

# 1 Three decades of marine bioregions evolution through 2 analysis of phytoplankton phenology

3 Wilhem Riom<sup>1</sup>, Nicolas Mayot<sup>1</sup>, Alexandre Mignot<sup>2</sup>, Vincent Taillandier<sup>1</sup>, Fabrizio  
4 D’Ortenzio<sup>1</sup>

5 <sup>1</sup> Sorbonne Université & CNRS, Laboratoire d’Océanographie de Villefranche, UMR 7093 LOV, 06230 Villefranche-sur-Mer, France

6 <sup>2</sup> Mercator Ocean International, 31400 Toulouse, France

7 *Correspondence to:* Wilhem Riom (wilhem.riom@imev-mer.fr)

## 8 Abstract

9 Ocean biogeochemistry is undergoing significant modification in response to climate change. To better  
10 track these evolutions, we present a novel ocean monitoring indicator that follows the temporal  
11 evolution of marine bioregions of similar phytoplankton phenologies. Chlorophyll-a concentration  
12 observations from remotely sensed ocean color describe seven distinct marine bioregions characterized  
13 by their unique patterns of phytoplankton biomass seasonality. The sizes and locations of these  
14 bioregions are monitored from 1998 to 2024 using a multi-sensor merged L4 ocean color product. While  
15 the bioregions’ extents appear to follow interannual and decadal climate variability, their long term  
16 evolution suggests a poleward extension of less seasonal phytoplankton phenology, which is generally  
17 characteristic of the tropical and subtropical bands. This innovative approach allows the systematic  
18 monitoring of how phytoplankton adapt their seasonal cycle in response to changes in environmental  
19 conditions, hence giving valuable insights into the evolution of marine ecosystems over the past three  
20 decades and helping advance our understanding of global ocean biological responses to environmental  
21 change.

## 22 1 Introduction

23 Phytoplankton, the main primary producers in the ocean, sustain marine food webs (Fenchel, 1988;  
24 Kiørboe, 1993) and play a central role in regulating oceanic carbon fluxes (Falkowski *et al.*, 1994).  
25 Environmental conditions shape phytoplankton growth and losses through “bottom-up” (e.g., light and  
26 nutrients availability) and “top-down” (e.g., grazing) processes. Over the past three decades, satellite  
27 ocean color measurements make it possible to estimate phytoplankton biomass (Behrenfeld *et al.*, 2005)  
28 proxied by chlorophyll-a concentration (Huot *et al.*, 2007). This, in turn, has enabled the study of  
29 phytoplankton phenology (i.e. the temporal succession of main biological events) (Longhurst, 2007;  
30 Racault *et al.*, 2012; Sapiano *et al.*, 2012, Boyce *et al.*, 2017). Climate influences the distribution of

31 environmental factors that, in turn, regulate the spatiotemporal dynamics of phytoplankton biomass  
32 (Falkowski and Oliver, 2007). Distinct seasonal patterns emerge along latitudinal gradients, from the  
33 equator to the poles (Longhurst, 1995). At high latitudes, primary production is mainly light limited,  
34 whereas in tropical and subtropical regions, phytoplankton production is essentially nutrient limited  
35 (Boyce *et al.*, 2017). Like the marine environment itself, phytoplankton biomass responds to both annual  
36 and decadal climate variability (Li *et al.*, 2024).

37 Climate change is altering oceanic ecosystems (ref from OSR #10 chapter 1), with complex impacts on  
38 phytoplankton growth. For instance, rising sea temperatures might directly affect metabolism (O'Connor  
39 *et al.*, 2009) but also environmental conditions through enhanced water column stratification  
40 (Yamaguchi and Suga, 2019), which in turn might further limit growth by hindering upward transport of  
41 nutrients to the sunlit layers (Sarmiento *et al.*, 2004; Fernández-González *et al.*, 2022). As for terrestrial  
42 plants (Cleland *et al.*, 2007; Inouye, 2022), marine phytoplankton are expected to respond to these  
43 environmental changes by adjusting their seasonal cycles (Winder and Sommer, 2012). Most of the  
44 documentation effort focused on variations in the onset, duration, and intensity of bloom events (e.g.,  
45 Sommer and Lengfellner, 2008; Martinez *et al.*, 2011; Henson *et al.*, 2018; Salgado-Hernanz, 2019). These  
46 changes may cause phenological mismatches hence disrupting energy transfer to higher trophic levels  
47 (Visser and Both 2005, Asch *et al.*, 2019) and have broader implications for the global carbon cycle (Fisher  
48 *et al.*, 2025). Consequently, establishing robust indicators monitoring interannual to decadal changes in  
49 phytoplankton phenology is critical to better address the evolution of the marine ecosystem with climate  
50 change.

51 With the large amount of remotely sensed ocean color observations, numerical clustering methods  
52 emerged as key tools to identify regions with similar seasonal dynamics of phytoplankton (hereafter  
53 referred to as bioregions) (International Ocean Color Coordinating Group, IOCCG, 2009). Several studies  
54 (e.g. D'Ortenzio and Ribera d'Alcalà, 2009; Lacour *et al.*, 2015; Ardyna *et al.*, 2017; Boyer *et al.*, 2017;  
55 Kheireddine *et al.*, 2021; Baudena *et al.*, 2025) have applied such methods to partition oceanic domains  
56 into bioregions characterized by similar seasonal patterns of chlorophyll-a concentration, which are  
57 often used as a basis for inferring provinces of similar biogeochemical functioning. Similarly to how  
58 Mayot *et al.* (2016) extended D'Ortenzio and Ribera d'Alcalà (2009) climatological partitioning of the  
59 Mediterranean Sea, this study presents an ocean monitoring approach built on Baudena *et al.* (2025)  
60 climatological bioregionalization of the global ocean. This method tracks variations in the extension of  
61 the bioregions in respect of time to reveal the trends in geographical changes of phytoplankton  
62 phenology. The main idea behind our approach is that tracking these variations may serve as a relevant  
63 proxy for assessing changes of phytoplankton dynamics, which, in turn, could inform on main variations  
64 of environmental factors of the marine ecosystem.

65 We introduce here a proof of concept for such an approach using the supervised clustering method  
66 introduced in Baudena *et al.*, 2025. Annual partition of the global ocean (56°S–56°N) from 1998 to 2024 is

67 obtained by classifying annual time series of remotely sensed chlorophyll-a concentration (Copernicus-  
68 GlobColor) into bioregions. After presenting the mean climatological state of the bioregions, we  
69 investigate their change in surface area over the last three decades. Then, building on D’Ortenzio *et al.*  
70 (2012) and adapting methods from Higgins *et al.* (2016), originally applied to terrestrial biomes, we  
71 compare the geographical extension of the bioregions between two decadal periods at the greatest extent  
72 of our dataset, (1998-2007 and 2015-2024) to identify the main trends in the reorganization of  
73 phytoplankton phenology. Finally, possible correlation with environmental changes and method  
74 limitations are evoked in the discussion section.

75 **2 Material and methods**

76 **2.1 Data**

77 Chlorophyll-a concentrations data were retrieved from the merged multi-sensor ocean color product ref.  
78 no. 1 (see Table 1). This product offers cloud free remotely sensed surface chlorophyll-a concentration at  
79 a 4 km spatial resolution and daily intervals. Using such a L4 product (an optimally interpolated, merged  
80 satellite dataset), as compared to L3 (merged product) in Baudena *et al.*, (2025), compensates for the lack  
81 of observation inherent to satellite ocean color (Stock *et al.*, 2020) and ensures a maximal spatialization  
82 of the bioregions at an annual temporal resolution.

| Product ref. no. | Product Id & type                                                | Data access                                       | Documentation                                                                                                                                   |
|------------------|------------------------------------------------------------------|---------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------|
| 1                | OCEANCOLOUR_GLO_<br>BGC_L4_MY_009_104,<br>Satellite observations | EU Copernicus<br>Marine Service<br>Product (2024) | Quality<br>Information<br>Document<br>(QUID):<br>Garnesson <i>et al.</i><br>(2025)<br>Product User<br>Manual (PUM):<br>Colella et<br>al. (2024) |

83 **Table 1: Product table**

84 **2.2 Supervised Clustering**

85 Annual ensembles of seasonal time series of chlorophyll-a concentration were built from 1998 to 2024.  
86 The time series composing them were all processed similarly to allow subsequent classification  
87 according to Baudena *et al.* (2025) supervised clustering method. In short, within each annual ensemble,  
88 each individual time series characterizes the seasonal evolution of chlorophyll-a concentration over a

89 1° × 1° grid. Following the method detailed in supplementary section S1, the time series were obtained  
90 averaging all available observations within each 1x1° pixel over a 8-day temporal window. To dampen  
91 sub-seasonal variations, time series were all smoothed with a 5 weeks centered rolling average method.  
92 Finally, all annual time series were normalized by their maximum to ensure that the clustering method  
93 focuses on their shape rather than on their magnitude.

94 Time series associated with pixels in the Arctic and Southern Oceans (respectively above 56°N and below  
95 56°S) were removed from every annual ensemble due to lack of continuous satellite observation through  
96 winter in relation to permanent cloud presence and polar night. Coastal pixels located within 111 km  
97 (~1°) from the coast were also discarded due to the uncertainty in chlorophyll-a concentration  
98 estimations within optically complex waters (Case 2 waters). As a result 80% of the global ocean area is  
99 considered. In the southern hemisphere, time series were all shifted six months backward, to ensure  
100 identical sequencing of seasons in the time series of all pixels.

101 Each annual ensemble was then partitioned into the seven clusters of Baudena *et al.*, 2025 based on their  
102 seasonality patterns. These seven clusters were found to optimally partition open ocean seasonal cycles  
103 of surface chlorophyll-a concentration in respect of multiple statistical tests discussed in the companion  
104 study. The assignment of a given time serie into one of the clusters was done according to its minimal  
105 euclidean distance (maximal similarity) with the central time series of Baudena *et al.*, 2025 clusters. To  
106 prevent assignment of too dissimilar seasonal patterns, a threshold distance was considered to accept  
107 (distance below the threshold) or refuse (distance above the threshold) an assignment. To account for the  
108 method's sensitivity to this hyperparameter, we discretized a range of possible values, defined by the  
109 minimum and maximum classification distances found among the most deviating elements of any  
110 cluster, from 1.33 (cluster 1) to 2.60 (cluster 7), based on the unsupervised clustering of Baudena *et al.*,  
111 (2025). Each annual ensemble was partitioned several times from a low (strict definition of the clusters)  
112 to high threshold values (lax definition of the clusters) selected within this range with a regular step of  
113 0.05 (see sensitivity analysis in supplementary section 2). At least 88 % of the time series were always  
114 successfully sorted within the seven clusters (see Fig. S2b). Unclassified time series, mostly located in  
115 regions of low satellite data availability region (see Fig. S2a), were all excluded from ulterior analysis.

## 116 2.3 Bioregions

117 The spatial projection of each pixel's membership over the global ocean forms large coherent spatial  
118 domains similarly classified. These oceanic domains correspond to the bioregions as defined by Baudena  
119 *et al.* (2025). As a reminder, bioregions share similar seasonal patterns in phytoplankton phenology  
120 suggesting a common biogeochemical functioning (Longhurst, 1995). Over time, the spatial definition of  
121 the bioregion might change with annual time series characteristic of a given pixel being attributed to  
122 different clusters over different years. A change of phytoplankton phenology is attributed to a pixel when  
123 its bioregion changes from one year to another. For a given pixel, the frequency of phenology change is

defined as the total sum of these changes over the study period. These changes might present oscillating patterns from annual to decadal period or long term trends.

Three climatological partitions of the global ocean were considered hereafter. They were constructed by keeping, in each pixel, the most frequent bioregion over the selected temporal extent. The three considered periods are: from 1998 to 2024 and two decadal periods from 1998 to 2007 and from 2015 to 2024. The former climatological period supports the documentation of the average bioregion extent while the molatter two decadals periods were chosen at the edge of the temporal span to support the documentation of long term changes in the bioregion's extent. The use of decadal bioregions also dampens interannual variability.

When comparing the decadal bioregions' extent between the 1998-2007 and the 2015-2024, we attribute a stable phenology change to a given pixel when its classification changed between the two periods and if this assignment remained identical for more than six years in each of the two decades. This temporal criterion was chosen strictly above half a decade to grant a reasonable and robust indicator of the bioregion persistence while remaining permissive in respect of inter annual climate variability.

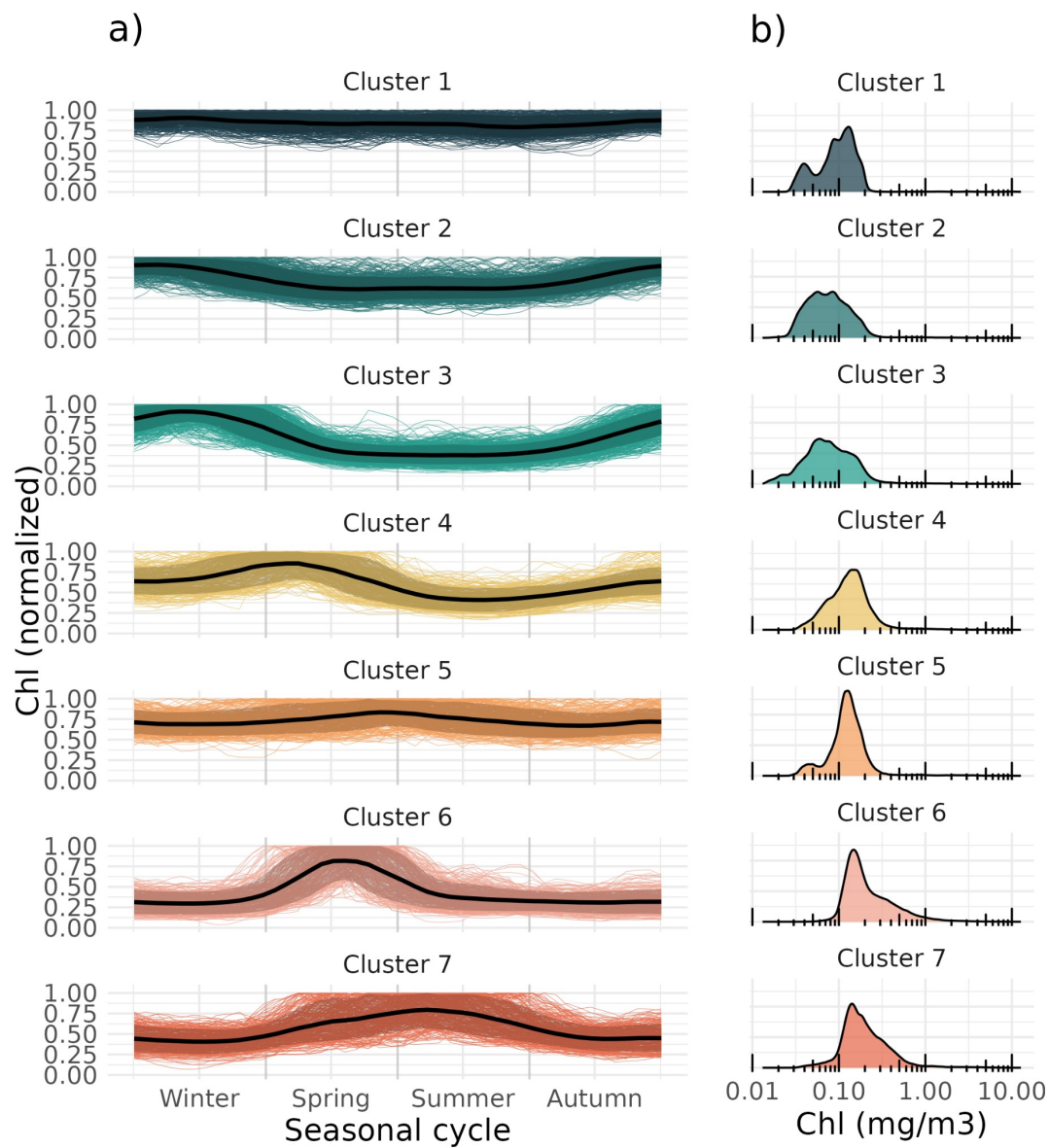
To assess phytoplanktonic biomass across the bioregions, we analyzed their chlorophyll-a concentrations, presented as probability distribution functions in Fig. 1b. The distribution for bioregion 1 is notably bimodal, showing a minor peak near  $0.03 \text{ mg.m}^{-3}$  and a dominant one just above  $0.1 \text{ mg.m}^{-3}$ . This finding prompted us to subdivide bioregion 1, after the clustering, based on a threshold of  $0.06 \text{ mg.m}^{-3}$  for yearly average chlorophyll-a, creating an oligotrophic group (below the threshold) and a mesotrophic group (above the threshold). Although both sub-regions exhibit a similar non-seasonal pattern, this subdivision reveals distinct phenologies, suggesting they are controlled by different environmental forcings that either sustain or inhibit year-round phytoplankton growth.

## 2.4 Uncertainties estimation

Following the set of threshold distance, each annual ensemble is partitioned twenty six times (see section 2.2). In each of these partitions, the distribution of the bioregion surface area relative to the set of threshold distances is characterised hereafter by its central value (the median) within its interquartile range (Q1–Q3). The interquartile range of surface area estimates accounts for the bioregionalization method uncertainty. All surface areas are reported relative to the total global ocean area. To identify long-term changes, we fitted a linear model to the central surface area estimates in respect of time. The statistical significance of these linear trends was determined using a Spearman rank correlation, with a trend considered significant at  $p < 0.1$ .

155 **3 Results**

156 Our analysis is presented in three parts. First, we recall the phytoplankton phenology and climatological  
157 repartition of the seven marine bioregions (described in more details in Baudena *et al.*, 2025). Second, we  
158 assess the interannual variability and long-term trends in the surface area evolution of each bioregion  
159 from 1998 to 2024. Finally, we identify the locations of stable phenological changes by comparing two  
160 distinct decades at the edges of the period.



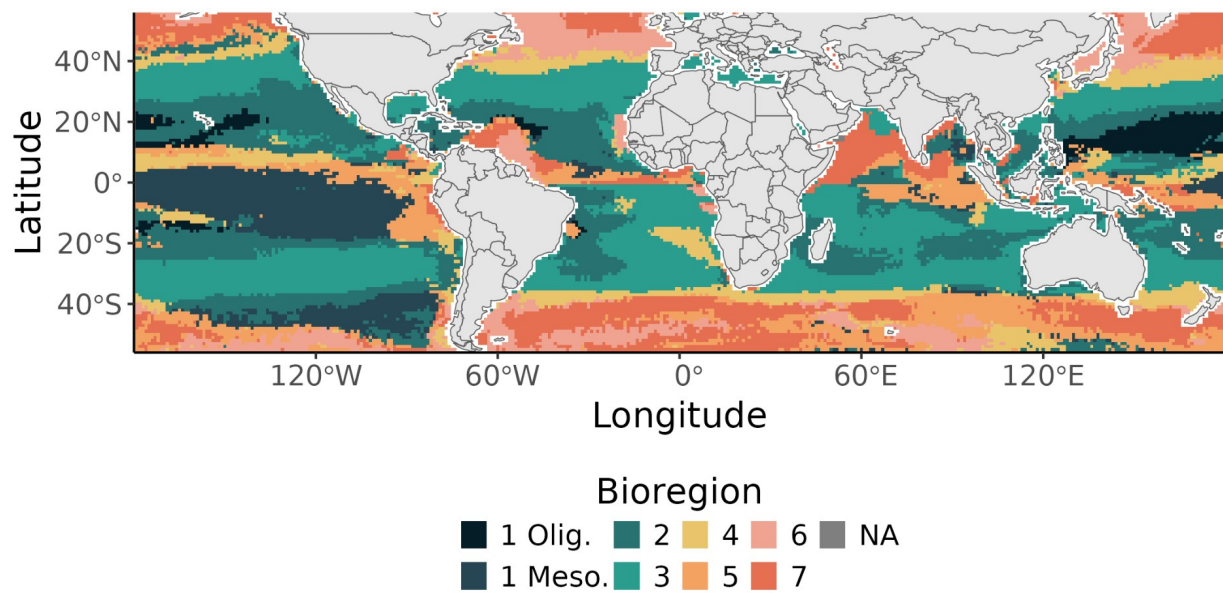
162  
163 **Figure 1: Clusters resulting from the supervised clustering of the ensemble of year 2024 from product ref. no.**  
164 **1 according to the strictest threshold. The left panel (a), shows the mean normalized seasonal cycles within**  
165 **each cluster (thick continuous black line) within its 10% and 90% percentiles (transparent black bands). In the**  
166 **background, examples of time series within that cluster are represented. The right panel (b), displays the**  
167 **distribution of chlorophyll concentration within each cluster.**

168 For each year, the supervised clustering method subdivides the ensemble into the seven clusters  
169 identified in Baudena *et al.* (2025). These clusters outline specific phenological patterns inferred from the  
170 mean seasonal cycle of chlorophyll-a concentration (Fig. 1a). These patterns range from no clear  
171 seasonality (bioregion 1) to those with pronounced single or double peak events (bioregions 7-6-4), which  
172 are typical of blooms in temperate and high-latitude systems, as we found in Fig. 2a.

173 In agreement with Baudena *et al.* (2025), the climatological distribution of the related bioregions over the  
174 1998-2024 period (Fig. 2a) follows a meridional distribution sketching coherent, large-scale structures  
175 corresponding to major oceanic domains, such as the subtropical gyres (bioregions 1 Olig., 2 and 3) and  
176 convergences zones (bioregion 4). The biogeochemical relevance of this partitioning is reinforced by the  
177 distribution of chlorophyll-a concentrations within each bioregion (Fig. 1b). A clear poleward  
178 productivity gradient emerges, with the lowest surface biomass in the perpetually stratified regimes of  
179 the subtropical band and the highest in the high-latitude bloom regions (bioregion 6-7). This aligns with  
180 established knowledge of global ocean productivity patterns (Behrenfeld *et al.*, 2005).

181 Baudena *et al.* (2025) offered a biogeochemical interpretation of the bioregions, summarized as follows.  
182 Bioregions 6 and 7 correspond to Longhurst's (1995) model 1 (*polar, irradiance-limited*). Bioregion 5  
183 exhibits features of both model 1 and model 2 (*mid-latitude, nutrient-limited spring production peak*).  
184 Bioregion 4 closely aligns with the Bloom bioregion identified by D'Ortenzio *et al.* (2012). Bioregion 3  
185 matches Longhurst's (1995) model 3 (*subtropical, winter nutrient-limited*), whereas Bioregion 2 closely  
186 resembles the Tropical bioregion described by D'Ortenzio *et al.* (2012). Finally, Bioregion 1 corresponds  
187 to Longhurst's model 4 (*tropical*). Its additional subdivision, introduced here, produces spatially coherent  
188 domains that distinguish between oligotrophic regions in the centers of subtropical gyres and  
189 mesotrophic regions primarily distributed around the equator.

(a) 1998-2024



(b) 1998-2024

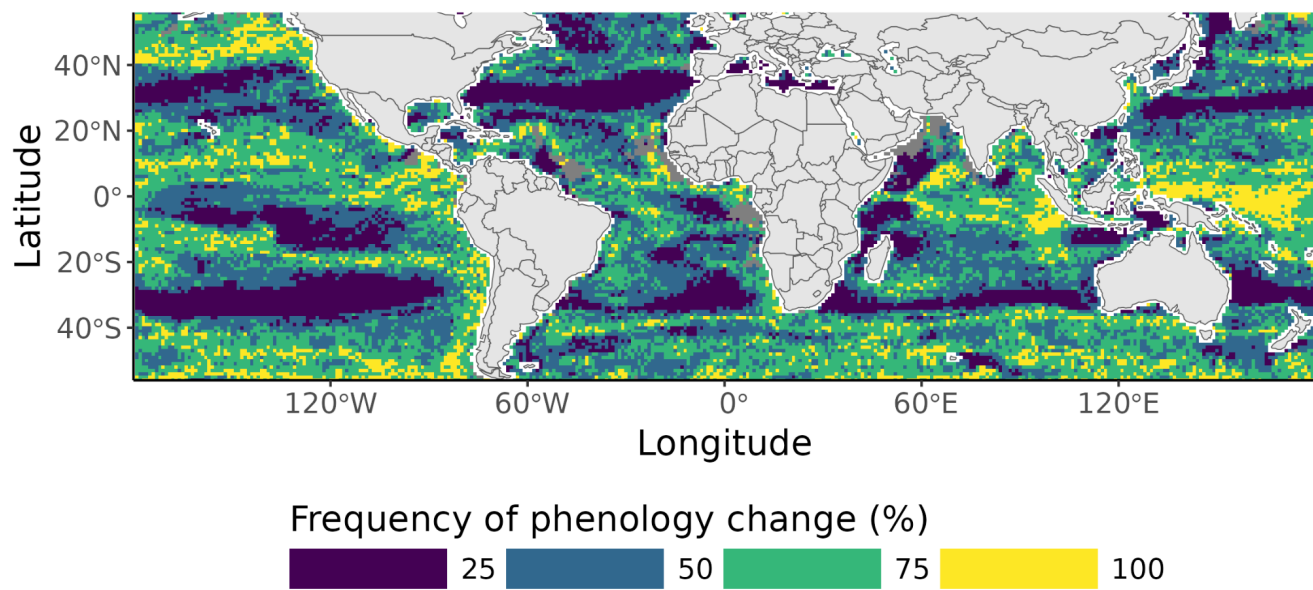


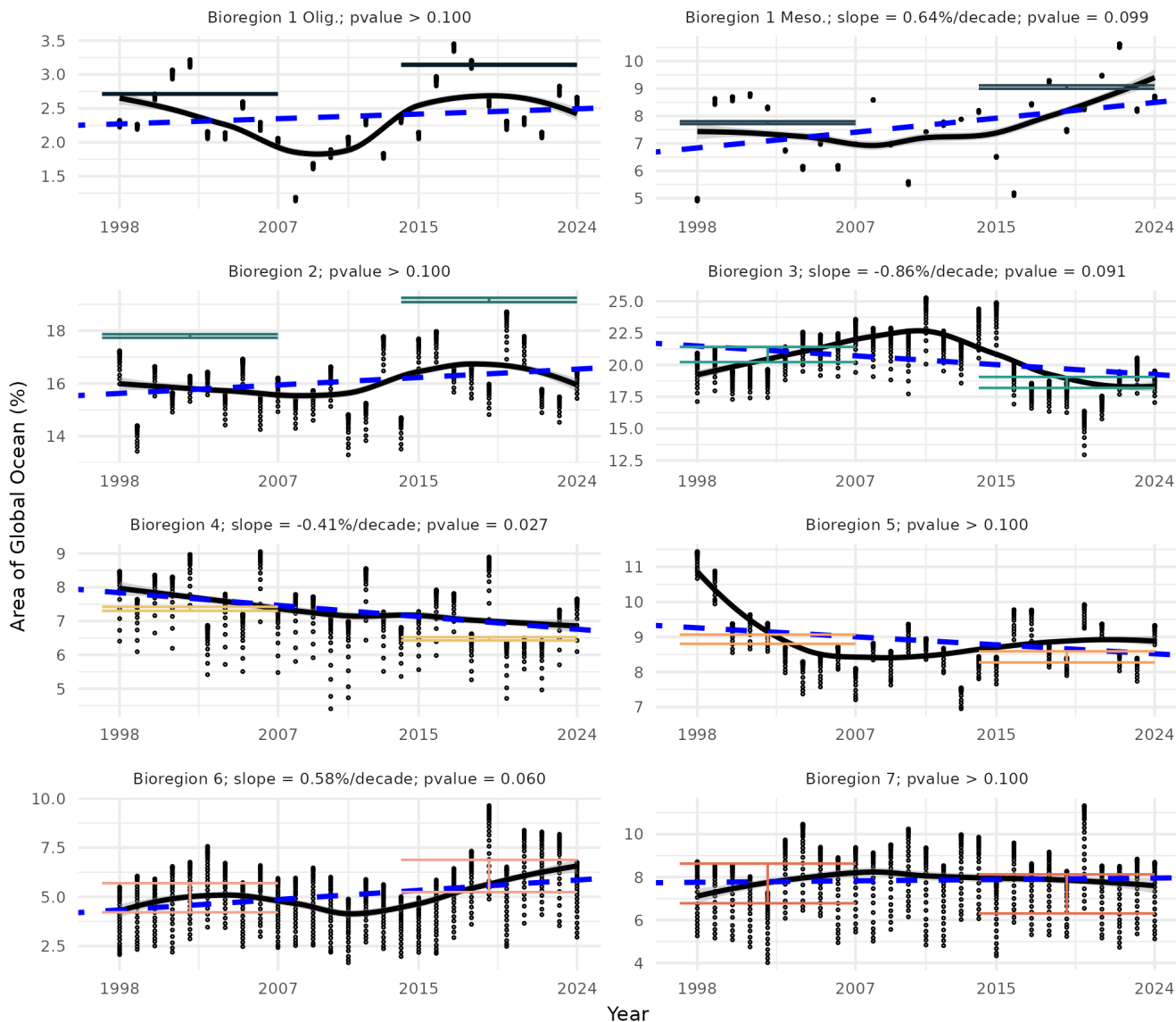
Figure 2: (a) Climatological distribution of the bioregions in the 1998-2024 period. (b) Amount of phenology change per pixel over the 1998-2024 period given in % of the total number of considered years. Both panels display the results obtained using the least strict clustering criteria on the ensemble processed from product ref. no. 1. Pixels designated as NA (in grey) refer to the position of the time series that were not successfully

196 **classified.**

197 **3.1 Temporal evolution of the bioregions**

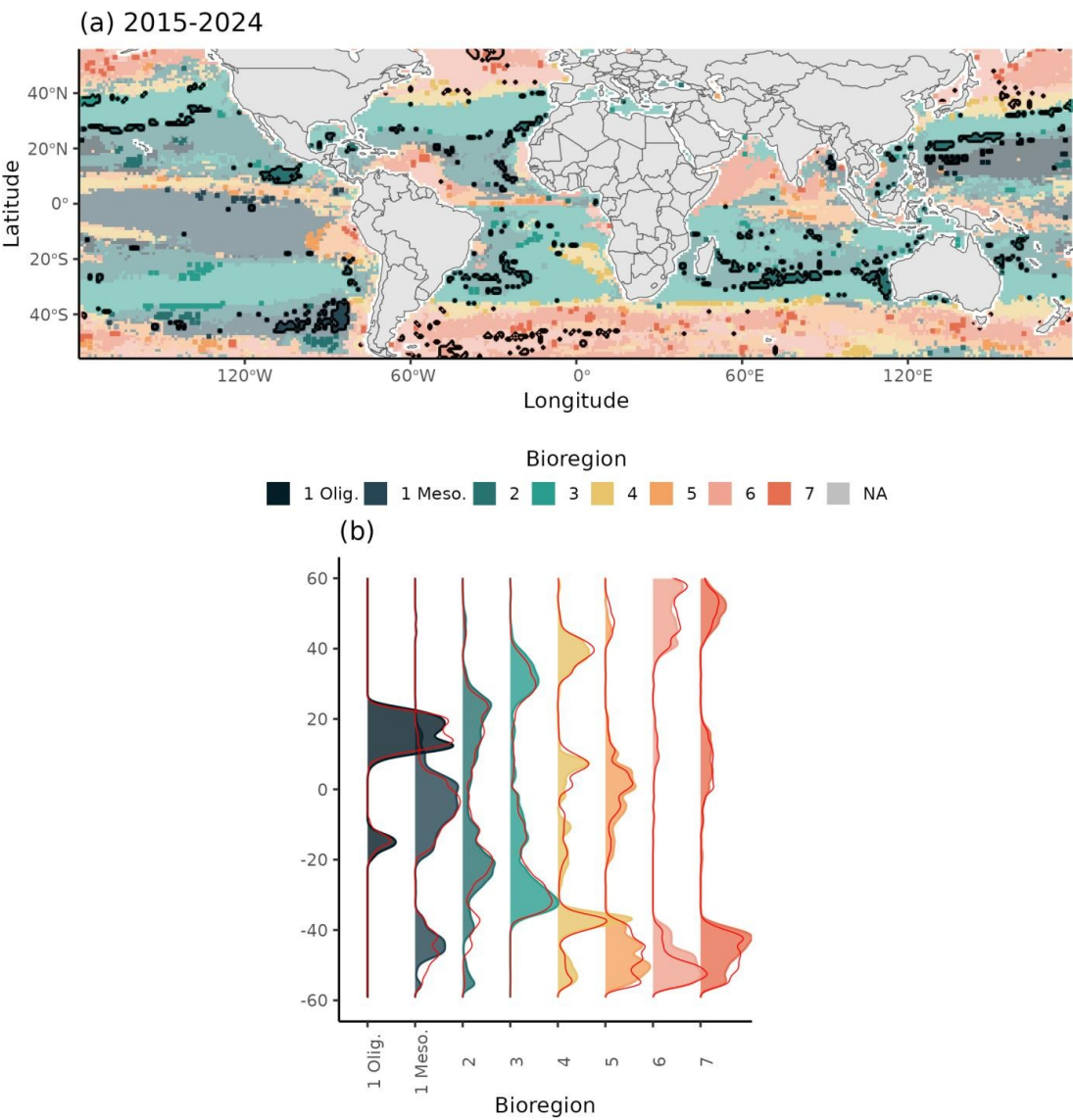
198 The boundaries of bioregions in Fig. 2a are not static. Fig. 2b displays the frequency of changes in each  
199 pixel bioregion's affiliation, interpreted as changes in phytoplankton phenology, over the 1998–2024  
200 period. These changes occur most frequently in transitional areas in-between major bioregions, as well  
201 as in coastal zones, over the equatorial band, and over high-latitude regions of the northern Pacific and  
202 Southern Ocean (Fig. 2b). Bioregion 3, centered at 30° in both hemispheres, appears as the most stable  
203 bioregion.

204 A visual analysis of the temporal evolution of each bioregion's surface area (Fig. 3) reveals strong  
205 interannual variabilities (time evolution of black dots) in all bioregions. Bioregions 1, 2, 3 and 6 also  
206 display high decadal variability (black lines). Linear trend analysis ( $p < 0.1$ ) indicates a significant  
207 reduction in the global surface area of bioregion 3 and bioregion 4. Conversely, the mesotrophic  
208 bioregion 1 shows a significant expansion. While surface areas of bioregions 6 and 7 exhibit large  
209 changes from one year to the other, their surface area estimates are associated with large method  
210 uncertainties (~50%), precluding the consideration of the trend significance.



211

212 **Figure 3 : Evolution of bioregions' surface area from 1998 to 2024. The time evolution of black dots represent**  
 213 **estimates of the areas following the varying acceptance thresholds. The black trend line displays the**  
 214 **smoothed centered 10-year rolling average, the blue dotted line corresponds to the linear tendency of the**  
 215 **annual median area estimate. Panel's titles show the linear trends on the condition that it was found**  
 216 **significant ( $p < 0.1$ ). First and third quartiles of the decadal bioregions (1998-2007 and 2015-2024) are indicated**  
 217 **as colored error bars. Note the varying y-scale across panels.**



219

220 **Figure 4: (a) Bioregions in the 2015-2024 decadal period with stable changes identified by black contours. (b)**

221 **displays the latitudinal distribution of bioregions between the 1998-2007 decadal period, as red line, and the**

222 **2015-2024 period, with colored and filled distributions, respectively.**

223 To isolate long-term trends from interannual variability, we identified areas with stable phenological

224 changes between the 1998–2007 and 2015–2024 decadal periods. As highlighted in Fig. 4a, these regions  
 225 are mostly located within the tropical and subtropical band. Overall 4.93% [4.56%, 5.06%] of the global  
 226 ocean is affected suggesting slow transitions in essentially steady conditions. The dominant pathways in  
 227 phenology transition are summarized in Table 2. The most prominent change (1.82% of the global ocean)  
 228 is the transition from bioregion 3 to the less seasonal bioregion 2, occurring primarily in the subtropical  
 229 Pacific and Indian Oceans. Other significant shifts include the expansions at lower latitude of bioregion 1  
 230 at the expense of bioregion 2 (0.62%) and of bioregion 3 at the expense of bioregion 4 (0.27%). In the  
 231 North Atlantic's temperate band, a notable net transition from bioregion 7 to 6 also occurred (0.09%). As  
 232 summarized by Fig.4b, the most prominent trend is a poleward expansion of bioregions of weaker  
 233 seasonality. These spatial patterns of change correspond to the surface area trends observed over the full  
 234 time series (Fig. 3).

|                                      |              | Oceanic Basins               |                               |                               |                               |                               | Total                         |
|--------------------------------------|--------------|------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|
|                                      |              | Indian Ocean                 | North Pacific Ocean           | South Pacific Ocean           | North Atlantic Ocean          | South Atlantic Ocean          |                               |
| Pathways of stable phenology changes | 2 to 1 Olig. | -                            | <b>0.12 %</b><br>[0.12, 0.12] | 0.01%<br>[0.01, 0.01]         | 0.03 %<br>[0.03, 0.03]        | -                             | <b>0.16 %</b><br>[0.16, 0.16] |
|                                      | 2 to 1 Meso. | 0.03 %<br>[0.03, 0.03]       | -                             | <b>0.36 %</b><br>[0.36, 0.36] | 0.07%<br>[0.07, 0.07]         | -                             | <b>0.46 %</b><br>[0.46, 0.46] |
|                                      | 3 to 2       | <b>0.67%</b><br>[0.66, 0.67] | <b>0.55%</b><br>[0.52, 0.55]  | <b>0.15 %</b><br>[0.15, 0.15] | <b>0.19 %</b><br>[0.18, 0.19] | <b>0.21 %</b><br>[0.21, 0.21] | <b>1.82 %</b><br>[1.78, 1.83] |
|                                      | 4 to 3       | 0.01 %<br>[0.01, 0.01]       | <b>0.16 %</b><br>[0.14, 0.16] | 0.02 %<br>[0.01, 0.02]        | 0.02 %<br>[0.02, 0.02]        | 0.06 %<br>[0.06, 0.06]        | <b>0.27 %</b><br>[0.24, 0.27] |
|                                      | 6 to 7       | -                            | 0.03 %<br>[0.02, 0.06]        | 0.02 %<br>[0.01, 0.02]        | 0.08 %<br>[0.03, 0.10]        | 0.01 %<br>[0.001, 0.10]       | <b>0.13 %</b><br>[0.06, 0.19] |
|                                      | 7 to 6       | 0.01%<br>[0.01, 0.01]        | 0.01%<br>[0.01, 0.02]         | -                             | <b>0.17 %</b><br>[0.13, 0.19] | <b>0.23 %</b><br>[0.19, 0.24] | <b>0.43 %</b><br>[0.33, 0.47] |

235  
 236 **Table 2: Major pathways among stable phenology changes. Changes in surface area from one bioregion to**  
 237 **another are given relatively to the global ocean. Estimates are given within their first and third quartiles and**  
 238 **grouped by oceanographic basins. Minor changes, associated with an area inferior to 0.1% of the global ocean,**  
 239 **are not represented. Estimates highlighted in bold indicate values greater than 0.1 % of the global ocean.**

240 **4 Discussion and conclusion**

241 Our analysis introduces a novel ocean indicator approach that distinguishes between intermittent, year-  
242 to-year variability and persistent, long-term shifts in phytoplankton phenology. While boundary regions  
243 exhibit frequent intermittent changes (Fig. 2b), our decadal analysis finds that nearly 5% (see Table 2) of  
244 the global ocean experienced a displacement of phytoplankton phenology suggesting persistent  
245 ecosystem reorganization over the past three decades. The cascading changes (i.e., transitions from  
246 bioregion 4 to 3, bioregion 3 to 2, and 2 to 1) identified above, are possibly driven by an intensification of  
247 upper-ocean stratification in relation to climate warming (Capotondi *et al.*, 2012). At these low latitudes  
248 (30°S-30°N), a shallower vertical mixing prevents entrainment of deeper nutrients (Vereshchaka and  
249 Shatravin, 2025) therefore hindering biomass accumulation of surface waters (Sarmiento *et al.*, 2004;  
250 Polovina *et al.*, 2008). The robustness of our ocean indicator approach is further validated in the  
251 temperate North Atlantic, where despite high method uncertainties, the documented shift from a double  
252 to a single bloom phenology (bioregion 7 to 6) linked to delayed autumnal mixing in Martinez *et al.*  
253 (2011) is successfully captured. The documented changes also echo the variations of micronekton  
254 habitats provinces monitored from sea surface temperature, stratification index and net primary  
255 production evolution in Alberne *et al.* (2025).

256 The proposed ocean monitoring approach is nevertheless subject to several limitations. First, satellite  
257 ocean color observations are sparse at high latitudes inducing increasing method uncertainties poleward  
258 and the exclusion of the subpolar and polar domains (above 60°). In these domains significant and rapid  
259 phenological changes are already documented (Kahru *et al.*, 2011; Thomalla *et al.*, 2023; Manizza *et al.*,  
260 2023), with potential propagating effects on higher trophic levels (Fossheim *et al.*, 2015). Second, because  
261 satellites only measure the ocean surface, our analysis cannot capture changes in subsurface  
262 productivity patterns, such as the deepening of the deep chlorophyll maximum (Mignot *et al.* 2014,  
263 Cornec *et al.*, 2021). Finally, while the twenty seven year long time series is substantial, it remains  
264 challenging to definitively disentangle long-term climate-driven trends from the influence of natural  
265 decadal-scale climate modes (e.g., D'Ortenzio *et al.*, 2012; Zhai *et al.*, 2013; Li *et al.*, 2024).

266 Despite these limitations, the ocean indicator approach presented here provides a powerful and  
267 pragmatic tool to effectively map the locations of potential long-term ecosystem shifts. This makes it a  
268 crucial complement to established indicators, such as the ocean indicator method for chlorophyll-a  
269 concentration (10.48670/moi-00230). While such concentration-based indicators quantify how much  
270 biomass is present, our phenology-based approach reveals how the ecosystem's seasonal dynamics are  
271 unfolding. It can therefore detect critical shifts in ecosystem structure and function even when the total  
272 annual biomass remains unchanged. Furthermore, identifying long term trends in the distribution of  
273 chlorophyll-a concentration was shown to be dependent on the type of ocean color product (Zhai *et al.*,  
274 2024, Pauthenet *et al.*, 2024). Investigating the presence and variability of the bioregions based on ESA's

275 Ocean Color Climate Change Initiative (Sathyendranath *et al.*, 2019) would further consolidate  
276 (invalidate) the highlighted trends. In this paper, we mainly propose an approach, a proof-of-concept,  
277 that could be further applied to other ocean colors time-series

278 Future work could integrate Global ocean hindcast, to overcome the limitations of remotely sensed ocean  
279 color and extend monitoring to regions with poor satellite coverage (10.48670/moi-00019) and other four  
280 dimensional products (10.48670/moi-00046) to account for in-depth process. Earth system models can  
281 also help predict future states according to climatic projections (Yamaguchi *et al.*, 2022; Fisher *et al.*,  
282 2025). The partitioning could also be refined by incorporating additional variables (e.g., the particulate  
283 backscattering coefficient) to better delineate bioregions. However, the current method's simplicity  
284 remains its main asset, ensuring a broad application range, ease of use, and making it an ideal candidate  
285 for immediate operational implementation.

286 **Data availability**

287 Ocean color data were collected from the OCEANCOLOUR\_GLO\_BGC\_L4\_MY\_009\_104 product, provided  
288 by the Copernicus Marine Environment Monitoring Service (CMEMS, <http://marine.copernicus.eu/>).  
289 Cluster centroids resulting from Baudena *et al.* (2025) were obtained directly from the author.

290 **Author Contribution CRediT**

291 **WR:** Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Visualization,  
292 Writing – Original Draft Preparation. **NM:** Conceptualization, Investigation, Methodology, Writing –  
293 Original Draft Preparation, Visualization, Writing – Review & Editing. **AM:** Conceptualization, Formal  
294 Analysis, Visualization, Writing – Review & Editing. **VT:** Conceptualization, Supervision, Writing – Review  
295 & Editing. **FDO:** Conceptualization, Funding Acquisition, Supervision, Writing – Review & Editing.

296 **Competing Interests**

297 The authors declare that they have no known competing financial interests or personal relationships that  
298 could have appeared to influence the work reported in this paper.

299 **Acknowledgement**

300 The authors gratefully acknowledge Karina von Schuckmann for her insightful guidance and valuable  
301 contributions throughout all stages of the present study.  
302 During the preparation of this work the authors used ChatGPT-4 from OpenAI (<https://chat.openai.com>)  
303 in order to improve the readability and language of the manuscript. After using this tool/service, the  
304 authors reviewed and edited the content as needed and take full responsibility for the content of the  
305 publication.

307 **Financial Support**

308 NM received in 2025 a postdoctoral research grant from the CNES (Centre National d'Etudes Spatiales).

309 WR acknowledge the financial support from the CNES through the APR - 2022 (project SEASONS) and  
310 BRIDGES-AVATAR (grant ANR-22-EXBR-0004) integrated in France (2030) and managed by Agence  
311 Nationale de la Recherche.

312 **References**

313 Albernhe, S., Gorgues, T., Titaud, O., Lehodey, P., Menkes, C., and Conchon, A.: Micronekton indicators  
314 evolution based on biophysically defined provinces, in: Ocean State Report 9, Copernicus GmbH,  
315 <https://doi.org/10.5194/sp-6-osr9>, 2025.

316 Ardyna, M., Claustre, H., Sallée, J., D'Ovidio, F., Gentili, B., Van Dijken, G., D'Ortenzio, F., and Arrigo, K. R.:  
317 Delineating environmental control of phytoplankton biomass and phenology in the Southern Ocean,  
318 *Geophysical Research Letters*, 44, 5016–5024, <https://doi.org/10.1002/2016GL072428>, 2017.

319 Asch, R. G., Stock, C. A., and Sarmiento, J. L.: Climate change impacts on mismatches between  
320 phytoplankton blooms and fish spawning phenology, *Global Change Biology*, 25, 2544–2559,  
321 <https://doi.org/10.1111/gcb.14650>, 2019.

322 Baudena, A., Riom, W., Taillandier, V., Mayot, N., Mignot, A., and D'Ortenzio, F.: Comparing satellite and  
323 BGC-Argo chlorophyll estimation: A phenological study, *Remote Sensing of Environment*, 326, 114743,  
324 <https://doi.org/10.1016/j.rse.2025.114743>, 2025.

325 Behrenfeld, M. J., Boss, E., Siegel, D. A., and Shea, D. M.: Carbon-based ocean productivity and  
326 phytoplankton physiology from space, *Global Biogeochemical Cycles*, 19, 2004GB002299,  
327 <https://doi.org/10.1029/2004GB002299>, 2005.

328 Boyce, D. G., Petrie, B., Frank, K. T., Worm, B., and Leggett, W. C.: Environmental structuring of marine  
329 plankton phenology, *Nat Ecol Evol*, 1, 1484–1494, <https://doi.org/10.1038/s41559-017-0287-3>, 2017.

330 Capotondi, A., Alexander, M. A., Bond, N. A., Curchitser, E. N., and Scott, J. D.: Enhanced upper ocean  
331 stratification with climate change in the CMIP3 models, *J. Geophys. Res.*, 117,  
332 <https://doi.org/10.1029/2011jc007409>, 2012.

333 Cleland, E., Chuine, I., Menzel, A., Mooney, H., and Schwartz, M.: Shifting plant phenology in response to  
334 global change, *Trends in Ecology & Evolution*, 22, 357–365, <https://doi.org/10.1016/j.tree.2007.04.003>, 2007.

335 Colella, S., Böhm, E., Cesarini, C., Jutard, Q., and Brando, V. E.: EU Copernicus Marine Service Product User  
336 Manual for Ocean Colour Products, OCEANCOLOUR\_GLO\_BGC\_L4\_MY\_009\_104, Issue 5.0, 2024.

337 Cornec, M., Claustre, H., Mignot, A., Guidi, L., Lacour, L., Poteau, A., D'Ortenzio, F., Gentili, B., and  
338 Schmechtig, C.: Deep Chlorophyll Maxima in the Global Ocean: Occurrences, Drivers and Characteristics,  
339 *Global Biogeochemical Cycles*, 35, <https://doi.org/10.1029/2020gb006759>, 2021.

340 D'Ortenzio, F. and Ribera d'Alcalà, M.: On the trophic regimes of the Mediterranean Sea: a satellite  
341 analysis, *Biogeosciences*, 6, 139–148, <https://doi.org/10.5194/bg-6-139-2009>, 2009.

342 D'Ortenzio, F., Antoine, D., Martinez, E., and Ribera d'Alcalà, M.: Phenological changes of oceanic  
343 phytoplankton in the 1980s and 2000s as revealed by remotely sensed ocean-color observations, *Global*  
344 *Biogeochemical Cycles*, 26, 2011GB004269, <https://doi.org/10.1029/2011GB004269>, 2012.

345 European Union-Copernicus Marine Service: Global ocean biogeochemistry hindcast,  
346 <https://doi.org/10.48670/MOI-00019>, 2018.

347 European Union-Copernicus Marine Service: Global Ocean 3D Chlorophyll-a concentration, Particulate  
348 Backscattering coefficient and Particulate Organic Carbon, <https://doi.org/10.48670/MOI-00046>, 2020a.

349 European Union-Copernicus Marine Service: Global Ocean Chlorophyll-a trend map from Observations  
350 Reprocessing, <https://doi.org/10.48670/MOI-00230>, 2020b.

351 European Union-Copernicus Marine Service: Global Ocean Colour (Copernicus-GlobColour), Bio-Geo-  
352 Chemical, L4 (monthly and interpolated) from Satellite Observations (1997-ongoing),  
353 <https://doi.org/10.48670/MOI-00281>, 2022.

354 Falkowski, P. G.: The role of phytoplankton photosynthesis in global biogeochemical cycles, *Photosynth*  
355 *Res*, 39, 235–258, <https://doi.org/10.1007/bf00014586>, 1994.

356 Falkowski, P. G. and Oliver, M. J.: Mix and match: how climate selects phytoplankton, *Nat Rev Microbiol*,  
357 5, 813–819, <https://doi.org/10.1038/nrmicro1751>, 2007.

358 Fenchel, T.: Marine Plankton Food Chains, *Annual Review of Ecology and Systematics*, 19, 19–38, 1988.

359 Fernández-González, C., Tarran, G. A., Schuback, N., Woodward, E. M. S., Aristegui, J., and Marañón, E.:  
360 Phytoplankton responses to changing temperature and nutrient availability are consistent across the  
361 tropical and subtropical Atlantic, *Commun Biol*, 5, 1035, <https://doi.org/10.1038/s42003-022-03971-z>, 2022.

362 Fisher, B. J., Poulton, A. J., Meredith, M. P., Baldry, K., Schofield, O., and Henley, S. F.: Climate-driven shifts  
363 in Southern Ocean primary producers and biogeochemistry in CMIP6 models, *Biogeosciences*, 22, 975–  
364 994, <https://doi.org/10.5194/bg-22-975-2025>, 2025.

365 Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., and Dolgov, A. V.: Recent  
366 warming leads to a rapid borealization of fish communities in the Arctic, *Nature Clim Change*, 5, 673–677,  
367 <https://doi.org/10.1038/nclimate2647>, 2015.

368 Garnesson, P., Mangin, A., and Jutard, Q.: EU Copernicus Marine Service Quality Information Document  
369 for the Global Ocean Colour (Copernicus-GlobColour), Bio-Geo-Chemical, L4 from Satellite Observations,  
370 OCEANCOLOUR\_GLO\_BGC\_L4\_MY\_009\_104, Issue 5.1, 2025.

371 Henson, S. A., Cole, H. S., Hopkins, J., Martin, A. P., and Yool, A.: Detection of climate change-driven trends  
 372 in phytoplankton phenology, *Global Change Biology*, 24, <https://doi.org/10.1111/gcb.13886>, 2018.

373 Higgins, S. I., Buitenwerf, R., and Moncrieff, G. R.: Defining functional biomes and monitoring their  
 374 change globally, *Global Change Biology*, 22, 3583–3593, <https://doi.org/10.1111/gcb.13367>, 2016.

375 Huot, Y., Babin, M., Bruyant, F., Grob, C., Twardowski, M. S., and Claustre, H.: Relationship between  
 376 photosynthetic parameters and different proxies of phytoplankton biomass in the subtropical ocean,  
 377 *Biogeosciences*, 4, 853–868, <https://doi.org/10.5194/bg-4-853-2007>, 2007.

378 Inouye, D. W.: Climate change and phenology, *WIREs Climate Change*, 13, e764,  
 379 <https://doi.org/10.1002/wcc.764>, 2022.

380 IOCCG, Dowell, M., and Platt, T.: Partition of the Ocean into Ecological Provinces: Role of Ocean-Colour  
 381 Radiometry., International Ocean Colour Coordinating Group (IOCCG), <https://doi.org/10.25607/OBP-99>,  
 382 2009.

383 Kahru, M., Brotas, V., Manzano-Sarabia, M., and Mitchell, B. G.: Are phytoplankton blooms occurring  
 384 earlier in the Arctic?: PHYTOPLANKTON BLOOMS IN THE ARCTIC, *Global Change Biology*, 17, 1733–1739,  
 385 <https://doi.org/10.1111/j.1365-2486.2010.02312.x>, 2011.

386 Kjørboe: Turbulence, Phytoplankton Cell Size, and the Structure of Pelagic Food Webs, in: *Advances in*  
 387 *Marine Biology*, Elsevier, 1–72, [https://doi.org/10.1016/s0065-2881\(08\)60129-7](https://doi.org/10.1016/s0065-2881(08)60129-7), 1993.

388 Kheireddine, M., Mayot, N., Ouhssain, M., and Jones, B. H.: Regionalization of the Red Sea Based on  
 389 Phytoplankton Phenology: A Satellite Analysis, *JGR Oceans*, 126, <https://doi.org/10.1029/2021jc017486>,  
 390 2021.

391 Lacour, L., Claustre, H., Prieur, L., and D’Ortenzio, F.: Phytoplankton biomass cycles in the North Atlantic  
 392 subpolar gyre: A similar mechanism for two different blooms in the Labrador Sea, *Geophysical Research*  
 393 *Letters*, 42, 5403–5410, <https://doi.org/10.1002/2015gl064540>, 2015.

394 Li, Z., Sun, D., Wang, S., Huan, Y., Zhang, H., Yuan, Y., and He, Y.: Ocean-scale patterns of environment  
 395 and climate changes driving global marine phytoplankton biomass dynamics, *Sci. Adv.*, 10,  
 396 <https://doi.org/10.1126/sciadv.adm7556>, 2024.

397 Longhurst, A.: Seasonal cycles of pelagic production and consumption, *Progress in Oceanography*,  
 398 36, 77–167, [https://doi.org/10.1016/0079-6611\(95\)00015-1](https://doi.org/10.1016/0079-6611(95)00015-1), 1995.

399 Longhurst, A. R.: *Ecological Geography of the Sea*, Second Edition., Elsevier, [https://doi.org/10.1016/b978-](https://doi.org/10.1016/b978-0-12-455521-1.x5000-1)  
 400 [0-12-455521-1.x5000-1](https://doi.org/10.1016/b978-0-12-455521-1.x5000-1), 2007.

401 Manizza, M., Carroll, D., Menemenlis, D., Zhang, H., and Miller, C. E.: Modeling the Recent Changes of  
 402 Phytoplankton Blooms Dynamics in the Arctic Ocean, *JGR Oceans*, 128, e2022JC019152,

403 <https://doi.org/10.1029/2022JC019152>, 2023.

404 Martinez, E., Antoine, D., D'Ortenzio, F., and De Boyer Montégut, C.: Phytoplankton spring and fall blooms  
 405 in the North Atlantic in the 1980s and 2000s, *J. Geophys. Res.*, 116, 2010JC006836,  
 406 <https://doi.org/10.1029/2010JC006836>, 2011.

407 Mayot, N., D'Ortenzio, F., Ribera d'Alcalà, M., Lavigne, H., and Claustre, H.: Interannual variability of the  
 408 Mediterranean trophic regimes from ocean color satellites, *Biogeosciences*, 13, 1901–1917,  
 409 <https://doi.org/10.5194/bg-13-1901-2016>, 2016.

410 Mignot, A., Claustre, H., Uitz, J., Poteau, A., D'Ortenzio, F., and Xing, X.: Understanding the seasonal  
 411 dynamics of phytoplankton biomass and the deep chlorophyll maximum in oligotrophic environments: A  
 412 Bio-Argo float investigation, *Global Biogeochemical Cycles*, 28, 856–876,  
 413 <https://doi.org/10.1002/2013gb004781>, 2014.

414 O'Connor, M. I., Piehler, M. F., Leech, D. M., Anton, A., and Bruno, J. F.: Warming and Resource  
 415 Availability Shift Food Web Structure and Metabolism, *PLoS Biol*, 7, e1000178,  
 416 <https://doi.org/10.1371/journal.pbio.1000178>, 2009.

417 Pauthenet, E., Martinez, E., Gorgues, T., Roussillon, J., Drumetz, L., Fablet, R., and Roux, M.: Contrasted  
 418 Trends in Chlorophyll- *a* Satellite Products, *Geophysical Research Letters*, 51, e2024GL108916,  
 419 <https://doi.org/10.1029/2024GL108916>, 2024.

420 Polovina, J. J., Howell, E. A., and Abecassis, M.: Ocean's least productive waters are expanding,  
 421 *Geophysical Research Letters*, 35, 2007GL031745, <https://doi.org/10.1029/2007GL031745>, 2008.

422 Racault, M.-F., Le Quéré, C., Buitenhuis, E., Sathyendranath, S., and Platt, T.: Phytoplankton phenology in  
 423 the global ocean, *Ecological Indicators*, 14, 152–163, <https://doi.org/10.1016/j.ecolind.2011.07.010>, 2012.

424 Salgado-Hernanz, P. M., Racault, M.-F., Font-Muñoz, J. S., and Basterretxea, G.: Trends in phytoplankton  
 425 phenology in the Mediterranean Sea based on ocean-colour remote sensing, *Remote Sensing of*  
 426 *Environment*, 221, 50–64, <https://doi.org/10.1016/j.rse.2018.10.036>, 2019.

427 Sapiano, M. R. P., Brown, C. W., Schollaert Uz, S., and Vargas, M.: Establishing a global climatology of  
 428 marine phytoplankton phenological characteristics, *J. Geophys. Res.*, 117, 2012JC007958,  
 429 <https://doi.org/10.1029/2012JC007958>, 2012.

430 Sarmiento, J. L., Slater, R., Barber, R., Bopp, L., Doney, S. C., Hirst, A. C., Kleypas, J., Matear, R.,  
 431 Mikolajewicz, U., Monfray, P., Soldatov, V., Spall, S. A., and Stouffer, R.: Response of ocean ecosystems to  
 432 climate warming, *Global Biogeochemical Cycles*, 18, 2003GB002134,  
 433 <https://doi.org/10.1029/2003GB002134>, 2004.

434 Sathyendranath, S., Brewin, R., Brockmann, C., Brotas, V., Calton, B., Chuprin, A., Cipollini, P., Couto, A.,  
 435 Dingle, J., Doerffer, R., Donlon, C., Dowell, M., Farman, A., Grant, M., Groom, S., Horseman, A., Jackson, T.,

436 Krasemann, H., Lavender, S., Martinez-Vicente, V., Mazeran, C., Mélin, F., Moore, T., Müller, D., Regner, P.,  
437 Roy, S., Steele, C., Steinmetz, F., Swinton, J., Taberner, M., Thompson, A., Valente, A., Zühlke, M., Brando,  
438 V., Feng, H., Feldman, G., Franz, B., Frouin, R., Gould, R., Hooker, S., Kahru, M., Kratzer, S., Mitchell, B.,  
439 Muller-Karger, F., Sosik, H., Voss, K., Werdell, J., and Platt, T.: An Ocean-Colour Time Series for Use in  
440 Climate Studies: The Experience of the Ocean-Colour Climate Change Initiative (OC-CCI), *Sensors*, 19,  
441 4285, <https://doi.org/10.3390/s19194285>, 2019.

442 Sommer, U. and Lengfellner, K.: Climate change and the timing, magnitude, and composition of the  
443 phytoplankton spring bloom, *Global Change Biology*, 14, 1199–1208, <https://doi.org/10.1111/j.1365->  
444 2486.2008.01571.x, 2008.

445 Stock, A., Subramaniam, A., Van Dijken, G. L., Wedding, L. M., Arrigo, K. R., Mills, M. M., Cameron, M. A.,  
446 and Micheli, F.: Comparison of Cloud-Filling Algorithms for Marine Satellite Data, *Remote Sensing*, 12,  
447 3313, <https://doi.org/10.3390/rs12203313>, 2020.

448 Thomalla, S. J., Nicholson, S.-A., Ryan-Keogh, T. J., and Smith, M. E.: Widespread changes in Southern  
449 Ocean phytoplankton blooms linked to climate drivers, *Nat. Clim. Chang.*, 13, 975–984,  
450 <https://doi.org/10.1038/s41558-023-01768-4>, 2023.

451 Vereshchaka, A. L. and Shatravin, A. V.: Chlorophyll dynamics in low latitudes unveils a new partition of  
452 the ocean, *Science of The Total Environment*, 966, 178697, <https://doi.org/10.1016/j.scitotenv.2025.178697>,  
453 2025.

454 Visser, M. E. and Both, C.: Shifts in phenology due to global climate change: the need for a yardstick, *Proc.*  
455 *R. Soc. B.*, 272, 2561–2569, <https://doi.org/10.1098/rsph.2005.3356>, 2005.

456 Winder, M. and Sommer, U.: Phytoplankton response to a changing climate, *Hydrobiologia*, 698,  
457 5–16, <https://doi.org/10.1007/s10750-012-1149-2>, 2012.

458 Yamaguchi, R. and Suga, T.: Trend and Variability in Global Upper-Ocean Stratification Since the 1960s,  
459 *JGR Oceans*, 124, 8933–8948, <https://doi.org/10.1029/2019jc015439>, 2019.

460 Yamaguchi, R., Rodgers, K. B., Timmermann, A., Stein, K., Schlunegger, S., Bianchi, D., Dunne, J. P., and  
461 Slater, R. D.: Trophic level decoupling drives future changes in phytoplankton bloom phenology, *Nat.*  
462 *Clim. Chang.*, 12, 469–476, <https://doi.org/10.1038/s41558-022-01353-1>, 2022.

463 Zhai, D., Beaulieu, C., and Kudela, R. M.: Long-Term Trends in the Distribution of Ocean Chlorophyll,  
464 *Geophysical Research Letters*, 51, e2023GL106577, <https://doi.org/10.1029/2023GL106577>, 2024.

465 Zhai, L., Platt, T., Tang, C., Sathyendranath, S., and Walne, A.: The response of phytoplankton to climate  
466 variability associated with the North Atlantic Oscillation, *Deep Sea Research Part II: Topical Studies in*  
467 *Oceanography*, 93, 159–168, <https://doi.org/10.1016/j.dsr2.2013.04.009>, 2013.