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**Carbon and nutrient  
cycling in the  
Norwegian Sea**

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# Carbon and nutrient mixed layer dynamics in the Norwegian Sea

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## Abstract

A coupled carbon-ecosystem model is compared to recent data from Ocean Weather Ship M (66° N, 02° E) and used to investigate nutrient and carbon processes within the Norwegian Sea. Nitrate is consumed by phytoplankton in the surface layers over the summer; however the data show that silicate does not become rapidly limiting for diatoms, in contrast to the model prediction and in contrast to data from other temperate locations. The model estimates atmosphere-ocean CO<sub>2</sub> flux to be 37 g C m<sup>-2</sup> yr<sup>-1</sup>. A detailed comparison of the carbonate system at other ocean locations reveals that although coccolithophore blooms occur at OWS M, they are not as prevalent here as other areas. The seasonal cycles of calcite saturation state and [CO<sub>3</sub><sup>2-</sup>] are similar in the model and in data: values range from ~3 and ~120 μmol kg<sup>-1</sup> respectively in winter, to ~4 and ~170 μmol kg<sup>-1</sup> respectively in summer. The timing of coccolithophore blooms within the year therefore coincides with a time of high calcite saturation state, as predicted by previous modelling work.

## 1 Introduction

The Norwegian Sea (Fig. 1) is an important high latitude region for processes including uptake and sequestration of CO<sub>2</sub>, primary production and large-scale ocean mixing. As with many other high latitude locations the mixed layer depth undergoes large seasonal fluctuations forcing seasonal dynamics of biology and chemistry in the upper ocean (Nilssen and Falck, 2006). High concentrations of nutrients in winter (nitrate >12 μmol L<sup>-1</sup>, phosphate >0.9 μmol L<sup>-1</sup> and silicate >5.5 μmol L<sup>-1</sup>, Dale et al., 1999) are reduced to low levels in the surface layer by consumption during spring and summer. Interannual variations in observations give a range of nitrate summer concentrations between near 0 μmol L<sup>-1</sup> and 2 μmol L<sup>-1</sup> (Kohly, 1998; Haupt et al., 1999, Dale et al., 1999). The lack of full depletion of nitrate in summer compared to other temperate sites (e.g. NABE (47° N, 20° W); OWS I (59° N, 19° W)) has been the subject of

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much speculation and two main hypotheses have been put forward to explain this phenomenon: 1) diatoms are present in low numbers and are limited by rapid consumption of silicate and hence do not bloom to the same magnitude as other areas (Dale et al., 1999); 2) large populations of grazers, both macro- and micro-zooplankton, rapidly consume the phytoplankton (Taylor et al., 1993).

The eastern Bering Sea is another high-latitude site that has been used to investigate the associated dynamics of plankton and carbonate systems. A detailed understanding of how plankton and carbonate interact with each other in the real ocean is of interest for predicting how the ocean will respond to ongoing and future ocean acidification. Merico et al. (2006)'s model study assessed the possible links between success of the coccolithophore *Emiliania huxleyi* in the natural environment and the ambient values of carbonate ion concentration ( $[\text{CO}_3^{2-}]$ ) following an earlier investigation addressing which environmental conditions may have contributed to the large *E. huxleyi* blooms in the eastern Bering Sea from 1996 to 2000 (Merico et al., 2004). Although the model calculated only minor interannual changes in calcite saturation state ( $\Omega_{\text{cal}}$ ), which were not thought to have caused the interannual differences in patterns of *E. huxleyi*, there did appear to be a possible link between the  $\Omega_{\text{cal}}$  and *E. huxleyi* success (Fig. 2). They predicted a sharp rise in  $[\text{CO}_3^{2-}]$  and  $\Omega_{\text{cal}}$  as a result of the spring blooms, leading to higher values in summer than in winter. Although  $[\text{CO}_3^{2-}]$ ,  $\Omega_{\text{cal}}$ ,  $\text{pCO}_2$ , etc. can be calculated from total dissolved inorganic carbon ( $C_T$ ) and total alkalinity ( $A_T$ ), very little data were available from the eastern Bering Sea to validate and test these hypotheses. The presence of a time series site in the Norwegian Sea (Ocean Weather Ship M (OWS M) at  $66^\circ \text{N}$ ,  $02^\circ \text{E}$ , Fig. 1) makes it ideal for further investigating the interactions between phytoplankton and the cycling of carbon and nutrients, which we carry out here using both data and modelling.

Seasonal fluctuations in  $C_T$  result from a combination of removal by photosynthesis and addition from respiration, mixing and ingassing from the atmosphere (Skjelvan et al., 2005). The process of biological precipitation of calcium carbonate ( $\text{CaCO}_3$ ) by calcifying organisms such as coccolithophores additionally impacts on the  $C_T$  dynamics

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(Najjar, 1992). Coccolithophores are present in the Norwegian Sea in low numbers during winter and spring with densities increasing in early summer (June) after the diatom bloom (Andruleit, 1997); with peaks up to  $3 \times 10^6$  coccospheres  $L^{-1}$  (Baumann et al., 2000). The seasonal succession of phytoplankton could play an important role in determining the cycling of carbon and nutrients.

This study aims to use an adaptation of Merico et al. (2006)'s model as a tool to investigate carbon and nutrient dynamics in the Norwegian Sea. Of particular interest are the relative influence of the physical system (including SST, SSS and MLD) compared to the biological system (including phytoplankton succession, growth rates, and zooplankton grazing rates) on the cycling of carbon and nitrate. Specifically, we consider the controls on nitrate and silicate consumption rates over the summer, phytoplankton succession and the seasonal and interannual patterns of the carbonate system, and test the hypothesis that coccolithophore success occurs at times of high calcite saturation state. The model outputs are compared to data from OWS M, satellite data and outputs of other models.

## 2 Methods

### 2.1 Model description

Merico et al. (2006)'s two-layer, time-dependent, coupled biological-physical-carbon model is adapted here to represent the Norwegian Sea, with specific reference to the location of OWS M. The main adaptations made relate to the physical conditions (i.e. the forcing conditions) and the parameterisation of the ecosystem values. They are described in more detail below.

The model is formulated as a bi-layer ocean system consisting of an upper, biologically active mixed layer (down to a seasonal thermocline), which contains phytoplankton, zooplankton and a limited amount of nutrients and chemical constituents; and a lower layer, containing no biology, but a source of nutrients and chemical constituents.

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The model also incorporates an atmospheric layer, with which air-sea fluxes of carbon dioxide can take place depending on the CO<sub>2</sub> partial pressure differences between the atmosphere and the surface water (Fig. 3).

The system of ordinary differential equations is solved numerically using a Fourth-order Runge-Kutta method with a time step of one hour and was run over a period of four years to allow the state variables to reach repeatable seasonal cycles and thus minimise the dependency of the results on the initial conditions. For the state variable equations readers are referred to Appendix A in Merico et al. (2006).

### 2.1.1 The physical system (physical forcing data are given in Fig. 4)

The two-layer water column model used here is influenced simply by vertical advection and does not include any horizontal advection. This approximation, as this study will demonstrate, is suitable for assessing average annual dynamics as the location of OWS M encompasses the North Atlantic inflow, which is not thought to vary greatly through the seasons (Oliver and Heywood, 2003; Orvik and Skagseth, 2003). However it may not be appropriate for smaller scale interpretations of individual events within a year period because of incursions of coastal water.

The biological activity was considered to take place in the upper mixed layer, while in the bottom layer, nutrient concentrations (nitrate (N<sub>0</sub>), silicate (Si<sub>0</sub>) and ammonium (A<sub>0</sub>)) and carbon state variables (C<sub>T0</sub> and A<sub>T0</sub>) were kept constant throughout the year. Nutrients were supplied to the upper layer by entrainment or diffusive mixing across the interface using the same method of Fasham (1993).

The model was forced with a variable mixed layer depth, calculated from monthly Levitus climatologies at the location of OWS M and linearly interpolated with time for each annual cycle (2002–2005). Annual sea surface PAR was calculated using astronomical formulae (taking into account latitude, daily sinusoidal variation in radiation and a fixed cloud cover parameter). This does not capture the short-term changes in cloud cover and mixing events that occur in natural systems and therefore represents approximate values for each annual cycle. The light limited growth for each phyto-

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plankton group was determined using a Steele's function, which includes the potential for saturation and inhibition of phytoplankton growth at high light levels. Initial investigations revealed that flagellate populations reached unrealistically high abundances when a simple Michaelis-Menten function for light limited growth was used. The effect of sea surface temperature (SST) on phytoplankton growth was simulated using Eppley's formulation (Eppley, 1972) and both sea surface salinity (SSS) and SST were used within the carbon system. Values were taken from OWS M averaged monthly data and linearly interpolated for each annual cycle. Wind speed data were taken from averaged daily recordings at OWS M.

### 2.1.2 The ecosystem

Phytoplankton were split into four groups: diatoms, dinoflagellates, flagellates and coccolithophores (*Emiliania huxleyi*). They were originally grouped in this way because they represented the most common species found in the Bering Sea (Merico et al., 2006). This appears to also be the case for the Norwegian Sea.

Zooplankton were split into two groups, these are microzooplankton and mesozooplankton. This distinction is important when considering more than one phytoplankton group because diatoms, dinoflagellates and microzooplankton are the food sources for mesozooplankton; whereas flagellates and *E. huxleyi* are the food sources for microzooplankton. Furthermore, although mesozooplankton, particularly copepods, have been well studied in the Nordic Seas (Dale et al., 2001; Halvorsen et al., 2003) and it is widely acknowledged that they have an important role in transferring energy to higher levels of the food web, they may be of secondary importance in terms of grazing of phytoplankton, and hence carbon flux, when compared to microzooplankton. There is a lack of microzooplankton grazing studies in the Norwegian Sea, yet reports from other areas suggest that microzooplankton impact significantly on phytoplankton populations (e.g. Burkhill et al., 1993; Calbet and Landry, 2004) and are the major loss term.

The Bering Sea model included a switching parameter for grazing rate on *E. huxleyi* and diatoms determined by the silicate concentration. When silicate was low diatoms

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are assumed to be unable to produce highly silicified tests and become more vulnerable to grazers, therefore microzooplankton switch feeding from *E. huxleyi* to diatoms when silicate is less than  $3 \mu\text{mol L}^{-1}$ . There is little evidence from data to back up this intuitive assumption of switching in the Norwegian Sea; however, mesocosm experiments have shown that diatom dominance ceases when silicate concentration fall below  $2\text{--}3 \mu\text{mol L}^{-1}$  (Egge and Aksnes, 1992). There is a relatively low silicate concentration year-round within the Norwegian Sea so it may be that there is little variation in grazer selection. However this assumption was left in the model and tests are carried out of the sensitivity of the *E. huxleyi* and diatom populations to this grazing assumption.

Silicate and nitrate are the two main nutrients modelled here. Phosphate was not included because preliminary data analysis of OWS M data suggested that phosphate levels were not limiting.

The primary objectives of this study are to investigate the nutrient and carbon cycling within the Norwegian Sea, rather than to accurately model the phytoplankton and zooplankton processes. However, some biological detail is necessary in order to represent biological impacts on nutrient and carbon cycles, and thus the ecosystem is constrained to approximately fit the data, while at the same time acknowledging considerable uncertainty over how to correctly represent competition between different phytoplankton functional groups (Anderson, 2005).

### 2.1.3 The carbonate system

The carbonate system is forced by deep total alkalinity ( $A_{T0}$ ), deep total dissolved inorganic carbon ( $C_{T0}$ ) and atmospheric  $\text{pCO}_2$  ( $\text{pCO}_2^{(\text{atm})}$ ).  $\text{pCO}_2^{(\text{atm})}$  was calculated as an interpolated trend taken from the annual cycle of atmospheric  $\text{CO}_2$  and then adjusted to a mean annual value of 377 ppm (averaged from OWS M observations for the time period 2002–2005; Tans and Conway, CDIAC) following the suggestion from Bellerby et al. (2005) that there is a seasonal fluctuation in  $\text{pCO}_2^{(\text{atm})}$ . Omitting this seasonal fluctuation leads to the flux of  $\text{CO}_2$  into the ocean during the summer period

being overestimated.

$C_T$  is removed from the upper layer of the water column by the consumption of inorganic carbon by phytoplankton but is added by respiration of organic material.  $C_T$  is also influenced by air-sea  $\text{CO}_2$  exchange with the atmosphere and by  $\text{CaCO}_3$  formation and dissolution. Seawater  $\text{pCO}_2$  was calculated from model variables of  $A_T$ , SST, salinity and  $C_T$  along with apparent dissociation constants of carbonic acid, boric acid, the solubility of  $\text{CO}_2$  and the hydrogen ion activity by using the iterative method presented by Peng et al. (1987). Changes in surface  $A_T$  were simply computed as the balance between calcification, dissolution and diffusive mixing; the effects of nitrate were not included.

## 2.2 Data analysis

The data were collected every month from January 2002 to December 2005 from the Norwegian Sea at Ocean Weather Station M, located at  $66^\circ \text{N}$ ,  $02^\circ \text{E}$  on the continental slope (Skjelvan et al., 2007; F. Rey, personal communication, 2007). Data used here includes nitrate concentration, silicate concentration, temperature, salinity,  $C_T$  and  $A_T$  and represents the values at depth  $\leq 20 \text{ m}$ .

## 3 Results

### 3.1 The standard run

#### 3.1.1 The nutrients

The OWS M data show that nitrate (Figs. 5a–c) is removed from the surface layer after  $\sim \text{JD } 120$  (April) at a rate of about  $183 \text{ mmol m}^{-3} \text{ d}^{-1}$  and becomes limiting (i.e.  $< 1 \text{ mmol m}^{-3}$ ) by  $\sim \text{JD } 180$  (July). Nitrate remains at relatively low concentrations until  $\sim \text{JD } 240$  when there is a more gradual increase ( $\sim 0.12 \text{ mmol m}^{-3} \text{ d}^{-1}$ ) as a result of cross-thermocline mixing and entrainment from the deep ocean as stratification

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breaks down. Maximum values are not reached until January. There is some interannual variability in the surface nitrate data during the summer seasons; however it does appear to reach  $<1 \text{ mmol m}^{-3}$ .

Silicate (Figs. 5d–f) decreases slowly during the spring and summer (at a rate of  $\sim 0.005 \text{ mmol m}^{-3} \text{ d}^{-1}$ ), reaching a minimum by August but almost immediately increasing again, while in another year (2005) it can be seen to decrease more rapidly ( $\sim 0.13 \text{ mmol m}^{-3} \text{ d}^{-1}$ ) but then fluctuate between  $1 \text{ mmol m}^{-3}$  and  $2 \text{ mmol m}^{-3}$  over the summer before increasing back to the winter maximum.

The standard run of the model (Fig. 5) demonstrates a similar pattern of nitrate consumption. Concentration decreases relatively rapidly during spring, remaining at relatively low concentrations over the summer and then slowly increasing back to the winter maximum value. The standard run is not able to reproduce the slow decline in silicate seen in 2002 and 2003, but is able to reproduce the more typical rapid decline in silicate as a result of diatom consumption seen in many other temperature locations (e.g. Larsson et al., 2001, Merico et al., 2004, Takahashi et al., 1993) and seen in the Norwegian Sea data in 2005.

### 3.1.2 The carbonate system

Figure 6 shows the standard run of the atmospheric and surface water  $\text{pCO}_2$  alongside data points from Gislefoss et al. (1998). The data points are from 1993 and 1994 and hence are at lower  $\text{pCO}_2$  than this model is set to. Modelled output has therefore been shifted down to demonstrate the similarities between the pattern and magnitude of the seasonal cycle. Figure 6 illustrates the atmospheric and surface water  $\text{pCO}_2$  when there are no coccolithophores present in the model (blue dots) and when all biology is turned off in the model (thin dashed line).

The model demonstrates clearly the role of biology in the seasonal cycle of the carbonate system. When biology is turned off  $A_T$  remains constant throughout the year (“no bio” in Fig. 7). Without biology, the slight increase in  $[\text{CO}_3^{2-}]$  over the summer period occurs as a result of loss of  $\text{CO}_2$  to the atmosphere, and the seasonal amplitude

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of calcite saturation state is small (0.4 units).  $p\text{CO}_2$  in the surface water decreases and increases with temperature over the seasons, with a peak ( $>400 \mu\text{atm}$ ) in August (JD 225), before declining again as SST decreases into winter (Fig. 6). In the run without biology again, the partial pressure in the surface waters is above the atmospheric partial pressure for most of the summer period, giving a net flux of  $\text{CO}_2$  out of the surface layer into the atmosphere.

With the biology included, the dynamics are very different (Figs. 6 and 7). Phytoplankton bloom over the spring and summer period consuming  $C_T$  from the surface layer. This consumption of carbon dioxide during photosynthesis causes a decrease in  $p\text{CO}_2$  in the surface water that is sufficient to keep the partial pressure below that of the atmosphere for the majority of the year, despite the warming of surface waters, in agreement with recent in situ observations of  $p\text{CO}_2$  at OWS M (data not shown).

$[\text{CO}_3^{2-}]$  and  $[C_T]$  in the standard run (with biology, SR in Fig. 7) follow similar patterns to the data:  $[\text{CO}_3^{2-}]$  increases over the summer period (from  $\sim 120$  to  $\sim 170 \mu\text{mol kg}^{-1}$ ) as a result of biological consumption of  $C_T$ . This causes an increase in  $\Omega_{\text{cal}}$  from about 3 to 4 following the spring bloom.  $A_T$  and carbonate ion data have large interannual variability, which is not easily replicated by the model. Modelled  $A_T$  and  $[\text{CO}_3^{2-}]$  are both low in years 2004 and 2005 compared to the data, at least when coccolithophores are included (SR in Fig. 7). This could imply that coccolithophores blooms did not occur during these years. During the coccolithophore growth period over the late summer in 2002 and 2003, there is a decrease in model  $A_T$  by about  $38 \mu\text{Eq kg}^{-1}$ , matching the data, as a result of  $\text{CaCO}_3$  formation by production of coccoliths.

### 3.2 Sensitivity analysis

There are some discrepancies between the standard run model output and the data – most notably the silicate removal in spring. The following sensitivity analyses were carried out to establish if the model could produce a better fit under different scenarios of forcing, grazing and growth rates. The sensitivity analysis also demonstrates why

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the standard parameters were chosen.

### 3.2.1 C: N ratio

It has recently been argued that the original Redfield ratio of C:N is not correct for all circumstances (Takahashi et al., 1985; Sambrotto et al., 1993; Anderson and Sarmento, 1994; Brostrom, 1998; Kahler and Koeve, 2001; Kortzinger et al., 2001; Falck and Anderson, 2005). Model sensitivity for C:N ratio demonstrated that a ratio of 1:6.6 (C:N) underestimated the  $C_T$  consumption over the summer period (Figure 8). When the ratio was increased to 1:9 the fit was much closer; and a high ratio (1:12) overestimated the carbon system values. A ratio of 1:9 was therefore considered the most appropriate and was used in the standard run and all further analyses.

### 3.2.2 Mixed layer depth

The MLD varies interannually; the timing and rate of shoaling of the mixed layer combined with levels of irradiance determines when the spring bloom occurs and its magnitude. Figure 9 shows three simulations of MLD: a rapidly shoaling and deepening mixed layer (MLD1) and a slowly shoaling and deepening mixed layer (MLD2) and an intermediate mixed layer (SR). MLD1 does not greatly alter the system during the spring bloom because at this time phytoplankton are limited by light; however the more rapid deepening in autumn stimulates an autumn phytoplankton bloom which maintains the nutrients and  $C_T$  at lower concentrations for a longer period into winter. MLD2 slows the shoaling of the mixed layer and hence the phytoplankton remain below the critical depth for a longer period of time. Alternative MLD variations do not improve the agreement with data and so are not used.

### 3.2.3 Growth rate of diatoms and flagellates

The OWS M data suggests that consumption of nitrate and silicate does not occur at equal rates as would be expected for a spring bloom dominated by diatoms. In fact

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silicate is depleted much more slowly. In order to assess why this happens the growth rates for flagellates and diatoms were both increased and decreased by 50% of the standard parameter (Fig. 10). When the growth rates are lower the diatoms are inhibited from blooming, the flagellates then bloom later, along with a larger coccolithophore bloom (~JD 160 compared to ~JD 140) causing a greater overall increase in chlorophyll than during the SR (~9.5 mg Chl m<sup>-3</sup> compared to ~5.5 mg Chl m<sup>-3</sup>). Silicate is not reduced until later in the summer when diatoms are finally able to bloom. Nitrate does not reach low concentrations over the summer as a result of the limited population growth. High growth rate allows the populations to bloom earlier in the spring (~JD 110, ~7 mg Chl m<sup>-3</sup>), rapidly depleting both nitrate and silicate. The high growth rate causes the phytoplankton and zooplankton to fall into tightly coupled predator-prey cycles.

### 3.2.4 Grazing

Microzooplankton and mesozooplankton occur at different times over the annual cycle. Microzooplankton are set to graze more efficiently on coccolithophores when the silicate concentration is >3 μM but then switch to grazing on diatoms when the silicate concentration falls below 3 μM. Silicate is low in the Norwegian Sea (~5 mmol m<sup>-3</sup> compared to ~30 μM prior to the spring blooms in the Bering Sea) therefore the switching becomes almost irrelevant. Mesozooplankton concentration is low and is food-limited mainly by the dinoflagellate population. With no grazers (i.e. all grazing rates set to zero in the model; Fig. 11) the nutrients follow a similar pattern over the annual cycle, except that they are maintained at limiting concentrations over the summer by the uncontrolled phytoplankton. There are, however, differences within the phytoplankton: the diatom bloom is similar in spring but have a second growth period in late summer (between JD 220 and JD 270); flagellates grow uncontrolled and become nitrate limited after JD 150 although their population declines only slowly throughout the summer maintaining nitrate at low levels. Dinoflagellates and coccolithophores are out-competed by the flagellates with no apparent growth over the year.

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## 4 Discussion

### 4.1 The ecosystem and nutrient dynamics

Previous data suggest that in some years Norwegian Sea nitrate concentrations never reach limiting levels, while in other years nitrate is fully depleted but not until later in summer (Kohly, 1998; Dale et al., 1999; Haupt et al., 1999). Various hypotheses have been proposed to explain this phenomenon including grazer levels (Taylor et al., 1993) and silicate-limited growth of diatoms (Dale et al., 1999). The OWS M data examined here suggest that there is interannual variation in the magnitude and timing of nitrate depletion which simply reflects the timing and magnitude of the spring bloom. In the model, diatoms are limited primarily by rapidly depleting the already low silicate concentration in spring, which results in them only having a relatively short bloom. After this, flagellates bloom and continue the nitrate depletion. Nitrate depletion can be delayed by both the time between phytoplankton blooms and the lack of large populations over the summer period. However the OWS M data do not necessarily agree with these simulations: silicate is not rapidly consumed, implying that either the diatoms are not rapidly blooming or that there is an influx of silicate which is able to counterbalance any rapid consumption. Neither the model nor the current data agree with previous observations that nitrate is not depleted in the summer months in some years. Minimum nitrate for 2002, 2003 and 2005, respectively, is 0.44, 0.50, and 0.63 mmol N m<sup>-3</sup> in the model and 0.26, 0.02, and 0.18 mmol N m<sup>-3</sup> in the data (Fig. 5).

This behaviour at OWS M is somewhat at odds with the most commonly observed pattern in temperate and sub-polar waters during spring: that nitrate and silicate are rapidly depleted as a consequence of intense phytoplankton blooms. Such a situation is seen in (1) the eastern Bering Sea (Merico et al., 2004), (2) the Irish Sea (Tyrrell et al., 2005), (3) the Baltic Sea (Larsson et al., 2001), and (4) the North Atlantic south of Iceland at about 60° N (Takahashi et al., 1993). On the other hand the Norwegian Sea data are more similar to concentrations observed during the North Atlantic Bloom Experiment (NABE) at 47° N, 20° W (Fasham et al., 2001; Takahashi et al., 1993). Al-

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though the data in Fig. 9 suggest that, in the Norwegian Sea, nitrate does get depleted to limiting levels each summer, the slow exhaustion rates of nitrate and, especially, silicate, are atypical compared to most other locations, and the peak springtime chlorophyll concentrations ( $\leq 3 \text{ mg chl-}a \text{ m}^{-3}$ ) are quite low compared to the other locations e.g.  $16 \text{ mg chl-}a \text{ m}^{-3}$  in the eastern Bering Sea and  $\sim 12 \text{ mg chl-}a \text{ m}^{-3}$  in the Irish Sea.

Analysis of longer term datasets for this area agree with these findings (F. Rey, personal communication, 2007). They suggest that the preferential grazing of zooplankton on diatoms may explain the relatively slow depletion of silicate. However, the selective grazing function in our model cannot account for the low chlorophyll levels and studies have shown that the dominant zooplankton grazers in the Norwegian Sea, *Calanus helgolandicus* and *Calanus finmarchicus* (Gaard, 2000) both have reduced reproductive output during diatom dominated blooms and hence preferentially graze on non-diatom species (Nejstgaard et al., 2001).

The data from OWS M clearly show that it is not a full High Nutrient Low Chlorophyll (HNLC) area, as, although peak chlorophyll concentrations are low, nutrient concentrations do fluctuate considerably across the seasonal cycle. However, the chlorophyll levels observed in the Norwegian Sea are more representative of those seen in HNLC areas, for example, the Subarctic Northeast Pacific (OWS P), which has constant low chlorophyll levels ( $< 3 \text{ mg chl-}a \text{ m}^{-3}$ ) throughout the annual cycle (Tyrrell et al., 2005).

Previous work suggests that phytoplankton growth in spring in the North Atlantic is influenced by levels of iron (Moore et al., 2006). This raises the question as to whether spring blooms at OWS M could also be restrained by low levels of iron in some years. OWS M lies on the continental slope and is subject to different conditions to shelf seas, but is also not an open ocean system. One possible explanation of the low chlorophyll levels and slow/incomplete nutrient depletion in some years could be that iron scarcity inhibits large phytoplankton blooms during some years but not others. The interannual variability could thus potentially be explained by the advection of coastal waters across OWS M only in some years (this often occurs around August time, as determined from sea surface salinity measurements). Coastal and shelf waters typically have higher

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iron content due to iron release from sediments (e.g. Aguilar-Islas et al., 2007).

## 4.2 Local CO<sub>2</sub> sink strengths

The annual cycle of carbon dioxide partial pressure in the surface waters ( $p\text{CO}_{2(SW)}$ ) has been explored here. At the start of the year  $p\text{CO}_{2(SW)}$  decreases as result of the colder water temperatures and the continued vertical exchange of carbon that carries on until the summer pycnocline has formed. The spring bloom rapidly consumes CO<sub>2</sub> from the surface water and hence decreases the partial pressure, (by up to 100  $\mu\text{atm}$ ) (Fig. 6). The removal of  $p\text{CO}_{2(SW)}$  occurs throughout the summer until the breakdown of stratification and the end of biological production.

For the first part of the year until the end of the biological production period, the waters act as a sink for carbon dioxide, with an average model CO<sub>2</sub> flux of 37 g C m<sup>-2</sup> yr<sup>-1</sup> from the atmosphere to the surface water. Falck and Anderson (2005) calculated a flux of CO<sub>2</sub> of 32 g C m<sup>-2</sup> yr<sup>-1</sup> for OWS M data during 1991 – 1994 and Skjelvan et al. (2005) suggest 20 g C m<sup>-2</sup> yr<sup>-1</sup> for the Norwegian Sea. Other estimates for the Nordic Seas area include a flux of 53 g C m<sup>-2</sup> yr<sup>-1</sup> into the Greenland Sea (Anderson et al., 2000) and 69 g C m<sup>-2</sup> yr<sup>-1</sup> into the Iceland Sea (Skjelvan et al., 1999). The model has demonstrated that without biological production occurring over the summer period there would only be a flux into the surface waters during the winter months when temperatures are low. The variability in fluxes between locations in the Nordic Seas may result from the varying amounts of primary production, the varying hydrographic conditions and/or the different water masses occurring at each location.

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## 4.3 Comparison to other carbonate system measurements in waters with abundant coccolithophores

### 4.3.1 Alkalinity

Robertson et al. (1994), in the North Atlantic, south of Iceland, gives  $A_T$  values within areas that do not have coccolithophores present of about  $2330 \mu\text{Eq kg}^{-1}$  (comparable to the modelled winter values in the Norwegian Sea:  $2320 \mu\text{Eq kg}^{-1}$ ). Areas where coccolithophore blooms had occurred, gave lower  $A_T$  values (lowest  $A_T < 2290 \mu\text{Eq kg}^{-1}$  at approximately  $63^\circ\text{N}$ ,  $22^\circ\text{W}$ ). This implies that areas harbouring intense coccolithophore blooms should experience reductions in  $A_T$  of about  $50\text{--}60 \mu\text{Eq kg}^{-1}$ . The decrease in alkalinity by  $38 \mu\text{Eq kg}^{-1}$  obtained from the Norwegian Sea model implies that there are relatively small blooms of coccolithophores present in late summer. Satellite data confirm this view: SeaWiFS derived calcite concentrations for the OWS M location range from about  $0.5 \text{ mmol CaCO}_3\text{-C m}^{-3}$  in winter to a maximum of  $4 \text{ mmol CaCO}_3\text{-C m}^{-3}$  in summer in some years (SeaWiFS Project, 2006). These values are in agreement with values of modelled calcite, produced as free coccoliths (range from  $0 \text{ mmol C m}^{-3}$  to  $3.5 \text{ mmol C m}^{-3}$ ). Interestingly, SeaWiFS images show that coccolithophore blooms commonly occur along the Norwegian coast but sometimes also extend out as far as the shelf break where OWS M is situated (SeaWiFS Project, 2006).

### 4.3.2 Dissolved inorganic carbon

$C_T$  concentration in the Norwegian Sea in winter was about  $2140 \mu\text{mol kg}^{-1}$ , while in June-July it was about  $2080 \mu\text{mol kg}^{-1}$ , which is a similar value to non-coccolithophore bloom areas in July 1991 in the North Atlantic (Robertson et al., 1994). The lowest  $C_T$  concentration reached in the Norwegian Sea was about  $2050 \mu\text{mol kg}^{-1}$ , again similar to values measured south of Iceland. Takahashi et al. (1993) show that in the northeastern North Atlantic  $C_T$  declined by about  $60 \mu\text{mol kg}^{-1}$  during the phytoplank-

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ton bloom period in late March through to late May (during the North Atlantic Bloom Experiment study in 1989).

#### 4.3.3 Partial pressure of CO<sub>2</sub>

Holligan et al. (1993) use data from the same cruise as Robertson et al. (1994) and propose that coccolith production caused a relative increase of up to 50  $\mu\text{atm}$  in  $\text{pCO}_{2(SW)}$  in association with  $A_T$  and  $C_T$  changes. The model of Merico et al. (2006), calculated an increase in  $\text{pCO}_2$  of about 40  $\mu\text{atm}$  associated with coccolithophore blooms in the eastern Bering Sea. Takahashi et al. (1993) measured a spring bloom reduction in  $\text{pCO}_{2(SW)}$  of about 60  $\mu\text{atm}$  in the northeastern North Atlantic. Murata (2006) addressed the cause-and-effect relationships associated with coccolithophore blooms and changes in  $\text{pCO}_2$ , demonstrating that  $\text{pCO}_2$  decreases only by 18  $\mu\text{atm}$  during a coccolithophore bloom compared with nearly 150  $\mu\text{atm}$  during a diatom bloom. Results in this study concur with the suggestion that where large coccolithophore blooms occur the local area may become a reduced sink of atmospheric CO<sub>2</sub>.

#### 4.3.4 Carbonate ion and calcite saturation state

Merico et al. (2006) modelled the seasonal cycle of carbonate chemistry in the eastern Bering Sea (specific location: 56.8° N, 164° W). The model calculated considerable seasonal variation in both carbonate ion (winter  $\sim 100 \mu\text{Mol kg}^{-1}$ , summer  $\sim 150 \mu\text{Mol kg}^{-1}$ ) and calcite saturation state (winter  $\sim 2.5$ , summer  $\sim 3.5$ ). Both variables were low in winter, rose sharply at the time of the spring blooms, and then stayed high during the summer until declining in autumn due to mixing. There was, however, a lack of data with which to test these model results in the eastern Bering Sea. In contrast, data are available for model comparison in this study. Our results from the Norwegian Sea shelf break (Ocean Weather Station M, 66° N, 2° E), agrees in outline with the model predictions for the eastern Bering Sea (compare Figs. 2 and 7). The Norwegian Sea data also show a seasonal oscillation in carbonate ion concentration (winter  $\sim 130 \mu\text{Mol}$

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$\text{kg}^{-1}$ , summer  $\sim 180 \mu\text{Mol kg}^{-1}$ ) and in calcite saturation state (winter  $\sim 3$ , summer  $\sim 4$ ). Values of both variables are slightly higher in this study than found in Merico et al. (2006).

The seasonal pattern in  $\Omega_{\text{cal}}$  is predominantly determined by the spring diatom blooms, because the intense  $C_T$  removal has the effect of driving up carbonate ion concentrations (Merico et al., 2006).

Annual averages of  $[\text{CO}_3^{2-}]$  and  $\Omega_{\text{cal}}$ , but not seasonal patterns, can also be compared to the GLODAP dataset (Key et al., 2004). This is a global dataset of carbonate chemistry ( $C_T$  and Alkalinity) measurements from open ocean cruises. Average annual values are calculated, with possible biases due to sampling of many locations at only one time of year (e.g. scarcity of winter measurements at high latitudes). The dataset does not extrapolate to the Norwegian Sea, but for the open North Atlantic at  $60^\circ \text{N}$ ,  $20^\circ \text{W}$ , the carbonate ion concentration derived from the GLODAP dataset (together with temperature and salinity taken from Levitus climatologies) is about  $170 \mu\text{Mol kg}^{-1}$ , and the calcite saturation state is about 4. Two stations close to OWS M were sampled in July 1981 during the Transient Tracers in the Ocean, North Atlantic Study (TTO-NAS) cruise programme, giving rise to carbonate ion concentration =  $\sim 178 \mu\text{Mol kg}^{-1}$  and  $\Omega_{\text{cal}} = \sim 4.3$  at  $\sim 65^\circ \text{N}$ ,  $06^\circ \text{W}$ , and carbonate ion concentration =  $\sim 172 \mu\text{Mol kg}^{-1}$  and  $\Omega_{\text{cal}} = \sim 4.2$  at  $\sim 68^\circ \text{N}$ ,  $03^\circ \text{W}$  (Brewer et al., 1986, applying the revisions to the data recommended by Tanhua and Wallace, 2005).

The OCCAM (Ocean Circulation and Climate Advanced Monitoring) model output for calcite saturation state gives, for the OWS M location, an annual range in calcite saturation state from  $\sim 3$  in winter to between 4 and 5 in summer (A. Yool, personal communication, 2007), in reasonable agreement with our data and model,

We also took two published datasets of  $C_T$ ,  $\text{pCO}_{2(\text{aq})}$ , SST and salinity (Takahashi et al., 1985, Table 2), from north and south of Iceland, and used them to calculate the seasonal cycles of carbonate ion and saturation state (Fig. 12). Both stations exhibit seasonal oscillation in carbonate ion concentration and saturation state, again with higher values in summer ( $\sim 190 \mu\text{Mol kg}^{-1}$  and 4.5–5 respectively), lower in winter

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(110-130  $\mu\text{Mol kg}^{-1}$ ,  $\sim 3$ ), and again in reasonable quantitative agreement with the numbers in this study.

## 5 Conclusions

Our results from a coupled carbon-ecosystem model combined with observational data from an ocean weather station in the Norwegian Sea provide additional evidence of a temporal association between phytoplankton and the carbonate system, with particular recognition that coccolithophore success may be related to the calcite saturation state, although coccolithophore blooms at OWS M are not as prevalent here as other areas, such as south of Iceland. The Norwegian Sea data show evidence that the calcite saturation state increases after (and as a result of) the spring bloom, with higher saturation states in summer than in winter. This has already been proposed by Merico et al. (2006) from model results, and is here confirmed with data.

Both the model and data show that silicate is not rapidly exhausted by diatoms during the spring bloom, in contrast to the typical dynamics elsewhere; the data also highlight the possibility that grazing and macro-nutrient dynamics are not alone in controlling the observed nutrient and chlorophyll concentrations at OWS M, suggesting that there may be partial iron limitation. This is in agreement with recent work revealing that other ocean regions, such as the North Atlantic, are influenced by iron availability (Moore et al., 2006).

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**Table 1.** Parameters of the standard model compared to other models (<sup>a</sup> Merico et al., 2004; <sup>b</sup> Evans and Parslow, 1985; <sup>c</sup> Fasham et al., 1990; <sup>d</sup> Taylor et al., 1993).

Parameter	Symbol	Units	MBS04 <sup>a</sup>	EP85 <sup>b</sup>	F90 <sup>c</sup>	T93 <sup>d</sup>	Current
<b>Diatoms (<math>P_d</math>)</b>							
Maximum growth rate at 0° C	$\mu_{0,d}$	day <sup>-1</sup>	1.2		2.9	0.9	1.3
Minimum sinking speed	$V_d$	m day <sup>-1</sup>	0.5				0.5
Mortality rate	$m_d$	day <sup>-1</sup>	0.08				0.08
Light saturation constant	$I_{s,d}$	W m <sup>-2</sup>	15				15
Nitrate half-saturation constant	$N_{h,d}$	mmol m <sup>-3</sup>	1.5		0.5	0.3	1.5
Ammonium half-saturation constant	$A_{h,d}$	mmol m <sup>-3</sup>	0.05			0.005	0.1
Silicate half-saturation constant	$S_h$	mmol m <sup>-3</sup>	3.5			0.3	3.5
<b>Flagellates (<math>P_f</math>)</b>							
Maximum growth rate at 0° C	$\mu_{0,f}$	day <sup>-1</sup>	0.65				0.6
Mortality rate	$m_f$	day <sup>-1</sup>	0.08				0.1
Light saturation constant	$I_{s,f}$	W m <sup>-2</sup>	15				15
Nitrate half-saturation constant	$N_{h,f}$	mmol m <sup>-3</sup>	1.5				1.5
Ammonium half-saturation constant	$A_{h,f}$	mmol m <sup>-3</sup>	0.05				0.1
<b>Dinoflagellates (<math>P_{df}</math>)</b>							
Maximum growth rate at 0° C	$\mu_{0,df}$	day <sup>-1</sup>	0.6				0.4
Mortality rate	$m_{df}$	day <sup>-1</sup>	0.08				0.12
Light saturation constant	$I_{s,df}$	W m <sup>-2</sup>	15				15
Nitrate half-saturation constant	$N_{h,df}$	mmol m <sup>-3</sup>	1.5				1.5
Ammonium half-saturation constant	$A_{h,df}$	mmol m <sup>-3</sup>	0.05				0.1
<b><i>E. huxleyi</i> (<math>P_{eh}</math>)</b>							
Maximum growth rate at 0° C	$\mu_{0,eh}$	day <sup>-1</sup>	1.15				0.5
Mortality rate	$m_{eh}$	day <sup>-1</sup>	0.08				0.08
Light saturation constant	$I_{s,eh}$	W m <sup>-2</sup>	45				45
Nitrate half-saturation constant	$N_{h,eh}$	mmol m <sup>-3</sup>	1.5		0.5	0.3	1.5
Ammonium half-saturation constant	$A_{h,eh}$	mmol m <sup>-3</sup>	0.05			0.005	0.1
<b>Nitrate (N)</b>							
Deep concentration	$N_0$	mmol m <sup>-3</sup>	20	10		10	12
Nitrification rate	$\Omega$	day <sup>-1</sup>	0.05				0.05
<b>Silicate (S)</b>							
Deep concentration	$S_0$	mmol m <sup>-3</sup>	35			6	5
<b>Microzooplankton (<math>Z_{mi}</math>)</b>							
Assimilation efficiency (S<3 uM)	$B_{eh,mi}, B_{f,mi}, B_{d,mi}$		0.75, 0.75, 0.75	0.5	0.75		0.75, 0.75, 0.75
Assimilation efficiency (S>3 uM)	$B_{eh,mi}, B_{f,mi}, B_{d,mi}$		0.75, 0.75, 0.75				0.75, 0.75, 0.75
Grazing preferences (S<3 uM)	$P_{eh,mi}, P_{f,mi}, P_{d,mi}$		0.33, 0.33, 0.33				0.2, 0.6, 0.2
Grazing preferences (S>3 uM)	$P_{eh,mi}, P_{f,mi}, P_{d,mi}$		0.5, 0.5, 0.0				0.3, 0.6, 0.1

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**Table 1.** Continued.

Parameter	Symbol	Units	MBS04 <sup>a</sup>	EP85 <sup>b</sup>	F90 <sup>c</sup>	T93 <sup>d</sup>	Current
Max. ingestion rates (S<3 uM)	$g_{eh,mi}, g_{f,mi}, g_{d,mi}$	day <sup>-1</sup>	0.175, 0.7, 0.7	1			0.7, 0.7, 0.7
Max. ingestion rates (S>3 uM)	$g_{eh,mi}, g_{f,mi}, g_{d,mi}$	day <sup>-1</sup>	0.7, 0.7, 0.0		1		0.7, 0.7, 0.7
Grazing half-saturation constant	$Z_{h,mi}$	mmol m <sup>-3</sup>	1	1			1
Mortality rate	$m_{mi}$	day <sup>-1</sup> (mmol m <sup>-3</sup> ) <sup>-1</sup>	0.05		0.05		0.05
Excretion rate	$e_{mi}$	day <sup>-1</sup>	0.025		0.1		0.025
Fraction of mort going to Ammonia	$\delta_{mi}$	day <sup>-1</sup>	0.1		0.75		0.1
Mesozooplankton ( $Z_{me}$ )							
Assimilation efficiency	$B_{d,me}, B_{mi,me}, B_{df,me}$		0.75, 0.75, 0.75				0.75, 0.75, 0.75
Grazing preferences	$P_{d,me}, P_{mi,me}, P_{df,me}$		0.33, 0.33, 0.33				0.33, 0.33, 0.33
Max. ingestion rate	$g_{d,me}, g_{mi,me}, g_{df,me}$	day <sup>-1</sup>	0.7, 0.7, 0.7				0.7, 0.7, 0.7
Grazing half-saturation constant	$Z_{h,me}$	mmol m <sup>-3</sup>	1				1
Mortality rate	$m_{me}$	day <sup>-1</sup> (mmol m <sup>-3</sup> ) <sup>-1</sup>	0.2				0.05
Excretion rate	$e_{me}$	day <sup>-1</sup>	0.1				0.1
Fraction of mort going to Ammonia	$\delta_{me}$		0.1				0.1
Detritus (D)							
Sinking speed	$V_D$	m day <sup>-1</sup>	0.4		1-10		0.4
Breakdown rate	$m_D$	day <sup>-1</sup>	0.05		0.05		0.05
Cross-thermocline mixing rate	$k$	m day <sup>-1</sup>	0.01	3	0.1	0.2	0.2
Cloud cover		PAR data	0.9	0.4	0.75		
Coccoliths as of Merico et al. (2004)							
Carbonate system ( $C_T, A_T$ )							
$C_T$ deep concentration	$C_{T0}$	$\mu\text{mol kg}^{-1}$	2100				2140
$A_T$ deep concentration	$A_{T0}$	$\mu\text{Eq kg}^{-1}$	2250				2320
Atmospheric $p\text{CO}_2$	$p\text{CO}_{2(\text{air})}$	$\mu\text{atm}$	345				377

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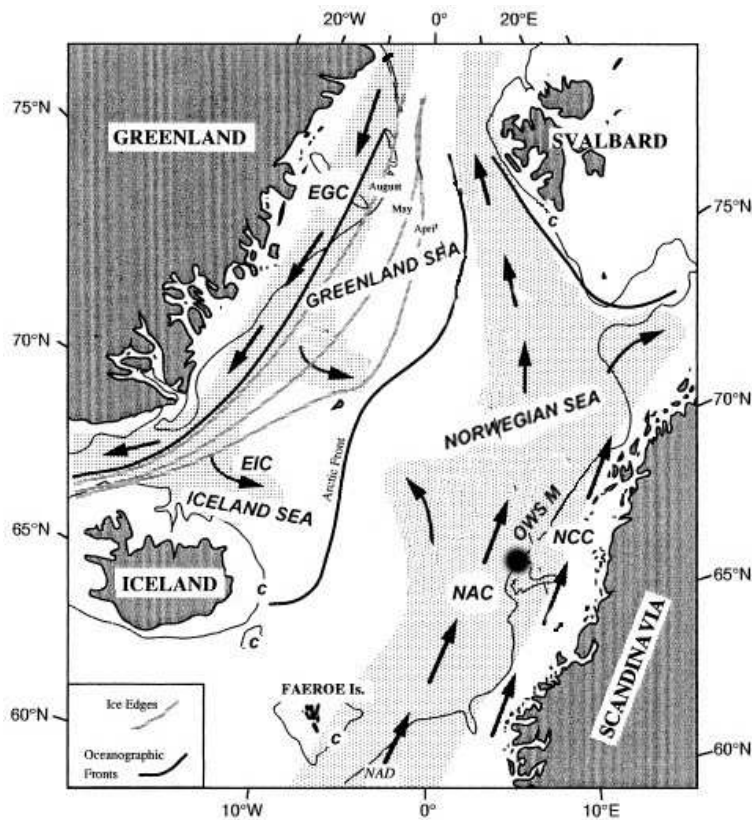
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**Fig. 1.** Map of the Nordic Seas including major surface currents and Ocean Weather Station M (OWS M) at 66° N, 02° E. Major oceanic fronts and approximate ice edges are also indicated and the continental shelf is marked by the c contour. EGC = East Greenland Current, EIC = East Icelandic Current, NAD = North Atlantic Drift, NAC = Norwegian Atlantic Current, NCC = Norwegian Coastal Current. Adapted from Andruleit (2000).

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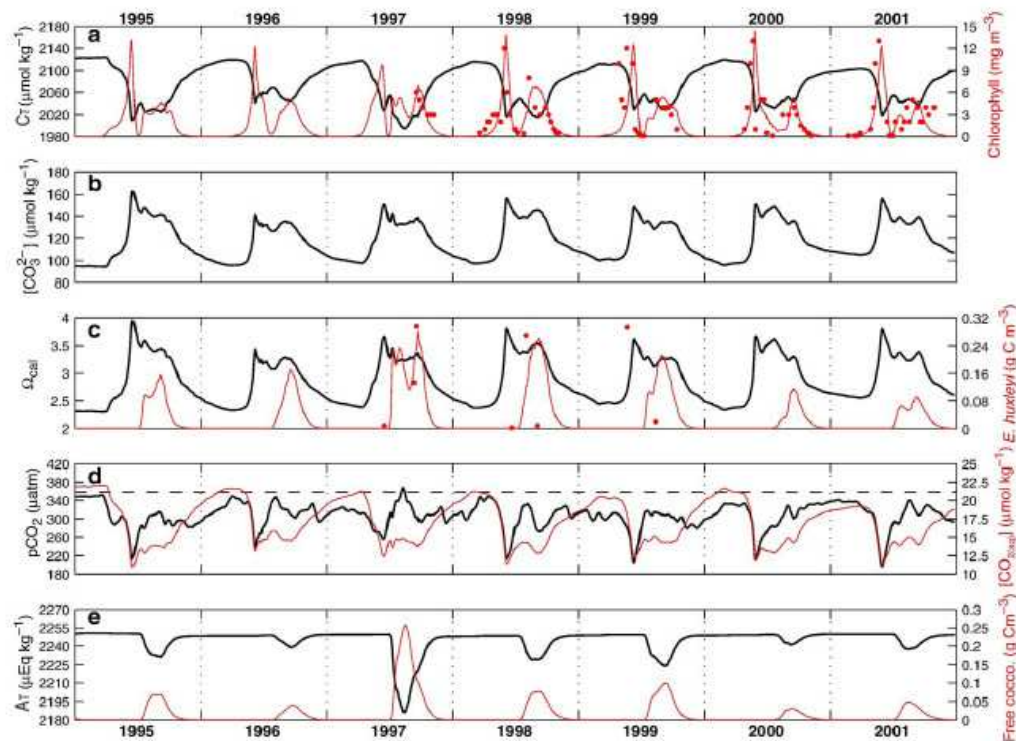
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**Fig. 2.** Biological and carbonate system variables in the eastern Bering Sea from 1995 to 2001. **(a)** Modelled  $C_T$  (black line) and modelled chlorophyll (red line) as compared with weekly averages of SeaWiFS-derived chlorophyll data (red dots); **(b)** modelled carbonate ion concentration; **(c)** modelled calcite saturation state (black line) and modelled *E. huxleyi* abundance (red line) as compared with observed concentrations (red dots); **(d)** modelled  $\text{CO}_2$  partial pressure in seawater (black line) and observed  $\text{CO}_2$  partial pressure in the atmosphere (dashed black line) and modelled dissolved  $\text{CO}_2$  (red line); **(e)** modelled alkalinity (black line) and modelled free coccolith concentration (red line). Adapted from Merico et al. (2006).

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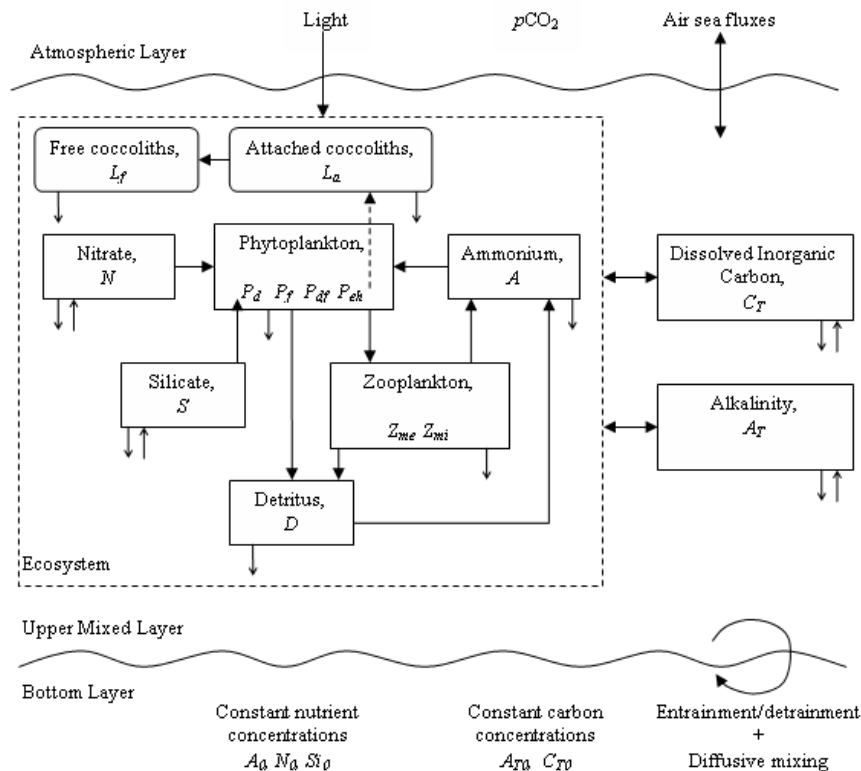
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**Fig. 3.** Physical structure of the model with main biological and chemical components. Arrows represent exchange of materials. Open arrows indicate the material flowing between the mixed layer and bottom layer. The arrow from *E. huxleyi* ( $P_{eh}$ ) to attached coccoliths ( $L_a$ ) is dashed indicating that attached coccoliths are produced proportionately to the *E. huxleyi* concentration rather than with a real flow of material between these two compartments. Note that mesozooplankton ( $Z_{me}$ ) also grazes on microzooplankton ( $Z_{mi}$ ). See text for more details. (Adapted from Merico et al., 2006).

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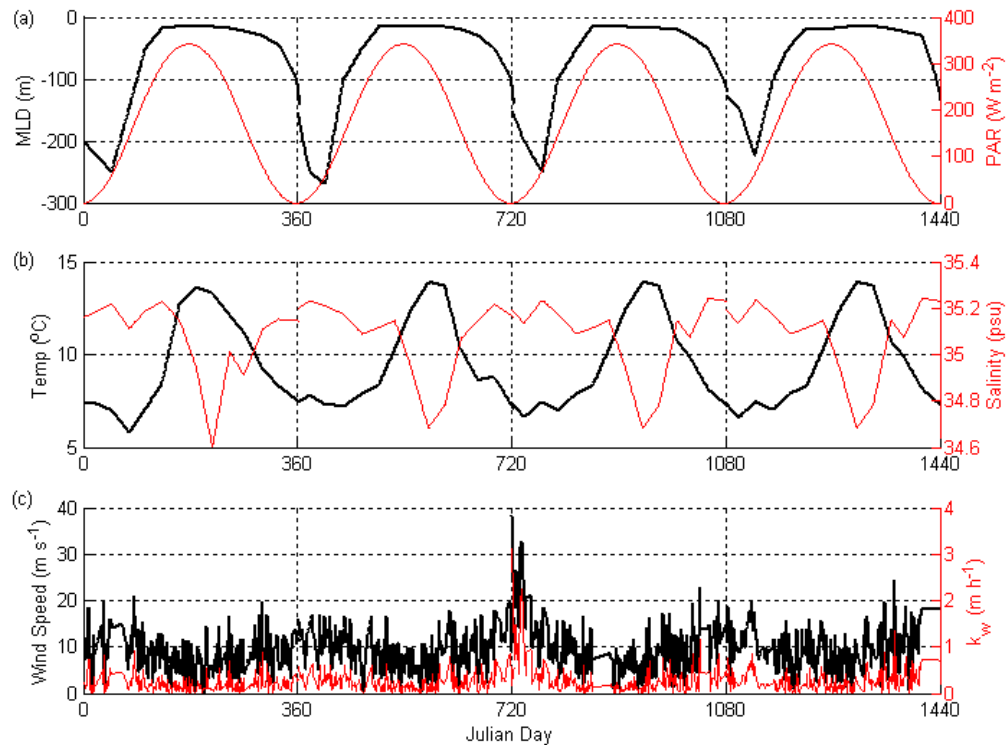
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**Fig. 4.** Physical data from OWS M which is used to force the model over each year, 2002 to 2005. **(a)** MLD (m) (thick line) and daily average light available for phytoplankton at the sea surface ( $\text{W m}^{-2}$ ) (thin line), **(b)** sea surface temperature ( $^{\circ}\text{C}$ ) (thick line) and sea surface salinity (psu) (thin line), and **(c)** wind speed ( $\text{m s}^{-1}$ ) (thick line) and gas transfer velocity ( $k_w$ ), ( $\text{m h}^{-1}$ ) (thin line).

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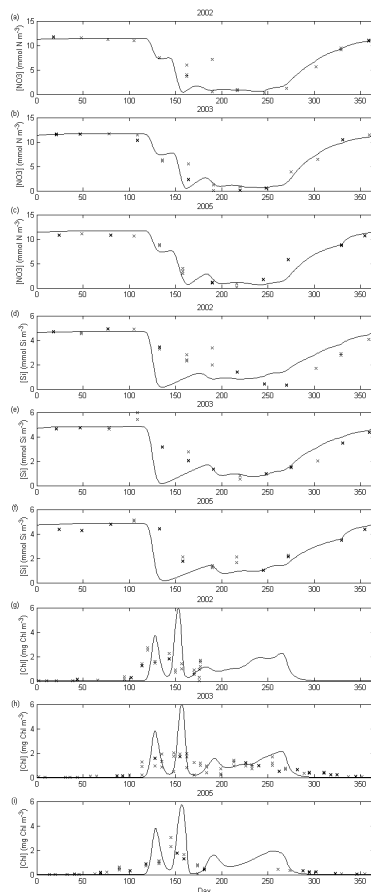
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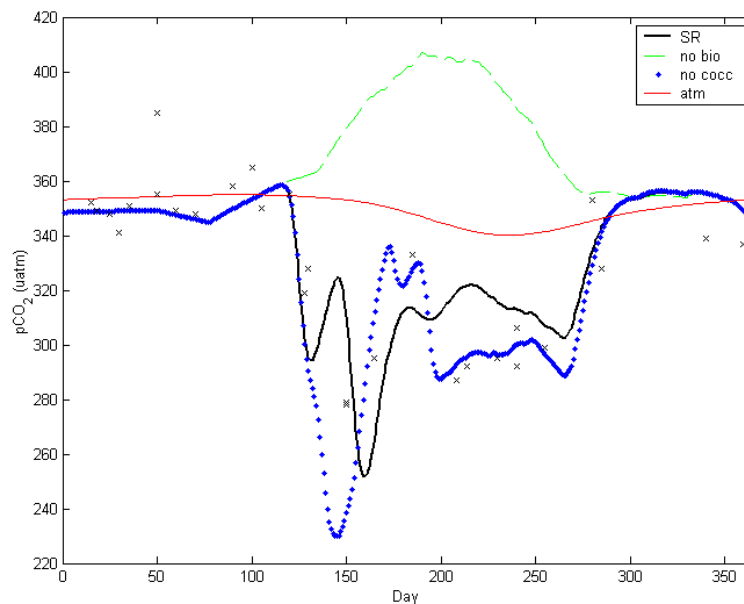


**Fig. 5.** The standard run output showing modelled data (black lines) and OWS M data ( $\leq 20$  m) (crosses) for **(a)** 2002 nitrate, **(b)** 2003 nitrate, **(c)** 2005 nitrate, **(d)** 2002 silicate, **(e)** 2003 silicate, **(f)** 2005 silicate, **(g)** 2002 chlorophyll, **(h)** 2003 chlorophyll, **(i)** 2005 chlorophyll. Year 2004 not included here because of lack of data.

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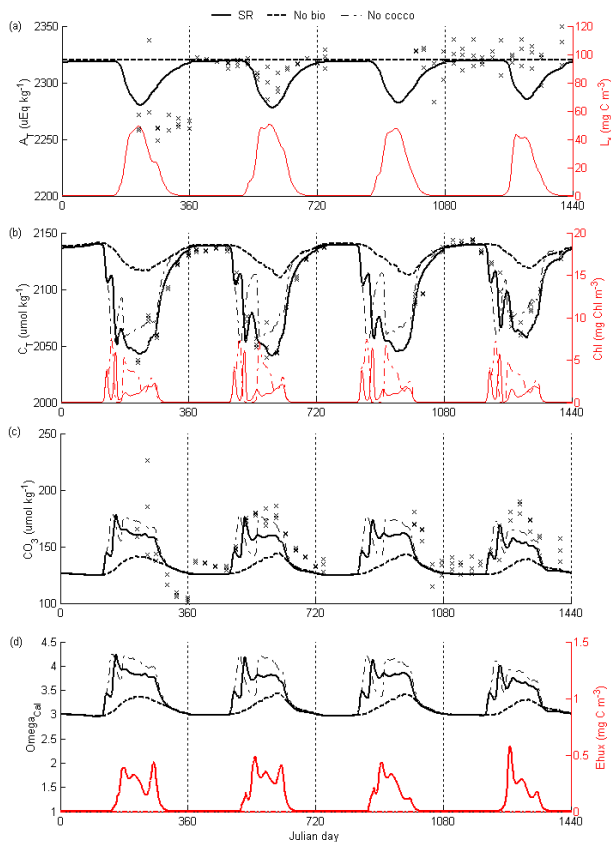


**Fig. 6.** Modelled output of carbon dioxide partial pressure in air (thin red line) and seawater with the standard run (thick black line), with no coccolithophores (thick dot blue line) and with all biology switched off (thin dashed green line) (averaged over the four modelled years). Data points (crosses) represent observed carbon dioxide partial pressure in seawater taken from Gislefoss et al. (1998). The data points are from 1993 and 1994 and hence they are at lower  $p\text{CO}_2$  than the current model is set to. Modelled output has therefore been shifted down to fit data points demonstrating the pattern and magnitude of the seasonal cycle.

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**Fig. 7.** Model output for carbonate system showing standard run (thick line), with biology turned off (thick dashed line) and with biology on but no coccolithophores (thin dashed line) compared to data (crosses) **(a)**  $A_T$  (black) and free coccoliths (red), **(b)**  $C_T$  (black) and chlorophyll concentration (red), **(c)** carbonate ion concentration and **(d)** calcite saturation state (black) and coccolithophore concentration (red).

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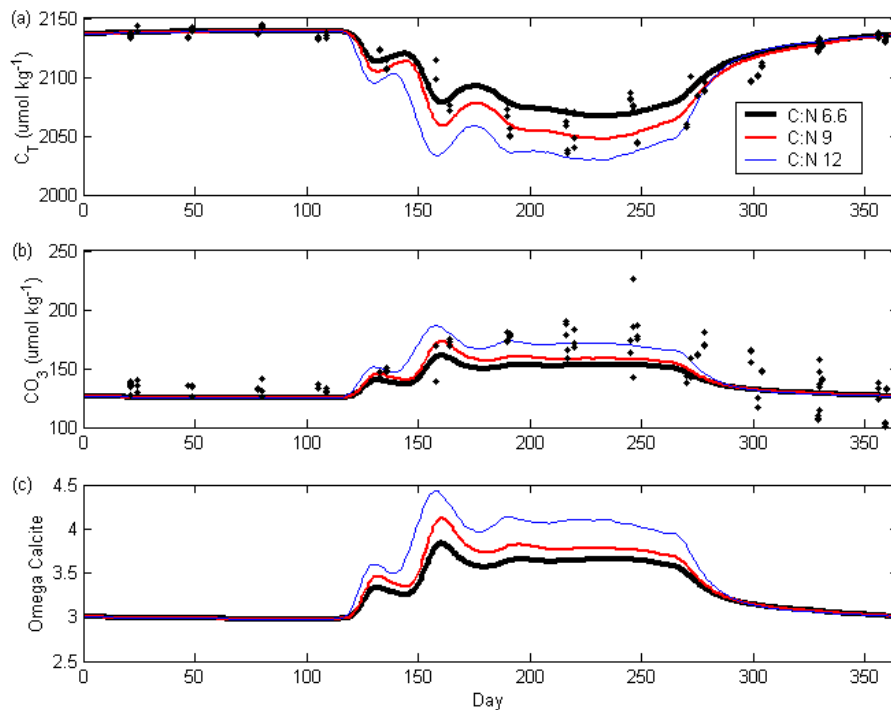
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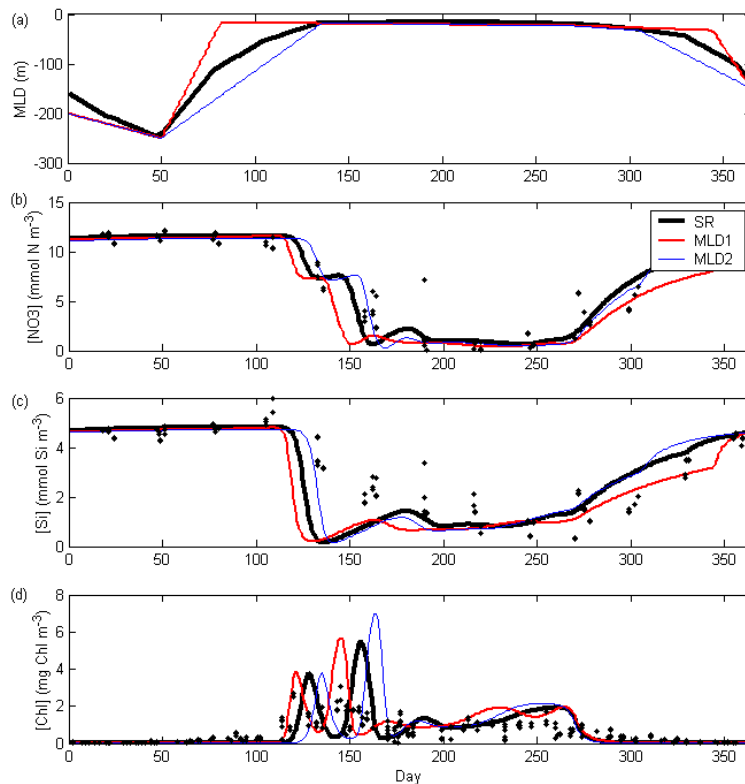


**Fig. 8.** Sensitivity analysis of the C:N ratio. Showing (a),  $C_T$  (b) and  $\text{CO}_3$  (c) Calcite saturation state for the standard run where the C:N = 6.6 high C:N = 12 and mid C:N ratio = 9. The dots represent the combined OWS M data ( $\leq 20$  m) from the period 2002–2005.

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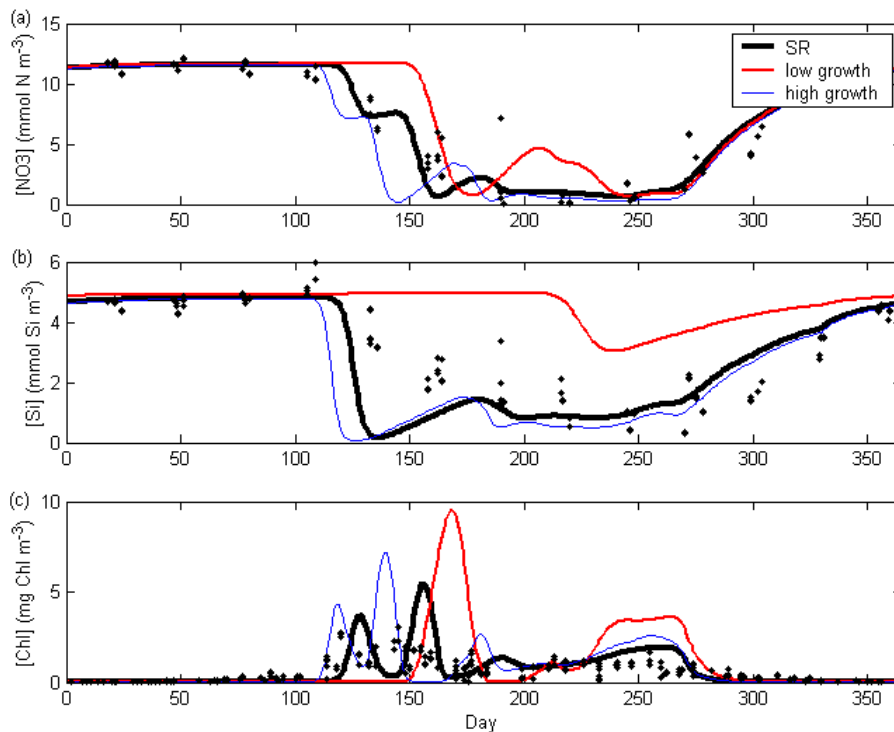


**Fig. 9.** Sensitivity of (a) MLD, (b) nitrate concentration, (c) silicate concentration, and (d) chlorophyll concentration in standard run (SR) compared to rapid shoaling and deepening of the mixed layer (MLD1) and slow shoaling and deepening of the mixed layer (MLD2). The dots represent the combined OWS M data ( $\leq 20$  m) from the period 2002–2005.

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**Fig. 10.** Sensitivity of (a) nitrate concentration, (b) silicate concentration and (c) chlorophyll concentration to changes diatom and flagellate growth rates (standard run, 50% higher growth rate (high growth) and 50% lower growth rate (low growth)). The black dots represent the combined OWS M data ( $\leq 20$  m) from the period 2002–2005.

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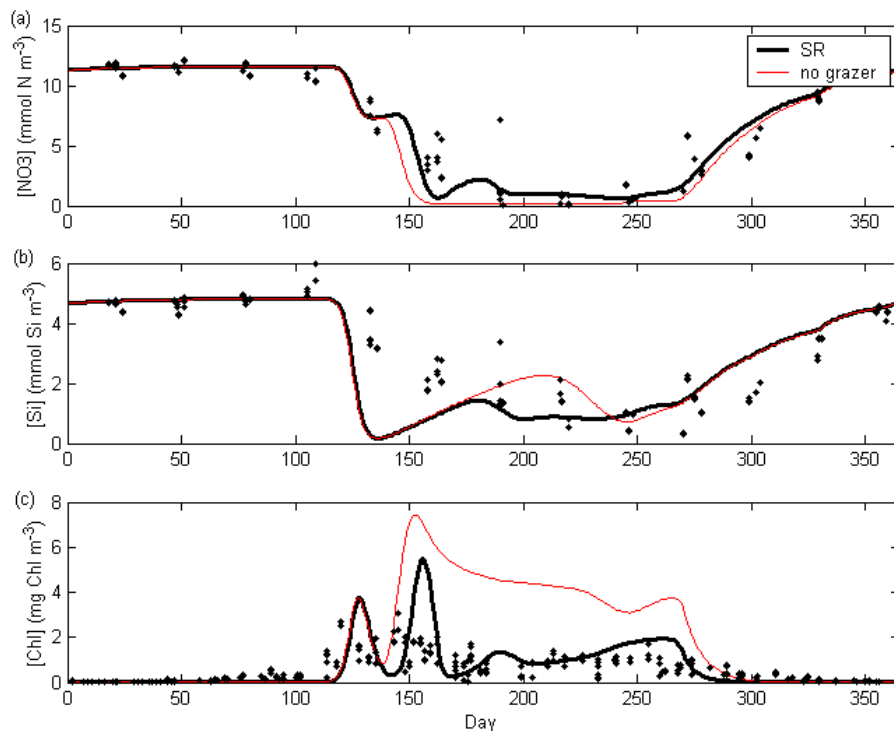
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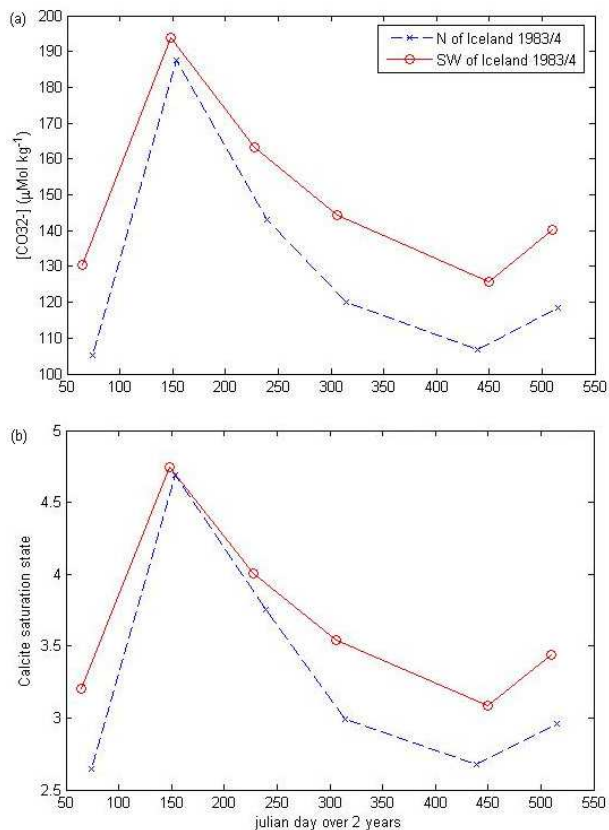


**Fig. 11.** Model simulations showing standard run and when no grazers are present, **(a)** nitrate concentration, **(b)** silicate concentration, **(c)** total chlorophyll concentration. The dots represent the combined OWS M data ( $\leq 20$  m) from the period 2002–2005.

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**Fig. 12.** Calculated seasonal cycles of **(a)** carbonate ion concentration and **(b)** calcite saturation state for north and south of Iceland (data taken from Table 2 of Takahashi et al., 1985).

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