Ocean Sci. Discuss., doi:10.5194/os-2017-39, 2017
Manuscript under review for journal Ocean Sci.
Discussion started: 29 May 2017

Ocean Science Discussions

Biological data assimilation for parameter estimation of a phytoplankton functional type model for the western North Pacific

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Abstract. Ecosystem models are used to understand ecosystem dynamics and ocean biogeochemical cycles and require optimum physiological parameters to best represent biological behaviours. These physiological parameters are often tuned up empirically, while ecosystem models have evolved to increase the number of physiological parameters. We developed a three-dimensional (3D) lower trophic level marine ecosystem model known as the Nitrogen, Silicon and Iron regulated Marine Ecosystem Model (NSI-MEM) and employed biological data assimilation using a micro-genetic algorithm to estimate 23 physiological parameters for two phytoplankton functional types in the western North Pacific. The approach used a one-dimensional emulator that referenced satellite data. The 3D NSI-MEM with biological parameters optimised by assimilation improved the timing of a modelled plankton bloom in the subarctic and subtropical regions compared to models without data assimilation. Furthermore, the model was able to simulate not only surface concentrations of phytoplankton but also subsurface maximum concentrations of phytoplankton. Our results show that surface data assimilation of biological parameters from two observatory stations benefits the representation of vertical plankton distribution in the western North Pacific.

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1 Introduction

Processes of growth, decay and interaction by plankton in the lower trophic level (LTL) marine ecosystem are critical to understand the oceanic biogeochemical cycles. There are many LTL marine ecosystem models ranging from simple nutrient, phytoplankton and zooplankton models to more complicated models including carbon-, oxygen-, silicate-, iron-cycles and so forth (e.g. Edwards and Brindley, 1996; Fasham et al., 1990; Shigemitsu et al., 2012; Yamanaka et al., 2004; Yoshikawa et al., 2005). Coupling LTL marine ecosystem models to ocean general circulation models (OGCMs) makes it possible to discuss the three-dimensional (3D) quantitative descriptions of the ecosystem and to investigate temporally fine variability (e.g. Aita et al., 2007; Hashioka et al., 2009; Hoshiba and Yamanaka, 2016; Masuda et al., 2017; Sumata et al., 2010). Physiological parameters are usually fixed on the basis of local estimations and applied homogeneously to a basin-scaled ocean, although the vales of physiological parameters should depend on the environments of regions. Physiological parameters have often been tuned up empirically and arbitrarily, although ecosystem models have recently added more parameters to increase the number of prognostic and diagnostic variables. A reasonable estimate of the physiological parameters in ecosystem models is required to reproduce the observed data such as the spatial distribution patterns of phytoplankton biomass and the timing of a plankton bloom.

In previous studies using LTL marine ecosystem models, various approaches for data assimilation were introduced as methods of estimating optimal physiological parameters (e.g. Kuroda and Kishi, 2004; Fiechter et al., 2013; Toyoda et al., 2013; Xiao and Friedrichs, 2014). In this study, to estimate the optimal parameter sets, we employed a data assimilative approach by using a micro-genetic algorithm (μ-GA) (Krishnakumar, 1990) with a LTL marine ecosystem model: the nitrogen, silicon and iron regulated marine ecosystem model (NSI-MEM) (Shigemitsu et al., 2012). This algorithm had already been adopted and confirmed to work well in the one-dimensional (1D) NSI-MEM of the western subarctic Pacific by Shigemitsu et al. (2012). Shigemitsu et al. (2012) had developed the NSI-MEM based on NEMURO (North pacific Ecosystem Model for Understanding Regional Oceanography: Kishi et al., 2007) the following points: (1) the introduction of an iron cycle, including dissolved and particulate iron, whereby the dissolved iron explicitly regulates phytoplankton-photosynthesis; (2) adoption of physiologically more consistent optimal nutrient-uptake (OU) kinetics compared to the classical Michaelis–Menten equation and (3) the division of detritus into two types of small and large sizes that exhibit different sinking rates among other things.

We used the 3D NSI-MEM and the Parameter-optimised approach for the phytoplankton components to improve the model's performance in terms of biomass and seasonal fluctuations of phytoplankton in the western North Pacific (WNP) region. In the WNP region, there are both subarctic and subtropical gyres comprising the Oyashio and the Kuroshio, respectively. Between the gyres (i.e. the Kuroshio–Oyashio transition region), horizontal gradients of temperature and phytoplankton concentration in the surface water are generally large due to meanders in the Kuroshio extension jet and mesoscale eddy activity (Qiu and Chen, 2010; Itoh et al., 2015). The WNP region is a high-nutrient, low-chlorophyll

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(HNLC) region where biological productivity is lower than expected for the prevailing surface macronutrient conditions. The relatively low productivity in the HNLC region is due to low dissolved iron concentrations (e.g. Tsuda et al., 2003), because iron is one of the essential micronutrients for many phytoplankton species. The source of iron for the WNP region is not only from air-born dust but also from iron transported in the intermediate water from the Sea of Okhotsk to the Oyashio region (Nishioka et al., 2011). Since the WNP region exhibits many complex physical and biogeochemical characteristics as referred to above, it is difficult even for state-of-the-art eddy-resolving models to reproduce them. As a trial toward better simulating the LTL ecosystem in the WNP region, we introduced the following into the NSI-MEM: (1) a data assimilated physical field by eddy-resolving OGCM with a horizontal resolution of 0.1° and (2) an assimilated physiological parameter estimation for two different phytoplankton groups. We also focused on the seasonal variations of phytoplankton.

2 Model and data description

2.1 Setting the 3D NSI-MEM

We used the marine ecosystem model, 3D NSI-MEM, and included two phytoplankton functional types (PFTs): non diatom small phytoplankton (PS) and large phytoplankton like diatoms (PL) (Fig. 1). We also used a physical field obtained from the Meteorological Research Institute Multivariate Ocean Variational Estimation for the WNP region (MOVE-WNP) (Usui et al., 2006). The MOVE-WNP system is composed of an OGCM and a multivariate 3D variational analysis scheme that synthesizes the observed information such as temperature, salinity and sea surface height.

The model domain extends from 15° N to 65° N and 117° E to 160° W, with a grid spacing of 1/10° × 1/10° around Japan and 1/6° to the north of 50° N and to the east of 160° E (Fig. 2 (a)). There are 54 vertical levels with layer thicknesses increasing from 1 m at the surface to 600 m at the bottom. The model is forced by factors including surface wind, heat flux and freshwater flux. The details of the surface forcing are presented by Tsujino et al. (2011). Dust flux for dissolved iron and short wave radiation input were similar to that of a global climate model (Model for Interdisciplinary Research on Climate; Watanabe et al., 2011), and river run-off as a nutrient supply was from CORE ver. 2 forcing (Large and Yeager, 2009). Nutrients near the boundary were restored to the values provided by a model, Marine Ecosystem Model CCSR Ocean Component Model (MEM-COCO), participating in MARine Ecosystem Model Intercomparison Project. The physical field used in our ecosystem model had already been confirmed to reproduce realistic salinity, velocity and temperature fields in a previous study (Usui et al., 2006). Using a physical one-day averaged field, we ran the NSI-MEM to simulate the years between 1985 and 1998. The results from 1998 were analysed in this study.

We divided the model domain into two provinces (green and yellow regions in Fig. 2 (b)) using the following province map instead of maps divided by latitude–longitude lines as in previous studies (e.g. Longhurst, 1995; Toyoda *et al.*, 2013). The province map is based on the dominant phytoplankton species and nutrient limitations (Hashioka et al., in preparation) and sets different ecosystem parameters (see details in Sect. 2.3) for each province (hereafter, ‘Parameter-optimised case’; Table

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1). The respective parameters for each province were estimated by the 1D NSI-MEM using the μ-GA employed by those in the 3D model. We also conducted model simulations with the similar parameters, as a parameter set for the whole domain, to Shigemitsu et al. (2012) (hereafter 'Default case', Table 1). In order to smooth the gap in parameter values at the boundary between the two provinces in Fig. 2 (b), the parameters were varied as a function of the sea surface temperature (SST) annually averaged for 1998 (Fig. 2 (c)) for our 'SST-dependent case' (Table 1). The parameters were interpolated/extrapolated according to the following equation:

$$P(x) = P_{St.S1} + \left(P_{St.KNOT} - P_{St.S1}\right) \times \frac{SST(x) - SST_{St.S1}}{SST_{St.KNOT} - SST_{St.S1}}, \quad (1)$$

where P (x), $P_{\text{St. S1}}$ and $P_{\text{St. KNOT}}$ are ecosystem parameters for a point (x), St. S1 and St. KNOT, respectively. St. KNOT and St. S1 are typical observational points in the subarctic and subtropical regions (green- and yellow-coloured areas in Fig. 2 (b), respectively). The parameters of all the 3D experimental cases, shown in Table 1, were not changed either vertically or temporally.

2.2 Satellite and in situ data

Global satellite data for 1998 for phytoplankton (i.e. chlorophyll a) were obtained from the Ocean Colour Climate Change Initiative dataset, European Space Agency, available online at http://www.esa-oceancolour-cci.org/, which utilises the data archives of ESAs MERIS/ENVISAT and NASAs SeaWiFS/SeaStar, Aqua/MODIS. The global satellite data were linearly interpolated to the grid (size 1/10° and 1/6°) in the model domain (Fig. 2 (a)), and the nitrogen-converted concentrations of both PL and PS were estimated by a satellite PFT algorithm (Hirata et al., 2011). The μ-GA cost function was defined from the 1998 monthly averaged PL and PS concentrations. Satellite data of the 1998 mean SST from the AVHRR Pathfinder Project (http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/) were also used to conduct our SST-dependent case study using the same interpolation as above.

To validate the vertical distribution of the model results, we utilised in situ data of phytoplankton and nutrients at St. KNOT (44° N, 155° E) obtained from the web site (http://www.mirc.jha.or.jp/CREST/KNOT/) (Tsurushima et al., 2002).

2.3 1D NSI-MEM process

The 1D NSI-MEM used in Shigemitsu et al. (2012) was employed as an emulator to determine the optimal set of ecosystem parameters at St. KNOT (44° N, 155° E) and S1 (30° N, 145° E), respectively. We modified the 1D NSI-MEM of Shigemitsu et al. (2012) by increasing the number of vertical layers to 54 and introducing the vertical advection of the 3D simulation. Twenty-three parameters in the NSI-MEM were selected, as shown in Table 2, which were responsible for PL and PS biomass relevant to the photosynthesis and grazing of zooplanktons. The other parameters were similar to those in the Default case. The initial (1st January 1998) and boundary conditions during the integration period were applied from those in the 3D model.

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2.4 μ-GA implementation

The μ-GA procedure included the following: (1) a cost function was defined; (2) higher evaluated model results of parameter information were maintained (following Step 2 to 5) and (3) optimized parameter set was estimated through repeating the process of (2) multiple times (following Step 6). To define the cost function, satellite PFT data were used as reference values for the μ-GA because satellite data have higher temporal and spatial resolution than in situ data.

Running the 1D NSI-MEM with the μ-GA, 23 optimal parameters were obtained through the following process:

Step 0 Define a range of parameter values (Table 2) based on previous studies (e.g. Jiang et al., 2003; Fujii et al., 2005; Yoshie et al., 2007) and prepare 23 population size being the same number of estimated parameters before running the μ-GA.

Step 1 Generate 23 initial random parameter strings using the μ-GA.

Step 2 Evaluate the 23 model runs with the different parameter strings using the following cost function:

$$Cost = \sum_{i}^{I} \frac{1}{N_i} \sum_{j}^{Ni} \frac{1}{\sigma^2{}_i} (m_{ij} - d_{ij})^2 , \qquad (2)$$

where m_i is the modelled monthly mean of phytoplankton type i (i = 1 for PL and 2 for PS) and d_i is the monthly satellite data of the type i. The index j denotes the number of months (N_i) for which satellite data of type i exists. The assigned weights for PL and PS are σ_{PL} = 0.1 μmol/l and σ_{PS} = 0.1 μmol/l.

Step 3 Determine the best parameter string and carry it forward to the next model run (or the next 'generation') (elitist strategy).

Step 4 Choose the remaining 22 strings for re-determination of the best parameter strings (or 'reproduction') based on a deterministic tournament selection strategy (the best string that gave the highest model performance in Step 3 also competes for its copy in the reproduction). In the tournament selection strategy, the strings are grouped randomly and adjacent pairs are made to compete. Apply crossover to the winning pairs and generate new parameter strings for the final 22 strings. Two copies of the same string mating for the next generation should be avoided.

Step 5 If the difference between the maximum and minimum cost function values of the populations becomes too small, renew all the parameter strings randomly except for the best-performed string for efficiently escaping from a local solution; the cost function may have local minimums.

Step 6 Repeat the procedure from Step 2 to Step 5 until the best parameter strings are un-changed (i.e. parameters are well converged within 2,000 generations (times) in the present study).

The 1D NSI-MEM was used as an emulator to determine ecosystem parameters through the process described above, and the parameter sets assimilated by the 1D model with the μ-GA at St. KNOT and St. S1 were applied to the 3D simulations which were conducted as the Parameter-optimised case and the SST-dependent case in Table 1.

3. Results and discussion

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3.1 1D model

The 1D NSI-MEM was employed as an emulator to determine ecosystem parameters. Seasonal variations in the Default and Parameter-optimised cases simulated those from the satellite data as follows: the PS biomass was larger than the PL biomass at both St. KNOT and St. S1, but the relative ratio of PL to the total biomass at St. KNOT was larger than that at St. S1 (Fig. 3). These results are consistent with the general understanding that the subarctic region biomass is larger than the subtropical region biomass. Moreover, diatoms, represented as PL, are a major group in the subarctic region.

The seasonal variations of PS in the Parameter-optimised case (dashed lines) for the two stations simulated by the satellite data (solid lines) were more accurate than those in the Default case (dotted lines). There were small seasonal variations with a winter peak of 0.6–0.7 molN/m^3 at St. KNOT, and a relatively large seasonal variation with a spring peak of 0.65 molN/m^3 at St. S1 except double the biomass observed by the satellite (0.33 molN/m^3). For PL, the seasonal peaks in winter at St. KNOT (0.57 molN/m^3) and in spring at St. S1 (0.08 molN/m^3) in the Parameter-optimised case captured those in the satellite data independent of the large differences in biomass.

3.2 3D model

The parameter sets assimilated by the 1D model at St. KNOT and St. S1 were applied to the 3D simulation. The seasonal variation features in the 3D simulation were similar to those seen in the 1D simulation (i.e. relatively small seasonal variations of PS biomass in the subarctic region and relatively high winter biomass in the Parameter-optimised case compared to the Default case). The PL biomass features were similar to those of the PS biomass, mentioned above, except that the PL biomass was lower in the subtropical region in the Parameter-optimised case than in the Default case. Seasonal peaks of PS and PL biomass also had the same features as those in the 1D simulations (i.e. the PS bloom in the Parameter-optimised case occurred from winter to spring (Fig. 4 (c), (g)), but that in the Default case occurred in summer (Fig. 4 (b)).

Higher phytoplankton concentrations were found in coastal areas throughout the year in the satellite data. The model could not simulate these high concentrations. This may be due to the inaccuracy of the satellite data resulting from the high concentrations of dissolved organic material and inorganic suspended matter (e.g. sand, silt and clay), and/or due to the uncertainty in the model introduced by unaccounted coastal dynamics such as small-scale mixing processes.

3.3 Amplitude and phase of seasonal phytoplankton fluctuations

At the St. KNOT and St. S1 stations, seasonal variation in total phytoplankton concentrations in the Parameter-optimised case were better reproduced to those in the satellite data than those in the Default case (Fig. 5). At St. KNOT (Fig. 5 (a)), the phytoplankton bloom in the Parameter-optimised case occurs in winter, and the phytoplankton bloom in the Default case occurs in summer with an anti-phase to that of the satellite. At St. S1 (Fig. 5 (b)), the timing of maximum phytoplankton concentration in the Parameter-optimised case matches that of the satellite regardless of its larger seasonal variation amplitude compared to those in the satellite and the Default cases. The seasonal variations for each of the PS and PL concentrations are similar to the total phytoplankton concentrations (not shown) compared with the two model cases.

Figure 6 shows the amplitude and the phase of seasonal variations in the three model cases (Default, Parameter-optimised and SST-dependent) compared with those from the satellite. Based on the seasonal variation from the satellite, the radius shows the relative amplitude of seasonal variation for each of the modelled cases, and the angle from the x-axis shows the maximum concentration time lag for each of the model cases (i.e. the point (1, 0) shown as 'True' is a perfect match to the satellite data). At St. KNOT, the point of the Parameter-optimised case (blue solid vector) was the closest to the satellite data for all the three modelled cases. The ratios of the amplitudes to the satellite data were as follows: 1.00 for the Parameter-optimised case (blue solid vector); 1.08 for the SST-dependent case (yellow solid vector) and 1.24 for the Default case (orange solid vector). The timings of the maximum concentration were as follows: a two-month delay for the Parameter-optimised case (blue solid vector); a three-month delay for the SST-dependent case and a six month delay (anti-phase) for the Default case. The timing of the Parameter-optimised case at St. S1 (blue broken vector) was improved, though its seasonal amplitude was not improved.

Optimisation of the physiological parameters by assimilating them to the satellite data at the two stations improved the seasonal variations of the phytoplankton concentrations such as the timing of the bloom and the seasonal amplitude of the WNP region.

3.4 Comparison with vertical distributions

The model-simulated vertical distributions of phytoplankton and nitrate concentrations from St. KNOT on 20th July, 1998 were compared with the observed on the same day in situ data (Fig. 7). The vertical distribution of phytoplankton in the Parameter-optimised case was closer to the in situ data compared to the Default case data (Fig. 7 (a)). The maximum phytoplankton concentration for the Parameter-optimised case and the in situ data were located in the subsurface around a depth of 50 m, while there was no subsurface maximum in the Default case. This was an interesting improvement because physiological parameters were optimised using only surface satellite data. Moreover, data assimilation not only improved the surface concentration but also the important characteristics of vertical plankton distribution such as the subsurface maximum by changing the physiological parameters.

In the NEMURO, the predecessor version of the NSI-MEM, the amplitude and timing of phytoplankton blooms are predominantly controlled by the photosynthesis rate (i.e. bottom-up effect of nutrient dependence) rather than the grazing rate (i.e. top-down effect of zooplanktons) (Hashioka et al., 2013). The former was determined by the smallest limited growth rate of nitrogen (NH_4 and NO_3), silicate ($Si(OH)_4$) and dissolved iron (FeD) (refer to Eq. (A15) and Eq. (A23) in Shigemitsu et al., 2012). For PS and PL in the Parameter-optimised case and Default case, the dissolved-iron-limited growth rates (yellow lines) dominate the photosynthesis (Fig 8). These increased remarkably in the subsurface layer (below a depth of 50 m) because of the parameter optimisation of the potential maximum growth rate (V_0) and the affinity (A_0) as shown in Table 2.

As a result, the uptake of dissolved iron was improved, particularly in the subsurface layer, leading to an increase of the phytoplankton biomass (Fig. 7 (a)). The larger biomass of phytoplankton also consumed more nitrate and silicate nutrients resulting in a lower nitrate concentration compared to that in the Default case above a depth of 140 m (Fig. 7 (b)).

The change in the dissolved-iron-limited growth rates resulted from the lower concentration of dissolved iron in the subarctic area (Fig. 9) because of the greater consumption of FeD by the phytoplankton compared to that in the Default case. In the Parameter-optimised case (Fig. 9 (b)), the low concentration of dissolved iron in the subarctic region (north of 40° N) is consistent with the conception of a HNLC region in the North Pacific Ocean (Moore et al., 2013).

3.5 Physiological parameter changes with ambient conditions

The SST-dependent case (i.e. smoothed changing parameters) was compared to the Parameter-optimised case (i.e. boundary-gap parameters). The horizontal distribution of the PS and PL concentrations in the SST-dependent case were not significantly different from those in the Parameter-optimised case (Fig. 4) except in two regions—the western region of low latitude (15° N to 25° N and 120° E to 150° E during January and April in Fig. 4 (h)), and the region adjacent to the Kuroshio Extension (around 40° N during July to October in Fig. 4 (h)). The former exception is due to the extrapolation of parameters with high SST and the latter is due to smoothing of parameters between the St. KNOT and St. S1 stations. The simulated seasonal variations of phytoplankton concentration in the SST-dependent case are slightly worse than those in the Parameter-optimised case at the two stations (Fig. 6). However, a smoothed set of parameters dependent on the SST prevents the artificial gap of the parameter value at the fixed boundary between the two provinces.

Physiological parameters in ecosystem models change with the surrounding conditions (e.g. nutrient abundance, light intensity and SST). Smith and Yamanaka (2007) and Smith et al. (2009) suggested the significance of photo-acclimation and nutrient affinity acclimation. Phytoplankton cells change their traits (e.g. nutrient channel, enzyme) in response to ambient nutrient concentrations, and typically large (small) cells adapt to low (high) light and high (low) nutrient concentrations (Smith et al., 2015). In the NSI-MEM, the effect of nutrient-uptake responses by plankton acclimated to different ambient nutrient conditions is applied as an OU kinetic formulation, but the effect of photo-acclimation has not yet been introduced. As a first trial of the 3D NSI-MEM, the effect of the physiological parameter change with time was not included in this study, due to the difficulties and complexities of the scientific interpretation (Schartau et al., 2016). However, the effects of seasonal variation on the physiological parameters seems significant; thus; the variation effects will be added to the data assimilation process.

4 Conclusions

We extended a LTL marine ecosystem model, NSI-MEM, into a 3D coupled OGCM. We also used a data assimilation approach with a μ-GA for two different PFTs in the WNP region: non-diatom PS and PL. Twenty-three parameters in the NSI-MEM were estimated using a 1D emulator with a μ-GA parameter-optimisation procedure, referred to as satellite data. By applying the optimised parameters to the 3D NSI-MEM Parameter-optimised case, the model performances were

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improved in terms of the seasonal variations of phytoplankton biomass, including the timing of the plankton bloom in the surface layer, compared to those using prior parameter values (Default case). The vertical distribution of phytoplankton such as in the subsurface maximum layer were also improved due to the easier-to-use of dissolved iron via the parameter changes, compared to that in the Default case.

Physiological parameters in this study were systematically determined by a μ-GA within the range of those used by numerical models in previous studies. It would be confirmed whether the values of the physiological parameters are consistent with those observed in situ and/or explained why each parameter is set to an estimated value based on the various processes (e.g. nutrient bottom-up, zooplankton top-down and particle sinking processes in the ecosystem model).

Acknowledgements

This study was supported by Core Research for Evolutional Science and Technology (CREST), Japan Science and Technology Agency, Grant Number JPMJCR11A5. The first author developed the 3D NSI-MEM and conducted simulations using this model at Hokkaido University and analysed the results supported by the Center for Earth Surface System Dynamics, Atmosphere and Ocean Research Institute, The University of Tokyo. The phytoplankton satellite data were gathered by the Ocean Colour Climate Change Initiative, ESA (European Space Agency). The SST-satellite data was provided by the National Oceanic and Atmospheric Administration Pathfinder project in GHRSST (The Group for High Resolution Sea Surface Temperature) and the US National Oceanographic Data Center.

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Table

Table 1. List of experiments

	Experiment name	Content of experiment
1D model experiments	Default	Use the almost same parameters as those in Shigemitsu et al. (2012)
	Parameter-optimised	Optimise the parameters with μ-GA at St. KNOT and St. S1
3D model experiments	Default	The same as default of 1-D model but applied to 3-D simulation
	Parameter-optimised	The same as Parameter-optimised of 1-D model but applied to 3-D simulation for two provinces of Fig. 2 (b)
	SST-dependent	The same as Parameter-optimised of 3-D simulation with interpolated parameters at St. KNOT and St. S1 with SST, instead of parameters for two provinces

Table 2. NSI-MEM physiological parameters estimated by the μ-GA. Max and Min values prescribe the upper and lower bounds of the parameter variations used in the previous studies. St. Knot and St. S1 indicate optimal estimated values in the provinces of Fig. 2 (b) while Default values are previous parameter values.

	Min	**KNOT**	**S1**	**Default**	**Max**	**Unit**	**Source of Min and Max range**
$V_{0,PS}$	0.1	2.7	0.7	0.6	3.2	/day	Shigemitsu et al. (2012)
$A_{0,NO3,PS}$	1	454	436	30	512	l/molN・s	Shigemitsu et al. (2012)
$K_{NO3,PS}$	0.50	1.87	2.92	1.00	3.00	μmolN/l	Chai et al. (2002), Eslinger et al. (2000)
$K_{NH4,PS}$	0.05	0.12	0.26	0.10	1.00	μmolN/l	Chai et al. (2002), Eslinger et al. (2000)
$K_{Fed,PS}$	0.035	0.100	0.060	0.040	0.100	nmol/l	Kudo et al. (2006), Price et al. (1994)
k_{PS}	0.0392	0.0693	0.0650	0.0693	0.0693	/degC	Eslinger et al. (2000), Fujii et al. (2005)
M_{PS0}	0.01208	0.01208	0.04321	0.05850	0.05878	l/μmolN・day	Fujii et al. (2005), Sugimoto et al. (2010)
$V_{0,PL}$	0.1	3.2	1.5	1.2	3.2	/day	Shigemitsu et al. (2012)

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$A_{0,NO3,PL}$	1	437	171	10	512	l/molN・s	Shigemitsu et al. (2012)
$K_{NO3,PL}$	0.50	3.00	2.92	3.00	3.00	μmolN/l	Eslinger et al. (2000), Jiang et al. (2003)
$K_{NH4,PL}$	0.50	0.50	1.31	0.30	2.30	μmolN/l	Eslinger et al. (2000), Fujii et al. (2005)
$K_{SiL,PL}$	3.0	6.0	4.3	6.0	6.0	μmol/l	Yoshie et al. (2007)
$K_{Fed,PL}$	0.050	0.050	0.089	0.090	0.200	nmol/l	Coale et al. (2003)
k_{PL}	0.0392	0.0693	0.0392	0.0693	0.0693	/degC	Eslinger et al. (2000), Fujii et al. (2005)
M_{PL0}	0.02900	0.03694	0.03496	0.02900	0.05878	l/μmolN・day	Fujii et al. (2005), Yamanaka et al. (2004)
G_{RmaxS}	0.30	0.79	0.30	0.31	4.00	/day	Yoshie et al. (2007), Yoshikawa et al. (2005)
PS_{ZS*}	0.040	0.364	0.364	0.043	0.364	μmolN/l	Eslinger et al. (2000), Sugimoto et al. (2010)
$G_{RmaxL,PS}$	0.05	0.05	0.05	0.10	0.54	/day	Eslinger et al. (2000), Fujii et al. (2005)
$G_{RmaxL,PL}$	0.14	0.25	0.14	0.49	0.54	/day	Fujii et al. (2005)
PS_{ZL*}	0.0143	0.0430	0.0430	0.0400	0.0430	μmolN/l	Eslinger et al. (2000), Fujii et al. (2005)
PL_{ZL*}	0.0143	0.0430	0.0184	0.0400	0.0430	μmolN/l	Eslinger et al. (2000), Fujii et al. (2005)
$G_{RmaxP,PL}$	0.10	0.40	0.14	0.20	0.40	/day	Eslinger et al. (2000)
PL_{ZP*}	0.0143	0.0430	0.0184	0.0400	0.0430	μmolN/l	Eslinger et al. (2000), Fujii et al. (2005)

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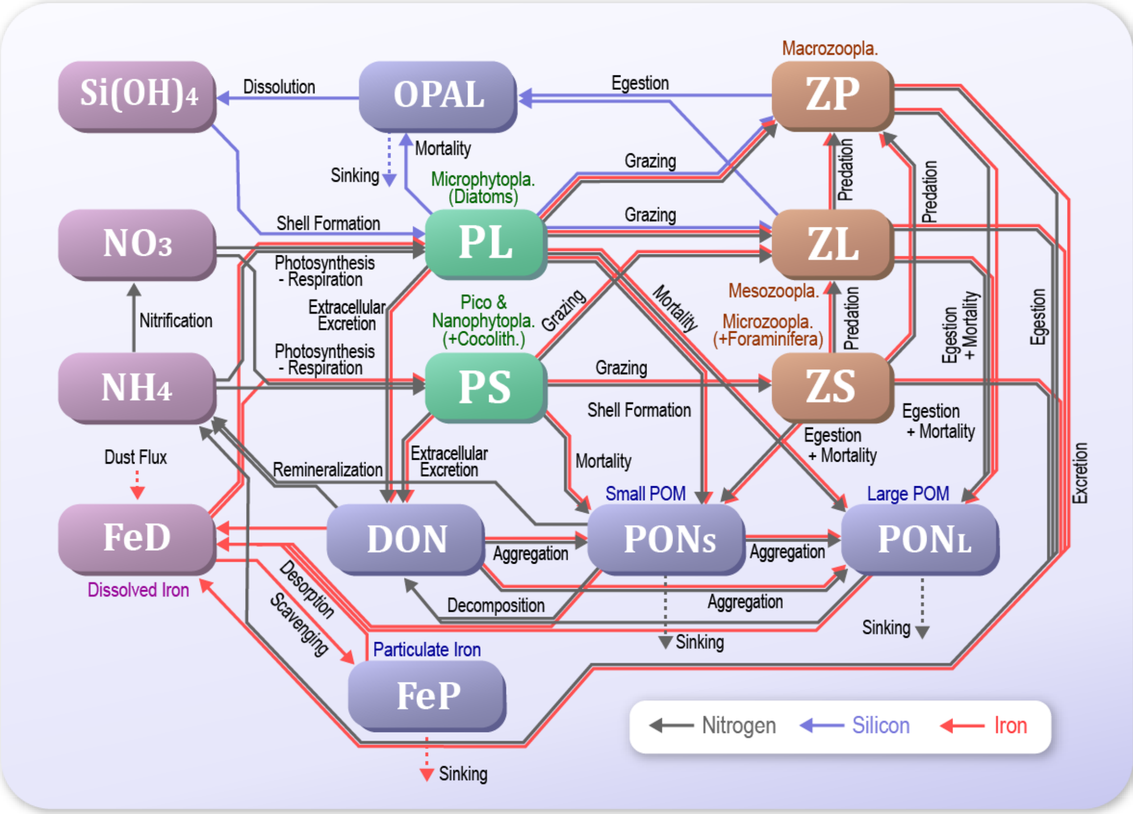

Figure 1. Schematic view of the NSI-MEM interactions among the fourteen components.

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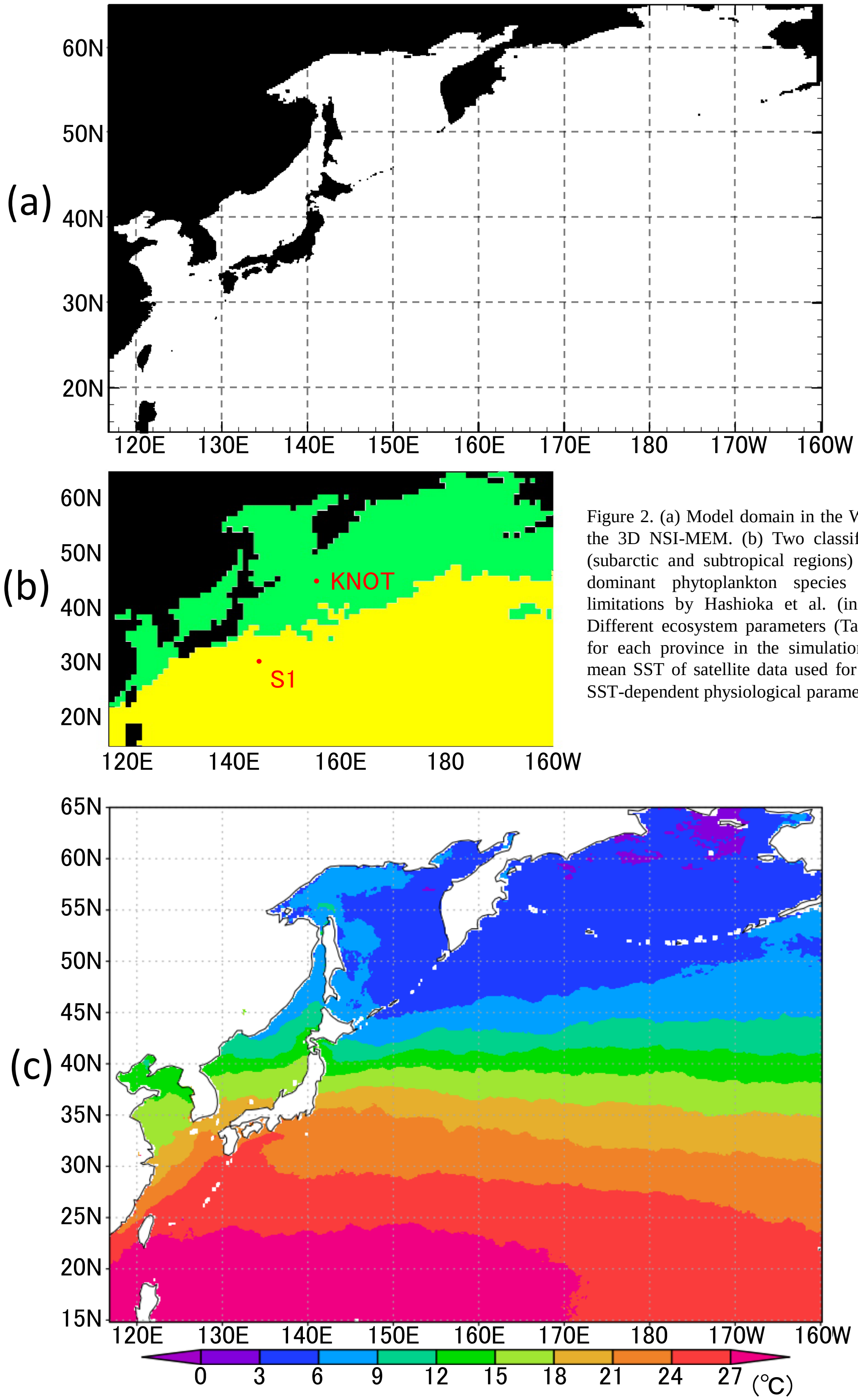

Figure 2. (a) Model domain in the WNP region of the 3D NSI-MEM. (b) Two classified provinces (subarctic and subtropical regions) based on the dominant phytoplankton species and nutrient limitations by Hashioka et al. (in preparation). Different ecosystem parameters (Table 2) are set for each province in the simulation. (c) Annual mean SST of satellite data used for simulation of SST-dependent physiological parameters.

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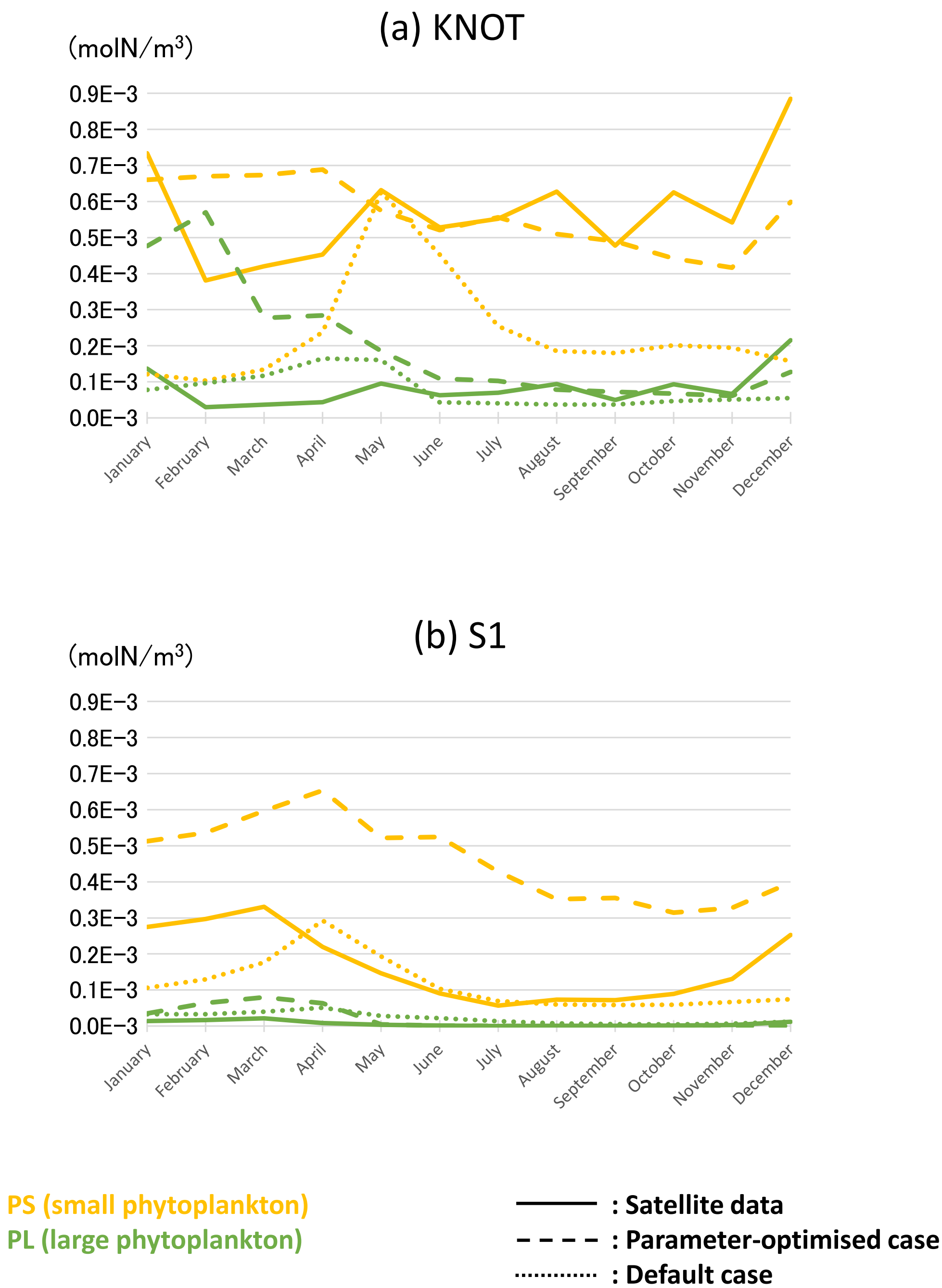

Figure 3. Seasonal variations of surface phytoplankton biomass in the 1D NSI-MEM and satellite data at (a) St. KNOT and (b) St. S1 are shown as typical observational points of the subarctic and the subtropical regions, respectively.

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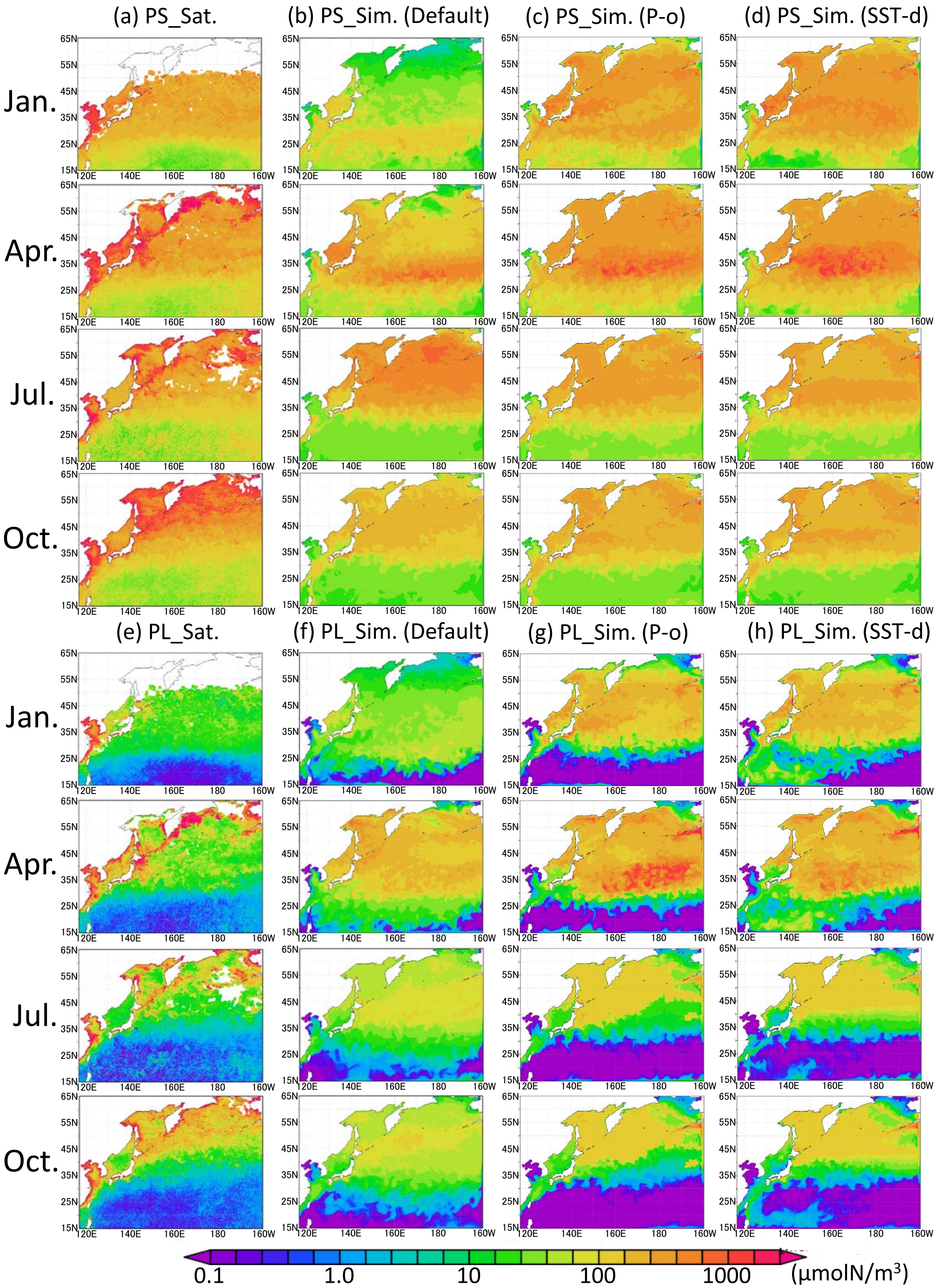

Figure 4. Horizontal distribution of phytoplankton at the surface in 1998. (a) PS (small phytoplankton) from satellites observations, (b) PS in Default case, (c) PS in the Parameter-optimised case, and (d) in the SST-dependent case. (e), (f), (g), (h) are the same except for PL (large phytoplankton). Areas without satellite data are left blank.

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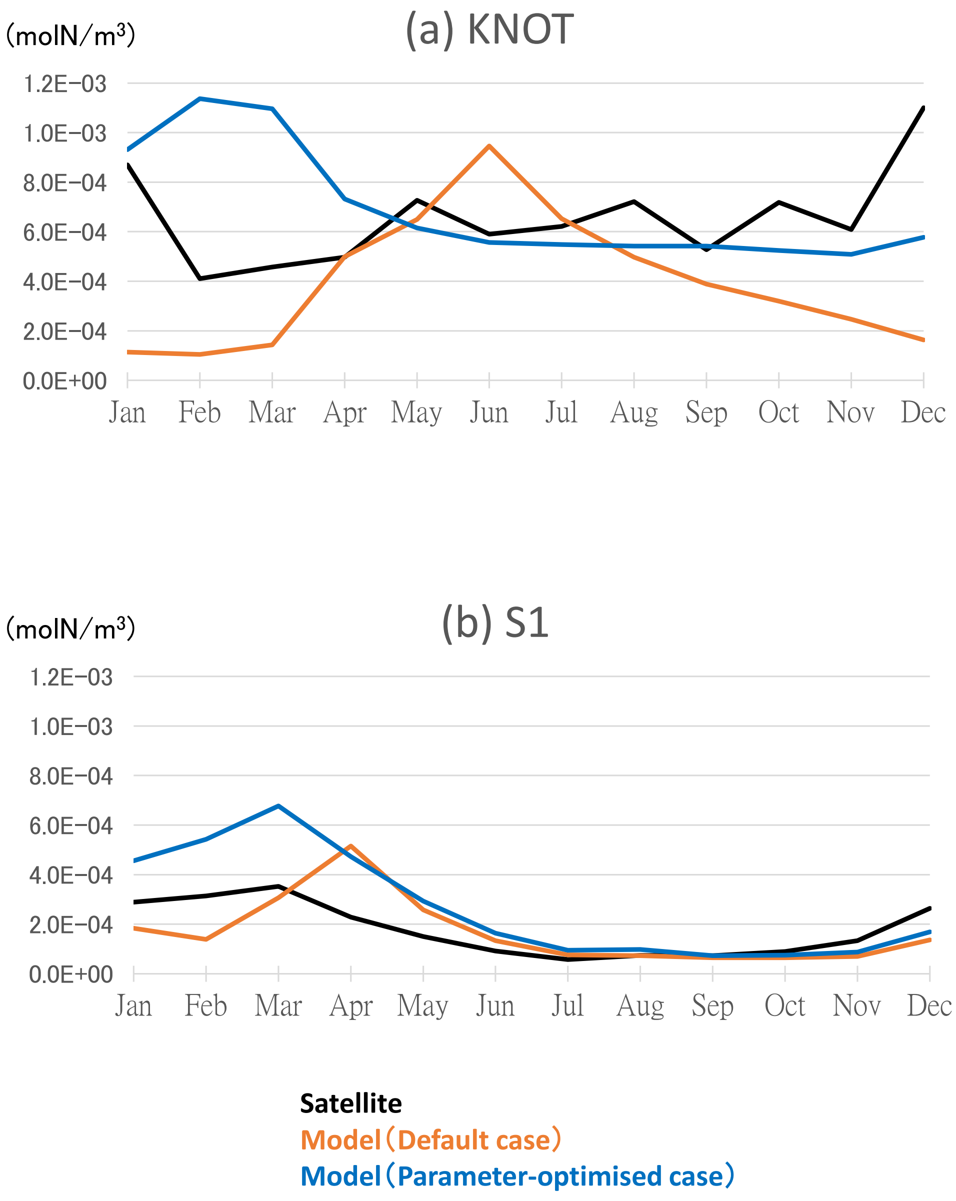

Figure 5. Time series of phytoplankton (PL+PS) concentration in the 3D NSI-MEM and satellite data at (a) St. KNOT and (b) St. S1.

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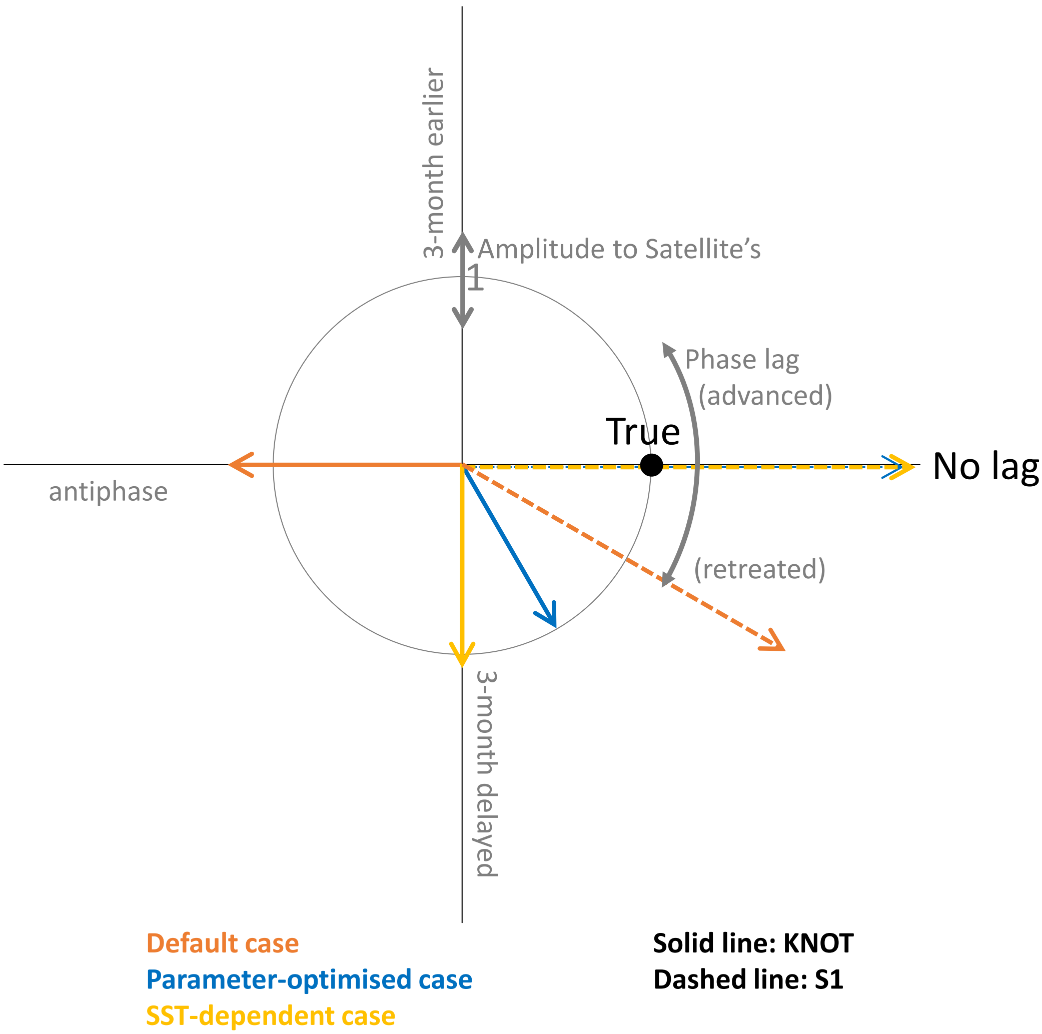

Figure 6. Diagram showing the amplitude and the phase of seasonal variations in the three model cases compared with those in the satellite data. Based on the seasonal variation in the satellite data, the radius indicates the relative amplitude (model/satellite) of seasonal variation for each model case and the angle from the positive x-axis shows the time lag of the maximum concentration for each model case (i.e. the point (1, 0) shown as 'True' is the perfect match to the satellite data). The blue dashed line (Parameter-optimised case at St. S1) and yellow dashed line (SST-dependent case at St. S1) overlap on the no-lagged x-axis.

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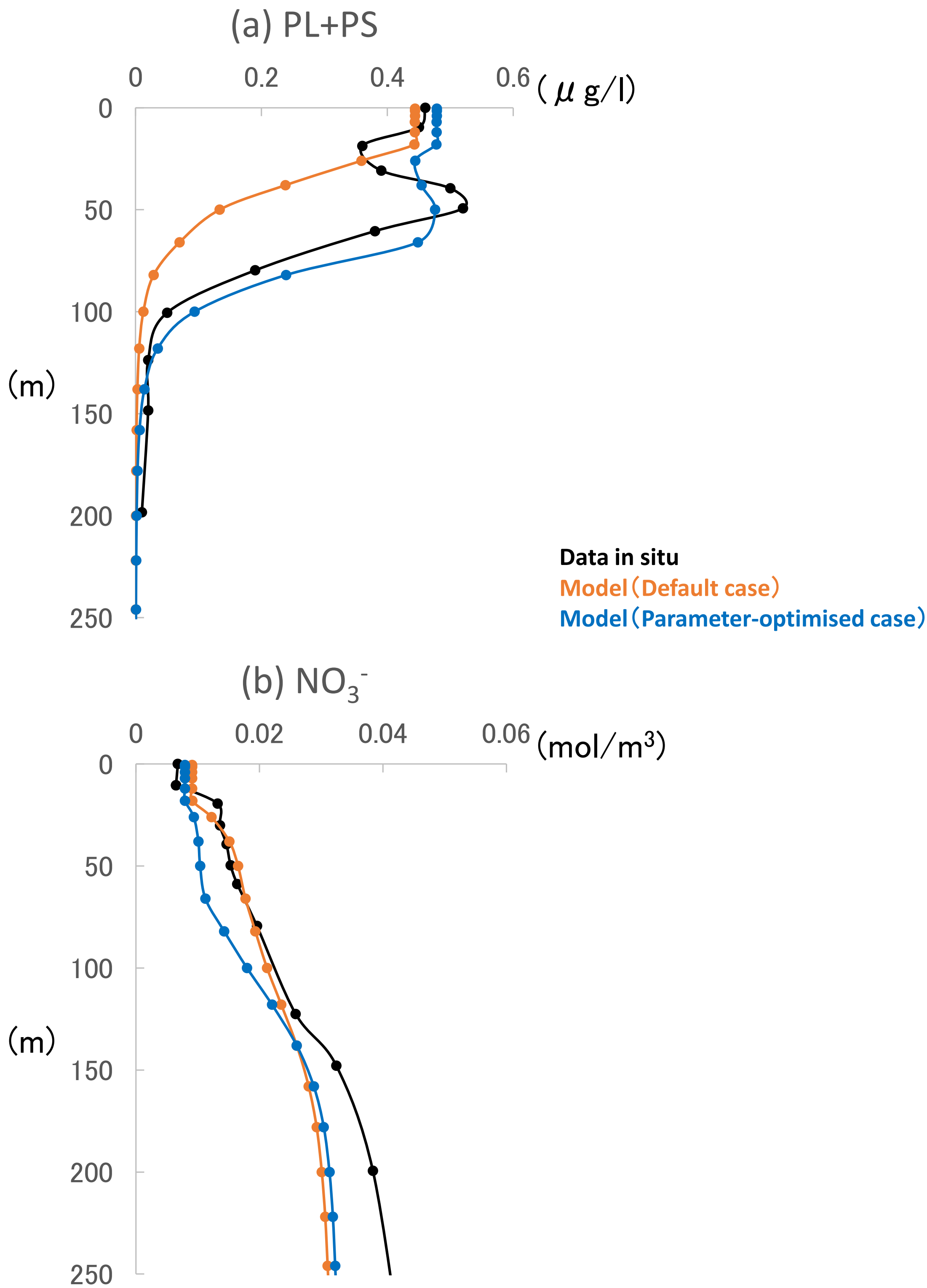

Figure 7. Vertical distributions of (a) phytoplankton (PL+PS) and (b) nitrate concentrations from the 3D model and in situ data at St. KNOT on 20th July, 1998.

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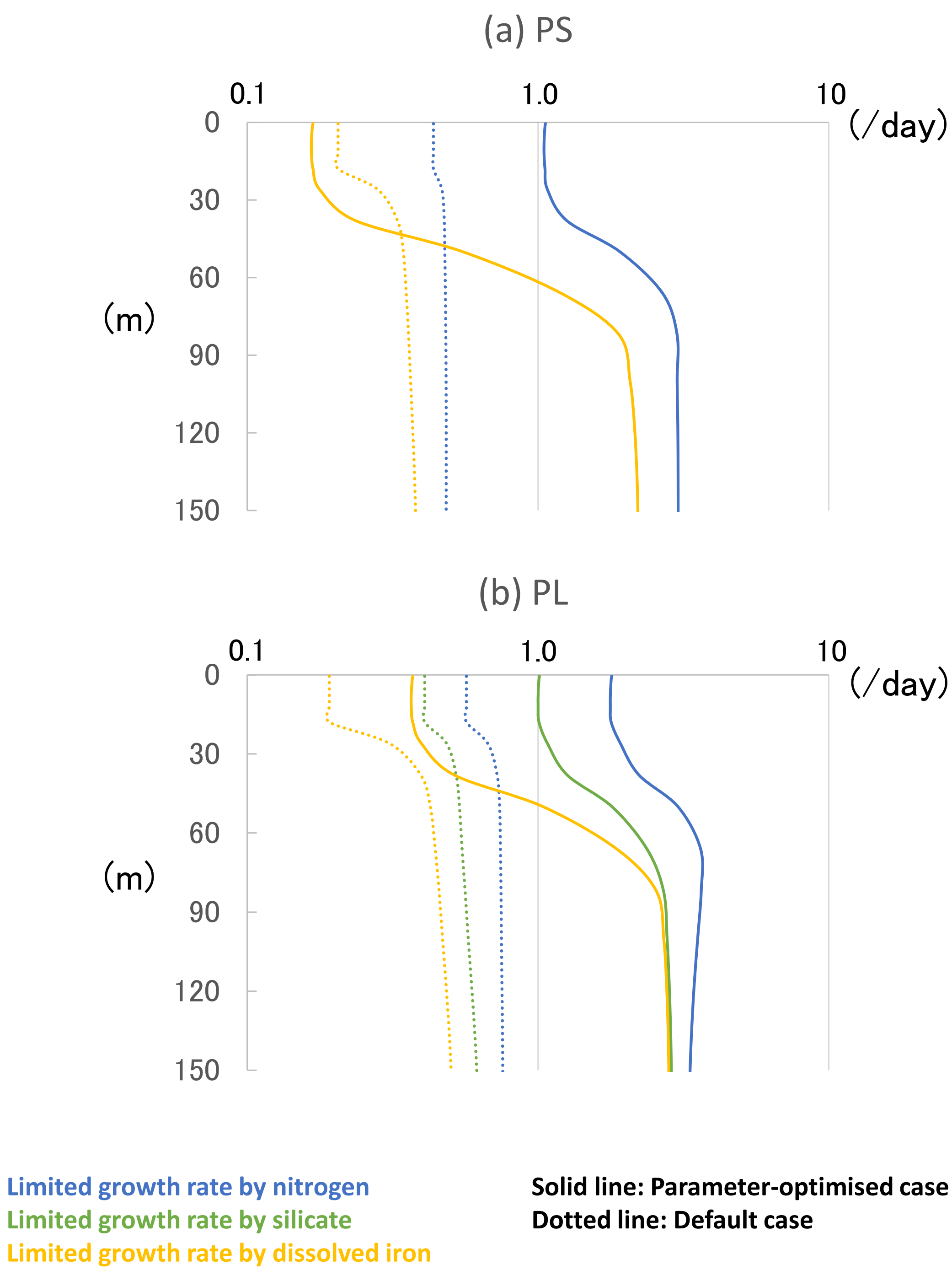

Figure 8. Vertical distributions of limited growth rates by nitrogen, silicate and dissolved iron simulated from the 3D model of (a) PS and (b) PL at St. KNOT on 20th July, 1998.

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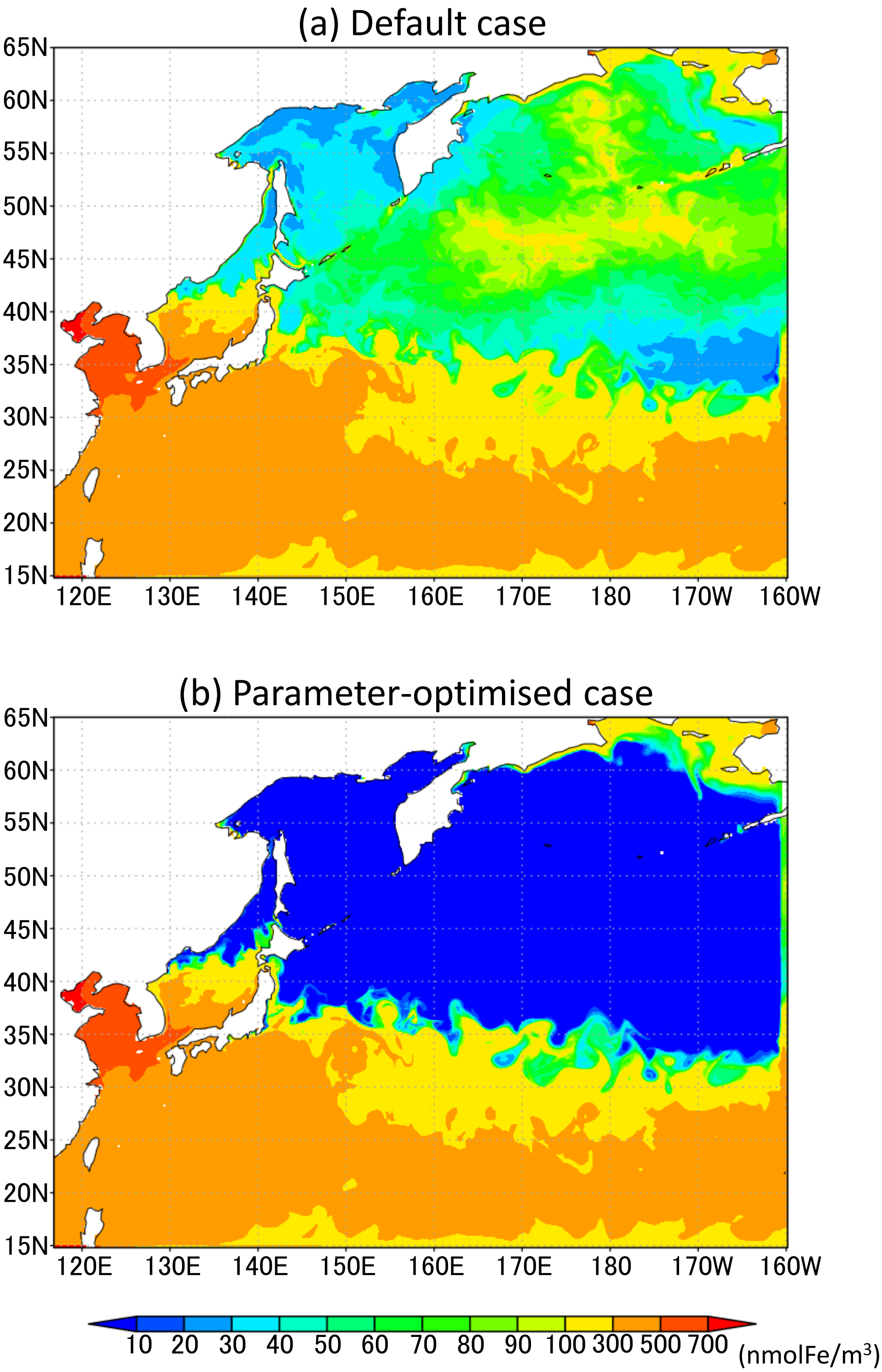

Figure 9. Horizontal distribution of dissolved iron in the surface sea water layer for July 1998; (a) the Default case and (b) the Parameter-optimised case.