17

ORIGIN AND IMPORTANCE OF PICOPLANKTONIC DMSP

M. Corn,[1] S. Belviso,[1] F. Partensky,[2] N. Simon,[2] and U. Christaki[1]

[1] Centre des Faibles Radioactivités
Laboratoire Mixte CNRSCEA
91198 Gif-sur-Yvette Cedex, France
[2] Station Biologique
CNRS et Université Paris 6, B.P. 74
29682 Roscoff Cedex, France

SUMMARY

The importance of picoplanktonic particulate DMSP (DMSPp GF/F-2 μm) was investigated using size fractionation during a time-series experiment in the Mediterranean Sea and in three areas of the subtropical Atlantic Ocean. Picoplanktonic DMSPp accounted for up to 25% of depth-integrated total DMSPp (GF/F-200 μm) in oligotrophic waters. In order to estimate the relative contribution of picophytoplankton to DMSPp in the GF/F-2 μm fraction, we measured the DMSPp content of representative strains of the three main groups of picophytoplankton, including *Prochlorococcus (*prochlorophytes), *Synechococcus* (cyanobacteria) and picoeukaryotes belonging to four classes (Prasinophyceae, Pelagophyceae, Chlorophyceae and Prymnesiophyceae). The average cellular DMSPp concentrations (mean ± 1SD) were $2.8.10^{-4} \pm 1.8.10^{-4}$, $5.1.10^{-3} \pm 7.8.10^{-3}$ and 46.5 ± 73.7 fg/cell for *Prochlorococcus* sp., *Synechococcus* sp. and the picoeukaryotes, respectively. The DMSP content was highly variable among taxonomic groups of picoeukaryotes even when normalized per unit biovolume. The prymnesiophytes produced the most DMSP (e.g. clone CCMP625, 196 mmol.liter cell volume^{-1}) and the chlorophyte the least (0.74 mmol.liter cell volume^{-1}). Using these average DMSP contents per cell and flow cytometric counts of natural populations of picophytoplankton, it is strongly suggested that the picoeukaryotes were the main DMSP producers in the GF/F-2 μm size class. The combined contribution of the two prokaryotes was negligible (less than 1%), even in oligotrophic waters.

INTRODUCTION

Dimethylsulfide (DMS) is an important gas which is involved in the sulfur cycle. It arises mainly from the enzymatic cleavage of dimethylsulfoniopropionate (DMSP) which is produced

Biological and Environmental Chemistry of DMSP and Related Sulfonium Compounds
edited by Ronald P. Kiene et al., Plenum Press, New York, 1996

by marine algae. In an extensive survey of marine phytoplankton, Keller and coworkers (11) demonstrated that DMSP was mainly produced by members of the Dinophyceae and Prymnesiophyceae, although some other chlorophyll ccontaining algae, including species of Chrysophyceae and Bacillariophyceae (i.e. diatoms) could also contain significant amounts of DMSP. While many species of nano and microphytoplankton have been screened for DMSP production (11,12), fewer species of picophytoplankton, i.e. photosynthetic organisms passing through 2 μm pore filters, have been studied. Flow cytometric analyses have revealed that this class includes both eukaryotes, belonging to most algal classes (20), and prokaryotes mainly belonging to two genera, *Synechococcus* (cyanobacteria) and the recently discovered *Prochlorococcus* (prochlorophytes) (4, 6, 7, 14, 17, 18). The latter occur at very large concentrations in the temperate and tropical open waters of Atlantic and Pacific oceans as well as in the Mediterranean sea (7, 10, 14, 18, 21). Their contribution to the integrated photosynthetic biomass of warm oligotrophic oceans may reach up to 58% (19). Thus, due to its wide distribution and its photosynthetic activity, *Prochlorococcus* most probably plays a very significant role in the global carbon cycle. Picoeukaryotes are also significant components of the picophytoplanktonic standing stock (20-46% in terms of carbon) in both the mesotrophic and oligotrophic parts of tropical oceans. On the other hand, *Synechococcus* is most significant in mesotrophic areas (4, 19).

In this study, we investigated the contribution of picoplanktonic DMSPp (GF/F-2 μm size fraction) to total planktonic DMSPp (GF/F200 μm size fraction) in two oceanographic areas (Mediterranean Sea and subtropical Atlantic). We also estimated the relative contribution of different picophytoplankton groups to the DMSP in the GF/F-2 μm size fraction in the latter area by converting flow cytometric cell counts of *Prochlorococcus*, *Synechococcus* and picoeukaryotes into cell DMSPp using conversion factors obtained by measuring the average DMSPp per cell of representative cultured species.

MATERIALS AND METHODS

Field Samples

Seawater samples were collected at a mesotrophic site (43°25′N 7°51′E) in the central Ligurian Sea off Villefranche-sur-Mer (France). This site of the northeastern Mediterranean Sea was selected by the JGOFS-France DYFAMED Program and was occupied every month from March 1993 to November 1994. Samples were also collected in the subtropical northeastern Atlantic Ocean (Table 1), at the three sites (EU, MESO and OLIGO) selected by the JGOFS-France EUMELI program, in September-October 1991 (EUMELI 3; 2) and in May-June 1992 (EUMELI 4). All water samples were taken using 12 Niskin bottles fixed to a CTD system.

Table 1. Position and date of hydrocasts during cruises EUMELI 3 (Sept. 1991; 2) and EUMELI 4 (June 1992) in the subtropical Atlantic

SITE	DATE	POSITION	NAME
OLIGO	23 sept 91	20°55N 31°05W	BSN 11
OLIGO	23 june 92	21°02N 31°10W	GOF 49
MESO	17 june 92	18°29N 21°07W	GOF 30
EU	13 june 92	20°30N 18°30W	CTD 192

Picophytoplanktonic Cultures

The origin and mean cell volume of algal strains used in this study are summarized in Table 3. The pigment and size characteristics of picoeukaryotic strains are described elsewhere (20). Although the equivalent diameters of the unidentified prymnesiophyte, CCMP625, and of *Imantonia* are slightly larger than 2 μm (20), these organisms were included in this study on picoplankton because a significant fraction (ca. 10-40%) of these flagellates may pass through 2 μm pore Nuclepore filters (unpublished data). All eukaryotic strains were grown in K medium (13); *Synechococcus* in f/2 medium (9); and *Prochlorococcus* in a modified K medium (6) with K/10 trace metals plus 10 nM $NiCl_2$, 10 nM H_2SeO_3, 10 μM glycerophosphate, 50 μM NH_4Cl and 50 μM urea (Keller, unpublished). All cultures were maintained at 19°C under continuous low blue light (14.5 μmol quanta m^{-2} s^{-1}) provided by Daylight fluorescent tubes (Sylvania) wrapped with a "moonlight blue" Lee filter (Panavision). This low blue light simulated the light available in the lower euphotic zone in oligotrophic waters. All measurements were made in duplicate during the exponential phase of cell growth, unless otherwise specified.

Cell Enumeration

Cells were counted using two types of flow cytometers. A FACScan™(Becton Dickinson, San José, CA) flow cytometer was used aboard the ship to count live picophytoplanktonic populations during the EUMELI 3 cruise. An EPICS 541 flow cytometer (Coulter, Hialeah, Fla.) was used to analyze both the fixed samples from the EUMELI 4 cruise and live laboratory cultures of picophytoplankton. Optical configurations and set up of these systems are described in (19) and (21). With both flow cytometers, cells were counted on biparametric histograms representing right angle light scatter vs. chlorophyll red fluorescence (see e.g. 21 for illustration).

Pigment Analyses

During the EUMELI cruises, chlorophyll *a* (data obtained courtesy of J. Neveux) was measured by filtering water through 47 mm Whatman GF/F filters, extracting the filters in 90% acetone and analyzing the extracts by fluorometry (16). In the Mediterranean Sea, measurements of chlorophyll *a* and divinylchlorophyll *a* (data obtained courtesy of J.C. Marty and H. Claustre), (cumulatively termed total chlorophyll *a*), were done by reverse-phase HPLC using a modification of the method of Williams and Claustre (22), as described in (2).

Size Fractionation

The picoplankton size class was defined as that which passed through a 2.0 Nuclepore filter by gravity filtration but was retained on a Whatman GF/F filter (nominal pore size of 0.7 μm). This size class is designated as GF/F-2.0 μm.

DMSP Analysis

The DMSP content of picoplankton (GF/F-2 μm) was indirectly measured by subtracting the total dissolved DMSP + DMS of a sample filtered through a GF/F filter from the total DMSP + DMS content of an 2.0μm unfiltered sample following the method described in (2). Seawater was collected from the surface to depths of either 110 m (Mediterranean Sea) or 150 m (Atlantic) and 60 ml sub-samples were used for the DMSP

analyses. These aliquots were filtered by gravity through 2 μm pore-size Nuclepore membranes (47 mm diameter) for the total DMSP + DMS sample and through Whatman GF/F glassfiber filters to produce the dissolved DMSP+DMS pool. After treatment of the samples with cold alkali, DMS analyses were performed by GC/FPD (3). Five aliquots were used to estimate the overall precision of the method with natural samples. Precision for DMSPp samples in the GF/F-2μm size class was 20-40%.

For the screening of picophytoplankton isolates, a new method was developed to increase sensitivity in order to quantify DMSPp levels in microorganisms containing small amounts of this

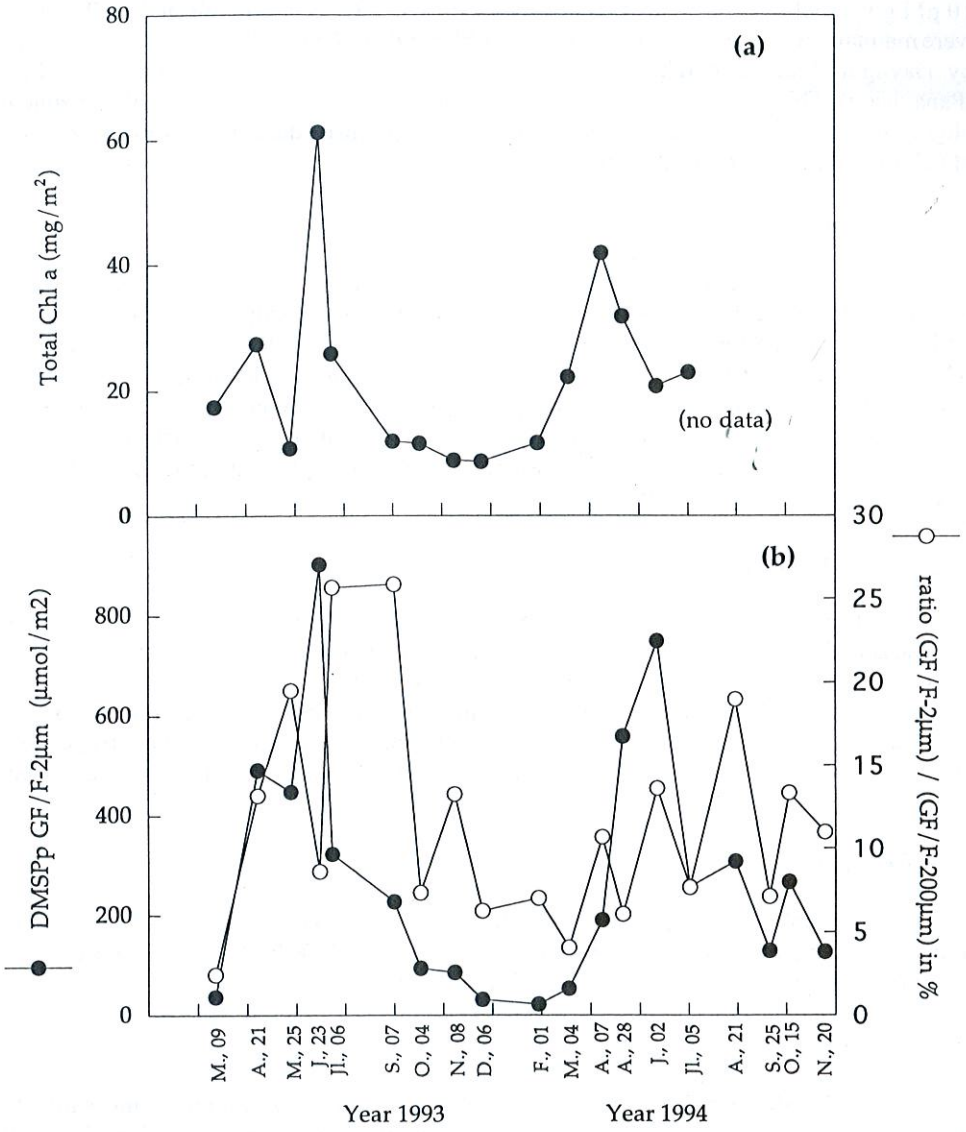

Figure 1. Seasonal variations of the depth-integrated concentrations of DMSPp in the size range GF/F-2 μm, the chlorophyll a and the ratio (DMSPp GF/F-2 μm)/(DMSPp GF/F-200 μm), in the Mediterranean Sea in 1993 and 1994 (Month in abbreviation, day).

compound. Culture samples (8 ml), either unfiltered or filtered on Whatman GF/F filters, were transferred into teflon-stoppered glassware and treated with cold alkali. After 12 h storage at room temperature, they were purged with high-grade helium. DMS was trapped cryogenically on the walls of Teflon tubing immersed in liquid nitrogen, and analyzed by gas chromatography with a Varian chromatograph equipped with a pulsed flame photometric detector (PFPD). PFPD is based on a flame source and combustible gas mixture rate that cannot sustain a continuous flame operation (5). With the PFPD, the sensitivity for sulfur is higher (detection limit of 1 pg S/sec), and the selectivity against hydrocarbons molecules is large (10^3 to 10^6 S/C), and the gas consumption is smaller than with a conventional FPD. The detection limit was 60 pg of DMS. Measurements were performed in duplicate and the agreement was generally better than 15%.

RESULTS AND DISCUSSION

Analysis of DMSPp in the Field

Mediterranean Sea. Nineteen vertical profiles were taken from March 1993 to November 1994 in the deep (> 2000 m) open waters of the central Ligurian Sea. From November to March, the seawater column was well mixed, with temperatures ca. 14°C and detectable nitrate concentrations, with a maximum of 4 μM in February (M.D. Pizay, pers. comm.). In summer, the water column became stratified, with a 10-20 m deep mixed layer and surface temperatures reaching 25°C. The upper layer was oligotrophic (nitrate was undetectable at the μM level) with a subsurface chlorophyll *a* maximum at 20-40 m (J.C. Marty, pers. comm.). The integrated concentration of chlorophyll *a* in the top 50 m, i.e. the layer where nearly all the DMSP was found, displayed interannual variability (Fig. 1a). In 1993, the Chl *a* standing stock peaked in June with a subsurface bloom of prymnesiophytes, whereas in 1994, the biomass peaked in April during a bloom of diatoms (J.C. Marty, pers. comm.). The integrated total picoplanktonic DMSPp standing stock showed a similar pattern in 1993 and 1994, with maximum levels of about 800 $\mu mol.m^{-2}$ in June and minima during winter (Fig 1b). The contribution of DMSPp in the picoplanktonic size range (GF/F-2 μm) to the total DMSPp pool (GF/F-200 μm) averaged 10% and ranged between 35% in March and 17-25% in July-September. There was a temporal displacement between the peak of total DMSPp and the maximum in the ratio of picoplanktonic to total DMSPp in both years (Fig. 1). The relative contribution of picoplanktonic DMSPp was highest during summer, i.e. when oceanographic conditions were the most oligotrophic.

Atlantic Ocean. In June 1992 (EUMELI 4), levels of particulate DMSP in the size ranges GF/F-2 μm and GF/F-200 μm were investigated in three areas of the subtropical northeastern Atlantic Ocean (Tables 1 and 2). A previously published result from the EUMELI 3 cruise (2) has been included in the data set to demonstrate that there was little seasonal variation at the OLIGO site. The depth integrated standing stock of DMSPp in the size range GF/F-2 μm was at least two times in oligotrophic waters than in eutrophic and mesotrophic waters (Table 2), although the total DMSPp (GF/F-200 μm) showed an inverse variation. This is consistent with an increase of the relative contribution of the biomass of picophytoplankton to total chlorophyll biomass along the nutrient gradient from the EU and OLIGO sites (19). The contribution of the picoplanktonic DMSPp pool to the total DMSPp pool was 12-22% in oligotrophic waters and 23% in eutrophic and mesotrophic waters.

Quantification of DMSPp in Picophytoplanktonic Species. Our filter fractionation studies in two different oceanic areas (Mediterranean Sea and Atlantic Ocean) have shown

Table 2. Depth-integrated concentrations of picoplanltonic (GF/F-2 μm) and total (GF/F-200μm) DMSPp fractions and ratio of these two fractions at three sites of the subtropical Atlantic. Intracellular DMSP was computed using cell counts for each group multiplied by the average DMSP cell content determined in cultures for the three picoplanktonic groups: Prochlorococcus = 2.8 10^{-4} fg /cell, Synechococcus = 5.1 10^{-3} fg/cell and picoeukaryotes = 46.5 fg / cell

Site-Date	Integrated depth	DMSPp GF/F-2μm pool	DMSPp GF/F-200μm pool	(DMSPp GF/F-2μm) / (DMSPp GF/F-200μm)
	(m)	(μmol/m²)	(μmol/m²)	(%)
OLIGO-Sept 91	0-160	459	2114	21.7
OLIGO-June 92	0-140	283	2328	12.2
MESO-June 92	0-75	118	6877	1.7
EU-June 92	0-70	122	3883	3.2

that DMSPp in the size range GF/F-2 μm may account for 2-25% of the total DMSPp reservoir. However, the relative contribution of the different picophytoplankton populations to the total picophytoplanktonic DMSPp, as well as any contribution by heterotrophs or picodetritus was not resolved. To estimate these fractions, we determined the intracellular DMSP content of representative species in culture in an attempt to obtain factors to convert cell numbers (obtained by flow cytometry) from natural populations into DMSPp values for these species.

With the sensitive PFPD system used, DMSPp ($> 10^4$ fg cell^{-1}) was detected in all the isolates screened except a clone of *Synechococcus,* EUM11, and an unidentified prasinophyte EUM16B (Table 3). The mean intracellular DMSP concentrations (±1 SD) in *Prochlorococcus*, *Synechococcus* and the eukaryote strains were $2.8\ 10^{-4} \pm 1.8\ 10^{-4}$ (n=9), $5.1\ .10^{-3} \pm 7.8\ 10^{-3}$ (n=3) and 46.5 ± 73.7 fg cell^{-1} (n=11) respectively.

The *Synechococcus* strains used in this study belonged to two pigment groups. Clones EUM11 and MAX42, which both possess phycoerythrin with high phycourobilin (PUB) and low phycoerythrobilin (PEB) content, were representative of the open ocean, while DC2, which possesses the converse pigment signature, was more typical of coastal waters (see e.g. 17). DMSPp was detected in clone MAX42 but not in EUM11 (Table 3). The coastal strain, DC2, was previously screened by Keller et al. (11), but with a less sensitive detection system, and they did not detect any DMSP. DMSP production does not appear to be related to the pigment signature in this genus.

Among the autotrophic picoeukaryotes, DMSP production varied up to 1,700-fold on a per cell basis (the non-DMSP producing EUM16B strain excluded). Variations in the DMSP levels per unit cell volume, which eliminates variability due to size differences among species, were also large (up to 265-fold). Three of the picoeukaryotic clones used in this study were previously screened by Keller and coworkers (11). The measured DMSP contents of *Imantonia rotunda* (11) and *Imantonia* sp. (this study) are similar. In contrast, Keller et al. (11) detected about 10 times more DMSP in *Micromonas* than we did. While we detected 0.74 mmol DMSP·liter cell volume^{-1} in *Nannochloris,* Keller et al. did not detect any DMSP in this clone. The prymnesiophytes (CCMP625 and *Imantonia*) and the prasinophytes produced the largest amounts of DMSP, while the chlorophytes produced the lowest (Table 3). *Pelagomonas*, the only representative of the newly described Pelagophyceae, previously classified as chrysophytes (1), had a moderate DMSP content. These observations support the findings of Keller et al. (11, 12), with prymnesiophytes being major producers, prasinophytes and pelagophytes (ex chrysophytes) moderate producers, and chlorophytes being non- or very small producers of DMSP.

Besides taxonomic position, which is probably the main factor of variation in DMSP production between different phytoplankton communities, intraspecific variations can also occur. Matrai and Keller (15) reported that for cultures of *Prorocentrum minimum* and *Amphidinium carterae* DMSPp varied according to the growth stage. We have confirmed that such variations can occur since DMSPp content varied by a factor of 4 in cultures of the strains EUM8 and CCMP625 sampled one week apart (Table 3).

It is possible that contaminating bacteria in xenic cultures (such as ours) may also contribute to the measured amounts of DMSP. Diaz et al. (8) showed that a marine bacterial strain could accumulate DMSP. Thus, the occurrence of contaminating bacteria may have somehow biased the determination of DMSPp in our cultures of *Prochlorococcus* and *Synechococcus*, which were both low DMSP producers. Bacteria able to pass through GF/F filters could also cause an overestimate of the dissolved DMSP pool. Since dissolved DMSP was subtracted from the total DMSP pool to calculate DMSPp, any interference of this type would be minimal. To further check possibility that bacteria in cultures might contribute to DMSPp, poststationary cultures of *Prochlorococcus,* grown at high light, were used. These conditions were deleterious to *Prochlorococcus* cells (which died), but not to contaminating

Table 3. Origin, mean cell volume and concentration of intracellular DMSP (per cell and per liter of biovolume) of the picophytoplankton surveyed. They were in exponential phase of growth except for CCMP 1192 and one of the CCMP625 samples which were in stationary phase. Clones CCMP 1426, CCMP1378 and MED4 originate from the same isolate. Average volumes of analyzed picoeukaryotes and prokaryotes species were determined conductrimetrically in a previous study (20) and by A.Morel (pers.comm.), repectively. na = information not available, <dl = <detection limit (10^{-4} fg / cell)

Family	Species	Strain	Area	Mean cell vl.	Intracellular DMSP (DMSPp)	
				µm³	fg/cell	mmol/l
Prochlorophyceae	*Prochlorococcus*	TATL1	Tropical Atlantic	0.1	1.6E-04	0.03
	Prochlorococcus	TATL2	Tropical Atlantic	0.1	1.6E-04	0.03
	Prochlorococcus	TATL4	Tropical Atlantic	0.1	1.9E-04	0.03
	Prochlorococcus	NATL1	N.W. Atlantic	0.1	1.1E-04	0.02
	Prochlorococcus	PAC1A[a]	Tropical Pacific	0.1	2.9E-04	0.05
	Prochlorococcus	CCMP 1426[b] -	Mediterranean Sea			
		MED 4[c] -	Mediterranean Sea	0.087	2.1 to 4.0	0.03 to 0.06
		CCMP 1378[b]	Mediterranean Sea		E-04	
	Prochlorococcus	SS120[c]	Sargasso Sea	0.1	7.1E-04	0.12
Cyanophyceae	*Synechococcus*	EUM11	Tropical Atlantic	0.52	<dl	<dl
	Synechococcus	DC2[b]	Atlantic	0.65	1E-3	0.03
	Synechococcus	MAX42	Sargasso Sea	0.32	14E-3	0.7
Prasinophyceae	*Pycnococcus* sp.	CCMP 1192[b]	Oceanus 83 sta II	5.47	19.9	58
	Pycnococcus provasolii	CCMP 1203[b]	Old WHOI sta II	9.03	32.0	57
	Unidentified	EUM 16B	Tropical Atlantic	1.49	<dl	<dl
	Micromonas pusilla	CCMP 490[b]	Woods Hole. MA	1.87	2.1	17.9
	Bathycoccus prasinos	type strain	Gulf of Naples	2.04	4.5	35.6
Pelagophyceae	*Pelagomonas* sp.	EUM 8	Tropical Atlantic	4.8	4.6 & 9.3	15.4 & 31.4[e]
Chlorophyceae	*Nannochloris* sp.	CCMP 515[b]	Cape Bolinas (Philippines)	2.48	0.12	0.74
Prymnesiophyceae	Unidentified	CCMP 625[b]	na	15.07	184 & 56	196 & 60[e]
	Imantonia sp.	PCC 18561[d]	Northeast Atlantic	21.48	199	149

[a] gift of Dr. L. Campbell
[b] strains obtained from the Center For the Culture of Marine Phytoplankton, Bigelow Laboratory
[c] gift of Drs. P. Chisholm and L. Moore
[d] strains obtained from the Pasteur Culture collection, Paris, France
[e] the two values are for cultures sampled 1 week apart

Table 4. Depth-integrated cell concentrations and calculated DMSP concentrations contributed by the three main populations of picoplankton (*Prochlorococcus, Synechococcus* and picoeukaryotes), measured concentrations of picoplanktonic (GF/F-2 µm) DMSPp fraction, and ratio of total calculated picophytoplanktonic DMSP to the measured GF / F-2 µm DMSPp fraction, at three sites of the subtropical Atlantic. Intracellular DMSP was computed using the actual cell counts multiplied by the average DMSP cell content determined in cultures for the three picoplankters: *Prochlorococcus* = 2.8 10^{-4} fg / cell, *Synechococcus* = 5.1 10^{-3} fg / cell and picoeukaryoted = 46.5 fg / cell

Site-Date	Integrated depth	*Prochlorococcus* sp.		*Synechococcus* sp.		Eukaryote strains		DMSPp GF/F-2µm pool	total picopl. DMSP/ (DMSPp GF/F-2µm)
	(m)	10^{11}cell/m^2	µmol DMSP/m^2	10^{11}cell/m^2	µmol DMSP/m^2	10^{11}cell/m^2	µmol DMSP/m^2	(µmol/m^2)	(%)
OLIGO-Sept 91	0-160	235.0	0.11	2.37	0.02	1.6	120	459	26
OLIGO-June 92	0-140	192.0	0.09	3.18	0.03	1.36	102	283	36
MESO-June 92	0-75	12.9	0.006	137.3	1.12	6.58	493	118	419
EU-June 92	0-70	0.6	0.0003	0.52	0.004	0.66	49	122	40

bacteria, which remained at high concentrations. These cultures had undetectable DMSP levels. Thus, there is no evidence that contaminating bacteria contribute to the DMSP pool in cultures.

Contribution of Autotrophic Picoplankton to Total Picoplankton. The relative contribution of autotrophic prokaryotes and eukaryotes to the DMSPp pool in the GF/F-2 μm size fraction in the tropical Atlantic Ocean was estimated using the average DMSP content per cell (measured in cultures) and flow cytometric cell counts of picophytoplankton. The integrated values of estimated picophytoplanktonic DMSP and their relative contribution to measured picoplanktonic DMSP are shown in Table 4. Both in June 1991 and September 1992, *Prochlorococcus* accounted for about half of the photosynthetic biomass at the OLIGO site (19). In contrast, *Synechococcus* numerically dominated at the MESO site, occupied during the EUMELI 4 cruise (June, 1992) (19). In both cases however, the DMSPp estimated for these prokaryotic groups was very low, either when compared to that contributed by the picoeukaryotes, or to the total measured picoplanktonic DMSPp (Table 4). The contribution of prokaryotes remained low even when using the highest DMSP contents measured in cultures of *Prochlorococcus* or *Synechococccus* as conversion factors (e.g. *Synechococcus* accounted for a maximum 2.5% of the picoplanktonic DMSP at the MESO site in June 1992).

The estimation of picoeukaryotic DMSP was more difficult because of the large variability in DMSP content observed between the different taxonomic groups. Thus, a precise estimate would require accurate determination of the species distribution within each sample, a goal which is presently unattainable by flow cytometric methods. Variability in species composition occurs both horizontally and vertically. With these caveats in mind, we applied an average DMSPp value, derived from our cultures, to estimate the picoeukaryotic contribution at the different EUMELI sites. We found that the contribution of autotrophic picoeukaryotes to the DMSP pool in the GF/F to 2 μm size fraction ranged from 26 to 36% at both the OLIGO and EU sites (Table 4). This leaves the majority of the DMSP in this size fraction unaccounted for and suggests that a significant fraction of DMSPp at these stations may be due to other sources, such as heterotrophs and/or picodetritus. At the MESO site however, the simulated picoeukaryotic DMSP was greatly overestimated, possibly because the dominant species at this station were low DMSPproducers, such as chlorophytes.

ACKNOWLEDGMENTS

The authors wish to thank the captains and crew of the research vessels L'ATALANTE and TETHYS II. This work was supported by CNRS, CEA, INSU, IFREMER and EEC under contract EV5VCT930326. This is CFR contribution number 1737.

REFERENCES

1. Andersen, R. A., Saunders, G. W., Pasking, M. P. and J. P. Sexton. 1993. Ultrastructure and 18S rRNA gene sequence for *Pelagomonas calceolata* gen. and sp. nov. and the description of a new algal class, the Pelagophyceae classis nov. J. Phycol. 29: 701-715.
2. Belviso, S., Buat—Ménard, P., Putaud, J.P., Nguyen, B.C., Claustre, H. and J. Neveux. 1993. Size distribution of dimethylsulfoniopropionate in areas of the tropical northeastern Atlantic Ocean and the Mediterranean Sea. Mar. Chem. 44: 55-71.
3. Belviso, S., Kim, S.K., Rassoulzadegan, F., Krajka, B., Nguyen, B.C., Mihalopoulos, N. and P. Buat-Ménard. 1990. Production of dimethylsulfonium propionate (DMSP) and dimethylsulfide (DMS) by a microbial food web. Limnol. Oceanogr. 35: 1810-1821.

4. Campbell, L. and D. Vaulot. 1993. Photosynthetic picoplankton community structure in the subtropical North Pacific Ocean near Hawaii (station ALOHA). Deep Sea Res. 40: 2043-2060.
5. Cheskis, S., Atar, E. and A. Amirav. 1993. Pulsed-flame photometer: a novel chromatography detector. Anal. Chem. 85: 539-555.
6. Chisholm, S.W., Frankel, S.L., Goericke, R., Olson, R.J., Palenik, B., Waterbury, J., West-Johnsrud, L. and E.R. Zettler. 1992. *Prochlorococcus marinus* nov. gen. nov. sp.: an oxyphototrophic marine procaryote containing divinyl chlorophyll a and b. Arch. Microbiol. 157: 297-300.
7. Chisholm, S.W., Olson, R.J., Zettler, E.R., Waterbury, J., Goericke, R. and N. Welschmeyer. 1988. A novel freeliving prochlorophyte occurs at high cell concentrations in the oceanic euphotic zone. Nature 334: 340-343.
8. Diaz, M.R., Visscher, P.T. and B.F. Taylor. 1992. Metabolism of dimethylsulfoniopropionate and glycine betaine by a marine bacterium. FEMS Microbiol. Lett. 96: 61-66.
9. Guillard, R.R.L. and J.H. Ryther. 1962. Studies of marine planktonic diatoms. I. *Cyclotella nana* Hustedt and *Denotula confervacea* (Cleve) Gran. Can. J. Microbiol. 8: 229-239.
10. Ishizaka, J., Kiyosawa, H., Ishida, K., Ishikawa, K. and M. Takahashi. 1994. Meridional distribution and carbon biomass of autotrophic picoplankton in the Central North Pacific Ocean during Late Northern Summer 1990. Deep- Sea Res. 41: 1745-1766.
11. Keller, M.D., Bellows, W.K. and R.R.L. Guillard. 1989. Dimethylsulfide production in marine phytoplankton, p. 167-182. *In* E. Saltzman and W. Cooper (eds), Biogenic Sulfur in the Environment. Am. Chem. Soc., Washington.
12. Keller, M.D. 1989. Dimethyl sulfide production and marine phytoplankton: the importance of species composition and cell size. Biol. Oceanogr. 6: 375-382.
13. Keller, M.D.,Selvin, R.C. and R.R.L. Guillard. 1987. Media for the culture of oceanic ultraphytoplankton. J. Phycol. 23: 633-638.
14. Li, W.K.W., Dickie, P.M., Irwin, B.D. and A. M. Wood. 1992. Biomass of bacteria, cyanobacteria, prochlorophytes and photosynthetic eucaryotes in the Sargasso Sea. Deep Sea Res. 39: 501-519.
15. Matrai, P.A. and M.D. Keller. 1994. Total organic sulfur and dimethylsulfoniopropionate in marine phytoplankton: intracellular variations. Mar. Biol. 119: 61-68.
16. Neveux, J. and F. Lantoine. 1993. Spectrofluorometric assay of chlorophylls and phaeopigments using the least squares approximation technique. Deep Sea Res. 40: 1747-1765.
17. Olson, R. J., Chisholm, S. W., Zettler, E. R. and E. V. Armbrust. 1988. Analysis of *Synechococcus* pigment types in the sea using single and dual beam flow cytometry. Deep-Sea Res. 35: 425-440.
18. Olson, R.J., Chisholm, S.W., Zettler, E.R., Altabet, M. and J. Dusenberry. 1990. Spatial and temporal distributions of prochlorophytes picoplankton in the North Atlantic Ocean. Deep Sea Res. 37: 1033-1051.
19. Partensky, F., Blanchot, J., Lantoine, F., Neveux, J. and D. Marie. Vertical structure of picoplankton at different trophic sites of the subtropical Northeastern Atlantic Ocean. Deep- Sea Res, in press.
20. Simon, N., Barlow, R.G., Marie, D., Partensky, F. and D. Vaulot. 1994. Characterization of oceanic photosynthetic picoeukaryotes by flow cytometry. J. Phycol. 30: 922-935.
21. Vaulot, D., Partensky, F., Neveux, J., Mantoura, R.F.C. and C. Llewellyn. 1990. Winter presence of prochlorophytes in surface waters of the northwestern Mediterranean Sea. Limnol. Oceanogr. 35: 1156-1164.
22. Williams, R. and H. Claustre. 1991. Photosynthe tic pigments as biomarkers of phytoplankton populations and processes involved in the transformation of particulate organic matter at the BIOTRANS site (47°N, 20°W). Deep Sea Res. 38: 347-355.