Seasonal and inter-annual variability of net primary production in the NW Iberian margin (1998-2016) in relation to wind stress and sea surface temperature

P.P. Beca-Carretero^{1, 2}, J. Otero¹, P. E. Land³, S. Groom³, X.A. Álvarez-Salgado^{1,*}

¹CSIC Instituto de Investigaciones Marinas, Eduardo Cabello 6, E36208 Vigo, Spain

²Martin Ryan Institute, National University of Ireland, Galway, Ireland

³Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK

*Corresponding author:

E-mail: xsalgado@iim.csic.es; Phone: +34 986231930; Fax: +34 986292762

Abstract

Seasonal and inter-annual variability of satellite-derived net primary production (NPP) in the NW Iberian margin and its relationship with the offshore Ekman transport ($-Q_x$) and a variety of sea surface temperature (SST) indices have been examined over the period 1998-2016. Seasonality explained about 55% of NPP variability over the shelf and the adjacent ocean. Maximum NPP rates occurred by May in the adjacent ocean, and were delayed until July over the shelf. The excess production (ΔNPP) over the shelf compared to the ocean domain represented $0.45 \pm 0.02 \text{ g C m}^{-2} \text{ d}^{-1}$ or $37 \pm 2\%$ of the total NPP and peaked in August, in between the maximum $-Q_x$ and the maximum SST difference between the shelf and the adjacent ocean (ΔSST). During the upwelling season, the inter-annual variability of NPP in the adjacent ocean correlated positively with the spring stratification (SST_{str}) and the average $-Q_x$ over the upwelling season and ΔNPP correlated inversely with ΔSST . Conversely, during the downwelling season, ΔNPP correlated with the average stratification (SST_{down}) over the downwelling season. The rates of change of NPP with the climate-related variables ($-Q_x$, ΔSST , SST_{str} , SST_{down}), obtained from these regressions, may be used to test the sensitivity of the NW Iberian upwelling productivity to climate change.

Keyword: net primary production, new production, satellite imagery, coastal upwelling, NW Spain

1. Introduction

Eastern boundary upwelling ecosystems (EBUEs) represent less than 1% of the total ocean volume, however, more than 10% of the marine new production occurs in these systems, and they support roughly 25% of the total worldwide fisheries (Fréon et al., 2009; Messié and Chavez, 2015). Furthermore, due to the high partial CO₂ pressure (pCO₂) of upwelled waters, these areas usually operate as CO₂ sources to the atmosphere (Borges et al., 2005; Chen and Borges, 2009). The Canary Current EBUE is an exception to this rule because the photosynthetic activity of phytoplankton is able to reduce seawater pCO₂ below the saturation level, thus functioning as a carbon sink (Laruelle et al., 2010). Particularly, in the NW Iberian margin, relatively low pCO₂ levels in the source Eastern North Atlantic Central Water (ENACW), moderate coastal wind intensities, and prolonged residence times of upwelled water over the shelf compared with the other major EBUEs are the reasons behind this particular behaviour (Álvarez-Salgado et al., 2010).

The NW Iberian margin is markedly sensitive to climate change because it is located at the boundary between the subtropical and subpolar regimes of the North Atlantic, under the influence of the North Atlantic and Azores currents (Álvarez-Salgado et al., 2010; Pérez et al., 2010). At these latitudes coastal winds are seasonal: in spring and summer the prevailing northerly winds favour coastal upwelling and associated high primary production, while in autumn and winter southerly winds are dominant, favouring coastal downwelling concomitant with low primary production (Aristegui et al., 2009). Any significant change in these patterns may also affect both the sustainable exploitation of its abundant marine living resources and their economic value (Guisande et al., 2001; Otero et al., 2008; Álvarez-Salgado et al., 2008; Pérez et al., 2010; Bode et al., 2015) as well as the role of this area as a sink for anthropogenic CO₂ (Borges and Frankignoulle, 2002; Gago et al., 2003; Álvarez-Salgado et al., 2010).

The response of marine primary producers in terms of biomass and productivity is mainly associated with changes in irradiance, temperature and nutrient availability in the surface layer (Behrenfeld and Boss, 2018). At temperate latitudes, nutrient supply is the most limiting factor of phytoplankton productivity. Its availability is controlled by physical processes, mainly vertical advection and turbulent mixing, which respond to temporary changes in climate conditions (Deutsch and Weber, 2012). In EBUEs, nutrient inputs and, hence, primary production are particularly dependent on the frequency and intensity of upwelling-favourable winds (Carr, 2002; Demarq, 2009; Chavez et al., 2011; Messié and Chavez, 2015). In the NW Iberian margin, phytoplankton net primary production (NPP) maxima usually occur during two periods: 1) in early spring, associated with the onset of seasonal stratification and limited by the nutrient concentrations reached in the water column during previous winter convection (Nogueira et al., 1997; Bode et al., 2011); and 2) through the summer, in response to the intermittent upwelling-favourable events that occur every 5-15 days (Pérez et al., 2000; Cermeño et al., 2006).

Bakun (1990) hypothesised that global warming is strengthening the atmospheric temperature difference between the ocean and the adjacent land mass. This would provoke increased atmospheric pressure gradients in the coastal zone and, therefore, favour the development of more intense upwelling-favourable alongshore winds. Current empirical evidences of this hypothesis are rather weak (Bakun et al., 2015) and forecasting of future climate scenarios indicate that the likely cause of upwelling intensification will be more related to changes in the position of the oceanic high-pressure systems (García-Reyes et al., 2015). Particularly, summer time winds at higher latitudes are projected to intensify, while at lower latitudes are projected to weaken within the boundaries of the coastal upwelling systems (Rykaczewski et al., 2015). For the case of the NW Iberian margin, some studies have suggested a decrease of northerly winds intensity and persistence over the last 60 years (e.g.

Lemos and Pires, 2004; Álvarez-Salgado et al., 2008; Pérez et al., 2010) while others concluded that the trend was not clear (e.g. Barton et al., 2013) or even reversed (Demarcq, 2009; Leitaó et al., 2018). Climate projections for the area predict a significant increase of coastal upwelling (Casabella et al., 2014; Álvarez et al., 2016) related to a strengthening of the land-ocean temperature gradient and an intensification of the Azores High, which will drift northeastward during the 21st century (Sousa et al., 2017) in agreement with the global study of Rykaczewski et al. (2015).

Despite the uncertainty of future climate estimations, quantifying the response of NPP to changing primary climate variables, such as sea surface temperature or coastal winds, would help to assess the sensitivity of EBUEs to climate change and their associated socioeconomic consequences (Pauly and Christensen, 1995; Bakun and Weeks, 2004; Barth et al., 2007; Bakun et al., 2015; García-Reyes et al., 2015). In this regard, artisanal fisheries and extensive mussel aquaculture are climate-dependent key components of the economy of the NW Iberian margin (Alonso-Fernández et al., 2019; Labarta and Reiriz, 2019). With these considerations in mind, here we report the seasonal and inter-annual variability of the NPP of the NW Iberian margin over the period 1998–2016 in relation to two climate-related indices: the intensity and direction of coastal winds and sea surface temperature (SST), including the shelf-ocean SST difference (Δ SST). Parameterization of the response of NPP as a function of these indices is demonstrated to be a valuable tool to explore the sensitivity of the productivity of this area to climate change. Satellite-derived NPP and SST and coastal winds calculated from atmospheric pressure charts were assembled to achieve these goals.

2. Methods

2.1. Data set

This study was conducted in the NW Iberian margin from 42° to 43°N and 8° to 10° W, at the northern boundary of the Canary Current EBUE. The study area was divided into three separate zones: continental shelf (water depths < 200 m), slope (water depths between 200 and 2000 m) and adjacent ocean (water depths > 2000 m; Fig. 1). Seamounts (isolated areas of slope surrounded by ocean) were reassigned to ocean. Sea surface temperatures (SST) in the study area were estimated from Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) reanalysis data up to 2007 (Roberts-Jones et al., 2012) and near-real-time OSTIA data from 2008 (Donlon et al., 2012), both downloaded from <http://marine.copernicus.eu/services-portfolio/access-to-products/>. Chlorophyll *a* (Chl) concentrations and photosynthetically available radiation (PAR) were estimated from Sea-Viewing Wide Field-of-View (SeaWiFS) and Moderate Resolution Imaging Spectroradiometer (MODIS) satellite sensor records, downloaded from <https://oceancolor.gsfc.nasa.gov/cgi/browse.pl?sen=am>. The time series of SST, Chl and PAR consisted of daily mean values for the three zones over the period 1998–2016. On cloudy days (days with less than 10 valid measurements in a given region, which corresponds to 0.3% of the shelf, 0.4% of the slope and 0.5% of the ocean zone) Chl and PAR values were neither reported nor interpolated. Winds at 43°N 11°W (Fig. 1) were calculated by the Spanish Institute of Oceanography (Instituto Español de Oceanografía, IEO) from sea level pressure fields over the ocean supplied at 6 hours intervals (0, 6, 12, and 18 hours) by the US Navy Operational Global Atmospheric Prediction System (NOGAPS) model maintained by FNMOC (Fleet Numerical Meteorology and Oceanography Center) (<http://www.indicedeafloramiento.ieo.es/afloramiento.html>; González-Nuevo et al., 2014). These winds were used to calculate the offshore Ekman transport ($-Q_x$) perpendicular to the

coast, which is a rough estimation of the volume of upwelled water per unit of time and unit of coast length (Lavín et al., 1991).

2.2. Satellite-derived net primary production estimates

Satellite estimates of Chl were used to compute net primary production rates (NPP) using the model of Morel (1991) with the modifications described in Smyth et al (2005) and Groom et al. (2005). The NPP model was forced with daily estimates of Chl, SST and PAR, along with calculated day length and the assumption of typical oceanic levels of coloured dissolved organic material. Modelled NPP values were validated in the study area with measurements of NPP obtained from 24 h in situ incubations of samples labelled with $H^{14}CO_3^-$ (see Joint et al., 2002 for details). Model uncertainty, estimated from the root-mean square error (RMSE) between the measured and modelled NPP values ranges from 27% to 42%. The numerical expression for the computation of PP with Morel's (1991; equation 27) model is:

$$PP = 12 \cdot a_{max}^* \cdot \phi_{\mu,max} \cdot \int_0^D \int_0^Z \int_{400}^{700} C(z) \cdot PUR(z, t, \lambda) \cdot F(I_0(z, t)) \cdot d\lambda \cdot dz \cdot dt \quad (2)$$

where a_{max}^* (in $m^{-1} [mg \text{ Chl } m^{-3}]^{-1}$) is the maximum value of the Chl specific phytoplankton absorption spectrum; $\phi_{\mu,max}$ (in mole carbon $[mol \text{ photons absorbed}]^{-1}$) is the quantum yield for growth; $C(z)$ is the Chl concentration (in $mg \text{ } m^{-3}$) at depth z ; $PUR(z, t, \lambda)$ is the photosynthetically usable radiation (spectral photosynthetically active radiation weighted by the spectral phytoplankton absorption, in $E \text{ } m^{-2} \text{ } d^{-1}$) at depth z , time t and wavelength λ ; F is a function that relates carbon production I_0 to total usable light at depth z and time t expressed as a dimensionless parameter equal to $PUR/irradiance$ scaling factor (KPUR). This parameter was set at $80 \mu E \text{ } m^{-2} \text{ } s^{-1}$ at $20^\circ C$ and the variation with temperature is modelled with the following equation:

$$KPUR(T) = KPUR(20) \times 1.065^{(T-20)} \quad (3)$$

To obtain the daily average PP, the functions of $C(z)$, $PUR(z, t, \lambda)$ and $F(I_0(z, t))$, modelled with the optical water model Hydrolight, are integrated from sunrise until sunset (where D is the number of hours of daylight), between the surface and the base of the euphotic region (fixed at the depth at which downwelling PAR is 0.1% of its surface value) and between 400 and 700 nm wavelength, i.e. in the range of wavelengths useful for photosynthesis. $PUR(0, t, \lambda)$ is estimated from daily integrated PAR by assuming a diurnal variation of PAR and multiplying by chlorophyll-specific phytoplankton absorption divided by its maximum spectral value. Daily estimates of SeaWiFS-derived Chl and PAR were available from October 1997 to November 2010 and MODIS-derived Chl and PAR from July 2002 to December 2016. We used MODIS data where available, SeaWiFS data otherwise. A slight but consistent discrepancy was noticed between the maximum SeaWiFS and MODIS PAR in the overlap period. To remove this, we regressed SeaWiFS PAR against MODIS PAR using all available overlaps in the region and used this regression to make SeaWiFS PAR consistent with MODIS PAR. SeaWiFS Chl was found to be statistically indistinguishable (two-tailed Student's t -test with $p < 0.05$) from MODIS Chl. OSTIA reanalysis SST was available up to the end of 2007, and near real time SST from the start of 2007. Reanalysis SST was used where available, and the two were found to be statistically indistinguishable (two-tailed Student's t -test with $p < 0.05$) during 2007.

As the PP model was parameterized with 24 h incubations, the primary production values obtained correspond with net primary production (NPP), i.e. the gross phytoplankton production minus the microbial (bacteria, phytoplankton and microzooplankton) respiration and phytoplankton exudation (Joint et al., 2002).

2.3. Statistical analysis of the time series

For each year (1998 to 2016, or all data to obtain a climatology), position or zone (43°N 11°W for -Qx; shelf, slope, offshore and adjacent ocean for SST, PAR, Chl and NPP) and variable (-Qx, SST, PAR, Chl and NPP) the coefficients that define the first and second harmonic of their respective seasonal cycles (SC) were calculated by fitting the following harmonic equation to the data:

$$SC = A_0 + A_1 \cdot \sin\left(\frac{2\pi}{365} \cdot t + \varphi_1\right) + A_2 \cdot \sin\left(\frac{4\pi}{365} \cdot t + \varphi_2\right) \quad (4)$$

where A_0 is the annual average of the variable, A_1 and A_2 are the amplitudes of the first and second harmonic, φ_1 and φ_2 are their respective phase shifts, and t is the day of year (DOY), 1 to 365 or 366. The standard error of the estimation of each coefficient, and the goodness-of-fit, i.e. the Pearson's R, between response variable and predicted values were reported to objectively assess the proper functioning of eq. 4. With this procedure, we reduced the maximum of 365 (or 366) values per year to just 5 coefficients (A_0 , A_1 , A_2 , φ_1 and φ_2). A_0 , A_1 and A_2 were expressed in the same units as the fitted variables; and φ_1 and φ_2 were obtained in radians but converted into days of the year when the seasonal maxima of the first and second harmonics occur to better appreciate the phase shifts.

Depending on the direction of coastal winds, -Qx takes positive or negative values. A value of -Qx > 0 denotes upwelling and -Qx < 0 downwelling. A climatological fit of eq. 4 to -Qx shows a clear distinction between upwelling from mid-March to early October and downwelling for the rest of the year (Fig. 2A). Hence, the upwelling- and downwelling-favourable seasons are defined by their climatological start and end dates, and these are used to calculate seasonal average values of SST, Chl and NPP, both climatologically and in each year.

The inter-annual variability of the coefficients derived from the time series of $-Q_x$, SST, Chl and NPP (A_0 , A_1 , A_2 , ϕ_1 and ϕ_2) were analysed on the basis of their correlation with the year (1998 to 2016) using ordinary least squares (OLS) regression. Regression equations between the coefficients of the time series of the explanatory ($-Q_x$ and SST) and the response (Chl and NPP) variables were obtained using the standardized (or reduced) major-axis method (SMA).

All data treatments and analyses were performed with the software R (version 3.5.0, R Core Team, 2018). Harmonic models were specifically fitted using Levenberg-Marquardt algorithm implemented in the package ‘minpack.lm 1.2-1’ (Elzohv et al., 2016), and SMA regressions were fitted using the package ‘smatr 3.4-8’ (Warton et al., 2012). Results were considered significant if $p < 0.05$.

3. Results

3.1. Average 1998-2016 annual cycles of $-Q_x$, SST, PAR, Chl and NPP

Harmonic eq. (4) applied to the whole daily time series of $-Q_x$ from 1998 to 2016 explained 6% of the $-Q_x$ variability (Table 1, Fig. 2A). Despite R being relatively low, the coefficients of the first and second harmonics of eq. (4) were highly significant ($p < 0.0001$). The average value ($\pm$ SE) of the time series (A_0), $25.7 \pm 14.1 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$, is slightly positive over the study period. The amplitude of the first harmonic ($409.1 \pm 19.9 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$) was more than 6-fold greater than that of the second harmonic ($66.7 \pm 19.9 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$), indicating that the long-term (1998-2016) seasonal cycle is well described by division of the year into an upwelling- and a downwelling-favourable season (Fig. 2A). The upwelling-favourable season ($-Q_x > 0$) was, therefore, defined as extending from mid March (DOY 77) to early October (DOY 278), i.e. 202 days, giving a substantially shorter downwelling-favourable season of 163 days (Fig. 2A). The average seasonal maximum of $414 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$

was reached by mid June (DOY 199) and the seasonal minimum of $-433 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ by mid December (DOY 352).

The average 1998-2016 annual SST cycle as obtained by fitting eq. (4) to the whole daily SST time series accounted for 81% and 90% of the total SST variability over the shelf and the adjacent ocean, respectively (Table 1, Fig. 2B). A_0 over the shelf ($15.27 \pm 0.01 \text{ }^\circ\text{C}$) was significantly lower ($p < 0.001$) than in the adjacent ocean ($15.90 \pm 0.01 \text{ }^\circ\text{C}$). The amplitude of the first harmonic was 1-2 orders of magnitude larger than that of the second harmonic. Average SST reached a minimum of $12.95 \text{ }^\circ\text{C}$ by the end of February (DOY 53) over the shelf and $13.28 \text{ }^\circ\text{C}$ (DOY 60) in the adjacent ocean. Conversely, the average value reached a maximum of $17.54 \text{ }^\circ\text{C}$ over the period 1998-2016 by late August (DOY 234) over the shelf, and $18.83 \text{ }^\circ\text{C}$ on DOY 239 in the adjacent ocean. Fig. 2B also shows the average 1998–2016 seasonal cycle of the difference between the SST over the shelf and the adjacent ocean (ΔSST), which accounted for 55% of the total variability of the daily time series (Table 1). On average, the shelf was $0.63 \pm 0.004 \text{ }^\circ\text{C}$ colder than the adjacent ocean. This difference reached a minimum of $-0.08 \text{ }^\circ\text{C}$ in late April (DOY 117) and increased during the upwelling season, reaching a maximum of $-1.31 \text{ }^\circ\text{C}$ by early September (DOY 248).

The harmonic analysis of the daily time series of PAR resulted in a climatological seasonal cycle accounting for 76% of the total variability observed over the shelf and 77% in the adjacent ocean (Table 1, Fig. 2C). The seasonal cycle was roughly the same on both areas reaching a maximum of 55.3 and $55.8 \text{ E m}^{-2} \text{ d}^{-1}$ by the end of June (DOY 180 and 181, respectively). The amplitude of the first harmonic was more than 20-fold larger than that of the second harmonic.

The harmonic analysis of the daily time series of Chl resulted in the seasonal cycle explaining just 3% of the total variability observed over the shelf and 21% in the adjacent ocean (Table 1, Fig. 2D). However, in both cases, the coefficients of the first and second

harmonic of eq. (4) were highly significant ($p < 0.0001$). A_0 over the shelf ($1.03 \pm 0.01 \text{ mg m}^{-3}$) was more than twice than in the adjacent ocean ($0.42 \pm 0.004 \text{ mg m}^{-3}$). Interestingly, while the amplitude of the first harmonic was larger (about 1.8-fold) than that of the second harmonic in the adjacent ocean, this pattern reverses over the shelf, where the second harmonic is 1.4-fold larger than the first harmonic. The annual cycle of Chl showed two seasonal maxima, occurring in late winter-early spring and in late summer (Fig. 2D). While over the shelf the late summer peak was slightly higher (1.22 mg m^{-3}) than the early spring peak (1.11 mg m^{-3}), in the adjacent ocean the early spring maximum (0.67 mg m^{-3}) was considerably higher than the late summer peak (0.35 mg m^{-3}). The Chl maxima over the shelf took place on DOY 80 (mid March) and DOY 249 (early September), whereas in the adjacent ocean both maxima occurred somewhat later, on DOY 91 (early April) and DOY 278 (early October).

The harmonic analysis of the daily time series of NPP indicates that the seasonal cycle explained 56% of the total variability observed over the shelf and 55% in the adjacent ocean (Table 1, Fig. 2E). The excess production over the shelf as compared with the adjacent ocean (ΔNPP) also exhibited a seasonal cycle that explained 33% of the total variability of the daily time series (Table 1). The shelf showed the highest NPP rates throughout the seasonal cycle, with an A_0 of $0.94 \pm 0.004 \text{ g C m}^{-2} \text{ d}^{-1}$ over the period 1998–2016. Conversely, the lowest values corresponded to the adjacent ocean, with an A_0 of $0.59 \pm 0.003 \text{ g C m}^{-2} \text{ d}^{-1}$ which was significantly lower than over the shelf ($p < 0.001$). In both sites, the amplitude of the first harmonic was > 3.5 -fold greater than that of the second harmonic for NPP and ΔNPP . The average NPP rate reached a maximum of $1.37 \text{ g C m}^{-2} \text{ d}^{-1}$ over the shelf by late July (DOY 211), and of $0.83 \text{ g C m}^{-2} \text{ d}^{-1}$ in the adjacent ocean by mid-May (DOY 131) (Fig. 2E). The NPP excess over the shelf (ΔNPP) was $0.45 \pm 0.02 \text{ g C m}^{-2} \text{ d}^{-1}$ on average during the 1998–2016 upwelling season, which represents $37 \pm 2 \%$ of the average shelf NPP, increasing from

22% in late March (DOY 90) to 48% in late August (DOY 235; Fig. 2E). Δ NPP itself reached a maximum of $0.65 \text{ g C m}^{-2} \text{ d}^{-1}$ by early August (DOY 221), coinciding with the period of maximum NPP production over the shelf (Fig. 2E). It is noticeable that, on average over the period 1998-2016, the Δ NPP maximum occurred 27 days before the Δ SST maximum. During the downwelling-favourable season, the average Δ NPP reduced to $0.22 \pm 0.02 \text{ g C m}^{-2} \text{ d}^{-1}$, which represented $36 \pm 1\%$ of the total NPP.

The annual patterns for SST, Chl and NPP on the slope zone were similar to those observed in the adjacent ocean (Fig. 2B-E), thus they were not further used in subsequent analyses. We choose to compare the two zones, shelf and open ocean, that presented the largest mutual contrast.

3.2. Inter-annual variability of the annual cycles between 1998 and 2016

The annual cycles of -Qx for the individual years explained from 2.1% in 2003 to 21.0% in 2009 (average 11.3%, SD 5.1%) of the total variability of the daily data and exhibited a marked difference from year to year (Fig. 3A). For some of the study years (e.g. 1998, 2010 and 2013) northerly winds were very intense during the upwelling season, 2013 being the year with the highest average -Qx of $531 \pm 279 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$. By contrast, 2003 showed the lowest upwelling season average -Qx of $144 \pm 73 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$. The beginning and end of the upwelling season was also highly variable from year to year, with starting dates fluctuating between early February (day 33) in 2015 to mid June (day 171) in 2009. Indeed, the duration of the upwelling-favourable season also changed widely, ranging between 115 days in 2014 and 277 days in 2008. Moreover, 2005 and 2012 are marked by unusually long and intense winter upwelling events: upwelling was dominant for January to mid March 2005, with an average (SD) intensity of $284 (113) \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$, and from February to mid April 2012, with an average (SD) intensity of $170 (82) \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ (Fig. 3A).

The seasonal cycles of SST for the individual years explained from 88.3% to 96.6% of the total variability of the daily data in the adjacent ocean and from 79.1% to 95.3% over the shelf and showed contrasting inter-annual trends. In the adjacent ocean, maximum and minimum annual average temperatures (A_0) occurred in 2006 with 16.25 ± 0.03 °C and in 2002 with 15.54 ± 0.02 °C, respectively (Fig. 3B). Over the shelf, the annual average temperature reached a maximum of 15.74 ± 0.03 °C in 2006, and a minimum of 14.94 ± 0.05 °C in 2013 (Fig. 3C). The timing when maximum and minimum temperatures occurred also varied from year to year in both zones, though no significant temporal trends were found (Fig. 3B, C). In addition, the adjacent ocean was generally warmer than the shelf during the upwelling season, attaining the highest contrast in 2007 with 1.83 °C (Fig. 3D).

The seasonal cycles of Chl for the individual years explained from 4.5% in 2010 to 58.2% in 2003 (average 35.0%, SD 16.2%) of the total variability in the adjacent ocean and from 2.0% in 2003 to 23.1% in 2002 (average 14.4%, SD 7.3%) over the shelf. Therefore, seasonality is better represented by harmonic eq. 4 in the adjacent ocean than over the shelf. Furthermore, a marked Chl seasonal maximum generally occurred at the beginning of the spring in the adjacent ocean with the highest value attained in 2009 (0.51 ± 0.02 mg m⁻³) (Fig. 3E). However, over the shelf, the seasonal maximum tended to be located at the end of the summer, though in some years (e.g. 2001, 2009, 2014) this peak also occurred at the beginning of the spring (Fig. 3F).

Again, inter-annual differences in the annual cycles of NPP between 1998 and 2016 showed substantial dissimilarities between the shelf and the adjacent ocean, explaining from 41.7% to 70.7% (average 60.7%, SD 8.1%) of the total variability over the shelf and from 38.7% to 78.9% (average 66.6%, SD 10.3%) in the adjacent ocean. The highest annual average productivity in the adjacent ocean was in 2010, with 0.68 ± 0.01 g C m⁻² d⁻¹, and the lowest in 2003, 0.51 ± 0.01 g C m⁻² d⁻¹, being 25% lower (Fig. 3G). Over the shelf, annual

NPP average in 2000 ($0.81 \pm 0.02 \text{ g C m}^{-2} \text{ d}^{-1}$) was 26.4 % lower than in 2010, the year with the highest value (Fig. 3H). The timing when maximum NPP was attained remained relatively stable over the shelf (Fig. 3H); however, maximum NPP on the adjacent ocean tended to occur later during the study period at a rate of 3 ± 1 day per year (Fig. 3G). In addition, ΔNPP ranged from $0.26 \pm 0.01 \text{ g C m}^{-2} \text{ d}^{-1}$ in 1999 to $0.43 \pm 0.02 \text{ g C m}^{-2} \text{ d}^{-1}$ in 2006. During the upwelling season, ΔNPP was greater, reaching a maximum of $0.87 \text{ g C m}^{-2} \text{ d}^{-1}$ in 2009 (Fig. 3I).

3.3. Inter-annual trends in the parameters that define the seasonal cycle

The occurrence of an inter-annual trend in the ability of eq. 4 to describe the seasonal cycle of -Qx, SST, Chl and NPP during the period 1998-2016 was tested by examining the time course of RMSE between eq. 4 and the fit data for each variable. The RMSEs of -Qx, and SST did not show significant linear trends through the studied period, though a non-linear decadal variation in -Qx was apparent, with RMSE maxima in 1999-2002 and 2013-14 (Fig. S1). Concerning Chl and NPP, a significant linear increase ($p < 0.05$) was observed in the RMSE through the study period both in the ocean and shelf zones. This result indicates that the ability of eq. 4 to describe the seasonal cycles of Chl and NPP gets worst over time, suggesting an increase of the variability of Chl and NPP into frequencies higher than the second harmonic (a six-month cycle) of eq. 4 (Fig. S1). RMSE is particularly high in years 2005 and 2009-10 for Chl and in year 2005 for NPP. Similarly, RMSE of ΔNPP increased linearly ($p < 0.05$) over time indicating a poorer fit of eq. 4 in recent years although in year 2005 the fitting was particularly poor (Fig. S1).

Although all parameters obtained from fitting eq. 4 (A_0 , A_1 , A_2 , ϕ_1 and ϕ_2) exhibited marked inter-annual fluctuations (Fig. 3), linear trends were mostly not significant during the 19-year study period (Fig. 4). Exceptions were found for the annual average (A_0) Chl

concentration and NPP over the shelf that showed an increase of $0.015 \pm 0.006 \text{ mg m}^{-3}$ per year ($p = 0.02$) and $0.007 \pm 0.003 \text{ g C m}^{-2} \text{ d}^{-1}$ per year ($p = 0.03$), respectively (Fig. 4). However, a detailed inspection of these trends reveals 2010 was a break point: Chl and NPP increased from 1998 to 2010 and then decreased from 2010 to 2016. Furthermore, the phase of the second harmonic (ϕ_2) of the SST over the shelf presented a decrease of 4.7 ± 1.9 days per year ($p = 0.02$) (Fig. 4).

3.4. Relationship of NPP changes with Ekman transport and SST

We tested the covariance of the inter-annual variability of NPP with the inter-annual changes in -Qx and SST over the shelf and the adjacent ocean. Some significant relationships emerged from these tests. The upwelling season includes both the spring and late summer Chl maxima (Fig. 2D) and, therefore, it is the period of maximum sustained NPP (Fig. 2E) over both the shelf and the adjacent ocean. The inter-annual variability of NPP over the upwelling season in the adjacent ocean was related to the water column stratification from the annual minimum of SST (a proxy for winter convection) to the annual maximum of Chl (a proxy for the occurrence of the spring bloom in the adjacent ocean). The higher the stratification, obtained as the SST difference between the time of the spring bloom and the time of the winter mixing (SSTstr), the higher the NPP at a rate (95% C.I.) of 184.4 (132.4 – 256.8) $\text{mg C m}^{-2} \text{ d}^{-1}$ per $^{\circ}\text{C}$ of SSTstr (SMA regression, $R^2 = 0.57$, $n = 19$, $p = 0.0002$) (Fig. 5A). The NPP in the adjacent ocean is also positively correlated with the average offshore Ekman transport over the upwelling season (proxy to the horizontal nutrient transport from the coast) at a rate of 0.66 (0.428 – 1.01) $\text{mg C m}^{-2} \text{ d}^{-1}$ per $\text{m}^3 \text{ s}^{-1} \text{ km}^{-1}$ (SMA regression, $R^2 = 0.26$, $n = 19$, $p = 0.027$) (Fig. 5B).

The inter-annual variability of the NPP over the shelf during the upwelling season was positively related with the NPP in the adjacent ocean during the upwelling season (SMA

regression, $R^2 = 0.49$, $n = 19$, $p = 0.0008$) (Fig. 5C) and ΔNPP decreased with ΔSST at a rate of -0.76 (0.50 – 1.15) $g\ C\ m^{-2}\ d^{-1}$ per $^{\circ}C$ (SMA regression, $R^2 = 0.29$, $n = 19$, $p = 0.018$) (Fig. 5D). Therefore, NPP over the shelf during the upwelling season can be modelled by a multiple linear relationship involving NPP in the adjacent ocean and ΔSST during the upwelling season ($R^2 = 0.64$, $n = 19$, $p = 0.0003$).

For the downwelling season, none of the tested explanatory variables (annual minimum SST, SSTstr, average SST and average $-Q_x$ over the downwelling season) were able to explain the interannual variability of the NPP in the adjacent ocean. For the case of the NPP over the shelf, this was related to NPP in the adjacent ocean (SMA regression, $R^2 = 0.62$, $n = 19$, $p < 0.0001$) (Fig. 5E) and ΔNPP increased with the difference between the average and the minimum SST over the shelf (SSTdown) at a rate of 69.5 (45.5 – 106.0) $mg\ C\ m^{-2}\ d^{-1}$ per $^{\circ}C$ (SMA regression, $R^2 = 0.27$, $n = 19$, $p = 0.021$) (Fig. 5F). Therefore, NPP over the shelf during the downwelling season can be modelled by a multiple linear relationship involving NPP in the adjacent ocean and SSTdown ($R^2 = 0.74$, $n = 19$, $p < 0.0001$).

4. Discussion

4.1. Ekman transport vs sea surface temperature

Previous studies in the NW Iberian margin have reported a marked decrease of the offshore Ekman transport through the second half of the 20th century and the beginning of the 21st century (Álvarez-Salgado et al., 2008; Pérez et al., 2010; Pardo et al., 2011; Gómez-Gesteira et al., 2011). This decrease has been associated with a relaxation of the zonal atmospheric pressure gradient in the Bay of Biscay (Pérez et al., 2010). More recently, Barton et al. (2013) have suggested that the evolution of upwelling intensity over the last decades in the Canary EBUE is uncertain. All these observations contradict the hypothesis of Bakun (1990), which predicts an intensification of upwelling in parallel to global warming. A recent

review by Sydeman et al. (2014) pointed out that, over the last 60 years, coastal winds have strengthened in the Benguela, Humboldt and California EBUEs in response to global warming but the wind pattern was unclear in the Canary EBUE. Conversely, an increase of the duration and intensification of upwelling in the Canary, Benguela and Humboldt EBUEs but not in the California EBUE has been suggested by Wang et al. (2015). In our study, restricted to the period 1998 to 2016, the offshore Ekman transport did not exhibit a significant trend because of the alternation of short periods (< 5 years) of upwelling-favourable wind intensification and weakening as described by Santos et al. (2011). Discrepancies among studies are related with the sources of the wind data (Barton et al., 2013), methodological refinements in the calculation of geostrophic winds (González-Nuevo et al., 2014) and the length of the time series as well as the fitting procedure used to analyse the data (Santos et al., 2011).

Our results, for the period 1998–2016, show no significant SST trends both over the shelf and in the adjacent ocean (Fig. 4). However, a significant SST rise of 0.1–0.3 °C per decade was observed in previous works in this area when covering longer periods (de Castro et al., 2009; Gómez-Gesteira et al., 2008; 2011; Santos et al., 2011; Pérez et al., 2010). The annual average SST decreases significantly from the adjacent ocean to the coast, reaching maximum differences during the upwelling season. The maximum temperature difference was observed by early September because of: i) the uplift of the cold and nutrient-rich oceanic ENACW onto the shelf in response to the offshore Ekman transport promoted by the dominant northerly winds (Otero et al., 2008; de Castro et al., 2008; González-Nuevo et al., 2014); and ii) the maximum SST reached at this time of the year in the adjacent ocean as a consequence of the seasonal warming at our latitudes (Gómez-Gesteira et al., 2011). In this regard, the inter-annual variability of SST over the shelf during the upwelling season was

correlated inversely with $-Q_x$ (SMA regression, $R^2 = 0.30$, $n = 19$, $p = 0.016$), showing a decrease of $2.4 (1.6-3.6) 10^{-3} \text{ }^\circ\text{C per m}^3 \text{ s}^{-1} \text{ km}^{-1}$.

The SST difference between shelf and adjacent ocean waters during the downwelling season is mainly due to the contributions of inland cool water to the shelf, from the rivers Miño and Douro and the rivers that drain into the Rías Baixas to form the so-called Western Iberian Buoyant Plume (WIBP; Peliz et al., 2005; Sousa et al., 2014; Mendes et al., 2016). Minimum SST differences between the shelf and the adjacent ocean are reached by the end of April, when the flow of inland waters begins to weaken (Álvarez-Salgado et al., 2003; Peliz et al., 2005).

The maximum ΔNPP (DOY 221) occurred in between the maxima of the two environmental variables that we are using as upwelling indices: (i) the day of the maximum offshore Ekman transport (DOY 197) and (ii) the day with maximum ΔSST (DOY 242). Therefore, the day of the maximum offshore Ekman transport may be used to predict the maximum peak of productivity better than the maximum ΔSST because the first occurred 24 days before the NPP maximum, whereas the second happened 21 days after the phytoplankton peak. This is because ΔSST depends not only on the cooling of surface waters by coastal upwelling but also on the parallel warming of the adjacent ocean waters.

4.2. New Production in the NW Iberian margin

Despite the low percentage of the total variability of the daily time series of Chl explained by eq. 4, the average seasonal cycle described by this equation (Fig. 3) fits with previous descriptions of the coast-ocean and temporal variability of Chl in the NW Iberian margin (Demarq, 2009; Bode et al., 2011; Otero et al., 2018; Álvarez et al., 2012; Picado et al., 2014; Ferreira et al., 2019). In agreement with these studies, a significant increase of the seasonal average Chl was observed in shelf waters over the study period, but 2010

represented a breakpoint in that trend (Fig. 4). Previous studies did not comprise up to year 2010 and the recent paper by Ferreira et al. (2019) did not highlight this specific trend off the NW Iberian shelf. A significant increase of NPP was also observed in shelf waters over the study period, being again interrupted by the 2010 break point (Fig. 4). Chl and NPP increased over time in the adjacent ocean too, although not significantly. Previous studies also observed an increase in the primary production between 1990 and 2006 in this area (Bode et al., 2011; Chávez et al., 2011) but the decrease after 2010 has been reported for the first time in this work. Inter-annual differences in NPP between shelf and adjacent ocean waters during the upwelling period indicate an excess of NPP over the shelf (Δ NPP). This excess can be considered as a new production (NP) estimate assuming that it is associated to the new nutrients transported by the upwelled ENACW (Joint et al., 2001). Calculation of the magnitude of NP allows us to assess the carrying capacity of the NW Iberian shelf as well as its potential to absorb the anthropogenic CO₂ accumulated in the atmosphere. NP of the NW Iberian shelf represents $37 \pm 2\%$ of the total NPP over the upwelling season, indicating that 37% of the NPP is supported by new upwelled nutrients and, therefore 63% come from nutrient mineralization processes in the aphotic layer and the pelagic sediments of the shelf, in agreement with previous estimates (Joint et al., 2002; Arístegui et al., 2009). By contrast, in other upwelling systems NP represents $> 50\%$ of the total NPP (e.g. Wilkerson and Dugdale, 2008.). This difference is caused by the lower intensity of coastal winds and higher residence time of upwelled water over the Iberian shelf compared to the other EBUEs (Arístegui et al., 2006; Álvarez-Salgado et al., 2010), which leads to a higher nutrient recycling efficiency. Moreover, during the downwelling favourable season the excess of NPP over the shelf should be sustained by the new nutrients from continental inputs, mainly from the River Miño (Álvarez et al., 2012; Picado et al., 2014).

It is remarkable the overall increase with time of the RSME between eq. 4 and the values for Chl, NPP and Δ NPP over the period 1998-2016 (Fig. S1). Given that eq. 4 models the first (period, 1 year) and second (period, $\frac{1}{2}$ year) harmonics of the seasonal cycles of Chl, NPP and Δ NPP, an increase in the error of estimation of eq. 4 suggests that the variability of these parameters would be preferentially centred on shorter time periods.

4.3. Potential climate drivers of NPP variability in the NW Iberian margin

The annual maximum of NPP in the adjacent ocean occurs in spring, enabled by the nutrients accumulated in the surface layer during winter convection. The spring bloom takes place when SST increases enough to trigger stratification of the surface layer, which is essential for the accumulation of phytoplankton growing from nutrients accumulated during the winter (Cloern et al., 1996). On this basis, a positive relationship should be expected between the water column stratification after winter mixing and the NPP during the spring bloom in the adjacent ocean. In this sense, we observed a significant increase of NPP with the SST difference between the SST minimum and the Chl maximum (SST_{str}), demonstrating the expected positive response of NPP to stratification after winter mixing (Fig. 5A). Noticeably, despite the fact that the lower the temperature during the winter mixing period, the higher the surface nutrient concentrations before the spring bloom (Pérez et al., 2005), annual minimum SST does not help to explain the inter-annual variability of the adjacent ocean NPP. Furthermore, we observed that the higher the offshore Ekman transport, the higher the NPP in the adjacent ocean during the upwelling season (Fig. 5B). This result suggests that the inorganic nutrients upwelled over the shelf are partly returned to the adjacent ocean and/or that the phytoplankton populations grown on the coast are exported via upwelling filaments (Álvarez-Salgado et al., 2001). Finally, the estimated new production over the shelf (NP) during the upwelling season, ranging from 0.31 to 0.57 g C m⁻² d⁻¹, can

be modelled by means of the cooling of the shelf compared with the adjacent ocean, Δ SST (Fig. 5D), in agreement with the nutrient enrichment of shelf waters with upwelled ENACW through the upwelling season (Joint et al., 2002; Otero et al., 2008).

The slopes of these linear relationships of NPP with $-Q_X$ and the different SST indices allow to roughly testing the sensitivity of NPP to these climate-related indices. Future climate scenarios for the NW Iberian margin predict an enhancement of upwelling favourable winds, particularly between April and September, i.e. the upwelling favourable season (Casabella et al., 2014; Álvarez et al., 2016). These projections are in agreement with the general results of Rykaczewski et al. (2015), who predicted that summertime winds in the poleward boundary of an upwelling system, 42-43°N in our case, are projected to intensify. The California Current System was an exception (Rykaczewski et al. 2015; Brady et al., 2017). Álvarez et al. (2016) reported increments of the offshore Ekman transport of $5.03 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ per decade (IPCC RCP 4.5) to $11.21 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ per decade (IPCC RCP8.5) for the study area. Considering the NPP to $-Q_X$ slope obtained for the upwelling season in the adjacent ocean ($0.66 \text{ mg C m}^{-2} \text{ d}^{-1} \text{ per m}^3 \text{ s}^{-1} \text{ km}^{-1}$; Fig. 5B), a coarse estimate of the expected increase of NPP due to coastal upwelling increase would be between 3.3 and $7.4 \text{ mg C m}^{-2} \text{ d}^{-1}$ per decade depending on the IPCC scenario, RCP4.5 and 8.5, respectively. Future $-Q_X$ values also allow a rough projection of shelf SST decrease based on the slope of the linear relationship between both variables ($-2.4 \cdot 10^{-3} \text{ }^\circ\text{C per m}^3 \text{ s}^{-1} \text{ km}^{-1}$): from -0.012 for RCP4.5 to $-0.027 \text{ }^\circ\text{C decade}^{-1}$ for RCP8.5. This brief decrease can slightly compensate the overall increase of $0.1\text{--}0.3^\circ\text{C decade}^{-1}$ in the area. Furthermore, using the slope of the relationship between Δ NPP and Δ SST ($-0.76 \text{ g C m}^{-2} \text{ d}^{-1} \text{ per }^\circ\text{C}$; Fig. 5D), the shelf SST decrease can be converted into a NPP increase of 9 for RCP4.5 to $20 \text{ mg C m}^{-2} \text{ d}^{-1} \text{ decade}^{-1}$ for RCP8.5.

Although the impact of future warming on the stratification of surface waters of the NW Iberian margin has not been examined yet, a brief analysis of the historical SST data for

the study area indicates that both SST_{str} and SST_{down} have experienced minimal non-significant increases of $< 0.007\text{ }^{\circ}\text{C decade}^{-1}$. If this warming rate continues over this century, it would translate into insignificant increases of the NPP over the shelf and the adjacent ocean of $< 1\text{ mg C m}^{-2}\text{ d}^{-1}\text{ decade}^{-1}$ as derived from the slope of the relationships of NPP with SST_{str} ($184.4\text{ mg C m}^{-2}\text{ d}^{-1}\text{ per }^{\circ}\text{C}$; Fig. 5A) and SST_{down} ($69.5\text{ mg C m}^{-2}\text{ d}^{-1}\text{ per }^{\circ}\text{C}$; Fig. 5F).

We have shown the sensitivity of primary producers to climate-related variables ($-Q_x$, ΔSST , SST_{str}, SST_{down}), in the NW Iberian margin, one the most productive marine regions of Europe in terms of fisheries and allied activities, which are essentially influenced by the upwelling regime. These results are in line with the numerical modelling study by Fortes Lopes et al. (2014) off Northern Portugal confirming that changes in the strength and frequency of northerly winds could have a direct impact of the distribution of phytoplankton. So shifts in upwelling intensity and duration will have consequences in these associated activities, and thus in the communities which depend on this sector.

5. Conclusions

We have studied the seasonal and inter-annual variability of net primary production (NPP) in the NW Iberian margin over the period 1998–2016, in relation to two climate-related indices: offshore Ekman transport ($-Q_x$) and sea surface temperature (SST). We present parametric equations relating NPP with $-Q_x$ and SST indices that allow testing of the sensitivity of NPP to climate variability. In particular, during the upwelling-favourable season both the NPP of the adjacent ocean and the NP over the shelf are related with water column stratification and upwelling intensity. Concerning upwelling, its effect on shelf NPP (and NP) was direct, whereas its effect on ocean NPP was indirect, through the lateral import

of nutrients and/or phytoplankton biomass from the shelf. Our results should be treated with caution given the limited time span of our dataset.

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Figure captions

Fig. 1. Map of the study area. White shaded areas show the three zones (shelf, slope and adjacent ocean) for which daily mean sea surface temperature, photosynthetically available radiation and satellite derived chlorophyll *a* net primary production data were obtained. The blue shaded area shows the cell of $2^\circ \times 2^\circ$ centred at 43°N 11°W where geostrophic winds were obtained to calculate the upwelling index.

Fig. 2. Seasonal cycle obtained from fitting eq. 4 to the whole daily time series of (A) the offshore Ekman transport ($-Q_x$, in $\text{m}^3 \text{s}^{-1} \text{km}^{-1}$) estimated for 43°N 11°W , and to (B) SST in left Y-axis and ΔSST in right Y-axis (both in, $^\circ\text{C}$), (C) PAR (in $\text{E m}^{-2} \text{d}^{-1}$), (D) chlorophyll (in mg m^{-3}), and (E) NPP (in $\text{g C m}^{-2} \text{d}^{-1}$) measured on the shelf (orange line), slope (light blue line), adjacent ocean (dark green line) in left Y-axis, and the shelf-ocean NPP difference (blue dots) and % excess NP over the shelf (red line) in the right Y-axes, between 1998 and 2016. The shaded area highlights the upwelling season as determined in panel A.

Fig. 3. Inter-annual evolution of the predicted seasonal cycle of the (A) upwelling index measured at 43°N 11°W , the SST on the adjacent ocean (B), on the shelf (C) and the shelf-ocean difference in SST (D), the chlorophyll on the adjacent ocean (E) and on the shelf (F), the NPP on the adjacent ocean (G), on the shelf (H), and the shelf-ocean difference in NPP (I) between 1998 and 2016. Shown are also the trends for the day when the predicted maximum (black lines and dots) and minimum (white lines and dots) occurs.

Fig. 4. Inter-annual trends for the annual average (A_0), the amplitudes of the first (A_1) and second (A_2) harmonic, and their respective phase shifts (ϕ_1 and ϕ_2) between 1998 and 2016 for the upwelling index estimated at 43°N 11°W , the SST on the adjacent ocean, on the shelf

and their difference, the Chl on the adjacent ocean and on the shelf, and the NPP on the adjacent ocean, on the shelf and their difference. Lines show fits of linear (solid) and non-linear (dotted) models fitted by OLS and Generalized Additive Models, respectively. Blue (red) colour indicates significant (non-significant) relationships ($p < 0.05$). The DOY when the first harmonic is maximum is calculated as $(\pi/2 - \phi_1) \cdot 365/(2\pi)$ and the DOY when the second harmonic is maximum as $(\pi/2 - \phi_2) \cdot 365/(4\pi)$.

Fig. 5. Bivariate plots showing the relationships between (A) ocean NPP over the upwelling season and SST difference between the minimum temperature and the temperature at the spring Chl a maximum (SSTstr); (B) ocean NPP over the upwelling season and the offshore Ekman transport over the upwelling season ($-Q_x$); (C) shelf NPP over the upwelling season and ocean NPP over the upwelling season; (D) shelf NPP excess (ΔNPP) over the upwelling season and temperature difference between the shelf and the ocean (ΔSST) over the upwelling season; (E) shelf NPP over the downwelling season and ocean NPP over the downwelling season; (F) shelf NPP excess (ΔNPP) over the upwelling season and difference between the minimum and the average temperature over the shelf (SSTdown) over the downwelling season. Black line shows OLS regression and dashed lines shows SMA regression.

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Year (1998–2016)

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Table 1. Coefficients ($\pm$ SE) obtained from fitting eq. 4 to $-Qx$ (in $m^3 s^{-1} km^{-1}$), SST (in $^{\circ}C$), PAR (in $E m^{-2} d^{-1}$), Chl (in $mg m^{-3}$) and NPP (in $g C m^{-2} d^{-1}$) in each zone (adjacent ocean and over the shelf, see Fig. 1). R, Pearson's correlation coefficient between the response variable and the model predictions. Note that ϕ_1 and ϕ_2 are shown in radians while in Fig. 4 they were converted into the DOY when the first and second harmonics are maxima.

Variable	A_0	A_1	A_2	ϕ_1	ϕ_2	R
$-Qx$	25.67 (± 14.07)	409.12 (± 19.86)	66.74 (± 19.87)	4.76 (± 0.05)	5.74 (± 0.30)	0.24
SST_{ocean}	15.90 (± 0.01)	2.77 (± 0.01)	0.16 (± 0.01)	3.71 (± 0.004)	6.08 (± 0.07)	0.95
SST_{shelf}	15.27 (± 0.01)	2.29 (± 0.01)	0.03 (± 0.01)	3.81 (± 0.01)	2.47 (± 0.49)	0.90
PAR_{ocean}	33.15 (± 0.11)	22.62 (± 0.16)	1.02 (± 0.15)	4.84 (± 0.01)	6.02 (± 0.15)	0.88
PAR_{shelf}	32.79 (± 0.11)	22.92 (± 0.16)	1.09 (± 0.16)	4.83 (± 0.01)	0.18 (± 0.15)	0.87
Chl_{ocean}	0.42 (± 0.004)	0.16 (± 0.01)	0.09 (± 0.01)	0.06 (± 0.03)	4.67 (± 0.06)	0.46
Chl_{shelf}	1.03 (± 0.01)	0.08 (± 0.01)	0.13 (± 0.01)	4.26 (± 0.15)	5.35 (± 0.09)	0.18
NPP_{ocean}	0.59 (± 0.003)	0.27 (± 0.004)	0.07 (± 0.004)	5.06 (± 0.01)	4.79 (± 0.05)	0.74
NPP_{shelf}	0.94 (± 0.004)	0.44 (± 0.01)	0.09 (± 0.01)	4.62 (± 0.01)	5.58 (± 0.06)	0.75
ΔSST	-0.63 (± 0.004)	0.53 (± 0.01)	0.18 (± 0.01)	6.45 (± 0.01)	2.87 (± 0.03)	0.74
ΔNPP	0.35 (± 0.004)	0.23 (± 0.01)	0.06 (± 0.01)	4.11 (± 0.02)	0.14 (± 0.09)	0.57

Supplementary Material

Fig. S1. Inter-annual trends for the root-mean square error (RMSE) of eq. 4 for each variable. Lines show fits of linear (solid) and non-linear (dotted) models fitted by OLS and Generalized Additive Models, respectively. Blue (red) colour indicate significant (non-significant) relationships ($p < 0.05$). Lower RMSE values indicate a better fit.