Vol. 27(2):197-203 | Ocean and Polar Research | June 2005

Article

Dimethylsulfide and Dimethylsulfoniopropionate Production in the Antarctic Pelagic Food Web

Nobue Kasamatsu[1,2*], Tsuneo Odate[1,2], and Mitsuo Fukuchi[1,2]

[1]*The Graduate University for Advanced Studies*
[2]*National Institute of Polar Research*
Research Organization of Information and Systems
173-8515, 1-9-10 Kaga, Itabashi-ku, Tokyo, Japan

Abstract : Dimethylsulfide (DMS) is the most abundant form of volatile sulfurs in the ocean. Many biogeochemical studies have been conducted in the past several decades to unveil the processes driving the production, transformation and removal of DMS. They have shown that the Southern Ocean is an area with one of the highest levels of DMS concentrations during the austral summer in the global oceans. It has recently been observed that Antarctic krill, *Euphausia superba*, produces DMS and dissolved dimethylsulfoniopropionate (DMSP) in its grazing process. Copepods also produce DMS, and the potential production rates of DMS in the Southern Ocean by krill and copepods are estimated to be as much as 21 μmol m^{-2} d^{-1} and 0.6 μmol m^{-2} d^{-1}, respectively. These production rates of zooplankton and the presence of phytoplankton, which have high DMSP contents in their cells, might facilitate *in situ* DMS production in the Southern Ocean.

Key words : Dimethylsulfide, Dimethylsulfoniopropionate, Zooplankton, Krill, Food web, Southern Ocean

1. Introduction

Dimethylsulfide (DMS) is the most abundant form of volatile sulfurs in the ocean and constitutes up to half of the global biogenic sulfur flux to the atmosphere (Liss *et al.* 1997). In the ocean, DMS is produced by the enzymatic cleavage of dimethylsulfoniopropionate (DMSP), an organic compound synthesized by many marine phytoplankton species (e.g. Keller *et al.* 1989). The volatility of DMS and the concentration gradient across the sea-air interface lead to the ocean being the major source of DMS for the atmosphere (Liss *et al.* 1997). In the troposphere, DMS is oxidized primarily by hydroxyl radicals. The main atmospheric oxidation products are methanesulfonic acid (MSA) and sulfur dioxide (SO_2). Oxidation of DMS in the atmosphere produces sulfate aerosols that, either directly or by acting as cloud condensation nuclei, scatter solar radiation, thereby influencing the radiative balance of the Earth. The system involving phytoplankton, DMS, sulfate aerosol formation, cloud albedo and ocean surface temperature has been suggested as an element of the feedback mechanisms linking global biosphere and climate (Charlson *et al.* 1987), although the existence of this linkage has not been unequivocally proven.

The stocks and processes determining the sinks and the sources of DMS in the oceans have been extensively discussed by others (e.g. Liss *et al.* 1997; Simó 2001) (Fig. 1). DMSP is the principal source of DMS in surface waters, and it is known that oceanic phytoplankton produces DMSP as a compatible solute, antioxidant products, a cryoprotectant, and a grazing deterrent (Sunda *et al.* 2002). There are generally poor positive correlations between DMS and phytoplankton biomass (chlorophyll *a* concentrations). This is largely caused by differences in the production of a DMS precursor, DMSP, between phytoplankton species and their physiological states (Keller *et al.* 1989; Kasamatsu *et al.* 2004a). The conversion of DMSP into DMS is also influenced by complex biological processes such as

*Corresponding author. E-mail : kasa@nipr.ac.jp

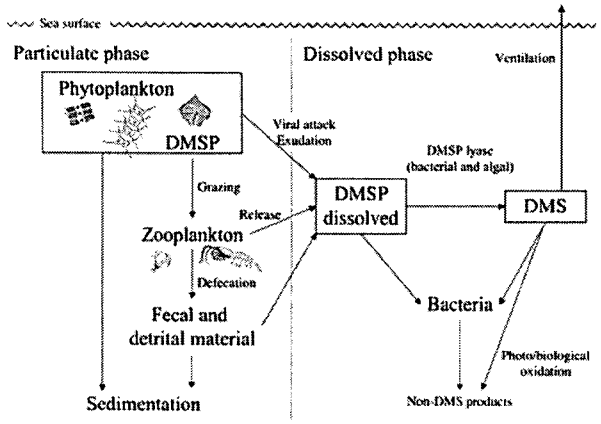

Fig. 1. Schematic representation of dimethylated sulfur processes in the surface ocean.

phytoplankton exudation, cell lysis, viral attack, zooplankton grazing, phytoplanktonic enzymes, and bacterial activities (Stefels and van Leeuwe 1998; Simó 2001; Kasamatsu *et al.* 2004b). Some DMSP released into seawater can be degraded to DMS and acrylic acid by algal and bacterial lyase. Dissolved DMSP ($DMSP_d$) and DMS are consumed by bacteria, since DMSP and DMS both act as a source of carbon and sulfur for bacteria (Liss *et al.* 1997). Microbial consumption of $DMSP_d$ and DMS resulting in the production of non-DMS products appears to be a significant sink for oceanic DMS and DMSP, although it is extremely variable in both space and time in the ocean (Simó 2001). DMS is also converted into dimethylsulfoxide (DMSO) via photochemical and microbial oxidation (Liss *et al.* 1997). Consequently, sea-air exchange may represent only a minor sink for seawater DMS and DMSP. Burkill *et al.* (2002) reported DMS flux to atmosphere was only 1% of the DMSP sulfur produced in the surface mixed layer within a coccolithophore bloom.

It has been assumed that zooplankton grazing on phytoplankton could be the major route to release DMSP from algal cells to seawater (e.g. Dacey and Wakeham 1986). Dacey and Wakeham (1986) found that one third of the phytoplankton DMSP ingested by copepods was released in the seawater as DMS. During shipboard experiments, Daly and DiTullio (1996) reported DMS concentrations in the incubation bottles increased when krill were added. Kasamatsu *et al.* (2004b) recently demonstrated that DMS and $DMSP_d$ production was positively correlated with phytoplankton ingestion by krill, *Euphausia superba,* whereas grazing by salps, *Salpa thompsoni,* did not produce DMS and $DMSP_d$. In their mouthpart, *E. Superba* has mandibles that macerate any large particles, and the food passes to the mouth (Mauchiline and Fisher 1969). Breakage of phytoplankton cells by krill causes the release of organic matter into seawater, whereas salps ingest whole phytoplankton and repackage the ingested chemicals into rapidly sinking pellets. It seems that these different mechanisms of grazing cause differences in DMS and $DMSP_d$ production. Antarctic krill and salps are the dominant herbivores in the Southern Ocean (Pakhomov *et al.* 2002). It is possible that the changes in their respective dominance and the resulting corresponding impact on DMS production could be responsible for variations in distribution of DMS concentrations in the Southern Ocean.

The Southern Ocean (south of the Subtropical Front) surrounding the Antarctic continent covers about 20% of the total world ocean surface (Curran and Jones 2000). Liss *et al.* (1997) reported the majority of atmospheric sulfur comes from oceanic DMS originating in the Southern Ocean. High DMSP and DMS concentrations have been observed in association with high productivities in summer and in the ice edge bloom (Curran and Jones 2000). Curran and Jones (2000) estimated the annual emission of DMS from the Southern Ocean to be as much as 139 Gmol S yr^{-1}, which represents 28% of the global emissions (500 Gmol S yr^{-1}). The Southern Ocean is also thought to be where the largest changes in DMS flux are expected under global warming (Bopp *et al.* 2003). However, current studies of DMS models do not satisfactorily reproduce surface DMS concentrations in the Southern Ocean (Belviso *et al.* 2004), since data sets are sparse in both space and time. The objectives of this study are to estimate the production of biogenic sulfers by zooplankton in the Southern Ocean and to discuss the potential production of biogenic sulfurs in the Antarctic pelagic food web.

2. Methods and materials

Water sampling

Sampling was carried out in the Australian sector of the Southern Ocean from 61°S to 65°S latitude along 140°E longitude during the R/V *Hakuho-Maru* cruise KH01-3 (the University of Tokyo) in January 2002. Water samples were collected at 10 or 11 depths between 2 and 200 m with a rosette sampler equipped with 12 *l* Niskin bottles and a conductivity-temperature-depth (CTD) probe (SeaBird SBE911 plus). In addition, surface seawater was taken with a plastic bucket. These samples were used for the determination of DMS, $DMSP_d$, and chlorophyll *a* (chl *a*). For DMS(P) analyses, water samples were transferred

with 100 m*l* glass syringes to avoid gas exchange (Terazaki *et al.* 2003).

Sulfur determinations

DMS and DMSP concentrations (11 or 12 measurements for each sulfur compound at each sampling station) were measured with a purge and trap apparatus as described by Kasamatsu *et al.* (2004b). DMS concentration was determined on a gas chromatograph equipped with a flame photometric detector (Shimadzu GC-14B). For determination of $DMSP_d$, an aliquot of seawater was filtered through a Whatman GF/F filter and the filtrate poured into a serum bottle containing 4 m*l* of 6 M NaOH. Serum bottles were stored at 4°C for at least 24 h to complete the cleavage before analyses, and were purged with pure nitrogen gas. Analytical error for each measurement was 11%.

Pigment analysis

Water samples for chl *a* measurements were filtered through Whatman GF/F filters. Chl *a* was extracted in dimethylformamide (Suzuki and Ishimaru 1990) for 24 h at approximately −80°C. Concentrations of chl *a* were determined onboard the ship with a model 10AU Turner Designs fluorometer using a method described by Parsons *et al.* (1984).

3. Results and discussion

The potential impacts of zooplankton grazing in the Southern Ocean

The potential effects of zooplankton grazing on the production of DMS and $DMSP_d$ have been investigated both in the laboratory and in the field in a variety of phytoplankton species (Table 1). Individual-normalized production rates can be compared and indicate that the effect of krill is larger than those of other mesozooplankton (Table 1). Copepods are also identified as the most important filter-feeding metazoans in the Southern Ocean in terms of total dry and carbon mass (Pakhomov *et al.* 2002). In spite of their abundance in the Southern Ocean, the effects of copepods on the DMS dynamics in the Southern Ocean have not been investigated. Leck *et al.* (1990) found significant correlations of DMS concentrations with copepods for samples collected in the Baltic Sea. In the North Water of northern Baffin Bay, Lee *et al.* (2003) incubated copepods and found that *in vitro* copepod grazing was highly statistically significant in DMS and $DMSP_d$ production, although *in situ* production rates by copepod grazing were unimportant as a release mechanism for *in situ* levels of DMS and $DMSP_d$ in the North Water. They estimated weight-specific production rates for DMS

Table 1. Effect of zooplankton grazing on DMS and $DMSP_d$ production rates as reported in the literature, together with information on types of zooplankton used for grazers and phytoplankton used for food items.

Study site	Phytoplankton	Zooplankton (inds. l^{-1})	Production rates (nmol ind.$^{-1}$ d^{-1})		Literature
			DMS	$DMSP_d$	
Laboratory	Dinoflagellate culture (*Gymnodinium nelsoni*)	Copepods (*Centropages hamatus, Labidocera aestiva*, 30-40 l^{-1})	4.8	-	Dacey and Wakeham (1996)
Northeastern Gulf of St. Lawrence	Phytoplankton	Pteropods (*Limacina helicina*, 2.5 l^{-1})	-	9.6-44*	Levasseur *et al.* (1994)
Central Gulf of St. Lawrence	Phytoplankton	Copepods (*Calanus finmarchicus*, 20 l^{-1})	0-0.185	0.12-0.214	Cantin *et al.* (1996)
Antarctic peninsula	Phytoplankton (ice-algal communities)	Juvenile krill (*Euphausia superba*, 1.3 l^{-1})	1.68-89.5	-	Daly and DiTullio (1996)
Laboratory	Cultures (*Phaeodactylum tricornatum, Thalassiosira weissflogii*)	Copepods (*Eurytemora affinis*, 50 l^{-1})	-	0.14	Kwint *et al.* (1996)
North Water	Phytoplankton (large diatoms)	Copepods (mixed assemblages)	0.004-1.42	0.003-1.57	Lee *et al.* (2003)
Southern Ocean	Phytoplankton	Krill (*Euphausia superba*, 0.1 l^{-1})	−17-174	−14-237*	Kasamatsu *et al.* (2004b)
Southern Ocean	Phytoplankton	Salps (*Salpa thompsoni*, 0.1 l^{-1})	Not detectable	Not detectable	Kasamatsu *et al.* (2004b)

*These results were reported as DMS+$DMSP_d$ production rates.

at 0.011-2 nmol mg^{-1} DW d^{-1} (median = 0.23 nmol mg^{-1} DW d^{-1}) and for $DMSP_d$ at 0.005-6.86 nmol mg^{-1} DW d^{-1} (median = 0.71 nmol mg^{-1} DW d^{-1}) in the North Water (Lee *et al.* 2003). Average copepod biomass in the Southern Ocean is estimated to be 1161 mg C m^{-2} (Pakhomov *et al.* 2002). It is equivalent to 2,700 mg DW m^{-2}, if the carbon weight of copepods is assumed to be 43% of the dry weight in the Southern Ocean (Pakhomov *et al.* 2002). Although there must be differences in the relation between carbon and dry weights of copepods between the North Water and the Southern Ocean, extrapolation of the results from the North Water for the copepod biomass in the Southern Ocean shows that Southern Ocean copepods produce DMS at 0.6 μmol m^{-2} d^{-1}. The values for dry weight for *E. superba* can be estimated from the body length using published conversion factors as follows:

$W = 1.58 \times 10^{-6} L^{3.40}$ (Kils 1981),

$C = 72.77\ W^{1.0242}$ (Nishikawa *et al.* 1995),

D = C/0.39 (Davis and Wiebe 1985),

where W is wet weight (g), L is body length (mm), C is carbon weight (mg) and D is dry weight (mg). Body length of the Antarctic krill used in Kasamatsu *et al.* (2004b) was about 35 mm, which corresponds to 19.8 mg C and 50.7 mg DW. The DMS production rates estimated in that study ranged from −16.8 to 174.2 nmol $ind.^{-1}$ d^{-1} (mean = 69.8 nmol $ind.^{-1}$ d^{-1}, n = 12) (Table 1). Then, average weight-specific production rates for DMS should be 1.4 nmol mg^{-1} DW d^{-1} (3.5 nmol mg^{-1} C d^{-1}). Throughout the Southern Ocean, the average biomass of *E. superba*, which are mostly distributed south of the Polar Front, is estimated to be 5,950 mg C m^{-2} and 220 mg C m^{-2} in regions of dense and low krill concentrations, respectively (Pakhomov *et al.* 2002). As a result, DMS production rates in dense and in low krill concentrations are estimated to be 21 μmol m^{-2} d^{-1} (3.5 nmol mg^{-1} C d^{-1} multiplied by 5,950 mg C m^{-2}) and 0.8 μmol m^{-2} d^{-1} (3.5 nmol mg^{-1} C d^{-1} multiplied by 220 mg C m^{-2}), respectively. Hence, krill seems to be the major producer of DMS and $DMSP_d$ among the macrozooplankton dominating the Southern Ocean. It is also reported that the density of *E. superba* in swarms could reach as many as 60,000 individuals m^{-3} (Mauchline 1980). At that high density, the potential DMS production rate by krill could be 170 nmol-DMS l^{-1} h^{-1}.

In January 2002, the southernmost sampling station was occupied near the ice edge and the macrozooplankton community was found to be dominated by krill (Oka 2004). Chl *a* concentrations integrated from 0 m to 200 m

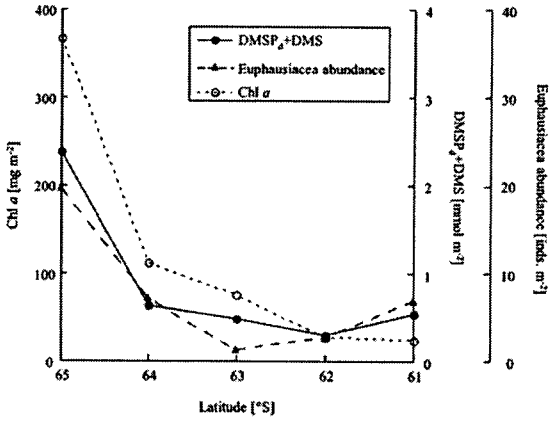

Fig. 2. DMS+$DMSP_d$ concentrations (mmol m^{-2}) with concentrations of euphausiids (inds. m^{-2}) and chl *a* (mg m^{-2}) along 140 °E in January 2002. Concentrations of $DMSP_d$+DMS and chl *a* are integrated from 0-200 m in the water column. Euphausiacea abundance obtained by RMT net (0-200 m) was inferred from the data sets of Oka (2004). All data were obtained during the KH01-3 cruise in January 2002.

were high in the south and decreased toward the north (Fig. 2). The distributions of DMS+$DMSP_d$ concentrations and euphausiid abundances, including that of *E. superba*, followed the same trend. High densities of euphausiids were recorded at 65°S in accordance with high concentrations of DMS and $DMSP_d$. Miki (2003) estimated the contributions of the different algal classes to total chl *a* by CHEMTAX analysis of HPLC pigment signatures. Seven algal categories, defined operationally by their pigment contents, i.e., Diatoms, two categories of haptophytes: Hapto3s (typified by coccolithophorids) and Hapto4s (including *Phaeocystis antarctica* plus Parmales and other chrysophytes), Dinoflagellates, Prasinophytes, Chlorophytes and Cryptophytes were observed. The categories of Diatoms contributed more than 60% to total chl *a* throughout the observation. At 65°S contributions of Hapto3s and Hapto4s to total chl *a* were 1.2 and 0.5 $\mu g\ l^{-1}$, which constituted 13.7% and 6.3%, respectively, as a percentage of the total chl *a*. It has been reported that Prymnesiophyceae, coccolithophorid and *Phaeocystis* sp., have much higher concentrations of intracellular DMSP than diatoms (Keller *et al.* 1989). Furthermore, *in vitro* enzyme assays showed high DMSP lyase activity of *Phaeocystis* sp. (Stefels and van Leeuwe 1998). To clarify the differences of DMS(P) distributions in the south (high) and in the north (low), further investigations, such as advection of different water masses, differences in phytoplankton growth phase, and

microbial activity are necessary. Our results nevertheless suggest that, in addition to the presence of Haptophytes that have high intracellular DMSP and high DMSP lyase activity, the krill encounters with such phytoplankton facilitated *in situ* DMS and $DMSP_d$ production at 65°S.

The effects of various prey

Effects of zooplankton grazing on DMS and DMSP production, as previously reported, might be varied by the abundance and types of food items encountered by zooplankton (Table 1). Kasamatsu *et al.* (2004b) investigated the grazing effects of salps and reported that they produced no detectable amounts of DMS. Chl *a* concentrations of seawater used in the experiments with salps were relatively low and were found to be in a narrow range of 0.1 to 0.3 $\mu g\ l^{-1}$. Further studies over a wider range of prey densities will allow the effects of salps in DMS and $DMSP_d$ production to be more fully understood. It is known that intracellular DMSP are different between phytoplankton species (Keller *et al.* 1989). It is also reported that phytoplankton cultured in the laboratory changed their chl *a*-normalized DMSP contents with their growth phase; DMSP contents gradually increase during the stationary growth phase (Kasamatsu *et al.* 2004*a*). Additionally, there are some reports that high DMSP concentrations were observed in sea ice, seemingly derived from ice algae (e.g. Curran and Jones 2000). Curran and Jones (2000) also reported that phytoplankton species exhibited higher levels of DMSP in the seasonal ice zone. It is possible that DMSP production by phytoplankton that grow at lower temperatures and higher salinity in sea ice in the polar regions is much higher than that by phytoplankton found in temperate or tropical environments, since phytoplankton seems to produce DMSP as a cryoprotectant and osmolyte. Sunda *et al.* (2002) found that intracellular DMSP serves as an antioxidant. This finding was supported by increased DMSP concentrations when phytoplankton was exposed to oxidative stressors, including solar UV radiation and Fe limitation. The Antarctic Ocean is a turbulent environment, where phytoplankton may experience high UV stress in addition to iron limitations. (Stefels and van Leeuwe 1998; Qian *et al.* 2001). This would result in an increase of intracellular DMSP contents of phytoplankton; hence a higher release of DMSP from phytoplankton by zooplankton grazing could be expected in the Antarctic regions of the Southern Ocean.

Other roles of zooplankton in DMS(P) dynamics

Tang *et al.* (1999) suggested that some copepod species could accumulate a considerable amount of DMSP in their bodies, thereby changing the partitioning of DMSP between the particulate and dissolved phases with a potential effect on ambient DMS concentrations. Furthermore, macrozooplankton are able to re-package small particles like algal cells into sinking feces efficiently (Pakhmov *et al.* 2002). It is now recognized that macrozooplankton in the Southern Ocean such as krill, salps and copepods are omnivores. The fate of $DMSP_p$ in the fecal pellets needs to be investigated, as these pellets are broken down not only by bacteria and microzooplankton, but also by the macrozooplankton themselves until the fecal pellets are deposited below the mixed layer. The differences between DMS production by zooplankton types may also arise from differences in life stage, size and the physiological state of grazers.

Recently, the relative dominance and importance of microzooplankton grazing on phytoplankton has been more widely recognized. Within a coccolithophore bloom, shipboard experiments showed that microzooplankton grazing accounted for >90% of $DMSP_p$ degradation (Burkill *et al.* 2002). Bacteria are also known to play an important role in the transformation of DMSP and DMS (Scarratt *et al.* 2000). To improve our understanding of the biogenic sulfur in the Southern Ocean, links between these biogenic sulfur compounds and the whole Antarctic pelagic food web structure should be the subject of continued investigation.

Acknowledgements

Intensive discussions with several colleagues encouraged us to refine the ideas presented in this paper. We would particularly like to thank So Kawaguchi, Shuichi Watanabe and Kunio Takahashi. Thanks are also extended to Makoto Terazaki, Hiroshi Ogawa and the crew of the R/V *Hakuho-Maru* for their marvelous hospitality in the Southern Ocean. The manuscript was considerably improved by critical and constructive comments made by the two anonymous referees. We appreciate that Korea Polar Research Institute offered us an opportunity to present our research at the Symposium. We would also like to thank Hyoung-Chul Shin for useful comments on the contents and suggestions on the English.

References

Belviso, S., L. Bopp, C. Moulin, J.C. Orr, T.R. Anderson, O. Aumont, S. Chu, S. Elliott, M.E. Maltrud, and R. Simo. 2004. Comparison of global climatological maps

of sea surface dimethylsulfide. *Global Biogeochem. Cycles*, 18, GB3013.

Bopp, L., O. Aumont, S. Belviso, and P. Monfray. 2003. Potential impact of climate change on marine dimethyl sulfide emissions. *Tellus*, 55B, 11-22.

Burkill, P.E., S.D. Archer, C. Robinson, P.D. Nightingale, S.B. Groom, G.A. Tarran, and M.V. Zubkov. 2002. Dimethyl sulphide biogeochemistry within a coccolithophore bloom (DISCO): an overview. *Deep-Sea Res. II*, 49, 2863-2885.

Cantin, G., M. Levasseur, M. Gosselin, and S. Michaud. 1996. Role of zooplankton in the mesoscale distribution of surface dimethylsulfide concentrations in the Gulf of St. Lawrence, Canada. *Mar. Ecol. Prog. Ser.*, 141, 103-117.

Charlson, R.J., J.E. Lovelock, M.O. Andreae, and S.G. Warren. 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature*, 326, 655-661.

Curran, M.A.J. and G.B. Jones. 2000. Dimethyl sulfide in the Southern Ocean: Seasonality and flux. *J. Geophys. Res.*, 105, 20451-20459.

Dacey, J.W.H. and S.G. Wakeham. 1986. Oceanic dimethylsulfide: production during zooplankton grazing on phytoplankton. *Science*, 233, 1314-1316.

Daly, K.L. and G.R. DiTullio. 1996. Particulate dimethylsulfoniopropionate removal and dimethylsulfide production by zooplankton in the Southern Ocean. p. 223-238. In: *Biological and environmental chemistry of DMSP and related sulfonium compound.* eds. by R.P. Kiene, P.T. Visscher, M.D. Keller, and G.O. Kirst. Plenum Press, New York.

Davis, C.S. and P.H. Weibe. 1985. Macrozooplankton biomass in a warm-core Gulr Stream ring: Time series change in size structure, taxanomic composition, and vertical distribution. *J. Geophys. Res.*, 90, 8871-8884.

Kasamatsu, N., T. Hirano, S. Kudoh, T. Odate, and M. Fukuchi. 2004a. Dimethylsulfoniopropionate production by psychrophilic diatom isolates. *J. Phycol.*, 40, 874-878.

Kasamatsu, N., S. Kawaguchi, S. Watanabe, T. Odate, and M. Fukuchi. 2004b. Possible impacts of zooplankton grazing on dimethylsulfide production in the Antarctic Ocean. *Can. J. Fish. Aquat. Sci.*, 61, 736-743.

Keller, M.D., W.K. Bellows, and R.R.L. Guillard. 1989. Dimethyl sulfide production in marine phytoplankton. p. 183-200. In: *Biogenic sulfur in the environment*, eds. by E.S. Saltsman, and W.J. Cooper. American Chemical Society, Washington DC.

Kils, U. 1981. The suimming behavior, swimming performance and energy balance of Antarctic krill, *Euphausia superba. BIOMASS Sci. Ser.*, 3, 1-233.

Kwint, R.L.J., X. Irigoien, and K.J.M. Kramer. 1996. Copepods and DMSP. In: *Biological and Environmental Chemistry of DMSP and Related Sulfonium Compound.* eds. by R.P. Kiene, P.T. Visscher, M.D. Keller, and G.O. Kirst. Plenum Press, New York.

Leck, C., U. Larsson, L.E. Bagander, S. Johansson, and S. Hadju. 1990. DMS in the Baltic Sea - annual variability in relation to biological activity. *J. Geophys. Res.*, 95, 3353-3363.

Lee, P.A., P.A. Saunders, S.J. De Mora, D. Deibel, and M. Levasseur. 2003. Influence of copepod grazing on concentrations of dissolved dimethylsulfoxide and related sulfur compounds in the North Water, northern Baffin Bay. *Mar. Ecol. Prog. Ser.*, 255, 235-248.

Levasseur, M., M.D. Keller, E. Bonneau, D. D'Amours, and W.K. Bellows. 1994. Oceanographic basis of DMS-related atlantic cod (*Gadus morhua*) fishery problem: blackeberry feed. *Can. J. Fish. Aquat. Sci.*, 51, 881-889.

Liss, P.S., A.D. Hatton, G. Malin, P.D. Nightingale, and S.M. Turner. 1997. Marine sulphur emissions. *Phil. Trans. R. Soc. Lond. B*, 352, 159-169.

Mauchline, J. and L.R. Fisher. 1969. The biology of euphausiids. *Adv. Mar. Biol.*, 7, 1-454.

Mauchline, J. 1980. Studies on patches of krill, Euphausia superba Dana. *BIOMASS Handb.*, 6, 1-36.

Miki, M. 2003. The study of phytoplankton population dynamics using algal pigments. Master Thesis, The Univ. Tokyo. 66 p.

Nishikawa, J., M. Naganobu, T. Ichii, H. Ishii, M. Terazaki, and K. Kawaguchi. 1995. Distribution of salps near the South Shetlands during austral summer, 1990-1991 with special reference to krill distribution. *Polar Biol.*, 15, 31-39.

Oka, N. 2004. Comparison of macrozooplankton community structure in 2002 and 2003 summer along 140°E line in the Southern Ocean with special reference to geological distribution of *Euphausia superba* and *Salpa thompsonoi*. Master Thesis, Mie University. 77 p.

Pakhomov, E.A., P.W. Froneman, and R. Perissinotto. 2002. Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. *Deep-Sea Res. II*, 49, 1881-1907.

Parsons, T.R., Y. Maita, and C.M. Lalli. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press, New York, 173 p.

Qian, J., K. Mopper, and D.J. Kieber. 2001. Photochemical production of the hydroxyl radical in Antarctic waters. *Deep-Sea Res. I*, 48, 741-759.

Scarratt, M., G. Cantin, M. Levasseur, and S. Michaud. 2000. Particulate size-fractionated kinetics of DMS production: where does DMSP cleavage occur at the microscale? *J. Sea Res.*, 43, 245-252.

Simó, R. 2001. Production of atmospheric sulfur by oceanic plankton: biological, ecological and evolutionary links. *Trends Ecol. Evol.*, 16, 287-294.

Stefels, J. and M.A. van Leeuwe. 1998. Effects of iron and light stress on the biochemical composition of Antarctic *Phaeocystis* sp. (Prymnesiophyceae). I. Intracellular DMSP concentrations. *J. Phycol.*, 34, 486-495.

Sunda, W., D.J. Kieber, R.P. Kiene, and S. Huntsman. 2002. An antioxidant function for DMSP and DMS in marine algae. *Nature*, 418, 317-320.

Suzuki, R. and T. Ishimaru. 1990. An improved method for the determination of phytoplankton chlorophyll using N, N-Dimethylformamide. *J. Oceanogr. Soc. Jap.*, 46, 190-194.

Tang, K.W., H.G. Dam, P.T. Visscher, and T.D. Fenn. 1999. Dimethylsulfoniopropionate (DMSP) in marine copepods and its relation with diets and salinity. *Mar. Ecol. Prog. Ser.*, 179, 71-79.

Terazaki, M., H. Ogawa, and K. Tamaki. 2003. Preliminary report of Hakuho Maru cruise KH-01-3. Ocean Research Institute, University of Tokyo. 170 p.

Received Oct. 12, 2004
Accepted May 10, 2005