Tellus (2006), 58B, 242–254
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TELLUS

Changes in DMS production and flux in relation to decadal shifts in ocean circulation

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(Manuscript received 6 July 2005; in final form 9 January 2006)

ABSTRACT

A fundamental question is are the biological processes regulating dimethylsulphide (DMS) production by the marine ecosystem interconnected and responding to atmospheric or ocean signals at decadal timescales? Related to this is a need to quantify how climate change affects these interconnections and understand the expected levels of natural variability on decadal timescales. To explore this we have used indicators of climate variability [the Gulf Stream North Wall (GSNW) and the North Atlantic Oscillation (NAO) indices] as probes to demonstrate that a marine ecosystem model, incorporating DMS production, can extract and amplify a climatic signal, which is spread across a variety of meteorological variables. The GSNW signal is imparted through the wind and cloud forcing, despite the fact there was not significant relationship observed between the GSNW index and the meteorological forcing data. The model simulations appear to reproduce observed decadal variability in phytoplankton community structure in the eastern North Atlantic and imply that DMS(P) biogeochemistry may vary on decadal timescales as a consequence of changes in community structure. The GSNW index is a potential indicator of such changes and there may have been a regime shift in DMSP production in the eastern North Atlantic coincident with that observed for plankton. Sensitivity analysis indicates that the impact of climate variability on DMS biogeochemistry may potentially be damped by the ability of microbial communities to adapt physiologically to the effects of changes in light and nutrients.

1. Introduction

Dimethylsulphide (DMS) is a climatically important trace gas that is generated by biological transformation processes from dimethylsulphoniopropionate (DMSP), synthesized in varying amounts by a variety of phytoplankton species. It has been hypothesized to play a significant role in maintaining the Earth's temperature within bounds conducive to the existence of life. The DMS concentration in surface waters and hence, sea to air flux, is governed by a complex web of biological and physio-chemical processes (Liss et al., 1997; Kiene et al., 2000). On the few occasions when a comprehensive budget has been generated, estimates of the proportion of DMSP production that is transformed to DMS in the surface ocean varies between 11% and 56%, while sea to air flux of DMS accounts for approximately 1% of the DMSP produced (Bates et al., 1994; Simó and Pedrós-Alió, 1999; Archer et al., 2002). Climate change is likely to alter these yields but it is uncertain in which direction and through which key processes.

Year-to-year biological variability has been observed to track fluctuations in large-scale climatic indices and it may be expected that DMS production will show similar associations. Statistical relationships between the position of the North Wall of the Gulf Stream (GSNW) and biological populations in Northern Europe Waters have been reported by several authors. This association has been found in Continuous Plankton Recorder data in and around the North Sea (Taylor et al., 1992; Taylor, 1995), coastal North Sea data (Frid and Huliselan, 1996), jellyfish data (Lyman et al., 2005) and young fish (Lindley et al., 2003) in freshwater data (George & Taylor, 1995; George, 2000) and in terrestrial data from a roadside verge in the UK (Willis et al., 1995). The latter examples implying that the association must be transferred via the atmosphere. Similar relationships between long-term biological/planktonic time-series and the North Atlantic Oscillation (NAO) have also been found (e.g. Fromentin and Planque, 1996; Reid et al., 1998). The NAO is the dominant atmospheric pattern over the North Atlantic and Western Europe and is associated with changes in the winter surface westerly winds. Similar relationships between long-term biological/planktonic time-series and the NAO have also been found (e.g. Fromentin and Planque, 1996; Reid et al., 1998).

The associations between ecosystem components and the GSNW and NAO seen around the British Isles and in the North

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DOI: 10.1111/j.1600-0889.2006.00183.x

Sea may be because these areas lie in the paths of weather systems originating over the North Atlantic. This association is obvious for the NAO but how do these associations with the GSNW arise? Although the GSNW is derived from current shifts very close to the US coast, it is likely the index is recording more widespread circulation changes. Curry and McCartney (2001) have constructed a measure of the large scale transport of the Gulf Stream from the 1950's onwards using as an index the difference in potential energy anomaly at the surface relative to 2000 db between Bermuda and the central Labrador basin. It appears that the Gulf Stream is an indicator of the overall ocean transport. This is the reason that the position of the Gulf Stream accumulates atmospheric changes across the North Atlantic over several years (Gangopadhyay et al., 1992; Taylor et al., 1998; Taylor and Gangopadhyay, 2001).

Previous modelling work has demonstrated that model ecosystems can amplify weak climatic signals (Taylor et al., 2002). The observed association between plankton populations around the UK and the position of the Gulf Stream was used as a probe to illustrate how a modelled complex marine ecosystem extracts a weak signal that is spread across different meteorological variables. This demonstrates that biological systems may respond to climatic signals, which are not those most apparent in the driving variables. Correspondingly, the response to global warming of the complex network of processes that govern DMS concentration in surface waters may not result directly from increased insolation and/or temperature but from more subtle climatic changes or ecosystem responses.

The purpose of this work is to address the questions: what is the interannual variability of DMS(P) biogeochemistry, can the GSNW and the NAO signals be detected amongst these processes and if so how do these signals manifest themselves and what are the potential mechanisms? As no sufficiently long-term time-series of observations exist to answer these questions, a modelling approach is used. In order to determine how the GSNW and NAO signals find their way into the plankton we have followed the methodology of Taylor et al. (2002) whereby time-series of hourly meteorological observations made at Dublin from 1966 to 1998 were used to drive a coupled physical-ecological water-column model. This model is a synthesis of the European Regional Seas Ecosystem Model (ERSEM) (Baretta et al., 1995) adapted to include DMS production (Archer et al., 2002, 2004) and the General Ocean Turbulence Model (GOTM) (Burchard et al., 1999). The simulations are of a generic water column in the central North Sea (56°N) typical of the seasonally stratified North West European shelf.

2. Methodology

2.1. The physical model

GOTM is a 1-D physical model that is designed as a generic system for marine modelling. In this case the GOTM *Mellor Yamada* turbulence closure option (Mellor and Yamada, 1982) is applied and forced with hourly resolution sea surface meteorology. The meteorological forcing data (air temperature at 2m, 10 m winds speed and direction, cloud cover and relative humidity) were obtained from Dublin Airport. Although not data from the North Sea, Dublin lies directly in the path of weather systems, which commonly move from the Gulf Stream to the North Sea (Taylor et al., 2002). As the GSNW and NAO indices are found in a wide variety of aquatic, benthic and terrestrial ecosystems in the British Isles and NW European Shelf (George and Taylor, 1995; Taylor, 1995; Reid et al., 1998; Lindley and Batten 2002) we infer that these signals are to be found in the general weather patterns over the region and, therefore, assume the Dublin data set to be typical.

This physical forcing is used to calculate the time evolution of temperature, salinity, turbulence and hence the coefficients of vertical eddy diffusivity throughout the water column. This method has been demonstrated to give good simulations of observed turbulent dissipation data in the stratified waters of the Northern North Sea (Burchard et al., 2002). At the sea surface, fluxes of heat and momentum are calculated using the bulk formulas outlined in Castelari et al. (1998). Evaporation and precipitation are not considered.

2.2. The ecosystem model

ERSEM is a generic ecosystem model originally used in the North Sea (Baretta et al., 1995; Allen et al., 2001, 2004) but recently applied successfully to more oligotrophic waters (Zavaterelli et al., 2000; Allen et al., 2002) and oceanic upwelling systems (Blackford and Burkill, 2002). Detailed descriptions of ERSEM and its pelagic submodels are given in Baretta et al. (1995), Baretta-Bekker et al. (1997) and Ebenhöh et al. (1997). In ERSEM the ecosystem is represented as a network of interacting physical, chemical and biological processes. A 'functional group' approach is used to describe the biological components consisting of primary producers, consumers and decomposers, which in turn are subdivided on the basis of trophic links and/or size. A schematic of the ERSEM DMS model trophic links is given in Fig. 1a. The dynamics of each functional group are dictated by physiological (ingestion, respiration, excretion and egestion) and population (growth, mortality and migration) processes that are described by fluxes of nutrients between groups. The adaption of phytoplankton to variability in the light field assumes that the optimal growth parameter in the photosynthesis-irradiance equation adjusts enabling optimization of growth rates in a variety of regimes. (Ebenhöh et al., 1997) Phytoplankton biomass is described by carbon, nitrogen, phosphorous and in the case of diatoms silicon components, because variable C/N/P cell quotas are allowed. Nutrient uptake is decoupled from the carbon processes that are dependent on internal cell nutrient quotas. Gross primary production is a function of temperature, availability of and adaptation to light, silicate concentration in the case of

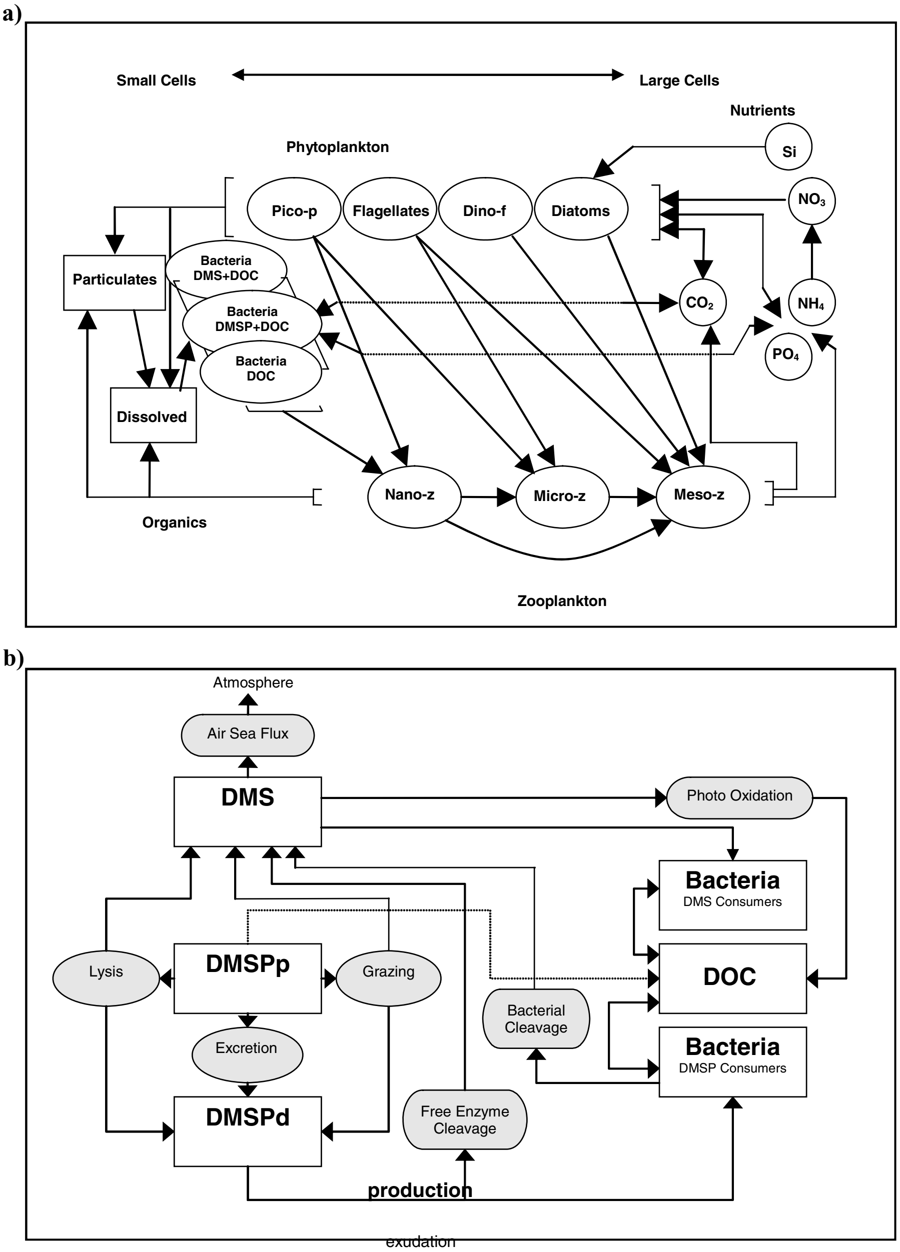


Fig. 1. Diagrammatic representation of (a) The ERSEM-DMS foodweb and (b) the dimethyl sulphide (DMS) and dimethylsulphoniopropionate (DMSP)-related processes incorporated into ERSEM.

diatoms and phytoplankton biomass. The required nutrient uptake is calculated as a combination of uptake commensurate with carbon productivity and uptake necessary to address any internal shortfall of nutrients. Actual uptake is constrained by a maximum uptake dependent on an affinity parameter and external nutrient concentration. If there is a shortfall in the available nutrients, which prevent the entire gross production being fixed, the excess carbon is diverted to the DOC pool via nutrient stressed lysis.

The phytoplankton community consists of four functional types: picophytoplankton (0.2–2.0 μm), phytoflagellates (2–20 μm), phototrophic dinoflagellates (20–200 μm) and diatoms (20–200 μm). Photosynthetically active light (PAR) at the sea surface is modelled from astronomical values that are corrected for cloud cover. Extinction of light through the water column is a function of particulate concentrations and phytoplankton biomass and is given a background extinction parameter. Mesozooplankton, microzooplankton and heterotrophic flagellates make up the consumers. Grazing uptake is a function of maximal ingestion rate, temperature, food availability and the zooplankton biomass. Zooplankton mortality occurs in the model at a constant rate and may be triggered by low oxygen concentration. Each zooplankton functional group is predated upon (Fig. 1a).

2.3. The DMS model

The processes included in the DMS model and incorporated in ERSEM are shown in Fig. 1b and are mathematically described in equations 1–21 of Archer et al. (2004). This is a modification of the model described in Archer et al. (2002). The process rates that transform DMSP to DMS and standing stocks of particulate DMSP (DMSPp), dissolved DMSP (DMSPd) and DMS quantified during a 6 d Lagrangian experiment in the northern North Sea were well represented by the parameters applied in the original model (Archer et al., 2002).

The four phytoplankton functional groups invest a constant proportion of gross carbon production in DMSP synthesis; this fraction varies by functional group as follows, diatoms = 0.01, flagellates = 0.05, picoplankton = 0.025 and dinoflagellates = 0.08 (Archer et al., 2004). There are three bacterioplankton functional groups in the model that differ in the dissolved food source that they can utilize. One group utilizes only dissolved organic matter (DOM), one group is able to take up DMSPd and DOM and the third group is able to consume DMS and DOM. In natural waters whether the same bacteria are able to utilize DMSPd and DMS (e.g. González et al., 1999) or the different processes are carried out by different taxonomic/functional groups (e.g. Visscher et al., 1992) is uncertain. Bacterial uptake is a function of potential assimilation rate, temperature, oxygen availability, nutrient quotient and the concentration of the food source. A full description of the model and its parameters can be found in Archer et al. (2004) and the references within.

2.4. Model set-up

The physical model was initialized with a fully mixed, winter temperature and salinity profile appropriate to the central North Sea. The ERSEM formulation of the biogeochemical processes defining biological dynamics is retained in the present model as are the parameter values described in Archer et al. (2004) and references within. The ecological model was initialized with *in situ* winter nutrient concentrations measured during the North Sea Project (Lowry et al., 1992) and the winter biomass estimates used to initialize the simulations described in Baretta et al. (1995). The model was then spun-up for 5 yr with a repeating annual forcing to generate the initial conditions. The model was run as a series of independent simulations, each starting from the same initial conditions, one for each year for the period 1966–1994. The simulations were run independently to allow the investigation of the impact of the meteorology of a specific year on the ecosystem. We can do this because sensitivity analysis using an ensemble of 100 simulations and a Gaussian perturbation of each pelagic state variable by up 10% demonstrates that model phytoplankton is insensitive to perturbations in initial conditions of the ecosystem as long as the physical environment remains constant (R. Torres 2004, personal communication), implying the carry over of ecosystem information from one year to the next does not significantly influence the simulations.

2.5. Climate indices

The NAO index is updated from Hurrell (1995). It represents the difference between the winter (December to March) sea level pressures of the Iceland low (measured at Stykkisholmur in Iceland) and the Azores high (measured at Lisbon in Portugal).

The Gulf Stream North Wall (GSNW) index is a measure of the latitudinal position of the north wall of the Gulf Stream where it breaks away from the east coast of North America. It is calculated from monthly charts of the north wall's position (Taylor and Stephens, 1980) available from 1966. Six time-series of positions were generated by reading the latitude of the north wall from each chart at the longitudes 79, 75, 72, 67 and 65W. An index of monthly position is then calculated as the first principle component of these six series (Kendall and Stuart, 1966). The first principle component is the weighted sum of the series, which contains as much of the variance as possible (Taylor, 1995).

2.6. CUSUM

The Cumulative Sums (CUSUM) technique was used to analyse the relationships between the climatic indicators and the model output. The CUSUM is the square of the difference between the data generated by the model and GSNW or NAO index after each data set has been converted to a mean of zero and unit standard deviation.

$$\mathrm{CUSUM} = \sum\nolimits_{i=1,n} (Index - Data)^2.$$

CUSUMs provide a sensitive test of whether the relationship is constant with time and are a commonly used control technique in process engineering. Variables are positively correlated when the slope of successively plotted CUSUM values is close to zero. The slope rises to 2.0 if the variables are uncorrelated. To calculate the probabilities of the CUSUM occurring by chance 2000 random data series were generated, each having the same serial (auto) correlation (i.e. the *correlation* of a variable with itself over successive time intervals) as the data set being tested. A slope was calculated between every pair of points (adjacent and non-adjacent), and these values were averaged. The average slope was then compared with those calculated by applying exactly the same procedure to each of the random data sets. The number of random series giving a slope at least as small as the average gives an estimate of the probability that such a small slope would arise by chance. The CUSUM analysis is performed by comparing each climatic index with the mean values from the spring and summer productive period (days 90–240) for biological rates and state variables from the model. Previous work (Taylor et al., 2002) has shown that the signal is only found when the ecosystem is active.

3. Results

3.1. Validation

A 1-D modelling approach removes horizontal hydrodynamic effects from the simulations. Consequently the results presented are purely the response of the ecosystem to the meteorological forcing. A detailed validation of the ecosystem model and the sulphur cycle model can be found in Allen et al. (2004) and Archer et al. (2004), respectively. As an illustration, Fig. 2 shows the validation of a simulation of near surface concentration of DMS, DMSPp and DMSPd for the year 1989 at station CS (55°30′N, 0°55′E) compared with data from the NERC North Sea project (Lowry et al., 1992; Turner et al., 1996). Similarly, Fig. 3 shows the validation of the ecosystem model with chlorophyll, nitrate, phosphate, silicate, microzooplankton and mesozooplankton. In all cases the model shows good correspondence with both the magnitude and trend of the data. Comparison of our results with continuous plankton recorder data from the central North Sea (WinCPR Vezzulli et al., 2005) using the CUSUM method demonstrates that the model reproduces the observed interannual variability in Plankton Colour Index, dinoflagellates and some species of diatom. The probabilities that these relationships are statistically significant are summarized in Table 1.

3.2. Interannual and decadal variability

The interannual variability of gross DMSPp production is in the range ±10% of the mean value over the period of the simulation (Fig. 4). Similar ranges are observed for the concentration of DMSPd and DMS (Fig. 4). However the range of interannual variability of the sea–air flux is ±30% (Fig. 4).

The cumulative summation technique of Ibanez et al. (1993) illustrates the intensity and duration of any changes in a variable. There are clear decadal changes in the gross DMSPp production (Fig. 5a); between 1966 and 1975 the production is variable, from 1975 to 1985 it systematically decreases and after 1985 it steadily increases. DMSPd and DMS (not shown) exhibit similar behaviour. Decadal changes of the contributions of each phytoplankton type to gross DMSPp production are shown in Fig. 5b. The impact of diatoms (the smallest contributor) remains fairly constant throughout the period, production by flagellates slowly decreases until 1985 then increases in parallel with the increasing DMSPp production, picoplankton production increases up to 1971, remains stable till 1977, decreases to 1981 and thereafter fluctuates evenly about the mean, while dinoflagellate production decreases steadily until 1977 then increases to the end of the simulation period.

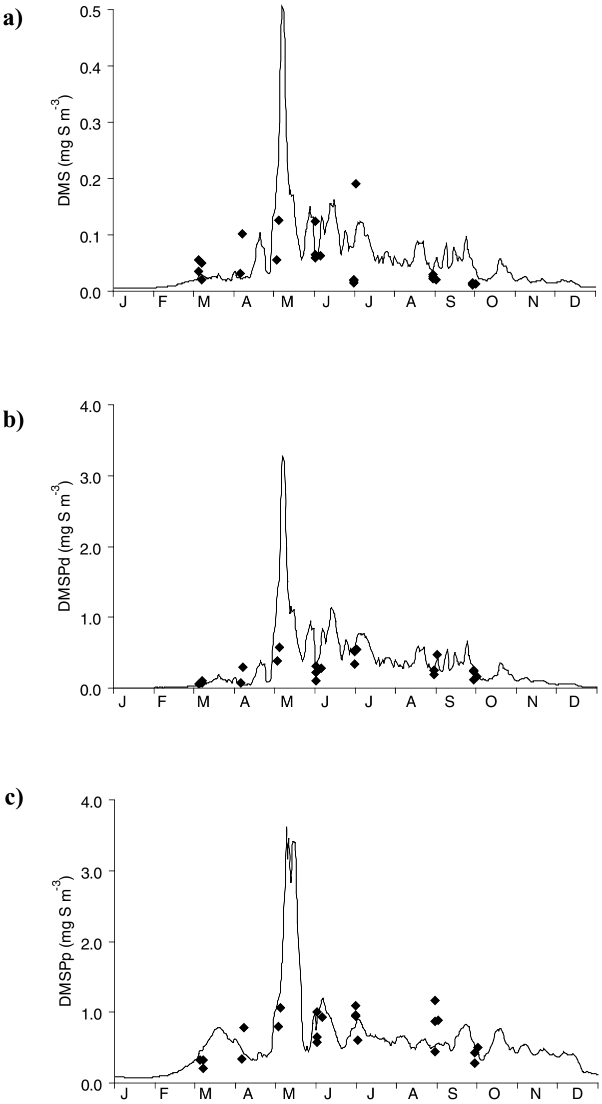


Fig. 2. Comparison of simulated concentrations and field data collected during the North Sea Project (NSP) for (a) dimethyl sulphide (DMS), (b) dissolved dimethylsulphoniopropionate (DMSPd) and (c) particulate dimethylsulphoniopropionate (DMSPp) for 1989. Graphs (a), (b) and (c) illustrate the temporal trend in simulated daily concentration in the surface mixed layer and measurements (filled diamonds) made in surface waters at CS or one of three stations with similar physical characteristics within ICES box 7′ and 20 km of CS.

3.3. CUSUM analysis

CUSUM analysis indicates that the GSNW signal can be found in modelled DMS concentration, DMSPd concentration, gross

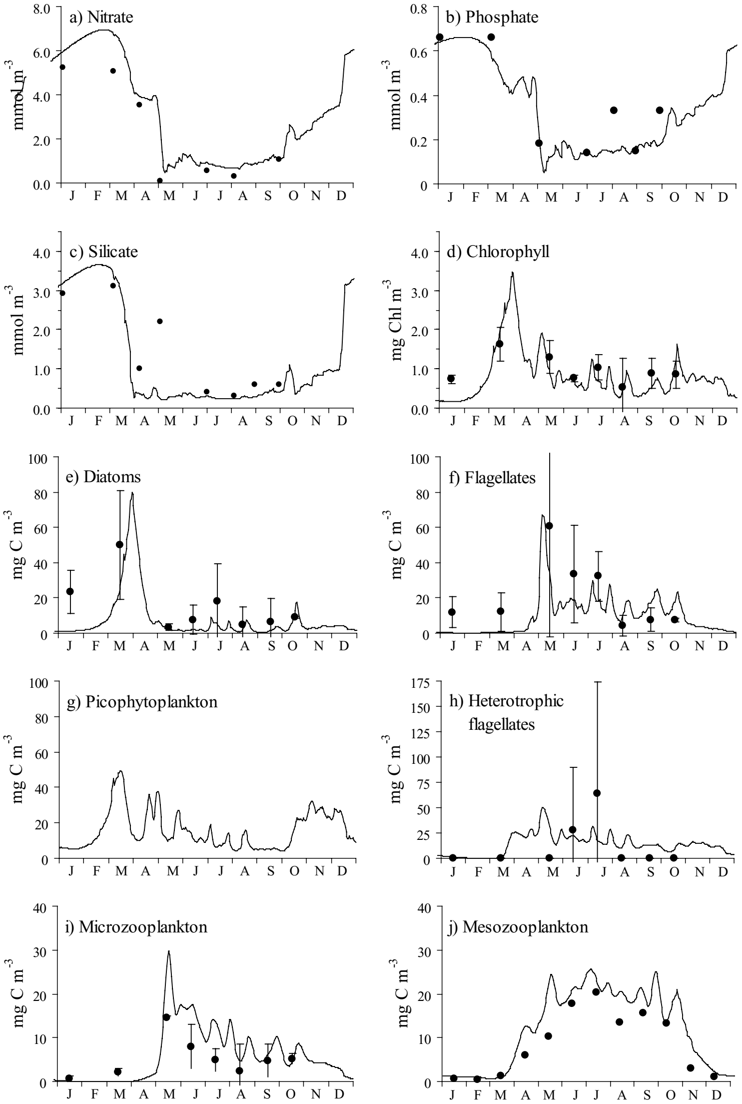


Fig. 3. Seasonal succession graph for August 1989 to September 1999 of modelled (line) and measured (circles) chlorophyll (mg-C m^{-3}) for (a) NSP data, depths 0–10 m, model data at 5 m, (b) NSP data, depths 15–25 m, model data at 20 m, (c) NSP data, depths 35–40 m, model data at 40 m and ERBAS biomass (mg-C m^{-3}) for (d) Diatoms (e) Flagellates (f) Mesozooplankton (g) Microzooplankton and (h) Heterotrophic Flagellates.

DMSPp production, bacterial production, primary production (except diatom and flagellate production), nutrient concentration and recycling and mesozooplankton and microzooplankton biomass. Some examples are shown in Fig. 6. The relationship of simulated variables with the GSNW is strongest between 1973 and 1994, evident as the shallowness of slope on the graph for all variables that show a statistically significant CUSUM. The probabilities that these relationships are statistically significant are summarized for the GSNW in Fig. 7. In general the signal is found in all components of the ecosystem apart from the biomass and production of both diatoms and flagellates. It is particularly strong in the standing stocks and production of the heterotrophic components and sulphur compounds. In contrast the NAO signal is found in relatively few components of the ecosystem: mesozooplankton; microzooplankton; the biomass and production of DMSPd consuming bacteria;, ammonia recycling; bacterial phosphorous uptake; and diatom production. Again, some examples are given in Fig. 8. The probabilities that these relationships are statistically significant are summarized in Fig. 9.

CUSUM analysis of the relationship between the meteorological forcings and the climatic indices reveals that the GSNW is scattered through the variables rather than localized in any subset. The CUSUM probabilities (not shown) are in excess of 0.1 implying that the GSNW signal is not a statistically significant component of the atmospheric data. This relative weakness of the signal in the meteorological observations has been previously noted (Taylor 1995; Taylor et al., 2002). In contrast the NAO signal is found in the wind speed and the temperature ($p < 0.05$) but not in the cloud cover (not shown).

Table 1. A comparison between the annual average of phytoplankton functional group and total biomass generated by the model corresponding annual average CPR data. The values are the probability of the CUSUM relationship between the model output and CPR data being random. The CPR data is for the stratified central North Sea (WinCPR Vezzulli et al., 2005), the region simulated by the model. Probabilities of less than 10% are highlighted. The species were chosen to match those used by Leterme et al. (2005) in their analysis of North Atlantic phytoplankton change

	Model diatoms	Model flagellates	Model dinoflagellates	Model total phytoplankton
Diatoms				
Thalassionema nitzschiodes	0.15	0.4	0.16	0.19
Thalassiothrix longissima	**0.05**	**0.06**	**0.09**	**0.05**
Thalassiosira spp.	**0.06**	0.62	0.8	0.14
Dinoflagellates				
Ceratium furca	0.14	0.12	**0.007**	**0.09**
Ceratium fusus	0.2	0.31	**0.04**	0.15
Ceratium horridum	0.34	0.28	**0.01**	0.35
Phytoplankton colour index (PCI)	**0.01**	0.44	0.44	**0.004**

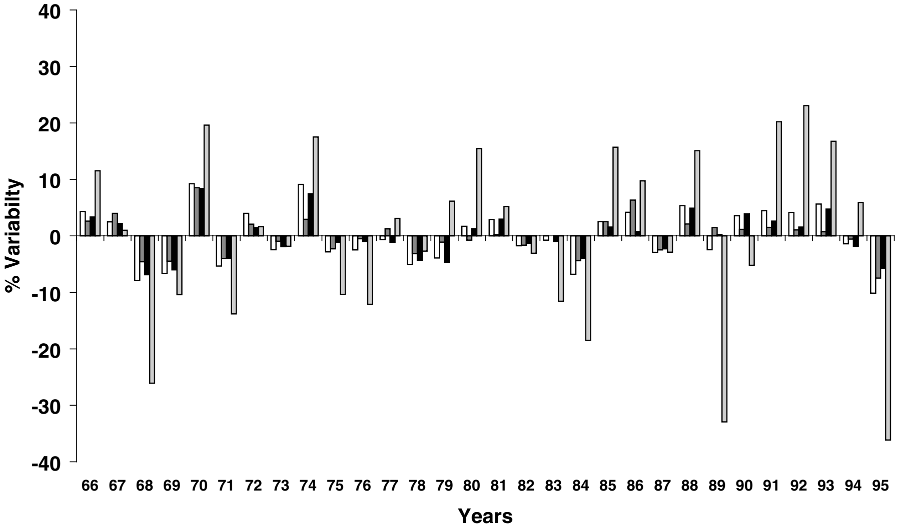


Fig. 4. The simulated percentage interannual variability of spring/summer mean (days 90–240) gross production of DMSPp concentration, DMSPd concentration, DMS and DMS sea to air flux for the period 1966–1995. Gross production of DMSPp (white), DMS (black), DMSPd (dark grey) and sea to air flux of DMS (light grey).

DMSPp production, DMSPd and DMS concentrations all have a significant relationship with the GSNW index as do a wide range of ecosystem variables during the spring and summer. DMS concentration is significantly related to the NAO. The GSNW signal is not found in the DMS sea to air flux but the NAO signal is (CUSUM probabilities are $p = 0.3$ and $p = 0.008$, respectively). This is a consequence of the formulation of the sea to air gas exchange rate, which is a function of the seawater concentration of DMS and the square of the wind speed (Nightingale et al., 2000). The power law wind speed term in the equation outweighs the DMS term, which contains the GSNW signal. However the NAO signal is also found in the wind ($p = 0.025$) and, therefore, through the power law wind speed term, in the sea to air DMS flux.

3.4. Sensitivity analysis

Sensitivity analysis of the relationship between model output and climatic indices to meteorological forcing was undertaken by rerunning the simulations with (1) constant wind, variable cloud and then with (2) constant cloud cover and variable wind. The results indicate that the GSNW signal is propagated by the wind variability and to a lesser extent the cloud variability (Table 2). In contrast, the NAO signal in the simulations remains fairly constant even when the variability of the cloud or the wind is removed (Table 2). Simple regression analysis of the relationship between spring and summer gross DMSPp production and spring and summer mean wind speed indicates that production increases with increasing wind speed ($R^2 = 0.5$, R is significantly different

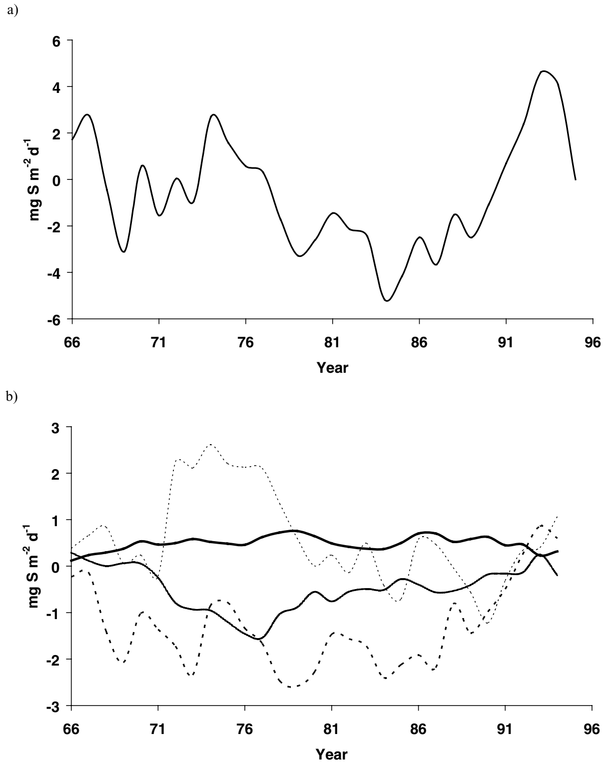


Fig. 5. Summation plots of decadal variability of (a) annual daily mean gross production of DMSP and (b) the annual daily mean gross production of DMSP by diatoms (solid black line), flagellates (heavy dash), picoplankton (light dash) and dinoflagellates (grey). The calculation consists of subtracting a reference value (the mean of the series) from the data and successively adding the residuals. Successive positive residuals produce an increasing slope, while successive negative residuals produce a decreasing slope. A succession of values similar to the mean show no slope.

from 0 at a probability of $p = 0.999$). The probability that the CUSUM relationship between the GSNW index and wind speed occurs by chance is 0.27 (i.e. a 27% chance the relationship is random) indicating that it is not significant.

To investigate the model sensitivity to changes in the magnitude of the wind speed, the model was run with 1977 forcing and the wind speed scaled by plus or minus 20% (i.e. the magnitude of the wind varies but not the variability). In this case the spring and summer gross production of DMSPp was found to be independent of the magnitude of the wind (Fig. 10a). At first glance these results appear to be contradictory but it implies that the variability in timing of wind events and the associated changes in other meteorological variables rather than the magnitude of the wind may be more significant for transferring the climatic signal to the ecosystem. A combination of increased transfer of energy through wind mixing and surface cooling determine the variability of the stability of the mixed layer.

Additionally, the sensitivity of the simulated sulphur cycle to changes in air temperature has been investigated (Fig. 10b). Essentially, the response is linear over the range of changes explored (±3°C). For example increasing the air temperature by 2°C causes a 5% increase in DMSPp production and a 7% increase in the sea to air DMS flux, while a decrease of 2°C leads to a 4% decrease in DMSPp production and a 6% decrease in sea to air DMS flux. This is due to a combination of the physiological response of phytoplankton to temperature (growth rate increase with temperature) and the temperature dependence of the gas transfer rate through the Schmidt number (gas transfer increasing with temperature). The changes in DMSPp production balance the changes in sea to air flux of DMS, consequently there is little net change in the concentration of DMS.

Further analysis of the model's sensitivity to external forcing demonstrates that increasing the annual mean cloud cover from 0% to 100% (corresponding to a 72% reduction in the available light) results in a 13% reduction in gross DMSPp production (Fig. 10c). The reduction in gross DMSPp production decreases linearly with the increase in cloud cover. Similar behaviour is found for concentrations of DMSPd, DMS and the sea to air flux, the magnitude of the effect decreasing as the processes are further removed from the production term. Unsurprisingly this indicates that an increase in albedo may reduce DMSPp production. However the magnitude of this change is not as large as might have been expected and is buffered by the ability of model (and observed) phytoplankton to optimize their growth rates in response to changes in the light regime.

4. Discussion

DMS biogeochemistry is hypothesized to respond to changing climate, particularly elevated temperature (Charlson et al., 1987). One purpose of the present study was to establish the levels of interannual variability in DMS biogeochemistry and determine whether large-scale climatic indices could be detected amongst this variability. In the temperate, central North Sea modelled interannual variability in the mean spring and summer DMS sea to air flux rates (±30%) was higher than for the concentrations of DMS and DMSP or for the gross production of DMSP (±10%). (Fig. 4). Few observational data sets exist from which interannual variability of DMS biogeochemistry can be assessed. Low interannual variation in DMS seawater concentration was observed in the Equatorial Pacific between 1982 and 1996 (Bates and Quinn, 1997). This is despite large interannual variations in oceanic and atmospheric properties associated with three El Niño-Southern Oscillation events during this period. In contrast, in the temperate Southern Indian Ocean atmospheric measurements of DMS over a 10 yr period (1990–1999) showed up to 100% variation in mean monthly concentration (Sciare et al., 2000). These anomalies in atmospheric DMS concentration generally correlated with anomalies in sea surface temperature. These contrasting observations may be because variability in atmospheric DMS

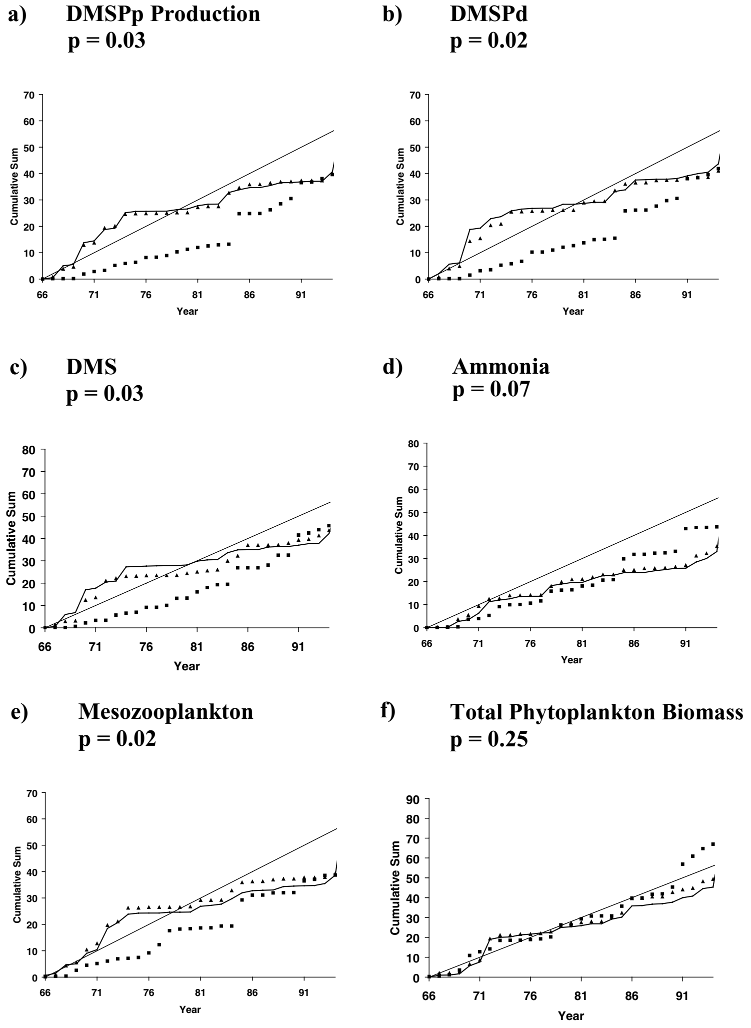


Fig. 6. CUSUM plots for the GSNW and modelled (a) gross production of DMSPp (mg S m^{-2} d^{-1}), (b) DMSPd (mg S m^{-3}), (c) DMS (mg S m^{-3}) (d) ammonia (mmol N m^{-3}), (e) mesozooplankton (mg C m^{-3}) and (f) total phytoplankton biomass (mg C m^{-3}). The thick solid line is the standard simulation, squares represent the simulation with constant wind forcing and triangles with constant cloud cover. The probability that the standard run occurs by chance is also given. The thin solid line indicates the random relationship.

concentrations are greater than occur within the surface seawater because sea to air flux is more variable (Fig. 4). More likely, they indicate substantial latitudinal variability in the key forcing factors controlling DMS biogeochemistry and how these forcing factors alter annually.

The North Atlantic and NW European shelf displays strong decadal changes in planktonic biomass (e.g. Reid et al., 1998). In particular the CPR shows strong decadal changes in the plankton colour index (PCI), and abundance of diatoms and dinoflagellates (Leterme et al., 2005); PCI and dinoflagellate abundance increase over time while diatom abundance decreases. Our simulations (Fig. 5a) show clear decadal variability in gross production of DMSP, with a significant change in sign occurring in the mid eighties (decreasing before 1985, increasing after) coincident with the observed regime shift in plankton in the North Sea (Reid et al., 1998). As different phytoplankton functional groups have differing DMSP to carbon ratios, we would expect climatically induced shifts in phytoplankton community structure to drive these changes in DMSP production. In a qualitative sense our model can capture the observed variability of some diatoms species, dinoflagellates and the PCI (Table 1). The discrete nature of CPR cell counts and inherent uncertainties in their conversion to carbon biomass precludes a quantitative comparison. The simulated decadal changes in DMSP production are at least in part due to changes in the model phytoplankton community structure; in particular the increasing flagellate contribution after 1985.

Indices such as GSNW and NAO are important for detecting climate change. If the impact of climate change is concealed by interannual variability correlation with large-scale climate indicators may provide a way of detecting it. Our results illustrate that there are at least two types of ecosystem response to climatic variations. The first case is typified by the NAO index where a few components of the ecosystem respond while most are hardly affected. In the second case a climatic signal (GSNW), which is spread broadly through the meteorological variables is picked up by a wide range of ecosystem components. Consequently, ecosystems can be more sensitive to a weaker signal (GSNW)

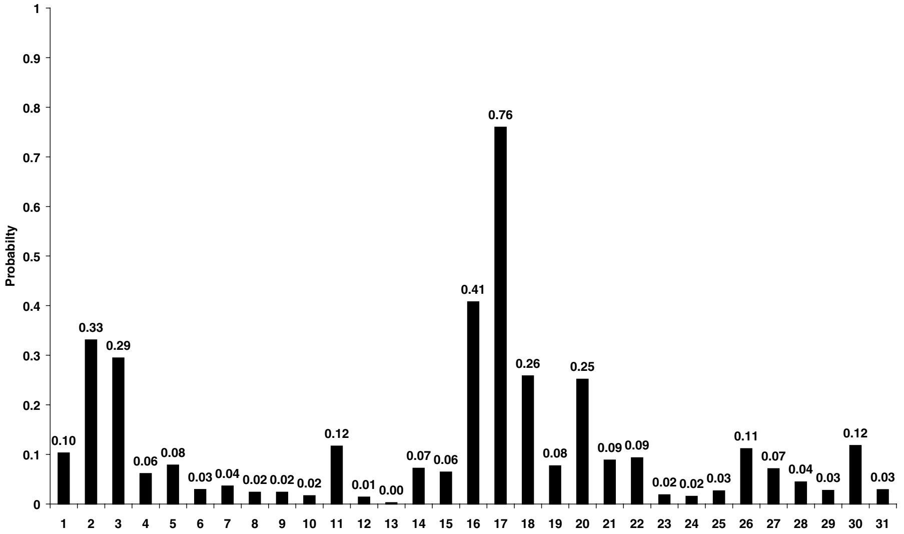
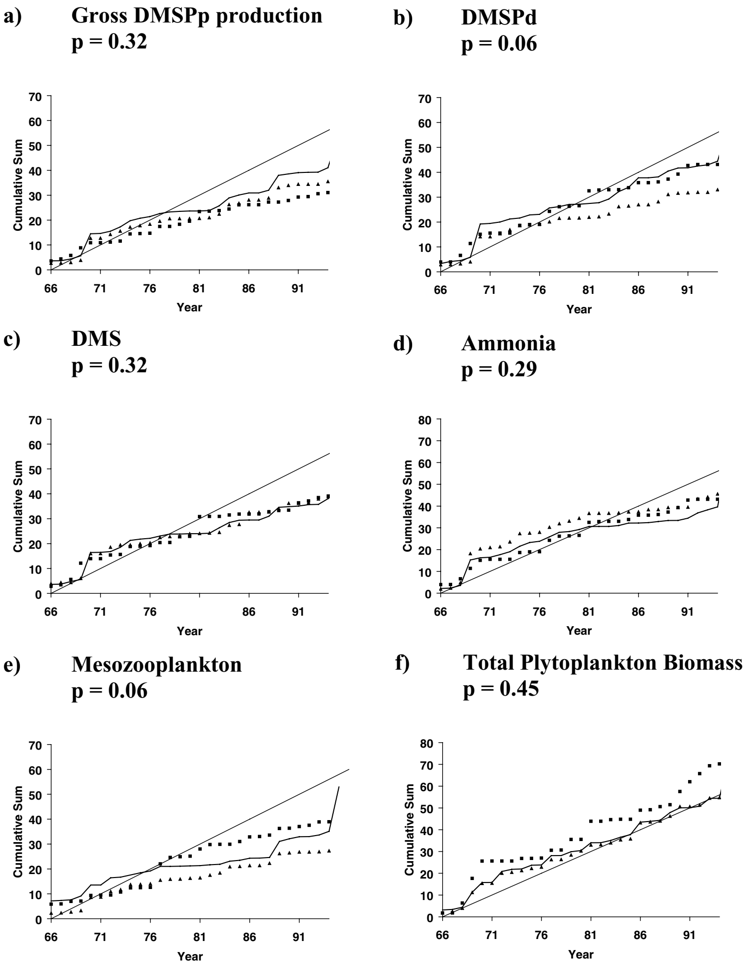


Fig. 7. Bar chart showing the probabilities that the CUSUM relationships with the GSNW occur by chance. (1) net primary production, (2) diatom production, (3) flagellate production, (4) picoplankton production, (5) large flagellate production, (6) bacterial production, (7) DMS consuming bacterial production, (8) DMSPd consuming bacterial production, (9) mesozooplankton, (10) Microzooplankton, (11) heterotrophic flagellate biomass, (12) phosphate, (13) nitrate, (14) ammonium, (15) silicate, (16) diatom biomass, (17) flagellate biomass, (18) picoplankton biomass, (19) large flagellate biomass, (20) total phytoplankton biomass, (21) bacterial biomass, (22) DMS consuming bacterial biomass, (23) DMSPd consuming bacterial biomass, (24) DMSPd, (25) DMS, (26) phytoplankton nitrogen uptake, (27) phytoplankton phosphate uptake, (28) ammonia release by zooplankton, (29) phosphate release by zooplankton, (30) bacterial phosphate demand, (31) gross production of DMSPp.

through many variables in the spring summer growing season than to a strong one (NAO) concentrated in the biologically less active winter season. The production of DMSPp and its consequent biological mediation to DMSPd and DMS primarily takes place in the spring and summer and consequently the GSNW signal is evident in these components. The sea to air exchange of DMS is primarily under wind control and unsurprisingly is related to the NAO index. CUSUM analysis demonstrates that a strong link between the NAO signal and wind speed (and hence DMS sea to air flux) persists through to the spring and summer.

Our results indicate that the GSNW signal is propagated in spring/summer through climatic conditions that have an instantaneous impact on planktonic ecosystems and DMS(P) cycling, while the NAO signal is generated from the persistence of winter conditions. The reason it does not dominate in the ecosystem model results was demonstrated by Taylor et al., 2002. The NAO most clearly represents the winter but the GSNW signal introduces a bias to various weather variables into the more ecologically significant seasons of the spring and summer. For instance, the presence of the NAO signal and the absence of the GSNW index in diatom biomass (Figs. 7 and 9) is because the modelled blooms take place in late winter before the GSNW becomes an important influence.

An important factor that may obscure correlations between climatic indices and DMS biogeochemistry is physiological adaptation by planktonic microbial communities. Cloud cover regulates the photosynthetically available radiation in the ocean and hence the maximum achievable production by phytoplankton. In most marine systems the ability of the phytoplankton to achieve this maximum production is constrained by the availability of nutrients, which in turn is controlled by the physical environment of the ocean. In the seasonally stratified shelf seas we are simulating, the stability of the summer thermocline is strongly influenced by buoyancy and shear production induced by interactions with the atmosphere. So for example, an increase in DMS production leading to increased cloud cover should result in a reduction in the maximum achievable phytoplankton production. At the same time it reduces the incident solar radiation, which potentially decreases the stability of the water column (reducing potential production if the enhanced mixing limits the time phytoplankton can spend in the light e.g. Huisman et al., 1999) and enhances the nutrient supply to the euphotic zone (increasing potential production e.g. Sharples et al., 2001). These effects are to some extent masked by the ability of both modelled and real phytoplankton to buffer change though adaptation to the ambient light field to optimize growth and through adjusting their internal C:N and C:P ratios according to the ambient nutrient availability. The influence of photosynthetic adaptation is shown in Fig 10c, where 100% cloud cover, a 72% reduction in available light, results in a decrease in DMSPp production of only 13%. The implication being that future attempts to predict the response of DMS(P) biogeochemistry to climate change should unlike previous attempts account for biological adaptations that potentially buffer the response to physical change.



a) Gross DMSPp production p = 0.32

b) DMSPd p = 0.06

c) DMS p = 0.32

d) Ammonia p = 0.29

e) Mesozooplankton p = 0.06

f) Total Plytoplankton Biomass p = 0.45

Fig. 8. CUSUM plots for the NAO and modelled (a) gross production of DMSPp (mg S m^{-2} d^{-1}), (b) DMSPd (mg S m^{-3}), (c) DMS (mg S m^{-3}) (d) ammonia (mmol N m^{-3}), (e) mesozooplankton (mg C m^{-3}) and (f) total phytoplankton biomass (mg C m^{-3}). The thick solid line is the standard simulation, squares represent the simulation with constant wind forcing and triangles with constant cloud cover. The probability that the standard run occurs by chance is also given. The thin solid line indicates the random relationship.

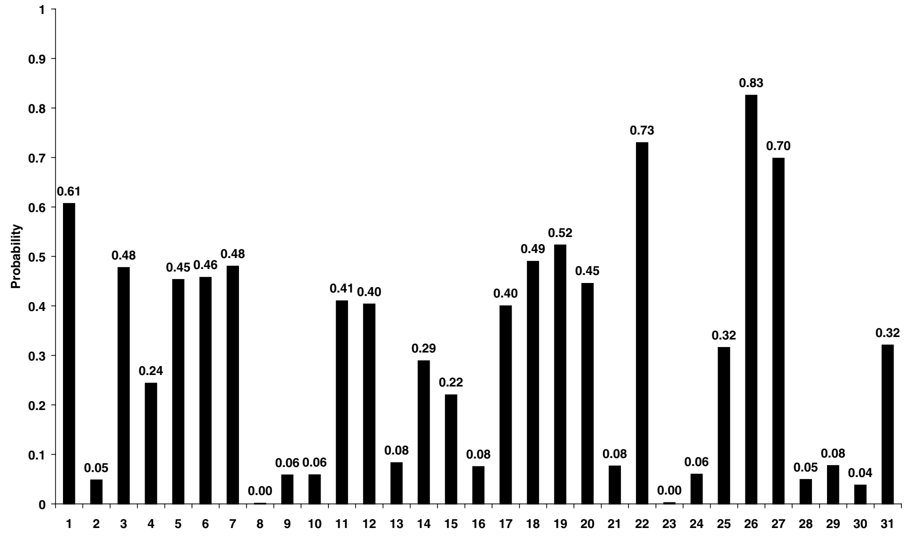


Fig. 9. Bar chart showing the probabilities that the CUSUM relationships with the NAO occur by chance. Nomenclature as in Fig. 6.

Table 2. Number of variables showing a probability of less than 10% of a random CUSUM relationship with the climate indices

	Standard	Constant cloud Variable wind	Constant wind Variable cloud
GSNW	21	8	2
NAO	12	10	12

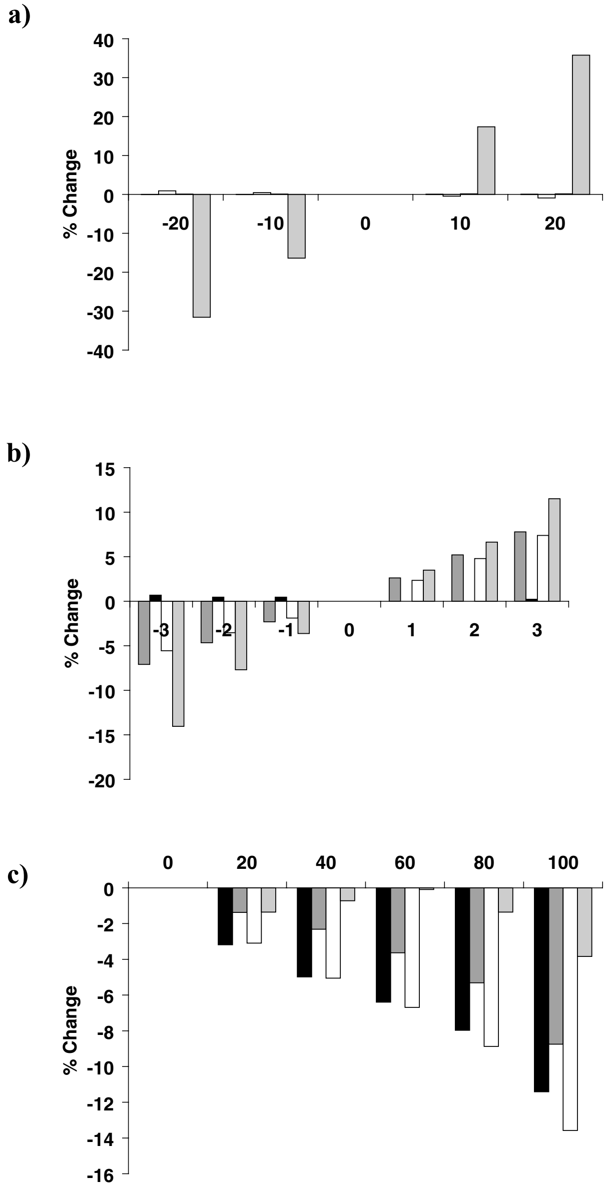


Fig. 10. Sensitivity of DMS(P) concentration, DMSPp production and sea air exchange to (a) wind, (b) temperature and (c) cloud cover expressed as the % change in the seasonal total with reference to the standard (1977) for (a) and zero cloud cover for (c). DMS (black), DMSPd (dark grey), gross production of DMSPp (white) and sea air flux of DMS (light grey).

5. Acknowledgments

This work was undertaken as a part of the core strategic research program of the Plymouth Marine Laboratory, which is funded by the UK Natural Environmental Research Council. We would like to thank R. Torres (PML) for the ensemble sensitivity analysis of the model to initial conditions.

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