Indian Ocean warming as a potential trigger for super phytoplankton blooms in the eastern equatorial Pacific from El Niño to La Niña transitions

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Abstract

During El Niño to La Niña transitions in 1998 and 2010, satellite observations revealed a sharp increase in surface chlorophyll in the eastern equatorial Pacific (EEP), exceeding the interannual amplitude by threefold; however, the causes of such super phytoplankton blooms (SPBs) remain unclear. Here, observational data, climate model simulations, and coupled ocean-biogeochemical modeling experiments are adopted to show that Indian Ocean (IO) warming plays an active role in remotely triggering SPBs in the EEP. During the previous boreal winter in an El Niño year, IO warming generates anomalous easterlies over the western edge of the tropical Pacific, which excite upwelling Kelvin waves propagating into the EEP during the following boreal spring, remotely causing an uplift of the nutricline in the EEP. Seasonally, the mixed layer deepens and the upper ocean warms during the following late spring, and large amounts of nutrient-rich cold subsurface waters entrain into the mixed layer; interannually, the local grazing pressure is low after the peak of El Niño. These remote and local factors jointly promote SPBs in the EEP.

1. Introduction

El Niño and the related Southern Oscillation (ENSO) phenomenon is the strongest signal in the interannual variation of the coupled ocean-atmosphere system, exerting a significant influence on weather conditions, ecosystems, and agriculture around the world (Behrenfeld et al 2006, McPhaden et al 2006, Su et al 2018a, Gregory et al 2019, Rifai et al 2019, Zhang et al 2020). As the negative phase of ENSO, La Niña events manifest colder-than-normal conditions in the central-eastern equatorial Pacific (EEP), and these conditions are associated with enhanced upwelling and subsurface upward nutrient transport, consequently leading to an increase in primary productivity in this region (Radenac et al 2012, Gierach et al 2013). Since September 1997, unprecedented volumes of global coverage ocean-color data have become available, which have been widely used for ENSO-related studies (McClain et al 2002, Kang et al 2017, Zhang et al 2011, Gregg and Rousseaux 2019, Zhang et al 2019a). For example, satellite ocean-color data revealed that while La Niña events frequently occurred in the tropical Pacific, sudden phytoplankton blooms occurred twice in the EEP during the transition between El Niño and La Niña (figure 1(a)). During the El Niño/La Niña transitions in 1998 and 2010, the interannual anomalies of the surface chlorophyll concentration quickly reversed from a negative to a positive state, exceeding
Figure 1. Observed super phytoplankton blooms during the satellite-era. (a) Normalized interannual anomalies of SST (shaded) and surface chlorophyll (black curve) over the Niño3 region from January 1998 to December 2019. (b), and (c) Temporal evolution of SST (shaded) and sea level anomalies (SLA, contours) along the equator (averaged over 2° S to 2° N) in 1998 and 2010; (d) and (e) are the same as (b) and (c) but for surface chlorophyll (shaded) and surface zonal winds (contours). Green circles in (a) denote SPBs (1998 and 2010), with interannual anomalies exceeding threefold the corresponding standard deviation. The contour intervals are 5 cm in (a) and (b), and 1 m s$^{-1}$ in (c) and (d).
standard deviations of the interannual anomalies more than threefold (figure 1(a), green circle), and such events are referred to as super-phytoplankton blooms (SPBs). This biological response exerts a pronounced influence on pelagic ecosystem variability, fisheries, the food web, and the carbon cycle on the interannual timescales (Brainard et al. 2018). Therefore, identifying the processes responsible for SPBs is of great importance for biogeochemical studies, fisheries, and the economy in the eastern Pacific and Southern American coastal countries.

The first SPB was observed by satellite around mid-1998, when physical conditions exhibited drastic changes in the tropical Pacific (Chavez et al. 1999, Murtugudde et al. 1999). In May 1998, an unprecedented La Niña event occurred, and easterly winds resumed in the central EEP, which subsequently enhanced the upwelling of nutrient-rich cold subsurface waters. After 3 weeks, with the rapid decrease in sea surface temperature (SST), the positive chlorophyll anomaly exceeded its interannual variations more than fivefold in the Niño3 region (150° W–90° W, 5° S—5° N, figures 1(a), (b), and S1 (available online at stacks.iop.org/ERL/16/054040/mmedia)). Various processes responsible for this SPB have been suggested by previous studies as follows (Ryan et al. 2006, Gorgues et al. 2010). (a) After the El Niño peak, the thermocline (nutricline) was anomalously shallow, leading to the entry of subsurface nutrients into the euphotic zone, which fueled the growth of phytoplankton. Additionally, the equatorial undercurrent (EUC) may serve as an important source for macro and micro-nutrients (e.g. Chavez et al. 1998, Christian et al. 2002, Ryan et al. 2002, Qin et al. 2016). (b) The low concentration in zooplankton tends to relieve grazing pressure on phytoplankton after an El Niño event (e.g. Landry et al. 1997, Wang et al. 2005, Gorgues et al. 2010). (c) A significant increase in the percentage of large phytoplankton (e.g. diatoms) by 10%–30% contributed to an increase in the total chlorophyll concentration (e.g. Chai et al. 2007, Dugdale et al. 2007, Strutton et al. 2008, Masotti et al. 2011).

The local physical and biogeochemical conditions favor the occurrence of an SPB in the EEP during the El Niño/La Niña transition. However, SPBs occurred only twice during the rapid transition phase from El Niño to La Niña in 1998 and 2010 (figure 1(a)). Previous studies use a self-sustained oscillatory mode such as a delayed oscillator or recharge–discharge oscillator to explain the ENSO cycle (Schopf and Suarez 1988, Jin 1997, Wang 2018). Recent studies have found that interocean interactions can initiate or modulate El Niño/La Niña transitions (Xie et al. 2009, 2016, Izumo et al. 2010, Luo et al. 2012, Wang 2019, Duan et al. 2020). For example, a previous study suggested that the Indian Ocean (IO) warming might have contributed to the rapid transition from El Niño to La Niña during 2009–2010 (Kim et al. 2011). This ENSO phase transition coincidentally corresponded to the timing of the recent SPB occurring in May 2010 (figure 1). Additionally, other coupled modeling studies have suggested that the Indian Ocean dipole (IOD) and Indian Ocean basin (IOB) modes can contribute to the rapid phase transition of ENSO in the tropical Pacific (Ohba and Ueda 2007, Ha et al. 2017, Le et al. 2020, Yoo et al. 2020). Specifically, the SST warming in the tropical Indian Ocean (TIO) generates anomalous easterlies over the western edge of the Pacific, which excite upwelling Kelvin waves that propagate into the EEP during the following boreal spring. The strong subsurface cooling due to upwelling Kelvin waves quickly reverses El Niño to the La Niña phase (Kim et al. 2011). At the appropriate time (e.g. the late-spring seasonal phytoplankton bloom, the deepening of the seasonal mixed layer, and spring SST warming in the EEP), anomalous shoaling of thermocline/nutricline induced by IO warming may further promote the growth of phytoplankton. Additionally, local processes (e.g. low grazing pressure after the peak of El Niño) may jointly promote an IO warming-induced SPB.

Clearly, the processes responsible for SPB occurrences remain unclear at present. Here, we first examine the recent SPBs events occurring during the recent El Niño/La Niña transition using observational data. To demonstrate the role of IO warming in triggering SPBs, we evaluated historical experiments (1850–2014) in Earth System Models (ESMs) participating in the Coupled Model Intercomparison Project Phase 6 (CMIP6). Moreover, we performed a series of regional ocean-biogeochemical modeling experiments to investigate the potential role of other local processes (the delivery of iron to the EEP by the EUC and low grazing pressure from zooplankton) in promoting SPBs.

2. Method

2.1. Observational data and CMIP6 historical simulation products

We used a series of observed monthly mean data to examine the SPB events during 1998–2019. The SST data were from the Optimally Interpolated Reynolds SST version 2 (Reynolds et al. 2002). Surface chlorophyll data were from the GlobColor Project (Maritorena et al. 2010). The sea surface height was from AVISO data (Ducet et al. 2000). The climatological mean nutrients (nitrate, silicate, and phosphorus) concentrations were from the WOA 2018 (Boyer et al. 2019). The mixed layer depth was obtained from Argo floats (2005–2019) and EN4 (1998–2019) (Good et al. 2013). The monthly mean wind stress was from European Centre for Medium-Range Weather Forecasts (ECMWF)/ERA-interim (Dee et al. 2011). Ocean temperature was from the Global Ocean Data Assimilation System (Saha et al. 2006). CMIP6 historical simulations in
14 ESMs with biogeochemical components were utilized to examine the possible SPB events (table S1). Four monthly mean variables (SST, surface chlorophyll, sea surface height, and surface wind stress) were used from the ‘r1i1p1f0’ simulations. The long-term trends for all simulations were removed before they were used to compute the corresponding interannual anomalies.

2.2. A coupled ocean–biogeochemical model and experimental design

A regional coupled ocean–biogeochemical model was utilized in this study (Gent and Cane 1989, Christian et al 2001, Wang et al 2009, Zhang et al 2018). The ocean model was configured to the tropical Pacific basin (120°E–76°W, 30°S–30°N), with a horizontal resolution of 0.3–0.6°. The model had 20 sigma layers, with the first layer being the mixed layer, which was explicitly computed by a bulk mixed-layer model (Chen et al 1994).

To simulate the 1998 and 2010 SPB events, we utilized daily atmospheric forcing from ECMWF/ERA-interim reanalysis to drive the ocean model from 1997 (2009) to 1998 (2010) as a control run. Next, we examined the surface chlorophyll responses under different grazing pressures during these two SPB events. Four sensitivity experiments were performed with varying maximum grazing rates of zooplankton from 3.0 d−1 (low grazing pressure) to 6.0 d−1 (high grazing pressure) with intervals of 1.0 d−1 under the same atmospheric forcing as in the control run.

To identify the potential role of iron transported by the EUC in promoting the eastern Pacific SPB, we performed two simplified simulations. The model settings were the same as those in the control run except for its initial condition starting on 1st January 1998 (2010), in which iron was artificially added except for its initial condition starting on 1st January 1997 (2009) (2010), in which iron was artificially added. Four monthly mean variables (SST, surface chlorophyll, sea surface height, and surface wind stress) were used from the ‘r1i1p1f0’ simulations. The long-term trends for all simulations were removed before they were used to compute the corresponding interannual anomalies.

3. Results

3.1. The observed SPB occurrence in the EEP

As the initial motivation, we first examined the recent SPB event that developed in the boreal spring and summer of 2010 (figure 1(a)). In terms of physical response, unprecedented central Pacific warming emerged in boreal winter, and then quickly reversed to a cooling state in the following boreal spring and summer (figures 1(a), (c), and S2; Feng et al 2015, Gao and Zhang 2017). Kim et al (2011) documented that this fast phase transition of the 2009–2010 event was mainly attributed to the strong eastward-propagating subsurface cold anomaly (figures S3–S5). As a precursor of the fast transition from warm pool El Niño to La Niña, persistent SST warming emerged in the TIO and SST cooling appeared in the far-western tropical Pacific from January to April 2010 (figure 1(c)). This SST pattern tended to generate anomalous easterly winds over the western edge of the Pacific (figure 1(e)). Anomalous easterly winds excited a series of eastward-propagating upwelling Kelvin waves (represented by sea level anomalies) and reached the eastern boundary of the Pacific after approximately three months (figures 1(c) and S2). The subsurface cold anomalies (−2°C) associated with eastward upwelling Kelvin waves further resulted in surface cooling in the eastern Pacific during boreal spring and terminated the El Niño state (figures 1(c) and S5). Therefore, IO warming plays an active role in promoting the ENSO transition from El Niño to La Niña in the tropical Pacific.

In terms of biological response, during boreal winter and early spring, a reduction in chlorophyll was observed in the central equatorial Pacific (figures 1(a) and (e)). In the following months (April–May 2010), as a response to IO warming, negative sea level anomalies quickly emerged in the EEP, which corresponds to the shoaling of the thermocline (or nutricline). Thus, increased subsurface nutrients due to an uplifted nutricline can promote the growth of phytoplankton (i.e. an increase in chlorophyll), with its maximum amplitude reaching triple of the interannual variability, and this phenomenon can be referred to as an SPB (figure 1(a)).

As shown in figure 1, the time length for which the 1998/2010 blooms persisted and the extent that they covered are significantly different from each other. The 1998 bloom tended to occur eastward in 180°–120°W from June to August, exceeding the interannual amplitude by fivefold. The 2010 bloom tended to occur relatively westward in 150°W–120°W from April to June, exceeding the interannual amplitude by threefold (figure 1). The different bloom timings should be related to different local factors. As shown in figure 2(b), the mixed layer attains its minimum depth value from February to April in the eastern Pacific, then deepens from April and reverses its seasonally deep depth in the boreal summer. During the 1998 ENSO phase transition, the proper seasonal variations in physical (deepening of the seasonal mixed layer, figure 2(b)) and biological conditions (figures 2(c)–(f)) were superimposed on the IO warming-induced shoaling thermocline on the interannual timescale (figures 1(b) and (d)). Therefore, the subsurface nutrients were easily transported into the mixed layer through entrainment, which further triggered an extreme increase of chlorophyll in the middle of 1998. In terms of the 2010 bloom, the timing of bloom is not consistent with the seasonal deepening mixed layer, so MLD change is not the key factor to promote the increase in chlorophyll. Conversely, the SST spring warming (figure 2(a)) further promoted the phytoplankton bloom of more than
Figure 2. Observed seasonal anomalies of physical and biogeochemical fields along the equator (averaged over 2°S to 2°N). (a) SST; (b) MLD; (c) chlorophyll; (d) nitrate; (e) silicate; (f) phosphorus. The SST data were from the Optimally Interpolated Reynolds SST version 2; surface chlorophyll data were from the GlobColor Project; mixed layer depth was obtained from EN4 during 1998–2019. The climatological mean nutrients (nitrate, silicate, and phosphorus) concentrations were from the WOA 2018.

0.2 mg m\(^{-3}\) in 2010. Therefore, except for the IO-warming triggering the bloom, the local factors (seasonal SST warming and MLD deepening) can further promote the individual blooms.

Note that an El Niño-La Niña transition occurred in February 2007; however, the positive chlorophyll anomalies in the EEP were small. The small change in chlorophyll could be partially attributed to the inappropriate timing of the ENSO phase transition (shoaling of the seasonal mixed layer during boreal winter (figure S7)) and the lack of the remote effect from the IO (figure S6). An exceptional case occurred during the 2016 El Niño/La Niña transition, similar to the physical condition in 2010. Although SST warming emerged in the TIO during boreal winter, weakened trade winds from the subtropical effect tended to weaken the SST amplitude during the 2016 La Niña (Su et al. 2018b). The negative SST anomalies (SSTA) in the EEP maintained a relatively weak amplitude (approximately \(-0.6^\circ\)C, figures S6 and S7); negative SLA anomalies were weak, and positive chlorophyll anomalies were also small in the EEP in the summer of 2016 (figure S6). Therefore, IO warming is solely an active factor promoting SPB events; other atmospheric processes may hinder the development of SPB events triggered by IO warming.

3.2. SPB events analyzed in CMIP6 models

To further demonstrate the role of IO warming in triggering an SPB, we examined SPB events that occurred in the CMIP6 historical simulation. We define that SPB events emerge when the standardized surface chlorophyll in the Niño3 region exceeds the threefold standard deviation of interannual
Figure 3. (a) Composite SST (shaded) and sea level anomalies (contour) along the equator (averaged over 2°S to 2°N) during SPBs from the CESM2 historical run. (b) The same as (a) but for chlorophyll (shaded) and surface zonal winds (contour). (c) Relationship between SST anomalies of ND(0)JF(+1) over the tropical Indian Ocean (20°S–20°N, 60°E–100°E) and chlorophyll anomalies of MJJA(+1) over the Niño3 region based on six available climate model simulations during 1850–2014. The contour intervals are 1 cm in (a) and 0.1 m s⁻¹ in (b); red, green and orange dots indicate extreme (with |Niño3 chlorophyll| > 2 s.d.), moderate (1.5 s.d.<|Niño3 chlorophyll|< 2 s.d.) and weak (1.0 s.d.<|Niño3 chlorophyll| < 1.5 s.d.) bloom events, respectively. Black dots indicate all the years when the chlorophyll anomalies do not fall into these criteria. Note that Niño3 chlorophyll in (c) is the averaged chlorophyll from May to August, which is below 3 s.d. Criteria of super bloom in 1998 and 2010. The numerals ‘0’ and ‘+1’ denote the previous and current SPB years, respectively.

chlorophyll anomalies, which captures the SPB events of 1998 and 2010 well (figure 1, dashed black lines). Unfortunately, only CESM2 (CESM2_WACCM), GFDL-ESM4, IPSL-CM6A-LR, and NorESM2-LM (MM) could capture several SPB events, and only the CESM2 (CESM2_WACCM) could simulate more than 13 events during the ENSO transition from 1850 to 2014 (figure S8). Therefore, we performed a composite analysis of SPBs based on the CESM2 historical run (Danabasoglu et al 2020) according to the selective condition of SPBs.

Figures 3(a) and (b) show that the CESM2 simulated SPBs tend to occur in the following spring–summer after the El Niño peak phase, which is associated with a fast transition between El Niño and La Niña or even before the transition. After the peak phase of El Niño, persistent warming emerges in the TIO during boreal winter, which is associated with anomalous easterlies over the western edge of the Pacific (figure 3(b)). As a response, a negative SLA propagates from the western to the eastern Pacific basin, which reaches the EEP in the late spring and early summer of next year (figure 3(a)). These characteristics are consistent with those described during the 2010 SPB events (figures 1(c) and 3(b)), suggesting that the previous hypothesis for SPB events triggered by IO-warming is reasonable.

To further confirm this hypothesis, figure 3(c) shows the relationship between the TIO SSTA during November (0)–February (+1) (ND(0)JF(+1)) and the surface chlorophyll over the Niño3 region during May (+1) – August (+1) (MJJA(+1)), derived from six CMIP6 models with more samples. The numerals ‘0’ and ‘+1’ denote the previous and current SPB years, respectively. The averaged Niño3 Chl anomalies that exceeded double standard deviations of chlorophyll anomalies over MJJA (+1) (>89%) were mainly located in the first quadrant (red dots). When looking at the Niño3 Chl anomalies that exceeded one standard deviation of chlorophyll anomalies (colored dots), more than 74% of the events were still located in the first quadrant. Additionally, the correlation
coefficient between ND(0)JF(+1) SSTA in TIO and MJJA(+1) chlorophyll in the Niño3 region was 0.416 ($P < 0.01$), these results further confirm that the IO warming in boreal winter indeed plays an active role in triggering the SPB events in the eastern Pacific.

### 3.3. The local factors promoting SPB events induced by IO-warming: modeling experiments

Although IO warming acts as a potential trigger for SPB events in the EEP, previous studies suggested that local factors can strengthen SPBs in the Pacific (Gorgues et al 2010). These factors include low grazing pressure from zooplankton after El Niño, and increased iron transportation by the eastward EUC. Therefore, we performed a series of experiments (see section 2.2) to examine the effects of local factors on SPBs.

#### 3.3.1. The effect of zooplankton-related grazing pressure on SPBs in the EEP

As shown in figures 4(a) and (b), a dynamic response exists to grazing pressure: the bloom is initiated under low grazing pressure, but is limited by grazing as time progresses. Under high grazing pressure (e.g. $g_{zw} = 6.0$), the surface chlorophyll exhibited small changes during the 1998 and 2010 SPB events. Conversely, under low grazing pressure ($g_{zw} = 3.0$, red lines in figures 4(a) and (b)), surface chlorophyll in the EEP still sustained a relatively low level before the boreal spring. Surprisingly, during boreal spring (April–July), surface chlorophyll sharply increased by 0.35 mg m$^{-3}$ (July 1998) and 0.2 mg m$^{-3}$ (May 2010) in the Niño3 region, closely following the satellite-observed temporal evolution (black lines in figures 4(a) and (b)). The different bloom timings (June–September for 1998, whereas April–July for 2010) are related to different local factors (seasonally deepening mixed layer or spring warming) as suggested previously. Under these seasonally favorable conditions, low grazing pressure can help strengthen IO-warming-induced SPB events at the appropriate time.

#### 3.3.2. The effect of EUC-accompanied iron transport on SPBs

The EUC flows eastward and shoals with the thermocline along the equator, supplying rich iron to the euphotic zone in the EEP. Thus, previous studies suggested that the variations in the EUC that are associated with ENSO may affect the phytoplankton biomass in the EEP through modulating iron concentration (Ryan et al 2002, 2006, Qin et al 2016). To validate the role of the EUC transporting iron in promoting SPB events, we conducted two extremely simplified coupled ocean physics-biogeochemistry simulations as proposed previous study (Gorgues et al 2010). We continuously imposed additional iron on the modeled iron concentration at 140°E, 0° at depths 100–220 m; this location is widely recognized as the source of the EUC at the equator, where the New Guinea Coastal Undercurrent-associated iron from the New Guinea continental margin was imported into the EUC. Under realistic atmospheric forcing, the imposed iron was indeed transported eastward by the EUC, leading to an increase in chlorophyll west of 120°W associated with the interannual MLD anomalies (figures 4(c) and (d)). However, the artificially imposed iron decreases to zero in the far eastern Pacific due to the scavenging losses and uptake of phytoplankton (figures S9 and S10), indicating that iron transport due to the EUC does not significantly promote SPB events in the far EEP due to the ENSO transition. Consistent results were found in previous studies for the mid-1998 SPB event (Gorgues et al 2010).

### 4. Conclusions and implications

SPB events occasionally emerge in the EEP during El Niño/La Niña transitions (e.g. mid-2010), and these events are associated with a rapid increase in the surface chlorophyll concentration, exceeding the threefold standard deviation of interannual chlorophyll variations in the Niño3 region. This biological response exerts a pronounced influence on pelagic ecosystems, fisheries, and the carbon cycle in the tropical Pacific.

In this study, we found that IO warming plays an active role in remotely triggering SPB events (figure 4(e)). During the previous boreal winter in an El Niño year, IO warming generates anomalous eastern equatorial upwellings over the western edge of the Pacific, which further excite the propagation of upwelled Kelvin waves into the EEP. Together with low grazing pressure after the peak of El Niño, seasonal deepening of the mixed layer, and seasonal SST warming in the late spring-summer, jointly promoting a sharp increase in phytoplankton biomass in the EEP.

Also, other local processes in the EEP were found to possibly further contribute to SPBs. (a) Due to enhanced ocean-atmosphere coupling during early summer, the seasonally deepened mixed layer in the far EEP superimposes onto the shoaling thermocline induced by IO warming on the interannual timescale. So, the subsurface nutrients are easily transported into the mixed layer through entrainment; in some cases, bloom emerges when seasonal SST warms in boreal spring. As a result, these two local factors both lead to an increase in chlorophyll. (b) Due to the reduction in grazer biomass after the peak phase of El Niño, the low grazing pressure might be insufficient to limit phytoplankton growth, which indirectly promotes an increase in phytoplankton biomass.

Previous studies suggested that iron transport eastward by the EUC along the equator may promote an increase in chlorophyll during La Niña events. However, as found in our modeling study and previous study, iron transport due to the EUC hardly
reaches the far EEP where the SPB occurs. Additionally, as suggested in a pioneer modeling and observational study (Gorgues et al 2005, Evans et al 2009), tropical instability waves (TIWs) cannot efficiently transport subsurface iron into the mixed layer and induce an increase in chlorophyll. Due to the weakening of the South Equatorial Current (SEC) during boreal spring, the current shear between the SEC and
EUC tends to be weak, leading to a weak TIW activity. Thus, during the SPB season (April–August), the weakened TIWs may hardly result in SPBs in the EEP. Additionally, the frontal activities in association with ENSO may further contribute to the phytoplankton blooms in the EEP (Tian et al. 2018, 2019, Wang et al. 2021), which should be investigated in the future high-resolution modeling study.

It is noted that the low SST in the EEP is not always consistent with the high chlorophyll in the observations (figure 1(a)), but the relationship is robust in the CESM2 historic run (figure S8). The possible causes can be discussed as follows. (a) Satellite observation shows that the maximum center of chlorophyll variability tends to be located in the western-central equatorial Pacific (Zhang et al. 2018, 2019b), which may be related to zonal migration of nutrient front and ENSO induced EUC-transported iron change in the central Pacific. Thus, the variability of chlorophyll in the central-eastern Pacific is relatively weak and hardly follows or responds to the evolution of SSTA. (b) A previous study found that the response of chlorophyll (phytoplankton) in the equatorial Pacific generally leads SST responses by 1–3 months (Park et al. 2018), which is related to the rapid response of phytoplankton to subsurface nutrients anomalies (e.g. iron) associated with thermocline variations in the central equatorial Pacific. (c) The biological components in the ESMs are simplified to one to four phytoplankton groups with fixed half-saturation and grazing constants (Bopp et al. 2013), and the nonlinear response of phytoplankton may hardly capture precisely by modeling. For the earlier bloom timing in CESM2 (i.e. March), the related mechanisms still need to be investigated further by performing inter-model comparison studies; e.g. different phytoplankton function groups may show diverse responses to physical environment change (Moore et al. 2013).

Previous studies have demonstrated that the interannual variability in biological response is tightly associated with physical processes induced by ENSO (Messié and Chavez 2012). However, in this study, we found that IO warming can remotely excite SPBs in the eastern Pacific. Recent studies have shown that the IOD and IOB induce pronounced atmospheric and oceanic responses in the western tropical Pacific (Cai et al. 2019), which may further promote the ENSO phase transition. Given the prominent role of IO warming and even Atlantic SST changes in ENSO and interdecadal climate fluctuations (Izumo et al. 2010, Luo et al. 2012, Li et al. 2016), the interbasin interactions between climate and ecosystem variability need to be investigated. Further work is necessary to confirm our results using complex ESMs in the future and more in situ observations (Chai et al. 2020a, 2020b). For example, widely adopted pacemaker experiments can be performed to separate climate and biogeochemical effects from other ocean basins (Kosaka and Xie 2016).

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.6084/m9.figshare.13347599.v2.

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Conflict of interest

The authors declare no competing interests.

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