



1 **Two different phytoplankton blooming mechanisms over the**
2 **East China Sea during El-Niño decaying summers**

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9 **Abstract.** During an El Niño-decaying summer, the East China Sea (ECS) has experienced anomalous
10 phytoplankton blooming, but the understanding of associated generating mechanisms remains limited. Here, we
11 analyzed observational (25 years) and long-term simulation data (1,000 years) to investigate the underlying
12 mechanisms for the anomalous phytoplankton blooming in ECS. Results highlight two mechanisms associated
13 with enhanced phytoplankton blooming in ECS during El Niño-decaying summers: inland runoff-driven and
14 oceanic sub-surface upwelling-driven blooming mechanisms. Firstly, increased river discharge from the Yangtze
15 River (YR) induces phytoplankton blooms. Secondly, wind-driven Ekman upwelling in ECS provides nutrients
16 for phytoplankton from the sub-surface to the surface water layer. Rossby wave propagations from Western North
17 Pacific Anti-Cyclone (WNPAC) cause a distinctive cyclonic atmospheric circulation over ECS that induces
18 Ekman upwelling. The climate model simulation supports these two mechanisms, and thus our results suggest that
19 both mechanisms contribute to the phytoplankton bloom concurrently.



20 1. Introduction

21 Numerous rivers, including The Yangtze River (YR), run into East China Sea (ECS). YR is the longest
22 river in Eurasia, contributing to a shallow continental shelf with high marine primary productivity (Liu et al., 2010,
23 2003; Tong et al., 2015; Zhai et al., 2023; Zhang, 1996; Zhao and Guo, 2011). Particularly, the Yellow Sea (YS)
24 and ECS, which belong to the East Asian Marginal Seas (EAMS), are known for being among the most productive
25 marine environments globally. Nutrients for phytoplankton growth are ample from the intrusion of nutrient-rich
26 Kuroshio intermediate water (Chen, 1996; Chen et al., 1995; Zhang et al., 2007), atmospheric deposition (Kim et
27 al., 2011; Zhang et al., 2010), and primarily riverine input from the YR (Huang et al., 2019; Wang et al., 2003).

28 Marine phytoplankton plays a role in the marine trophic chain (Danielsdottir et al., 2007), ocean carbon,
29 and biogeochemical cycles (Behrenfeld et al., 2006; Field et al., 1998). Chlorophyll-a (Chl-a) concentration is
30 widely used as a proxy for phytoplankton biomass and it has strength for handiness to measure from satellite
31 (Henson et al., 2010). The ECS region is surrounded by highly populated and developed nations with hundreds of
32 millions of people, which can have a profound impact on fisheries and marine ecosystems. Therefore,
33 understanding the spatio-temporal variability of phytoplankton in the ECS region associated with changes in river
34 discharge has great socio-economic importance, particularly in coastal communities.

35 ENSO plays a key role as a climate regulator for East Asia through its teleconnection. Western North
36 Pacific Anti-Cyclone (WNPAC) regulates the East Asian climate during ENSO events from the developing to
37 decaying phase (Kim and Kug, 2018; Li et al., 2017; Son et al., 2014; Wang et al., 2000). ENSO-induced changes
38 in the atmospheric and oceanic circulation alter physical properties in the ECS region, which can also affect the
39 marine ecosystems of the ECS region (Racault et al., 2017). During a decaying El-Niño summer season,
40 anomalous WNPAC transports warm and moist air from lower latitudes to East Asia, which increases regional
41 precipitation (Kwon et al., 2005; Li et al., 2021) and thus river discharge, carrying abundant nutrients into the
42 YECS region (Beardsley et al., 1985; Shi and Wang, 2012). This augmented river discharge impacts the coastal
43 ecosystems of eastern China and the western part of the Korean peninsula, potentially triggering anomalous
44 phytoplankton blooming (He et al., 2013; Park et al., 2015; Yamaguchi et al., 2012). The recent increasing trend
45 in surface chlorophyll-a in the ECS is correlated with nutrient concentrations without an increase in river discharge
46 (He et al., 2013). In addition, increased river discharge can cause anomalous phytoplankton blooming after strong
47 El Niño cases (Wu et al., 2023). These results suggest that there can be another process to induce the enhanced
48 phytoplankton blooming during El Niño decaying summer.

49 The WNPAC generated during the El Niño period not only increases riverine flows but also
50 accompanies anomalous cyclonic circulation over the EAMS region by the atmospheric Rossby wave propagation.
51 This induces Ekman upwelling (EKU) in the ECS region, transporting nutrients from the oceanic sub-surface to
52 the surface layer, and fostering anomalous phytoplankton blooming. An improved understanding of the additional
53 mechanism in conjunction with the existing one, will allow us to more accurately estimate the magnitude of
54 phytoplankton blooms in the ECS region during post El Niño summers. This could have implications for marine
55 resource management and fisheries in many neighboring countries.

56 Here, we propose another mechanism other than nutrient fluxes from the enhanced inland river



57 discharge. This study aims to understand the variability of phytoplankton concentrations in the ECS region during
58 the El Niño-decaying summers. We investigate both inland runoff-driven and oceanic sub-surface upwelling-
59 driven blooming mechanisms during El Niño decaying summers. The climate model long-term simulation and
60 observational data support these findings, highlighting the concurrent roles of both mechanisms in enhancing
61 phytoplankton blooming.



62 2. Data and Methods

63 2.1. Reanalysis & Observation data

64 We used the ocean colour satellite data from the European Space Agency Climate Change Initiative
65 Version (ESA-CCI) for chlorophyll-a data, serving as a proxy for phytoplankton biomass, covering 25-year
66 periods from 1998 to 2022 (Sathyendranath et al., 2019). El Niño events were identified using Extended
67 Reconstructed Sea Surface Temperature version 5 (ERSSTv5; Huang et al., 2017) Sea Surface Temperature (SST)
68 data from National Oceanic and Atmospheric Administration (NOAA), with anomalies greater than 1 standard
69 deviation during the winter season (December – January – February; DJF) index in the Nino3.4 (5°S-5°N / 170°
70 W-120°W) region. Furthermore, to examine atmospheric circulation such as wind, precipitation, and geopotential
71 height (GPH) changes, we analyzed the re-analysis data from the National Centers for Environmental Prediction
72 reanalysis version 2 / the National Center for Atmospheric Research (NCEP2 / NCAR; Kanamitsu et al., 2002).
73 Lastly, wind stress (τ) and wind stress curl ($\text{Curl}_{(\tau)}$; Kessler, 2006) are calculated followed as Eqs. (1)-(2) with
74 typical value for drag coefficient ($C_D = 0.0015$; Trenberth et al., 1990; Wyrтки and Meyers, 1976) and sea level
75 air density ($\rho_{\text{air}} = 1.225 \text{ kg m}^{-3}$; Cavcar, 2000) with the square of zonal & meridional wind speed (V^2) from
76 NCEP2 re-analysis data.

$$77 \quad \tau = \rho_{\text{air}} C_D V^2$$

78 (1)

$$79 \quad \text{Curl}_{(\tau)} = \frac{\partial \tau_y}{\partial x} - \frac{\partial \tau_x}{\partial y} \quad (2)$$

80 2.2. Model data

81 We used the present climate-based (1990-year atmospheric CO₂ concentration level; 353 parts per
82 million (ppm)) long-term integrated simulations of the Geophysical Fluid Dynamic Laboratory (GFDL) - CM2.1
83 Earth System Model (ESM) fully coupled with the marine ecosystem model TOPAZv2 (Tracers of Ocean
84 Phytoplankton with Allometric Zooplankton Version 2; Dunne et al., 2013). The model incorporates various
85 external nutrient inputs such as atmospheric deposition, river nitrogen (N) input, and river inputs of dissolved
86 carbon, alkalinity, and lithogenic material; however not includes river phosphorus (P) inputs (Dunne et al., 2013).
87 The growth rate of phytoplankton is computed using a function of chlorophyll to carbon ratio and limited by
88 various factors in TOPAZ (Dunne et al., 2010). Nutrient limitation terms are determined by minimum limitation
89 values among micronutrients (Fe, PO₄, Si(OH)₄, NO₃ + NH₄).

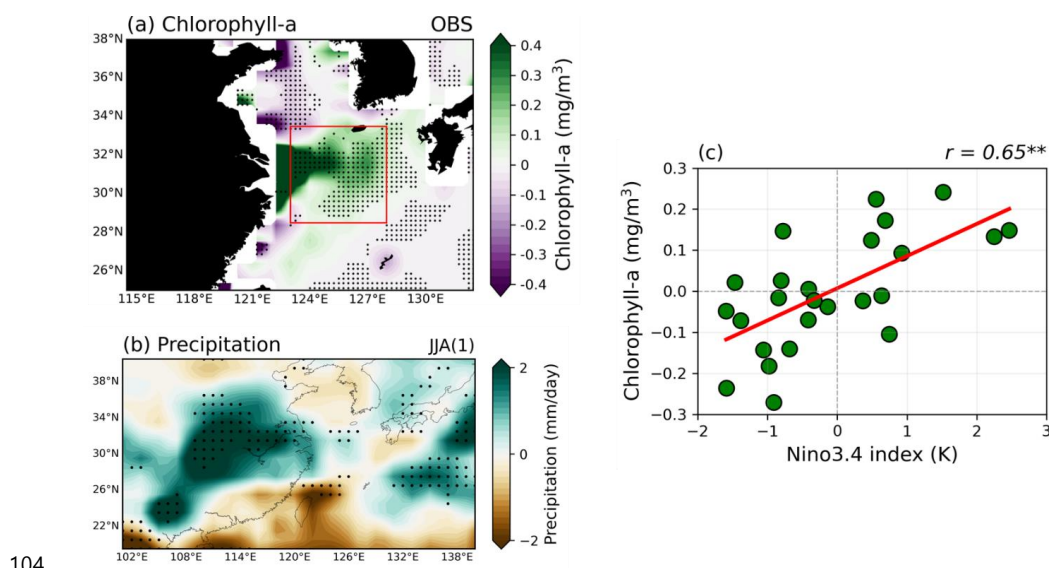
90 Surface values in the model data were averaged to 30-meter depths, with spatial grid and temporal scale
91 set at 1° x 1° grid and monthly mean data, respectively. El Niño events were defined in the same methodology as
92 in the observation data. Statistical significance was calculated using the non-parametric bootstrap method, with
93 10,000 random samples replacing as many numbers of El Niño cases in observation and model results, respectively.



94 **3. Results**

95 **3.1. Runoff-driven blooming mechanism - Insight from Observations**

96 Figures 1a-b display the composite maps illustrating the spatial distribution of surface chlorophyll-a
97 anomalies (SCHL) and precipitation anomalies during the El Niño decaying summer season (June-July-August;
98 JJA). The pronounced anomalous SCHL blooming is observed from the Yangtze River Estuary (YRE) to the
99 southern part of the Korean Peninsular. It has consistent patterns with the dispersal of strong river discharge from
100 the YR (Park et al., 2015; Yamaguchi et al., 2012). In addition to the estuary of the YR region, there are also broad
101 weak diagonal patterns of positive signal from northeastern Taiwan to the Korean Strait. This is in agreement with
102 the relationship between Yangtze River Discharge (YRD) and SCHL in Yamaguchi et al, which has a lagged
103 correlation from June to August and extends over a wide region from Jeju Island to the Korean Strait.



104

105 **Figure 1.** Composite maps exhibiting the 3-month average of (a) surface Chlorophyll-a (SCHL) anomalies, and
106 (b) precipitation anomalies for El Niño decaying summer season (June-July-August; JJA) of all El Niño cases,
107 using re-analysis and satellite data. (c) The relationship between the Niño3.4-DJF index which indicates the
108 strength of El Niño mature phase and area-averaged SCHL anomalies over the research target area during the El
109 Niño decaying summer season (Red box in Fig. 1a; 28.5°N-33.5°N / 122.5°E-128.5°E). All the black dots indicate
110 where the responses are significant at the 95% confidence level by using the bootstrap method. ** marks indicate
111 statistically significant correlation at the 99% confidence level.

112

113 This anomalous phytoplankton bloom during the boreal summer season of the following El Niño events
114 has been explained by enhanced precipitation. In the El Niño years, the intensification of southwesterly winds by
115 the Western North Pacific (WNP) high-pressure flow brings in warm and humid air from lower latitudes. This, in
116 turn, leads to anomalous rainfall in the East Asian region (Figure 1b). Given the strong association between the
117 variability of the YRD and precipitation, it is reasonable to anticipate that an increase in riverine input corresponds



118 to increased precipitation (Park et al., 2015). The lagged correlation between the Nino3.4 D(0)JF(1) index and the
119 SCHL anomalies in the ECS region (28.5°N-33.5°N, 123°E-128°E; target region indicated as red box in Fig. 1a)
120 during El-Niño decaying summers (JJA(1)) indicate significant positive relationship ($r = 0.65^{**}$) at the 99%
121 confidence level (Figure 1c).

122 To comprehensively understand the mechanisms of phytoplankton blooms over the ECS during the
123 summer season after the ENSO mature phase, we first re-assessed the runoff-driven blooming mechanism,
124 commonly well-known from several previous studies. The robust positive signal in the precipitation anomalies is
125 centered in the southeastern part of China, where the YR flows. The intensified precipitation, consequently,
126 triggers an increase in river discharge, leading to anomalous SCHL blooming broadly over the YECS (Runoff-
127 driven blooming mechanism).

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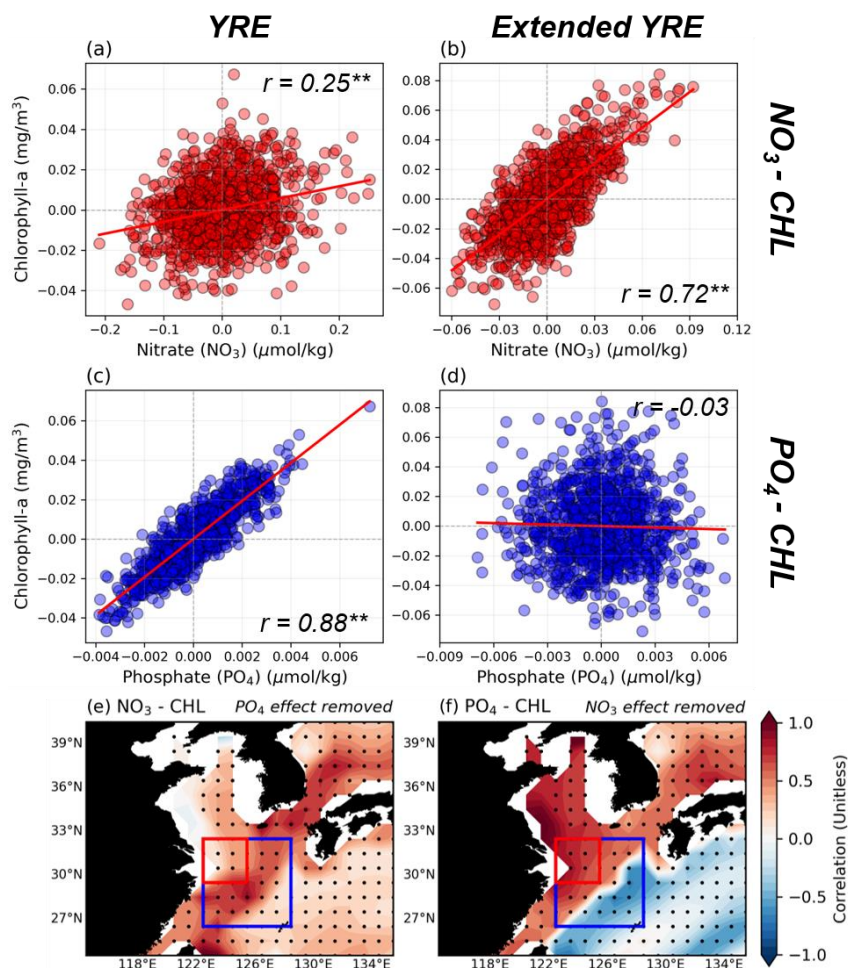
129 3.2. Runoff-driven blooming mechanism - Insight from Model

130 We further analyzed a long-term simulation using GFDL-CM2.1 ESM with a fully coupled
131 biogeochemical model to understand blooming mechanisms as well as the well-known runoff-driven blooming
132 mechanism. Notably, the GFDL-CM2.1 ESM does not simulate inputs of P from riverine inflows. In our target
133 area, the ECS region, climatologically, there is a strong influx of riverine runoff from the YR, which contains
134 excess Nitrate (N) concentrations (Kim et al., 2011; Moon et al., 2021; Wang et al., 2003). Under these marine
135 environmental characteristics, P is relatively constrained, and phytoplankton growth is controlled by changes in P
136 concentrations. In the oceans where P is the dominant factor regulating phytoplankton growth, especially in the
137 target region, the deficiency of P riverine inputs in the models may underestimate phytoplankton variability.
138 However, it affords us the advantage of exploring phytoplankton blooming mechanisms from another perspective,
139 not just a runoff-driven mechanism centered on the YRE region.

140 Prior to delving into further analyses, we verified that GFDL-CM2.1 ESM adequately simulates the
141 nutrient limitation in the target region (26.5°N-32.5°N, 122.5°E-128.5°E; target region in the model), with strong
142 P limitation observed in the YRE region and stronger N limitation appearing getting farther out (Figure 2). We
143 confirmed the nutrient limitation by separating the target region into the YRE and the extended YRE region (red
144 & blue box in Figs. 2e-f). In Figs. 2a-b, there is a relatively weak positive correlation ($r = 0.25^{**}$) between surface
145 NO_3 and SCHL anomalies in the YRE region, while a higher significant positive correlation ($r = 0.72^{**}$) in the
146 extended YRE region, indicating that N limitation begins to prevail. On the other hand, Figures 2c-d show a
147 significantly strong positive correlation ($r = 0.88^{**}$) between surface PO_4 and SCHL anomalies in the YRE region
148 and no correlation ($r = -0.03$) over the extended YRE region. In particular, the partial correlation between the
149 surface PO_4 and SCHL anomalies after removing the effect of NO_3 in the YRE region is almost unchanged at
150 0.86^{**} , while the opposite effect is even lower at 0.1^{**} . The spatial distribution of partial correlations shows that
151 the effect of surface NO_3 on SCHL anomalies after removing the effect of surface PO_4 is stronger in the extended
152 YRE region. On the other hand, the effect of surface PO_4 on SCHL anomalies after removing the influence of
153 surface NO_3 is very strong not only in the YRE region but also over the YECS and Bohai Sea (Figures 2e-f). These
154 support the dominant P limitation in the YRE region, implying that the strong P limitation in the YRE region is



155 applied as well as the observations. These findings indicate the GFDL-CM2.1 ESM's ability to simulate the
 156 relationship between phytoplankton growth and nutrients in the ECS region.



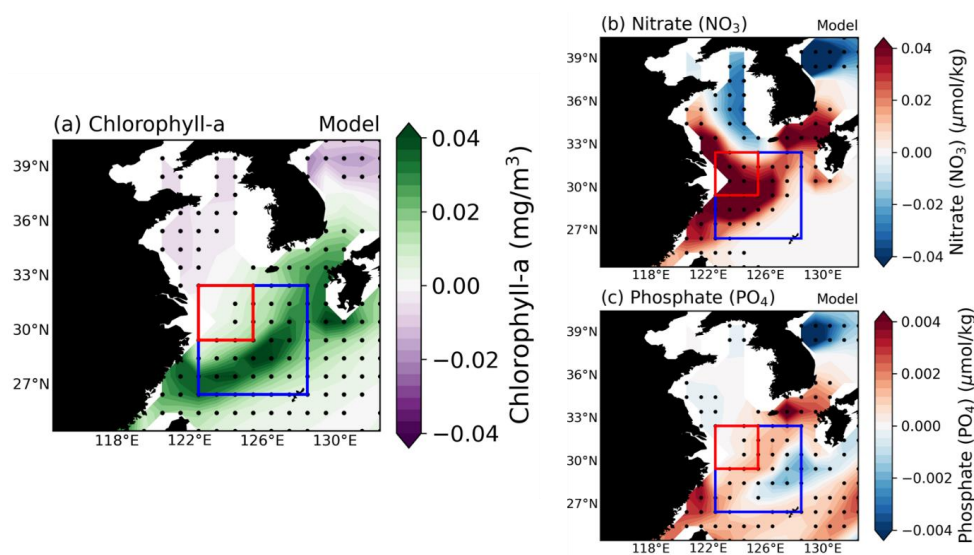
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 158 **Figure 2.** (a-d) The relationship between area-averaged surface nutrients and SCHL anomalies across the target
 159 area. The upper panels (a-b) focus on the relationship between surface nitrate (NO₃) and SCHL anomalies in the
 160 Yangtze River Estuary (YRE) [Left Panel; Fig. 2a] and extended YRE [Right Panel; Fig. 2b]. The lower panels
 161 (c-d) indicate the relationship between surface phosphate (PO₄) and SCHL anomalies in YRE [Left Panel; Fig. 2c]
 162 and extended YRE [Right Panel; Fig. 2d] within the ECS region respectively. (e-f) Partial correlation distribution
 163 of the effect of surface NO₃ on SCHL anomalies after removing the effect of surface PO₄ and opposite case
 164 respectively.

165

166 Figures 3a-c present the composites of SCHL anomalies, surface NO₃, and surface PO₄ anomalies during
 167 the decaying summer season following the mature phase of El Niño from all El-Niño cases in the GFDL-CM2.1
 168 ESM model over a total period of 1,000 years. Unlike the satellite-observed SCHL anomalies shown in Fig. 1a
 169 which are concentrated in the YRE region and gradually weakened outwards, the model results depict a diagonal



170 band pattern extending from the southeastern part of China to the Korean Strait (Figure 3a). This anomalous SCHL
171 pattern is somewhat consistent with the weak rightward diagonal pattern shown in Fig. 1a. Surface NO_3 anomalies
172 in Fig. 3b exhibit strong signals primarily in the YRE region, akin to the SCHL anomalies observed in Fig. 1a.
173 This similarity can be attributed to the ESM's incorporation of N inputs from riverine runoff, effectively capturing
174 the observed patterns. In contrast, surface PO_4 anomalies (Figure 3c) show a diagonal shape with a positive signal
175 from the northeastern part of Taiwan to the Korean strait. Given that the ESM does not include P input from
176 riverine sources, this anomalous PO_4 pattern can be driven by alternative processes. Therefore, it is essential to
177 explore additional mechanisms for phytoplankton blooming beyond the runoff-driven mechanisms.



178

179 **Figure 3.** (a-c) Composite maps illustrate the SCHL, surface NO_3 and surface PO_4 distribution of El Niño
180 decaying summer season over the East China Sea (ECS) for all El Niño cases (176 years) which were selected in
181 GFDL-CM2.1 ESM results. All the black dots indicate where the responses are statistically significant at the 95%
182 confidence level, determined using the bootstrap method.

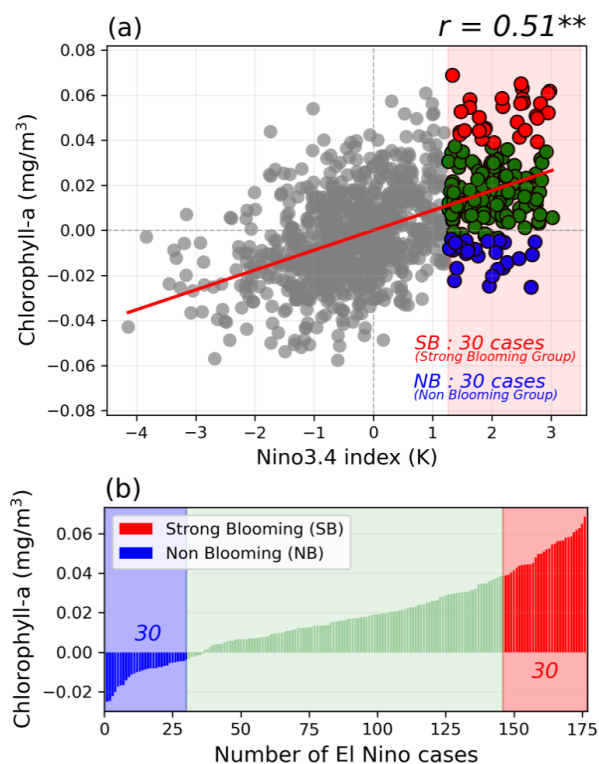
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184 We examined the relationship between the DJF Niño3.4 index and SCHL anomalies in the ECS region,
185 showing a significant positive correlation ($r = 0.51^{**}$) at the 99% confidence level (Figure 4a). From the long-
186 term integrated ESM results, we identified a total of 176 El Niño cases. Most of these cases result in positive
187 anomalous SCHL blooming, however, about 25% of the total El Niño cases exhibit negative SCHL anomalies. To
188 identify the processes responsible for the differing blooming outcomes, we divided the El Niño cases into two
189 groups based on the magnitude of anomalous SCHL blooming in the target region. The Strong Blooming (SB)
190 group, comprising the top 30 cases exhibiting strong blooming colored in reds, and the Non-Blooming (NB) group,
191 comprising the bottom 30 cases colored in blues (Figure 4b).

192 The composite map of SCHL anomalies during the El Niño decaying summer of the SB group reveals
193 pronounced anomalous blooming across the ECS region, while the NB group is characterized by negative SCHL

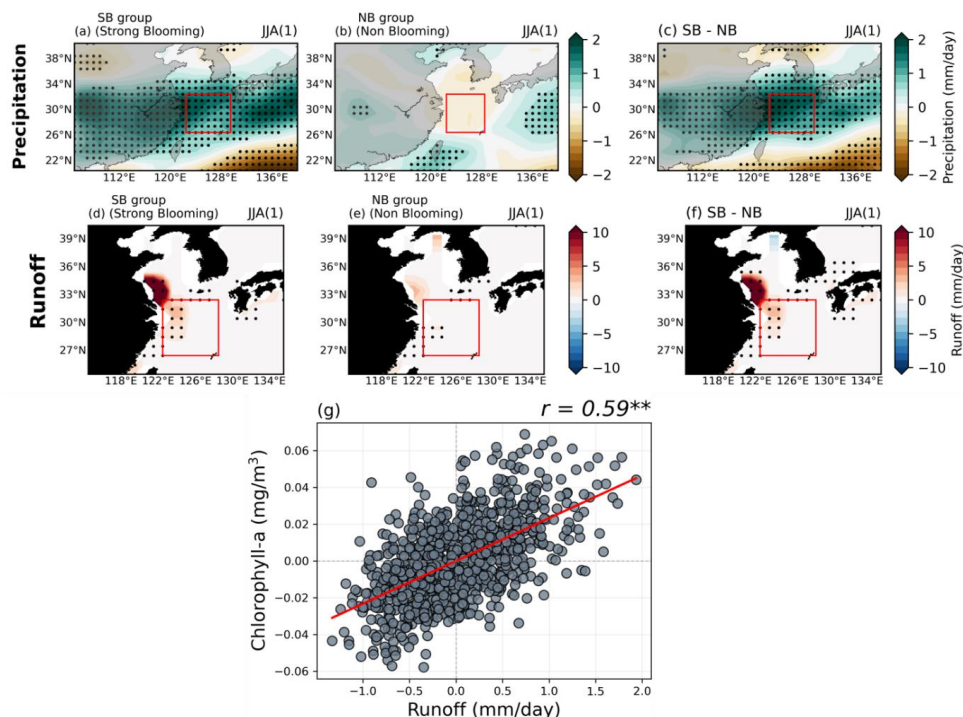


194 anomalies (Figure 4b, Figs. S1a-c). Surface nutrient distributions from the composite maps also show contrasting
195 results between the two groups during the El Niño decaying summer (Figs. S1d-i). To investigate the runoff-driven
196 phytoplankton blooming mechanism, as discussed in previous studies and above, we analyzed the composite
197 patterns of precipitation and runoff anomalies during the El Niño decaying summer season by comparing the two
198 groups (Figure 5). In terms of precipitation patterns, the SB group exhibits a broad positive rainfall band extending
199 over the entire East Asia region, from central China to Japan. In contrast, the NB group shows only weak positive
200 precipitation anomalies, confined to a narrow region of China, Taiwan, and the southern part of Japan. Similarly,
201 the runoff anomaly patterns display positive signals centered on the YRE region and the northern part of the YRE
202 region for both groups, with significance observed only in the SB group. The NB group, however, exhibits only
203 weakly significant positive patterns around the southern part of the YRE region. Moreover, the relationship
204 between runoff anomalies and the SCHL anomalies in the target region demonstrates a significantly positive
205 correlation ($r = 0.59^{**}$) at the 99% confidence level, indicating that the runoff-driven mechanism is well simulated
206 in the model (Figure 5g).



207

208 **Figure 4. (a)** The relationship between Niño3.4 DJF index and area-averaged SCHL anomalies over the target
209 region in GFDL-CM2.1 Earth System Model (ESM). **(b)** Categorization of all El Niño cases by the magnitude of
210 SCHL blooming in the target region of the ECS during El Niño decaying summers. The top 30 and bottom 30
211 cases, distinguished by SCHL anomaly magnitudes over the target region, colored in red and blue are grouped
212 into the Strong Blooming El Niño (SB) group and the Non-Blooming El Niño (NB) group, respectively.



213

214 **Figure 5.** (a-c) Composite maps exhibiting precipitation anomalies during the El Niño decaying summer season
215 for both groups, as well as the difference between the two groups. (d-f) Similar to Figs. 5a-c, these maps
216 demonstrate a composite map of runoff anomalies during the El Niño decaying summer season for both groups,
217 as well as the difference between the two groups. (g) The relationship between area-averaged runoff and SCHL
218 anomalies over the target region.

219

220 3.3. Upwelling-driven blooming mechanism - Insight from Model

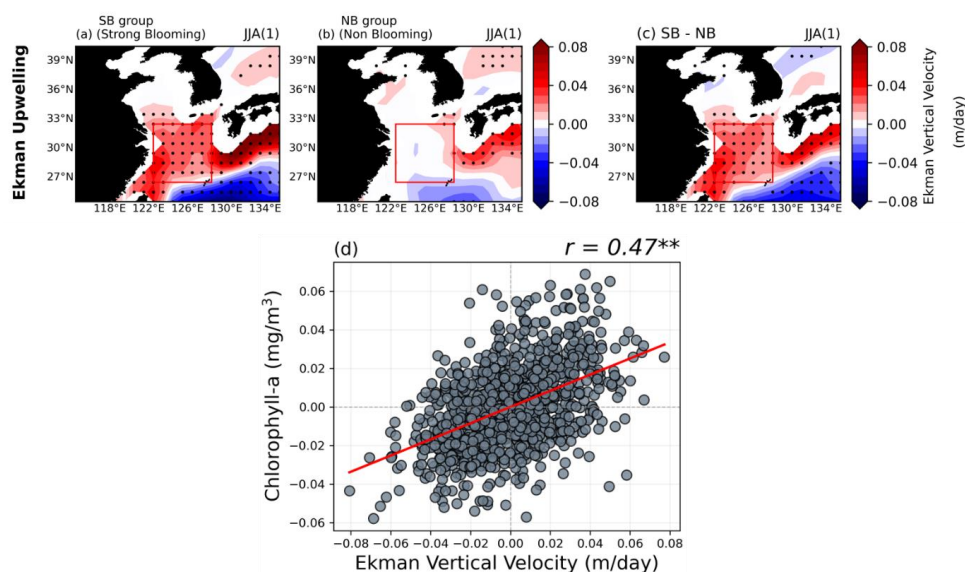
221 In addition to precipitation and runoff, there was a distinctive difference in the magnitude of upwelling
222 between the two groups. Figures 6a-b show the composite map of Ekman Upwelling (EKU) anomalies during the
223 El Niño decaying summer season. For the SB group, a significant positive EKU pattern dominates the ECS region,
224 with significantly negative EKU distribution in the WNP region, far south of Japan (Figure 6a). On the other hand,
225 the NB group does not exhibit any significant EKU anomaly patterns in the target region, with significant positive
226 EKU patterns over the southern part of Japan and negative EKU anomalies in the WNP but without significance
227 (Figure 6b). The difference between the two groups highlights distinct EKU anomaly patterns in the target region
228 (Figure 6c). The intensified EKU in the target region facilitates the transport of abundant nutrients from the
229 subsurface layer to the surface layer, thereby enhancing phytoplankton growth. This is supported by the
230 significantly positive correlation ($r = 0.47^{**}$) at the 99% confidence level between EKU anomalies and SCHL
231 anomalies in the target region, indicating that EKU can significantly contribute to anomalous phytoplankton
232 blooming, similar to the runoff-driven mechanism (Figure 6d).

233

EKU is primarily generated by cyclonic atmospheric circulations. The presence of robust upwelling in



234 the ECS region signifies the formation of cyclonic circulation, i.e. the EKV and wind stress curl (WSCL) are fully
235 positively correlated (Fig. S2a). During the El Niño mature phase, suppressed convection in the western Pacific
236 induces the Western North Pacific Anticyclone (WNPAC) in the lower-troposphere structure (Gill, 1980; Matsuno,
237 1966). Moreover, the WNPAC leads to cyclonic circulation in the northwestward ECS region via low-level Rossby
238 wave energy propagation (Wang et al., 2000). This sequence of wave patterns in the lower troposphere can
239 generate the WNPAC and atmospheric cyclonic circulation in the ECS region during the El Niño decaying summer
240 seasons. Given the significant differences in the magnitude and extent of rainfall band between the two groups,
241 we would expect distinct differences in the growth of WNPAC between the two groups as well. This suggests that
242 the differences in WNPAC development contribute to the variability in EKV and, consequently, the extent of
243 phytoplankton blooming in the ECS region during El Niño decaying summers.



244

245 **Figure 6.** (a-c) Composite maps exhibiting Ekman Upwelling (EKU) anomalies during the El Niño decaying
246 summer season for both groups, as well as the difference between the two groups. (d) The relationship between
247 area-averaged EKU and SCHL anomalies over the target region.

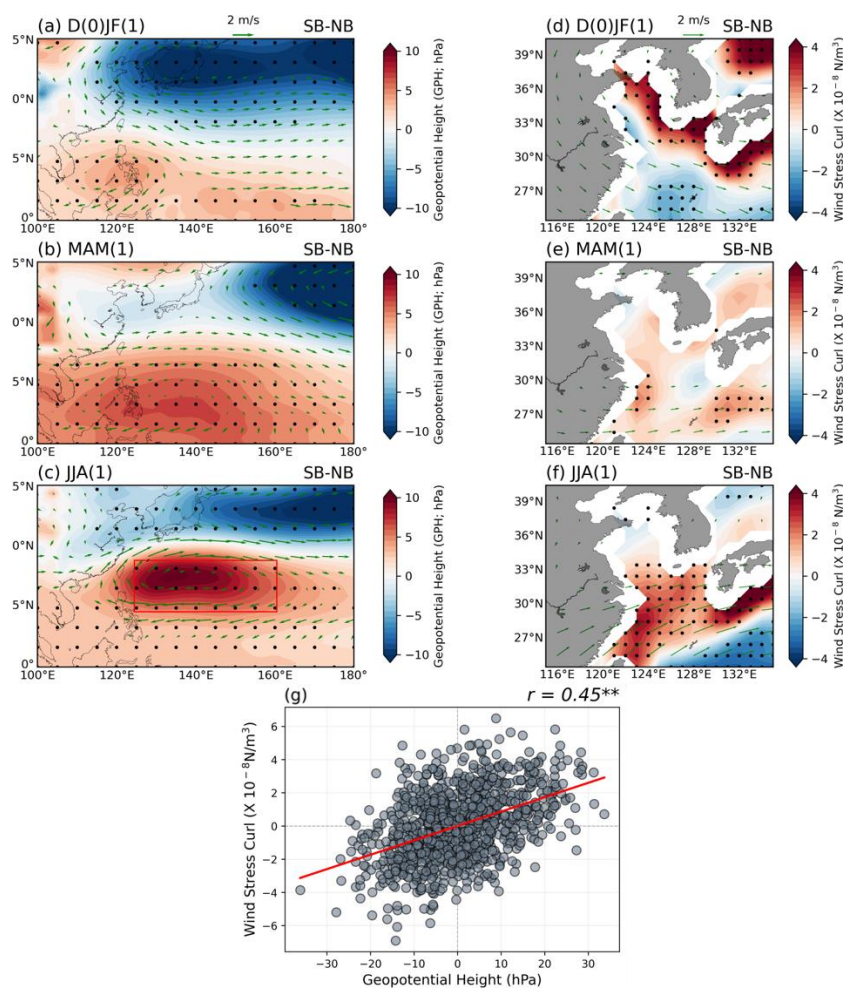
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249 Figure 7 illustrates the evolution of geopotential height (GPH) differences with 850hPa wind (Left
250 panels) and WSCL anomalies (Right panels) between two groups in the WNP across three seasons (D(0)JF(1)-
251 MAM(1)-JJA(1)) following El Niño mature phase. In the SB group, the WNPAC and North Pacific Cyclone (NPC)
252 are prominently stronger, positioned over the Philippines and North Pacific, respectively (Figure 7a). These
253 atmospheric circulations result in anomalous positive WSCL around the Korean Peninsula, Japan, and East Sea,
254 while negative WSCL is observed southeastern of China (Figure 7d). As the seasons progress, the WNPAC
255 migrates northeastward, becoming more pronounced in the SB group compared to the NB group, continuing into
256 the subsequent summer (Figures 7b-c). Positive WSCL anomalies begin to emerge in the ECS region from El
257 Niño decaying spring season, coinciding with the developed WNPAC (Figure 7e). By summer, the WNPAC in



258 the SB group is intensely and broadly developed, dominating the WNP, leading to a stronger cyclonic circulation
259 in the ECS region and enhanced wind-driven EKV due to positive WSCL (Figure 7c and Figure 7f). The
260 correlation between WSCL and the WNPAC index calculated from GPH anomalies within the red box in Fig. 7g
261 exhibits a significantly positive relationship ($r = 0.45^{**}$) at the 99% confidence level. This implies that the
262 development of a stronger WNPAC may lead to the generation of anomalous positive WSCL, prompting
263 upwelling and facilitating anomalous phytoplankton blooming during El Niño decaying summers.

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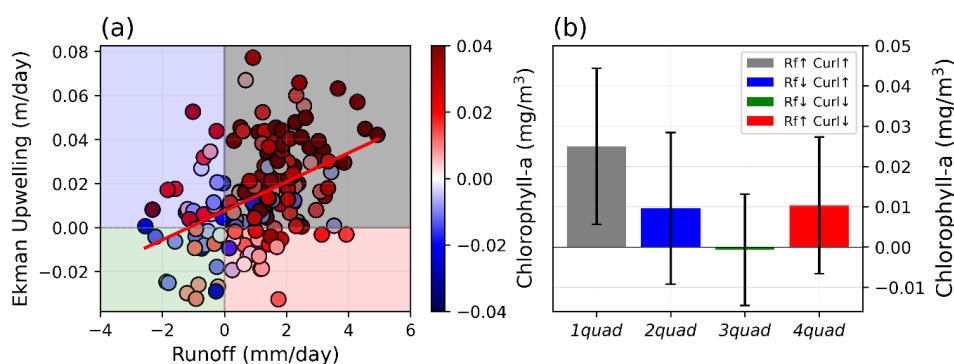
266 **Figure 7.** Evolution map of El Niño composite of (a-c) geopotential height (GPH; Left panels) and (d-f) Wind
267 Stress Curl (WSCL; Right panels) with 850hPa wind anomalies (vectors) from El Niño mature phase to decaying
268 summer season for the differences between two groups. (g) The relationship between area-averaged Western North
269 Pacific (WNP) GPH anomalies (highlighted as a red box in Fig. 7c) and Wind Stress Curl (WSCL) anomalies
270 over the target region. All the black dots indicate where the responses are statistically significant at the 95%
271 confidence level, determined using the bootstrap method.



272 As shown in Fig. 5 and Fig. 6, both the runoff-driven and upwelling-driven mechanisms work to
273 contribute to the strong blooming observed in the SB group. To quantify the relative contributions of these
274 mechanisms, we applied partial correlation and joint composite analyses. The partial correlation analysis revealed
275 that the impact of the runoff-driven mechanism on phytoplankton blooming, after removing the effect of the
276 upwelling-driven mechanism, is 0.49**. Conversely, the effect of the upwelling-driven mechanism on
277 phytoplankton blooming, after accounting for the runoff-driven mechanism, is 0.31**. These results indicate that
278 while both mechanisms play significant roles, the runoff-driven mechanism has a relatively stronger influence.

279 Additionally, the joint composite analysis further demonstrated that both mechanisms contribute to
280 anomalous phytoplankton blooming. We performed this analysis by assessing the relative strengths of runoff and
281 WSCL in the target region (Figure 8a). We categorized the 176 El Niño cases into four groups based on whether
282 the runoff and WSCL anomalies were positive or negative during the decaying summer season of El Niño events
283 (Figure 8b). The results showed that 62% (109 cases) of the El Niño cases exhibited both positive runoff and
284 WSCL anomalies. Furthermore, 13% (22 cases) and 11% (19 cases) displayed positive anomalies for either WSCL
285 or runoff, respectively, while 15% (26 cases) were negative for both. The magnitude of anomalous blooming was
286 highest when both WSCL and runoff anomalies were positive. The average blooming magnitude when WSCL
287 was positive but runoff anomalies were negative was almost the same, with little weakness of about 8% (0.0007
288 mg m^{-3}) compared to vice versa. When both were negative, the blooming magnitude was negative on average.
289 Importantly, a statistically significant positive blooming magnitude was observed only when both mechanisms
290 were positively contributing. Therefore, the combined effect of both mechanisms is crucial for the anomalous
291 phytoplankton blooming observed in the ECS region during the El Niño decaying summers.

292



293

294 **Figure 8.** (a) The scatter plot indicates the runoff and wind stress curl in the target region during the following
295 summer season of all El Niño cases selected from the GFDL-CM2.1 ESM. Colored scatters show the anomalous
296 blooming magnitude in the target region. (b) Bar plots indicate the averaged anomalous blooming magnitude of
297 the selected El Niño cases of each quadrant in Fig. 8a over the target region. Crosses indicate the range of ± 1
298 standard deviation.

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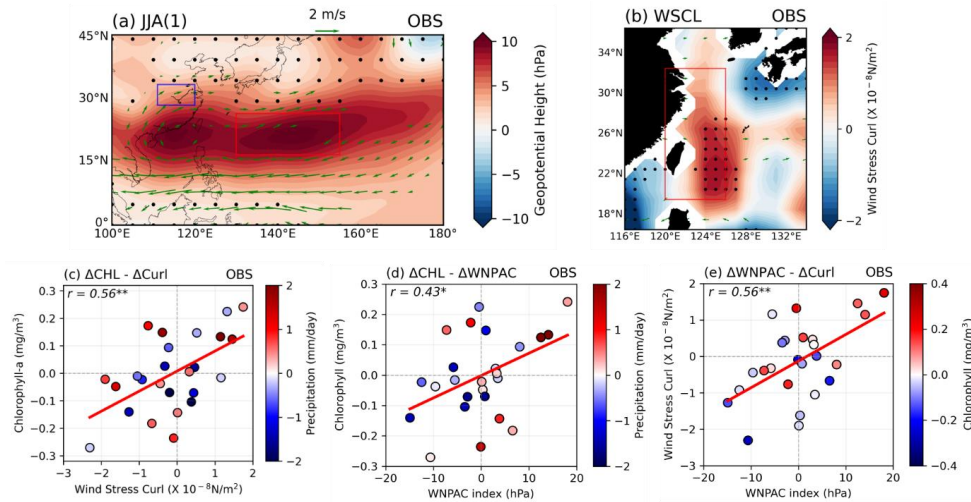
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301 **3.4. Upwelling-driven blooming mechanism - Insight from Observations**

302 So far, we have re-evaluated the runoff-driven mechanism using model results and identified an
303 upwelling-driven mechanism. Lastly, we examined the upwelling-driven mechanism using reanalysis data for
304 physical variables and chlorophyll-a satellite data to verify its application to the real world. Figure 9a shows the
305 composite map of GPH anomalies during the El Niño decaying summer, using NCEP2 re-analysis data. To identify
306 the typical WNPAC and 850hPa wind anomalies during El Niño decaying summers, we defined a WNPAC index
307 using the full period of available NCEP2 re-analysis data (1979-2022; 44 years). The WNPAC index was defined
308 as the area-averaged (16.5°N-26.5°N, 130°E-155°E) GPH anomalies; over the WNP region indicated by the red
309 box in Fig. 9a. The WNPAC pattern and anticyclonic 850hPa wind anomalies ranging from the South China Sea
310 to the WNP, are well represented in the re-analysis data. We calculated the WSCL using surface winds from the
311 NCEP2 re-analysis data, revealing significant positive WSCL (cyclonic circulation) anomalies over a large area
312 of southeastern China (Figure 9b). Furthermore, we found a significant positive correlation ($r = 0.56^{**}$) at the 99%
313 confidence level between the WSCL index (red box in Fig. 9b) and SCHL anomalies in the target region (Figure
314 9c). Additionally, there is a significant positive correlation ($r = 0.43^*$) at the 95% confidence level between the
315 WNPAC index and the SCHL anomalies in the target region (Figure 9d). A strong positive relationship ($r = 0.56^{**}$)
316 at the 99% confidence level between the WNPAC index and WSCL in the target region was also observed (Figure
317 9e). Several instances of negative SCHL anomalies occurred despite positive anomalous rainfall (blue box in Fig.
318 9a; 28.5°N-33.5°N, 111°E-120°E). However, interestingly, cases exhibiting strong anomalous SCHL blooming
319 mostly coincided with either strong WNPAC indices or robust cyclonic WSCL in the ECS region (Figure 9e).
320 These remarkable associations among these variables suggest that the upwelling-driven blooming mechanism is
321 indeed operating in the real world. Therefore, both the runoff-driven and upwelling-driven mechanisms must be
322 considered together to fully understand the dynamics of phytoplankton blooming in the ECS region during El
323 Niño decaying summers.

324



325

326 **Figure 9.** (a) The composite map exhibits the GPH anomalies over the WNP and 850hPa wind anomaly patterns
 327 during the El Niño decaying summer season for the available period of re-analysis data (1979-2022; 44 years).
 328 Red and blue boxes indicate the area-averaged WNPAC index (16.5°N-26.5°N, 130°E-155°E) and precipitation
 329 index (28.5°N- 33.5°N, 111°E-120°E) respectively. Black dots indicate the insignificance at the 90% confidence
 330 level using the bootstrap method. (b) The composite map shows WSCL anomaly patterns and 850hPa wind
 331 anomaly patterns during the El Niño decaying summer season within the same period with Fig. 9a. The red box
 332 indicates the area-averaged WSCL index. Black dots indicate the significance at the 90% confidence level using
 333 the bootstrap method. (c-d) The relationship between SCHL anomalies in the target region and the WSCL index
 334 and the WNPAC index respectively. Colored scatters show the precipitation index over the eastern part of China.
 335 (e) The relationship between the WNPAC index and the WSCL index. Colored scatters show the magnitude of
 336 SCHL anomalies in the target region.



337 **4. Discussions**

338 This study investigates the comprehensive mechanisms of anomalous phytoplankton blooms in the East
339 China Sea during the summer following El Niño events. We re-evaluated the existing runoff-driven phytoplankton
340 blooming mechanism using the observational data and long-term integrated ESM results based on present climate
341 conditions. Notably, the ESM we used does not simulate P riverine input, a crucial factor in the YRE region, our
342 research target region. Despite the absence of P riverine inputs, significant positive phytoplankton blooms still
343 emerged, we hence proposed an additional mechanism to trigger anomalous phytoplankton blooming during the
344 summers following the El Niño mature phase.

345 Firstly, we sorted all El Niño cases selected from long-term climate simulation results based on the
346 magnitude of SCHL blooming in the ECS region and classified the El Niño cases into two groups (SB & NB
347 group). There were clear differences between the two groups in climatic factors such as precipitation and runoff,
348 which drive existing blooming mechanisms. In the SB group, stronger and broader rainfall band and riverine
349 inputs into the ECS region were significantly predominant. The rainfall band generated over East Asia during the
350 summer season of post-El Niño is related to the development of the WNPAC, suggesting that the WNPAC is more
351 potently advanced in the SB group.

352 In addition, distinct differences between the two groups were observed, evident in both the magnitude
353 of EKV anomalies induced by atmospheric circulation and the WSCL anomaly patterns. Consequently, We found
354 a more robust and expansive WNPAC that persisted and extended its influence until the summer season, impacting
355 a broader area of East Asia in the SB group. This well-developed WNPAC triggers stronger wind anomalies in the
356 target region, leading to active EKV with positive WSCL. It facilitates upwelling in the water column as the
357 cyclonic atmospheric circulation, driven by the strong clockwise circulation over WNP, prevailed across the entire
358 ECS region.

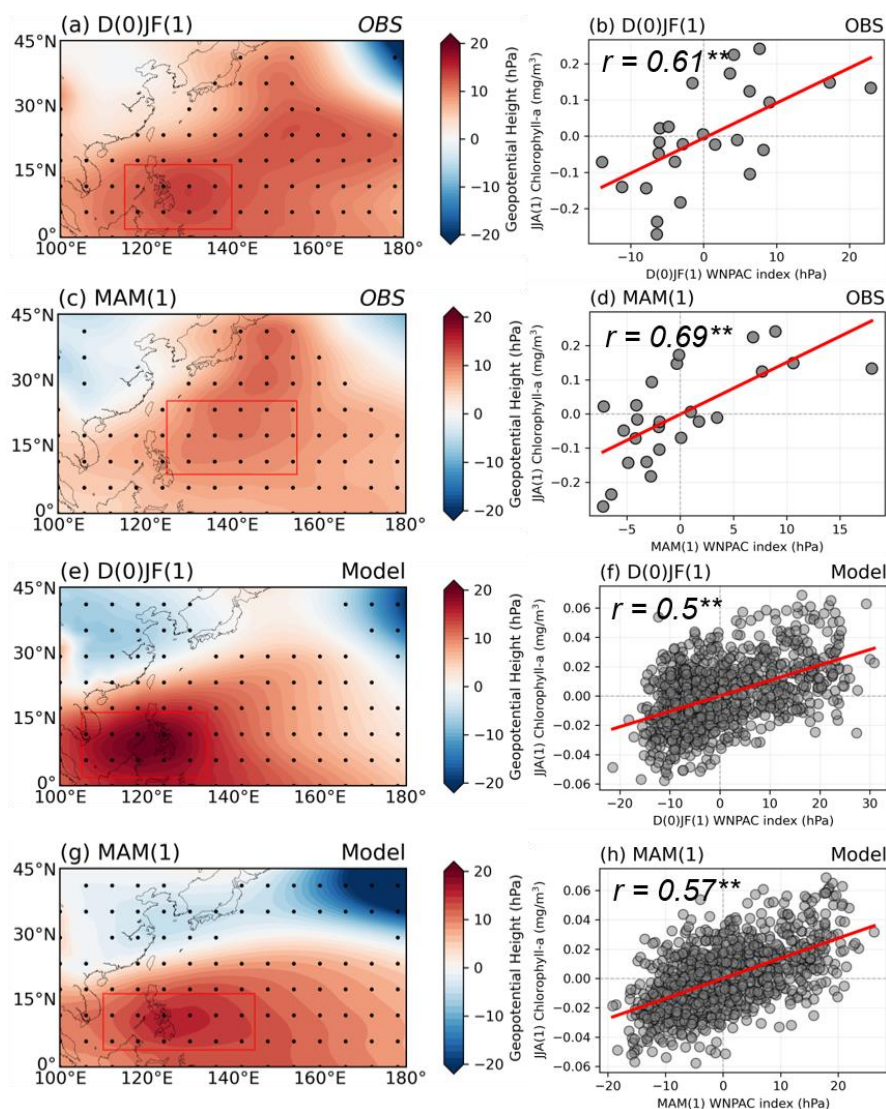
359 Lastly, we validated the upwelling-driven phytoplankton blooming mechanism elucidated by the model
360 results using reanalysis data and satellite chlorophyll-a data. There was a significantly positive relationship
361 between WNPAC and SCHL anomalies, as well as WNPAC and WSCL anomalies in the target region. Thus,
362 depending on the development of WNPAC during the El Niño decaying summers, anomalous phytoplankton
363 blooms can be triggered by a conjunction of different mechanisms: runoff-driven accompanied by strong
364 precipitation in the ECS region, as well as upwelling-driven mechanism induced by positive WSCL and EKV.

365 We investigated that the more vigorous development and expansion of the WNPAC can influence the
366 marine ecosystems of the ECS region with sufficient El Niño cases using ESM results. The intensity and extent
367 of WNPAC development between the SB and NB groups were distinct, which means that anomalous
368 phytoplankton blooming can be predicted as early as two seasons before it occurs during the El Niño mature phase.
369 We found a significantly positive lagged relationship between the WNPAC index and blooming magnitude in the
370 ECS region in both observations and ESM results (Figure 10). There were significant 2 seasons (D(0)JF(1) –
371 JJA(1)) lagged positive correlations ($r = 0.61^{**}$) and ESM results ($r = 0.5^{**}$). In addition, the case of a short-term,
372 1 season lagged relationship (MAM(1) – JJA(1)) has higher lagged positive correlations in both observations ($r =$
373 0.69^{**}) and ESM results (0.57^{**}) at the 99% confidence level. These results demonstrate that the magnitude of



374 WNPAC during the El Niño mature phase can be a good predictor of the magnitude of phytoplankton blooms in
375 the ECS region during the following summers of El Niño events.

376 The present climate-based long-term integrated ESM (GFDL-CM2.1) utilized in this study, possesses a
377 relatively low spatial resolution, leading to coarse representations of features like continental shelves and slopes
378 like those in the YECS region. This limitation may hinder the accurate depiction of regional currents and local
379 eddies, which are crucial for understanding ocean circulation dynamics, including the intrusion of the Kuroshio
380 current near the north-eastern part of Taiwan Island, as mentioned in previous studies (Chen, 1996; Chen et al.,
381 1995; Lee et al., 2023). However, since we are arguing for an upwelling mechanism in the ocean driven by
382 atmospheric circulation rather than horizontal transport, the resolution limitation may not significantly impact our
383 findings. Furthermore, our analyses are based on the present climate-based long-term integrated ESM, and there
384 may be changes in the pattern of WNPAC development due to changes in the ENSO teleconnection resulting from
385 changes in the El Niño mean state under global warming scenarios (Kim et al., 2024; Shin et al., 2022; Yang et
386 al., 2022; Yeh et al., 2009). Here, we primarily focused on the biological aspect of the phytoplankton blooming
387 mechanism and did not extensively explore the dynamic mechanisms driving differences in WNPAC development
388 intensity between the two groups. In Fig. S3, we identified differences in the decaying speed of the El Niño
389 strength between the two groups and the warmer SST anomalies in the Central Pacific (CP) region during El Niño
390 mature phase in the SB group. Therefore, further studies will be necessary to investigate the blooming magnitude
391 variations associated with different El Niño types such as CP and Eastern Pacific (EP) El Niño (Kug et al., 2009,
392 2010; Yuan and Yang, 2012). Moreover, Xie et al mentioned that the anomalous large-scale anti-cyclone in the
393 WNP during the summer season of the El Niño decaying is associated with the Indian Ocean (IO), named the IO
394 Capacitor theory. These dynamic aspects will require further detailed exploration in subsequent studies.
395 Additionally, quantitative analyses between runoff-driven and upwelling-driven blooming mechanisms through
396 model experiments will be necessary to provide a detailed understanding of the contribution of both mechanisms
397 to phytoplankton blooms during the El Niño decaying summer season.



398

399 **Figure 10.** (a-d) Evolution maps indicate the distribution of GPH anomalies from the mature phase (D(0)JF(1))
 400 of El Niño to the following spring season (MAM(1)) in the observations. Scatter plots show the lagged relationship
 401 between the area-averaged WNPAC index (red box in the left panels) during each period and the anomalous SCHL
 402 blooming magnitude in the target region during the decaying summers of the El Niño in observations. (e-h) Same
 403 as (a-d), but with model results.



404 **Data availability**

405 The chlorophyll satellite observation data used in this study is available on [https://esa-](https://esa-oceancolour-cci.org)
406 [oceancolour-cci.org](https://esa-oceancolour-cci.org). The ERSST (SST), wind, wind stress, GPH re-analysis data are provided
407 at <https://psl.noaa.gov/>.

408

409 **Code availability**

410 The computer codes that support the analysis within this paper are available from the
411 corresponding author on request.

412

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418

419 **Ethical approval**

420 Not applicable

421

422 **Declaration of Competing interests**

423 The authors declare no competing interests.

424



425 **CrediT authorship contribution statement**

426 **Dong-Geon Lee:** compiled the data, conducted analyses, prepared the figures, and wrote the
427 manuscript. **Jong-Seong Kug:** Designed the research and wrote the majority of the manuscript
428 content. All the authors discussed the study results and reviewed the manuscript.



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