Progress in Oceanography 165 (2018) 233–256

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Patterns and drivers of phytoplankton phenology off SW Iberia: A phenoregion based perspective

Lilian Anne Krug[a,*], Trevor Platt[b], Shubha Sathyendranath[c], Ana B. Barbosa[a]

[a] University of the Algarve/Centre for Marine and Environmental Research (CIMA), Campus de Gambelas, 8005-139 Faro, Portugal
[b] Plymouth Marine Laboratory, Prospect Place, The Hoe, PL1 3DH Plymouth, Devon, United Kingdom
[c] National Centre for Earth Observation, Plymouth Marine Laboratory, Prospect Place, The Hoe, PL1 3DH Plymouth, Devon, United Kingdom

ARTICLE INFO

Keywords:
Phytoplankton phenology
Phytoplankton blooms
Phytoplankton drivers
Partitioning
Ocean colour

ABSTRACT

Phytoplankton patterns, tightly linked to the dynamics of the ocean surface layer and its atmospheric forcing, have major impacts on ecosystem functioning and are valuable indicators of its response to environmental variability and change. Phytoplankton phenology and its underlying drivers are spatially variable, and the study of its patterns, particularly over heterogeneous regions, benefits from a delineation of regions with specific phenological properties, or phenoregions. The area Southwest off the Iberian Peninsula (SWIP, NE Atlantic) integrates a highly complex set of coastal and ocean domains that collectively challenge the understanding of regional phytoplankton phenology and related forcing mechanisms. This study aims to evaluate phytoplankton phenology patterns over the SWIP area, during an 18-year period (September 1997 – August 2015), using an objective, unsupervised partition strategy (Hierarchical Agglomerative Clustering – HAC) based on phenological indices derived from satellite ocean colour data. The partition is then used to describe region-specific phytoplankton phenological patterns related to bloom magnitude, frequency, duration and timing. Region-specific variability patterns in phenological indices and their linkages with environmental determinants, including local ocean physical-chemical variables, hydrodynamic variables and large scale climate indices, were explored using Generalized Additive Models (GAM). HAC analyses identified five coherent phenoregions over SWIP, with distinctive phytoplankton phenological properties: two open ocean and three coastal regions. Over the open ocean, a single, low magnitude and long bloom event per year, was regularly observed. Coastal phenoregions exhibited up to six short bloom events per year, and higher intra-annual and variability. GAM models explained 50–90% of the variance of all phenological indices except bloom initiation timing, and revealed that interannual patterns in phytoplankton phenology and their environmental drivers varied markedly among the five phenoregions. Over the oceanic phenoregions, large-scale climate indices (Eastern Atlantic Pattern, Atlantic Meridional Oscillation), mixed layer depth (MLD) and nitrate concentration preceding primary bloom events were influential predictors, reflecting the relevance of nutrient limitation. For the Coastal-Slope, a relatively more light-limited phenoregion, North Atlantic Oscillation and wind speed were more relevant, and bloom magnitude was also positively influenced by riverine discharge. This variable was a significant predictor of bloom frequency, magnitude and duration over the Riverine-influenced region. Over the Upwelling-influenced region, upwelling intensity and mean annual MLD showed stronger partial effects on phytoplankton phenology. Overall, our phenology-based unsupervised approach produced a biologically-relevant SWIP partition, providing an evaluation of the complexity of interactions between phytoplankton and multiple environmental forcing, particularly over coastal areas.

1. Introduction

Phytoplankton are the dominant primary producers of marine ecosystems, responsible for about 50% of global primary production (Field et al., 1998), and a key component of the biological carbon pump (Gregg et al., 2003; Cermeño et al., 2008). Phytoplankton growth is mostly controlled by light and nutrient availability and, therefore, tightly linked to the dynamics of the ocean surface mixed layer (Longhurst, 2007; Cloern and Dufford, 2005) and regulated by atmospheric forcing and large scale climate variability patterns (Martinez et al., 2009, 2011, 2016; Boyce et al., 2010; Racault et al., 2012, 2017; Zhai et al., 2013). Over coastal zones, terrestrial nutrient inputs and

* Corresponding author.
E-mail addresses: lakrug@ualg.pt (L.A. Krug), tplatt@dal.ca (T. Platt), ssat@pml.ac.uk (S. Sathyendranath), abarbosa@ualg.pt (A.B. Barbosa).

https://doi.org/10.1016/j.pocean.2018.06.010
Received 31 March 2018; Accepted 25 June 2018
Available online 26 June 2018
0079-6611/

topographic irregularities increase the complexity of phytoplankton patterns and driving forces (Carstensen et al., 2015; Cloern et al., 2016). Together with top-down controls, these environmental determinants modulate phytoplankton phenology, i.e., their periodically-recurring variability patterns, including the timing and intensity of phytoplankton blooms, short-term events that can represent a substantial fraction of the annual primary production in marine ecosystems (Behrenfeld, 2014; Sallée et al., 2015; Martinez et al., 2016). Phytoplankton phenology patterns, and alterations therein, have large impacts on ecosystem functioning (see review by Ji et al. 2010), affecting the efficiency of carbon transfer to higher trophic levels (Edwards and Richardson, 2004; Barth et al., 2007; Friedland et al., 2016), the recruitment success of economically important fish and invertebrate resources (Platt et al., 2003; Fuentes-Yaco et al., 2007; Koeller et al., 2009; Malick et al., 2015), benthic-pelagic coupling (Nixon et al., 2009), the carbon export efficiency and the depth of remineralization (Lutz et al., 2007). Through such mechanisms, phytoplankton provide a critical connection between environmental changes and ecosystem dynamics and productivity.

Phytoplankton phenology has been the subject of intense research in the last decade, mostly stimulated by the availability of satellite-retrieved surface chlorophyll-a concentration (Chl-a) and the anticipated climate-induced changes in marine ecosystems (e.g., Platt and Sathyendranath, 2008; Platt et al., 2010; Racault et al., 2012, 2014a; Friedland et al., 2018; Henson et al., 2018). As an integrative environmental science (Schwartz, 2003), phenological studies have evaluated phytoplankton periodic events as well as their interactions with environmental conditions and climatic forcing (e.g., Henson et al., 2006, 2018; Demarcq et al., 2012; Racault et al., 2012; Sapiano et al., 2012; Cabré et al., 2016; Kostadinov et al., 2017). Phytoplankton phenology has usually been synthesized into a set of ecologically relevant indices: the timing, duration and magnitude of bloom events (Platt and Sathyendranath, 2008; Platt et al., 2009, 2010; Racault et al., 2014a). These indices are currently considered key indicators of ecosystem functioning and its response to climate variability and change, at multiple scales (see Platt and Sathyendranath, 2008; Winder and Cloern, 2010; Racault et al., 2014a; Scheffers et al., 2016).

Global (Demarcq et al., 2012; D'Ortenzio et al., 2012; Racault et al., 2012, 2017; Sapiano et al., 2012; Friedland et al., 2018) and regional phenological studies, based on satellite-remote sensing and *in situ* sampling, have reported significant interannual changes in phytoplankton phenology for a wide diversity of marine ecosystems including epipelagic, neritic (e.g., North Atlantic – Harrison et al., 2013; Henson et al., 2010; Land et al., 2014; Martinez et al., 2011; González Taboada and Anadón, 2014; Mediterranean – Lavigne et al., 2013; North Sea – Edwards and Richardson, 2004; North Pacific – Yoo et al., 2008; California Current – Foukal and Thomas, 2014; Arctic and Southern Ocean – Kahru et al., 2010; Ardyna et al., 2014; Soppa et al., 2016; Oziel et al., 2017) and confined or estuarine ecosystems (Wiltshire et al., 2008; Nixon et al., 2009; Kromkamp and van Engeland, 2010; Groetsch et al., 2016; Kahru et al., 2015). However, most interannual changes in phytoplankton phenology and their underlying drivers are spatially variable, even over particular ocean basins (e.g., Yoo et al., 2008; Henson et al., 2010; Kahru et al., 2010; Martinez et al., 2011; Sasaoka et al., 2011; Friedland et al., 2016, 2018) or domains (e.g., Song et al., 2010; Lavigne et al., 2013; Zhao et al., 2013; Foukal and Thomas, 2014), depending on region-specific properties and factors controlling the initiation, collapse and magnitude of phytoplankton blooms. These results indicate that a proper geographic partitioning of marine ecosystems should be implemented for the investigation of phytoplankton phenology (e.g., Zhao et al., 2013).

Due to their ecological relevance, the shape of phytoplankton climatological seasonal cycles, extracted from Chl-a time series, has been used for objectively partitioning the complex spatial organization of ocean surface into biologically meaningful regions (bioregions, trophic regimes or bloom phenology regimes), at global (D'Ortenzio et al., 2012) or regional scales (D'Ortenzio and d'Alcalà, 2009; Sasaoka et al., 2011; Foukal and Thomas, 2014; Lacour et al., 2015; Mayot et al., 2015; Ardyna et al., 2017; Eliasen et al., 2017; Krug et al., 2017b). In some cases, phytoplankton phenology indices were used directly as input variables for delineating ocean surface "phenological provinces" or (pheno)regions (see Sasaoka et al., 2011; Xu et al., 2013; Land et al., 2014). Ocean partition represents a relevant strategy to simplify ocean complexity and disentangle the interactions between phytoplankton and multiple environmental determinants, particularly relevant for heterogeneous marine domains, providing a framework for assessing marine ecosystem status and trends, as well as its resilience and vulnerability to climate change (see reviews IOCCG, 2009; Krug et al., 2017a).

The southwest area off the Iberian Peninsula (SWIP; NE Atlantic), located at a transition zone between temperate and subtropical waters, constitutes a highly heterogeneous domain, particularly vulnerable to climate change (Kovats et al., 2014). A wide diversity of processes, including local and large scale oceanic and atmospheric circulation patterns, topographic irregularities, coastal upwelling and continental freshwater outflows, impacts phytoplankton spatial and temporal dynamics (e.g., Navarro and Ruiz, 2006; García-Lafuente and Ruiz, 2007; Prieto et al., 2009; Navarro et al., 2012; Bruno et al., 2013; Goela et al., 2013; Caballero et al., 2014; Sala et al., 2018), promoting the occurrence of distinct regions where phytoplankton are driven, differently, by specific combinations of physical and climatic environmental drivers (see Krug et al., 2017b). Due to its geographical location (eastern boundary of the North Atlantic basin), SWIP and its complex coastal areas are often overlooked (Follows and Dutkiewicz, 2002; Vargas et al., 2009; Racault et al., 2012; Ferreira et al., 2014) or sparsely resolved (e.g., Siegel et al., 2002; Ueyama and Monger, 2005; Henson et al., 2009; Kahru et al., 2010; Martinez et al., 2011; Demarcq et al., 2012; D'Ortenzio et al., 2012; Sapiano et al., 2012; Land et al., 2014; Racault et al., 2014b, 2017; González Taboada and Anadón, 2014; Cole et al., 2015; Cabré et al., 2016; Friedland et al., 2016, 2018; Zhang et al., 2017) in global or basin-scale phenological analysis. The analysis of phytoplankton phenology over SWIP at a finer, regional-scale resolution, however, has been restricted to the central Gulf of Cadiz area (Navarro et al., 2012). Thus, knowledge on phytoplankton phenology over the SWIP area, its interannual variability and underlying environmental drivers, is still limited.

In this context, our study aims to evaluate phytoplankton phenology patterns over the SWIP area, during an 18-year period (September 1997 – August 2015), using satellite ocean colour data, and to identify underlying environmental determinants. Our specific objectives are: (i) to evaluate the distribution of phytoplankton phenological indices over the study area and period, on a pixel-by-pixel basis; (ii) to partition the highly heterogeneous surface SWIP area into phenoregions using an objective, unsupervised partition based on phenological indices; (iii) to describe region-specific phytoplankton phenological indices and their interannual variability patterns; and (iv) to evaluate region-specific environmental determinants of phytoplankton phenology, including local ocean physical-chemical variables (mixed layer depth, photosynthetically available radiation and dissolved inorganic nutrients), hydrodynamic variables (riverine discharges and coastal upwelling intensity), and large scale climate indices.

2. Materials and methods

2.1. Study area

SWIP comprises a variety of oceanic and coastal domains. Open ocean domains are interspersed with submarine seamounts and canyons and, over the coast, a 5–35 km wide continental shelf shifts orientation, from meridional to zonal, at Cape São Vicente (CSV). CSV is the northwest limit of the Gulf of Cadiz (GoC), a basin that connects the Mediterranean Sea and the Atlantic Ocean. The main continental