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**Key Points:**

- Various marine environmental conditions in the East/Japan Sea were closely related to the Pacific Decadal Oscillation (PDO)
- Primary production and phytoplankton community structure in the East/Japan Sea could be changed according to the PDO
- A conceptual model for the responses of phytoplankton and potential changes according to the PDO phase in the East/Japan Sea was suggested

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# Variations in Phytoplankton Primary Production Driven by the Pacific Decadal Oscillation in the East/Japan Sea

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**Abstract** The Pacific Decadal Oscillation (PDO) regime is a major factor not only for the physical properties of the ocean but also for fishery and water resources. However, only a few studies have examined the impact of the PDO on the marine ecosystem in the East/Japan Sea. Therefore, in this study, the relationship between PDO and primary production (PP), and subsequent effects on the marine ecosystem were investigated in the East/Japan Sea using satellite data sets. PDO index showed a negative relationship with sea surface temperature (SST) and the contribution of the small phytoplankton to the total PP during the study period, whereas the mixed layer depth (MLD) and the PP showed a positive relationship with PDO index. The shallower MLD during the negative PDO phase indicates that vertical mixing may be weakened due to the stronger stratification caused by the higher SST than observed during the positive PDO phase. Consequently, we hypothesized that weakened vertical mixing may reduce nutrient supply to the euphotic layer, providing small-sized phytoplankton favored environmental conditions during the negative PDO. It is noteworthy that PDO-induced shoaling of the MLD was mainly observed in winter, which may influence the annual PP of the following year. This study shows that the annual PP in the East/Japan Sea can be largely affected through interactions between SST, MLD and subsequent changes in nutrient regime according to the PDO regime, which subsequently affects potential fishery resources in the East/Japan Sea.

**Plain Language Summary** Pacific Decadal Oscillation (PDO) is very important climatological factor that can affect ocean environmental conditions and its various components. However, only a few studies were conducted to examine the impact of the PDO on the marine ecosystem in the East/Japan Sea. In order to understand how the marine ecosystem will change according to the PDO in the East/Japan Sea, we investigated changes in marine environmental conditions according to the PDO using satellite data sets. Sea surface temperature was warmer, and mixed layer depth was shallower during the negative phase of the PDO. In addition, total primary production of phytoplankton was lower, while the contribution of small-sized phytoplankton to the total primary production was higher during the negative phase. The higher ocean surface temperature and shallower mixed layer depth suggest that the ocean is more stratified, which can lead to weakening of vertical mixing. Weakened vertical mixing may reduce nutrient supply to the euphotic layer, providing small-sized phytoplankton favored environmental conditions. Primary production of phytoplankton in the East/Japan Sea can be affected through environmental changes in related to the PDO, which can subsequently affect potential fisheries in the East/Japan Sea.

## 1. Introduction

The East/Japan Sea is a semi-enclosed, marginal sea bordered by Korea, Japan, and Russia, and it is well-known for its high productivity and dynamic marine environment including eddies, sub-polar fronts, and coastal upwelling (Y. S. Kang et al., 2002; D. Kim et al., 2012; S. H. Lee et al., 2017; J. H. Lim et al., 2012). The Ulleung/Tsushima Basin, located in the southwestern East/Japan Sea, has remarkably high productivity and is also called a "biological hotspot" (Jo et al., 2017; Joo et al., 2014; J. J. Kang et al., 2020; Kwak et al., 2013; D. Lee et al., 2017). Recently, dramatic environmental changes in the East/Japan Sea have caused alterations in the area's

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physical and biological characteristics (Joo et al., 2014, 2017; D. J. Kang et al., 2003; K. Kim et al., 2001; S. H. Lee et al., 2014). Moreover, the East/Japan Sea is a sensitively responding area to climate change. E. Y. Lee and Park (2019) reported that an ocean warming trend in the East/Japan Sea is faster than global warming trends seen elsewhere in recent decades. In addition, Joo et al. (2014) addressed a significant declining trend in annual primary production in the Ulleung/Tsushima Basin. Thus, the East/Japan Sea can be considered a suitable region for further studies on the response of the marine ecosystem to climate-induced marine environmental changes.

The Pacific Decadal Oscillation (PDO) is a multi-decadal variability in Pacific climate and the leading mode of sea surface temperature (SST) anomalies in the north Pacific (Mantua & Hare, 2002). The PDO regime is a major factor for the physical and biological properties of the ocean, such as SST, and fishery and water resources in the northeastern Pacific (Chavez et al., 2003; Mantua & Hare, 2002; Nigam et al., 1999). Although the PDO index is derived from SST anomalies in the northeastern Pacific (Andres et al., 2009; Chang et al., 2016; Chiba et al., 2012; Gordon & Giulivi, 2004), changes in environmental conditions due to the PDO are also observed in the northwestern Pacific region. Despite the ecological importance of the PDO, only a few studies on the impact of the PDO on marine ecosystems have been conducted in the East/Japan Sea (Chiba et al., 2008; Joo et al., 2014, 2016). Chiba et al. (2008) suggested that cold subsurface water can be shoaled, and the thickness of the warm surface Tsushima Current can be reduced during the negative PDO phase in the East/Japan Sea. In addition, these changes in water column structure lead to stronger stratification, which can cause depletion of nutrients in the upper layers and inhibition of lower-trophic level productivity (Chiba et al., 2008). Joo, Lee, Kang, et al. (2018) also found a strong negative relationship between PDO and nutrient concentration in the Ulleung/Tsushima Basin, East/Japan Sea.

The primary production (PP) of phytoplankton is generally obtained from shipboard measurements. However, it is hard to obtain long-term continuous observation data set in wide region through shipboard PP measurements. Thus, there is a limitation to studying low-frequency climate variability such as the PDO and its impact on the PP based on in situ measurements only. By contrast, remotely sensed ocean color data set can supplement the limitations of filed observation through the simultaneous observation over a wide spatial range. We used ocean color satellite data sets to understand the long-term variability in physical and ecological conditions such as SST, mixed layer depth (MLD)and PP in the East/Japan Sea. Since the East/Japan Sea is a region sensitive to climate change, we studied oceanic environmental conditions and PP in relation to the PDO regime using remote sensing data, and it will allow us to predict future changes in the East/Japan Sea marine environment due to global-scale climate changes such as global warming.

The aims of this study were as follows: (a) to investigate changes in environmental conditions in the East/Japan Sea with respect to the PDO regime, (b) to verify the impact of the PDO on PP, and (c) to understand the mechanism by which PP is altered by the PDO.

## 2. Materials and Methods

### 2.1. Remote Sensing Data

The satellite data used in this study included ocean color (OC) and sea surface temperature (SST) data. We collected SST data from the AVHRR Pathfinder and MODIS-Aqua. OC data was collected from SeaWiFS and MODIS-Aqua. These long-term data sets covering the study area (Figure 1) from 1998 to 2018. The OC data set includes the chlorophyll-a concentration (Chl-a), photosynthetic available radiation (PAR), and diffuse attenuation coefficient at 490 nm (Kd (490)). AVHRR Pathfinder version 5.3 level-3 collated SST data were obtained at 4-km/daily of space/time resolution. The data were provided by the NOAA National Centers for Environmental Information (NCEI; http://www.ncei.noaa.gov/). MODIS-Aqua and SeaWiFS level-3 monthly composited OC data were obtained from the Ocean Biology Processing Group (OBPG) at the NASA Goddard Space Flight Center (http://oceandata.sci.gsfc.nasa.gov/). Spatial resolution for MODIS-Aqua and SeaWiFS data sets were 4 and 9-km, respectively. Among the long-term data, we used AVHRR Pathfinder SST data and SeaWiFS OC data for the period from January 1998 to June 2002 and MODIS-Aqua data for the period from July 2002 to December 2018.

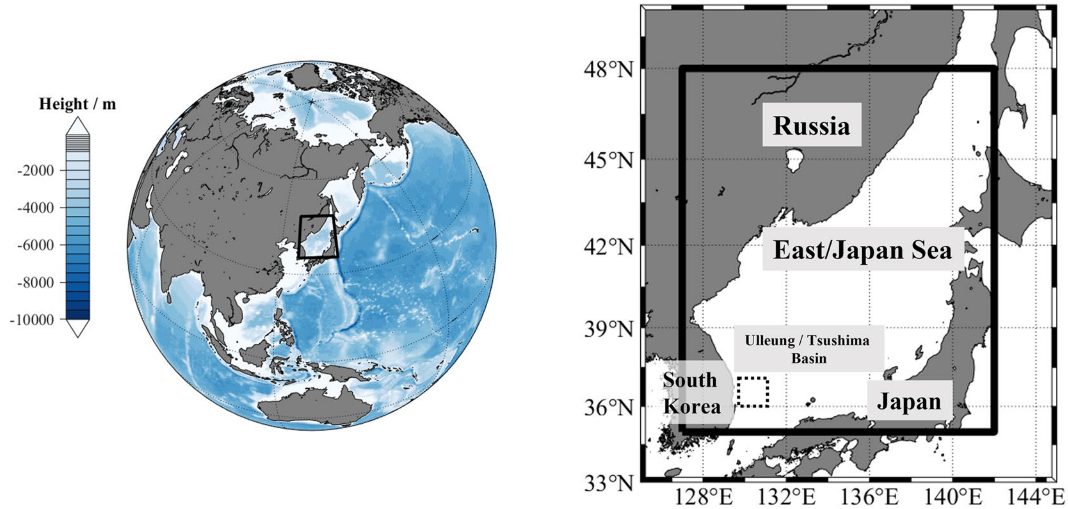


**Figure 1.** Study area in the East/Japan Sea located in the northwestern Pacific Ocean. The black square indicates the boundary of the study area defined in this study.

### 2.2. Estimation of Primary Production

PP was derived using a regional algorithm based on the Vertically Generalized Productivity Model (VGPM; Behrenfeld & Falkowski, 1997), with satellite ocean color data described as follows:

$$PP = 0.66125 \times P^{B}_{opt} \times \left[E_0/(E_0 + 4.1)\right] \times Z_{eu} \times Chl - a \times DL \quad (1)$$

where PP is the daily primary production integrated from the euphotic depth (mg C m$^{-2}$ d$^{-1}$), $P^{B}{}_{opt}$ is the optimal carbon fixation rate (mg C (mg Chl)$^{-1}$ hr$^{-1}$), $E_0$ is the amount of incident photosynthetically available radiation (PAR) during the day (E m$^{-2}$ d$^{-1}$), Zeu is the euphotic depth (m), which is derived by equation 4.6/$K_d$(490) that represents a 1% penetration depth of 490 nm radiation (Kirk, 1983), Chl-a is the concentration of chlorophyll-a (mg Chl m$^{-2}$), and DL is the photoperiod (hr), which is computed mathematically according to latitude and date.

$P^{B}{}_{opt}$ is derived from a multiple regression equation with SST and Chl-a (Kameda & Ishizaka, 2005) as follows:

$$P^{B}_{opt} = \frac{0.071 \times SST - 3.2 \times 10^{-3} \times SST^2 + 3.0 \times 10^{-5} \times SST^3}{Chl - a} + \left(1.0 + 0.17 \times SST - 2.5 \times 10^{-3} \times SST^2 + 8.0 \times 10^{-5} \times SST^3\right) \quad (2)$$

$P^{B}{}_{opt}$ in their model (K-I model) is the sum of large- and small phytoplankton groups. $P^{B}{}_{opt}$ for the micro- and nanophytoplankton (phytoplankton larger than 2 μm; $P^{B}{}_{opt\text{-}large}$) and picophytoplankton (smaller than 2 μm; $P^{B}{}_{opt\text{-}small}$) is defined as follows:

$$P^{B}_{opt-large} = 1.0 + 0.17 \times SST - 2.5 \times 10^{-3} \times SST^2 + 8.0 \times 10^{-5} \times SST^3 \quad (3)$$

$$P^{B}_{opt-small} = \frac{0.071 \times SST - 3.2 \times 10^{-3} \times SST^2 + 3.0 \times 10^{-5} \times SST^3}{Chl - a} \quad (4)$$

The contribution of small-sized phytoplankton to the total PP (small phytoplankton contribution) was calculated by dividing $PP_{small}$ by total PP.

Several previous studies already found a high correlation between in situ measured PP and model-derived PP based on the K-I model in the East/Japan Sea (Joo et al., 2014, 2016; Yamada et al., 2004). Size-fractionated PP also showed a strong linear relationship between in situ measurements and model estimates in the Ulleung/Tsushima Basin, East/Japan Sea (Joo et al., 2017).

### 2.3. Mixed Layer Depth Data

MLD data during 1998–2017 were obtained from the Estimating the Circulation and Climate of the Ocean (ECCO) ocean state estimate data (Forget et al., 2015). The ECCO state estimates provide a reproduced multi-decadal data set covering global oceans including the Arctic Ocean at a spatial resolution of ~0.8° × 1° (Forget et al., 2015). The ECCO model contains a large number of ocean observations from the satellite instruments and in situ measurements including CTDs, moorings, Argo floats, and gliders.

### 2.4. Pacific Decadal Oscillation Index

The monthly PDO index from the NCEI, which is based on the NOAA-extended reconstruction of SSTs (ERSST), was used in this study. These data were provided by the NOAA National Climatic Data Center (NCDC; http://www.ncdc.noaa.gov/). The NCEI PDO index is derived through a regression analysis of ERSST anomalies against the Mantua PDO index (Mantua et al., 1997) for their overlap period. The NCEI PDO index is computed with the ERSST anomalies.

### 2.5. Statistical Analysis

Before the statistical analyses, seasonal signals and linear trends were removed from all time-series data via the Climate Data Toolbox (CDT) for MATLAB (Greene et al., 2019) to separate seasonal effects from the long-term variability of environmental parameters. To deseasonalize, typical seasonal cycle of variability was subtracted from the time-series data. The typical seasonal cycle was derived by climatology of the time series after removing the linear least squares trend.

With these detrended and deseasonalized data, statistical analyses (principal component analysis, Pearson's correlation analysis, *t*-test) were performed by using the R software (version 2022.02.3, Inc., Boston, MA, USA). Principal component analysis (PCA) was conducted on six parameters we obtained from remote sensing data sets to find relationships between variables during the study period. Pearson's correlation analysis and *t*-test were conducted to assess the correlation and compare differences among variables.

## 3. Results

### 3.1. PDO Phase

The annual PDO index was derived by averaging the monthly PDO index for each year. The negative PDO phases appeared in most of the years during the study period, whereas the positive PDO phases were observed in 2003, 2014, 2015, and 2016 (Figure 2). The strongest positive annual PDO phase was observed in 2015 (0.9442), and the strongest negative PDO phase was observed in 2011 (−1.9142). The longest negative period during the study period lasted for 10 years, from 2004 to 2013.

### 3.2. Environmental Conditions

The high spatial variation in the monthly mean SST observed in the East/Japan Sea depended on the PDO phase (Figures 3a–3c). To distinguish the effects of PDO phase from the SST variability, time-series of the mean SST in the East/Japan Sea was deseasonalized and detrended. As a result, during the negative PDO phase, the mean SST in the East/Japan Sea was statistically significantly higher than during the positive PDO phase (*t*-test, $p < 0.01$). The average SST in the entire East/Japan Sea was 12.44 ± 0.67°C and 12.05 ± 0.59°C in the negative and positive PDO phases, respectively (Figure 4a). In addition, we observed a negative relationship between the PDO index and SST in the East/Japan Sea ($y = -0.15x + 13.01$, $r = 0.4638$, $p < 0.01$; Figure 4b).

The spatial distribution of the mean MLD from the ECCO state estimates in the East/Japan Sea also showed large differences according to the PDO phase (Figures 3d–3f). In particular, the difference was larger in the central and southern parts than in the northern part of the East/Japan Sea. The monthly mean MLD in the East/Japan Sea ranged from 15.21 to 124.89 m, with an average of 50.39 ± 33.38 m from 1998 to 2017. Seasonal variability of the mean MLD in the East/Japan Sea was also removed to understand the effect of PDO phase. The average MLDs for the East/Japan Sea during the negative and positive PDO phase from 1998 to 2017 were 50.13 ± 5.13 m and

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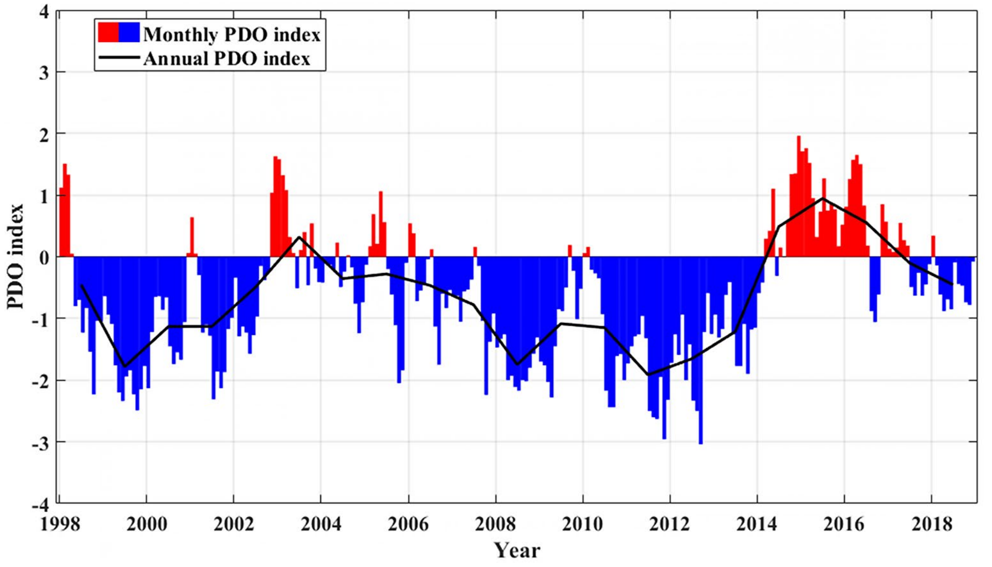


**Figure 2.** Time series of the monthly Pacific Decadal Oscillation (PDO) index (bar) and the annual PDO index (line) from 1998 to 2018.

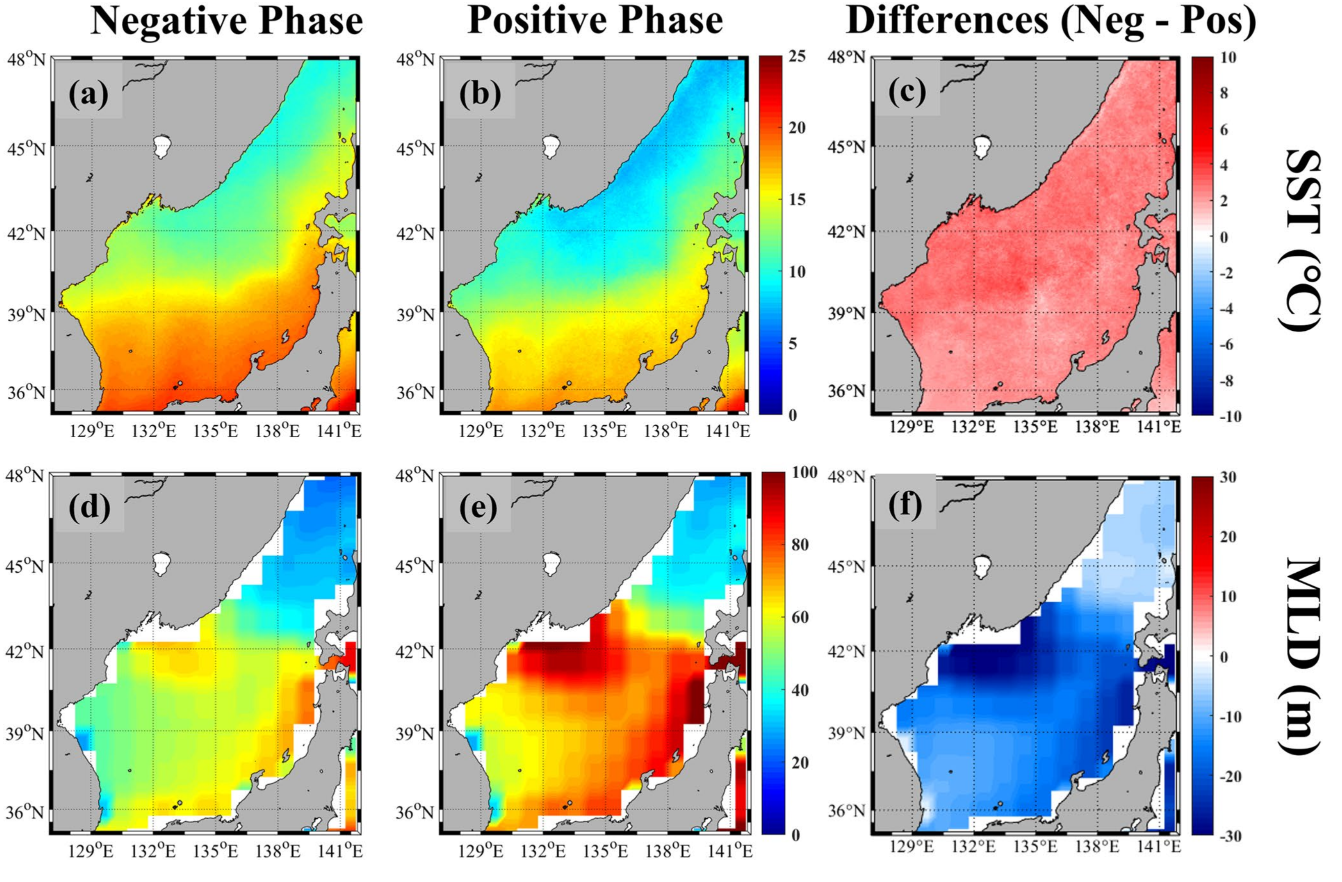


**Figure 3.** Spatial distribution of the mean sea surface temperature (SST, °C) and mean mixed layer depth (MLD, m). (a and b) Mean SST (°C) during the negative Pacific Decadal Oscillation (PDO) phase and the positive PDO phase, respectively. (c) Difference in the mean SST between the negative and positive PDO phases. (d and e) Mean MLD (m) during the negative PDO phase and the positive PDO phase, respectively. (f) Difference in the mean MLD between the negative and positive PDO phases.

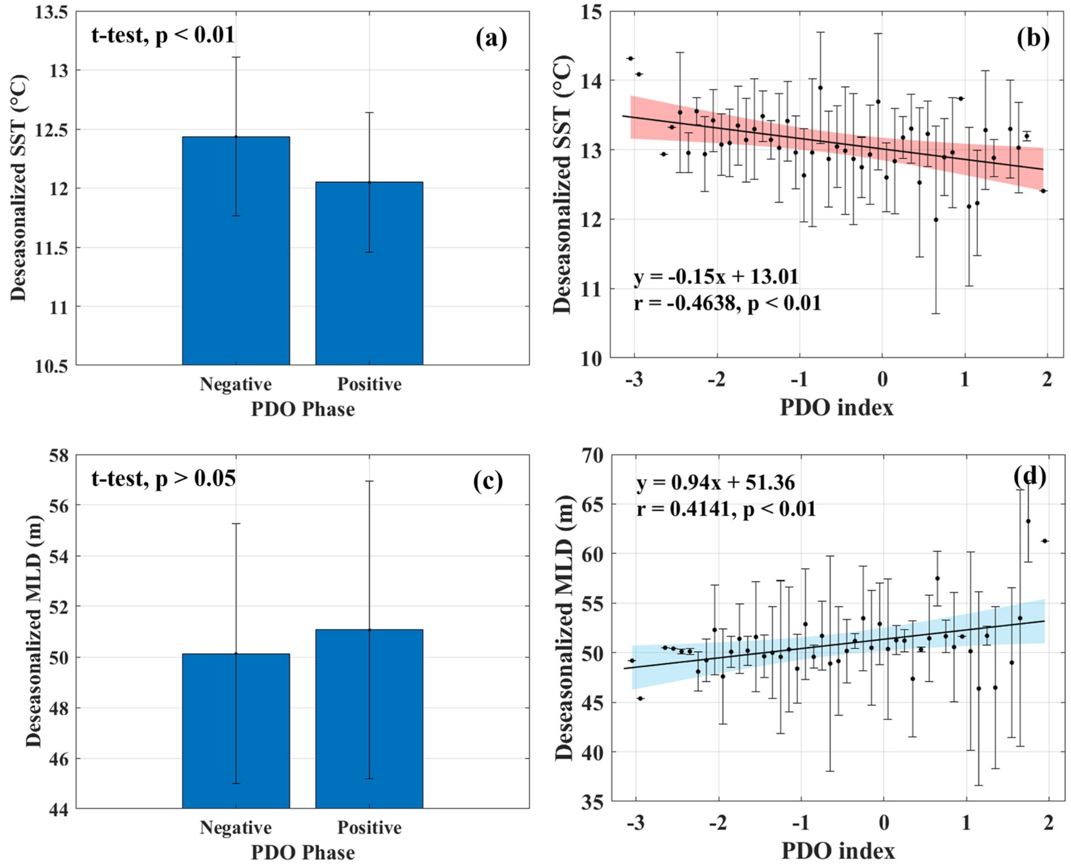


**Figure 4.** (a) Difference in the sea surface temperature (SST, °C) according to the Pacific Decadal Oscillation (PDO) phase. (b) Relationship between the PDO index and the mean SST (°C). (c) Difference in the mixed layer depth (MLD, m) according to the PDO phase. (d) Relationship between the PDO index and the mean MLD (m). Sample numbers (*n*) for the negative and positive PDO phases were 184 and 68, respectively. Error bars indicating standard deviations, and shaded area represents the 95% confidence intervals for the regression line. Seasonal variation and linear trend were removed from each variable.

51.07 ± 5.87 m, respectively (Figure 4c). Although difference of the mean MLD in the East/Japan Sea according to the PDO phase was not statistically significant (*t*-test, $p > 0.05$), MLD showed a positive relationship with the PDO index in the East/Japan Sea (Figure 4d; $y = 0.94x + 51.36$, $r = 0.4141$, $p < 0.01$). Consequently, the SST and the MLD in the East/Japan Sea during the negative PDO phase were significantly higher and shallower than during the positive PDO phase.

Seasonal mean SST and MLD in the East/Japan Sea was derived to investigate seasonal variations of environmental conditions during each PDO phase. Spring was defined as March–May, summer as June–August, fall as September–November, and winter as December–February. The mean SST and MLD in the entire East/Japan Sea according to the PDO phase showed seasonal variations (Table 1). The mean SST during the negative PDO phase ranged from 12.9 ± 0.6°C to 13.2 ± 0.6°C. Regarding the positive PDO phase, the mean SST ranged from 12.5 ± 0.6°C to 13.3 ± 0.5°C. The mean SST was relatively warmer during the negative PDO phase except during the spring seasons. The mean MLD during the negative PDO phase was also relatively shallower except during the spring. The mean MLD ranged from 49.7 ± 7 m to 51 ± 7.8 m during the negative PDO phase and from 48.9 ± 6.3 m to 52.7 ± 8.8 m during the positive PDO phase. When comparing the mean SST and MLD during the negative PDO phase to those during the positive PDO phase, differences in SST and MLD also showed high seasonality (Figure 5). The SST from summer to winter was relatively warmer during the negative PDO phase (Figure 5a). In contrast to the SST, the MLD was relatively shallower from summer to winter. The intensity of MLD shoaling was also stronger in the fall and winter seasons (Figure 5b).

**Table 1**
*Seasonally Averaged Environmental Parameters During Both PDO Phases*

| | | SST (°C) | MLD (m) | PP (mg C $m^{-2}$ $d^{-1}$) | $PP_{small}$ (mg C $m^{-2}$ $d^{-1}$) | Small contribution (%) |
|---|---|---|---|---|---|---|
| Negative PDO | Spring | 12.9 ± 0.6 | 51 ± 7.8 | 665.1 ± 55.2 | 161.2 ± 16.3 | 23.7 ± 2.6 |
| | Summer | 13.1 ± 0.8 | 50.3 ± 0.2 | 670.8 ± 38.6 | 159 ± 19.9 | 23.7 ± 2.8 |
| | Fall | 13.2 ± 0.6 | 49.8 ± 1.5 | 674.1 ± 33.6 | 160 ± 13.8 | 23.7 ± 2.3 |
| | Winter | 13.1 ± 0.7 | 49.7 ± 7 | 684.1 ± 32.4 | 159.5 ± 9.6 | 23.1 ± 2.6 |
| | Mean | 13.1 ± 0.7 | 50.2 ± 5.3 | 673.7 ± 41.1 | 159.9 ± 15.2 | 23.6 ± 2.6 |
| Positive PDO | Spring | 13.3 ± 0.5 | 48.9 ± 6.3 | 722.5 ± 51.4 | 155.2 ± 14.8 | 22.2 ± 2.9 |
| | Summer | 12.7 ± 0.8 | 50.6 ± 0.4 | 723 ± 33.7 | 164.4 ± 30.9 | 22.4 ± 3.6 |
| | Fall | 12.5 ± 0.6 | 52 ± 2.7 | 705.1 ± 32.7 | 159.9 ± 15.9 | 22.4 ± 2.8 |
| | Winter | 12.8 ± 0.8 | 52.7 ± 8.8 | 675.7 ± 34.8 | 159.4 ± 11.6 | 23.6 ± 3.3 |
| | Mean | 12.8 ± 0.7 | 51 ± 5.5 | 708.0 ± 42.5 | 159.7 ± 19.9 | 22.6 ± 3.1 |

### 3.3. Primary Production

The mean PP in each PDO phase showed similar spatial patterns (Figures 6a–6c). The mean PP was generally higher in the southern part of the East/Japan Sea during the positive PDO phase than during the negative phase while PP was lower in the northern part of the East/Japan Sea during the positive PDO phase However, the PP in the coastal regions was similar in both PDO phases. In contrast to the PP, the mean $PP_{small}$ was relatively higher during the negative PDO phase (Figures 6d–6f). Small phytoplankton contribution was derived from PP and $PP_{small}$. The mean small phytoplankton contribution also showed similar spatial distributions with the mean $PP_{small}$ (Figures 6g–6i). In addition, the spatial variations in the mean small phytoplankton contribution according to the PDO phase were similar to those of the mean $PP_{small}$. To investigate the spatial variability of PP according to the PDO phase, PP was annually averaged to minimize seasonal variations. Then, we defined three sub-regions in study area (Figure 7a). Changes in the annual PP during the negative PDO phase when compared to the positive PDO phase in Areas 1, 2, and 3 were 33.79 ± 23.09, 47.11 ± 20.27, and 45.84 ± 23.89 g C $m^{-2}$ $y^{-1}$, respectively (Figure 7b). As a result, the variability in the annual PP between negative and positive PDO phase was greater in the central region of the East/Japan Sea, indicated as Area 2 ($t$-test, $p < 0.01$).

To investigate the temporal variability without seasonal variations, the average of PP, $PP_{small}$ and small phytoplankton contribution were deseasonalized and time-series analysis were conducted. The average of PP and $PP_{small}$ showed high temporal variability in the East/Japan Sea (Figure 8). Of special note, the temporal variation pattern of the annual PP was similar to that of the annual PDO index (Figure 8a). Mean PP ranged from 632.90 ± 35.69 to 747.96 ± 37.02 mg C $m^{-2}$ $d^{-1}$, with an average of 683.16 ± 43.68 mg C $m^{-2}$ $d^{-1}$ during the study period. The highest PP was observed in 2015, whereas the lowest PP was observed in 2000. Mean $PP_{small}$ ranged from 142.79 ± 12.22 to 181.27 ± 14.26 mg C $m^{-2}$ $d^{-1}$, with an average of 159.80 ± 10.03 mg C $m^{-2}$ $d^{-1}$ (Figure 8b). Average of mean PP during the negative and positive PDO phases were 675.74 ± 40.56 mg C $m^{-2}$ $d^{-1}$ and 703.25 ± 45.74 mg C $m^{-2}$ $d^{-1}$, respectively (Figure 9a). The difference in the PP between positive and negative PDO phases was 27.51 mg C $m^{-2}$ $d^{-1}$, and the PP was significantly higher when the PDO was in the positive phase (Figure 9a; $t$-test, $p < 0.01$). PDO index and PP also showed a positive correlation ($y = 13.66x + 690.8$, $r = 0.5337$, $p < 0.01$; Figure 9b). On the other hand, $PP_{small}$ was lower during the positive PDO phase, but there was no statistically significant difference between positive and negative PDO phases (Figure 9c; $t$-test, $p > 0.05$). Moreover, although the relationship between $PP_{small}$ and PDO index is not always significant statistically, a negative relationship was found ($y = -1.05x + 157.64$, $r = -0.1627$, $p > 0.05$; Figure 9d). In case of small phytoplankton contribution, a negative linear relationship with PDO index was found (Figure 10a; $y = -0.56x + 22.94$, $r = -0.4815$, $p < 0.01$). The small phytoplankton contribution also showed a positive linear relationship with the SST (Figure 10b; $y = 0.90x + 13.42$, $r = 0.4677$, $p < 0.01$).

Similar to abiotic environmental conditions, Mean PP, $PP_{small}$, and small phytoplankton contribution showed high seasonal variabilities according to the PDO phase (Table 1). The mean PP during the negative PDO phase ranged from 665.1 ± 55.2 mg C $m^{-2}$ $d^{-1}$ to 684.1 ± 32.4 mg C $m^{-2}$ $d^{-1}$ (difference: ~19 mg C $m^{-2}$ $d^{-1}$) while,

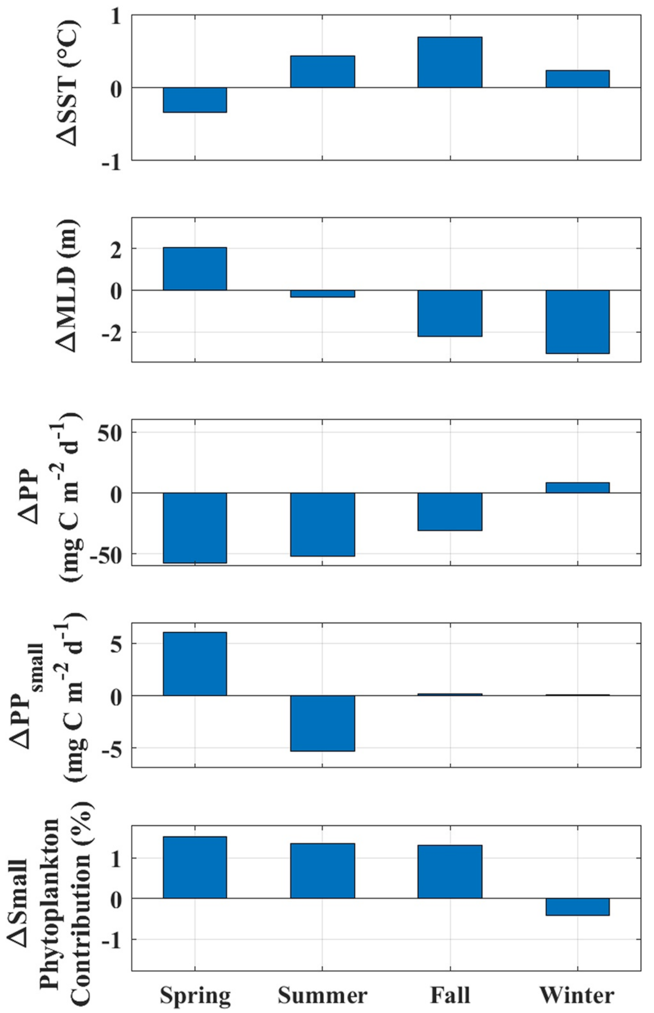


**Figure 5.** Seasonal distributions of differences according to the Pacific Decadal Oscillation (PDO) phase for the mean SST, MLD, PP, $PP_{small}$ and small phytoplankton contribution (a–e, respectively) when the average during the negative PDO phase is compared with the average during the positive PDO phase.

in the positive PDO phase, the mean PP ranged from 675.7 ± 34.8 mg C $m^{-2}$ $d^{-1}$ to 723 ± 33.7 mg C $m^{-2}$ $d^{-1}$ (difference: ~47 mg C $m^{-2}$ $d^{-1}$). The mean PP was generally lower during the negative PDO phase except during the winter season. On the other hand, mean $PP_{small}$ during the negative PDO phase was relatively higher than during the positive PDO phase except during the summer seasons. The mean $PP_{small}$ ranged from 159 ± 19.9 mg C $m^{-2}$ $d^{-1}$ to 161.2 ± 16.3 mg C $m^{-2}$ $d^{-1}$ during the negative PDO phase and from 155.2 ± 14.8 mg C $m^{-2}$ $d^{-1}$ to 164.4 ± 30.9 mg C $m^{-2}$ $d^{-1}$ during the positive PDO phase. Seasonal variation in the small phytoplankton contribution showed the opposite pattern to that of PP. Small phytoplankton contributions during the negative PDO phase were generally higher than those during the positive PDO phase. Small phytoplankton contribution ranged from 23.1 ± 2.6% to 23.7 ± 2.3% during the negative PDO phase and from 22.2 ± 2.9% to 23.6 ± 3.3% during the positive phase. Differences in the mean PP, mean $PP_{small}$ and mean small phytoplankton contribution also showed high seasonality (Figure 5). Declining trends in the mean PP during the negative PDO phase were relatively stronger in spring and summer than fall and winter (Figure 5c). Regarding the mean $PP_{small}$, it was generally higher during the negative PDO phase in summer season (Figure 5d). The average small phytoplankton contribution during the negative PDO phase was also generally higher during the negative PDO phase but relatively lower in winter (Figure 5e).

### 3.4. Principal Component Analysis

The results of PCA to find relationship between PDO and other variables are shown in Figure 11. The first three ordination axes (PC1, PC2, and PC3) of the PCA explained 79.8% of the variance. In the plane PC1-PC2, SST was negatively correlated with the PDO index and MLD (Figure 11a). In addition, negative relationships between PP and $PP_{small}$ and small phytoplankton contribution were found. On the other hand, PDO and PP showed strong positive correlation in plane PC1–PC3 (Figure 11b). $PP_{small}$ and small phytoplankton contribution was negatively related in both planes.

## 4. Discussion

### 4.1. Spatial Variability in Primary Production

In general, during negative (or positive) PDO phase, SST in the northwestern Pacific region is higher (or lower) than oppositive PDO phase (Mantua & Hare, 2002). The results from this study also showed that the SST in the East/Japan Sea during the negative PDO phase was higher than that during the positive PDO phase (Figures 3a and 4a).

The difference in the mean PP according to the PDO phase showed spatial variation in the study area, but the annual mean PP was generally lower in the East/Japan Sea during the negative PDO phase except coastal region located in the northern part of the East/Japan Sea (Figures 6a–6c). To compare the regional differences in the annual mean PP in response to the PDO, three sub-regions were defined as shown in Figure 7a. The smallest difference according to the PDO phase was observed in Area 1 (Figure 7b). Area 1, located in the southwestern East/Japan Sea, includes the Ulleung/Tsushima Basin, a well-known high productivity region in the East/Japan Sea. Several previous studies have suggested that the Ulleung/Tsushima Basin is a biological "hot spot" in the East/Japan Sea (Hyun et al., 2009; Joo et al., 2014; Kwak et al., 2013; J.-Y. Y. Lee et al., 2009; Yoo & Park, 2009). The characteristically high productivity in the Ulleung/Tsushima Basin is mainly induced by eddies (D. Kim et al., 2012; J. H. Lim et al., 2012). In the Ulleung/Tsushima Basin, eddy-induced upwelling can supply nutrients to the euphotic layer during the nutrient-depleted summer seasons (D. Kim et al., 2012). In addition, the high PP during early spring was observed by using the Geostationary Ocean Color Imager (GOCI), even before

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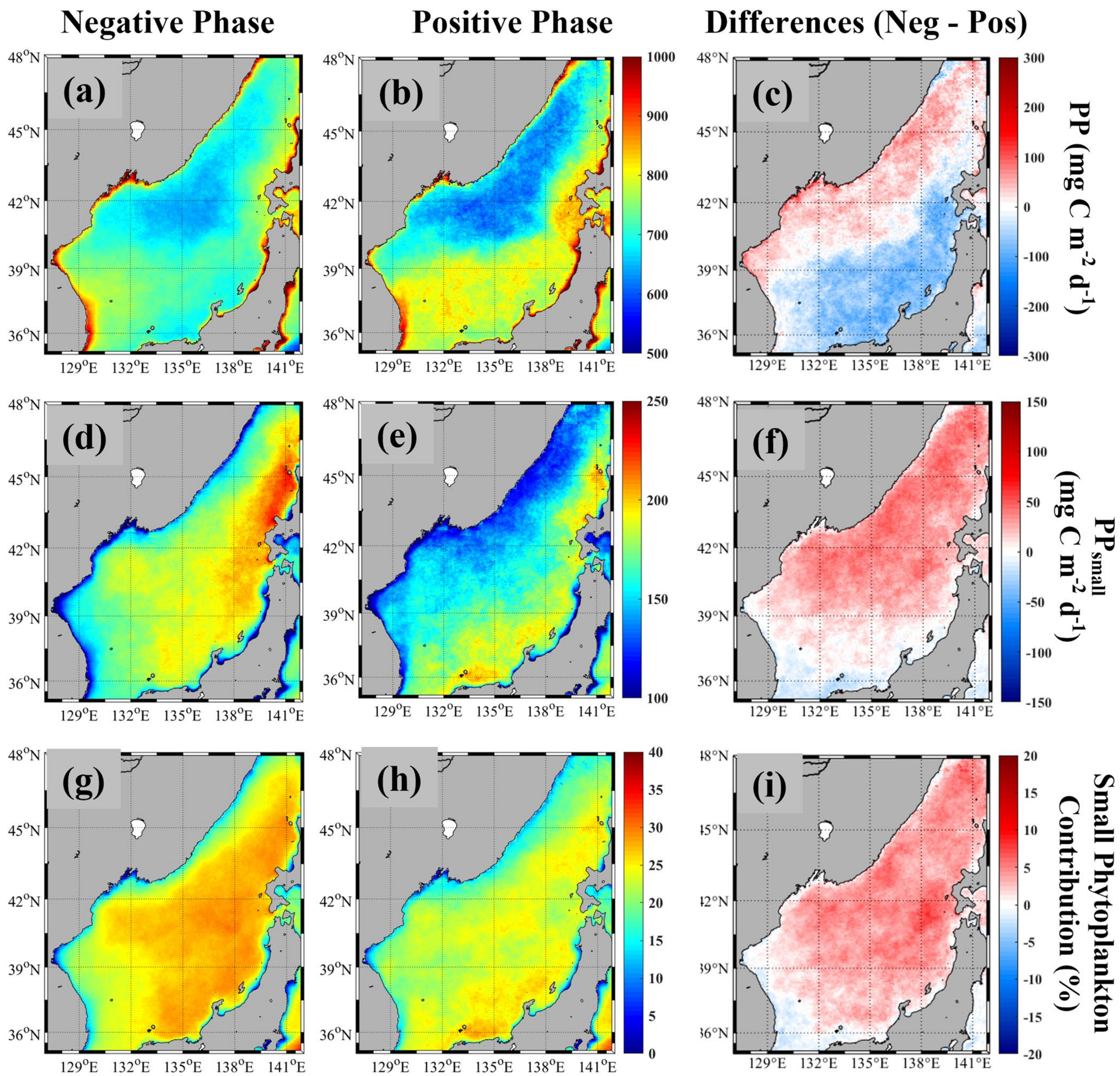


**Figure 6.** Spatial distribution of the mean PP (mg C m$^{-2}$ d$^{-1}$), mean $PP_{small}$ (mg C m$^{-2}$ d$^{-1}$) and small phytoplankton contribution (%) (a and b) Mean PP during the negative Pacific Decadal Oscillation (PDO) phase and the positive PDO phase, respectively. (c) Difference in the mean PP between the negative and positive PDO phases. (d and e) Mean $PP_{small}$ during the negative PDO phase and the positive PDO phase, respectively. (f) Difference in the mean $PP_{small}$ between the negative and positive PDO phases (g and h) Mean small phytoplankton contribution during the negative PDO phase and the positive PDO phase, respectively. (i) Difference in the mean small phytoplankton contribution between the negative and positive PDO phases.

the development of the stratification suitable for spring bloom (J. H. Lim et al., 2012). According to J. H. Lim et al. (2012), an upward water flux at the periphery of anticyclonic eddies can enhance primary productivity by allowing phytoplankton to remain within the euphotic layer before stratification fully develops. The differences in the annual PP due to the PDO were relatively small not only in the Ulleung/Tsushima Basin but also in several coastal areas (Figures 7a and 7b). The east coast of South Korea is well known for its frequent coastal upwelling, which contributes greatly to the PP in the East/Japan Sea (Hahm et al., 2019; T. S. Kim et al., 2014; Park & Kim, 2010). According to previous studies, changes in ocean temperature associated with the PDO occur not only in the surface layer but also extend to subsurface layer (Kumar & Wen, 2016; Wang et al., 2012). However,

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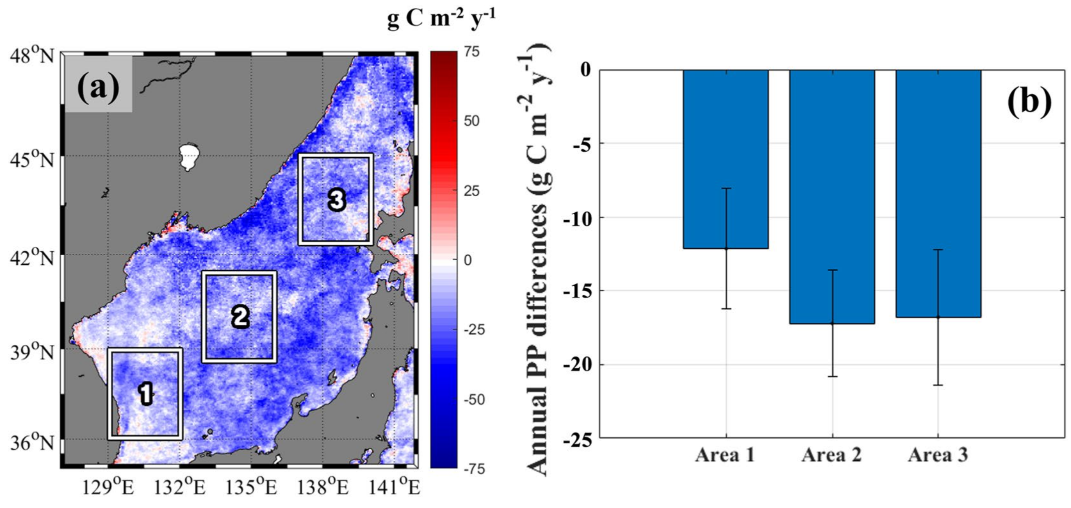


**Figure 7.** (a) Changes in the annual PP (g C $m^{-2}$ $y^{-1}$) during the negative Pacific Decadal Oscillation (PDO) phase when compared to the positive PDO phase. White boxes indicate the three sub-regions defined in this study. (b) Differences in the annual PP (g C $m^{-2}$ $y^{-1}$) according to the PDO phase in the three sub-regions.

although PDO-related ocean temperature changes occur in subsurface layers, the affected water depth is only up to 300 m in spring and even decreases to around 100 m in summer (Wang et al., 2012). Therefore, eddy-induced upwelling or wind-induced coastal upwelling still plays a role in supplying nutrients to the euphotic layer during summer, even as ocean temperature changes related to the PDO can intensify stratification, which tends to inhibit nutrient supply. In both the Ulleung/Tsushima Basin and coastal regions in South Korea, which showed a relatively minor change in the annual PP related to the PDO, upwelling contributes greatly to the annual PP, as mentioned above.

Consequently, ocean temperature changes related to the PDO would not significantly affect nutrient supply through upwelling. Accordingly, the difference in the annual PP according to the PDO phase would be relatively small in Area 1, where upwelling contributes greatly to the annual PP. However, changes in nutrient supply and the PP should be investigated, and a further detailed study is essential to clarify the mechanism suggested in this study.

### 4.2. Phytoplankton Community Response to PDO-Related Changes in Environmental Conditions

The higher SST during the negative PDO phase can alter the vertical structure of the water column, leading to a change in nutrient supply in the euphotic layer from below (Behrenfeld et al., 2006; McGowan et al., 2003; Roemmich & McGowan, 1995). A more stabilized water column due to the high temperature of the surface layer can intensify stratification and inhibit vertical mixing of the water column. In other words, the PP of phytoplankton can be inhibited due to the lower nutrient supply from the deeper layer during the negative PDO phase. The negative relationship between MLD and PDO index (Figures 4d and 11a) suggest that the stabilization of the ocean surface layer might be affected by PDO-related SST changes. In particular, shoaling of the MLD in relation to the PDO phase occurred mainly in winter (Figure 5b; *t*-test, $p < 0.05$). A shallower winter MLD during the negative PDO phase indicates that vertical mixing in winter might be weaker than that during the positive PDO phase. Generally, nutrient entrainment into the euphotic layer through vertical mixing in winter appears to be an important mechanism that can influence the intensity of the following spring bloom and the annual primary productivity of the following year (Freeland et al., 1997; Joo, Lee, Son, et al., 2018; S. H. Lee et al., 2014; Polovina et al., 1995). The anomaly in the mean PP was also relatively lower in the spring and summer during the negative PDO phase (Figure 5c). Consequently, PP of phytoplankton can be reduced due to the higher SST and the shallower MLD during the negative PDO phase.

In case of $PP_{small}$, although not statistically significant, an inverse relationship between the $PP_{small}$ and PDO index was found (Figures 9c, 9d, and 11). Generally, small-sized phytoplankton (0.7–2 μm) require less nutrients for PP and uptake ammonium ($NH_4$) preferentially (Agawin et al., 2000; Dortch, 1990; Glibert et al., 1982; S. H. Lee

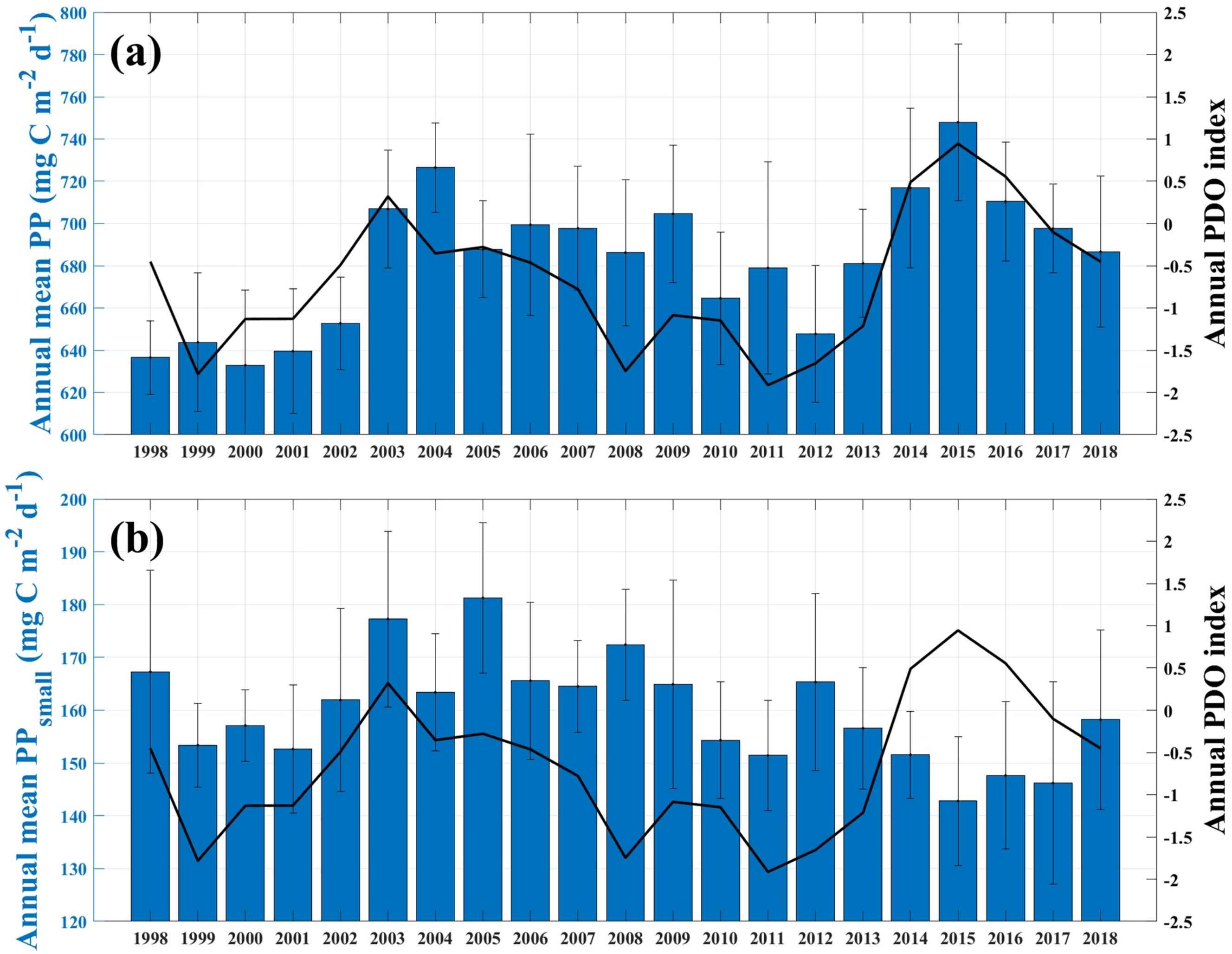


**Figure 8.** Time-series of (a) the annual mean PP (mg C m$^{-2}$ d$^{-1}$) and (b) the annual mean $PP_{small}$ (mg C m$^{-2}$ d$^{-1}$) from 1998 to 2018. Error bars indicate the standard deviations for annual mean PP and $PP_{small}$. Black lines indicate the annual Pacific Decadal Oscillation index.

& Whitledge, 2005). The PP of phytoplankton based on ammonium, which represents regenerated production, serves to maintain their population at a constant level rather than population growth (Dugdale & Goering, 1967; S. H. Lee & Whitledge, 2005). The main source of ammonium in the water column is bacterial degradation or excretion by heterotrophic grazers (Clark et al., 2008; Eppley & Peterson, 1979). Thus, the PP of small phytoplankton, or ammonium-based regenerated production, will not decrease, even if the nutrient supply from deeper waters is reduced.

The small phytoplankton contribution was higher in the negative PDO phase than in the positive PDO phase (Figures 10 and 11a). The higher small phytoplankton contribution during the negative PDO phase might be related to temperature changes. Morán et al. (2010) reported that the contribution of the picophytoplankton biomass increases with temperature. Moreover, PDO-related environmental changes can alter phytoplankton community structures in the western North Pacific Ocean (Chiba et al., 2012). Nutrient entrainment from deep water is among one of the most important sources of nitrates ($NO_3$), the primary stimulant of new production (Dugdale & Goering, 1967; Eppley & Peterson, 1979). Generally, large-sized phytoplankton (>2 μm) dominate in a nutrient-rich environment, and they uptake nitrates preferentially for carbon fixation (Agawin et al., 2000; Dortch, 1990; Glibert et al., 1982; S. H. Lee & Whitledge, 2005). In contrast to large-sized phytoplankton, small-sized phytoplankton are well-known to predominate in nitrate-poor oligotrophic waters since they have an advantage for utilizing nutrients in nutrient-poor regime (Agawin et al., 2000). Therefore, decreased upward nutrient flux during the negative PDO phase will provide a favorable environmental condition for small-sized

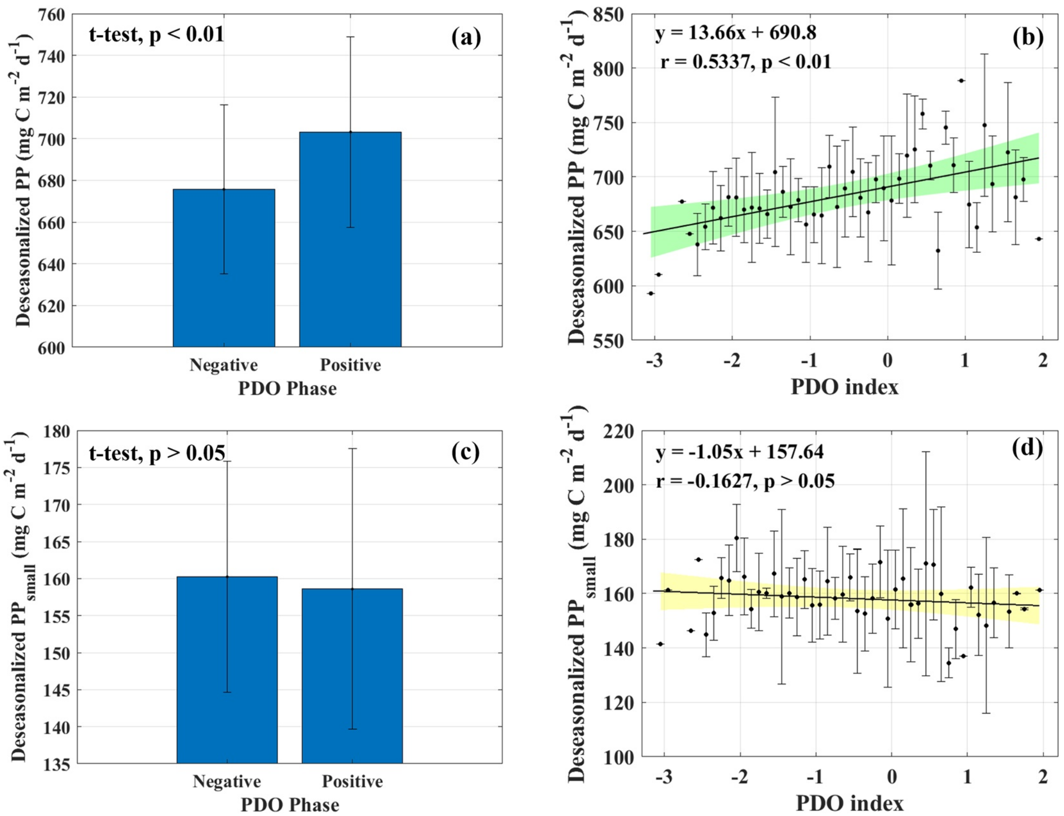


**Figure 9.** (a) Difference in the mean PP (mg C m$^{-2}$ d$^{-1}$) according to the Pacific Decadal Oscillation (PDO) phase. (b) Relationship between the PDO index and PP (mg C m$^{-2}$ d$^{-1}$). (c) Difference in the mean $PP_{small}$ (mg C m$^{-2}$ d$^{-1}$) according to the PDO phase. (d) Relationship between the PDO index and the $PP_{small}$ (mg C m$^{-2}$ d$^{-1}$). The shaded area represents the 95% confidence intervals for the regression line.

phytoplankton, allowing their contribution to the total biomass of phytoplankton community to increase. As a result, a higher small phytoplankton contribution indicates the relatively lower new production (Joo et al., 2017; Siegel et al., 2014). New production based on nitrates is generally considered as export production, which can be provided as an energy source for higher trophic levels (Dugdale & Goering, 1967; Siegel et al., 2014). Such changes in phytoplankton community structures can alter food-web structures, even up to the level of large pelagic fish species. Since predators generally tend to prefer prey of a certain size (Finkel, 2007; Hansen et al., 1994;

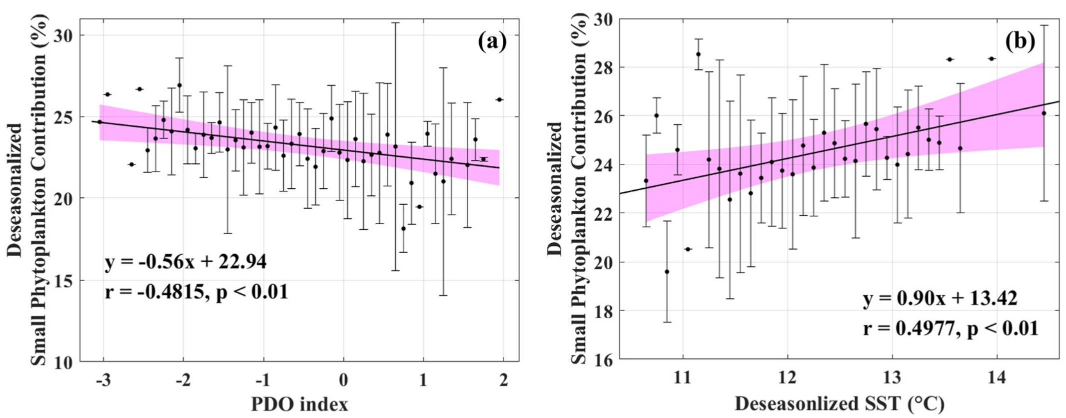


**Figure 10.** (a) Relationship between the Pacific Decadal Oscillation index and the small phytoplankton contribution (%). (b) Relationship between the SST (°C) and the small phytoplankton contribution (%). The shaded area represents the 95% confidence intervals for the regression line.

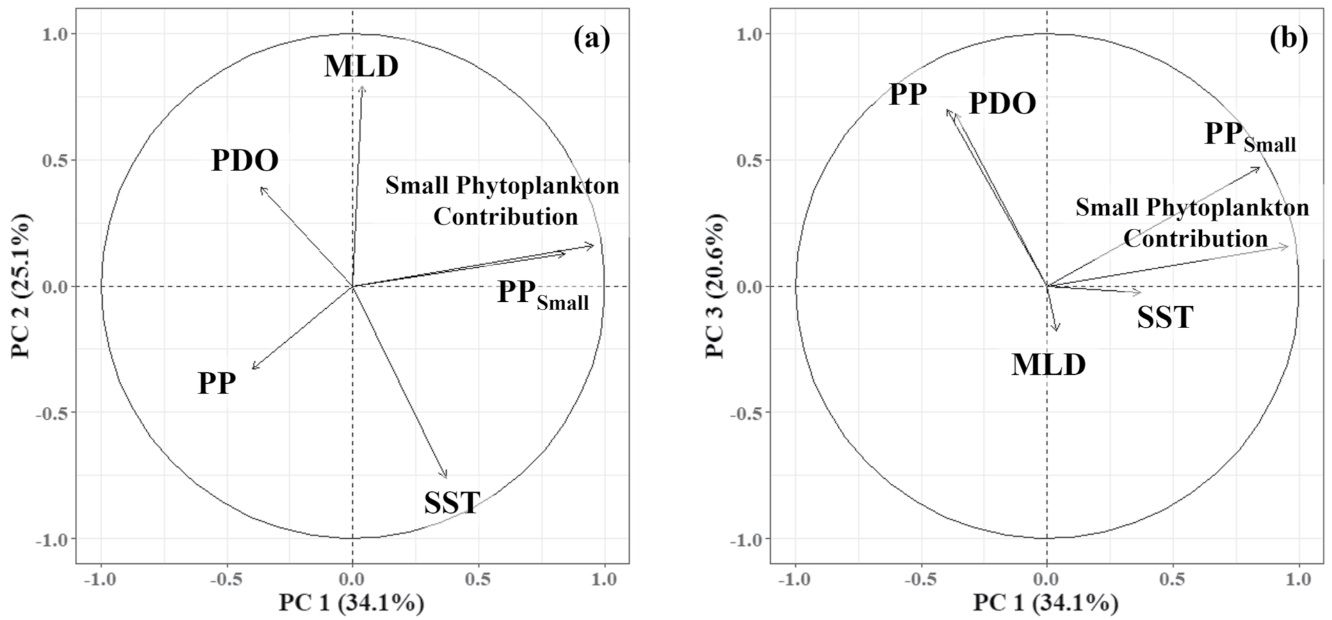


**Figure 11.** Principal components analysis (PCA) ordination plots of axes 1, 2, and 3 showing relationships between Pacific Decadal Oscillation and other variables on (a) PC 1 versus PC 2 and (b) PC 1 versus PC 3.

Irigoien et al., 2003; Parsons et al., 1967), shifts in the phytoplankton community size structure may cause changes in the species composition of herbivores and ultimately affect fishery resources. Several previous studies showed that the total PP of phytoplankton subsequently decreases when the small phytoplankton contribution increases (Jang et al., 2018; Joo et al., 2017; S. H. Lee et al., 2017; Y. J. Lim et al., 2019). It is well known that primary producers can affect not only herbivores but also carnivores through a bottom-up process (Hunter & Price, 1992). Several previous studies have shown that the chlorophyll-a concentration and PP of phytoplankton have a positive relationship with fishery yield (Chassot et al., 2007; Friedland et al., 2012). D. Lee et al. (2017) also reported that the spatial distribution of common Minke Whale (*Balaenoptera acutorostrata*) is positively related to the surface chlorophyll-a concentration in the East/Japan Sea. In addition, it has been reported in previous studies that the PP of phytoplankton can play an important role in the formation of the fishing ground for major fish species in the East/Japan Sea (D. Lee et al., 2018, 2019). Thus, the PP and biomass of the phytoplankton community can influence carnivorous fish populations, even though phytoplankton is not a direct dietary component for pelagic fish species. Based on the results of this study and the strong positive relationship between phytoplankton and fishery landings described in other research (Chassot et al., 2007; Friedland et al., 2012), a conceptual model for the link between PP and fishery according to the PDO phase in the East/Japan Sea was derived (Figure 12). It can be expected that the lower PP during the negative PDO phase will lead to a decrease in fishery production and vice versa during the positive PDO phase.

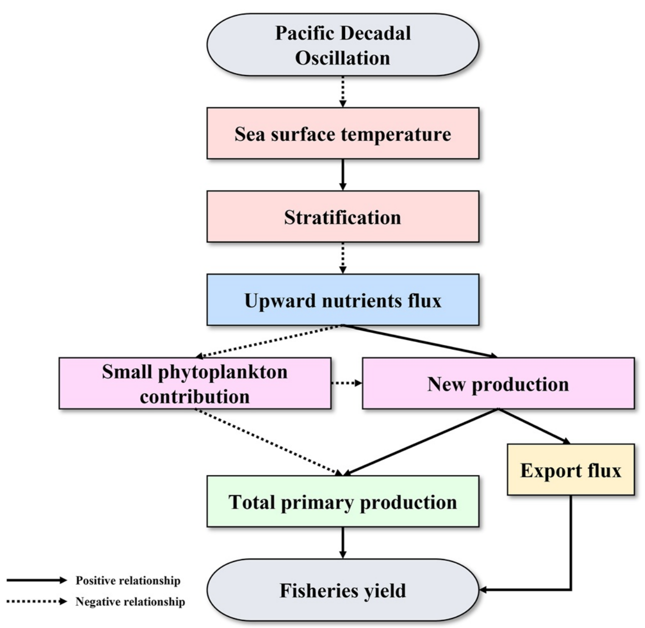


**Figure 12.** Conceptual model describing how environmental conditions, the phytoplankton community and fishery yield will be changed according to the Pacific Decadal Oscillation phase.

Consequently, the importance of small-sized phytoplankton could increase in the East/Japan Sea due to the changes in environmental conditions in relation to the PDO phase. Increases in the small phytoplankton contribution will lead not only to a lower total PP but also to reduced new production of the phytoplankton community. Furthermore, such alterations may affect energy transfer to the food web, leading to changes in the higher trophic levels. However, increase in SST itself also can influence phytoplankton dynamics. It is well known that growth rate and biochemical process such as cellular resource allocation and metabolism of phytoplankton are directly affected by water temperature (Eppley, 1972; Toseland et al., 2013). The growth rate of phytoplankton and the grazing pressure of zooplankton also have a complex interaction and are largely impacted by temperature (Chen et al., 2012; Schulhof et al., 2019). Therefore, further studies would be needed to understand the relationship between temperature changes and phytoplankton community dynamics more clearly. Additional research on the responses of the phytoplankton community dynamics and subsequent marine food-web to changes in environmental conditions through an integrated study encompassing physical and biogeochemical approaches will ultimately allow us to understand how marine ecosystems will respond to ongoing climate changes such as global warming and, furthermore, to establish strategies for fishery resource management.

## 5. Summary and Concluding Remarks

In this study, the relationship between the PDO and PP in the East/Japan Sea was investigated using various satellite data sets from 1998 to 2018. The annual PP showed high variability according to the PDO phase in the East/Japan Sea. The annual PP was significantly lower during the negative PDO phase. PDO-related changes in the annual PP in the East/Japan Sea were closely related to the size structure of the phytoplankton community. The small phytoplankton contribution to the annual PP increased during the negative PDO phase, since the higher SST can alter the vertical structure of the water column and inhibit nutrient supply from the deep ocean. Increases in the small phytoplankton contribution resulted in a lower total annual PP. A lowered annual PP can reduce the energy supply to the entire food web and even affect fishery resources. Moreover, PP in the euphotic layer is closely related to the biological pump efficiency (Ducklow et al., 2001). Consequently, the PP changes due to the PDO could affect not only the euphotic layer, but also pelagic ocean and even the benthic environments.

Results from this study suggest that the global-scale climate force can regulate not only the PP, but also community structure of phytoplankton through physical and biogeochemical mechanisms such as upper layer stratification and nutrient supply restriction. Since the PDO is a global scale climate variation, it can be expected that the PDO-induced changes in the marine ecosystem and biogeochemical cycles could occur in other regions although this study was conducted in the East/Japan Sea. Indeed, there are several studies on the relationship between the PDO and the variation in biogeochemical conditions (Duteil et al., 2018; Kuwae et al., 2006; Patterson et al., 2013). Since the SST anomaly according to the PDO varies depending on region, the relationship between the PDO and PP in other regions could be different from the results of this study. The lowered PP and change in the phytoplankton size structure observed in this study can be considered an oscillatory variation in the East/Japan Sea caused by the phase change in the PDO. However, the IPCC's SSP5-8.5 scenario (fossil-fuel based development with no additional climate policy) suggests that the global average surface temperature will increase by 5°C by 2100 (IPCC, 2022). The change in the SST suggested in the SSP5-8.5 scenario is more than double the difference in the SST according to the PDO phase observed in this study. This finding suggests that permanent changes in the PP and further influences on higher trophic levels can occur not only in the East/Japan Sea but also in the global ocean due to the global warming.

## Data Availability Statement

The remote sensing data obtained from SeaWiFS and MODIS-Aqua used in the study are available at NASA OceanColor Web (https://oceandata.sci.gsfc.nasa.gov/). AVHRR SST data are available at NOAA NCEI website (https://www.ncei.noaa.gov/products/avhrr-pathfinder-sst). MLD data from ECCO estimates are available at NASA PO.DAAC website (https://podaac.jpl.nasa.gov/dataset/ECCO_L4_MIXED_LAYER_DEPTH_05DEG_DAILY_V4R4). Data for this research are available at the Havard Dataverse (https://doi.org/10.7910/DVN/MDWZUZ) with a Creative Commons CC0 1.0 Universal Public Domain Dedication.

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## Erratum

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