1	Wind-driven interannual variability of sea ice algal production
2	in the western Arctic Chukchi Borderland
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15 Abstract

16 Seasonal and interannual variability in the biogenic particle sinking flux was recorded 17 using multi-year bottom-tethered sediment trap mooring systems in the Northwind Abyssal 18 Plain (Station NAP: 75°N, 162°W, 1975-m water depth) of the western Arctic Chukchi 19 Borderland. Trapped particle flux at a median depth of 184 m had an obvious peak and 20 dominance of sea ice-related diatom assemblages in August 2011. The observed particle flux 21 was considerably suppressed throughout summer 2012. In the present study, the response of ice 22 algal production and biomass to wind-driven changes in the physical environment was 23 addressed using a pan-Arctic sea ice-ocean modeling approach. A sea ice ecosystem with ice 24 algae was newly incorporated into the lower-trophic marine ecosystem model, which was 25 previously coupled with a high-resolution (i.e., 5-km horizontal grid size) sea ice-ocean general 26 circulation model. Seasonal model experiments covering two-year mooring periods indicated 27 that primary productivity of ice algae around the Chukchi Borderland depended on basin-scale 28 wind patterns via various processes. Easterly winds in the southern part of a distinct Beaufort 29 High supplied nutrient-rich water for euphotic zones of the NAP region via both surface Ekman 30 transport of Chukchi shelf water and vertical turbulent mixing with underlying nutricline water 31 in 2011. In contrast, northwesterly winds flowing in the northern part of an extended Siberian 32 High transported oligotrophic water within the Beaufort Gyre circulation toward the NAP 33 region in 2012. The modeled ice algal biomass during summer reflected the differences in 34 nutrient distribution. The modeled sinking flux of particulate organic nitrogen (PON) was 35 comparable with the time series obtained from sediment trap data in summer 2011. In contrast, 36 lateral advection of ice algal patches of shelf origin during a great cyclone event may have

- 37 caused a modeled PON flux bias in 2012. Extending the year-long measurements is expected to
- 38 help illustrate the more general features of ice-related biological processes in the Arctic Ocean.
- 39 Keywords: Arctic Ocean, Northwind Abyssal Plain, ice algae model, primary production, wind pattern

40 1. Introduction

41 The response of biogeochemical cycles to the decline in Arctic sea ice has become an 42 important topic for a variety of communities. Improved light conditions during summer have 43 enhanced phytoplankton photosynthesis activity in the Eurasian pelagic area of the Arctic 44 Ocean (Wassmann, 2011). A widespread massive deposition of ice algal biomass was detected 45 on the deep seafloor of the eastern Arctic basin (Boetius et al., 2013). On the other hand, the 46 under-ice export of particulate organic carbon (POC) was limited by insufficient nutrient supply 47 in the stratified central Arctic (Lalande et al., 2014). In the Beaufort Gyre region of the western 48 Arctic, freshwater accumulation suppressed primary production during the 2000s (McLaughlin 49 et al., 2010; Nishino et al., 2011). It is necessary to fill in the observational gaps to understand 50 spatial and temporal variability in the biological processes of the Arctic Ocean.

51 Sediment trap measurements are useful to capture year-long biological activity signals. The 52 locations of bottom-tethered traps have been confined to the north of the Laptev Sea (Fahl and 53 Nöthig, 2007), Mackenzie shelf (Forest et al., 2007), and the deep Canada Basin (Honjo et al., 54 2010; Hwang et al., 2015). In our field campaign, year-round bottom-tethered moorings, 55 including sediment trap instruments, have been deployed in the Northwind Abyssal Plain 56 (NAP) of the Chukchi Borderland since October 2010 (Fig. 1). Early-winter maxima of sinking 57 particle flux with fresh organic material have been captured annually at Station NAP (75°N, 58 162°W, 1,975 m water depth) (Watanabe et al., 2014; Onodera et al., 2015). The substantial 59 quantities of lithogenic minerals in the trapped particles suggest shelf-origin water transport 60 toward the NAP region. Seasonal experiments using an eddy-resolving (5 km grid size) pan-61 Arctic sea ice-ocean model indicated the effective role of Beaufort shelf-break eddies in the 62 transport of Chukchi shelf water with high biological productivity and in the consequent earlywinter peaks of sinking biogenic flux at Station NAP (Watanabe et al., 2014). It should be noted
that biological production continued inside these eddies moving in the southern Canada Basin.

65 Another finding obtained at Station NAP was remarkable interannual variability in summer 66 particle flux (Onodera et al., 2015; Ikenoue et al. 2015; Matsuno et al., 2015). Trapped particle 67 flux peaked sharply in August 2011 but was suppressed considerably during summer 2012. The 68 diatom assemblage compositions suggest that year-to-year changes in the distribution of shelf-69 origin water and relatively oligotrophic water originating from the interior of the Canada Basin 70 controls the particle flux around the Chukchi Borderland (Onodera et al., 2015). This situation 71 was supported by ocean current fields simulated in a medium-resolution (25 km grid size) 72 framework by the pan-Arctic physical oceanographic model (Onodera et al., 2015). However, 73 reliable *in-situ* biological productivity and water mass transport data above the shallow trap 74 depth (approximately 180–260 m) could not be available at Station NAP during the mooring 75 periods (October 2010-September 2012). In particular, chlorophyll, nutrient concentration, and 76 ocean velocity data from winter to early summer were insufficient. Further detailed 77 investigation of the background mechanisms associated with summer biogenic flux would be 78 highly valuable and possible using a coupled physical and marine ecosystem model. Whereas 79 the main content of observed diatom valves was the sea ice-related species (e.g., Fossula 80 arctica, Onodera et al., 2015), sea ice ecosystem was not included in our previous model 81 experiment (Watanabe et al., 2014). The lack of ice algae was a plausible factor for the summer 82 delay of the simulated biogenic flux peak behind the trap data. These issues raised our 83 motivation to incorporate ice-related biogeochemical processes in the model.

Ice algae models have a long history of development. Pioneering work was conducted on the Antarctic fast ice ecosystem (Arrigo et al., 1993). For the Arctic Ocean, one-dimensional ice

86 algae models were applied to landfast ice in Resolute Passage of the Canadian Archipelago 87 (Lavoie et al., 2005; Pogson et al., 2011) and offshore Barrow (Jin et al., 2006). The modeled 88 region has been extended in recent years to include the entire Arctic Ocean (Dupont, 2012) and 89 global domain (Deal et al., 2011; Jin et al., 2012). The analysis period covered from seasonal 90 transition (Lavoie, 2005; Deal et al., 2011) to decadal variability (Jin et al., 2012; Dupont, 91 2012) and future projections (Lavoie et al., 2010). Most models assume that ice algal activity 92 occurs primarily in the skeletal layer of the sea ice bottom (i.e., ice-water interface), where the 93 layer thickness is fixed at 2 cm (Lavoie et al., 2005), 3 cm (Jin et al., 2012), and 5 cm (Dupont, 94 2012). The ice algal biomass sometimes reaches values three orders of magnitude larger at the 95 ice-water interface than that in the upper part of the sea ice column (e.g., Jin et al., 2006). 96 Ocean surface water is a major nutrient supplier for ice algae in the skeletal layer. Tidal mixing 97 controls nutrient exchange rates at the ice-water interface in the narrow shallow straits of the 98 Canadian Archipelago (Lavoie et al., 2005). In a general viewpoint, it is reasonable that nutrient 99 flux is calculated as a function of the sea ice freezing/melting rate (Arrigo et al., 1993; Jin et al., 100 2006). However, Dupont (2012) did not calculate nutrient import due to sea ice freezing, 101 following an observational view where nutrients trapped inside the sea ice column have minor 102 contributions to an ice algal bloom (Cota et al., 1991; Cota and Smith, 1991). As grazing 103 pressure on ice algae is considered weak in the sea ice column, most previous models excluded 104 zooplankton biology in the skeletal layer (Jin et al., 2006; Dupont, 2012) or prescribed a small 105 grazing rate to potential grazers (e.g., amphipods) (Lavoie, 2005). The habitat of ice algae in the 106 skeletal layer disappears gradually due to melting sea ice. The assemblages released from the 107 sea ice bottom partially act as phytoplankton and become a food source for pelagic grazers in the water column (Michel et al., 1993, 1996). Thus, complex ice algal processes have beenproposed and numerically formulated in various ways.

110 In the present study, seasonal and interannual variability of ice algal production and 111 biomass in the Chukchi Borderland were addressed using a pan-Arctic sea ice-ocean modeling 112 approach (Fig. 1). We focused particularly on the relationships between ice-related biogeochemical processes and wind-driven dynamics, such as shelf-basin exchanges, local 113 114 upwelling/downwelling, and vertical turbulent mixing. To represent the summer biogenic 115 particle flux captured by sediment trap measurements, the simple sea ice ecosystem was newly 116 incorporated into a lower-trophic marine ecosystem model. Our model coupled with a 117 sophisticated high-resolution physical component is a powerful tool for the above-mentioned 118 subjects because of following issues. The Chukchi Borderland is composed of complex 119 topography such as long ridges, deep-sea plateaus, and steep shelf breaks. The sinking biogenic 120 flux available for comparison was obtained from the single-point mooring measurements in this 121 area. The source regions of surface water are distributed over the Chukchi Sea, the East 122 Siberian Sea, and the Canada Basin. The water mass transports are closely related to shelf-basin 123 boundary currents and baroclinic eddies. These complex topography and mesoscale 124 hydrographic features have been unresolved by previous basin-scale ice algae models, which 125 horizontal resolution was much coarser than the typical internal Rossby radius of deformation 126 in the polar region. The linkages between wind patterns, light and nutrient preconditioning of 127 ice algal bloom, and particle sinking are also unique viewpoints in the present work. Modeling 128 configurations and sediment trap analyses are described in Section 2. Seasonal transitions of the 129 modeled ice-ocean field, particularly those around the NAP region, are traced in Section 3. 130 Relationships between the interannual variability in biogeochemical properties and wind patterns are examined in Section 4. Uncertainties of the modeled processes are discussed in
Section 5, based on sensitivity experiments. The obtained findings are summarized in Section 6.

134 **2. Model configuration and experimental design**

135 **2.1 Physical oceanographic model**

136 The physical part of the coupled sea ice-ocean model is the "Center for Climate System 137 Research Ocean Component Model (COCO)" version 4.9 (Hasumi, 2006). The sea ice 138 component includes a multi-thickness-category configuration based on that of Bitz et al. (2001) 139 with a one-layer thermodynamic formulation (Bitz and Lipscomb, 1999), the linear-remapping 140 method for category transfer (Lipscomb, 2001), and the elastic-viscous-plastic rheology (Hunke 141 and Dukowicz, 1997). In addition to the open water category, the lower limit of sea ice 142 thickness in each category is set to 10, 30, 60, 100, 250, and 500 cm, respectively (i.e., 7 143 categories). The ocean component is a free-surface general circulation model formulated using 144 the advection scheme of Leonard et al. (1994) and the turbulence closure mixed-layer scheme 145 of Noh and Kim (1999).

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147 **2.2 Marine ecosystem model**

148 The COCO model was coupled with a lower-trophic marine ecosystem model, "North 149 Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO)". The 150 detailed configuration of the original NEMURO model, which represented pelagic plankton 151 species (i.e., diatom, flagellate, and copepod), was described in Kishi et al. (2007). To address 152 seasonality and interannual variability in ice algal production and biomass, a sea ice ecosystem 153 was incorporated in the present work, (Fig. 2 and Table 1). In the developed model (called 154 "Arctic NEMURO", hereafter), the habitat of ice algae is confined to the 2-cm skeletal layer. 155 The biogeochemical variables in the sea ice component comprise ice algae (IA), ice-related 156 fauna (IF), nitrate (NO3), ammonium (NH4), silicate (SIL), dissolved organic nitrogen (DON), particulate organic nitrogen (PON), and opal (OPL). Each model grid has a single value per 157

variable independent of the ice thickness category. As the sea ice bottom temperature is always kept at the freezing point of underlying seawater, a relationship of $Q_{10} = 2$ adopted in the present model did not have substantial impacts on biogeochemical cycles in the sea ice column. The growth rate of ice algae (GR) is calculated depending on light condition (L) and nutrient uptake (N_{up}) terms:

163 $GR = GR_{max} \times L \times N_{up},$

164 where the maximum growth rate GR_{max} is fixed at a constant value of 0.8 d⁻¹.

165 The light condition term followed the original NEMURO formulation:

166 $\mathbf{L} = \mathbf{I} / \mathbf{I}_{opti} \times \exp(1 - \mathbf{I} / \mathbf{I}_{opti}),$

167
$$I = PAR_{frac} \times SW^{\downarrow} \times (1 - \alpha_{sfc}) \times exp(-k_{snow} H_{snow} - k_{ice} H_{ice}),$$

168 where I is photosynthetically active radiation (PAR) in the skeletal layer. The conversion coefficient from shortwave radiation to PAR (PAR_{frac}) is 0.43 following the previous models 169 170 (Zhang et al., 2010; Dupont, 2012) so that 43% of shortwave flux is available for 171 photosynthesis activity. Light transmission through the snow and sea ice columns is given by downward shortwave radiation from atmosphere (SW^{\downarrow}), snow/ice surface albedo (α_{sfc}), column 172 thickness (H_{snow}, H_{ice}), and empirical extinction rates (k_{snow}, k_{ice}). The surface albedo (α_{sfc}) 173 174 changes from 0.8 to 0.6 depending on snow/ice type and surface temperature during summer. The light extinction rate (k_{snow} , k_{ice}) is set to 0.12 cm⁻¹ for snow and 0.045 cm⁻¹ for sea ice based 175 176 on Aota and Ishikawa (1982). According to this constant rate, for example, the light intensity in 177 the skeletal layer corresponds to approximately 10% (1%) of that absorbed into the surface of 178 sea ice with its thickness of 50 cm (100 cm) (Fig. 3a). The light transmission is calculated in 179 each thickness category (see the category arrangement in Section 2.1), and the under-ice 180 average intensity is then obtained in each model grid. A self-shading effect of ice algae is 181 neglected. For weak-light adaptation of ice algae, the optimal light intensity (I_{opti}) is set to 10 W 182 m⁻² (cf., 104 W m⁻² for pelagic phytoplankton (Kishi et al., 2007)). A PAR of 5 and 20 W m⁻² 183 results in a light condition term of 0.82 and 0.73, respectively (Fig. 3b).

The vertical exchange of biogeochemical variables between the skeletal layer and the ocean surface layer (suffixed as SKL and OCN, respectively, hereafter) is formulated in a different manner for sea ice freezing and melting periods. During the freezing period, ocean-to-ice fluxes F_{OI} are proportional to sea ice freezing rate IFR:

188
$$F_{OI} = CF_{OI} \times (NO3, NH4, SIL, DON)_{OCN} \times IFR.$$

189 The proportional coefficient CF_{OI} is set to 0.3, since first-year ice salinity is able to reach approximately 30% of ocean salinity. In addition, all of the imported nutrients are accumulated 190 191 only in the skeletal layer. The actual ice algae respond to nutrients concentrated in brine pockets 192 and channels. However, the incorporation of such detailed structures in sea ice interiors is 193 generally difficult for three-dimensional climate models. Here, we regard the skeletal layer as 194 the reservoir of total imported nutrients under an idealized assumption. There is no import of 195 particles such as pelagic planktons, PON, and OPL. During the melting period, ice-to-ocean 196 fluxes F_{IO} are proportional to the sea ice melting rate IMR:

197
$$F_{IO} = (IA, IF, NO3, NH4, SIL, DON, PON, OPL)_{SKL} \times IMR.$$

According to this formulation, the concentration of all biogeochemical variables in the sea ice component decreases to zero when sea ice entirely disappears due to the melting process in each model grid. Although sea ice melts from its surface, bottom, and flank, respectively, it is difficult to separate these melting processes in terms of particle export. In general, ice surface meltwater sinks through internal brine channels and flushes out a part of materials in the skeletal layer (Vancoppenolle et al., 2010). Besides, ice algae have an ability to maintain their position under a slow melting rate, and the habitat is not immediately lost even after ice bottom
melting. The methods adopted in the present work idealize ice-ocean exchange of
biogeochemical variables within reasonable scopes.

The nutrient source of ice algal growth can be divided to the sea ice column and underlying seawater. The present study assumes that ice algae utilize both ice/ocean nutrients depending on their biomass:

210
$$N_{up} = RN_{upSKL} \times N_{upSKL} + (1 - RN_{upSKL}) \times N_{upOCN},$$

211
$$\text{RN}_{upSKL} = 0.5 \times \{ \cos(\pi \times \text{IA} / \text{KN}_{upSKL}) + 1 \}, \text{ for IA} \leq \text{KN}_{upSKL} \}$$

212 where RN_{upSKL} is the ice algal uptake ratio of nutrient in the skeletal layer, and KN_{upSKL} is a 213 threshold value (Fig. 3c). When ice algal biomass IA exceeds KN_{upSKL} only seawater nutrients are utilized for the growth. The value of KN_{upSKL} is set to 1 mmol N $m^{\text{-}2}$ in the present 214 215 experiments. As reported in Section 3.2, sea ice nutrients are consumed preferentially for the 216 initial bloom of small-sized ice algae in early summer. According to the growth of ice algae, 217 their nutrient source shifts to seawater for the mature period. The "hybrid-type" formulation of 218 nutrient uptake represents more realistic ice algal biology, where ice algae anchoring under ice 219 floes gradually raise meter-long filaments in the water column (Boetius et al., 2013). In each 220 model time step, the Michaelis-Menten relationship is applied to nutrient concentration in the 221 skeletal layer and in the ocean surface layer (i.e., the uppermost ocean grid), respectively (Fig. 222 3d):

223
$$N_{upSKL} = min\{ NO3_{SKL} / (NO3_{SKL} + K_{NO3}) \times exp(-\Psi_{NH4} \times NH4_{SKL}) \}$$

$$+ NH4_{SKL} / (NH4_{SKL} + K_{NH4}), SIL_{SKL} / (SIL_{SKL} + K_{SIL}) \}$$

225
$$N_{upOCN} = \min\{ NO3_{OCN} / (NO3_{OCN} + K_{NO3}) \times exp(-\Psi_{NH4} \times NH4_{OCN}) \}$$

where the constant coefficients of half saturation for nitrate (K_{NO3}), ammonium (K_{NH4}), and silicate (K_{SIL}) and of ammonium inhibition (Ψ_{NH4}) have the same values (Table 1) as those of pelagic diatoms (i.e., large phytoplankton PL in the NEMURO model) (Kishi et al., 2007).

230 The ice algal biomass decreases due to mortality, grazing, and sea ice melting. The 231 respiration and mortality terms are functions of the ice algal biomass itself (under the freezing 232 temperature assumption). In the present experiments, there is no biomass of ice-related fauna, 233 and the grazing pressure on ice algae is neglected except for a sensitivity experiment in Section 234 5.4. All ice algae are included in ice-derived PON without any biological activities after their 235 export into the water column by melting sea ice. Sea ice assemblages sink faster than other 236 particles derived from pelagic plankton because ice algae aggregate before the release from the 237 sea ice bottom. Boetius et al. (2013) indicated rapid sinking of ice-related species. Hence, the 238 modeled PON is divided into two components with different sinking speeds. The sinking speeds of PON derived from ice algae (pelagic plankton) are from 50-200 m d⁻¹ (2-200 m d⁻¹), 239 following a cosine curve (Fig. 3e). The sinking speed is maintained at 200 m d⁻¹ below a depth 240 241 of 1,000 m. These profiles are reasonable, because sinking of particulate organic materials 242 generally accelerates with depth due to particle densification processes (e.g., aggregation in 243 shallow depths and elimination of light/fragile organic materials at middle depths) (Honda et al., 244 2013). The modeled OPL is treated in the same manner. We refer to the fast- and slow-sinking 245 PON/OPL as fPON/fOPL and sPON/sOPL, respectively.

The horizontal advection of biogeochemical variables in the sea ice component is also calculated, as the Arctic NEMURO is implemented in a three-dimensional framework. The divergence (convergence) of sea ice velocity causes loss (accumulation) of each material as well as snow and ice volumes. The actual ridging process is accompanied by complex deformation, whereas the modeled sea ice ecosystem is kept consistently in the skeletal layerwith a constant 2-cm thickness for simplicity.

252

253 2.3 Experimental design

254 The model domain contains the entire Arctic Ocean, the Greenland-Iceland-Norwegian Seas, 255 and the northern part of the North Atlantic (Fig. 1). The horizontal resolution is 5 km, and there 256 are $1,400 \times 1,000$ grids. There are 42 hybrid σ -z vertical levels. Vertical resolution varies from 2 257 m at the top to 500 m at the bottom. The σ -coordinate composed of three levels is applied to the 258 uppermost 10 m. We performed two one-year experiments (called the 2011 and 2012 cases), in 259 which the 5-km grid model was integrated from October 2010 (2011) to September 2011 (2012) 260 to examine seasonal and interannual variability in ice algae. The initial sea ice and ocean 261 physical fields for these experiments were obtained from a 1979-2011 decadal experiment 262 using the 25-km grid version (Onodera et al., 2015). The atmospheric forcing components were 263 constructed from the National Centers for Environmental Prediction/Climate Forecast System 264 Reanalysis (NCEP/CFSR) 6-hourly dataset (Saha et al., 2010). Pacific water inflow is provided 265 at the Bering Strait, based on Woodgate et al. (2005). Following our previous modeling study (e.g., Watanabe, 2011), the idealized seasonal cycles of northward velocity, temperature, and 266 salinity are prescribed such that the annual mean inflow is 0.8 Sv (1 Sv $\equiv 10^6$ m³ s⁻¹) and 267 268 temperature (salinity) reaches a maximum in September (March). Monthly nitrate and silicate 269 concentrations derived from the World Ocean Atlas 2013 (Garcia et al., 2013) are used for a 270 restoring along the lateral boundary region of the model domain, and summer climatology is 271 assigned to the initial fields of ocean nutrients. As PON and opal in sea bottom sediments are 272 crucial nutrient sources for the Arctic shelves via decomposition and remineralization processes, the fluxes in ammonium, DON, and silicate are added to the deepest layers just above the shelf bottom as in Watanabe et al. (2014). Sea ice nutrients are initially non-existent in the skeletal layer, and the lowest ice algal concentration of 0.02 mmol N m⁻³ is given for initial growth (i.e., seeding). The relationship of 1 mmol N = 80 mgC = 1.6 mgChl is assumed using a C/Chl mass ratio of 50 and a C/N Redfield ratio of 6.625 to compare the model outputs with observational estimates, as in Watanabe et al. (2012).

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280 **2.4 Sediment trap analysis**

281 The bottom-tethered sediment traps (SMD26S-6000, NiGK Cooperation) have been 282 moored at Station NAP (75°N, 162°W, 1,975-m water depth) since October 2010. Deployment 283 and turnaround were conducted by the Japanese R/V Mirai and the Canadian Coast Guard Ship 284 Sir Wilfrid Laurier. Sinking particles were sampled at depths of 181–218 m (median, 184 m) 285 during the first year from October 4, 2010 to September 27, 2011. The trap depth was 247-319 286 m (median, 256 m) during the second year from October 4, 2011 to September 17, 2012. These 287 sediment traps collected 26 samples approximately every two weeks during their one-year 288 deployment. The recovered trap samples were sieved through 1-mm mesh to remove swimmers, 289 and particles < 1 mm were divided evenly into 10 sub-samples. One of 10 aliquot samples was 290 filtered, and was desalted using Milli-W water. The dried sample was weighed, and it was then 291 ground and mixed using an agate mill. PON and POC contents were analyzed in one sequence. 292 The powdered samples were decalcified in hydrochloric acid vapor in a desiccator for eight 293 hours to remove particulate inorganic carbon. Sodium hydroxide pellets were placed in the 294 desiccator to neutralize the samples. PON content in the treated samples was sequentially 295 analyzed by a CHN analyzer (NCS2500, Thermo Quest). Sinking PON flux was calculated based on PON content, sampling period, open area of the sediment trap (0.5 m²), and aliquot 296

size of the treated sample (1/10). The detailed analysis method and diatom valve fluxes were
described in Onodera et al. (2015). The structures of radiolarians and copepods captured in the
same traps were reported in Ikenoue et al. (2015) and Matsuno et al. (2015), respectively.

301 3. Seasonal transition in the Chukchi Borderland

302 3.1 Physical environments

We defined the NAP region as that enclosed by 74°-76°N and 159°-165°W for the 303 304 following analyses (Fig. 1). Monthly mean values of the NCEP/CFSR cloud fraction, 305 downward shortwave radiation, wind speed at a height of 10 m, snow depth, sea ice thickness, 306 and sea ice concentration averaged in the NAP region are summarized in Table 2. The modeled 307 physical variables were checked (Fig. 4). The NAP region was entirely covered by sea ice 308 during the winter and spring seasons from December to April, and sea ice concentration 309 decreased gradually from May to September in both the 2011 and 2012 cases (Fig. 4a). The 310 area-mean sea ice thickness reached approximately 200 cm in April (Fig. 4b), which was a 311 typical value north of the Chukchi Sea (Haas et al., 2010). The declines in sea ice concentration 312 and thickness were consistent with the sea ice melting period from May to September (Fig. 4c). The mechanical divergence of sea ice flow fluctuated within the range of ± 0.2 d⁻¹ in early 313 314 winter and late summer (Fig. 4d).

315 Compared with the sea ice conditions simulated in the 2011 case, the early-winter covering 316 of sea ice was somewhat delayed in the 2012 case. Although sea ice continued to melt until 317 mid-November, winter sea ice thickness was greater in the 2012 case. The anomalous wind 318 pattern could account for thicker ice transport toward the NAP region, as suggested in Section 319 4.1. The negative anomaly of sea ice thickness in the 2011 case was additionally caused by two 320 melting events in November and December (Fig. 4c) and the blanket effect of more snow 321 accumulation on top of the sea ice (not shown). The faster rate of sea ice decline caused earlier 322 sea ice opening in the 2012 case (Figs. 4a-b), partly due to lower surface albedo from less snow 323 cover. These snow and sea ice differences were compatible with the NCEP/CFSR data (Table 2). In addition, the enhanced mechanical divergence of sea ice flow from mid-July to August accelerated the sea ice reduction in 2012 (Fig. 4d). Ice algal biomass in a specific region can change based on sea ice divergence events. The detailed processes associated with cyclone activities are discussed in Section 4.4.

328 As ice algal primary production depends highly on nutrient conditions in the underlying 329 ocean surface layer, replenishment of nitrate and silicate from depths in the nutricline is 330 substantially important. The Ekman upwelling and downwelling velocities were calculated 331 from the modeled ocean surface stress fields (i.e., the combination of wind stress in open water 332 area and ice-ocean stress under sea ice). The week-long Ekman downwelling occurred in both 333 cases during the winter, as usually seen inside the Beaufort Sea (Yang, 2009), and a strong 334 upwelling event appeared in the 2011 case (Fig. 4e). In July-August, the Ekman velocity sign 335 was opposite between the two cases. The mid-summer Ekman downwelling (upwelling) played 336 a role in the nutricline deepening (shoaling) in the 2011 (2012) case. The vertical turbulent 337 mixing was characterized by vertical diffusivity diagnosed using the closure scheme of Noh and 338 Kim (1999) in the present model. Turbulent mixing was activated during winter in the 2011 339 case (Fig. 4f). During the other periods, the smaller values of modeled vertical diffusivity by 340 one or two orders indicated that the mixing process had a relatively minor impact on nutrient 341 entrainment in the NAP region.

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343 **3.2 Ice algal production**

344 The modeled ice algal production demonstrated remarkable spatial and interannual variability in the western Arctic Ocean (Fig. 5). Annual production exceeded 0.6 mmol N m⁻² 345 over most of the Chukchi Sea shelf, whereas low productivity $< 0.1 \text{ mmol N m}^{-2}$ was located in 346 347 the central Canada Basin. The shelf-basin contrast in ice algal production was previously 348 detected by the trans-Arctic Ocean expedition in the 1990s (Gosselin et al., 1997) and 349 represented by decadal model simulations (Jin et al., 2012; Dupont, 2012). In the 2011 case, the 350 local maximum appeared north of the Chukchi and Beaufort shelf breaks (Fig. 5a), whereas ice 351 algal productivity was suppressed considerably around the Beaufort Gyre region in the 2012 352 case (Fig. 5b). The negative anomaly widely covered the western Arctic except the coastal 353 shelves and the northern part of Chukchi Borderland (Fig. 5c). Station NAP was located near 354 the shelf-basin boundary and also showed the negative anomaly.

355 In the NAP region, the modeled ice algal bloom started in June and produced a peak biomass of 0.7 mmol N m^{-2} at the beginning of August in the 2011 case (Fig. 6a). The peak 356 357 timing was a few months later than the pan-Arctic averages simulated in previous models (Jin 358 et al., 2012; Deal et al., 2011), partly because the NAP region is located north of highly 359 productive shelves. An additional reason for the lagged peak phase may be attributed to a lower 360 photosynthetic response to incoming solar irradiance in the present model setting. Sensitivity to 361 optimum light intensity is shown in Section 5.1. The Hovmöller diagram visualized the vivid shelf-basin contrast along the 75°N line (Fig. 6b). The bloom signal was quite weak inside the 362 Canada Basin. A massive ice algal bloom up to 10 mmol N m⁻² was simulated in July over the 363 Chukchi northern shelf to the west of the NAP region. The modeled ice algal biomass north of 364 the Chukchi Sea was within the lower range of $1-340 \text{ mgChl m}^{-2}$ in Arctic sea ice (Arrigo et al., 365

2010) and an order of magnitude smaller than that measured in Resolute Passage (160 mgChl m⁻²; Michel et al., 1996). The Chukchi Borderland has shifted from a perennial ice-covered area to a seasonal ice zone in recent years. Multi-year ice would have dimmed the ice algal bloom until the past decades in this area. It is also reasonable that substantially less amounts of nutrients restricted ice algal growth to the level below the pan-Arctic averages. In the 2012 case, initial bloom timing was further delayed by one month and ice algal biomass was clearly smaller than that of the 2011 case (Figs. 6a, c).

373 As introduced in Section 2.2, ice algal production rate was calculated using the empirical 374 functions of light condition and nutrient uptake terms. The light condition in the skeletal layer 375 of the sea ice column was recovered slowly after the end of polar night (February in the NAP region) and then increased rapidly due to thinning of snow/ice in May (Fig. 7a). Peak values of 376 PAR (3.5 W m⁻² in the 2011 case, and 2.2 W m⁻² in the 2012 case) were recorded in mid-July 377 378 after the summer solstice. Although sea ice melting continued until September, light intensity 379 turned to decrease in accordance with the annual cycle of solar radiation. As the optimal light intensity for ice algal growth (I_{onti}) was set to 10 W m⁻² in the present experiments, the light 380 381 condition term varied in phase with the PAR transition (Fig. 7b). The weaker summer light 382 intensity in the 2012 case could be attributed to the depressed shortwave radiation due to more 383 cloud cover (Table 2), despite thinner sea ice in August (Fig. 4b). The cyclone impact on light 384 conditions is described in Section 4.4.

The nutrient conditions in the sea ice and water columns showed remarkable interannual variability. Sea ice nitrate content peaked at 0.6 mmol N m⁻² (0.2 mmol N m⁻²) in the 2011 (2012) case (Fig. 8a), which was an order of magnitude smaller than in landfast ice in Resolute Passage of the Canadian Archipelago (Cota and Smith, 1991). Potential factors contributing to 389 the difference include the nutrient environment in the underlying water column and the sea ice 390 freezing rate, because nutrient accumulation in the skeletal layer was induced by ocean-to-ice 391 flux during the sea ice freezing period (see formulation in Section 2.2). At the beginning period 392 of the one-year model integration, the nutricline depth was located at 20 m in the NAP region 393 (Figs. 8b-c). Ekman downwelling helped deepen the nutricline from October to early November in both cases (Fig. 4e). In the 2011 case, Ekman upwelling was also evident in November. 394 However, the duration was just one week, so the Ekman contribution with a peak of 0.8 m d^{-1} 395 396 played a minor role in nutrient entrainment. The more important contributory process was 397 strong mixing during winter in the 2011 case, as shown by the enhanced vertical diffusivity (Fig. 4f). According to these processes, the surface nitrate concentration reached 2 mmol N m⁻³ (Fig. 398 399 8b), and a significant part was imported into the skeletal layer (Fig. 8a). In contrast, the 400 oligotrophic water stayed over the nutricline, which was at a nearly constant depth or somewhat 401 deepened during winter in the 2012 case (Fig. 8c). Sea ice nitrate content reflected the ocean surface value of $< 1 \text{ mmol N m}^{-3}$. Sea ice silicate, which had a similar difference to nitrate, was 402 403 not a limiting factor for ice algal growth in the NAP region (not shown). The rate of sea ice 404 freezing also differed between the two cases. The total amount of thermal sea ice growth from 405 October to April was 160 (136) cm in the 2011 (2012) cases. Whereas we focused on the 406 seasonal transitions from winter to early summer, *in-situ* data of nutrient concentration and sea 407 ice freezing rate were unavailable for the target region and period. Accordingly, proper 408 evaluations of the modeled properties, particularly during winter, were difficult at this stage. At 409 least, the model results suggest that preconditioning of nutrient accumulation in the sea ice 410 column during the freezing period controlled the interannual variability in the ice algal bloom. 411 The influences of the basin-scale wind pattern and water mass transport on the nutrient412 environment are analyzed in Section 4.

413 Nutrient availability for ice algal production reflected the difference in this preconditioning. 414 Based on the present model formulation, sea ice nutrients were consumed primarily during an 415 initial stage of the ice algal bloom, and nutrients in the ocean surface layer were utilized for 416 further blooms. According to ice algal growth (Fig. 6a), the uptake ratio of sea ice nutrients 417 (RN_{upSKL}) shifted from 1 to 0.7 within a few weeks of July in the 2011 case (Fig. 7c). When the half-saturation constant for nitrate uptake (K_{NO3}) was set to 6 mmol N m⁻³ for ice algae as well 418 419 as pelagic diatoms (PL in the present model), the nitrate uptake term before the ice algal bloom 420 was approximately 0.9 (0.7) in the 2011 (2012) case (Fig. 7d). The growth ratio between the 421 two cases became 1.8 at the beginning of June after multiplying the light condition term (Fig. 422 7b). The larger growth rate accounted for the earlier initial ice algal bloom in the 2011 case (Fig. 423 6a). Sea ice nitrate was depleted rapidly by this initial bloom and partially by export to the 424 water column with melting sea ice (Fig. 8a). The subsequent decrease in the RN_{upSKL} value 425 represented utilization of the underlying seawater nutrients (Fig. 7c). The additional bloom 426 occurred in late July (Fig. 6a). In the 2012 case, the decrease in the nutrient uptake term lagged 427 behind the 2011 case in accordance with the delay of the initial bloom (Fig. 7d). The ocean 428 nutrient uptake term, which had lower values during the ice freezing period, gradually became 429 comparable with the 2011 case. However, the higher RN_{upSKL} value, except in early August, 430 restricted ocean nutrient uptake in the 2012 case (Fig. 7c).

431 As expected, the seasonal transition of the ice algal biomass was similar to daily primary 432 productivity (Figs. 9a-b). In the present model experiments, primary production derived from 433 nutrients in the skeletal layer and in the water column was calculated separately. In the 2011 434 case, the nutrient source for the ice algal bloom changed from the sea ice column for the first primary production peak of 23 μ mol N m⁻² d⁻¹ to seawater for the second larger peak of 82 μ mol 435 N m⁻² d⁻¹. The second peak value of ~ 6.6 mgC m⁻² d⁻¹ was close to the field-based estimates of 436 4–9 mgC m⁻² d⁻¹ on the Beaufort shelf and slopes (Gradinger, 2009) and < 10 mgC m⁻² d⁻¹ in 437 the Arctic basins (Deal et al., 2011). The model results indicate that nutrients imported in the 438 439 sea ice column determine the beginning of the ice algal bloom, and that ocean nutrients have a 440 greater contribution to annual ice algal production, as reported previously (Gradinger, 2009). 441 The comparison with the PON export to the underlying water column suggested that more than 442 half of the organic nitrogen was remineralized in the sea ice column (Fig. 9a). In the 2012 case, the peak of primary production simulated in early August was 35 μ mol N m⁻² d⁻¹ (Fig. 9b). The 443 444 relative contribution of ocean nutrients to primary productivity was less than that in the 2011 445 case. The August peak in PON export flux exceeding ice algal productivity was attributed to 446 lateral advection of shelf-origin sea ice floes. The detailed discussions are presented in Section 447 4.3 and 4.4.

448

449 **4.** Wind-driven dynamics associated with ice algal productivity

450 To examine background mechanisms for year-to-year changes in ice algal productivity, 451 wind-driven sea ice and ocean dynamics in the western Arctic Ocean were addressed.

452

453 **4.1 Wind and sea ice patterns**

454 Interannual variabilities in sea ice motion and ocean surface currents in the Beaufort Sea 455 are closely related to the atmospheric circulation pattern (Yang, 2009; Proshutinsky et al., 2009). 456 We compared the winter mean sea level pressure (SLP) and wind stress fields constructed from 457 the NCEP/CFSR reanalysis data between the two years. Wind stress was calculated from the 458 daily mean SLP using a protocol of the Arctic Ocean Model Intercomparison Project (AOMIP) (http://www.whoi.edu/page.do?pid=30576). An anti-cyclonic wind pattern was accompanied by 459 460 a weak Beaufort High around the Canada Basin during winter 2010-2011 (Fig. 10a). The 461 easterly wind in the southern Beaufort Sea was favorable for transporting Chukchi shelf water 462 toward the southern Canada Basin and the NAP region via the Ekman process. Ekman transport was analytically estimated with a seawater density of 1.025×10^3 kg m⁻³ and a Coriolis 463 coefficient of 1.4×10^{-4} s⁻¹. A sea ice-ocean stress value of 0.1 Pa, which was frequently 464 465 recorded along the Chukchi shelf break during early winter in the 2011 case, yielded an Ekman transport value of 0.7 m² s⁻¹ (1.8 km² mon⁻¹). This value is close to the November climatology 466 467 in the southern Beaufort Sea (Yang, 2009) and indicates a shelf-basin water exchange of 900 km³ mon⁻¹ for a shelf break axis length of 500 km. In contrast, high SLP extended from the 468 469 Siberian Arctic to the western Arctic Ocean in winter 2011–2012 (Fig. 10b). Accordingly, a 470 northwesterly wind prevailed in the Beaufort Sea. In this situation, no definite shelf water 471 transport toward the NAP region was expected by the winter wind fields.

472 The changes in wind patterns were consistent with the modeled physical environments in 473 the NAP region, where several differences between the 2011 and 2012 cases were described in 474 Section 3.1. For October to early November 2011 (i.e., the beginning period of in the 2012 475 case), localized anti-cyclonic wind forcing was closely related to the modeled negative rate of 476 sea ice growth, convergence of sea ice velocity, and Ekman downwelling in the NAP region 477 (Figs. 4c-e). The wind-driven warm water intrusion toward the marginal ice zone induced 478 lateral/bottom melting of sea ice floes (not shown). The convergence in sea ice velocity 479 increased sea ice thickness via mechanical ridging processes, in contrast to sea ice melting 480 occurring during the same period. The continuous Ekman downwelling was also accompanied 481 by the sea ice convergence. For the period afterwards, the positive anomaly of sea ice thickness 482 was produced by southward transport of thicker sea ice from the central Arctic in the 2012 case 483 (Fig. 4b). The direction of sea ice flow around the NAP region clearly differed between the two 484 years (Figs. 10c-f), as detected previously by satellite-based and modeled spatial patterns 485 (Onodera et al., 2015). Both the daily time series in the Polar Pathfinder sea ice motion vectors 486 (Fowler et al., 2013) and in the simulation results showed the successive southward advection 487 of sea ice from late October 2011 to January 2012 (Figs. 10d, f). The distance of sea ice movement reached several hundred km during this period when sea ice velocity was 5 cm s⁻¹ 488 (ca. 130 km mon⁻¹). These results suggest that the anomalous wind pattern forced southward 489 490 transport of oligotrophic sea ice and water masses within the Beaufort Gyre and eventually 491 lessened nutrient availability in the Chukchi Borderland.

492

493 **4.2 Nutrient and shelf-break tracer distributions**

494 The nutrient preconditioning that occurred before the ice algal blooming period reflected 495 the wind-driven sea ice and water mass transport, as suggested in Section 4.1. The spatial 496 distribution of the ocean nitrate concentration was characterized by a sharp meridional gradient 497 across the Chukchi and Beaufort shelf breaks (Figs. 11a-b), as captured by a number of ship-498 based observations (e.g., Nishino et al., 2011). The modeled vertical average in the top 30 m reached 10 mmol N m⁻³ in the central Chukchi Sea and was < 1 mmol N m⁻³ in the Canada 499 500 Basin. As shown in Fig. 8, nitrate content around the NAP region tended to differ. In the 2011 501 case, relatively high nitrate concentrations were distributed from the northern shelf of the 502 Chukchi Sea to east of Northwind Ridge along 75°N (Fig. 11a). On the other hand, the shelf-503 basin contrast in nitrate content was still apparent even in the southern area of Chukchi 504 Borderland in the 2012 case (Fig. 11b).

505 To explore the paths of the shelf-break water, a virtual passive tracer was provided along 506 the shelf-basin boundary. We chose the tracer source region sandwiched by the 100-200-m 507 isobaths. The tracer value was fixed continuously to one (i.e., 100% concentration) at depths of 508 0-200 m in the defined region through each one-year experiment. Advection and diffusion of 509 the tracer in the other regions were calculated as well as seawater temperature and salinity. The 510 modeled distribution in March 2011 indicated that the tracer provided along the shelf-basin 511 boundary region was transported from the Chukchi northern shelf toward the interior of the Canada Basin. The northern edge of the tracer matched the nitrate-rich area in the 2011 case 512 513 (Fig. 11a). The vertical profile of nitrate concentration in the NAP region reflected the 514 deepening nutricline driven by the Ekman downwelling in October (Figs. 4e and 11c). 515 Subsequently, nitrate content in the upper 50 m showed a net increase during December-516 January, which could be explained by lateral input rather than local vertical mixing. Hence, the 517 model results indicate that Ekman transport of Chukchi shelf water along with energetic 518 turbulent mixing enhanced nutrient availability for ice algae in the NAP region. In contrast, in 519 March 2012, the tracer signal was quite weak over the Chukchi Borderland (Fig. 11b). No 520 significant change appeared in the vertical nitrate profile during winter after the wind-driven 521 downward shift (Fig. 11d). The spread of fresher basin water blocked the intrusion of shelf 522 water and weakened the turbulent mixing. The density stratification plausibly controlled ocean 523 subsurface mixing, as wind speed averaged from November to January of the 2011 and 2012 524 winter periods was comparable (Table 2). This mechanism was consistent with previous 525 findings, in which the mixed layer depth correlated with hydrographic structures rather than 526 wind forcing in the western Arctic (Peralta-Ferriz et al., 2015).

527 Onodera et al. (2015) categorized the sinking diatom assemblages in the sediment trap 528 samples at Station NAP into 98 taxa. The dominant species during summer 2011 were Fossula 529 arctica and the Fragilariopsis group (F. cylindrus and F. oceanica), which are common in ice 530 algae in the shelf region (Cremer, 1999). Their relative abundances were minor in the sinking 531 diatom flora during summer 2012. Instead, the major diatom in August 2012 was planktic 532 species such as Thalassionema nitzschioides, which was commonly observed in the Canada 533 Basin. In addition, the sinking flux of total diatom valves in August 2012 was considerably 534 lower than that in August 2011. The observed diatom compositions and valve fluxes were 535 consistent with the above-mentioned physical backgrounds. The modeled nitrate distribution 536 and tracer pathway supported the suggestion that winter transport of oligotrophic water from 537 the interior of the Canada Basin toward the NAP region was an important factor suppressing ice 538 algal productivity during summer 2012.

539

540 **4.3 PON flux**

541 The time series of sinking PON flux in the NAP region was compared with the sediment 542 trap data. The modeled PON flux at 180 m in the 2011 case increased gradually from June and

peaked at 18 μ mol N m⁻² d⁻¹ in mid-August following the ice algal bloom (Fig. 9c). Flux > 8 543 umol N m⁻² d⁻¹ continued until the end of the model integration (i.e., September). The flux 544 545 amount was underestimated in August and became comparable afterward with the trap values. 546 PON flux at 180 m corresponded to 79% of the ocean surface value exported from the sea ice 547 bottom during July-September 2011 (Figs. 9a, c). It should be noted that ice algae released 548 from the skeletal layer were included immediately in the ice-derived PON without being 549 suspended and seeding in the present model setting. The major component of PON flux 550 originating from ice algae, as observed in the analysis of diatom valve compositions (Onodera 551 et al., 2015). PON flux derived from pelagic phytoplankton and zooplankton increased gradually in August and peaked at 6 µmol N m⁻² d⁻¹ in early September (Fig. 9c). In the 2011 552 case, the dominance of the ice-derived PON for the sinking flux was associated with its faster 553 554 sinking speed (Section 2.2 and Fig. 3e), although the total biomass of pelagic plankton groups 555 was an order of magnitude larger than that of the ice algal biomass (not shown). The sediment 556 trap data captured another peak in PON flux during May 2011, when the model experiment 557 could not reproduce the peak. Neither spring bloom of ice algae nor pelagic phytoplankton was 558 expected due to the thick ice cover in the NAP region (Fig. 4b and Table 2). This event may 559 have been caused by transport of shelf water with lithogenic materials of sea bottom sediment. 560 A candidate driver was a cold-core eddy generated from a narrow jet along the Chukchi shelf 561 break (Spall et al., 2008; Llinás et al., 2009). The background mechanisms for the spring peak 562 are beyond the scope in the present study and will be analyzed in the future.

563 PON flux in the 2012 case produced a distinct mid-summer peak at the ocean surface and 564 at 180 m, although the trapped sample volume was too low to estimate nitrogen content in 565 summer 2012 (Fig. 9b, d). The trap depth of 247–319 m in 2012, which was deeper than that of 566 181-218 m in 2011, may have caused biases in the comparison between the two years. 567 Importantly, PON flux in 2012 was markedly lower than the 1,300-m flux in 2011 (Onodera et 568 al., 2015). Again, most of the modeled PON flux was ice-derived. The contribution of pelagic-569 derived PON in the 2012 case was rather less than in the 2011 case. Enhanced sea ice melting of up to 4 cm d⁻¹ assisted the peak flux in early August (Fig. 4c). The ice-ocean flux was 570 remarkably greater than the ice algal production rate, indicating that one-dimensional sea ice 571 572 processes cannot account for PON flux in the NAP region (Figs. 9b). We trace lateral advection 573 of the ice algal biomass around the Chukchi Borderland in the next section.

574

575 **4.4 Impact of great cyclone activity**

576 It was suggested that an extreme cyclone event was a supplementary factor for the drastic 577 sea ice reduction, particularly in the western Arctic, and the subsequent record minimum extent 578 of Arctic sea ice in summer 2012 (Simmonds and Rudeva, 2012; Zhang et al., 2013). A 579 previous modeling analysis indicated that plankton productivity over the Chukchi, East Siberian, 580 and Laptev shelves was enhanced by vertical mixing with nutrient replenishment and lateral 581 plankton transport of from the western Arctic basin during the cyclone storm (Zhang et al., 582 2014). It is assumed that synoptic cyclone activities have both positive and negative 583 contributions to ice algal production. In the 2012 case, the event-like shoaling of the upper part 584 of the nutricline was caused by mixing and upwelling processes in the NAP region, where the 585 southern part of the great cyclone passed and marginal ice floes were located in early August 586 (Fig. 12a). The modeled vertical diffusivity was maintained at background values partly 587 because strong density stratification suppressed turbulent mixing until July 2012 (Fig. 4f). During the cyclone event with high wind speeds (Table 2), vertical mixing of nearly $10 \text{ cm}^2 \text{ s}^{-1}$ 588 589 reached a depth of 20 m (Figs. 4f). Besides, the Ekman upwelling that continued from July 15

590 to August 29 could have worked on nutricline shoaling of 3.3 m (Fig. 4e). However, this timing 591 of nutrient replenishment overlapped with the release of ice algae from the skeletal layer due to 592 active sea ice melting (Fig. 8c), and the mixing and upwelling processes hardly enhanced ice 593 algal productivity. Mechanical sea ice divergence associated with cyclonic wind fields rather 594 contributed to the reduction in ice algal biomass in the specific region (Fig. 4d). Whereas the 595 outward movement of sea ice floes itself did not lead to loss of ice algae, solar heat absorption 596 into the exposed open water fractions enhanced lateral/bottom melting of sea ice and 597 corresponding release of ice algae. The light conditions for ice algal growth also changed by 598 during the cyclone event with extensive cloud cover. The NCEP/CFSR reanalysis data showed 599 a depression in solar irradiance in the southern part of the cyclone passage, where an early August shortwave flux in 2012 was lower than that in 2011 by approximately 20 W m⁻² (not 600 601 shown). The negative anomaly of light intensity corresponded to a decrease in the light 602 condition term for ice algal growth by less than 0.1.

603 Here, we performed a sensitivity experiment in which all biogeochemical processes in the 604 sea ice ecosystem were halted in August 2012. In this idealized experiment (called the "no ice 605 algal activity case"), only lateral advection and sea ice-ocean fluxes were allowed in the sea ice 606 column. All physical and pelagic marine ecosystem processes were calculated as in the original 607 2012 case. Although there was no ice algal production in August, both the modeled ice algal 608 biomass and PON flux increased in the NAP region (Figs. 12c-d). These enhanced signals could 609 only be explained by horizontal transport of larger biomass from neighboring regions. The 610 differences from the original case corresponded to additional production of ice algae flowing 611 into the NAP region. Thus, lateral advection was essentially important during the 2012 cyclone 612 period.

613 In the 2012 case, westerly winds were intensified in the southern part of a cyclone passage 614 and transported shelf-origin ice algal patches toward the Northwind Ridge. Each sea ice floe 615 moved approximately 150 km eastward during August 3–10 (Fig. 12b). Although the direction 616 of sea ice motion (87.4°T) was similar to the satellite-based vectors (82.8°T), the modeled drift speed (20.3 cm s⁻¹) was markedly faster than the latter (5.1 cm s⁻¹) during the cyclone period. It 617 is plausible that the peculiar advection caused a sudden increase in ice algal biomass and an 618 619 overestimation of the modeled PON flux in the NAP region (Figs. 6a and 12b). Local biases on 620 sea ice velocity may have arisen from atmospheric momentum input and sea ice dynamics. In 621 the present experiments, the conversion from SLP to the wind stress field (i.e., the AOMIP 622 protocol referred to in Section 4.1) was formulated with specific turning angles, which varied 623 depending on geostrophic wind speed (Proshutinsky and Johnson, 1997). Uncertainties in the 624 reanalysis SLP data should also be considered, because the maximum strength of the great 625 cyclone in August 2012 calculated from the data assimilation system depended on the number 626 of radiosonde profiles (Yamazaki et al., 2015). In addition, the traditional rheology of sea ice 627 internal stress has been developed for climate models with grid spacing much coarser than 10 628 km and does not guarantee the accuracy of ice floe dynamics, especially in the marginal ice 629 zone. Thus, speed and direction of the modeled ice algal advection around the Chukchi 630 Borderland may have deviated in August 2012. These biases had less impact on the basin-scale 631 sea ice and ocean circulation.

Another concern is the event-like deepening of the shallow sediment trap at Station NAP in July 2012 (Onodera et al., 2015). An intensified ocean current occasionally inclines the upper part of the bottom-tethered mooring system during storms. The anchored sea bottom depth of 1,975 m and deepening of the trap from 260 to 320 m suggests an inclination angle of

approximately 15°. It was reported that trapping efficiency and particle components were 636 remarkably influenced by tilting $> 30^{\circ}$ (Gardner, 1985). If this previous examination can be 637 applied despite the different trap shape, a 15° tilt should not significantly impact trapping 638 efficiency. In addition, strong ocean currents > 10 cm s⁻¹ sometimes reduce trapping efficiency 639 640 (Baker et al., 1988). However, the modeled horizontal velocity at the trap depths was below 2 cm s^{-1} , even during the cyclone period (not shown). It should also be noted that the trapped 641 PON flux was continuously negligible throughout summer 2012, not only for the temporal 642 643 cyclone event.

644

645 **5.** Sensitivity experiments

646 Although the present model experiments show the interannual variability in ice algal 647 primary production and sinking biogenic particle flux in the NAP region, various sea ice-related 648 processes still need to be considered. Here, we refer to the 2011 case analyzed in previous 649 sections as the original case and performed sensitivity experiments using different model 650 settings (Fig. 13). The first three cases (Cases 1–3) address uncertainties in the model parameters. In the next three cases (Cases 4-6), the grazing pressure on ice algae and the 651 652 treatments of ice algae released into the water column are discussed. All the sensitivity 653 experiments were initiated from the modeled fields at the beginning of March in the original 654 case for the saving of computational resources and conducted until September (i.e., seven 655 months integration).

656

657 **5.1 Optimum light intensity for ice algal production (Case 1)**

658 It is difficult to estimate accurately the photosynthesis-irradiance relationships of ice-659 related flora. Ice algae adapt well to weaker light intensity compared with that of pelagic phytoplankton (Arrigo et al., 2010). In the original case, the optimum light intensity for ice 660 algal production I_{opti} was set to 10 W m⁻². Gradinger (2009) reported that the minimum 661 requirement for ice algal growth was typically $< 1 \ \mu E \ m^{-2} \ s^{-1}$ based on laboratory incubation 662 experiments. When the relationship of 1 W m⁻² \sim 4.56 μ E m⁻² s⁻¹ is applied following Lavoie et 663 al. (2005), I_{opti} may be a smaller value. Here, we performed two sensitivity experiments with 664 different I_{opti} values (Case 1). When I_{opti} was set to 5 W m⁻² (20 W m⁻²), the summer peak in the 665 light condition term was 0.9 (0.3) in the NAP region (Figs. 3b and 7a). Relaxing the light 666 667 limitation resulted in an earlier and stronger ice algal bloom (Fig. 14a). The initial bloom

occurred in early June and the second peak of ice algal biomass increased to 1.2 mmol N m⁻² (cf. 668 0.7 mmol N m⁻² in the original case). The phase and magnitude of the modeled PON flux 669 shifted similarly and were still comparable with the trap data (Fig. 14b). In contrast, restricted 670 light conditions dampened the ice algal productivity to a peak biomass of 0.1 mmol N m^{-2} (Fig. 671 672 14a). The resultant decreased release of ice algae into the water column delayed the seasonal 673 increase in the PON flux (Fig. 14b). The difference in ice algal biomass did not alter the flux during late summer, which was derived mainly from pelagic plankton. Based on these 674 sensitivity experiments, an optimum light intensity of 10 W m⁻² or below was recommended for 675 676 the formulation adopted. Other choices can be made for the light condition term. Ice algae may not suffer from photo-inhibition even when the skeletal layer receives strong irradiance diffused 677 678 from neighboring open leads during ice melting periods. A saturated light condition in 679 accordance with increasing PAR can be represented, for example, by the hyperbolic tangent 680 function used in Lavoie et al. (2005). Besides, the shelf-shading effect of ice algae reduces ice 681 algal productivity in massive blooming regions (Pogson et al., 2011).

682

683 **5.2** Nutrient sources for ice algal production (Case 2)

The present model adopted the hybrid nutrient uptake formulation. Ice algal productivity depends on the uptake ratio between sea ice and water nutrients. Here, we performed three experiments (Case 2). When the threshold value KN_{upSKL} is increased to 1.5 mmol N m⁻², (cf. 1.0 mmol N m⁻² in the original case), the ice algal growth rate reflects nutrient availability in the sea ice column more strongly (Fig. 3c). Conversely, the decrease in KN_{upSKL} to 0.5 mmol N m⁻² accelerates the uptake of seawater nutrients. However, the modeled ice algal biomass and PON flux were not sensitive to this range of KN_{upSKL} (Figs. 14c-d). As in the original case (Figs. 691 7c and 9a), the major source of ice algal production was seawater nutrients, even when only 692 20% of the biomass could utilize (i.e., $RN_{upSKL} = 0.8$). On the other hand, both the ice algal 693 biomass and PON flux dropped remarkably in another experiment, in which uptake of sea ice 694 nutrients was halted throughout the integration period (Figs. 14c-d). The slower growth rate 695 with lower concentrations of seawater nutrients prevented ice algal seeds from blooming to the 696 same level as in the original case before sea ice melting loss (Fig. 7d). The nutrient reservoir 697 (and high concentration) in the sea ice column is important for the initial acceleration in an ice 698 algal bloom, and nutrient availability in the ocean surface layer controls peak biomass.

699 The exchange rate of dissolved materials at the ice-water interface generally depends on 700 molecular and turbulent diffusion processes. Lavoie et al. (2005) assumed that nutrient 701 replenishment from the underlying mixed layer was proportional to friction velocity varying 702 with the tidal cycle. The tidal effect is important in some regions such as the narrow straits of 703 the Canadian Archipelago. However, the essential improvement would be necessary for its 704 application to the entire Arctic Ocean. In this connection, the ocean-to-ice nutrient flux is 705 proportional to the CF_{OI} coefficient during the ice freezing period. A CF_{OI} value of 0 or 1 is 706 clearly unrealistic, because a significant portion of *in-situ* seawater nutrients remains inside the 707 sea ice column, and the residual is ejected to the underlying water column after sea ice freezing 708 as well as salinity. The original case adopted a CF_{OI} value of 0.3, following a first-year ice 709 salinity of ~ 10 psu. Smaller CF_{OI} values suppress nutrient accumulation in the skeletal layer 710 during the freezing period and delay the initial ice algal bloom. Another assumption in the present model is that all of the sea ice nutrients are concentrated only in the skeletal layer with 711 712 its constant thickness (cf. 2 cm in the original case), instead of brine pockets and channels that 713 were not represented in the present model. An increase in the layer thickness reduces nutrient 714 "concentration" (not total amount integrated in the entire sea ice column) and consequently delays an ice algal bloom. For example, a nitrate content of 0.6 mmol N m⁻², which was 715 recorded in April of the original 2011 case (Fig. 8a), yields a concentration of 30 mmol N m⁻³ 716 (12 mmol N m⁻³) and a nitrate condition term of 0.91 (0.80) in the skeletal layer with 2-cm (5-717 718 cm) thickness. A time-varying biologically active layer with brine volumes (Tedesco et al., 2010) and multiple separate sea ice layers (Pogson et al., 2011) have been proposed to represent 719 720 ice algal habitats more precisely. These uncertainties in sea ice nutrients seem to have an impact 721 on ice algal production.

722

723 **5.3** Sinking speed of ice-derived PON (Case 3)

The present model prescribed the fixed vertical profile of particle sinking speed (Fig. 3e). 724 In the original case, the sinking speed of ice-derived PON varied from 50 m d⁻¹ in the 725 uppermost model layer to 200 m d⁻¹ at a depth of 1.000 m. This speed range was comparable 726 with the previous estimate of $> 85 \text{ m d}^{-1}$ between the shallow (180 m) and deep (1,300 m) traps 727 at Station NAP in August 2011 (Onodera et al., 2015). The PON exported from the sea ice 728 729 bottom reached a depth of 180 m within four days under the model profile. As the decomposition rate from PON to ammonium and DON was set to 0.2 d⁻¹ at 0 °C, approximately 730 731 half (47%) of the ice-derived PON was dissolved above a depth of 180 m. Here, we performed two experiments (Case 3), in which the minimum sinking speed was set to 200 (20) m d^{-1} in the 732 faster (slower) sinking case (cf. 50 m d^{-1} in the original case). The remaining ratio of ice-733 734 derived PON after dissolution in these cases is theoretically 82% and 20% at a 180-m depth, respectively. Sinking speed hardly affected ice algal biomass (Fig. 14e), although the vertical 735 736 nutrient profile in the water column had quite minor changes. On the other hand, PON flux differed significantly between the two cases (Fig. 14f). The earlier and larger peak in the PON
flux appeared in the faster sinking case. The flux range obtained in Case 3 was smaller than the
sensitivity to the optimum light intensity evaluated in Case 1.

740 Actual sedimentation of biogenic particles depends on the ballast distribution in addition to 741 aggregation and elimination of light/fragile organic materials. When the source region of sea ice 742 and surface water in the NAP region was the central Canada Basin, an insufficient quantity of 743 ballast particles would have allowed slower PON sinking (Honjo et al., 2010). A variable 744 sinking speed depending ballast particles may improve a model performance on the PON flux. 745 Besides, the PON derived from phytoplankton and zooplankton possibly has a different sinking 746 speed. The faster sinking speed of fecal pellets may account for a substantial portion of the particle flux as observed in Resolute Passage (Michel et al., 1996). Thus, many uncertainties 747 748 remain with respect to the PON sinking process.

749

750 **5.4 Grazing on ice algae (Case 4)**

751 Previous observations detected a significant quantity of ice-related fauna including 752 amphipods in the sea ice column (Bluhm et al., 2010). It was also reported that ice algal 753 assemblages suspended under the ice bottom layer were an important food source for pelagic 754 grazers (e.g., copepods) during the early stages of sea ice melting (Michel et al., 1996). Here, 755 the impact of the grazing process on ice algal biomass was examined (Fig. 13). In Case 4, the 756 concentration of ice-related fauna (IF) changed from zero in the original case (i.e., no grazing pressure on ice algae throughout the integration period) to 0.02 mmol N m⁻³ on March 1. The 757 758 rate of IF grazing on ice algae was calculated following the Ivlev relationship:

759
$$\operatorname{Grz} = \max\{0, \operatorname{Grz}_{\max} \times (1 - \exp\{\lambda (\operatorname{IA}^* - \operatorname{IA})\})\},\$$

where the maximum grazing rate Grz_{max} of 0.4 d⁻¹ at 0 °C, the Ivlev constant λ of 1.4 (mmol N 760 m⁻³)⁻¹, and the feeding threshold value IA* of 0.04 mmol N m⁻³ were given, as well as the 761 grazing of mesozooplankton (ZL) on pelagic diatom (PL) in the original NEMURO model 762 (Kishi et al., 2007). The Ivley formulation assumes that no grazing occurs at an ice algal 763 764 concentration IA lower than IA*. The modeled ice algal biomass showed the rapid decline after a similar peak compared with the original case (Fig. 4g). The ice-related fauna gradually 765 766 increased following the ice algal bloom. A resultant peak of the IF biomass was 0.07 mmol N m⁻². This grazing process slightly contributed to the reduced PON flux (Fig. 14h). After sea ice 767 768 melting, the released IF was included in ZL in the water column. For the sake of the enhanced 769 grazing pressure in the water column, the phytoplankton biomass was also smaller than in the 770 original case (not shown). We used same parameter values of the grazing process as pelagic 771 planktons. When the skeletal layer is regarded as a refuge for ice algae from potential grazers, 772 the maximum rate and consequent impact of grazing in the sea ice column should be smaller.

773

774 **5.5** Transfer from ice algae to phytoplankton (Case 5)

775 It has been reported that a part of ice algae exported to the water column could continue 776 their production activities as phytoplankton and become a zooplankton food source (Michel et al., 1993; Leventer, 2003; Gradinger et al., 2009). In Case 5, a constant ratio of ice algae 777 778 released from the sea ice bottom was included in pelagic diatom (PL). The seeding partition 779 was set to 0.5, assuming that a half of the released algae behaved in the form of living intact 780 cells and the residual was included in the ice-related PON. Although the increased PL became a 781 competitor of ice algae for the uptake of seawater nutrients in the uppermost ocean layer, the 782 comparison with the original case showed little difference in the ice algal biomass (Figs. 14i).

On the other hand, the ice-derived algae staying alive in the water column were eventually included in the slower-sinking PON produced from pelagic species. These processes contributed to the decrease in PON flux at the trap depth (Fig. 14j). There is a wide uncertainty of seeding ratios of the released ice algae. For example, the ratio was set to 0.1 by Jin et al. (2012). To assess an impact of ice algal seeding to phytoplankton bloom and sinking biogenic fluxes more accurately, simultaneous measurements of diatom compositions both in the sea ice and water columns would be necessary.

790

791 **5.6 Grazing on ice-derived PON (Case 6)**

Zooplankton grazing on sinking biogenic particles could influence the quantity and
composition of export fluxes in the water column. In Case 6, ZL grazing on ice-derived PON
(fPON in the present model) was considered using the Ivlev equation:

795 $Grz = \max\{0, Grz_{max} \times (1 - \exp\{\lambda (fPON^* - fPON)\})\},\$

where Grz_{max} of 0.4 d⁻¹ and λ of 1.4 (mmol N m⁻³)⁻¹ were given as well as Case 4. The feeding 796 threshold value fPON* was set to zero, and the contributions of other potential grazers (ZS and 797 798 ZP in the present model) were neglected, for simplicity. This type of grazing hardly affected the 799 ice algal biomass as in Case 3 (Fig. 14k), and the PON flux also showed little difference from the original case (Fig. 141). A fPON concentration of 0.5 µmol N m⁻³ arising in mid-August 800 yielded a grazing rate Grz of $2.8 \times 10^{-4} \text{ d}^{-1}$. As the ZL concentration was still nearly 50 µmol N 801 m^{-3} in the upper 50 m, the grazed amount of fPON was 0.014 µmol N $m^{-3} d^{-1}$ at the flux peak. 802 The grazed ratio of 0.028 d⁻¹ based on the above estimate was an order of magnitude smaller 803 than the decomposition rate (see Section 5.3). This result indicated that the impact of 804 805 zooplankton grazing on ice-derived PON was negligible, at least in the NAP region. In addition,

zooplankton would not efficiently capture fast-sinking aggregates as shown in Lake Saroma
(Nishi and Tabeta, 2005). Suspended algae are rather preferable for zooplankton growth
(Michel et al., 1996).

810 **6. Summary**

Biogeochemical structures in the western Arctic were addressed using a sea ice-ocean modeling approach. In the present work, the sea ice ecosystem with ice algal activity was newly incorporated into a pelagic marine ecosystem model. We assumed that ice algae could utilize nutrients (nitrate, ammonium, and silicate) both in the skeletal layer of sea ice and in the ocean surface layer (i.e., seawater nutrients). The ratio of the nutrient source varied depending on ice algal biomass. This "hybrid-type" nutrient uptake formulation is an option to represent more realistic characteristics of ice algal biology.

818 The modeled ice algal primary production demonstrated noticeable interannual variability 819 as suggested by previous sediment trap analyses in the NAP region. It was found that year-to-820 year changes in ice algal production were closely related to pan-Arctic wind patterns. In winter 821 2010-2011, strong easterly winds around the Beaufort High induced basin-ward Ekman 822 transport of shelf-origin surface water and vertical turbulent mixing with underlying nutricline 823 waters. The higher nitrate concentrations were then distributed in the southern Beaufort Sea and 824 the Chukchi Borderland. On the other hand, in winter 2011-2012, northwesterly winds 825 associated with an extension of the Siberian High distributed oligotrophic water from the 826 central Canada Basin toward the northern Chukchi shelf. Hence, ice algal productivity in the 827 NAP region was suppressed by a deeper nutricline, in addition to cloud shading of solar 828 irradiance, until early summer.

The modeled summer biogenic particle flux in the NAP region was comparable with the sediment trap data in 2011 and but was remarkably overestimated in 2012. In summer 2012, lateral advection processes resulted in the enhanced PON flux, because the ice-ocean flux exceeded ice algal production in the same location. In August, westerly winds intensified in the 833 southern part of the cyclone transported the shelf-origin ice algal patches toward the NAP 834 region. This cyclone event may have caused the model biases on sea ice motion and biogenic 835 particle flux. We further considered several model uncertainties through the sensitivity 836 experiments. The modeled ice algal biomass was highly sensitive to optimum light intensity. 837 PON flux in the water column varied depending on particle sinking speed in addition to ice 838 algal productivity. The impacts of various grazing processes on PON flux were relatively minor 839 within the present cases. However, more possibilities should also be addressed in future studies. 840 Successive observations and model improvements are indispensable to gather ubiquitous 841 findings on ice-related biological processes.

842

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849 **References**

- 850 Aota, M. and Ishikawa, M.: On the extinction coefficient of sea ice, Low Temperature Science
- 851 Series A., 40, 127–135, 1982.
- Arrigo, K., Kremer, J. N., and Sullivan, C. W.: A simulated Antarctic fast ice ecosystem, J.
 Geophys. Res., 98, 6929–6946, 1993.
- Arrigo, K. R., Mock T., and Lizotte, M. P.: Primary producers and sea ice. In: Thomas, D. N.,
 Dieckmann, G. S. (Eds.), Sea Ice. Wiley-Blackwell, Oxford, pp. 283–325, 2010.
- 856 Baker, E. T., Milburn, H. B., and Tennant, D. A.: Field assessment of sediment trap efficiency
- under varying flow conditions, J. Mar. Res., 46, 573–592, 1998.
- Bitz, C. M., Holland, M. M., Weaver, A. J., and Eby, M.: Simulating the ice-thickness
 distribution in a coupled climate model, J. Geophys. Res., 106, 2441–2463, 2001.
- Bitz, C. M. and Lipscomb, W. H.: An energy-conserving thermodynamic model of sea ice, J.
 Geophys. Res., 104, 15,669–15,677, 1999.
- Bluhm, B. A., Gradinger, R. R., Schnack-Schiel, S. B.: Sea ice meio- and macro-fauna. In:
 Thomas, D. N., Dieckmann, G. S. (Eds.), Sea Ice. Wiley-Blackwell, Oxford, pp. 357–393,
 2010.
- Boetius, A. et al.: Export of algal biomass from the melting Arctic sea ice, Science, 339, 1430–
 1432, 2013.
- Cota, G. F., Legendre, L., Gosselin, M., and Ingram, R. G.: Ecology of bottom ice algae: I.
 Environmental controls and variability, J. Mar. Sys., 2, 257–277, 1991.
- Cota, G. F. and Smith, R. E. H.: Ecology of bottom ice algae: II. Dynamics, distributions and
 productivity, J. Mar. Sys., 2, 279–295, 1991.

- 871 Cremer, H: Distribution patterns of diatom surface sediment assemblages in the Laptev Sea
 872 (Arctic Ocean). Mar. Micropal., 38, 39–67, 1999.
- 873 Deal, C., Jin, M., Elliot S., Hunke, E., Maltrud, M., and Jeffery, N.: Large-scale modeling of
- primary production and ice algal biomass within arctic sea ice in 1992, J. Geophys. Res.,
- 875 116, C07004, doi:10.1029/2010JC006409, 2011.
- B76 Dupont, F.: Impact of sea-ice biology on overall primary production in a biophysical model of
 the pan-Arctic Ocean, J. Geophys. Res., 117, C00D17, doi:10.1029/2011JC006983, 2012.
- 878 Fahl, K. and Nöthig, E.-M.: Lithogenic and biogenic particle fluxes on the Lomonosov Ridge
- 879 (central Arctic Ocean) and their relevance for sediment accumulation: Vertical vs. lateral
 880 transport, Deep Sea Res- I, 54, 1256–1272, 2007.
- Forest, A., et al.: Particulate organic carbon fluxes on the slope of the Mackenzie Shelf
 (Beaufort Sea): Physical and biological forcing of shelf-basin exchanges. J. Mar. Sys., 68,
 39–54, 2007.
- Garcia, H. E., Locarnini, R. A., Boyer, T. P., Antonov, J. I., Baranova, O. K., Zweng, M. M.,
- Reagan, J. R., and Johnson, D. R.: World Ocean Atlas 2013, Volume 4: Dissolved Inorganic
 Nutrients (phosphate, nitrate, silicate). Levitus, S., Ed., Mishonov, A. Technical Ed.;
- 887 NOAA Atlas NESDIS, 76, 25pp., 2013.
- Gardner, D. H.: The effect of tilt on sediment trap efficiency, Deep Sea Res.-A, 32, 349–361,
 1985.
- 890 Gosselin, M., Levasseur, M., Wheeler, P. A., Horner, R. A., and Booth, B. C.: New
- 891 measurements of phytoplankton and ice algal production in the Arctic Ocean, Deep Sea
- 892 Res.-II, 44, 1623–1644, 1997.

893 Gradinger, R.: Sea-ice algae: Major contributors to primary production and algal biomass in the

Chukchi and Beaufort Seas during May/June 2002, Deep Sea Res.-II, 56, 1201–1212, 2009.

- 895 Haas, C., Hendricks, S., Eicken, H., and Herber, A.: Synoptic airborne thickness surveys reveal
- state of Arctic sea ice cover, Geophys. Res. Lett., 37, L09501, doi:10.1029/2010GL042652,
 2010.
- Hasumi, H.: CCSR Ocean Component Model (COCO) version 4.0, Center for Climate System
 Research Report, Univ. of Tokyo, 25, 103pp., 2006.
- 900 Honda, M. C., Kawakami, H., Watanabe, S., and Saino, T.: Concentration and vertical flux of
- 901 Fukushima-derived radiocesium in sinking particles from two sites in the Northwestern
- 902 Pacific Ocean, Biogeosciences, 10, 3525–3534, doi:10.5194.bg-10-3525-2013, 2013.
- Honjo, S., et al.: Biological pump processes in the cryopelagic and hemipelagic Arctic Ocean:
 Canada Basin and Chukchi Rise, Prog. Oceanogr., 85, 137–170, 2010.
- Hunke, E. C. and Dukowicz, J. K.: An elastic-viscous-plastic model for sea ice dynamics, J.
 Phys. Oceanogr., 27, 1849–1867, 1997.
- 907 Hwang, J., Kim, M., Manganini, S. J., McIntyre, C. P., Haghipour, N., Park, J. J., Krishfield, R.
- A., Macdonald, R. W., McLaughlin, F. A., and Eglinton, T. I.: Temporal and spatial
 variability of particle transport in the deep Arctic Canada Basin, J. Geophys. Res., 120,
 2784–2799, doi:10.1002/2014JC010643, 2015.
- 911 Ikenoue, T., Bjorklund, K. R., Kruglikova, S. B., Onodera, J., Kimoto, K., and Harada, N.: Flux
- 912 variations and vertical distributions of siliceous Rhizaria (Radiolaria and Phaeodaria) in the
- 913 western Arctic Ocean: indices of environmental changes, Biogeosciences, 12, 2019–2046,
- 914 doi:10.5194/bg-12-2019-2015, 2015.

- Jin, M., Deal, C. J., Wang, J., Shin, K.-H., Tanaka, N., Whitledge, T. E., Lee, S. H., Gradinger,
 R. R.: Controls of the landfast ice-ocean ecosystem offshore Barrow, Alaska, Ann. Glaciol.,
 44, 63–72, 2006.
- Jin, M., Deal, C., Lee, S. H., Elliott, S., Hunke, E., Maltrud, and M., Jeffery, N.: Investigation
- 919 of Arctic sea ice and ocean primary production for the period 1992-2007 using a 3-D global
- 920 ice-ocean ecosystem model, Deep Sea Res.-II, 81–84, 28–35,
 921 doi:10.1016/j.dsr2.2011.06.003, 2012.
- Kishi, M. J., et al.: NEMURO-a lower trophic level model for the North Pacific marine
 ecosystem, Ecol. Model., 202, 12–25, 2007.
- Lalande, C., Nöthig, E.-M., Somavilla, R., Bauerfeind, E., Shevchenko, V., and Okolodkov, Y.:
 Variability in under-ice export fluxes of biogenic matter in the Arctic Ocean, Global
 Biogeochem. Cycles, 28, doi:10.1002/2013GB004735, 2014.
- Lavoie, D., Denman, K., and Michel, C.: Modeling ice algal growth and decline in a seasonally
 ice-covered region of the Arctic (Resolute Passage, Canadian Archipelago), J. Geophys.
- 929 Res., 110, C11009, doi:10.1029/2005JC002922, 2005.
- 930 Lavoie, D., Denman, K. L., and Macdonald, R. W.: Effects of future climate change on primary
- productivity and export fluxes in the Beaufort Sea, J. Geophys. Res., 115, C04018,
 doi:10.1029/2009JC005493, 2010.
- Leonard, B. P., MacVean, M. K., and Lock, A. P.: The flux-integral method for multidimensional convection and diffusion, NASA Tech. Memo, 106679/ICOMP-94-13, NASA,
 Washington, D. C., 1994.
- 936 Leventer, A.: Particulate flux from sea ice in polar waters. In: Thomas, D. N. and Dieckmann G.
- 937 S. (Eds.), Sea Ice. Wiley-Blackwell, Oxford, pp. 303–332, 2003.

- 938 Llinas, L., Pickart, R. S., Mathis, J. T., and Smith, S. L.: Deep Sea Res.-II, 56, 1290–1304, 2009.
- Lipscomb, W. H.: Remapping the thickness distribution in sea ice models, J. Geophys. Res.,
 106, 13,989–14,000, 2001.
- 941 Matsuno, K., Yamaguchi, A., Fujiwara, A., Onodera, J., Watanabe, E., Harada, N., and Kikuchi,
- T.: Seasonal changes in the population structure of dominant planktonic copepods collected
 using a sediment trap moored in the western Arctic Ocean, J. Natural History, in press.,
 2015.
- McLaughlin, F. A. and Carmack, E. C.: Deepening of the nutricline and chlorophyll maximum
 in the Canada Basin interior, 2003–2009, Geophys. Res. Lett., 37, L24602,
 doi:10.1029/2010GL045459, 2010.
- Michel, C., Legendre, L. L., Therriault, J.-C., Demers, S., and Vandevelde T.: Springtime
 coupling between ice algal and phytoplankton assemblages in southeastern Hudson Bay,
 Canadian Arctic, Polar Biol., 13, 441–449, 1993.
- 951 Michel, C., Legendre, L., Ingram, R. G., Gosselin, M., and Levasseur, M.: Carbon budget of
- 952 sea-ice algae in spring: Evidence of a significant transfer to zooplankton grazers, J.
 953 Geophys. Res., 101, 18,345–18,360, 1996.
- Nishi, Y., and Tabeta, S.: Analysis of the contribution of ice algae to the ice-covered ecosystem
 in Lake Saroma by means of a coupled ice-ocean ecosystem model. J. Mar. Sys., 55, 249–
 270, 2005
- 957 Nishino, S., Kikuchi, T., Yamamoto-Kawai, M., Kawaguchi, Y., Hirawake, T., and Itoh, M.:
- 958 Enhancement/reduction of biological pump depends on ocean circulation in the sea-ice
- reduction regions of the Arctic Ocean. J. Oceanogr., 67, 305–314, 2011.

- Noh, Y. and Kim, H. J.: Simulations of temperature and turbulence structure of the oceanic
 boundary layer with the improved near-surface process, J. Geophys. Res., 104, 15,621–
 15,634, 1999.
- Onodera, J., Watanabe, E., Harada, N., and Honda, M. C.: Diatom flux reflects water-mass
 conditions on the southern Northwind Abyssal Plain, Arctic Ocean, Biogeosciences, 12,
 1373–1385, doi:10.5194/bg-12-1373-2015, 2015.
- Peralta-Ferriz, C. and Woodgate, R. A.: Seasonal and interannual variability of pan-Arctic
 surface mixed layer properties from 1979 to 2012 from hydrographic data, and the
 dominance of stratification for multiyear mixed layer depth shoaling, Prog. Oceanogr., in
 press, doi:10.1016/j.pocean.2014.12.005, 2015.
- Pogson, L., Tremblay, B., Lavoie, D., Michel, C., and Vancoppenolle, M.: Development and 970 971 validation of a one-dimensional snow-ice algae model against observations in Resolute 972 Passage. Canadian Arctic Archipelago, J. Geophys. Res. 116. C040110. 973 doi:10.1029/2010JC006119, 2011.
- 974 Proshutinsky, A. Y. and Johnson, M. A.: Two circulation regimes of the wind-driven Arctic
 975 Ocean, J. Geophys. Res., 102, 12,493–12,514, 1997.
- 976 Proshutinsky, A., Krishfield, R., Timmermans, M.-L., Toole, J., Carmack, E., McLaughlin, F.,
- 977 Williams, W. J., Zimmermann, S., Itoh, M., and Shimada, K.: Beaufort Gyre freshwater
- 978 reservoir: State and variability from observations, J. Geophys. Res., 114, C00A10,
 979 doi:10.1029/2008JC005104, 2009.
- 980 Saha, S., et al.: The NCEP Climate Forecast System reanalysis. Bull. Am. Meteorol. Soc., 91,
- 981 1015–1057, doi:10.1175/2010BAMS3001.1, 2010.

- Simmonds, I. and Rudeva, I.: The great Arctic cyclone of August 2012, Geophys. Res. Lett., 39,
 L23709, doi:10.1029/2012GL054259, 2012.
- Spall, M. A., Pickart, R. S., Frantantoni, P. S., and Plueddemann, A. J.: Western Arctic
 shelfbreak eddies: Formation and transport, J. Phys. Oceanogr., 38, 1644–1668, 2008.
- Steele, M., Morley, R., and Ermold, W.: PHC: A global ocean hydrography with a high-quality
 Arctic Ocean, J. Clim., 14, 2079–2087, 2001.
- Tedesco, L., Vichi, M., Haapala, J., and Stipa, T.: A dynamic Biologically Active Layer for
 numerical studies of the sea ice ecosystem, Ocean Model., 35, 89–104, 2010.
- 990 Vancoppenolle, M., Goosse, H., de Montety A., Fichefet, T., Tremblay, B., and Tison, J. -L.:
- 991 Modeling brine and nutrient dynamics in Antarctic sea ice: The case of dissolved silica, J.
- 992 Geophys. Res., 115, C02005, doi:10.1029/2009JC005359.
- Wassmann, P.: Arctic marine ecosystems in an era of rapid climate change. Prog. Oceanogr.. 90,
 1–17, 2011.
- 995 Watanabe, E.: Beaufort shelf break eddies and shelf-basin exchange of Pacific summer water in
- the western Arctic Ocean detected by satellite and modeling analyses, J. Geophys. Res.,
 116, C08034, doi:10.1029/2010JC006259, 2011.
- Watanabe, E., Kishi, M. J., Ishida, A., and Aita, M. N.: Western Arctic primary productivity
 regulated by shelf-break warm eddies, J. Oceanogr., 68, 703–718, doi:10.1007/s10872-012-
- 1000 0128-6, 2012.
- 1001 Watanabe, E., Onodera, J., Harada, N., Honda, M. C., Kimoto, K., Kikuchi, T., Nishino, S.,
- 1002 Matsuno, K., Yamaguchi, A., Ishida, A., and Kishi, M. J.: Enhanced role of eddies in the
- 1003 Arctic marine biological pump, Nature Comm., 5, doi:10.1038/ncomms4950, 2014.

- Woodgate, R. A., Aagaard, K., and Weingartner, T. J.: Monthly temperature, salinity, and
 transport variability of the Bering Strait through flow, Geophys. Res. Lett., 32, L04601,
 doi:10.1029/2004GL021880, 2005.
- 1007 Yamazaki, A., Inoue, J., Dethloff, K., Maturilli, M., and Kön
- 1007 Yamazaki, A., Inoue, J., Dethloff, K., Maturilli, M., and König-Langlo, G.: Impact of
- 1008 radiosonde observations on forecasting summertime Arctic cyclone formation, J. Geophys.
- 1009 Res., 120, doi:10.1002/2014JD022925, 2015.
- 1010 Yang, J.: Seasonal and interannual variability of downwelling in the Beaufort Sea, J. Geophys.

1011 Res., 114, C00A14, doi:10.1029/2008JC005084, 2009.

- 1012 Zhang, J., Spitz, Y. H., Steele, M., Ashjian, C., Campbell, R., Berline, L., and Matrai, P.:
- 1013 Modeling the impact of declining sea ice on the Arctic marine planktonic ecosystem, J.

1014 Geophys. Res., 115, C10015, doi:10.1029/2009JC005387, 2010.

- 1015 Zhang, J., Lindsay, R., Schweiger, A., and Steele, M.: The impact of an intense summer cyclone
 1016 on 2012 Arctic sea ice retreat, Geophys. Res. Lett., 40, doi:10.1002/grl.50190, 2013.
- 1017 Zhang, J., Ashjian, C., Campbell, R., Hill, V., Spitz, Y. H., and Steele, M.: The great 2012 Arctic
- 1018 Ocean summer cyclone enhanced biological productivity on the shelves, J. Geophys. Res.,
- 1019 119, 297–312, 2014.

1020

Table captions

Table 1. Parameters in the sea ice ecosystem model. The values of ice algae are same as those of large phytoplankton in the original NEMURO model (Kishi et al., 2007). The PAR fraction followed Zhang et al. (2010), and the light extinction rates were derived from Aota and Ishikawa (1982). The parameter values of nitrogen and silicon flows in the skeletal layer were same as those in the water column, which were also provided by Kishi et al. (2007).

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Table 2. Monthly mean values of NCEP/CFSR cloud fraction (n. d.), downward shortwave radiation (W m⁻²), 10 m wind speed (m s⁻¹), snow depth (cm), sea ice thickness (cm), and sea ice concentration (n. d.) averaged in the NAP region. 2011 (2012) corresponds to the period from October 2010 (2011) to September 2011 (2012) to compare the model results.

1032

1033 **Figure captions**

Figure 1. Bathymetry of the pan-Arctic sea ice-ocean model COCO. Location of Station NAP is indicated by a red dot in the left enlarged view. The NAP region defined in the present study is enclosed by 74°–76°N and 159°–165°W. The model integration period covers 33 years from 1979 to 2011 only for the physical oceanographic part using the 25 km resolution version, and the obtained fields are given as initial condition for one year experiment from October 2010 (2011) to September 2011 (2012) in the 2011 (2012) case using the 5 km resolution version with marine ecosystem components.

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Figure 2. Schematic image and configuration of the Arctic NEMURO model. Nitrogen and silicon flows are composed of photosynthesis (Photo), shell formation (Shell), respiration (Res), excretion (Exc), mortality (Mor), grazing (Grz), predation (Prd), egestion (Ege), decomposition (Dec), remineralization (Rem), nitrification (Nit), and sinking (Sink). Ice algal habitat is confined to the skeletal layer of sea ice bottom. Ice-related fauna (IF) is calculated only in a sensitivity experiment (Case 4). Exchange of biogeochemical variables with the pelagic ecosystem is allowed at the ice-ocean interface.

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Figure 3. Relationships of (a) light extinction rate (non-dimensional (n. d.)) v. s. thickness of (dashed line) snow and (solid line) sea ice (cm), (b) light condition term (n. d.) v. s. light intensity (PAR) (W m⁻²), (c) ice nutrient uptake ratio RN_{upSKL} (n. d.) v. s. ice algal biomass (mmol N m⁻²), (d) nitrate condition term (n. d.) v. s. nitrate concentration (mmol N m⁻³), and (e) sinking speed of PON derived from (solid line) ice algae and (dashed line) pelagic plankton groups (m d⁻¹) v. s. depth in the water column (m), respectively, in the Arctic NEMURO model.
See more information in Section 2.2.

1057

Figure 4. Seasonal transition of daily mean modeled variables in the NAP region. (a) Sea ice concentration (n. d.), (b) sea ice thickness (cm), (c) thermal growth rate of sea ice (cm d⁻¹), (d) divergence of sea ice velocity (d⁻¹), (e) Ekman upwelling velocity diagnosed using ocean surface stress fields (m d⁻¹), and (f) vertical diffusivity at the depth of 20 m (cm² s⁻¹) in the 2011 (red line) and 2012 (blue line) cases. Note that negative values in (c), (d), and (e) correspond to sea ice melting, convergence of sea ice velocity, and Ekman downwelling, respectively. Vertical diffusivity in (f) is shown in a logarithm scale.

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Figure 5. Modeled annual primary production of ice algae in the (a) 2011 and (b) 2012 cases (mmol N m⁻²). The difference between the two cases is shown in (c). Yellow dots denote the location of Station NAP. White dots represent the eastern and western limits of 75°N section in Figs. 6b-c.

1070

Figure 6. Modeled seasonal transition of ice algal biomass (a) in the NAP region and (b-c) along the 75°N line (mmol N m⁻²). Sea floor depths along the east-west section are also plotted (m). Red line in (a) and Hovmöller diagram in (b) correspond to the 2011 case. Blue line in (a) and the diagram in (c) correspond to the 2012 case. The content of 1 mmol N m⁻² in the sea ice column corresponds to the concentration of 50 mmol N m⁻³ when the skeletal layer thickness is set to 2 cm.

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Figure 7. Modeled seasonal transition of (a) light intensity (PAR) in the skeletal layer (W m⁻²), (b) light condition term (n. d.), (c) ice nutrient uptake ratio RN_{upSKL} (n. d.), and (d) nitrate condition term (n. d.) in the NAP region in the 2011 (red line) and 2012 (blue line) cases. Each term in (b-d) corresponds to ice algal value. In (d), the condition terms in the (thick lines) skeletal layer and (thin lines) ocean surface layer are shown.

1083

Figure 8. Modeled seasonal transition of nitrate concentration (a) in the skeletal layer (mmol N m^{-2}) and (b-c) in the top 100 m of water columns (mmol N m^{-3}). Red line in (a) and vertical profile in (b) correspond to the 2011 case. Blue line in (a) and the profile in (c) correspond to the 2012 case.

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Figure 9. Modeled (a-b) primary production rate of ice algae and (c-d) PON flux in the NAP 1089 region in the (a, c) 2011 and (b, d) 2012 cases (umol N $m^{-2} d^{-1}$). In (a-b), the daily rate of total 1090 1091 primary production (black lines) and those derived from nutrients in the skeletal layer (light 1092 blue lines) and water column (purple lines) are shown. The export flux of PON from the sea ice 1093 bottom to the underlying water column is overlaid by olive lines. In (c-d), the total simulated 1094 (black lines) and observed (gray bars) PON fluxes at 180 m are compared. The fluxes 1095 originating from ice algae (green lines) and pelagic plankton groups (orange lines) are also 1096 shown.

1097

1098 Figure 10. (a-b) (contours) Sea level pressure (SLP) (hPa) and (vectors) wind stress averaged 1099 (a) from November 2010 to January 2011 and (b) from November 2011 to January 2012. SLP is 1100 obtained from the NCEP/CFSR dataset, and wind stress vectors are calculated from the SLP 1101 field using the AOMIP formulation. Unit vector of wind stress is 0.1 Pa. Direction of (c-d) satellite-based and (e-f) modeled sea ice velocity in the NAP region (degree). Only daily 1102 averages whose velocity exceeded 5 cm s⁻¹ in the (c, e) 2011 and (d, f) 2012 periods are plotted. 1103 1104 Positive (negative) values of the direction correspond to northward (southward), and solid 1105 (dashed) bars indicate westward (eastward) motions, respectively. For example, a solid bar of -45° means southwestward direction of 225 °T. 1106

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Figure 11. Modeled nitrate concentration (mmol N m⁻³). The daily mean fields averaged in the 1108 1109 top 30 m of water columns on March 1 in the (a) 2011 and (b) 2012 cases are shown in the 1110 upper panels. In these experiments, a passive tracer is provided from the ocean surface to sea 1111 floor of 100-200 m depth along shelf-basin boundary sandwiched by white contours. Black 1112 contours correspond to a tracer value of 0.2 (0–30 m average). Orange lines denote the isobaths 1113 of 1,000 and 3,000 m. The vertical profile in the NAP region on (black) October 1, (blue) 1114 December 1, and (magenta) February 1 in the (c) 2011 and (d) 2012 cases are shown in the 1115 lower panels.

1116

Figure 12. (a) NCEP/CFSR (contours) sea level pressure (hPa) and (shade) sea ice concentration (n. d.) on August 6, 2012. (b) Modeled (contours) PON flux at the depth of 180 m and (vectors) sea ice motion averaged for August 3–10 in the 2012 case. The flux contours of 5, 10, and 20 µmol N m² d⁻¹ are shown around the Chukchi Borderland. The sea ice motion is overlaid every ten grid (i.e., approximately 50 km), and its unit vector is 20 cm s⁻¹. Red dots denote the location of Station NAP. August time series of the modeled (c) ice algal biomass (mmol N m⁻²) and (d) PON flux (μ mol N m⁻² d⁻¹) in the 2012 case (black lines) and the no ice algal activity case (blue lines).

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Figure 13. Schematic image of sensitivity experiments. In Case 4, the grazing pressure of icerelated fauna (IF) on ice algae (IA) and the transition from IF to mesozooplankton (ZL) after sea ice melting were calculated for the seeding. In Case 5, a part of IA was treated as large phytoplankton (PL) after sea ice melting. In Case 6, the ZL grazing on fast-sinking Particulate Organic Nitrogen (fPON) was calculated in the water column, and the formulation of slowsinking one (sPON) was not changed.

1132

Figure 14. Modeled seasonal transition of (a, c, e, g, i, k) ice algal biomass (mmol N m⁻²) and (b, d, f, h, j, l) PON flux (μ mol N m⁻² d⁻¹) in the NAP region in (a-b) Case 1, (c-d) Case 2, (e-f) Case 3, (g-h) Case 4, (i-j) Case 5, and (k-l) Case 6. Black thin lines correspond to the original 2011 case. The results with I_{opti} of 5 (20) W m⁻² in Case 1, KN_{upSKL} of 0.5 (1.5) mmol N m⁻² in Case 2, PON sinking speed of 200 (20) m d⁻¹ in Case 3 are shown by magenta (blue) lines, respectively. The biomass of ice-related fauna is shown by an olive line in Case 4.

Parameter	Definition	Value	Unit
[Ice algae]			
V _{max}	Maximum phytosynthetic rate at 0 °C	0.8	d^{-1}
K _{NO3}	Half saturation constant for nitrate	3.0	mmol-N m ⁻³
K _{NH4}	Half saturation constant for ammonium	0.1	mmol-N m ⁻³
K _{SIL}	Half saturation constant for silicate	6.0	mmol-N m ⁻³
$\Psi_{_{ m NH4}}$	Ammonium inhibition coefficient	1.5	(mmol-N m ⁻³) ⁻¹
K _{Gpp}	Temperature coefficient for photosynthetic rate	0.0693	°C ⁻¹
l _{opt}	Optimum light intensity	10	W m ⁻²
Reso	Respiration rate at 0 °C	0.03	d ⁻¹
K _{Res}	Temperature coefficient for respiration rate	0.0519	°C ⁻¹
γ	Extracellular excretion ratio to photosynthesis	0.135	n. d.
Mor _o	Mortality rate at 0 °C	0.029	(mmol-N m ⁻³) ⁻¹ d ⁻
K _{Mor}	Temperature coefficient for mortality rate	0.0693	°C ⁻¹
R _{sin}	Si:N ratio	2.0	n. d.
[Light property]			
PAR _{frac}	Fraction of PAR to shortwave radiation	0.43	n. d.
k _{snow}	light extinction rate for snow	0.12	cm ⁻¹
k _{ice}	light extinction rate for sea ice	0.045	cm ⁻¹
Nitrogen/Silicon flow]			
Nit _o	Nitrification rate at 0 °C	0.03	d ⁻¹
К _{Nit}	K _{Nit} Temperature coefficient for nitrification		°C ⁻¹
VP2N ₀	Decomposition rate from PON to ammonium at 0 $^{ m o}$ C	0.1	d ⁻¹
VP2D ₀	Decomposition rate from PON to DON at 0 $^{\circ}$ C	0.1	d ⁻¹
VD2N ₀	Decomposition rate from DON to ammonium at 0 $^{ m o}$ C	0.02	d ⁻¹
VP2Si ₀	Decomposition rate from opal to silicate at 0 $^{\circ}$ C	0.1	d ⁻¹
K _{P2N} /K _{P2D} /K _{D2N} /K _{P2Si}	Temperature coefficient for decomposition rate	0.0693	°C ⁻¹

Та	bl	e	2
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		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Cloud	2011	0.98	0.87	0.79	0.79	0.91	0.88	0.72	0.90	0.76	0.92	0.98	0.96
Fraction	2012	0.94	0.90	0.67	0.81	0.79	0.56	0.61	0.83	0.88	0.97	0.97	0.96
Shortwave	2011	9	0	0	0	4	51	165	236	305	217	102	45
Radiation	2012	10	0	0	0	4	62	170	245	264	184	92	46
Wind	2011	6.7	5.1	5.0	5.1	6.0	4.3	4.6	4.4	4.5	4.4	5.3	5.4
Speed	2012	8.1	5.0	4.8	5.1	4.7	4.5	4.1	3.9	4.7	4.7	7.1	7.1
Snow	2011	11	23	32	37	41	44	46	33	0	0	0	0
Depth	2012	8	23	22	21	23	23	22	13	0	0	0	0
Sea Ice	2011	60	209	216	261	276	281	268	249	228	169	78	0
Thickness	2012	60	210	232	271	279	278	286	259	207	141	62	0
Sea Ice	2011	0.21	0.89	0.98	0.99	0.99	0.99	0.99	0.99	0.99	0.83	0.19	0
Concentration	2012	0.19	0.90	0.98	0.98	0.98	0.98	0.99	0.97	0.87	0.70	0.18	0



Model Bathymetry



Spin up exp. 1979 forcing	Decadal exp. 1979-2011	25 km
10 years	33 years	
	Seasonal e	xp.
[201	1 case] 2010 Oct 201	1 Sep. 5 km
[201	2 case] 2011 Oct 201	2 Sep.

Fig. 1.

C4317



[Arctic NEMURO]

Fig. 2.









Fig. 4.



Annual primary production of ice algae [mmol N m-2]

Fig. 5.





Fig. 6.





C4323





Fig. 9.

C4325



Fig. 10.



Fig. 11.

C4327



Fig. 12.





C4329



Fig. 14.