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Climatic effect on DMS producers in the NE sub-Arctic Pacific: ENSO on the upper ocean

By CHI-SHING WONG[1]*, SHAU-KING EMMY WONG[1], ANGELICA PEÑA and MAURICE LEVASSEUR[2], [1]*Institute of Ocean Sciences, Fisheries and Oceans Canada, Sidney, British Columbia V8L 4B2, Canada;* [2]*Université Laval, Département de biologie (Québec-Océan), Québec, Québec, G1K 7P4, Canada*

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ABSTRACT

We examined dimethylsulphide (DMS) data of two locations (P26 and P20) 1996–2001 in sub-Arctic NE Pacific with emphasis on 2 yr of DMS production measured in June and September of 1999 and 2000. At Station P26, integrated DMS to mixed layer depth (MLD) in June during 1999–2001 La Niña period averaged 102 ± 25 μmol m^{-2} or only 42% of the average of 242 ± 27 μ mol m^{-2} measured during 1997–1998 El Niño period. The summer integrated DMS to MLD of 246 μmol m^{-2} in the year 2000 was 61% of summer average in the period 1996–1998 of 402 ± 115 μmol m^{-2}. At Station P20 where the mean DMS level of the MLD in June during the La Niña years of 1999–2001 was 77 ± 7 μmol m^{-2}, about 35% of 232 ± 22 μmol m^{-2} during the 1997–1998 El Niño. Phytoplankton species rich in DMSP (an algal precursor to DMS) were also more abundant in 1998 than in the years 1999–2001 with low DMS. The ENSO event was characterized by warmer, more stratified waters with MLD shallowing to about 19 m from 1996 to early 1998, compared to the following years. These results provide a first example of how climate fluctuations, through altering the physical and chemical properties of the upper ocean, may influence the structure of the phytoplankton assemblage and hence DMS concentrations in the open ocean.

1. Introduction

Emissions of oceanic dimethylsulphide (DMS) to the atmosphere are significant sources of biogenic sulphur in the global sulphur cycle (Lovelock et al., 1972). Oxidation of DMS to sulphate aerosols, which serve as cloud-condensation nuclei, can affect the global radiative balance, and hence the Earth's climate (Andreae and Crutzen, 1997). Since DMS is produced from its algal precursor (Malin and Kirst, 1997), dimethylsulphoniopropionate (DMSP), a hypothesis has been proposed (Charlson et al., 1987) for a phytoplankton-DMS-climate feedback link. Evidence supporting the influence of DMS on climate is increasing (Clarke et al., 1998). One report (Simó and Pedrós-Alió, 1999) also suggests a link between the seasonal yield of oceanic DMS and the mixed layer depth (MLD). However, there are as yet no direct observations linking long-term climatic variations and DMS production (Bates and Quinn, 1997). Our DMS time-series is the first comprehensive study (Kettle et al., 1999) in the sub-Arctic NE Pacific favourable to DMS producers, such as dinoflagellates and the coccolithophorid *Emiliania huxleyi* (Wong et al., 2005). Plankton species in the sub-Arctic NE Pacific are summarized in Harrison (2002) and Parsons et al. (1984).

Station P26 (also called P at 50°N, 145°W) and Station P20 (at 49°34′N, 138°40′W) are in the Gulf of Alaska in the Northeast Pacific Ocean, mainly in the waters traditionally covered by the research ships of the Institute of Ocean Sciences, Fisheries and Oceans Canada. The oceanography and ecology of this area are subjected to climatic forcing of El Niño, La Niña and regime shift.

2. Methods

The study area in NE Pacific waters with positions of stations P26 and P20 is shown in Fig. 1. Water properties of temperature, salinity, pressure or water depth, oxygen, silicate, phosphate, nitrate and chlorophyll-*a* (Chl-*a*) collected with DMS samples during 1996–2001 were also examined. A Technicon AutoAnalyzer^{TM} was used to determine the concentrations of silicate, phosphate and nitrate. Sea water samples for Chl-*a* were collected with DMS sampling whenever possible. Chl-*a* was determined by filtering sea water through a Whatman GF/F glassfibre filter to retain phytoplankton cells, which were then extracted with 90% acetone for fluorometric determination (Wong et al., 1995).

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*Corresponding author.
e-mail: WongCS@pac.dfo-mpo.gc.ca
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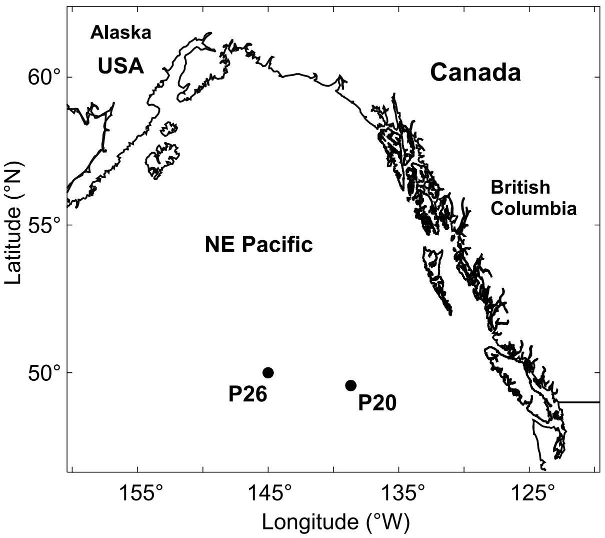

Fig. 1. Map of the Northeast Pacific Ocean showing Station P20 and Station P26.

Sea water samples for DMS were collected using a General Oceanic Rosette frame with 10L Niskin PVC samplers coupled to a CTD system, model SBE 11 plus (Seabird Electronics, Seattle, Washington, USA). Sea water was drawn from the Niskin samplers directly into 100 mL precision ground-glass syringes, which were then immersed in a bucket of surface sea water, stored in 4°C cooler in the dark. The samples are run as soon as they are taken. It takes about 4 hr to run a cast so the longest a sample is 'stored' before being run is 4 hr. The syringe is then attached to the system and a 25 mL calibration vessel is filled and subsequently drained into a 50 mL gas stripper and purged with UHP nitrogen flowing at 100 mL min^{-1} for 5 min. Gas transfer lines were made of Teflon tubing, except for the portion of fused silica-lined stainless steel located between the extraction system and the gas chromatograph. Water vapour was removed by a cold jacketed condenser set at 4 °C. DMS was captured by a trap (30 cm × 3.2 mm I.D., stainless steel) packed with Tenax TA, and immersed in an ethanol cold bath at -25 ° to -30 °C. The trap was quickly heated to 100 °C to release the DMS into a Hewlett-Packard 5880A gas chromatograph equipped with a flame photometric detector and a Chromasil 330 (Sulpelco # 1–1496) packed column that was kept at a constant oven temperature of 50 °C. The primary standard was prepared once a week from a stock solution of dimethylsulfide (Aldrich # 471577) in iso-propanol. The intermediate and working standards were made up fresh daily in purged, double Milli-Q water and run immediately before analysing each station profile. The detection limit was 0.08–0.1 nM with accuracy $>10\%$. The precision was 23% (S.D. ± 21%) for concentrations <0.2 nM, 15% (S.D. ± 14%) for concentrations 2–10 nM, 8% (S.D. ± 9%) for >10 nM. The overall precision for our data set was 18% (S.D. ± 17%). The DMS analytical method and calibration followed Uher (1999), who also described sampling and storage.

DMS has been known to absorb onto glass surface. Before year 2000, we did not silanize all glassware that came into contact with the DMS. All glassware was washed and baked before each cruise and cleaned before each cast. We have done a test by using a syringe treated with Chlorodimethylsilane versus one not treated and found no difference provided you clean the syringe not treated with Chlorodimethysilane after each cast.

Water samples for epifluorescence microscopy and light microscopy were collected using 10-L GoFLO bottles and fixed with Grade II glutaraldehyde (1.5% final concentration) and hexamethylenetriamine buffered formalin (0.4% final concentration), respectively. Within 24 hr of sample collection, 50 mL of glutaraldehyde preserved sea water was filtered; filtration and slide preparation procedures followed those of Booth et al. (1993). Filters were stored frozen at -20 °C in darkness until analysis (<6 weeks). Abundance and approximate dimensions of autotrophs ≤ 20 μm in size were determined using a Leitz Orthoplan epifluorescence microscope equipped with a 50 W Hg bulb and an ocular micrometer. Autotrophic flagellates (i.e. dinoflagellates, flagellates, and coccoid cells) were visualized using violet-blue excitation and enumerated at ×312 or ×1250 magnification. Samples preserved in formalin were analysed for coccolithophores, diatoms, and other autotrophs >20 μm in size using a Zeiss inverted light microscope within 20 weeks of collection. In general, 50 mL subsamples were settled for ~48 hr. For most taxa, the entire sample was enumerated at a magnification of ×250; however, for abundant taxa, transects were enumerated until ~100 cells or chains were counted. About 10 random dimension measurements were recorded per taxa per depth. For chain diatoms, dimension measurements of only one cell were taken per chain to avoid biasing the volume estimate. The biomass for each group was estimated as the product of cell abundance and cellular carbon. Following Booth et al. (1993), it was assumed that autotrophs <4 μm in size contain 0.22 pg Carbon μm^{-3}. Strathmann's (1967) equations were used to estimate carbon of diatoms and other autotrophs >4 μm in size. Average cell volumes were estimated using measurements of cell dimensions and formula outlined in Wetzel and Likens (1991). The volume of non-thecate cells (except dinoflagellates) <10 μm were corrected for shrinkage by multiplying the cell volume by 1.52 (Booth, 1987; Booth et al., 1993).

3. Results

Detail results from 1996 to 2001 were shown in Wong et al. (2005). Selected temperature, MLD, Chlorophyll-*a* and DMS concentrations are shown in Table 1.

Depth profiles of DMS at Station P26 and P20 in spring (June) and summer (August/September) of 1997–2001 are

Table 1. DMS concentration and oceanic habitat in the eastern sub-Arctic Pacific Ocean in spring (June) 1997–2001 and summer (August/September) 1996–2000

	June					August/September				
Parameter	1997	1998	1999	2000	2001	1996	1997	1998	1999	2000
Station P26 (50°N, 145°W)										
Mean sea surface temperature (°C)[a]	9.4	9.1	7.0	7.7	7.4	13.5	14.9	12.1	12.7	13.3
Mixed layer depth (m)[b]	25	15	28	33	36	19	12	32	31	31
Chlorophyll-*a*[c] (mg m^{-2}) up to MLD	8.5	8.0	7.4	9.0	17.7	4.7	5.6	8.1	–	18.2
DMS[c] (μmol m^{-2}) up to MLD	216	269	60	145	102	296	279	631	–	246
Station P20 (49° 34′N, 138° 40′W)										
Mean sea surface temperature (°C)	9.9	10.0	8.1	8.7	8.9	14.1	15.9	14.0	12.4	13.9
Mixed layer depth (m)	37	14	43	26	34	12	11	28	15	31
Chlorophyll-*a*[c] (mg m^{-2}) up to MLD	6.0	4.1	10.7	3.2	11.4	9.0	3.3	3.8	–	6.1
DMS[c] (μmol m^{-2}) up to MLD	201	244	91	70	70	259	105	352	–	86

[a] Sea surface temperatures are the means of available measurements from the top 5 m of the surface waters.

[b] Mixed layer depth is defined as the depth at which temperature dropped by 0.4 °C.

[c] Integrated.

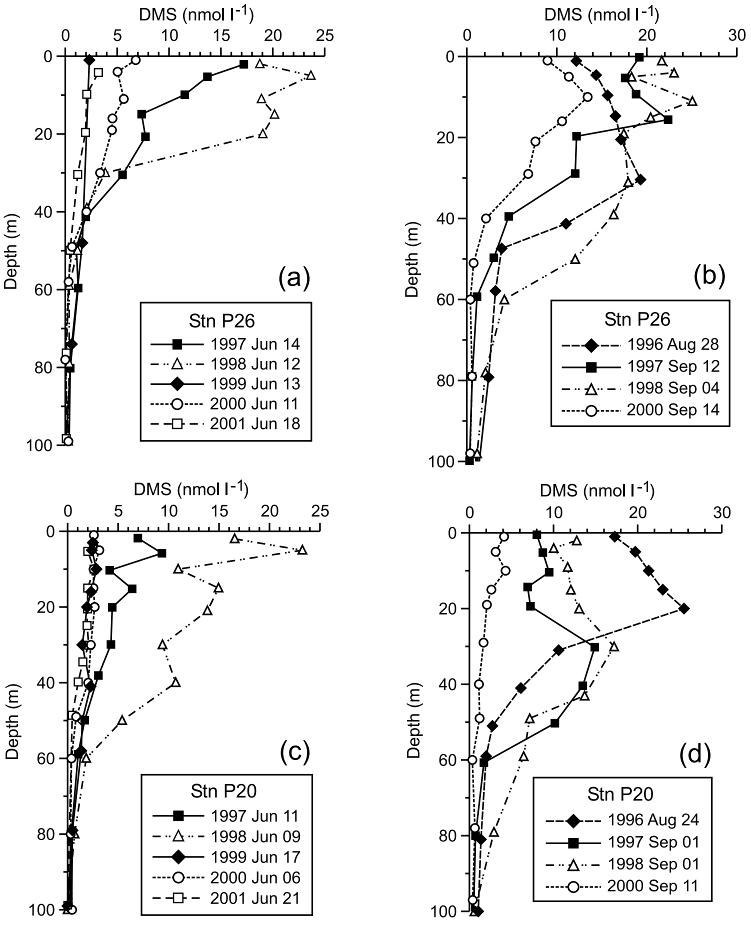

Fig.2. Depth profiles for DMS concentrations at P26 for (a) spring and (b) summer and at station P20 for (c) spring and (d) summer.

shown in Fig. 2. Depth profiles of biomass carbon of autotrophic dinoflagellates and coccolithophorids with location and date of collection in 1998–2000 are displayed in Fig. 3.

4. Discussion

Three cruises were conducted yearly from 1996 to 2001 in the winter (February/March), spring (June) and summer

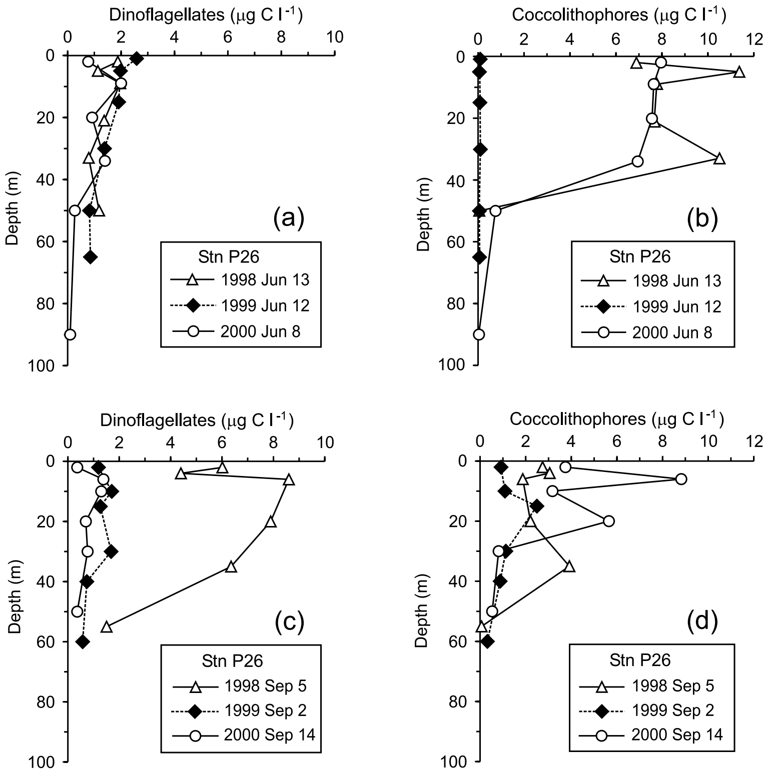

Fig.3. Depth profiles of the biomass carbon of autotrophic dinoflagellates and coccolithophorids in 1998–2000. (a) and (b) Samples collected in June. (c) and (d) Samples collected in September. Collection, identification and counting of samples followed the method described by Booth et al. (1993). Almost all the biomass of coccolithophorids in spring came from one species, *E. huxleyi*. Dinoflagellates also included many unidentified species.

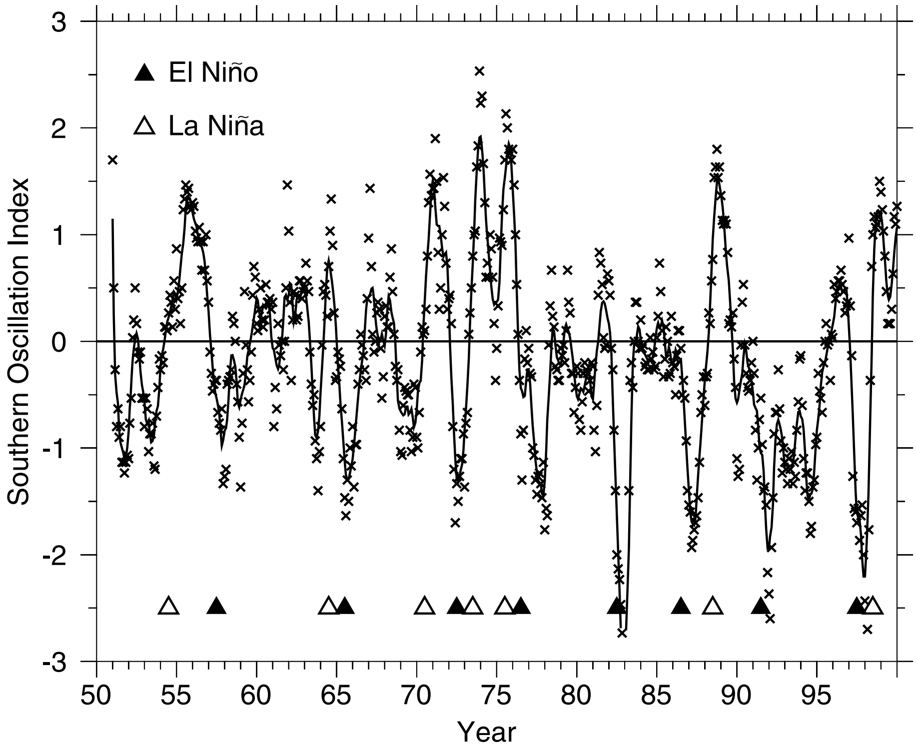

Fig.4. Warming and cooling during El Niño, La Niña and regime shift.

(August/September) by the Institute of Ocean Sciences (Fisheries and Oceans Canada). Water samples were taken at stations P20 (49°34′ N, 138°40′ W) and P26 (Ocean Station P or Station PAPA; 50°N, 145°W) in the open ocean off the west coast of Canada (Fig. 1) and analysed for chlorophyll-*a* and DMS. Between 1998 and 1999, we observed a dramatic decrease in the spring and summer concentrations of DMS at both stations (Fig. 2) and similar decrease in summer concentrations at P20. Both stations were located in a high-nutrient low-chlorophyll (HNLC) region characterized by lack of nutrient depletion and the absence of annual algal bloom events. We hypothesize that (1) MLD controls the oceanic condition, which in turn, affects the light and temperature which impact on the biology (2) the shift in DMS concentrations reflects the response of DMS-related processes to climate fluctuations during the ENSO transition. We divided our data set into 1996–1998 and 1999–2001 intervals and seasonally for winter (February and March), spring (May and June) and summer (August and September). In early May of 1996, maximum DMS concentrations at both stations were less than 2.5 nmol l^{-1}, or as low as the winter values. This was due to the colder temperature in May while June, a month later, is the month with more intensive production occurs. In other years, observations were done in June. At Station P26, integrated DMS to MLD levels in June during the 1999–2001 La Niña averaged 102 ± 25 μmol m^{-2}, or only 42% of the average of 242 ± 27 μmol m^{-2} measured during the 1997–1998 El Niño period (Table 1). Similarly, the summer integrated DMS to MLD level of 246 μmol m^{-2} in 2000 was 61% of the 1996–1998 summer average of 402 ± 115 μmol m^{-2}. Even larger decreases were observed at P20 where the mean DMS level of the MLD in June during the La Niña years of 1999–2001 was 77 ± 7 μmol m^{-2}, about 35% of 232 ± 22 μmol m^{-2} during the 1997–1998 El Niño. Only a single analysis was done for both years.

The DMS levels are examined for relationship to warming and cooling during El Niño, La Niña and regime shift (Fig. 4). The climatic regime is referred to the Niño-3.4 index, which is the average SST anomaly within the region 5°S–5°N, 170°–120°W, as one of the widely used ENSO indices (Barnston et al., 1997). 1997 and 2002 are dominant years for El Niño with event onset/demise in 1997/1998 and 2002/2003 respectively (Goddard and Dilley, 2005). For La Niña, dominant years are 1998, 1999 and 2000 with event onset/demise of 1998/1999 and 2000. The year 2001 is ENSO-neutral.

The oceanographic condition at Station P26 and Station P20 were examined in relation to the DMS levels. Oceanographically, at Station P26, the spring MLD was high at 150 m in 1996, and dropped to 120 m in 1997 and a very low value of ~85 m in 1998, an El Niño year. The summer MLD was very shallow at only 10 m in 1996 and ~15 m in 1998, an El Niño year, but deepened to ~35 m during La Niña years of 1999 and 30 m in 2001. For fall, the MLD was ~30 m in 1996 and in 1998, an El Niño year.

At Station P26 for the June values, during the El Niño period 1997 to 1998, temperature was higher and the MLD shallower, Chl-*a* lower, while the DMS levels were higher. In 1999, a La Niña year, Chl-*a* was lower. In 2000, at Station P26 for August, were similar to June condition of higher temperature, lower Chl-*a*, shallower MLD with high DMS. At Station P20, in June of El Niño years of 1997 and 1998, oceanographic condition of warmer temperature, shallower MLD, low Chl-*a* (particularly in 1998) and higher DMS, occurred.

Oceanographically, at Station P20, the spring MLD was at 30 m in 1996, ~30 m in 1997 and ~15 m in 1998 during an El Niño, and ~30 m 1999, 2000 and 2001, all during a La Niña.. In summer and fall, the MLD was at~15 m in 1996, ~15 m in 1997 and ~18 m in 1998 during an El Niño, but deepened to 40 m in 1999, ~30 m in 2000 and ~35 m in 2001 during a La Niña period. At Station P20 in August of El Niño years 1997 and 1998, temperature was not particularly warmer, although MLD was shallower, with high Chl-*a* in 1996 and high DMS in 1996 and 1998. In 1996 and 1997, Chl-*a* was low but high in 1998. At Station P20 in August, there was much higher DMS (three times that in other years) with much deeper MLD in 1998, and lower Chl-*a*. We speculate that the anomalous September value may be caused by possible anomalous change in DMS producers rather than by oceanographic condition. However, we do not have biological data during that period to support this hypothesis.

The El Niño–La Niña transition was marked by a dramatic decrease in sea surface temperature (SST). The 1997–1998 El Niño signals reached the NE Pacific by the summer of 1997 and persisted through the spring of 1998 (Strub, 2002). Warming of the Gulf of Alaska waters was driven by the prolonged El Niño with warmer waters moving towards Station P26 (DFO, 2004). The warm trend persisted at Station P26 and Station P20 until 1998 when it was interrupted during the prolonged La Niña from 1999 to 2002 in which SSTs at Station P26 and Station P20 were almost 2 °C lower than the values recorded in the early 1990s.

Warming of oceanic waters was accompanied by greater stratification of the upper water column. The MLD at Station P26 was relatively deeper at about 40 m during the period 1993–1995 but shallow to 19 m for summer 1995 to summer 1998. In the summers from 1999–2000, the MLD deepened to about 30 m. The shallower MLD during 1996–1998 also subjected phytoplankton and bacteria congregated in the mixed layer to higher levels of ultraviolet (UV-B) and solar radiation (Simó and Pedrós-Alió, 1999). Higher exposures of UV-B would inhibit the activities of a wide range of aerobic and anaerobic bacteria that mediate the production and consumption of both DMS and DMSP (Groene, 1995; Simó and Pedrós-Alió, 1999). However, we could not estimate the magnitude of these changes as turnover rates of DMS from bacterial degradations or photochemical processes in the NE sub-Arctic Pacific Ocean are lacking.

DMS production is known to depend directly on the species composition and cell size of DMSP-containing phytoplankton

(Keller, 1989), and on the physiological responses of these species to changing conditions of their habitats (Turner et al., 1996; Malin and Kirst, 1997). Indirectly, the production of DMS may also depend on the properties and turnover rates of those biological functions of production and consumption (Groene, 1995; Simó et al., 2000) that are integral parts of the biogeochemical cycle of DMS. Hence, climatic changes that modify substantially the habitats of DMSP-containing phytoplankton and their heterotrophic consumers (microzooplankton and bacteria) will inevitably affect the level of DMS in surface waters.

Several of the nanoplankton groups found near P26, such as dinoflagellates (e.g., *Amphidinium* spp, *Gymnodinium* spp. and *Prorocentrum minimum*) and prymnesiophytes (e.g., *Chrysochromulina* spp., *Phaeocystis pouchetii* and the coccolithophorid *Emiliana huxleyi*) are recognized as significant producers of DMSP (Keller et al., 1989). Surveys conducted in the spring and summer of 1984–1988 (Booth et al., 1993) near Station P26 found them relatively common or abundant. These species were also found in samples collected in 1998–2000. However, the biomass and cell counts of coccolithophorids revealed large differences between years. Almost all the coccolithophorid biomass in spring (Fig. 3b) came from a lone species, *E. huxleyi*. Its number in spring 1998 and 2000 reached $\sim 3.8 \times 10^5$ cells l^{-1}, but was almost two orders of magnitude less in spring 1999. In summer, *E. huxleyi* contributed 17%, 30% and 72% of the coccolithophorid biomass in 1999, 1998 and 2000, respectively. Thus, the biomass of coccolithophorids was much greater in 1998 and 2000 than in 1999. A smaller between-year difference in biomass occurred for the autotrophic dinoflagellates in the summer seasons, in which they were more abundant in 1998 than in 1999–2000 (Fig. 3c). Their summer biomass values were also higher than those of coccolithophorids (Fig. 3d). The most important dinoflagellates were several species of *Gymnodinium*. Since the biomass values of coccolithophorids and dinoflagellates in 1999 were about the same as those observed in the mid-1980s (Booth et al., 1993), the 1998 values most likely represented the results from a different algal assemblage dominated by exceptionally high density of DMS-containing phytoplankton. In general, coccolithophorids play a more important role relative to dinoflagellates, but with no clear indication of control of ecosystem structure.

During 1996–1998, the ecological conditions of high SST and shallower MLDs in the eastern sub-Arctic Pacific enable the small DMSP-rich phytoplankton to out-compete the large DMSP-poor diatoms (Boyd and Harrison, 1999). For example, *E. huxleyi* is known to proliferate in a nutrient-poor, open-ocean environment, including iron-stressed ones (Muggli and Harrison, 1996). Moreover, by producing more coccolithophorids cells when nutrients become depleted (Lecourt et al., 1996), *E. huxleyi* is able to sink to the nutricline (high nutrients and low light) below the mixed layer and exploit this deeper nutrient reservoir. Field observations (Turner et al., 1988) and laboratory cultures (Turner et al., 1988; Keller and Korjeff-Bellows, 1996; Stefels, 2000) also reveal that DMSP content of microalgae usually increases under nitrogen-depleted conditions. For the sub-Arctic strain of *E. huxleyi*, the temperature (16–17 °C) for maximum growth (Muggli and Harrrison, 1996; Lecourt et al., 1996) is slightly above the summer SST during the El Niño period (Table 1). The warmer SST would accelerate the turnover rates of DMSP in the sub-Arctic Pacific as it was observed in the subtropical oceanic region (Dacey et al., 1998). Change in DMS concentrations in the MLD is also linked to change to wind speed (Wong et al., 2005).

The step-like decreases of DMS concentrations at P26 and P20 during the ENSO transition are manifestations of the possible shifts in ecosystem structure and function caused by the climate variability in the eastern sub-Arctic Pacific Ocean. As warming in this region persisted for almost a decade in the early 1990s (Whitney and Freeland, 1999), the local phytoplankton communities would be dominated by small flagellates, dinoflagellates and coccolithophorids in the same period. Similar shifts of plankton population toward a prokaryote-dominated ecosystem happened in the North Pacific subtropical gyre during the last two decades (Karl et al., 2001), and might also occur in the equatorial region. However, efforts to detect the signals of increased DMS from the equatorial Pacific during El Niño events was not successful (Bates and Quinn, 1997). The result contradicts snow-core data from the Antarctic region (Legrand and Feniet-Saigne, 1991). These data suggest that the oxidation products of DMS in south polar snow increased in response to the short-term climate fluctuations induced by ENSO events during the last 60 yr. Most probably, the contradicting observations are the results of different species compositions in the two ecosystems. During warm periods, the equatorial region is dominated by prokaryotes that are not DMSP producers, whereas in the Southern Ocean, the dominant phytoplankton is the known DMSP- and DMS-producer *Phaeocystis* (Groene, 1995). DMSP content varies with species composition and cell size (Keller, 1989), as stated earlier, and implies high DMS evasion from waters with high DMSP.

Our observations have implications for the hypothesis proposed by Charlson et al. (1987). They postulated a self-regulating feedback mechanism between climate and the production of DMS by marine phytoplankton. One possible positive feedback link presumes that increased SST and/or light leads to increased DMS emissions. Experimental results of the physiological effects of temperature on DMS/DMSP production are inconclusive (Malin and Kirst, 1997). The only field observation on the link between DMS concentration and temperature (low in winter and high in summer) in an open ocean environment (Dacey et al., 1998) probably reflects the seasonal variability in the turnover rates of DMSP to DMS.

5. Conclusions

We hypothesize that temperature and light (via variation of the depth of the mixed layer) influence the production of DMS by altering the properties of the habitats in the temperate and sub-Arctic regions of the open oceans. As SST of a region rises, the stratification of the upper water column intensifies and oceanic upwelling weakens. In the nutrient-rich waters of the sub-Arctic Pacific, higher stratification and shallower mixed layer favour the growth of small-sized phytoplankton such as small flagellates, dinoflagellates and coccolithophorids. Most prolific DMSP producers are members of these phytoplankton groups, such as *E. huxleyi* that, in addition, possesses its own DMSP-lyase allowing it directly (with or without the intervention of bacteria) decrease or increase the production of DMS (*Wolfe and Steinke*, 1996). Consequently, the local ecosystem is shifted towards one with structure and function adapted to changing production of DMSP and DMS. However, bacteria abundance and productivity at Station P26 was relatively high and growth rates slow. The bacteria abundance and productivity were at their lowest in summer, 1998 when La Niña cooling had hit by that time and the MLDs were the deepest for any year. Bacterial abundance and productivity were anomalously low in association with El Niño, and even lower with La Niña (Sherry, 2002). Our speculation on the central role of ecosystem structure as a possible explanation of high DMS suffers from the unavailability of long-term time-series of DMS producers, and should not be regarded as a firm conclusion.

Recent studies have found that the climate-driven variations in the MLD exert a substantial influence on the seasonal production of DMS in the open ocean (Dacey et al., 1998; Simó and Pedrós-Alió, 1999). We have provided observational evidence of the central role of the ecosystem structure as an essential link between MLD and DMS production in large parts of the oceans on a longer (annual to 5 yr) timescale. Furthermore, we envisage these mechanisms of longer-term variations in DMS might be the regular *modus operandi* in a warming ocean caused by global climate change. In the Pacific Ocean, an increasing level of greenhouse gases in the atmosphere would lead to more frequent El Niño and fewer, but stronger, La Niña events (Timmermann et al., 1999). Globally, a larger part of the warming oceans may have highly stratified water for a longer part of the year. These conditions could enhance the shift in the marine ecosystem described herein, and might induce more rapid turnover of DMSP and higher production of DMS. Hence, in a warming global climate, we might anticipate an increasing emission of biogenic DMS from the ocean surface.

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