

# 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 estimation of the parameters was based on a one-dimensional simulation that referenced satellite data for constraining the physiological parameters. The 3-D NSI-MEM optimised by the data assimilation improved the timing of a modelled plankton bloom in the subarctic and subtropical regions compared to the model without data assimilation. Furthermore, the model was able to improve not only surface concentrations of phytoplankton but also their subsurface maximum concentrations. Our results showed that surface data assimilation of physiological parameters from two contrasting observatory stations benefits the representation of vertical plankton distribution in the western North Pacific.

25 The Western North Pacific (WNP) region is a high-nutrient, low-chlorophyll (HNLC) region where biological productivity  
26 is lower than expected for the prevailing surface macronutrient conditions. There are both Western Subarctic Gyre and  
27 Subtropical Gyre comprising the Oyashio and the Kuroshio, respectively (Fig. 1 (a)). Between the gyres (i.e. the Kuroshio–  
28 Oyashio transition region), horizontal gradients of temperature and phytoplankton concentration in the surface water are  
29 generally large due to meanders in the Kuroshio extension jet and mesoscale eddy activity (Qiu and Chen, 2010; Itoh et al.,  
30 2015). The relatively low productivity in the HNLC region is due to low dissolved iron concentrations (e.g., Tsuda et al., 2003),  
31 because iron is one of the essential micronutrients for many phytoplankton species. The source of iron for the WNP region is  
32 not only from air-born dust but also from iron transported in the intermediate water from the Sea of Okhotsk to the Oyashio  
33 region (Nishioka et al., 2011). Since the WNP region exhibits many complex physical and biogeochemical characteristics as  
34 referred to above, it is difficult even for state-of-the-art eddy-resolving models to reproduce them.

35 Processes of growth, decay and interaction by plankton are critical to understand the oceanic biogeochemical cycles and the  
36 lower trophic level (LTL) marine ecosystems. There are many LTL marine ecosystem models ranging from simple nutrient,  
37 phytoplankton and zooplankton models to more complicated models including carbon-, oxygen-, silicate-, iron-cycles and so  
38 forth (e.g., Fasham et al., 1990; Edwards and Brindley, 1996; Lancelot et al., 2000; Yamanaka et al., 2004; Blauw et al., 2009).  
39 Coupling LTL marine ecosystem models to ocean general circulation models (OGCMs) and earth system models enables  
40 three-dimensional (3D) quantitative descriptions of the ecosystem and its temporally fine variability (e.g., Aumont and Bopp,  
41 2006; Follows et al., 2007; Buitenhuis et al., 2010; Sumata et al., 2010; Hoshiba and Yamanaka, 2016).

42 Physiological parameters are usually fixed in the models on the basis of local estimations and applied homogeneously to a  
43 basin-scaled ocean, although the values of physiological parameters should depend on the environments of regions. Moreover,  
44 physiological parameters have been often tuned up empirically and arbitrarily. The fact that the number of parameters increases  
45 with prognostic and diagnostic variables makes it more difficult to tune them. In order to reproduce observed data such as  
46 spatial distribution of phytoplankton biomass and timing of a plankton bloom, it is required to reasonably estimate the  
47 physiological parameters.

48 In previous studies using LTL marine ecosystem models, various approaches for data assimilation were introduced as  
49 methods of estimating optimal physiological parameters (e.g., Kuroda and Kishi, 2004; Fiechter et al., 2013; Toyoda et al.,  
50 2013; Xiao and Friedrichs, 2014). On the other hand, Shigemitsu et al. (2012) applied a unique assimilative approach to a LTL  
51 marine ecosystem model, using a mirco-genetic algorithm ( $\mu$ -GA) (Krishnakumar, 1990). For the western subarctic Pacific,  
52 they showed that the  $\mu$ -GA worked well in the one-dimensional (1D) nitrogen-, silicon- and iron regulated marine ecosystem  
53 model (NSI-MEM: Fig. 2), that was based on NEMURO (North pacific Ecosystem Model for Understanding Regional  
54 Oceanography: Kishi et al., 2007) but differed in the following points: (1) the introduction of an iron cycle, including dissolved  
55 and particulate iron, whereby the dissolved iron explicitly regulates phytoplankton-photosynthesis; (2) adoption of  
56 physiologically more consistent optimal nutrient-uptake (OU) kinetics (Smith et al., 2009) **instead of** the Michaelis–Menten

57 equation (Michaelis et al., 2011) and (3) the division of detritus into two types of small and large sizes that exhibit different  
58 sinking rates.

59 Our objective is to improve simulation of the LTL ecosystem in the WNP region by further introducing: (1) a physical field  
60 from an eddy-resolving OGCM with a horizontal resolution of  $0.1^\circ$  and (2) an assimilated physiological parameter estimation  
61 for two different phytoplankton groups. The details of the model and  $\mu$ -GA settings are described in Section 2. We compare  
62 the simulation results with/without the parameter optimisation to observed data, and confirm the effects of changing parameters  
63 in Section 3. We mainly focused on the seasonal variations of phytoplankton in the pelagic region. Finally, the results are  
64 summarized in Section 4.

## 65 **2 Model and data description**

### 66 **2.1 3D NSI-MEM**

67 We used the marine ecosystem model, NSI-MEM that includes two phytoplankton functional types (PFTs), namely non-  
68 diatom small phytoplankton (PS) and large phytoplankton representing diatoms (PL) (Fig. 2). In order to run the NSI-MEM  
69 in three-dimensional space, we used a physical field obtained from the Meteorological Research Institute Multivariate Ocean  
70 Variational Estimation for the WNP region (MOVE-WNP) (Usui et al., 2006). The MOVE-WNP system is composed of the  
71 OGCM (the Meteorological Research Institute community ocean model) and a multivariate 3D variational analysis scheme  
72 that synthesizes the observed information such as temperature, salinity and sea surface height. **The 3D variational analysis  
73 scheme added an increment to the temperature and salinity field, but the amount of water mass was conserved (Fujii and  
74 Kamachi, 2003).**

75 The model domain extends from  $15^\circ$  N to  $65^\circ$  N and  $117^\circ$  E to  $160^\circ$  W in the WNP region, with a grid spacing of  $1/10^\circ \times$   
76  $1/10^\circ$  around Japan and  $1/6^\circ$  to the north of  $50^\circ$  N and to the east of  $160^\circ$  E (Fig. 1 (a)). There are 54 vertical levels with layer  
77 thicknesses increasing from 1 m at the surface to 600 m at the bottom. The model is forced by factors including surface wind,  
78 heat flux and freshwater flux. The details of the surface forcing are presented by Tsujino et al. (2011). Short wave radiation  
79 input and dust flux were the same as those of a global climate model (Model for Interdisciplinary Research on Climate,  
80 MIROC; Watanabe et al., 2011). A part of the dust flux (3.5 %; Shigemitsu et al., 2012) was regarded as the iron dust, and  
81 1 % of the iron dust was assumed to dissolve into the sea surface (Parekh et al., 2004). The other iron dust was transported to  
82 the lower layers and dissolved, which was the same process as Shigemitsu et al. (2012). River run-off as a freshwater supply  
83 was from CORE ver. 2 forcing (Large and Yeager, 2009), in which the river source had the nitrate concentration value of 29  
84  $\mu\text{mol/l}$  (Conha et al., 2007) and the silicate concentration value of 102  $\mu\text{mol/l}$  adjusted in the range between  $\text{Si/N} = 0.2$  to 4.3  
85 (Jickells, 1998). Nitrate and silicate sources were only rivers, and iron supply was only from the dust in the model setting. In  
86 order to buffer artificial high concentrations near the side edge of the model domain, nutrients near the southern and eastern  
87 boundary of the model domain were only restored for 43 minutes to 3.6 hours to the values provided by the Meteorological  
88 Research Institute Community Ocean Model (MEM-MRI.COM) participating in MARine Ecosystem Model Intercomparison

89 Project ([https://pft.ees.hokudai.ac.jp/maremip/data/MAREMIPh\\_var\\_list.html](https://pft.ees.hokudai.ac.jp/maremip/data/MAREMIPh_var_list.html)). The physical field used in our ecosystem  
90 model had already been confirmed to reproduce realistic salinity, velocity and temperature fields in a previous study (Usui et  
91 al., 2006). Using a physical one-day averaged field, we ran the NSI-MEM to simulate the years between 1985 and 1998.

92 We divided the model domain into two provinces (green and yellow regions in Fig. 1 (b)) using the following province map  
93 instead of maps divided by latitude–longitude lines as in previous studies (e.g., Longhurst, 1995; Toyoda *et al.*, 2013). The  
94 province map is based on the dominant phytoplankton species and nutrient limitations (Hashioka et al., in preparation) and  
95 sets different ecosystem parameters (see details in Section 2.3) for each province (hereafter, ‘Parameter-optimised case: **OPT**’;  
96 Table 1). For each province, the respective parameters estimated by the  $\mu$ -GA and the 1D NSI-MEM were employed to  
97 those in the 3D NSI-MEM. A large gap in a horizontal-distribution of phytoplankton can appear on the  
98 boundary of the two provinces in Fig. 1 (b), due to a gap in the different parameter sets at the boundary. In  
99 order to smooth the gap in parameter values at the boundary between the two provinces in Fig. 1 (b), the parameters were  
100 varied as a function of the sea surface temperature (SST) annually averaged for 1998 (Fig. 1 (c)) for our ‘SST-dependent case:  
101 **SST-OPT**’ (Table 1). **While phytoplankton fluctuate with not only SST but also other surrounding conditions such as nutrient**  
102 **abundance in the real ocean (Smith and Yamanaka, 2007; Smith et al., 2009), we chose SST because  $\mu$ -GA optimization is**  
103 **conducted for physiological parameters of both phytoplankton and zooplankton (Table 2) and the SST directly affects**  
104 **physiology of both of them whereas nutrients and light were essentially related to phytoplankton.** The parameters were  
105 interpolated/extrapolated according to the following equation:

$$106 \quad P(x) = P_{St.S1} + (P_{St.KNOT} - P_{St.S1}) \times \frac{SST(x) - SST_{St.S1}}{SST_{St.KNOT} - SST_{St.S1}}, \quad (1)$$

107 where  $P(x)$ ,  $P_{St.S1}$  and  $P_{St.KNOT}$  are ecosystem parameters for a point ( $x$ ), St. S1 and St. KNOT, respectively. St. KNOT and  
108 St. S1 are typical observational points in the subarctic and subtropical regions (green- and yellow-coloured areas in Fig. 1 (b),  
109 respectively). We also conducted model experiments with the parameters similar to Shigemitsu et al. (2012) for the whole  
110 domain (hereafter ‘Control case: **CTRL**’, Table 1). The parameters of all the 3D experimental cases, shown in Table 1, were  
111 not changed either vertically or temporally. In the parameter-optimised and SST-dependent cases, the parameters were the  
112 same as the Control case from 1<sup>st</sup> January 1985 to 31<sup>st</sup> December 1996. During the next one year (1997), the simulations were  
113 spun-up with the optimised or SST-dependent parameters. Then, simulation results on 1<sup>st</sup> Jan. 1998 were used as initial  
114 conditions for the 1998-year simulations. The **parameter** values used in the control case were not changed during the 1985-to-  
115 1998 period. The simulation results for the last year (i.e., 1998) were analysed and compared to observational data of 1998.

## 116 2.2 Satellite and in situ data

117 Global satellite data for 1998 for phytoplankton (i.e. chlorophyll a) were obtained from the Ocean Colour Climate Change  
118 Initiative, European Space Agency, available online at <http://www.esa-oceancolour-cci.org/>, which utilises the data archives  
119 of ESAs MERIS/ENVISAT and NASAs SeaWiFS/SeaStar, Aqua/MODIS. The global satellite data which have the horizontal  
120 resolution of  $0.042^\circ$  were linearly interpolated to the grid (size  $1/10^\circ$  and  $1/6^\circ$ ) in the model domain (Fig. 1 (a)), and the

121 nitrogen-converted concentrations of both PL and PS were estimated **based on** a satellite PFT algorithm (Hirata et al., 2011).  
122 The  $\mu$ -GA cost function was defined from the 1998 monthly averaged PL and PS concentrations. The satellite data of daily  
123 temporal resolution were not useful due to many regions of missing value. Therefore, we discuss the results for the monthly  
124 scale in the present study.

125 Satellite data of the 1998 mean SST (horizontal grids of  $0.088^\circ$ ) from the AVHRR Pathfinder Project  
126 (<http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/>) were also used to conduct our SST-dependent case study using the  
127 same interpolation procedure as above. The data was linearly interpolated between satellite- and model grids, which could  
128 introduce some uncertainty to the satellite data. In addition, the use of the global chlorophyll data in the regional study for the  
129 WNP region could be another error source of the observational data: the previous study (Gregg and Casey, 2004) showed that  
130 the regional Root Mean Square log % errors of the satellite data ranged from 24.7 to 31.6 in the North Pacific.

131 To validate the vertical distribution of the model results, we utilised in situ data of phytoplankton and nutrients in 1998 along  
132  $165^\circ$  E section taken from World Ocean Database 2013 (<https://www.nodc.noaa.gov/OC5/WOD13/>), and at St. KNOT ( $44^\circ$  N,  
133  $155^\circ$  E) obtained from the web site (<http://www.mirc.jha.or.jp/CREST/KNOT/>) (Tsurushima et al., 2002).

### 134 **2.3 1D NSI-MEM process**

135 The 1D NSI-MEM used in Shigemitsu et al. (2012) was employed as an emulator to determine the optimal set of ecosystem  
136 parameters at St. KNOT ( $44^\circ$  N,  $155^\circ$  E) and S1 ( $30^\circ$  N,  $145^\circ$  E), respectively. We modified the 1D NSI-MEM of Shigemitsu  
137 et al. (2012) by increasing the number of vertical layers to 54 and introducing the vertical advection of the 3D simulation.  
138 Twenty-three of 107 physiological parameters in the NSI-MEM were selected, as shown in Table 2, which were responsible  
139 for PL and PS biomass relevant to the photosynthesis and grazing of zooplanktons. In the previous study, Yoshie et al. (2007)  
140 also suggested that some parameters in the 23 parameters were relatively influential on PS and PL, more than the other  
141 physiological parameters such as those for sinking process of particulate matters (PON, OPAL in Fig. 2). The other parameters  
142 of the NSI-MEM were the same as those in the Control case. The initial (1<sup>st</sup> January 1998) and boundary conditions during the  
143 integration period were applied from those in the 3D model.

### 144 **2.4 $\mu$ -GA implementation**

145 The  $\mu$ -GA procedure requires a cost function. To define the cost function (Eq. (2)), satellite PFT data were used as reference  
146 values for the  $\mu$ -GA because satellite data have higher temporal and spatial resolution than in situ data. The  $\mu$ -GA procedure  
147 works in such a way that a parameter set of the lowest cost is retained, and then a new parameter set is determined by crossover  
148 and mutation methods using the retained set. An optimised parameter set is finally provided by repeating the process multiple  
149 times.

150 Running the 1D NSI-MEM with the  $\mu$ -GA, the 23 optimal parameters were obtained through the following process:

151 **Step 0** Define a range of parameter values (Table 2) based on previous studies (e.g., Jiang et al., 2003; Fujii et al., 2005;  
152 Yoshie et al., 2007) and prepare 23 model runs being the same number of estimated parameters before running the  $\mu$ -GA.

153 **Step 1** Generate 23 initial random parameter sets using the  $\mu$ -GA.

154 **Step 2** Evaluate the 23 model runs with the different parameter sets using the following cost function:

155 
$$Cost = \sum_i^I \frac{1}{N_i} \sum_j^{N_i} \frac{1}{\sigma_i^2} (m_{ij} - d_{ij})^2, \quad (2)$$

156 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  
157 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  
158 PL and PS were the same low value ( $\sigma_{PL} = 0.1 \mu\text{mol/l}$  and  $\sigma_{PS} = 0.1 \mu\text{mol/l}$ ) as some weights used in Shigemitsu et al. (2012).

159 **Step 3** Determine the best parameter set and carry it forward to the next model run (or the next ‘generation’) (elitist strategy).

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

165 **Step 5** If the difference between the maximum and minimum cost function values of the model runs becomes smaller than  
166 a threshold value, renew all the parameter sets randomly except for the best-performed set for efficiently escaping from a local  
167 solution; the cost function may have local minimums.

168 **Step 6** Repeat the procedure from Step 2 to Step 5 until the best parameter set is well converged within 2,000 generations  
169 (times) in the present study.

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

### 173 **3. Results and discussion**

#### 174 **3.1 1D model**

175 The 1D NSI-MEM was employed to determine ecosystem parameters for the 3D-model simulation. The 1D simulation results  
176 (Fig. 3) of Parameter-optimised case (blue dashed lines) are clearly closer to satellite data (solid lines) than those of Control  
177 case (orange dashed lines). The cost-function values estimated by the 1D simulations in the Parameter-optimised case (OPT),  
178 1.61 and 0.17 at KNOT and S1, are also about 8 and 6 times smaller than those in the Control case (CTRL), 13.55 and 1.11,  
179 respectively (not shown).

180 The total biomass (PL+PS) at St. KNOT in the subarctic region is larger than that at St. S1 in the subtropical region. The PS  
181 biomass (Fig. 3 (a), (c)) is larger than the PL biomass (Fig. 3 (b), (d)) at both St. KNOT and St. S1. As for the relative ratio of  
182 PL to the total biomass, the relative ratio at St. KNOT is larger than that at St. S1. These results are consistent with the general  
183 understanding that biomass in the subarctic region is larger than that in the subtropical region, and that the ratio of PL to the

184 total biomass in the subarctic region is also larger than that in the subtropical region.

185 Seasonal variations in the **OPT** for the two stations simulated with the satellite data assimilation are also improved drastically  
186 in comparison to the **CTRL**. The seasonal variations of PS and PL at St. KNOT (Fig. 3 (a), (b)) in the **OPT** have relatively  
187 high concentrations with a winter peak of  $630 \mu\text{molN/m}^3$  and  $130 \mu\text{molN/m}^3$ , respectively. In the **CTRL** of PS, however, there  
188 is a spring (May) peak of  $180 \mu\text{molN/m}^3$ , and the PL concentration remains low through the year. At St. S1, the PS seasonal  
189 variations tend towards high-concentration in winter and low concentration from summer to autumn in the **OPT**, while the PS  
190 concentration, in the **CTRL**, in summer to autumn is higher than that in winter. **The PL concentrations of the two model cases**  
191 **are almost zero, and that of satellite is also remarkably small ( $< 21.5 \mu\text{molN/m}^3$ ).** The parameter-optimisation process by 1D  
192 model works well in terms of the seasonal variations of surface phytoplankton.

### 193 3.2 3D model

194 The parameter set estimated by the 1D model at St. KNOT and St. S1 were applied to the 3D simulation (Fig. 4). The seasonal  
195 features in the 3D simulation are generally similar to those seen in the 1D simulation (i.e. relatively small seasonal variations  
196 of PS biomass in the subarctic region and a relatively high winter biomass in the **OPT**, than the **CTRL**). At St. KNOT, for  
197 instance, there is the smaller difference between the high ( $575 \mu\text{molN/m}^3$  in January) and low ( $398 \mu\text{molN/m}^3$  in October)  
198 concentrations in the **OPT** than the high ( $568 \mu\text{molN/m}^3$  in July) and low ( $59 \mu\text{molN/m}^3$  in January) in the **CTRL**. The PL  
199 biomass features are also similar to those of the PS biomass mentioned above, except that the PL biomass is lower in the  
200 subtropical region in the **OPT** than in the **CTRL**. Seasonal peaks of PS and PL biomass also have the same features as those in  
201 the 1D simulations (i.e. the PS bloom in the **OPT** occurs from winter to spring (Fig. 4 (c), (g)), but that in the **CTRL** occurred  
202 in summer (Fig. 4 (b)). The SST-dependent (**SST-OPT**) results are discussed later in Section 3.5.

203 Higher phytoplankton concentrations ( $> 1000 \mu\text{molN/m}^3$ ) were found in coastal areas throughout the year in the satellite data.  
204 The model could not simulate these high concentrations in the coastal areas. This may be due to the inaccuracy of the satellite  
205 data resulting from the high concentrations of dissolved organic material and inorganic suspended matter (e.g., sand, silt and  
206 clay), and/or due to the uncertainty in the model introduced by unaccounted coastal dynamics such as small-scale mixing  
207 processes (e.g., estuary circulation, tidal mixing and wave by local wind forcing). Any nutrient flux from the seabed was not  
208 considered in this study, which also may induce the low-biased phytoplankton biomass close to the coast. Hereafter, we focus  
209 on phytoplankton seasonal fluctuation in the pelagic and open ocean in this study.

210 Lagged (within  $\pm 2$  months) correlation coefficients were calculated for the monthly time series of the surface phytoplankton  
211 concentration between the simulations and satellite data in each grid (Fig. 5). Spatial distributions of the correlation show that  
212 the larger coefficient-value region ( $r > 0.7$ ) of the **OPT** (Fig. 5 (b)) in  $25^\circ \text{N}$  -  $45^\circ \text{N}$  becomes extended than that of the **CTRL**  
213 (Fig. 5 (a)) by 71 %, though the mean value of the **OPT** in the north part of  $50^\circ \text{N}$  ( $r=0.18$ ) is smaller than that in the **CTRL**  
214 ( $r=0.66$ ). The result is similar in the **SST-OPT** (Fig. 5 (c)). Our parameter estimation significantly improved the simulation  
215 result of the horizontal distribution of phytoplankton in the lower latitude ( $< 45^\circ \text{N}$ ), but not in the region ( $> 50^\circ \text{N}$ ) closer to  
216 the coasts.



217 Fig. 6 (a)-(c) shows vertical distributions of total phytoplankton along the 165° E transect. The parameter optimisation  
218 improves the distributions in that the phytoplankton maximum in the subsurface more deepens than that of CTRL (Fig. 6 (b-  
219 c)). Parameter-optimised total biomass through the vertical section above 200 m is also closer to the observed data than the  
220 CTRL. It is an interesting result because the vertical distribution is improved due to the data-assimilation process using only  
221 surface satellite data. The detailed reason is discussed in Section 3.4. In the nutrients distribution along the 165° E (Fig. 6 (d)  
222 to (i)), the concentrations of OPT (Fig. 6 (f), (i)) are lower than those of CTRL (Fig. 6 (e), (h)). The mean values along the  
223 transect of nitrate and silicate are 0.011 molN/m<sup>3</sup> and 0.025 molSi/m<sup>3</sup>, respectively, in the OPT, 0.014 molN/m<sup>3</sup> and 0.034  
224 molSi/m<sup>3</sup> in the CTRL, and 0.012 molN/m<sup>3</sup> and 0.022 molSi/m<sup>3</sup> in the observation (Fig. 6 (d), (g)). OPT than CTRL is better  
225 consistent with the observation, though the nitrate observed value is higher than the simulations in the surface (< 80 m) and  
226 subarctic (> 42° N) region. While nitrate is not the limiting nutrient compared with iron and silicate for phytoplankton's  
227 photosynthesis in the subarctic region (the detail is also mentioned in Section 3.4), the data-assimilation process improves even  
228 the nutrient field in addition to the phytoplankton field.

229 As for the temperature and salinity along the vertical section (Fig. 7), the physical field used by the model simulations is well  
230 reconstructed in terms of mixed layer depth and transition from the subarctic and the subtropical regions. Judging from the  
231 temperature and salinity distributions in the subarctic region (> 42° N), the water columns are well mixed vertically both in  
232 the observation and the simulation, and intensely stratified in the subtropical region (< 36° N). There is the transition region  
233 (36° N -40° N) of temperature between the subtropical and the subarctic.

### 234 3.3 Amplitude and phase of seasonal variation of phytoplankton

235 The model performances were significantly improved in terms of spatial distributions of phytoplankton biomass, as a result  
236 of the parameters optimized in Section 3.2. Also at the specific stations on the St. KNOT and St. S1 where the parameters were  
237 estimated by 1D simulations, seasonal variation in total phytoplankton concentrations in the OPT were generally better  
238 reproduced to those in the satellite data than those in the CTRL (Fig. 8). At St. KNOT (Fig. 8 (a)), the phytoplankton bloom  
239 in the OPT occurs in winter, and the phytoplankton bloom in the CTRL occurs in summer in an anti-phase to that of the satellite.  
240 At St. S1 (Fig. 8 (b)), OPT case reasonably captures the timing of the phytoplankton bloom by the satellite, although the  
241 amplitude is slightly overestimated. The seasonal variations of the PS and PL concentrations are similar to those of the total  
242 phytoplankton (not shown) in both cases.

243 Figure 9 shows comparisons of the amplitude and the phase of seasonal variations between three model cases (CTRL, OPT  
244 and SST-OPT) and the satellite data. The radius shows the amplitude of seasonal variation for each of the modelled cases  
245 relative to the satellite data, and the angle from the x-axis shows the maximum concentration time lag for each of the model  
246 cases (i.e. the point (1, 0) shown as 'True' is a perfect match to the satellite data). At St. KNOT, the OPT (blue solid vector)  
247 exhibits the phase closest to the satellite data among the three modelled cases. The ratios of the amplitudes to the satellite data  
248 were as follows: 1.00 for the OPT (blue solid vector), 1.08 for the SST-OPT (yellow solid vector) and 1.24 for the CTRL  
249 (orange solid vector). The timings of the maximum concentration were as follows: a two-month delay for the OPT, a three-



250 month delay for the **SST-OPT** and a six month delay (anti-phase) for the **CTRL**. The timing of the **OPT** at St. S1 (blue **dotted**  
251 vector) was improved, though its seasonal amplitude was not.

252 Optimisation of the physiological parameters by assimilating the satellite data at the two stations improved the seasonal  
253 variations of the phytoplankton concentrations such as the timing of the maximum concentration and the seasonal amplitude  
254 of the WNP region.

### 255 **3.4 Vertical distributions of phytoplankton and nutrients concentrations at St. KNOT**

256 The model-simulated vertical distributions of phytoplankton, nitrate and silicate concentrations at St. KNOT on 20<sup>th</sup> July,  
257 1998 were compared with the observed ones on the same day (Fig. 10). The vertical distribution of phytoplankton (Fig. 10 (a))  
258 by 3D simulations in the **OPT** (solid blue line) is closer to the in situ data (black line) as compared to the **CTRL** (solid orange  
259 line): the maximum phytoplankton concentration for the **OPT** and the in situ data are located in the subsurface around a depth  
260 of 50 m, while there is no subsurface maximum in the **CTRL**. The differences of the biomass between the **OPT** and **CTRL**  
261 become especially larger in the subsurface layer (40 m to 80 m). Thus, better physiological parameterisation through the data  
262 assimilation improves not only the surface concentration but also the important characteristics of vertical plankton distribution  
263 such as the subsurface maximum. This is an interesting improvement because the physiological parameters are optimised using  
264 only surface satellite data.

265 The vertical profile of phytoplankton obtained from the 3D simulation **reproduces** the observed ones better than the 1D  
266 simulation, too (Fig. 10 (a)). In addition, the difference in 3D (solid lines) and 1D (**dashed** lines) is larger in the upper layer (<  
267 80 m) than in the lower layer (> 100 m). Moreover error bars **and shade** for the 3D simulations, which depict the maximum  
268 and minimum values in  $\pm 0.3^\circ$  around the exact grid of St. KNOT, are also larger in the upper layer than the lower layer. **We**  
269 **assume that horizontal advection such as mesoscale eddies is in the O (100 km) radius scale and  $\geq 16$  weeks' lifetime (e.g.,**  
270 **Chelton et al., 2011) and can be detected within the  $\pm 0.3^\circ$  range in the physical field.** These suggests that effects of horizontal  
271 advection is important for the daily reconstruction of the profile in the upper layer as the effects are not included in the 1D  
272 model.

273 In the NEMURO, the predecessor version of the NSI-MEM, the amplitude and timing of phytoplankton blooms are  
274 predominantly controlled by the photosynthesis rate (i.e. bottom-up effect of nutrient dependence) rather than the grazing rate  
275 (i.e. top-down effect of zooplanktons) (Hashioka et al., 2013). The former is determined by the limited growth rate **which is a**  
276 **limitation function of growth rate by either nitrogen ( $\text{NH}_4+\text{NO}_3$ ), silicate ( $\text{Si}(\text{OH})_4$ ) or dissolved iron (FeD)** (refer to Eq. (A15)  
277 and Eq. (A23) in Shigemitsu et al., 2012). **The smallest limited growth rate among the three nutrient groups (i.e.  $\text{NH}_4+\text{NO}_3$ ,**  
278  **$\text{Si}(\text{OH})_4$  and FeD) is used to limit the rate of phytoplankton's photosynthesis.** For PS and PL in the **OPT** and **CTRL**, the  
279 dissolved-iron-limited growth rates (**red lines in Fig. 11**) dominate the photosynthesis, while the silicate-growth rate is the  
280 second-largest limiting factor for PL (**green lines in Fig. 11 (b)**). The mean iron-growth rates increase remarkably below a  
281 depth of 50 m (e.g., **0.37 to 1.86 day<sup>-1</sup>** and **0.48 to 2.47 day<sup>-1</sup>** in PS and PL, respectively) because of the parameter optimisation  
282 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

283 seems to be accelerated, particularly in the subsurface layer, leading to an increase of the phytoplankton biomass (Fig. 10 (a)).  
284 The larger biomass of phytoplankton may also consume more nitrate and silicate nutrients resulting in a lower nitrate  
285 concentration above a depth of 140 m (Fig. 10 (b)) and silicate (Fig. 10 (c)) as compared to that in the CTRL. The vertical  
286 gradients of nitrate and silicate in the OPT are closer to the observed data than that in the CTRL. In the OPT, nitrate and silicate  
287 concentrations are less than the data in situ, both at the depth of around 50 m (0.010 molN/m<sup>3</sup> and 0.015 molSi/m<sup>3</sup> in the OPT;  
288 0.015 molN/m<sup>3</sup> and 0.025 molSi/m<sup>3</sup> in the observation) and 200 m (0.031 molN/m<sup>3</sup> and 0.069 molSi/m<sup>3</sup>; 0.038 molN/m<sup>3</sup> and  
289 0.085 molSi/m<sup>3</sup>, respectively), while those at the depth of around 50 m in the CTRL (0.017 molN/m<sup>3</sup> and 0.037 molSi/m<sup>3</sup>) is  
290 higher than those in the OPT in which much smaller gradients than the observed gradients are found. In the upper layer, the  
291 nutrients are adequately supplied to phytoplankton as a result of the parameter optimisation. As in the lower layer below the  
292 depth of 120 m, the nutrient concentrations seem to be also determined by physical processes in the ocean-basin scale, not  
293 only local biological processes.

294 The change of the dissolved-iron-limited growth rates by optimisation results in the lower concentration of dissolved iron in  
295 the subarctic area (Fig. 12) because of the greater consumption of FeD by the phytoplankton than in the CTRL. The result is  
296 so far consistent with the conception of a HNLC region in the North Pacific Ocean (Moore et al., 2013), in spite that our model  
297 does not include iron source from the Sea of Okhotsk to the WNP region as another iron source (Nishioka et al., 2011). A  
298 further improvement is expected by adding such an iron supply into our model.

### 299 3.5 Physiological parameter changes with ambient conditions

300 The SST-OPT (i.e. smoothed changing parameters) was compared to the OPT (i.e. boundary-gap parameters). The horizontal  
301 distribution of the PS and PL concentrations in the SST-OPT were not significantly different from those in the OPT (Fig. 4)  
302 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  
303 Fig. 4 (h)), and the region adjacent to the Kuroshio Extension (around 40° N during July to October in Fig. 4 (h)). The former  
304 exception was due to the extrapolation of parameters with high SST and the latter was due to smoothing of parameters between  
305 the St. KNOT and St. S1 stations. The simulated seasonal variations of phytoplankton concentration in the SST-OPT was  
306 slightly worse than those in the OPT at the two stations (Fig. 9). The ratios of the seasonal amplitudes at St. S1, for instance,  
307 were 2.33 for the OPT and 2.39 for the SST-OPT. The maximum concentration for the both cases were found in the same  
308 month (March) as that for the satellite data (they overlap each other on the no-lagged x-axis in Fig. 9). However, a smoothed  
309 set of parameters dependent on the SST prevents the artificial gap of the parameter value at the fixed boundary between the  
310 two provinces.

311 Physiological parameters represented in ecosystem models were optimized in reference to 1998 while they may change with  
312 time. In addition, they may change with the surrounding conditions in the real ocean (e.g., SST, nutrient abundance, light  
313 intensity). Smith and Yamanaka (2007) and Smith et al. (2009) suggest the significance of photo-acclimation and nutrient  
314 affinity acclimation. Phytoplankton cells change their traits (e.g., nutrient channel, enzyme) in response to ambient nutrient  
315 concentrations, and typically large (small) cells adapt to low (high) light and high (low) nutrient concentrations (Smith et al.,

316 2015). In the NSI-MEM, the effect of nutrient-uptake responses by plankton acclimated to different ambient nutrient conditions  
317 is applied as an OU kinetic formulation, but the effect of photo-acclimation has not yet been introduced due to the difficulties  
318 and complexities of the scientific interpretation (Schartau et al., 2016). **However, incorporating temporal variation in the**  
319 **physiological parameters may be effective in the data assimilation process.**

#### 320 **4 Conclusions**

321 We extended a LTL marine ecosystem model, NSI-MEM, into a 3D coupled OGCM. We also used a data assimilation  
322 approach for two different PFTs in the WNP region: non-diatom PS and PL. Twenty-three **ecosystem** parameters in the NSI-  
323 MEM were estimated using a 1D emulator with a  $\mu$ -GA parameter-optimisation procedure. By applying the optimised  
324 parameters to the 3D NSI-MEM, the model performances were improved in terms of the seasonal variations of phytoplankton  
325 biomass, including the timing of the plankton bloom in the surface layer, compared to those using prior parameter values  
326 (Control case). **Notably, the vertical distribution of phytoplankton such as the subsurface maximum layer were also improved**  
327 **via the parameter optimisation, compared to that in the Control case. Thus, it was demonstrated that the 3D simulation**  
328 **performed better than the 1D simulation even to reproduce the vertical profile of phytoplankton.**

329 Physiological parameters in this study were systematically determined by a  $\mu$ -GA within the range of those used by numerical  
330 models in previous studies. **While our parameter estimation improved modelling skill of temporal and spatial variability of PL**  
331 **and PS in the WNP, the estimated parameter values themselves should also be confirmed with sufficient amount of data when**  
332 **they become available, in order to increase our confidence towards mechanistic and numerical understanding of the**  
333 **phytoplankton dynamics observed.**

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339 Atmosphere and Ocean Research Institute, The University of Tokyo. The phytoplankton satellite data were gathered by the  
340 Ocean Colour Climate Change Initiative, ESA (European Space Agency). The SST-satellite data was provided by the National  
341 Oceanic and Atmospheric Administration Pathfinder project in GHRSSST (The Group for High Resolution Sea Surface  
342 Temperature) and the US National Oceanographic Data Center. Data in situ used in this study were taken from World Ocean  
343 Database 2013 and Ocean Time-series Program in western North Pacific.

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471



472 Table

473

474 Table 1. List of experiments

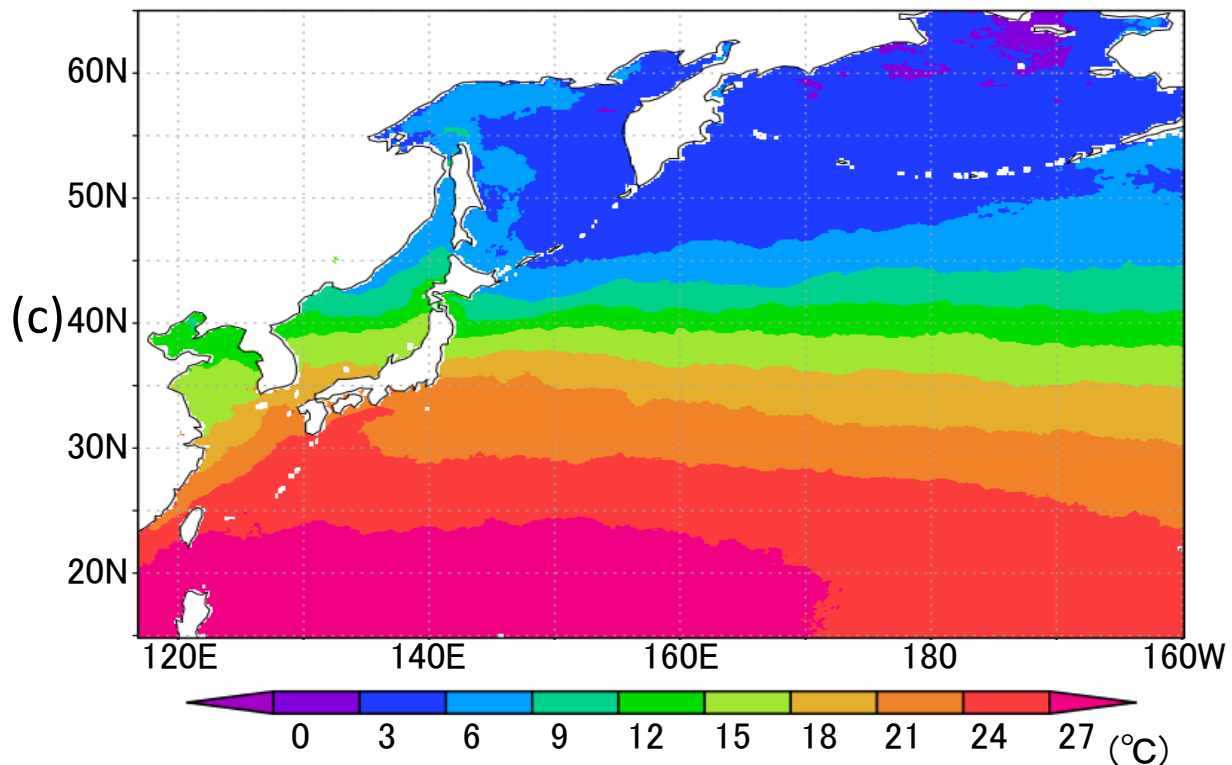
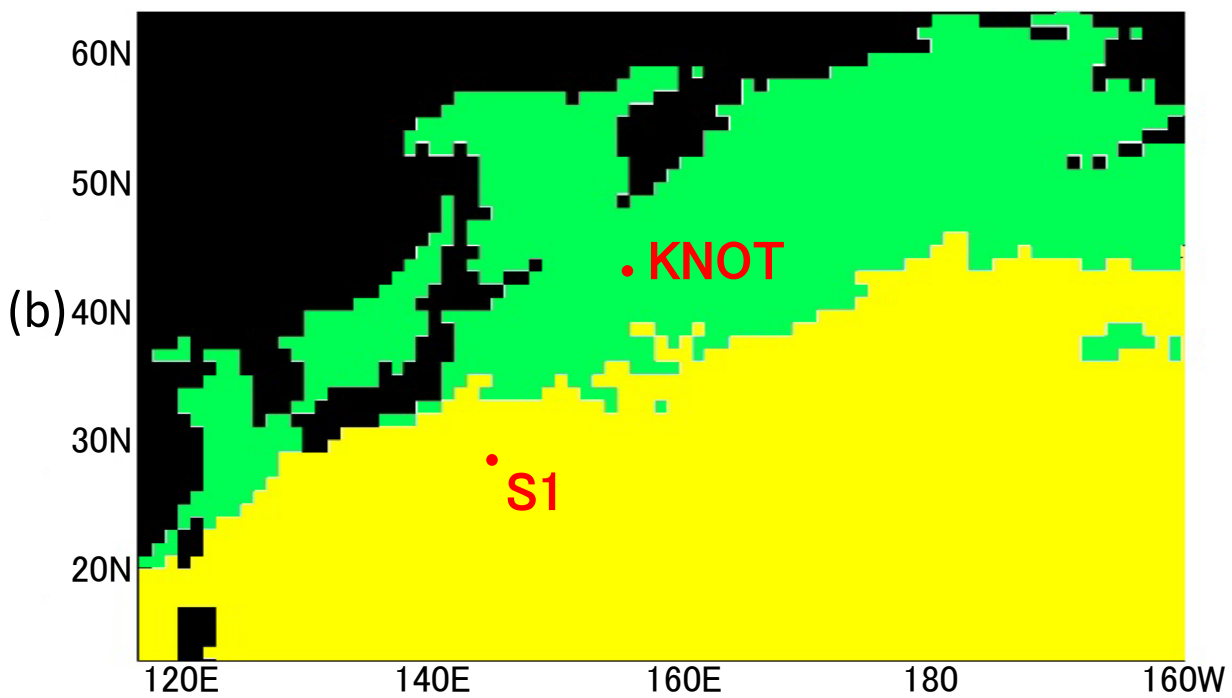
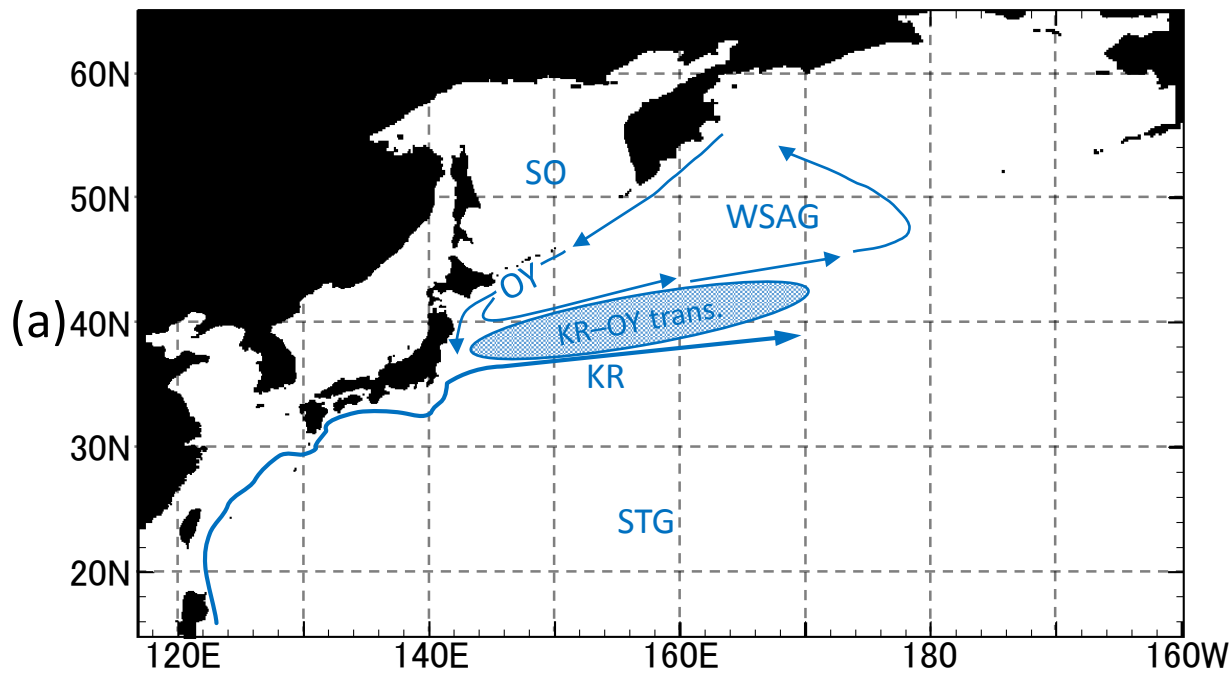
	Experiment name	Content of experiment
1D model experiments	Control	Use the almost same parameters as those in Shigemitsu et al. (2012)
	Parameter-optimised	Optimise the parameters with $\mu$ -GA at St. KNOT and St. S1
3D model experiments	Control	The same as Control of 1-D model but applied to 3-D simulation
	Parameter-optimised	The same as Parameter-optimised of 1-D model but applied to 3-D simulation for two provinces of Fig. 1 (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

475

476 Table 2. NSI-MEM physiological parameters estimated by the  $\mu$ -GA. Max and Min values prescribe the upper and  
 477 lower bounds of the parameter variations used in the previous studies. St. KNOT and St. S1 indicate optimal  
 478 estimated values in the provinces of Fig. 1 (b) while Control values are not optimised parameter values,  
 479 and the values of Shigemitsu et al. (2012) are the parameters of the previous study.

Parameter	Symbol	Min	KNOT	S1	Control	Shigemitsu et al. (2012)	Max	Unit	Sources of Min and Max range
PS Potential maximum growth rate at 0°C	$V_{0,PS}$	0.1	2.7	0.7	0.6	0.6	3.2	/day	Shigemitsu et al. (2012)
PS Potential maximum affinity for $NO_3$	$A_{0,NO_3,PS}$	1	454	436	30	282	512	l/molN · s	Shigemitsu et al. (2012)
PS Half saturation constant for $NO_3$	$K_{NO_3,PS}$	0.5	1.871	2.9194	1	1	3	$\mu$ molN/l	Chai et al. (2002), Eslinger et al. (2000)
PS Half saturation constant for $NH_4$	$K_{NH_4,PS}$	0.05	0.1225	0.2582	0.1	0.1	1	$\mu$ molN/l	Chai et al. (2002), Eslinger et al. (2000)
PS Half saturation constant for FeD	$K_{FeD,PS}$	0.035	0.1	0.0602	0.04	0.05	0.1	nmol/l	Kudo et al. (2006), Price et al. (1994)
PS Temperature coefficient for photosynthetic rate	$k_{PS}$	0.0392	0.0693	0.065	0.0693	0.0693	0.0693	/degC	Eslinger et al. (2000), Fujii et al. (2005)

PS Mortality rate at 0°C	$M_{PS0}$	0.012075	0.012075	0.043212	0.0585	0.0585	0.05878	$l/\mu\text{molN} \cdot \text{day}$	Fujii et al. (2005), Sugimoto et al. (2010)
PL Potential maximum growth rate at 0°C	$V_{0,PL}$	0.1	3.2	1.5	1.2	0.8	3.2	/day	Shigemitsu et al. (2012)
PL Potential maximum affinity for $\text{NO}_3^-$	$A_{0,\text{NO}_3,PL}$	1	437	171	10	252	512	$l/\text{molN} \cdot \text{s}$	Shigemitsu et al. (2012)
PL Half saturation constant for $\text{NO}_3^-$	$K_{\text{NO}_3,PL}$	0.5	3	2.9194	3	3	3	$\mu\text{molN/l}$	Eslinger et al. (2000), Jiang et al. (2003)
PL Half saturation constant for $\text{NH}_4^+$	$K_{\text{NH}_4,PL}$	0.5	0.5	1.3129	0.3	0.3	2.3	$\mu\text{molN/l}$	Eslinger et al. (2000), Fujii et al. (2005)
PL Half saturation constant for $\text{Si(OH)}_4$	$K_{\text{SiL},PL}$	3	6	4.2857	6	6	6	$\mu\text{mol/l}$	Yoshie et al. (2007)
PL Half saturation constant for FeD	$K_{\text{FeD},PL}$	0.05	0.05	0.0887	0.09	0.1	0.2	$\text{nmol/l}$	Coale et al. (2003)
PL Temperature coefficient for photosynthetic rate	$k_{PL}$	0.0392	0.0693	0.0392	0.0693	0.0693	0.0693	/degC	Eslinger et al. (2000), Fujii et al. (2005)
PL Mortality rate at 0°C	$M_{PL0}$	0.029	0.036941	0.034956	0.029	0.029	0.05878	$l/\mu\text{molN} \cdot \text{day}$	Fujii et al. (2005), Yamanaka et al. (2004)
ZS Maximum rate of grazing PS at 0°C	$G_{RmaxS}$	0.3	0.7933	0.3	0.31	0.4	4	/day	Yoshie et al. (2007), Yoshikawa et al. (2005)
ZS Threshold value for grazing PS	$PS_{ZS^*}$	0.04	0.364	0.364	0.043	0.043	0.364	$\mu\text{molN/l}$	Eslinger et al. (2000), Sugimoto et al. (2010)
ZL Maximum rate of grazing PS at 0°C	$G_{RmaxL,PS}$	0.05	0.05	0.05	0.1	0.1	0.541	/day	Eslinger et al. (2000), Fujii et al. (2005)
ZL Maximum rate of grazing PL at 0°C	$G_{RmaxL,PL}$	0.135	0.251	0.135	0.49	0.4	0.541	/day	Fujii et al. (2005)
ZL Threshold value for grazing PS	$PS_{ZL^*}$	0.01433	0.043	0.043	0.04	0.04	0.043	$\mu\text{molN/l}$	Eslinger et al. (2000), Fujii et al. (2005)
ZL Threshold value for grazing PL	$PL_{ZL^*}$	0.01433	0.043	0.018426	0.04	0.04	0.043	$\mu\text{molN/l}$	Eslinger et al. (2000), Fujii et al. (2005)
ZP Maximum rate of grazing PL at 0°C	$G_{RmaxP,PL}$	0.1	0.4	0.1429	0.2	0.2	0.4	/day	Eslinger et al. (2000)
ZP Threshold value for grazing PL	$PL_{ZP^*}$	0.01433	0.043	0.018426	0.04	0.04	0.043	$\mu\text{molN/l}$	Eslinger et al. (2000), Fujii et al. (2005)



**Figure 1.** (a) Model domain in the WNP region of the 3D NSI-MEM. Blue arrows and symbols depict a schematic representation of the main circulation features in the WNP (KR: Kuroshio, OY: Oyashio, KR-OY trans.: the Kuroshio–Oyashio transition region, STG: Subtropical Gyre region, WSAG: Western Subarctic Gyre and SO: the sea of Okhotsk). (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 (SST-dependent case).

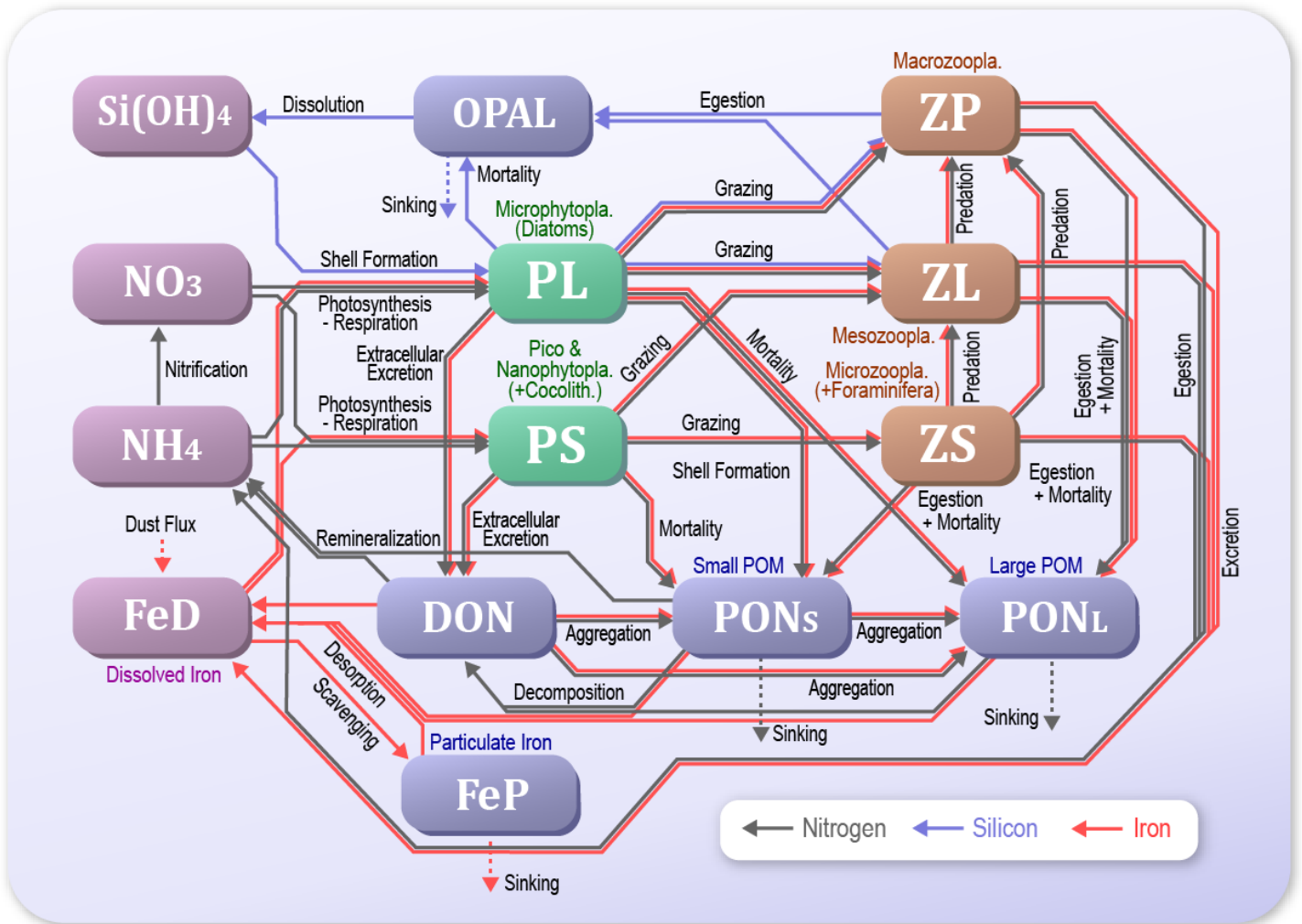
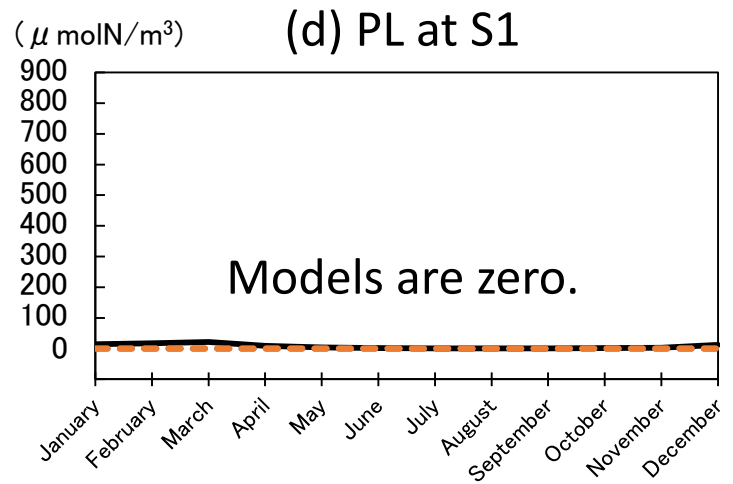
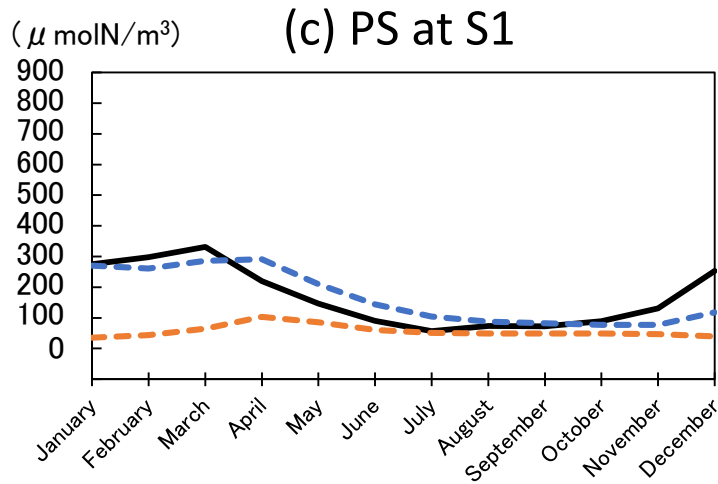
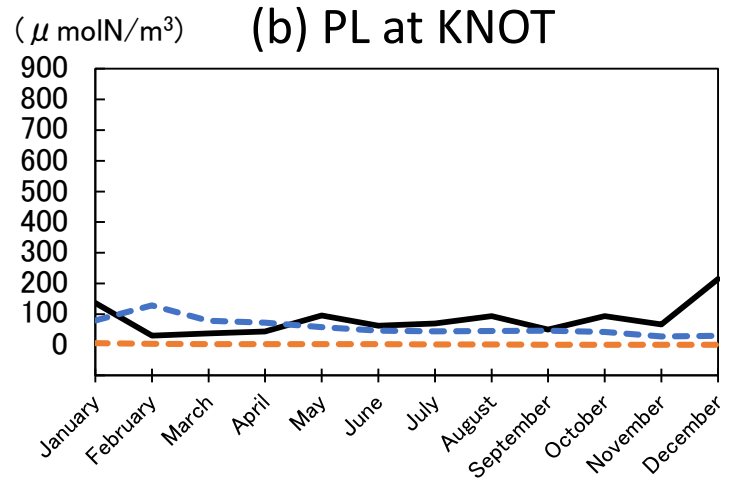
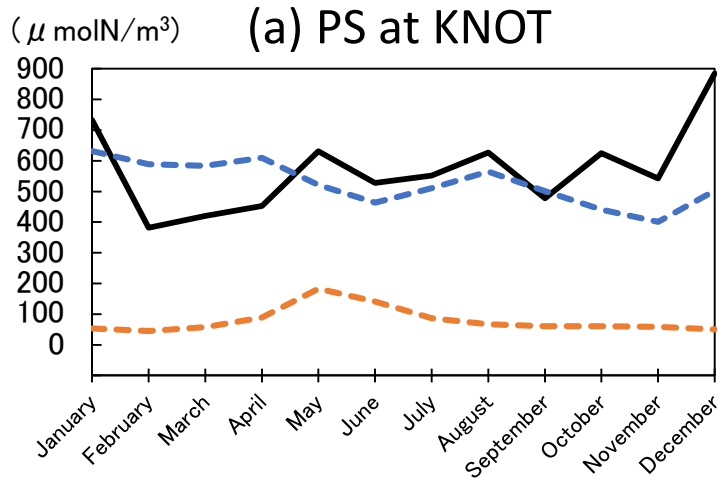


Figure 2. Schematic view of the NSI-MEM interactions among the fourteen components. Green colour boxes and brown boxes indicate phytoplankton and zooplankton, respectively. Blue boxes are particulate/dissolved matters. Violet boxes show nutrients and essential micronutrient.



— : Satellite data  
 - - - : Model (Parameter-optimised case)  
 - - - : Model (Control case)

Figure 3. Seasonal variations of surface phytoplankton (PS: small phytoplankton and PL: large phytoplankton) biomass in the 1D NSI-MEM and satellite data at St. KNOT and St. S1 shown as typical observational points of the subarctic and the subtropical regions, respectively. (a) PS at St. KNOT, (b) PL at St. KNOT, (c) PS at St. S1 and (d) PL at St. S1 where the concentrations of the two model cases are almost zero, and that of satellite is also remarkably small. The unit conversion between the simulation data ( $\mu\text{molN/m}^3$ ) and the satellite data ( $\text{gchl-a/m}^3$ ) is referred to as the nitrogen-chlorophyll ratio of PL= 1: 1.59 and PS= 1: 0.636 (Shigemitsu et al., 2012). The same conversion of nitrogen-chlorophyll is used to Fig. 4, Fig. 6, Fig. 8 and Fig. 10.



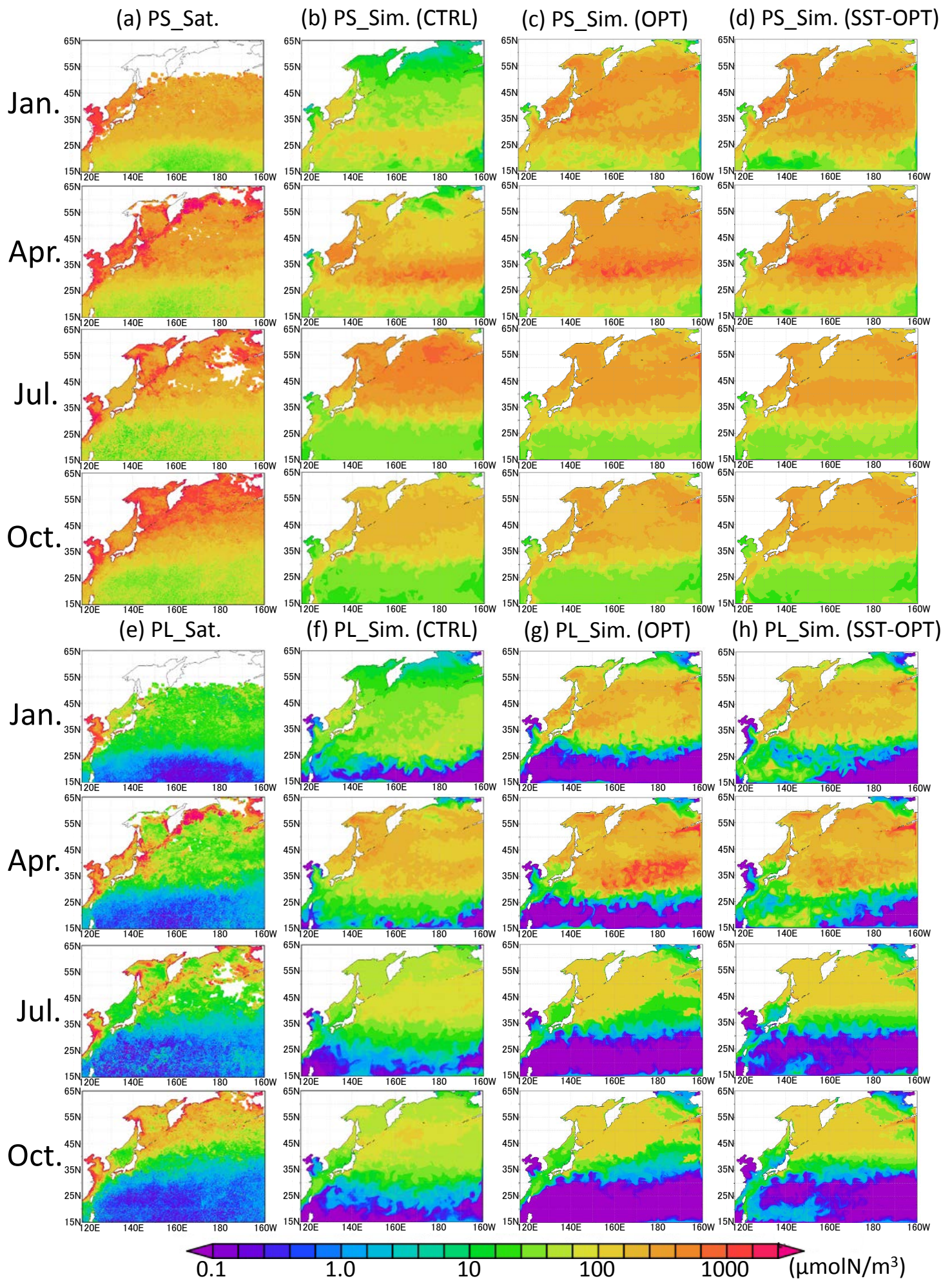
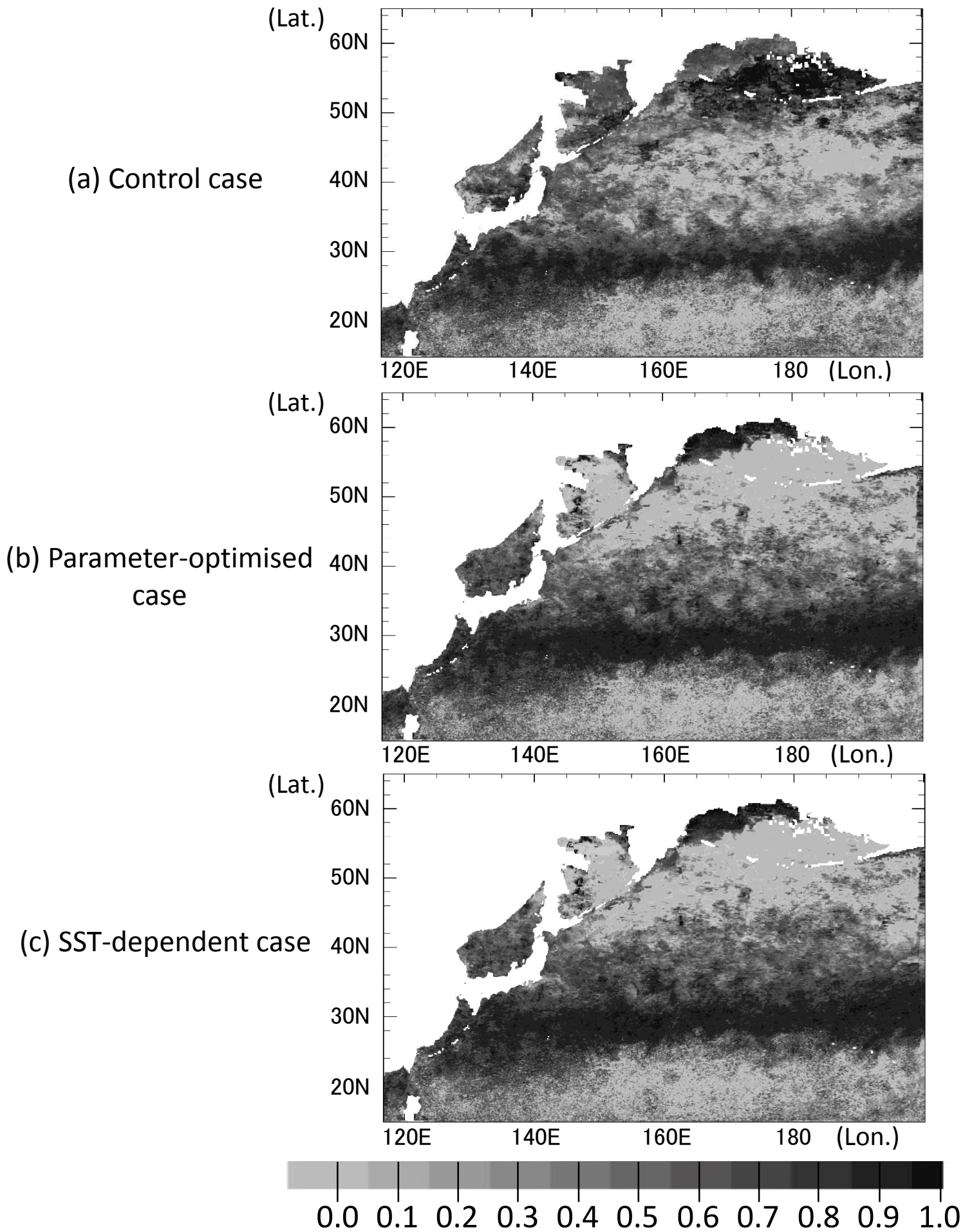


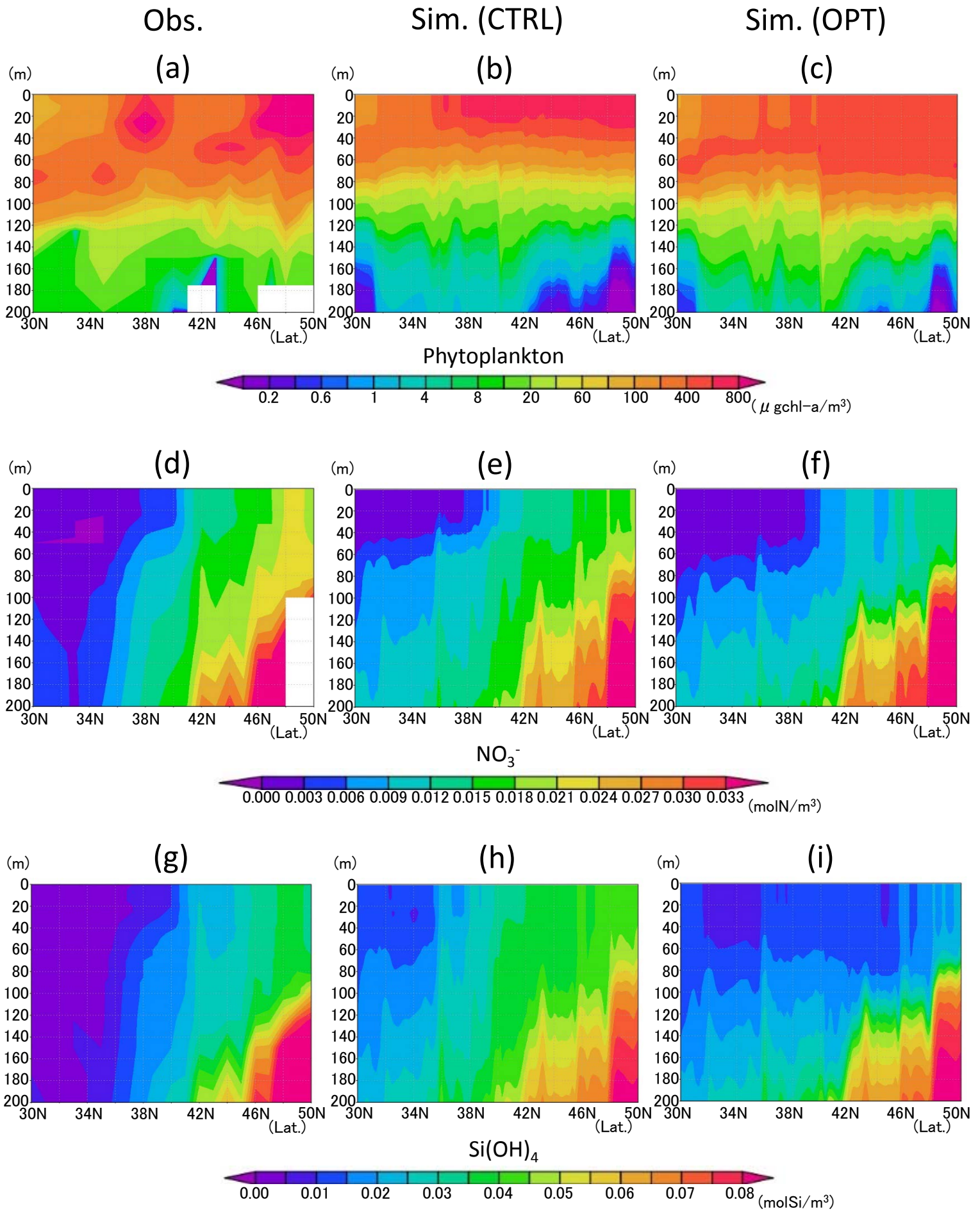
Figure 4. Horizontal distribution of phytoplankton at the surface in 1998. (a) PS (small phytoplankton) from satellites observations, (b) PS in Control case, (c) PS in the Parameter-optimised case, and (d) in the SST-dependent case. (e), (f), (g), (h) are the same except for PL (large phytoplankton).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



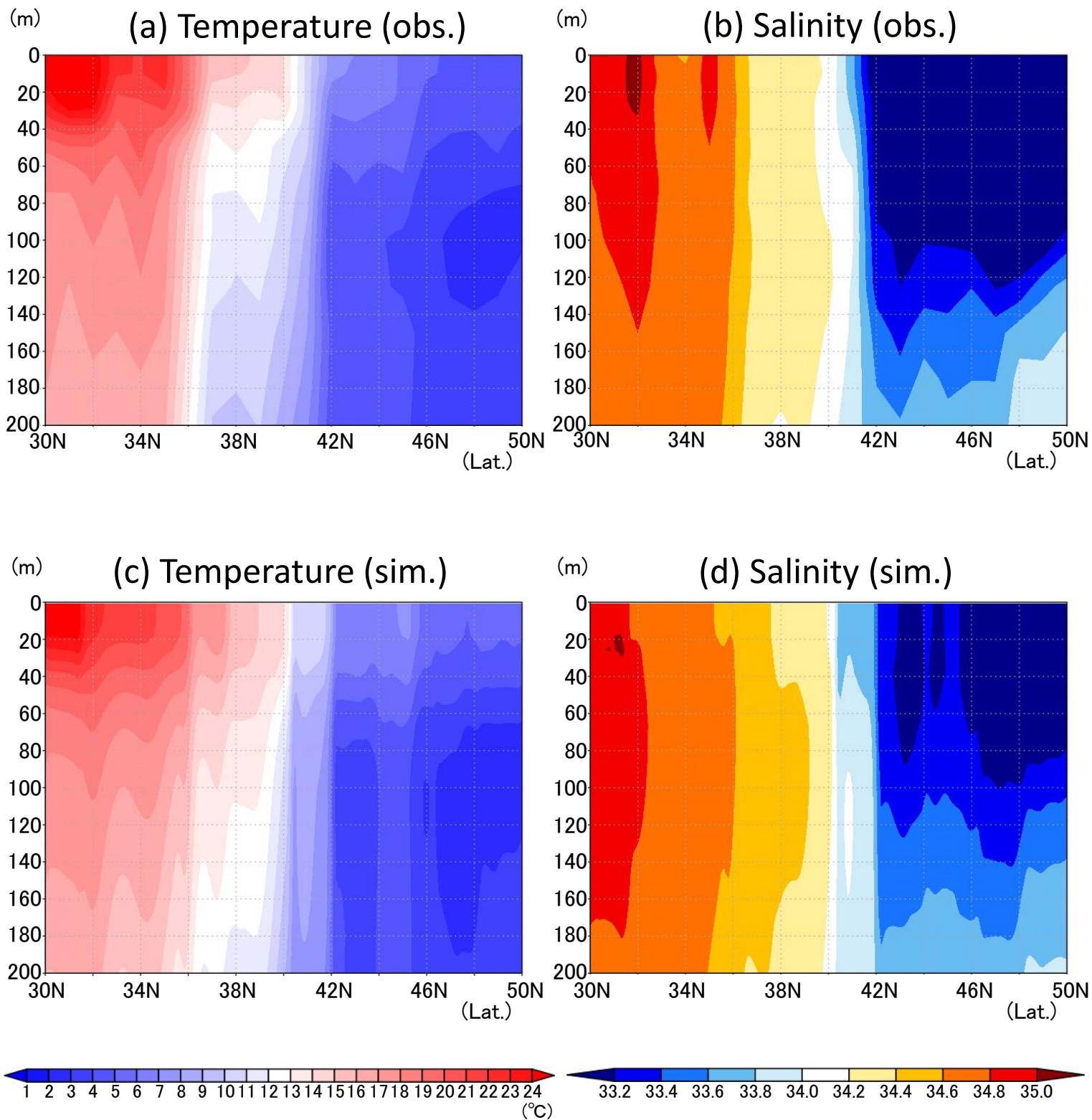


**Figure 5.** Horizontal distribution of lagged (within  $\pm 2$  months) correlation coefficients were calculated for the monthly time series of phytoplankton (PL+PS) concentration between the simulation and the satellite data in each grid at the surface in 1998. (a) Control case, (b) Parameter-optimised case and (c) SST-dependent case. Areas without satellite data and in the coastal regions where the bottoms are less than 200 m are left blank.





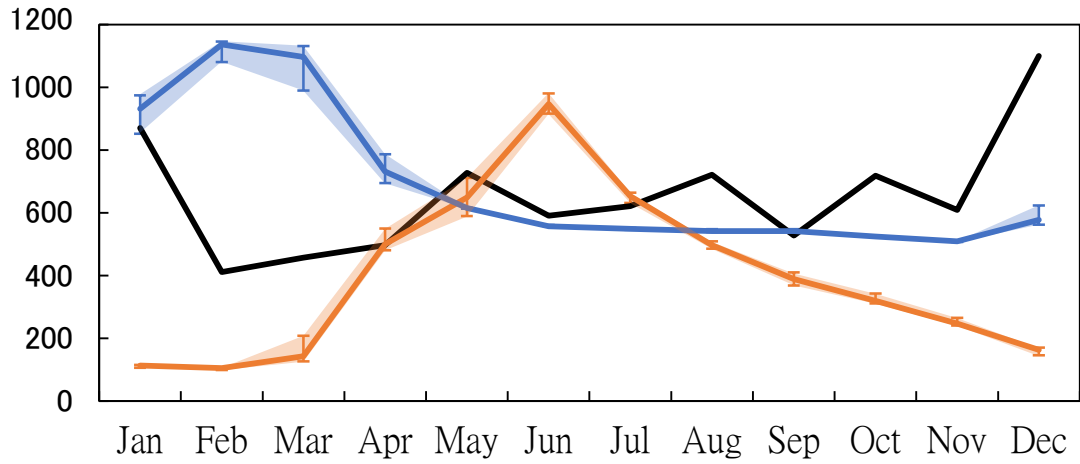
**Figure 6.** Vertical distribution of phytoplankton (a, b, c), nitrate (d, e, f) and silicate (g, h, i) along the 165° E section in June, 1998. (a, d, g) Data in situ observed during 16<sup>th</sup> June to 21<sup>st</sup> June in 1998 downloaded from World Ocean Database 2013. (b, e, h) Simulation result of Control case in June 1998 mean. (c, f, i) Simulation result of Parameter-optimised case in June 1998 mean. Areas of missing values are left blank.



**Figure 7.** Vertical distribution of temperature (a, c) and salinity (b, d) along the 165° E section in June, 1998. (a, b) Data in situ observed during 16<sup>th</sup> June to 21<sup>st</sup> June in 1998 downloaded from World Ocean Database 2013. (c, d) Physical field in June 1998 mean used in the 3D NSI-MEM.

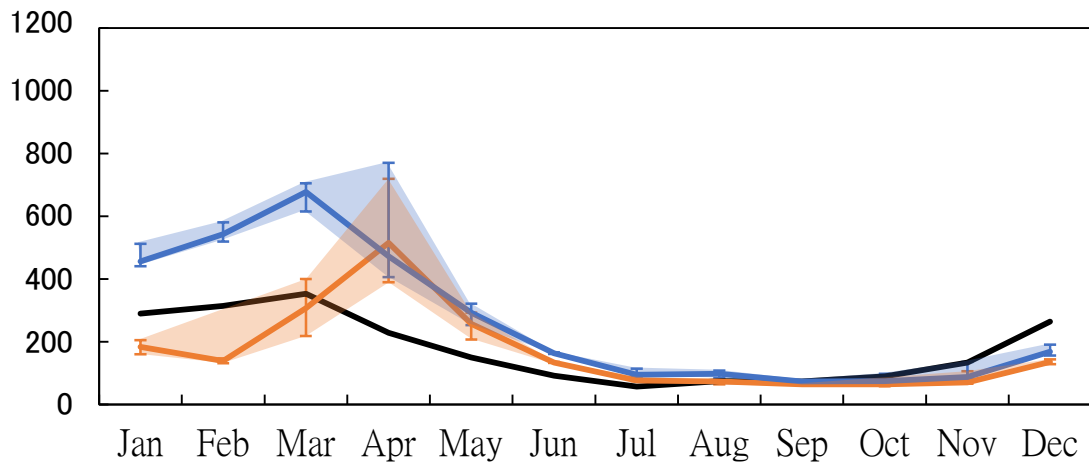
( $\mu\text{ molN/m}^3$ )

(a) KNOT



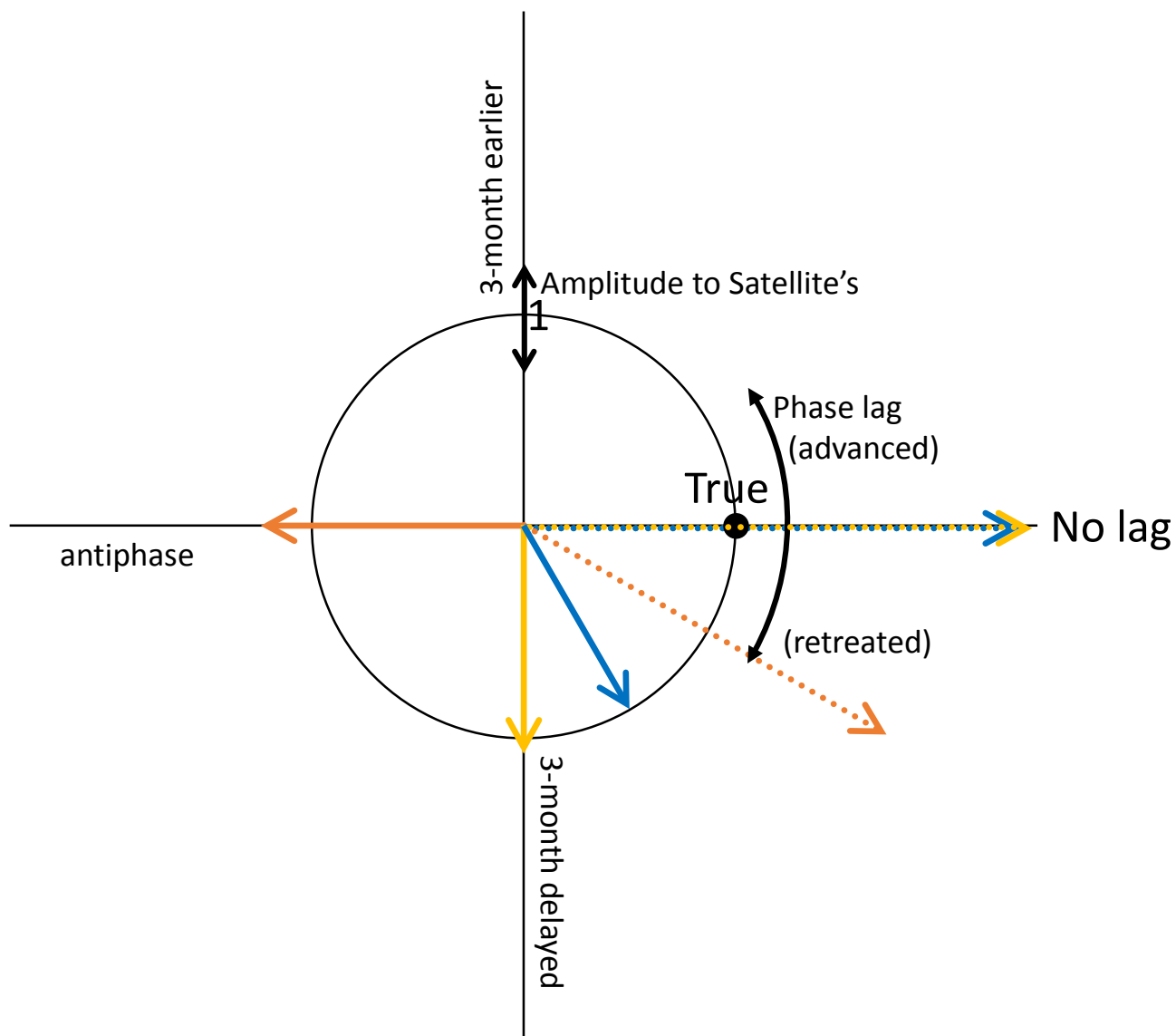
( $\mu\text{ molN/m}^3$ )

(b) S1



— : Satellite data  
— : Model (Parameter-optimised case)  
— : Model (Control case)

**Figure 8.** Time series of phytoplankton (PL+PS) concentration in the 3D NSI-MEM and satellite data at (a) St. KNOT and (b) St. S1. Error bars and shade of the simulations show the maximum and minimum values in  $\pm 0.3^\circ$  around the grids of St. KNOT and St. S1.



- : Control case (KNOT)
- : Parameter-optimised case (KNOT)
- : SST-dependent case (KNOT)
- ..... : Control case (S1)
- ..... : Parameter-optimised case (S1)
- ..... : SST-dependent case (S1)

**Figure 9.** 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 dotted line (Parameter-optimised case at St. S1) and yellow dotted line (SST-dependent case at St. S1) overlap on the no-lagged x-axis.

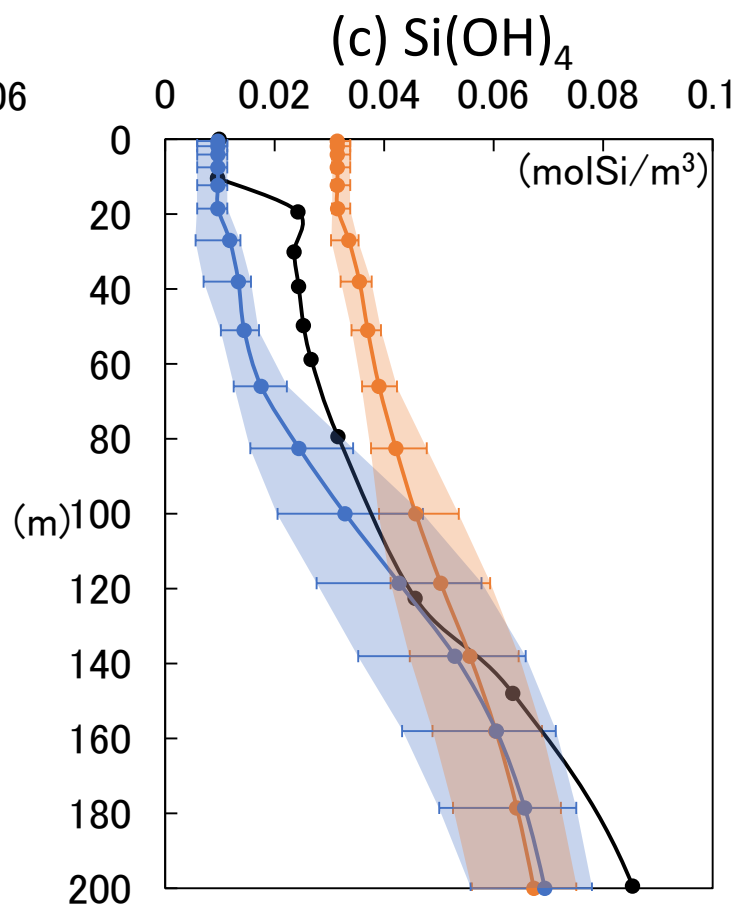
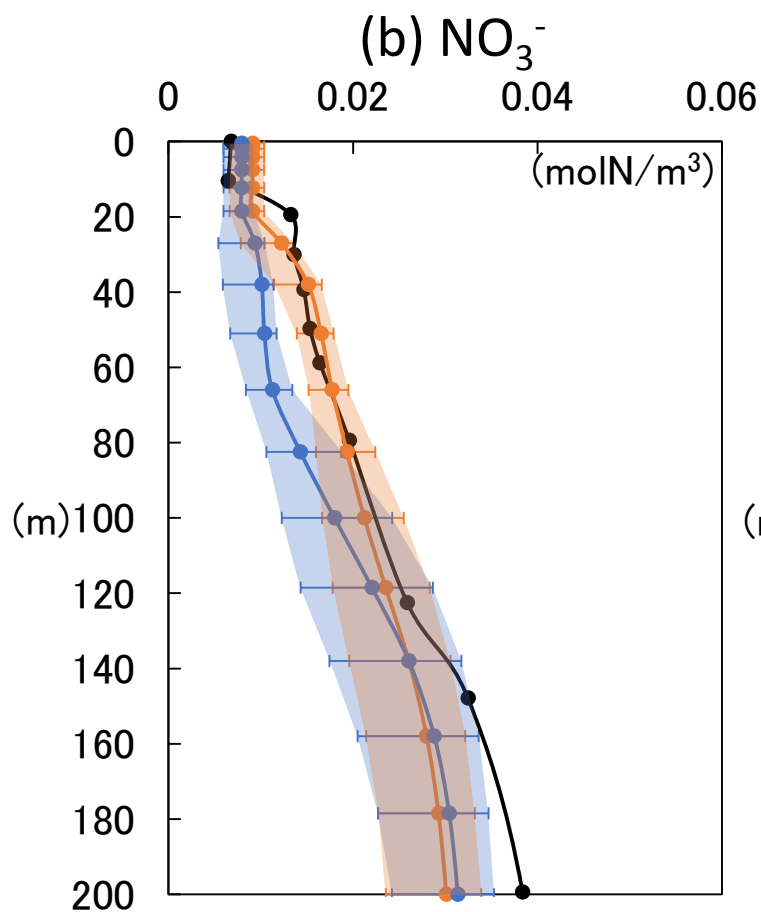
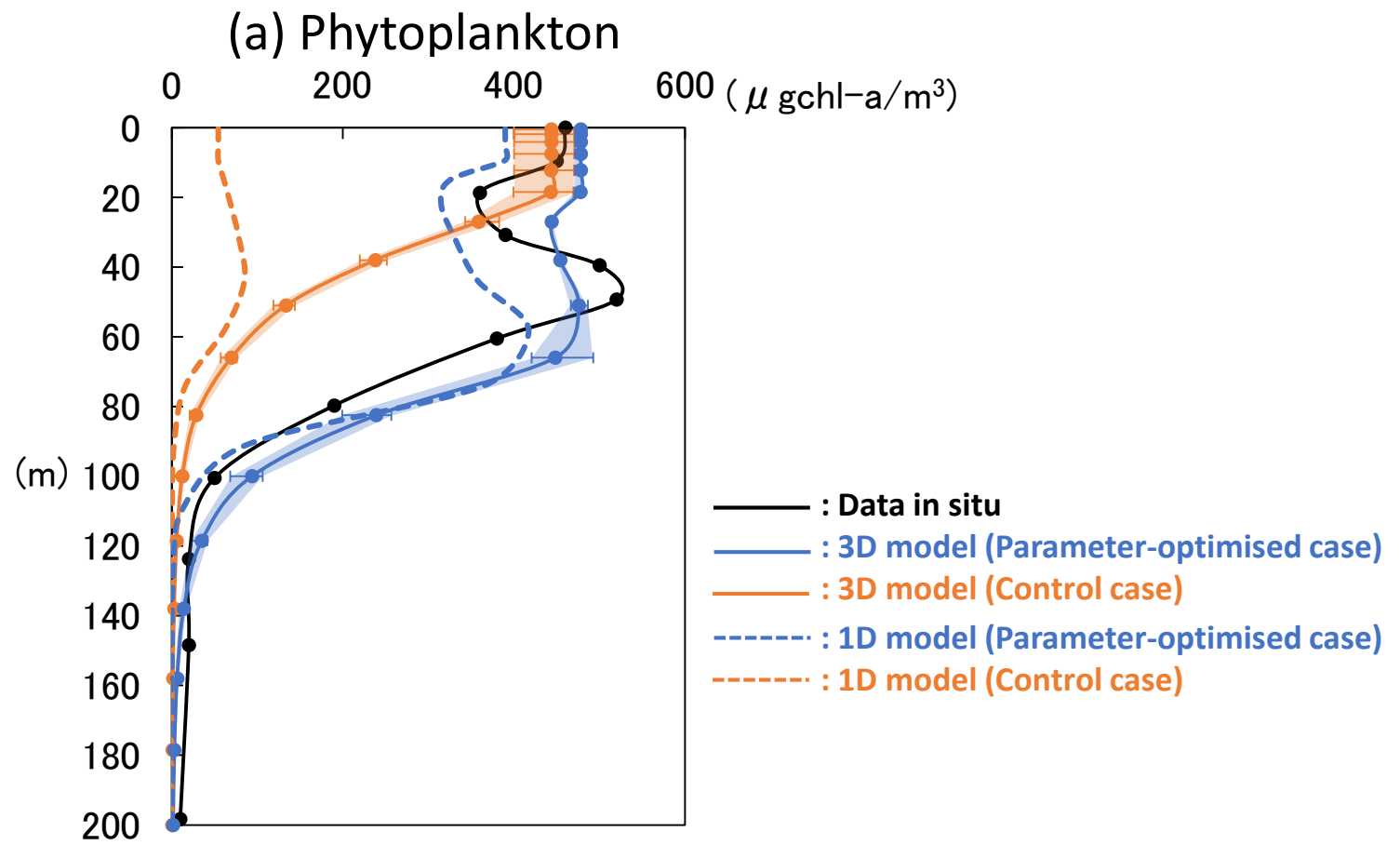
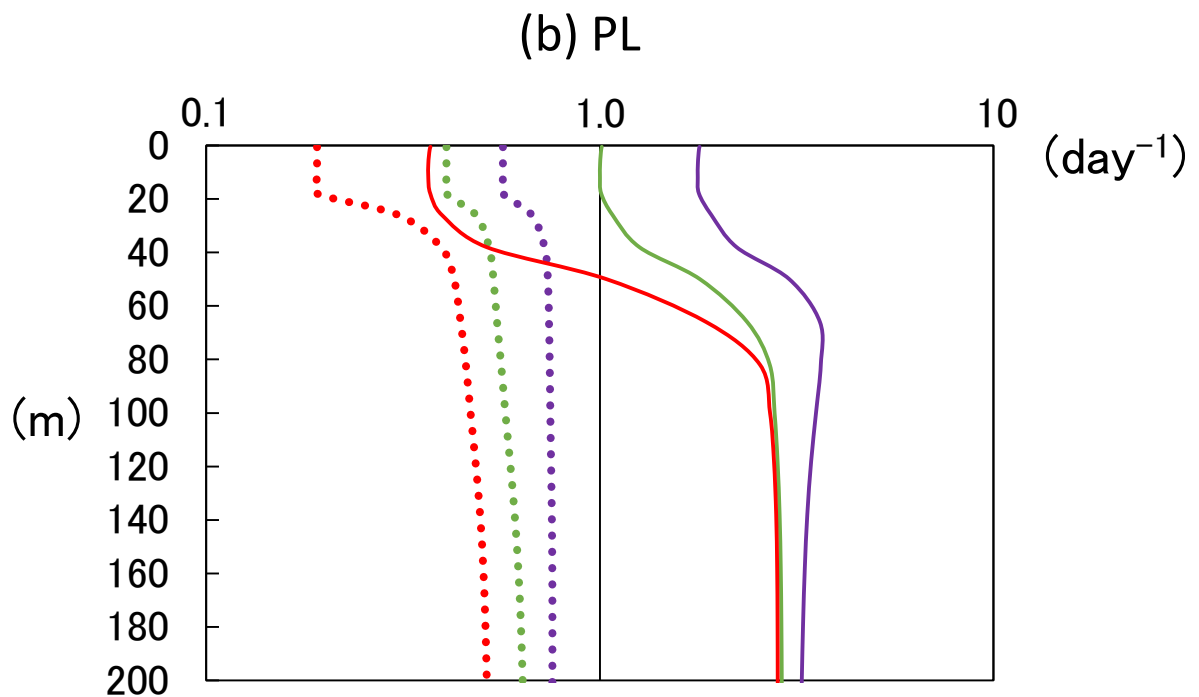
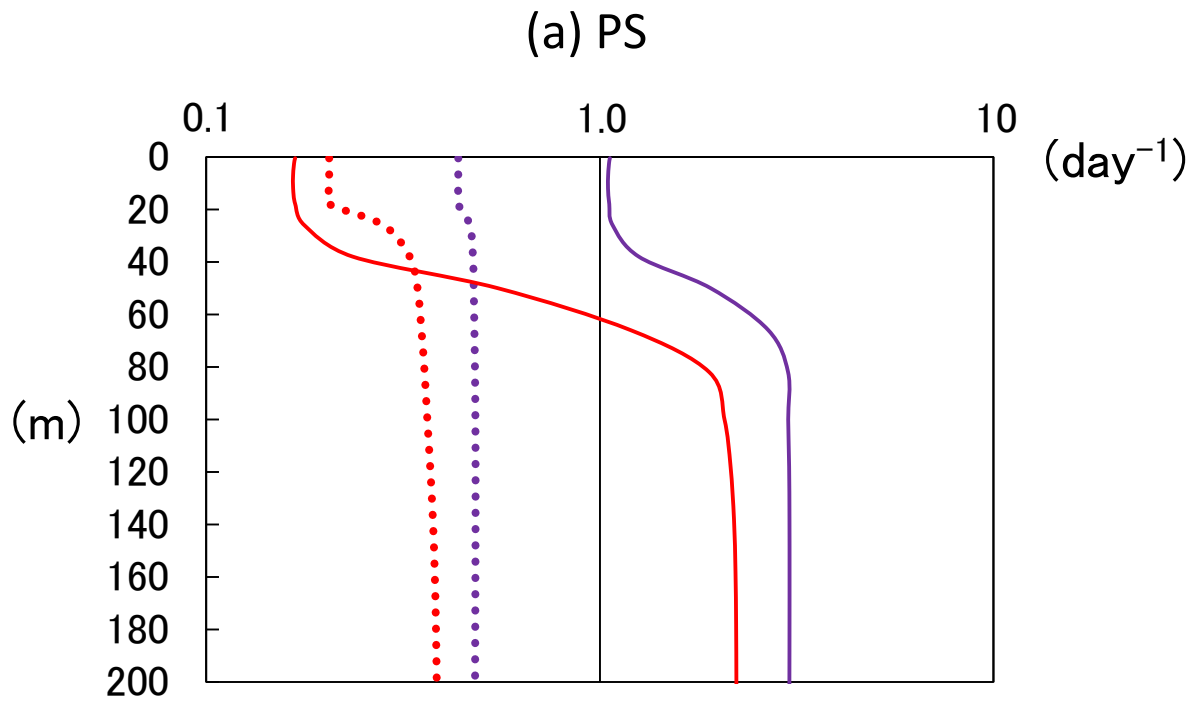


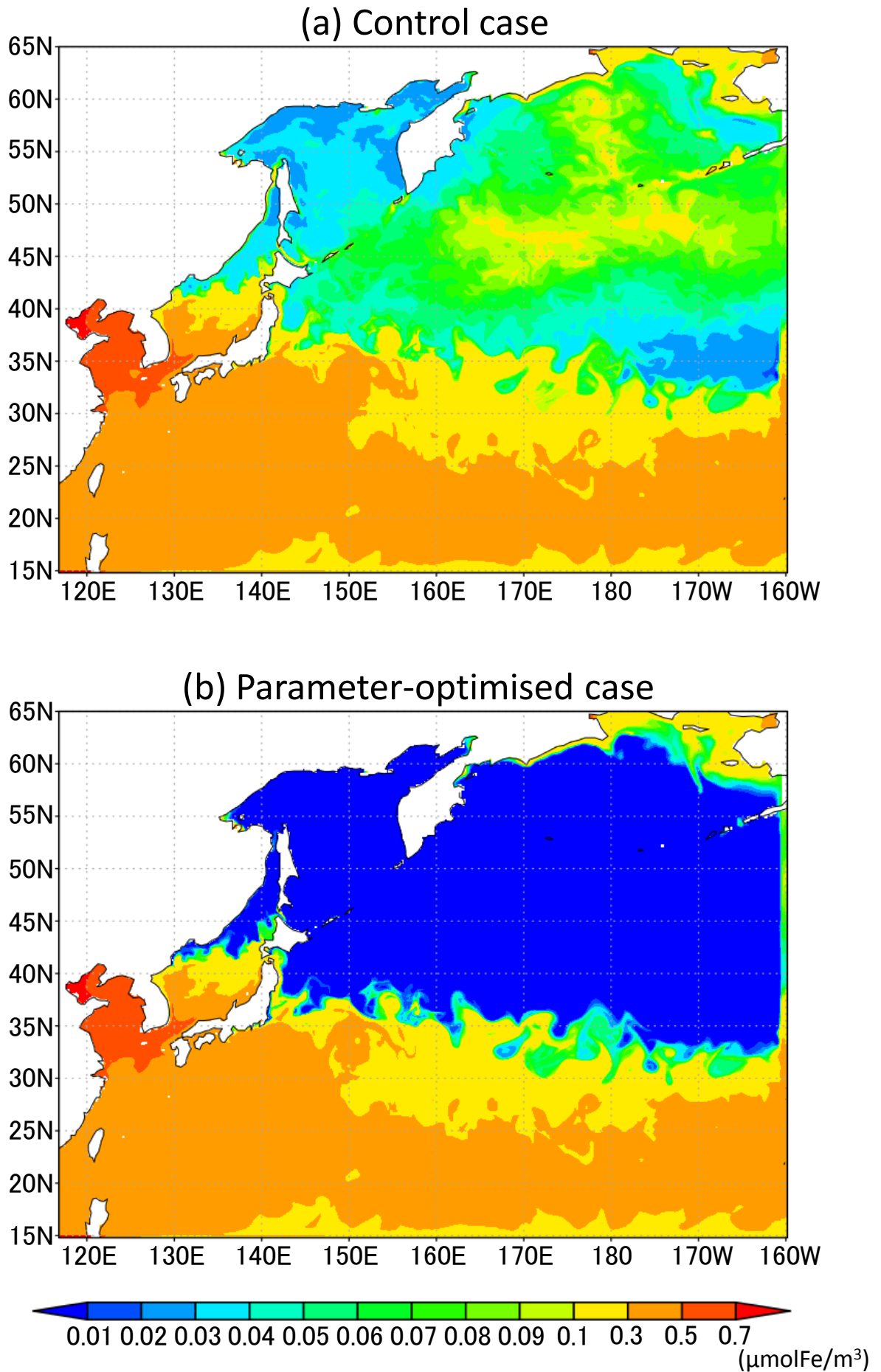
Figure 10. Vertical distributions of (a) phytoplankton (PL+PS) from the 3D model (solid line), 1D model (dashed line) and in situ data, (b) nitrate and (c) silicate concentrations from the 3D model (solid line) and in situ data at St. KNOT on 20<sup>th</sup> July, 1998. Error bars and shade of the 3D simulations show the same mean as those of Fig. 8.





— : by nitrogen (Parameter-optimised case)      ..... : by nitrogen (Control case )  
 — : by silicate (Parameter-optimised case)      ..... : by silicate (Control case)  
 — : by dissolved iron (Parameter-optimised case)      ..... : by dissolved iron (Control case)

Figure 11. 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 20<sup>th</sup> July, 1998. The smallest rate by dissolved iron most heavily limits the rate of phytoplankton's photosynthesis. These limited growth rates (molN/m<sup>3</sup>/day) were divided by the PS or PL biomass (molN/m<sup>3</sup>) to standardize.



**Figure 12.** Horizontal distribution of dissolved iron in the surface sea water layer for July 1998; (a) Control case and (b) Parameter-optimised case.