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Unravelling region-specific environmental drivers of phytoplankton across a complex marine domain (off SW Iberia)

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ABSTRACT

Phytoplankton, the dominant marine primary producers, are considered to be highly sensitive indicators of ecosystem condition and change. The southwest area off the Iberian Peninsula (SWIP, NE Atlantic) is located in a biogeographical transition zone between temperate and subtropical waters, and classified as being very vulnerable to climate change. SWIP includes a variety of oceanic and coastal domains, under the influence of topographic irregularities, coastal upwelling and continental freshwater outflows, that collectively challenge the understanding of phytoplankton dynamics and controls. This study aimed to evaluate patterns in seasonal and interannual variability in phytoplankton and underlying environmental determinants within specific regions of SWIP, during a 15-year period (1997–2012), and to assess whether climate variability affects the regions in different ways. Empirical Orthogonal Function (EOF) analysis of satellite-retrieved sea surface chlorophyll-a concentration (Chl-a), acquired from the Ocean Colour Climate Change Initiative (OC-CCI), 4-km, 16-day resolution, was used to regionalize the study area. Region-specific Chl-a variability patterns and their linkages with environmental determinants were explored using Generalized Additive Mixed Models (GAMM). A set of local physical-chemical variables, derived from satellite and model data, and large-scale climate indices, were used as environmental variables. EOF analysis of Chl-a variability over the heterogeneous SWIP area identified nine coherent regions, with distinctive variability patterns (4 coastals, 2 slopes and 3 open-ocean regions). Region-specific GAMM models explained between 32% and 82% of Chl-a variance, with higher explanatory power (>61%) for open ocean regions and coastal regions under increased riverine influence. Chl-a model predictors, as well as their effects, varied markedly among SWIP regions. However, climate-sensitive local environmental variables (sea surface temperature – SST and photosynthetically available radiation) emerged as the most influential general predictors overall, and large-scale climate indices showed significant but minor effects. Over oceanic SWIP regions, Chl-a (0.08–1.50 $\mu g\ L^{-1}$) showed a uni-modal annual cycle, with increases during the mixed-layer deepening and late-winter maxima, reflecting seasonal changes in SST and ocean stratification, and probably related to increased nutrient availability and/or decreased mortality. Over coastal regions south of 37°N, Chl-a (0.23–10 $\mu g\ L^{-1}$) also benefited from riverine discharges, mostly during winter, and upwelling induced by zonal westerly winds, stronger during summer. Over the Portuguese west coast region, Chl-a (0.26–2.20 $\mu g\ L^{-1}$) showed a uni-modal annual cycle, with summer maxima, associated with the stimulatory effects of meridional northerly winds and coastal upwelling that partially extended into slope waters. Chl-a interannual variability showed zonal differences within SWIP, with significant interannual patterns only for regions south of 37°N. Nonetheless, contrasting trends were detected in coastal (decline) and oceanic (increase) regions, possibly a consequence of between-region differences in the relative roles of nutrient and light limitation, corresponding to significant interannual increases in wind speed and mixed layer depth. Our study used a biologically-relevant objective regionalization of a heterogeneous area, to elucidate phytoplankton dynamics and controls. The region-specific associations observed between phytoplankton and multiple climate-sensitive environmental drivers over the SWIP area reinforce the role of phytoplankton as a strategic element for evaluating ecosystem responses to climate variability and change.

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1. Introduction

Phytoplankton are the dominant primary producers of marine ecosystems, responsible for ca. 50% of global primary production (Field et al., 1998), and are key contributors to carbon dioxide uptake by the ocean (Gregg et al., 2003; Smetacek and Cloern, 2008). The distribution and variability patterns of phytoplankton reflect the interplay between bottom-up forces, directly regulating growth rates, and top-down forces related to phytoplankton losses (e.g., grazing, sinking, lysis) processes. Both forces are, in turn, controlled by atmosphere and ocean circulation patterns and atmosphere-land-ocean interactions (Cloern and Dufford, 2005; Longhurst, 2007). Indeed, not only phytoplankton resources (e.g., light, inorganic nutrients), but also their dominant grazers, are controlled by atmosphere and ocean physical-forcing, being strongly affected by climate variability and change (Behrenfeld, 2014; Chavez et al., 2011; Cloern et al., 2016). The increasing concerns on the effects of anthropogenic and global climate changes, linked to the pivotal role of phytoplankton and their value as highly sensitive ecological indicators, make the study of phytoplankton regulation a key approach to evaluating ecosystem status and change, and to forecasting ecosystem responses under environmental change (Cloern et al., 2016; Platt and Sathyendranath, 2008; Racault et al., 2014a; Smetacek and Cloern, 2008).

Temporal and spatial phytoplankton variability patterns in the ocean can be assessed using satellite-retrieved surface chlorophyll-a concentration (Chl-a), a proxy for phytoplankton biomass, derived from ocean colour remote sensing (OCRS). Although limited to the top layers of the ocean, OCRS offers a unique synoptic, high spatial-temporal resolution, multi-decadal coverage of surface marine bio-optical environment. OCRS products are considered to belong to the Essential Climate Variables (ECV), a suite of environmental properties comprising physical, chemical and biological variables critical to the characterization of climate, and also measured systematically, direct or indirectly, at a global scale on an operational basis (Bojinski et al., 2014). Likewise, several biologically-relevant oceanographic and atmospheric variables are routinely measured or inferred from satellite remote sensing (Robinson, 2010) and coupled climate, hydrodynamic-biogeochemical models (Siedler et al., 2013). The integrated analysis of time series of Chl-a and concurrent environmental variables supports the identification of dominant drivers of phytoplankton variability, allowing the discrimination between local anthropogenic influences and climate-driven changes or the relative importance of physical forcing versus biological interactions (Cloern et al., 2016; Smetacek and Cloern, 2008). Accumulating evidence shows that climate variability is impacting marine phytoplankton but its effects are variable depending on period of analysis, phytoplankton controls and ecosystem properties (Boyd et al., 2016; Cloern and Jassby, 2010; Devred et al., 2009; Henson et al., 2016; Martinez et al., 2016). Comparative analysis, across different ecosystems, will then allow an increased perception of how phytoplankton controls and ecosystem-specific attributes may modulate phytoplankton responses to climate change. Ultimately, this information may be used to identify more climate-susceptible ecosystems, and to improve our ability to forecast marine ecosystem alterations under projected climate change scenarios.

The southwest area off the Iberian Peninsula (SWIP; NE Atlantic) constitutes a complex environment with distinct offshore and coastal domains, with meridional and zonal orientation (Fig. 1). SWIP south sector includes the Gulf of Cadiz, a basin that receives waters from the Mediterranean Sea. This heterogeneous area, located in a biogeographical transition zone between temperate and subtropical waters, is influenced by Atlantic and Mediterranean circulation patterns, coastline and topographic irregularities, coastal upwelling events, intense mesoscale activity and continental freshwater discharges (Arístegui et al., 2009; García-Lafuente and Ruiz, 2007; Muñoz et al., 2015; Relvas et al., 2007). Furthermore, SWIP, along with Southern Europe and Mediterranean, is classified as a region particularly vulnerable to climate change. Alterations projected for this region by the Intergovernmental Panel on Climate Change (IPCC) include decreased precipitation, increased frequency and intensity of heatwaves and decline in provision of ecosystem services (Kovats et al., 2014). Indeed, several climate-driven alterations over recent decades were already reported for the area including an enhancement in the frequency of heatwaves, a decrease in storm frequency and intensity (Trigo, 2006), sea surface warming (Belkin et al., 2009; Lima and Wethey, 2012; Goela et al., 2016), changes in upwelling intensity and patterns (Lemos and Pires, 2004; Lemos and Sansó, 2006; Relvas et al., 2009; review by Varela et al., 2015), fluctuations in the abundance of small pelagic fishes and fish landings (see Arístegui et al., 2009; Catalán et al., 2006; Gamito et al., 2016; Ruiz et al., 2009), and species range shifts with a northern expansion of subtropical species (Horta e Costa et al., 2014; Lourenço et al., 2012; Nicastro et al., 2013).

Phytoplankton studies in the SWIP area included in situ and remote-sensing-based observational approaches. In situ-based studies (Moita, 2001), usually involving irregular low frequency sampling and a limited time coverage, mostly addressed specific coastal zones located in the Gulf of Cadiz's northwestern (Cravo et al., 2010; Goela et al., 2014; Loureiro et al., 2005, 2011) and north-northeastern sectors (Cardeira et al., 2013; Echevarría et al., 2009; Huertas et al., 2005, 2006; Macías et al., 2008; Navarro et al., 2006; Reul et al., 2006). Observational studies based on OCRS products allowed a regular high-frequency sampling, covering most SWIP areas (Navarro et al., 2007, 2012, 2013; Peliz and Fiúza, 1999; Souza and Bricaud, 1992) or specific regions within the north margin of the Gulf of Cadiz (Caballero et al., 2014; Cravo et al., 2013; Cristina et al., 2016a, 2016b; Goela et al., 2015; Navarro and Ruiz, 2006; Prieto et al., 2009; Ramírez-Romero et al., 2012; Vázquez et al., 2009). Other study strategies have also included model-based inferences (Macías et al., 2014; Marta-Almeida et al., 2012; Reboreda et al., 2014a, 2014b) and dedicated experiments (Loureiro et al., 2008; Weissbach et al., 2011). Overall, these studies have contributed to our understanding of phytoplankton variability and regulation in some, mostly coastal, domains of the SWIP area. Additionally, these studies indicated that the influence of specific environmental drivers, including climate-related variables (e.g., wind forcing, coastal upwelling and mixing-stratification cycles; rainfall and riverine discharges; tidal currents and internal waves), depends on location and study period (e.g., Caballero et al., 2014; García-Lafuente and Ruiz, 2007; Navarro and Ruiz, 2006; Navarro et al., 2012; Peliz and Fiúza, 1999; Prieto et al., 2009). Indeed, 5-year Chl-a time series, retrieved from OCRS, were decomposed into dominant modes and used to regionalize the Gulf of Cadiz basin (Muñoz et al., 2015; Navarro and Ruiz, 2006). Despite the connectivity across-domains, recent studies mostly addressed the zonal and meridional Iberian margins separately, often overlooking the open ocean domain, so an integrated comprehensive view of phytoplankton dynamics and controls over the heterogeneous SWIP area is still lacking.

In this context, the objectives of our study are: (i) to evaluate phytoplankton seasonal and interannual variability patterns in the SWIP area, over a 15-year period (1997–2012); (ii) to identify region-specific phytoplankton environmental determinants within this heterogeneous study area; and (iii) to investigate whether climate variability affects specific SWIP regions in particular ways. To accomplish this goal, SWIP was partitioned into regions with similar phytoplankton variability, using satellite-retrieved Chl-a and Empirical Orthogonal Function analysis, and region-specific linkages between environmental drivers and phytoplankton were later explored using Generalized Additive Mixed Models. Phenology of phytoplankton blooms will be addressed specifically in a dedicated article.

2. Materials and methods

2.1. Study area

SWIP area is currently partitioned into distinct spatial functional units, depending on the global ocean classification scheme used (see

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