

1 **Sixteen-year phytoplankton biomass trends in the northwestern Pacific Ocean**
2 **observed by the SeaWiFS and MODIS ocean color sensors**

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12 **Abstract** Using multisensor/platform biophysical data collected from 1997 to 2013, we
13 investigated trends of the concentrations of phytoplankton biomass (Chl) in the
14 northwestern Pacific Ocean (NWPO) and the probable responsible factors. The trend of
15 rising sea surface temperature (SST) was the main factor maintaining phytoplankton
16 positive net growth and resulted in a trend of increasing Chl at high latitudes in all seasons.
17 At latitudes of 36–48°N, east of 160°E, the trend of rising SST was accompanied by a
18 trend of declining Chl, markedly in spring and fall, which could be ascribed to
19 strengthened stratification. The trends of environmental variables in the Oyashio area
20 have modified conditions in a way detrimental to phytoplankton growth, the result being
21 a trend of declining Chl from spring to fall. Chl south of roughly 36°N exhibited different
22 trends in different seasons because of the different trends of vertical stratification.

23 Whereas the observed 16-year Chl trends were not primarily influenced by interannual
24 climate variability, to some degree they were likely modified by decadal variability
25 associated with a weakened Aleutian Low pressure. This work prompts further
26 comprehensive studies to investigate the probable ecological consequences of the
27 observed Chl trend for high-trophic-level marine organisms in the NWPO.

28 **Keywords** Remote sensing · Ocean color · Chlorophyll-*a* · Phytoplankton growth ·
29 Light/nutrient limitation · Climate change

30 **1 Introduction**

31 The northwestern Pacific Ocean (NWPO) consists of a cyclonic subarctic and an anti-
32 cyclonic subtropical gyre. To the west, the subarctic and subtropical gyres are bordered
33 by the Oyashio and the Kuroshio currents, respectively, whereas meridionally, the two
34 gyres are separated by the Kuroshio-Oyashio confluence area (Fig. 1) (Hanawa and
35 Mitsudera 1986; Yasuda 2003). To enable comparative, long-term, biogeochemical
36 studies of the subarctic and subtropical gyres, two biogeochemical time-series stations,
37 K2 (47°N, 160°E, subarctic area) and S1 (30°N, 145°E, subtropical area), have been
38 established (see Honda et al. this volume).

39 Stations K2 and S1 exhibit distinct biogeochemical characteristics: at station K2 (S1)
40 nutrient concentrations are high (low), sea surface temperature (SST, °C) is low (high),
41 the critical depth is shallow (deep), and the winter phytoplankton chlorophyll-*a*
42 concentration (Chl, mg m⁻³) is low (high) (see Siswanto et al. 2015). The distinct
43 geophysical differences between stations K2 and S1 lead to a limitation of phytoplankton
44 growth by light/temperature and nutrients at stations K2 and S1, respectively (e.g.,
45 Matsumoto et al. 2014; Siswanto et al. 2015). On the basis of multiplatform-derived

46 biogeochemical data, Siswanto et al. (2015) have shown that not only do
47 light/temperature and nutrient limitation occur at stations K2 and S1, respectively, but
48 also that the limiting factors change meridionally during different seasons as a result of
49 seasonal changes in geophysical variables.

50 Meridional differences in the variability of phytoplankton Chl emerge not only at
51 seasonal time scales but also at interannual and decadal time scales in response to large-
52 scale climate variability (Goes et al. 2003; Aita et al. 2007; Chiba et al. 2008; Siswanto
53 et al. this volume). By pixel-based spatiotemporal analysis of satellite data, Siswanto et
54 al. (this volume) showed that there exists a meridional difference in the response of Chl
55 to climatic anomalies; i.e., Chl tends to decrease (increase) over the area north (south) of
56 42°N during the positive phase of the Pacific Decadal Oscillation (PDO), even though the
57 forcing factors (e.g., vertical mixing) are the same in the two areas. Such meridional
58 differences are consistent with the meridional difference in phytoplankton limiting factors
59 (e.g., Siswanto et al. 2015).

60 Considering that NWPO phytoplankton respond differently to the same forcing
61 factor(s) at different latitudes, it is thus likely that whether any geophysical variables (e.g.,
62 temperature, vertical mixing, stratification, light) that undergo long-term trends, perhaps
63 because of global warming, lead Chl to increase or decrease depends on latitude.
64 Behrenfeld et al. (2006) and Doney (2006), for instance, have postulated that
65 phytoplankton at high latitudes will indirectly benefit from warming of the ocean, because
66 a warmer ocean weakens vertical mixing and allows phytoplankton to spend more time
67 within the euphotic zone, the result being an increase of Chl. Toseland et al. (2013) also
68 suggest that phytoplankton at high latitudes directly benefit from a warming ocean
69 because rising temperatures promote phytoplankton growth. In contrast, a warmer ocean

70 will be detrimental to phytoplankton (decrease Chl) in low latitudes because of
71 strengthening of stratification, which will reduce vertical nutrient fluxes from deep layers
72 (e.g., Gregg et al. 2005; Polovina et al. 2008; Boyce et al. 2010).

73 In fact, on a global scale and in terms of annual means, Chl exhibits meridionally
74 different trends, as mentioned by Vantrepotte and Mélin (2009), but the trends are not
75 always consistent with the aforesaid hypotheses, because the Chl in high (low) latitudes
76 does not always increase (decrease) in response to warming (see Fig. 6b in their paper).
77 Their analysis, based on 10-year satellite Chl data, shows that the trend of Chl in the
78 NWPO is less obvious than the analogous trend in the northeastern Pacific Ocean. This
79 difference was possibly caused by cancellation between positive and negative trends in
80 different seasons.

81 We thus used a longer dataset (16 years, from September 1997 to June 2013) of Chl
82 derived from ocean color sensors to update Chl trends in the NWPO during the most
83 recent decades. We were interested in determining Chl trends in different seasons. Within
84 the same time span, we also used satellite-based and/or reanalyzed geophysical variables
85 that might have caused Chl trends to differ meridionally and seasonally. Understanding
86 Chl trends and the possible underlying factors at seasonal time scales is important; they
87 may bring ecological consequences for the biomass of high-trophic-level marine
88 organisms by shifting the timing of phytoplankton and zooplankton phenology, varying
89 the food resources for juvenile fish in their feeding ground, and shifting the locations of
90 fishing grounds.

91 **2 Methodology**

92 **2.1 Multiplatform data acquisition**

93 We used 16-year (September 1997 to June 2013) monthly composite Chl and
94 photosynthetically available radiation (PAR, Einstein $\text{m}^{-2} \text{d}^{-1}$) data with a 9-km spatial
95 resolution retrieved by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and the
96 Moderate Resolution Imaging Spectroradiometer-Aqua (MODIS). We acquired the
97 SeaWiFS and MODIS data from <http://oceancolor.gsfc.nasa.gov>. We also used concurrent
98 monthly SSTs retrieved by the Advanced Very High Resolution Radiometer (AVHRR,
99 <http://podaac.jpl.nasa.gov/AVHRR-Pathfinder>) with 4-km spatial resolution and the
100 MODIS (<http://oceancolor.gsfc.nasa.gov>) with a 9-km spatial resolution. The variables
101 SST and PAR were analyzed because temperature and light are important phytoplankton-
102 limiting factors, especially in high latitudes of the NWPO (e.g., Siswanto et al. 2015).

103 To generate recent 16-year wind speed (WS, m s^{-1}) data, an important variable driving
104 vertical mixing, we used the Cross-Calibrated Multiplatform (CCMP)- and WindSat-
105 derived WS, both of which we acquired from <http://apdrc.soest.hawaii.edu>. We also
106 investigated the mixed layer depth (MLD, m), a key variable controlling the degree of
107 light and/or nutrient availability. To generate a MLD dataset within the same time span,
108 we used MLDs from different platforms. One MLD dataset was acquired from the Global
109 Ocean Data Assimilation System (GODAS, <https://climatedataguide.ucar.edu>) with 1°
110 spatial resolution, and the other was the Argo float-based MLD dataset acquired from the
111 Japan Agency for Marine-Earth Science and Technology (JAMSTEC, http://www.jamstec.go.jp/ARGO/argo_web/argo/index.html).

113 2.2 Data interpolation and transformation

114 Although satellite remote sensing provides routine and consistent temporal observations,
115 satellite data, especially those retrieved by optical and infrared sensors, can contain gaps
116 due to cloud cover and rain belts. Gaps in satellite data are problematic for pixel-based

117 analyses of long-term trends and correlations between Chl and environmental variables,
118 because both analyses require spatially and temporally complete datasets. Therefore, prior
119 to spatial and temporal analyses, we applied a Data Interpolating Empirical Orthogonal
120 Function (DINEOF) method to the SeaWiFS, MODIS, AVHRR, and Argo float-derived
121 data to construct spatiotemporally complete SeaWiFS (Chl), MODIS (Chl, SST), AVHRR
122 (SST), and Argo float (MLD) datasets.

123 The applicability and effectiveness of DINEOF to fill in spatiotemporal gaps in
124 satellite data have been demonstrated in previous studies (e.g., Beckers and Rixen, 2003;
125 Alvera-Azcárate et al. 2005; Li and He 2014; Siswanto et al. 2015). DINEOF is able to
126 fill in gaps in pixels and represent spatial features of satellite images even with 80% cloud
127 coverage both in terms of single images (see Alvera-Azcárate et al. 2005) and temporal
128 means (see Li and He 2014). Our 16-year full dataset had mean cloud coverage of 24%
129 and only three images had cloud coverage of >80%. Mean cloud coverage was relatively
130 high at high latitudes >45°N, but was still <60% (data not shown). We thus expected that
131 DINEOF would also work well with our dataset. DINEOF was not applied to GODAS
132 MLD and CCMP WS because there were no spatiotemporal gaps in those datasets.

133 To ensure compatibility of the Chl and PAR data retrieved by SeaWiFS and MODIS,
134 a pixel-based linear regression was applied for the period from July 2002 to December
135 2010, when observations by both sensors were available. Regression coefficients obtained
136 in each pixel were then used to transform all MODIS Chl and PAR so that they were
137 compatible with SeaWiFS Chl and PAR. We finally used SeaWiFS Chl and PAR from
138 September 1997 to December 2007 and transformed MODIS Chl and PAR from January
139 2008 to June 2013 to derive Chl and PAR trends. Because the uncertainty of the SeaWiFS
140 Chl retrieval in the NWPO has been confirmed to be less than $\pm 35\%$ (Sasaoka et al. 2002),

141 which is the goal for the uncertainty of the NASA ocean color mission Chl product
142 (O'Reilly et al. 1998), we transformed Chl data from MODIS to SeaWiFS.

143 With the same data transformation, we derived pixel-by-pixel regression coefficients
144 of AVHRR on MODIS SSTs for the period from July 2002 to December 2009, when the
145 AVHRR and MODIS missions overlapped. We used them to transform MODIS SSTs so
146 that they were compatible with AVHRR SSTs. We then used AVHRR SSTs from
147 September 1997 to December 2009 and transformed MODIS SSTs from January 2010 to
148 June 2013 in the subsequent SST trend analysis. We also transformed GODAS MLDs so
149 that they were compatible with Argo float-based, in situ MLDs. Pixel-by-pixel regression
150 coefficients were derived by using MLD datasets collected from January 2007 to June
151 2013. For further analysis, we used transformed GODAS MLDs from June 1997 to
152 December 2006 and Argo float-based MLDs from January 2007 to June 2013. A similar
153 data transformation was used to transform Windsat WS so that it was compatible with
154 CCMP WS using regression coefficients derived for the observation period (February
155 2003 to December 2012) when the two datasets overlapped.

156 Siswanto et al. (2015) have shown that the aforesaid data transformation is effective
157 for making two datasets compatible. The merged datasets are also consistent with
158 measured data at stations K2 and S1, especially for Chl, for which the uncertainty was
159 less than that ($\pm 35\%$) targeted by the NASA Ocean Color mission.

160 2.3 Data analysis

161 Prior to trend analysis, seasonal means of all variables were removed by subtracting
162 monthly climatological means from the data time series. The trend analysis was therefore
163 based on variable anomalies. Rather than least-squares regressions, we carried out robust
164 regressions on biophysical variable anomalies against time (monthly basis), because

165 robust regressions are less sensitive (than least-squares regressions) to outliers, the
166 implication being that the observed trends are less influenced by extreme anomalies
167 associated with climatic anomalies on both interannual and decadal time scales. Like
168 Vantrepotte and Mélin (2009), we then used the slope of the robust regressions to
169 approximate the trend from 1997 to 2013. The significance of trend was statistically
170 defined by using Mann-Kendall test with 95% confidence level ($p < 0.05$) (e.g., Kahru et
171 al. 2012).

172 Although the long-term analysis was based on variable anomalies, hereafter we do not
173 explicitly express the ‘anomalies’ of the variables. Neither do we use the specific variable
174 name for variable anomaly values. We will use ‘Chl’ interchangeably to refer to Chl in
175 general terms and specifically when we discuss the results of our analysis. We inspected
176 the trends in different seasons, and following Cohen et al. (2009), we divided the boreal
177 seasons as follows: winter, from January to March; spring, from April to June; summer,
178 from July to September; and fall, from October to December.

179 **3 Results and discussion**

180 Phytoplankton Chl is a measure of phytoplankton standing stock, the spatiotemporal
181 variability of which can be an indication of phytoplankton net growth rate, basically
182 determined by the imbalance between phytoplankton growth and loss rates (Irwin and
183 Finkel 2008; Behrenfeld 2010; Marañón et al. 2014). A change in an environmental
184 variable can change environmental conditions in a way that is detrimental and/or
185 favorable for phytoplankton net growth as manifested by Chl changes. For instance,
186 increasing SST stimulates the net growth of phytoplankton at high latitudes (where
187 nutrients are not limiting factor) because it suppresses vertical mixing (thereby shortening
188 the period of time phytoplankton spend in deep, dimly lit waters) and promotes

189 phytoplankton growth (Eppley 1972; Behrenfeld and Falkowski 1997; Behrenfeld et al.
190 2006; Doney 2006; Toseland et al. 2013). On the other hand, increasing SST is detrimental
191 for phytoplankton in low latitudes where their growth is limited by nutrients, because it
192 strengthens stratification and thereby limits the supply of nutrients from deep layers
193 (Gregg et al. 2005; Polovina et al. 2008; Boyce et al. 2010).

194 Because phytoplankton limiting factors also change seasonally and meridionally (e.g.,
195 Siswanto et al. 2015), long-term changes of environmental conditions would likely affect
196 phytoplankton growth (or precede Chl trends) differently in different seasons and regions.
197 Below, divided into four seasons, we discuss the probable mechanisms underlying the
198 trends of Chl observed in various areas as summarized in Table 1.

199 3.1 Trends of Chl and probable responsible factors in different seasons

200 *3.1.1 Winter season*

201 In high latitudes mainly north of 42°N, Chl tended to increase at a rate of 0.006 mg m⁻³
202 yr⁻¹ and it increased by 0.090 mg m⁻³ within 16 years (Fig. 2a). Increased Chl indicated
203 that over the 16-year period, environment conditions there have changed and become
204 more favorable to positive net growth. Considering the facts that, 1) phytoplankton at
205 high latitudes were limited by light and temperature [inferred from the negative
206 coefficient of correlation (r) between Chl and MLD (Fig. 3a), positive r between Chl and
207 PAR (Fig. 3b), and positive r between Chl and SST (Fig. 3c); see also Fujiki et al. (2014)
208 and Matsumoto et al. (2014)]; and 2) PAR showed no trend (Fig. 2b), the increasing trend
209 of SST might thus produce favorable conditions that would allow phytoplankton net
210 growth to increase, as manifested by an increase of Chl. Moreover, the increasing trend
211 of the MLD (due to increased WS, Figs. 2d, e), rather than being detrimental (by

212 lengthening the low-light period), has likely caused environment conditions to be more
213 favorable for positive net growth through a dilution effect that reduced grazing pressure
214 (e.g., Yoshie et al. 2003; Matsumoto et al. 2014).

215 However, the most prominent trend of increasing SST at latitudes of 36–42°N (Fig.
216 2c) was not accompanied by a remarkable Chl trend (Fig. 2a). This finding can be
217 explained by the fact that light was a more important limiting factor than temperature, as
218 evidenced by the lower positive r between Chl and SST (Fig. 3c) than between Chl and
219 PAR (Fig. 3b) and the large negative r between Chl and MLD (Fig. 3a).

220 Over the area roughly south of 30°N, a small but significant decreasing trend in Chl
221 was observed (Fig. 2a). It changed at a rate of $-0.002 \text{ mg m}^{-3} \text{ yr}^{-1}$ (declined by 0.036 mg
222 m^{-3} in 16 years). The area south of 30°N is a nutrient-limited environment [see the positive
223 r for Chl vs MLD (Fig. 3a) and the negative r for Chl vs SST (Fig. 3c)] because the MLD
224 south of 30°N is shallower than the critical depth throughout the year (Obata et al. 1996;
225 Siswanto et al. 2015). Therefore, a decreasing trend in MLD south of 30°N (Fig. 2d)
226 might change environment conditions in a way detrimental (by declining nutrient
227 availability) for phytoplankton, the result being a decrease of Chl.

228 3.1.2 Spring season

229 Phytoplankton Chl north of 46°N tended to increase (Fig. 2f) at a rate of 0.014 mg m^{-3}
230 yr^{-1} and increased by 0.208 mg m^{-3} over the 16-year time span. Environmental conditions
231 have likely changed in a way more favorable for phytoplankton positive net growth. The
232 increase of growth was likely due to the increasing trend of SST (Fig. 2h). This
233 hypothesis is supported by the facts that, 1) Chl was positively correlated with PAR and
234 SST (Figs. 3e, f), the suggestion being that phytoplankton **growth** was controlled by light
235 and temperature; and 2) PAR tended to decline (Fig. 2g).

236 A trend of decreasing Chl at a rate of $0.008 \text{ mg m}^{-3} \text{ yr}^{-1}$ (decreased by 0.118 mg m^{-3}
237 over the 16 years) at latitudes of $36\text{--}46^\circ\text{N}$, east of 160°E was apparent (Fig. 2f). Although
238 light and temperature were still limiting factors [see the positive r between Chl and PAR
239 and Chl and SST (Figs. 3e, f)], the concomitant trend of increasing SST (Fig. 2h) did not
240 cause an increasing trend of net positive growth. Decreased light availability [due to
241 decreased PAR (Fig. 2g)] and decreased nutrient availability (due to strengthened
242 stratification attributed to higher SSTs) were likely responsible for the declining trend in
243 phytoplankton net growth, the result being a decline in Chl. The trend of decreasing MLD
244 in the winter (Fig. 2d) might also have reduced the availability of nutrients that could be
245 consumed by phytoplankton in the spring. Goes et al. (2000, 2003) also mentioned that
246 nutrients entrained by winter vertical mixing is crucial in determining the magnitude of
247 spring Chl.

248 The most prominent trend of decreasing Chl at a rate of $0.041 \text{ mg m}^{-3} \text{ yr}^{-1}$, however,
249 was observed in the Oyashio area, where Chl declined by 0.622 mg m^{-3} over the 16 years.
250 The negative r between Chl and MLD (Fig. 3d) and positive r between Chl and PAR (Fig.
251 3e) in the Oyashio area indicated that phytoplankton **growth** was more limited by light
252 than by nutrients (e.g., Saito et al. 2002; Liu et al. 2004; Siswanto et al. 2015). Thus, the
253 trends of declining PAR and increasing MLD (due to strengthened WS, Figs. 2i, j) that
254 lengthened the low-light period were detrimental to phytoplankton net growth. This
255 cause-and-effect reflects the fact that the MLD is about the same as the critical depth in
256 the Oyashio area during the spring (Siswanto et al. 2015). The change of environmental
257 conditions in a way detrimental to phytoplankton net growth might also be ascribed to the
258 trend of decreasing SST (due to increased MLD) that reduced phytoplankton growth.

259 A small but significant trend of increasing Chl at a rate $0.003 \text{ mg m}^{-3} \text{ yr}^{-1}$ (increased

260 by 0.048 mg m^{-3} within 16 years) was observed south of Japan centered at 30°N (Fig. 2f).
261 The positive r between Chl and MLD (Fig. 3d) and negative r between Chl and SST (Fig.
262 3f) indicated that phytoplankton **growth** in this area was more limited by nutrients than
263 by light. The trend of increasing Chl there was thus likely attributable to a trend of
264 increasing nutrient availability associated with the trend of surface cooling (Fig. 2h)
265 caused by strengthened wind-driven vertical mixing (see strengthened WS and increased
266 MLD in Figs. 2i, j).

267 *3.1.3 Summer season*

268 Summer Chl north of roughly 45°N tended to increase (Fig. 2k) at a rate of 0.015 mg m^{-3}
269 yr^{-1} and increased by 0.217 mg m^{-3} in 16 years. Summer phytoplankton **growth** at high
270 latitudes was more controlled by temperature and/or light than by nutrients (Figs. 3h, i,
271 see also Kudo et al. 2006; Fujiki et al. 2014; Matsumoto et al. 2014) because winter
272 mixing-entrained nutrients are not fully consumed by phytoplankton, even during the
273 summer. Because PAR tended to decline (Fig. 2l), phytoplankton north of 45°N likely
274 still benefited from the trend of increasing SST (Fig. 2m), and their net growth tended to
275 be positive within the 16-year time span.

276 In the Oyashio area, Chl tended to decline at rate of $0.018 \text{ mg m}^{-3} \text{ yr}^{-1}$ and declined by
277 0.248 mg m^{-3} over the study period. The correlations between Chl and MLD were both
278 negative and positive (Fig. 3g), but the correlations between Chl and PAR were
279 consistently positive (Fig. 3h), and the correlations between Chl and SST were
280 consistently negative (Fig. 3i). These relationships indicate that phytoplankton **growth**
281 was regulated by an interplay between light and nutrient availability. As a resource, light
282 was likely not severely limiting (as it was at high latitudes), and nutrients were not
283 severely limiting (as they were at low latitudes) until an environmental change reduced

284 one of the resources. Thus, the trends of declining nutrient concentrations (due to
285 decreased MLD, Fig. 2n), declining PAR, and perhaps increasing grazing pressure (due
286 to decreased MLD) were among the probable factors driving the trend of declining Chl.
287 The increasing trend of SST was unlikely to cause phytoplankton growth to increase, as
288 temperature was not a limiting factor in the Oyashio area (see Fig. 3i).

289 The prominent trend of increasing Chl at a rate of $0.004 \text{ mg m}^{-3} \text{ yr}^{-1}$ (increased by
290 0.053 mg m^{-3} within the 16 years) was also observed over an elongated area from latitude
291 36°N northeastward (Fig. 2k), where nutrient limitation is expected to occur due to strong
292 summer stratification [see the positive r between Chl and MLD (Fig. 3g) and the negative
293 r between Chl and SST (Fig. 3i)]. The factors responsible for the trend of increasing Chl
294 are unclear, because the observed trends of increasing SST and decreasing MLD (due to
295 increased SST and decreased WS, Fig. 2o) were expected to cause Chl to decrease by
296 reducing nutrient availability and increasing grazing pressure.

297 *3.1.4 Fall season*

298 Fall Chl north of 45°N increased at a rate of $0.012 \text{ mg m}^{-3} \text{ yr}^{-1}$ and increased by 0.176
299 mg m^{-3} within 16 years (Fig. 2p). Rather than nutrients, light and temperature were the
300 controlling factors for phytoplankton growth (see the positive r values between Chl and
301 PAR and between Chl and SST in Figs. 3k, l). Therefore, the accompanying trends of
302 increasing PAR and SST (Figs. 2q, r) modified environmental conditions in a way
303 favorable for phytoplankton positive net growth.

304 Over the area from the Oyashio area eastward along latitudes of $42\text{--}48^\circ\text{N}$, Chl tended
305 to decline at a rate of $0.009 \text{ mg m}^{-3} \text{ yr}^{-1}$ and it decreased by 0.134 mg m^{-3} within 16 years
306 (Fig. 2p). Although PAR and SST were still important controlling factors (see the positive
307 r between Chl and PAR and between Chl and SST, Figs. 3k, l), a prominent trend of

308 increasing SST (Fig. 2r) was unable to cause a trend of increasing positive net growth.
309 Therefore, the trends of decreasing PAR [to reduce light availability, (Fig. 2q)] and
310 decreasing MLD [to increase grazing pressure, (Fig. 2s)] might be responsible for the
311 decreasing net growth over the 16-year time span, as manifested by the declining trend of
312 Chl. The decreased MLD in this latitude band can also be ascribed to both increased SST
313 and decreased WS (Fig. 2t).

314 A prominent trend of declining Chl at latitudes of 33–42°N and east of 160°E at a rate
315 of $0.005 \text{ mg m}^{-3} \text{ yr}^{-1}$ (decreased by 0.078 mg m^{-3} in 16 years) was likely caused by a
316 tendency of declining nutrient availability attributed to a warming trend of SST.
317 Phytoplankton growth south of 42°N was likely controlled by nutrients [see the negative
318 r between Chl and SST (Fig. 3l)] especially south of 36°N [see the positive r between Chl
319 and MLD (Fig. 3j)]. Over the western area south of Japan, the trend of decreasing MLD
320 likely reduced nutrient availability and was the cause of the trend of declining Chl there.
321 The warming trend of SST that strengthened stratification in the eastern area south of
322 30°N was likely responsible for the small but significant trend of declining Chl a rate of
323 about $0.001 \text{ mg m}^{-3} \text{ yr}^{-1}$ (declined by 0.018 mg m^{-3} in 16 years).

324 3.2 Relevance to previous studies and discrepancies

325 When all seasons are included, annual mean Chl in the subarctic area north of roughly
326 45°N tended to increase (Fig. 4a). As discussed above, the trend of increasing SST, by
327 driving the trend of increasing phytoplankton positive net growth in all seasons, was the
328 main factor responsible for this Chl increase. Considering only significant increasing
329 trends ($p < 0.05$), annual mean Chl north of 45°N increased by 0.095 mg m^{-3} within the
330 16-year period of study. Previous studies that included all seasons reported different Chl

331 trends in the NWPO due to different periods of the SeaWiFS records and approaches. For
332 instance, by executing linear regression analysis on all data (including Chl data during El
333 Niño and La Niña periods) McClain et al. (2004) and Gregg et al. (2005) reported a
334 declining trend of Chl within a period of 6 years prior to 2003. On the other hand,
335 Behrenfeld et al. (2006) suggested a trend of increasing Chl in the NWPO from 1999 to
336 2004, because they excluded Chl data from the 1997 El Niño and 1988 La Niña periods.
337 These results indicate that a short time series of Chl is greatly influenced by El
338 Niño/Southern Oscillation (ENSO) variability, and thus is insufficient to derive long-term
339 trends of Chl.

340 Using a 10-year (from November 1997 to October 2007) SeaWiFS Chl record that
341 included all seasons, Vantrepotte and Mélin (2009) suggested that, except for the tropical
342 oceans, the overall pattern of Chl trends with and without data from El Niño and La Niña
343 periods are similar, the implication being that the temporally short climate variability of
344 ENSO did not mainly drive the 10-year trend of Chl in the NWPO, which showed a trend
345 of increasing Chl almost over the entire NWPO (see their Fig. 6b). With a robust
346 regression analysis and using the same 10-year Chl data, we found patterns of Chl trends
347 (Fig. 4b) similar to the results of Vantrepotte and Mélin (2009).

348 Extending satellite Chl record to June 2013 (16-year time span), we found an overall
349 Chl trend (Fig. 4a) different from Vantrepotte and Mélin's (2009) result or our result with
350 a 10-year data record (Fig. 4b). Spatial variation of the trend in Fig. 4a was the result of
351 using the full Chl dataset (gap-filled, and including El Niño and La Niña periods). The
352 features in Fig. 4a also appeared in Fig. 4c, which was the result of excluding data from
353 strong/moderate El Niño and La Niña periods (Fig. 4c). We also found that the spatial
354 feature of Chl trends derived from the original (with gaps) Chl data (Fig. 4d) resembled

355 that derived from the full (gap-filled) Chl dataset (Fig. 4a). This result indicated that the
356 ENSO variability and the use of interpolated (gap-filled) Chl data had little effect on the
357 observed 16-year Chl trends.

358 As discussed above, the ENSO variability was not superimposed on Vantrepotte and
359 Mélin's (2009) 10-year and our 16-year Chl trends. Therefore, the discrepancy between
360 Chl trends derived from 10-year and 16-year Chl records is probably associated with
361 longer (decadal) variability. The Aleutian Low pressure (ALP) has tended to weaken, as
362 indicated by the trend of decreasing PDO index (compared to the strengthening trend
363 before October 2007, Fig. 5). Especially since October 2007, the PDO index has been in
364 large negative phases (mean: -0.87 , compared to 0.06 before October 2007). A weakening
365 ALP is known to spin down the cyclonic subarctic gyre (to weaken Ekman divergence)
366 and the anti-cyclonic subtropical gyre (to weaken Ekman convergence) (Sugimoto and
367 Hanawa 2009). The weakened Ekman divergence in the subarctic region might be one
368 reason for the trend of increasing SST at high latitudes (Figs. 2c, h, m, r), which in turn
369 led to a more remarkable trend of increasing Chl compared to the trend before October
370 2007 (Figs. 4b, 5a). On the other hand, although weakened Ekman convergence in the
371 subtropical region is expected to decrease SST (Figs. 2c, h, m, r), Chl was almost constant
372 (Fig. 5b) because Chl in the subtropical region is no longer limited by temperature.

373 3.3 Probable consequences on marine ecosystems

374 The increase of SSTs at high latitudes during the winter and spring over the 16 years
375 implies a tendency toward strengthened stratification. The spring bloom onset is expected
376 to advance over the 16-year time span, and perhaps in the future, if such a trend of
377 increasing SST continues (Peeters et al. 2007; Chiba et al. 2008). In contrast, a cooler

378 SST in low latitudes (including the areas east of Japan) would likely delay the onset of
379 the spring bloom. The changes in phytoplankton phenology is further expected to
380 influence zooplankton phenology (e.g., Chiba et al. 2008) and perhaps fisheries resources
381 in this area.

382 Besides being influenced by changes of phytoplankton phenology, higher trophic level
383 marine organisms are expected to have been influenced by the changes of Chl and SST
384 over the 16-year period. For instance, the Oyashio area, one of the most productive areas
385 in the world, is an important feeding ground for Japanese sardine and Pacific saury (e.g.,
386 Sakurai et al. 2007 and reference therein). They feed on calanoid zooplankton that graze
387 on phytoplankton. The trend of decreasing Chl, especially during spring and summer (the
388 feeding period), might affect recruitment of sardine and saury. The fact that the biomass
389 of saury tended to decrease from 2004 to 2010 and that the spawning biomass of sardine
390 tended to decline from the mid-1990s to 2004 (Sakuramoto et al. 2010; Ito et al. 2013 and
391 reference therein) should prompt more comprehensive studies to investigate whether this
392 decline of a fisheries biomass is related to a declining trend of Chl in the Oyashio area.
393 The north-south contrast of SST trends east of Japan (Figs. 2c, h, m, r) is also expected to
394 influence biomass and fishing ground of saury, because saury feeding and spawning
395 migrations are regulated by SST in this region (see Fig. 2 and Fig. 3 in Ito et al. 2013).

396 It is probably also of interest to investigate whether the standing stock and fishing
397 ground of albacore in the NWPO have also changed because, 1) the main albacore fishing
398 ground during the fall is over almost the entire latitude band of 36–42°N and east of 160°E,
399 an area that showed the most prominent trends of increasing SST and declining Chl,
400 especially in fall (Figs. 2p, r) (see also Fig. 6 in Zainuddin et al. 2008); 2) albacore fishing
401 ground corresponds with the areas with SST range of 18.5–21.5°C and Chl range of 0.2–

402 0.4 mg m⁻³ (Zainuddin et al. 2008); and 3) these Chl and SST ranges might shift spatially
403 because of the Chl and SST trends, and so might the albacore fishing ground.

404 **4 Summary**

405 Phytoplankton Chl at high latitudes in the NWPO has tended to increase, but with
406 different spatial scales in different seasons. Such a trend of increasing Chl reflected a
407 change of environmental conditions that were able to keep phytoplankton growth greater
408 than losses, the result being phytoplankton positive net growth. We conclude that the trend
409 of increasing SST is the main factor maintaining phytoplankton positive net growth at
410 high latitudes north of roughly 45°N. In the mid-latitudes (~36–46°N and east of 160°E),
411 despite a trend of increasing SST, Chl has tended to decline. The trend of increasing SST
412 (to strengthen stratification) likely changed environmental conditions in a way that
413 resulted in a negative net growth, as manifested by the trend of declining Chl. In the
414 Oyashio area, although environmental variables showed different trends in different
415 seasons, the changed environmental conditions were likely detrimental for phytoplankton
416 net growth, the result being a trend of declining Chl from spring to fall. At latitudes south
417 of 36°N, Chl exhibited different trends in different seasons; these differences might be
418 attributable to the trend of nutrient availability associated with MLD trends. The NWPO
419 Chl trends within the 16-year time span were not primarily influenced by the ENSO
420 interannual variability. However, they were likely modified by the PDO, which has been
421 in a very negative phase (weakened ALP) since 2007. This work suggests that through
422 coupled atmosphere-ocean interactions, climate-driven long-term changes of
423 environmental variables drove the trend of phytoplankton biomass; this work should
424 prompt further study to investigate the ecological consequences for high-trophic-level
425 marine organisms in the NWPO.

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557 **Figure Captions**

558 **Fig. 1** Map of the study region showing the surface currents, including the Kuroshio (K),
 559 Kuroshio extension (KE), Oyashio (O), subarctic front (SF), and East Kamchatka (EK).
 560 The letters SO indicate the Sea of Okhotsk. Dashed ellipse indicates approximately the
 561 Oyashio area.

562 **Fig. 2** Spatial variations of significant trends during the winter ($p < 0.05$) for (a) Chl, (b)
 563 PAR, (c) SST, (d) MLD, and (e) WS derived from winter monthly data within the study
 564 period. The areas with insignificant trends are masked out (white areas). Panels (f–j), (k–
 565 o), and (p–t) are the same as panels (a–e), except that the analyses were conducted for
 566 spring, summer, and fall, respectively.

567 **Fig. 3** Spatial variations of significant ($p < 0.05$) correlation coefficients (r) between Chl
 568 and MLD (a), Chl and PAR (b), and Chl and SST (c) during the winter. The areas with
 569 insignificant r are masked out (white areas). Panels (d–f), (g–i), and (j–l) are the same as
 570 panels (a–c), except that the analyses were conducted for spring, summer, and fall,
 571 respectively.

572 **Fig. 4** Spatial variation of annual mean Chl significant trends ($p < 0.05$) derived by
 573 different procedures. (a) Trend was derived by using the full Chl dataset, i.e., gap-filled
 574 data within the 16-year period. (b) Same as panel (a), except within the 10-year period
 575 from November 1997 to September 2007. (c) Same as panel (a), except that the trend was
 576 derived by excluding Chl data during strong/moderate El Niño and La Niña periods. (d)
 577 Same as panel (a), except that the trend was derived by using original (including gaps)
 578 satellite Chl data. Green and blue boxes in (b) are the subarctic and subtropical regions,
 579 respectively, where the time series of mean Chl anomaly data in Fig. 5 were derived.

580 **Fig. 5** (a) Time series of mean Chl anomaly (red bars) derived from the subarctic region
581 (160–170°E and 47–52°N; see the green box in Fig. 4b) and the PDO index (black bars)
582 within the period from September 1997 to June 2013. The solid red and black lines are
583 regression lines for Chl and the PDO index, respectively. The dashed red and black lines
584 are the same as the solid lines, except that the regression lines were derived from
585 November 1997 to September 2007 (indicated by the vertical dashed blue line). Panel (b)
586 is the same as panel (a) except that the mean Chl anomaly was derived from the
587 subtropical region (130–140°E and 24–30°N; see the blue box in Fig. 4b).

Table 1 Summary of Chl trends observed within the 16-year time span (September 1997 to June 2013) in different areas of interest and the probable responsible factors and/or mechanisms during each of the four seasons

Season	Area of interest	Trend of Chl	Trend of environmental variables and probable factors/mechanisms
Winter	North of 42°N	Increase	Increased SST promoted phytoplankton growth Increased MLD reduced grazing pressure
	South of 30°N	Decrease	Decreased MLD decreased nutrient availability
Spring	North of 46°N	Increase	Increased SST promoted phytoplankton growth
	Latitudes 36–46°N, east of 160°E	Decrease	Increased SST (by strengthening stratification) decreased nutrient availability; Decreased PAR reduced light availability
	Oyashio area	Decrease	Increased MLD lengthened low-light period; Decreased PAR reduced light availability; Decreased SST decreased phytoplankton growth
	Along latitude 30°N	Weak increase	Increased MLD increased nutrient availability
Summer	North of 45°N	Increase	Increased SST promoted phytoplankton growth Decreased MLD decreased nutrient availability;
	Oyashio area	Decrease	Decreased PAR decrease light availability; Decreased MLD increased grazing pressure
	Along latitude 36°N	Weak increase	Unclear mechanisms
Fall	North of 45°N	Increase	Increased SST promoted phytoplankton growth; Increased PAR increased light availability
	Oyashio area and along 42–45°N	Decrease	Decreased PAR reduced light availability; Decreased MLD increased grazing pressure
	Latitudes 33–42°N, east of 160°E	Decrease	Increased SST (shoaled mixed layer) decreased nutrient supply
	South of Japan	Decrease	Decreased MLD decreased nutrient availability
	South of 30°N	Weak decrease	Increased SST (by strengthening stratification) decreased nutrient availability

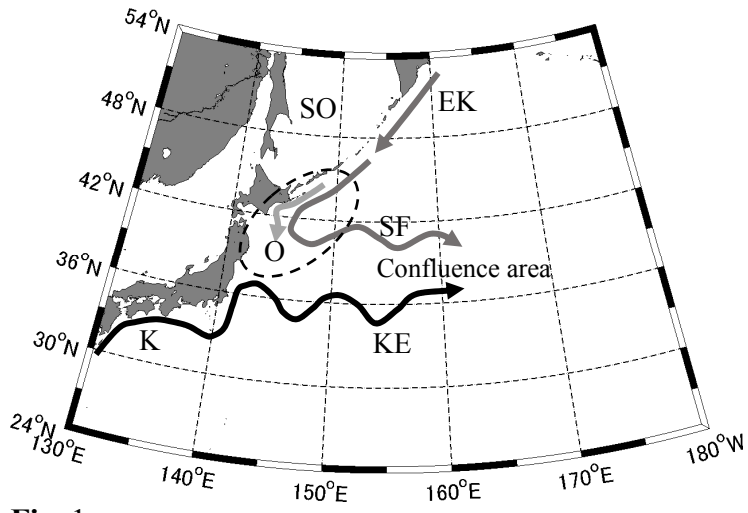


Fig. 1

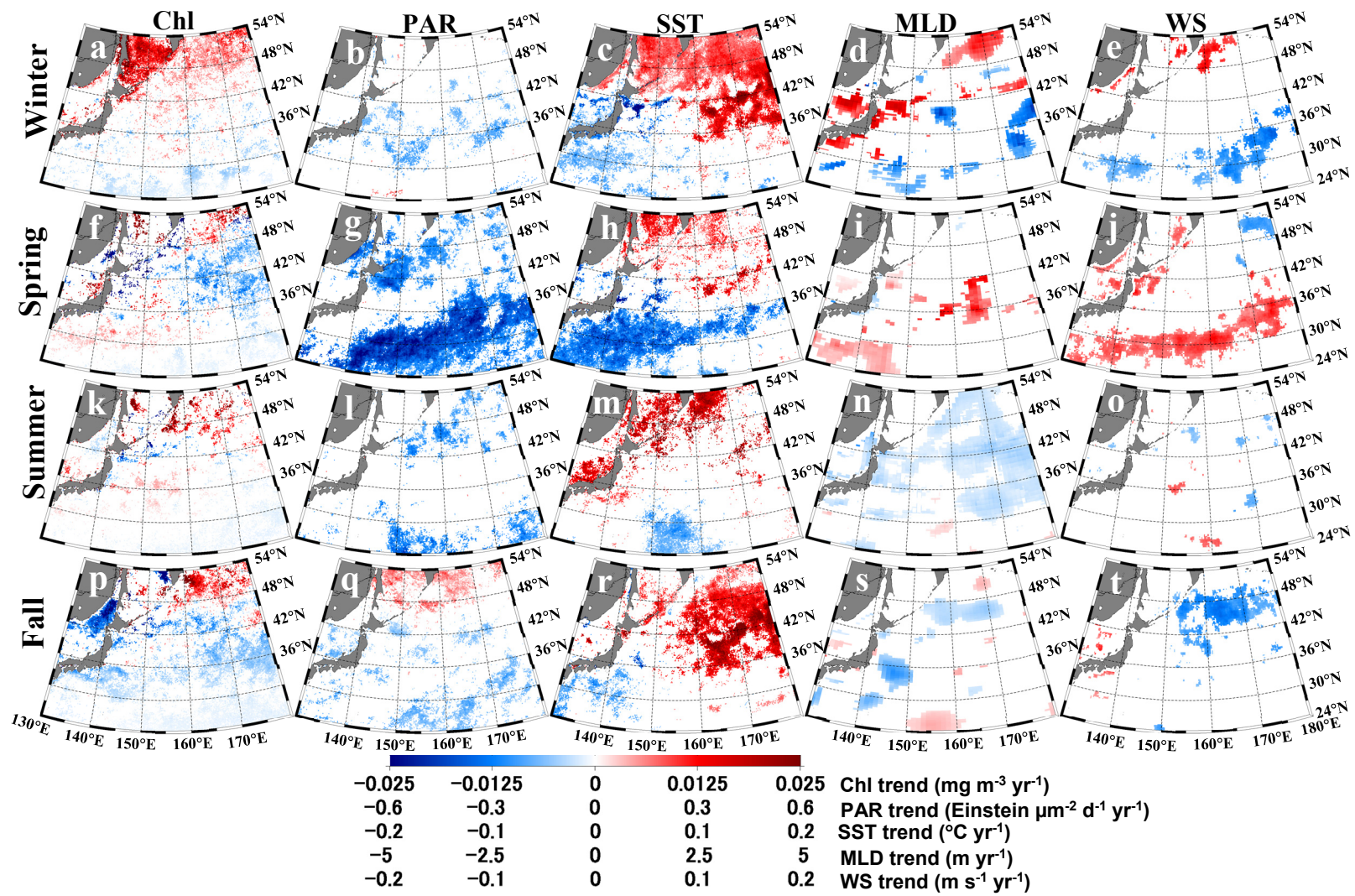


Fig. 2

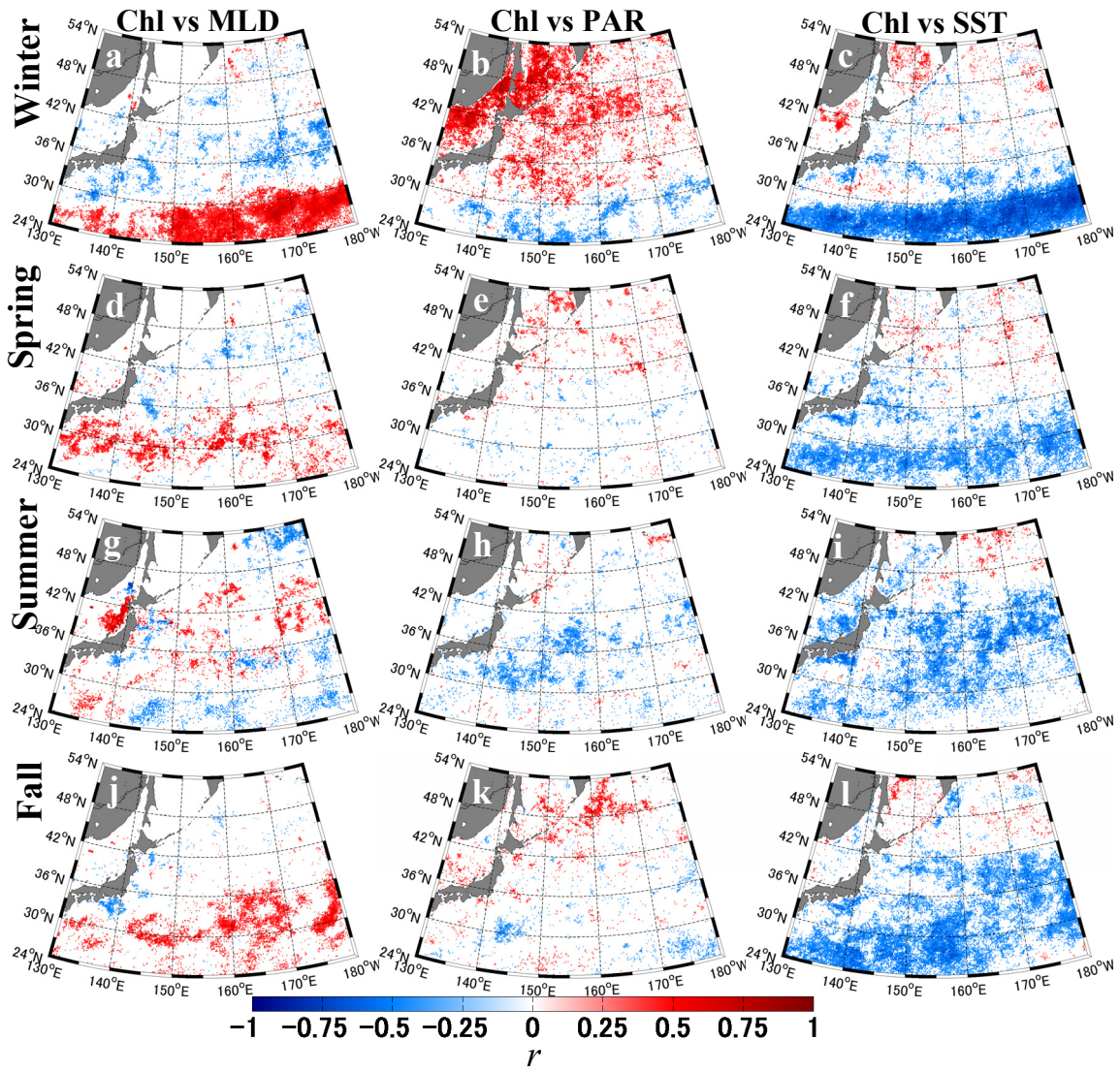


Fig. 3

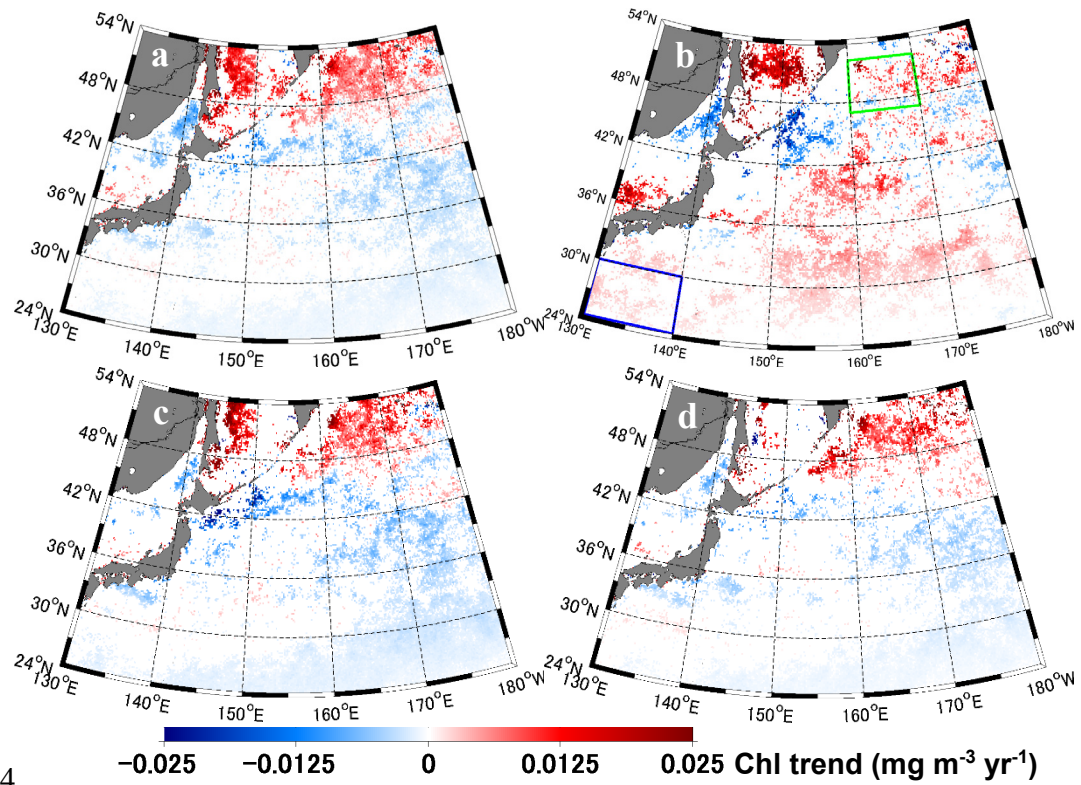


Fig. 4

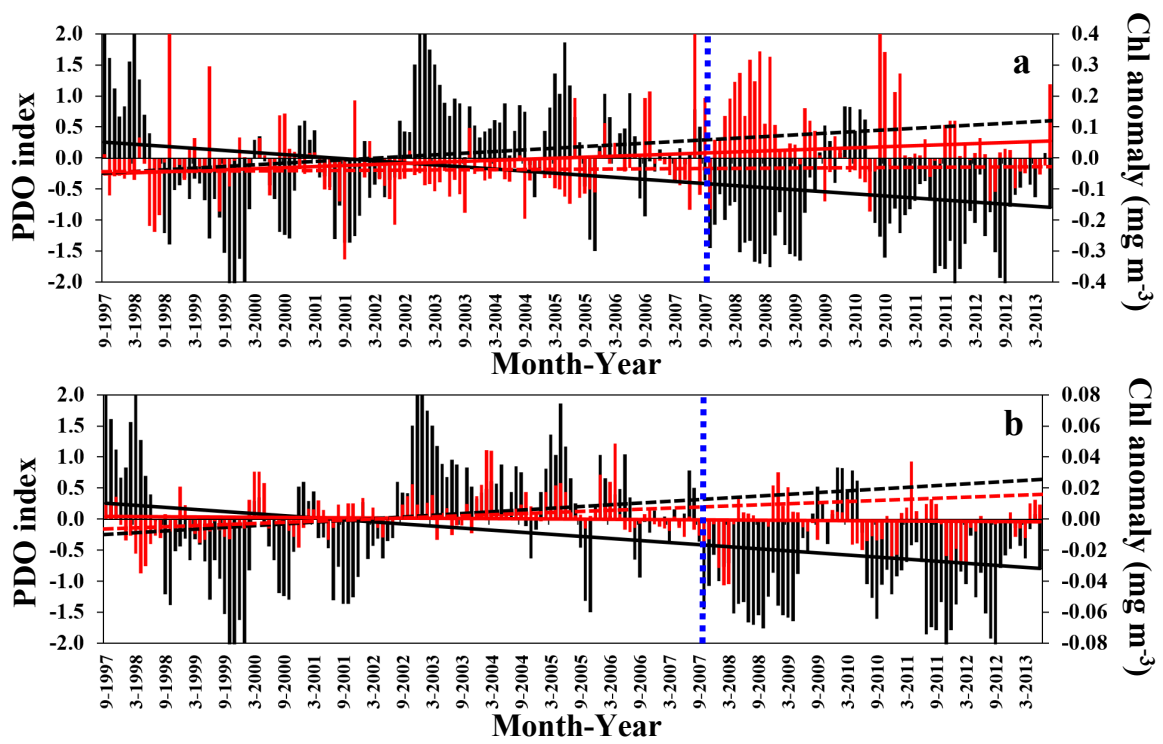


Fig. 5