 2) with a median of 2.8
111 $\mu g C L^{-1}$. The biomass decreases with depth, from $7.3 \pm 4.3 \mu g C L^{-1}$ at the surface to 0.36 ± 0.19
112 $\mu g C L^{-1}$ at 2750-4750 m depth (Figure 3). The average biomass in the top 225 m is slightly
113 higher in the Northern temperate region ($23^\circ N - 67^\circ N$, $5.5 \pm 3.7 \mu g C L^{-1}$, Figures 2, 3, 4) and
114 tropics ($5.5 \pm 3.6 \mu g C L^{-1}$) than in Antarctica ($3.2 \pm 1.9 \mu g C L^{-1}$), the Arctic ($2.4 \pm 2.1 \mu g C L^{-1}$)
115 and Southern temperate region ($3.1 \pm 1.9 \mu g C L^{-1}$). The differences between most of these
116 regions are significant (one-way ANOVA with violated homogeneity of variances, Games
117 Howell post-hoc test, $p < 0.001$), except for Antarctica, for which there are only 23 measurements
118 in the upper 225 m, and which was only significantly different from the tropics ($p = 0.014$). There
119 is no significant difference between abundance in coastal waters and in the upper 225 m of the
120 open ocean (Fig. 3, one-way ANOVA, $p = 0.86$).

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

129 4 Discussion

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

134 In addition, a higher conversion factor has been found in coastal waters (Fukuda et al.
135 1998). However, it has not been established how far this higher conversion factor extends
136 between the coastal bay waters and the open ocean. If we assume the higher conversion factor is
137 valid up to a water depth to the bottom of 225 m (i.e., the continental shelf), then, based on the
138 average profile of picoheterotroph biomass (Figure 3), increasing the conversion factor from 9.1
139 to 30.2 fg cell⁻¹ would only add 0.02 Pg C to the global inventory. Thus, at present the main
140 sources of uncertainty in picoheterotroph biomass appear to be the open ocean conversion factor
141 and lack of spatial coverage, and not the increase in the conversion factor near the coast. All of
142 the open ocean conversion factors in Table 1 were measured on samples from the upper 250 m,
143 so whether the conversion factor changes with depth is yet to be resolved.

144 Whitman et al. (1998) estimated the global ocean picoheterotroph inventory at 2.0 Pg C.
145 This higher estimate is entirely due to their use of a higher conversion factor of 20 fg C cell⁻¹. In
146 fact, the present database gives a 20% higher inventory of global picoheterotroph abundance of
147 $1.2 \cdot 10^{29}$ cells based on an averaged depth profile, or 30% higher, $1.3 \cdot 10^{29}$ cells, based on regional
148 inventories in the upper 225 m, but a considerably lower biomass inventory of 1.1 - 1.2 Pg C.
149 Despite the uncertainties that we discuss above, we judge that the direct measurements of cellular
150 carbon contents for open ocean picoheterotrophs that we have used here are the most precise
151 conversion factors. For applications where biomass rather than abundance of picoheterotrophs is
152 relevant (most notably in biogeochemical models), the database that is presented here has the
153 largest coverage and the best estimates that are available at present.

155 Acknowledgment

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158

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Tables.

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, unpubl.
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 - April 1995	Arabian Sea	Campbell et al., 1998
Delaware95	Apr 1995	North Atlantic	Li, unpubl.
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
ArabianTTN049	Jul - Aug 1995	Arabian Sea	Olson, unpubl.
ArabianTTN050	Aug - Sep 1995	Arabian Sea	Campbell et al., 1998
NOAA95	Sep - Oct 1995	Indian Ocean	Buck, unpubl.
ArabianTTN054	Dec 1995	Arabian Sea	Campbell et al., 1998
AZOMP	1995-2009	North Atlantic	Li, 2002; Li, 2009; Li et al., 2009
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.
Almo-2	Jan 1998	Mediterranean Sea	Jacquet et al., 2010
Kiwi8	Jan-Feb 1998	Antarctica	Landry, unpubl.
Kiwi9	Feb-Mar 1998	Antarctica	Landry, unpubl.
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
C3O	2007-2008	North Atlantic, Arctic	Li, 2002; Li, 2009; Li et al., 2009

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262

Table 2. Conversion factors

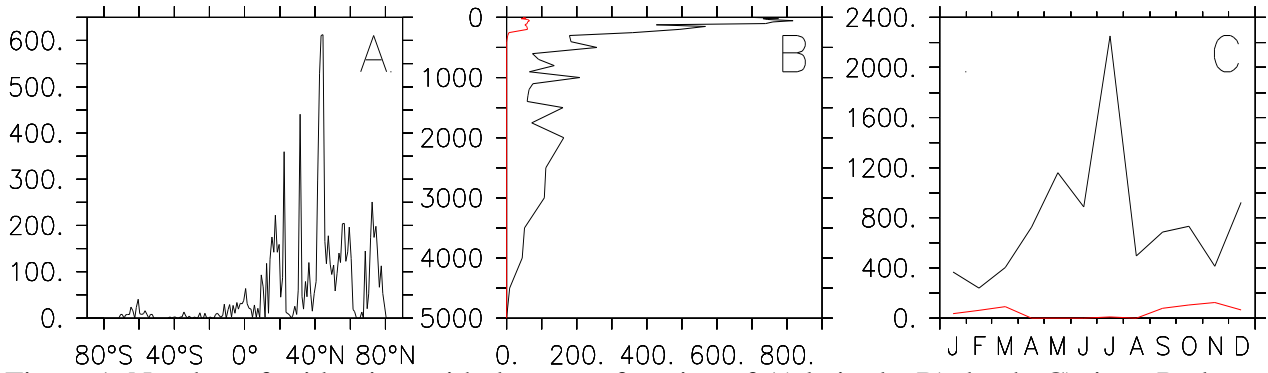
fg C cell ⁻¹	reference
7.7 (5.5, 9.8)	oceanic, Antarctica Carlson et al., 1999
12.4 ± 6.3 (n=6)	oceanic, Pacific Fukuda et al., 1998
30.2 ± 12.3 (n=5)	coastal, Japan Fukuda et al., 1998
7.1	oceanic, Atlantic, BATS

263

	Gundersen et al., 2002
9.1	average (oceanic only)

264 **Figures and captions**

265



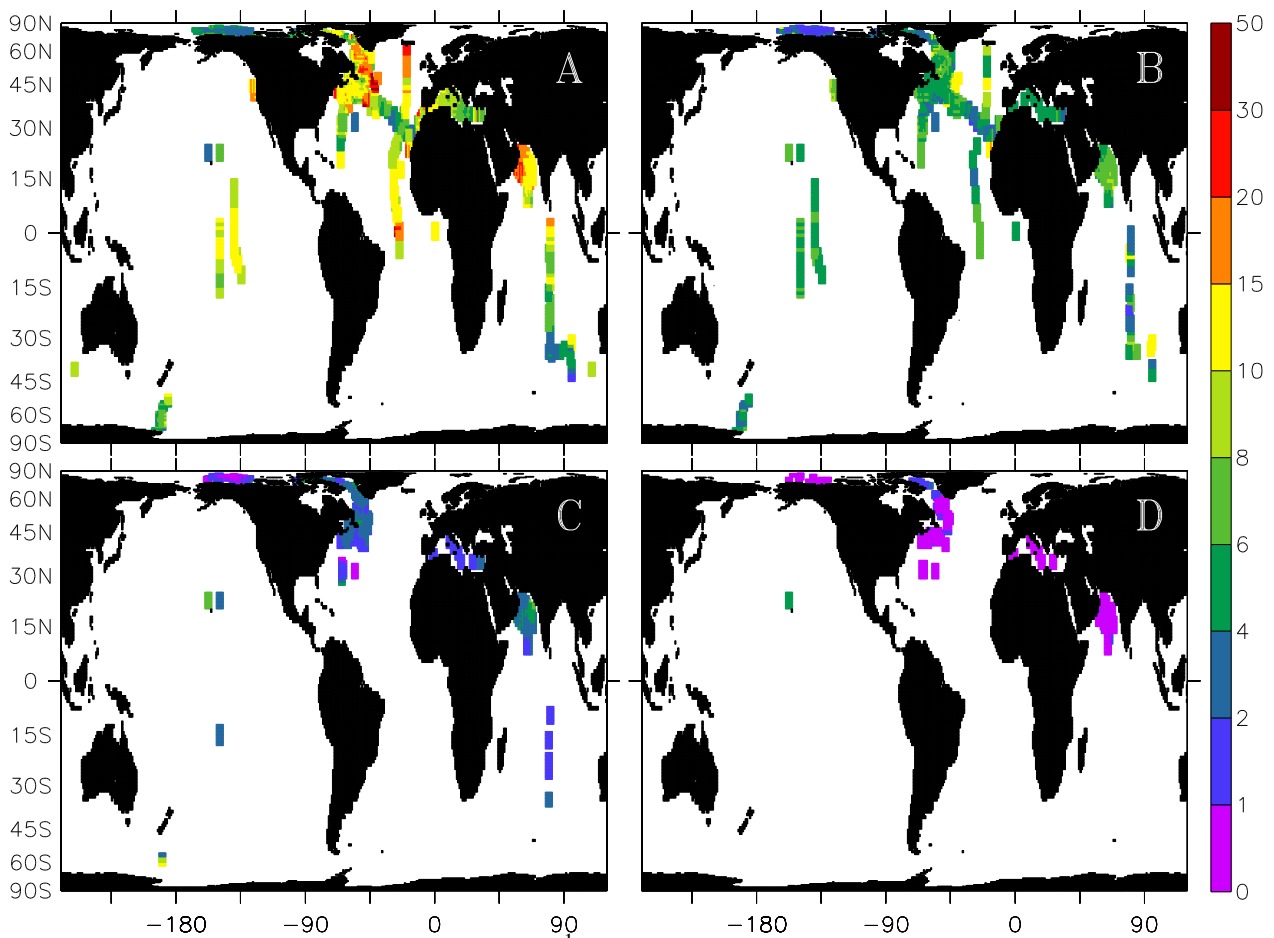
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Figure 1. Number of grid points with data, as a function of A) latitude. B) depth. C) time. Red: Southern Hemisphere, Black: total.

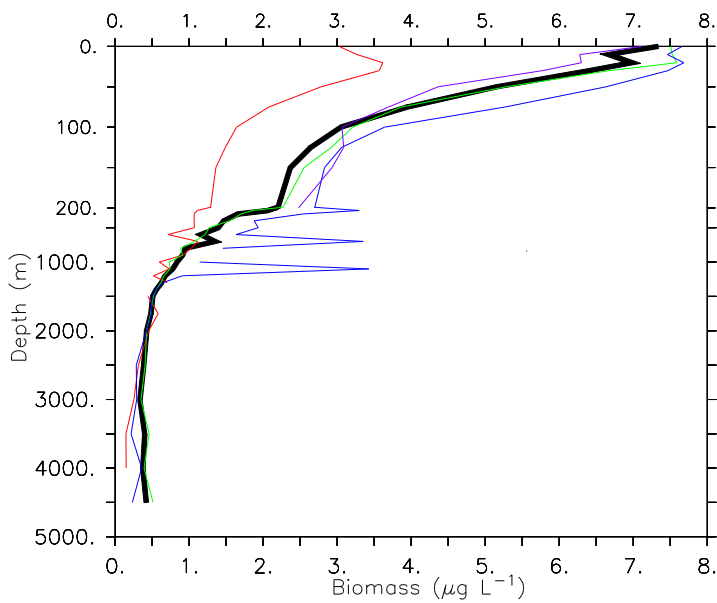


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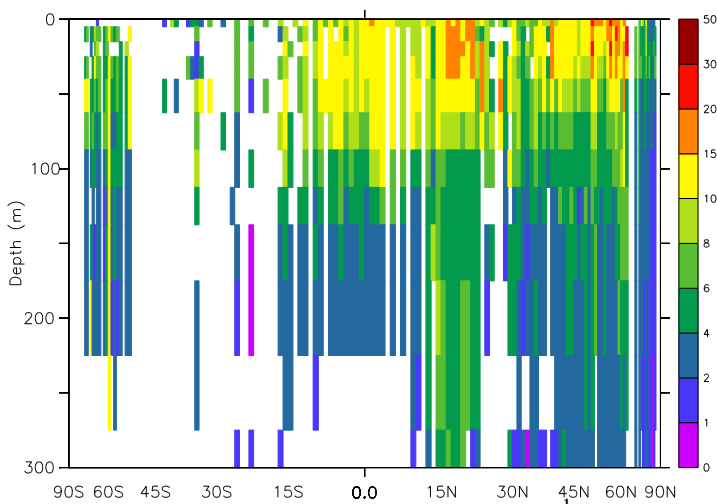
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Figure 2. Picoheterotroph biomass ($\mu\text{g C L}^{-1}$) averaged over all available months. A) 0-40 m, B) 40-225 m, C) 225-950 m, D) ≥ 950 m.



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 274 Figure 3. Picoheterotroph biomass averaged over all available longitudes, latitudes and months,
 275 as a function of depth, Black line) global average, blue line) tropical oceans, green line)
 276 temperate regions, red line) polar oceans, purple line) coastal ocean abundance × open ocean
 277 conversion factor.
 278



279
 280 Figure 4. Picoheterotroph biomass (µg C L⁻¹) averaged over all available longitudes and months
 281 in the top 300 m.