



Three decades of marine bioregions evolution through analysis of phytoplankton phenology

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Abstract

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

1 Introduction

Phytoplankton, the main primary producers in the ocean, sustain marine food webs (Fenchel, 1988; Kiørboe, 1993) and play a central role in regulating oceanic carbon fluxes (Falkowsky et al., 1994). Environmental conditions shape phytoplankton growth and losses through “bottom-up” (e.g., light and nutrients availability) and “top-down” (e.g., grazing) processes. Over the past three decades, satellite ocean color measurements make it possible to estimate phytoplankton biomass (Behrenfeld et al., 2005) proxied by chlorophyll-a concentration (Huot et al., 2007). This, in turn, has enabled the study of phytoplankton phenology (i.e. the temporal succession of main biological events) (Longhurst, 2007; Racault et al., 2012; Sapiano et al., 2012, Boyce et al., 2017). Climate influences the distribution of environmental factors that, in turn, regulate the spatiotemporal dynamics of phytoplankton biomass (Flawosky and Oliver, 2007). Distinct seasonal patterns emerge along



latitudinal gradients, from the equator to the poles (Longhurst, 1995). At high latitudes, primary production is mainly light limited, whereas in tropical and subtropical regions, phytoplankton production is essentially nutrient limited (Boyce et al., 2017). Like the marine environment itself, phytoplankton biomass responds to both annual and decadal climate variability (Li et al., 2024).

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

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

This study uses a supervised clustering method on remotely sensed chlorophyll-a seasonality to partition the global ocean (between 56°S-56°N) from 1998 to 2024. We first present an update of the bioregion climatological distribution from 1998 to 2024 and then look at their variability patterns over the last three decades. Lastly, building on D'Ortenzio et al. (2012) and adapting methods from Higgins et al. (2016), originally applied to terrestrial biomes, we compare the geographical extension



61 of the bioregions between two decadal periods, (1998-2007 and 2025-2014) to identify major trends in phenological changes
62 in response to a changing environment.

63 **2 Material and methods**

64 **2.1 Data**

65 Chlorophyll-a concentrations data were retrieved from the merged multi-sensor ocean color product ref. no. 1 (see Table 1)
66 therefore compensating for the lack of observation inherent to satellite ocean color (Stock et al., 2020).

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

67 **Table 1: Product table**

68 **2.2 Supervised Clustering**

69 Annual ensembles of seasonal time series of chlorophyll-a concentration were built from 1998 to 2024. The time series
70 composing them were all processed similarly to allow subsequent classification according to Baudena et al. (2025)
71 supervised clustering method. In short, within each annual ensemble, each individual time series characterizes the seasonal
72 evolution of chlorophyll-a concentration at the location of a $1^{\circ} \times 1^{\circ}$ pixel, defined on a fixed spatial grid that remains
73 constant across all annual ensembles. The time series were obtained averaging all observations within the pixel over a 8-day
74 temporal window. To dampen sub-seasonal variations, time series were all smoothed with a 5 weeks centered rolling average
75 method. Finally, all annual time series were normalized by their maximum to ensure that the clustering method focuses on
76 their shape rather than on their magnitude.



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

Each annual ensemble was then partitioned into seven distinct clusters characterized by their seasonal patterns. The classification of each time series is based on the minimal euclidean distance between the time series and the seven central time series of Baudena et al. (2025) clusters. For each individual year, this partitioning was repeated over a range of varying acceptance thresholds so as to identify the uncertainties around the clustering method. For each year, twenty six different supervised clustering were done using as many different threshold values ranging from low (strict definition of the clusters) to high threshold values (lax definition of the clusters). On average, 96% (+/-4%) of the time series were successfully sorted within the seven clusters. Unclassified time series were excluded from ulterior analysis.

2.3 Bioregions

When successful, the supervised clustering method assigns a pixel to one of the seven clusters of Baudena et al. (2025). The spatial projection of the pixel's membership over the global ocean forms large coherent spatial domains classified similarly. These oceanic domains correspond to the bioregions as defined by Baudena et al. (2025). As a reminder, bioregions share similar seasonal patterns in phytoplankton phenology suggesting a common biogeochemical functioning (Longhurst, 1995). Over time, the spatial definition of the bioregion might change with the annual time series characteristics of a pixel being attributed to different clusters in different years. A change of phytoplankton phenology is attributed to a pixel when its bioregion changes from one year to another. The frequency of phenology change, presented in Fig. 2b refers to the amount of years over the last 26 years a pixel saw a change in its attributed bioregion. These changes might present oscillating patterns at annual to decadal period or present long term trends.

Three climatological partitioning of the global ocean were considered hereafter. They were constructed by keeping, in each pixel, the most frequent bioregion over the climatology temporal extent. The three considered periods are: from 1998 to 2024 (see Fig. 2a) and two decadal periods from 1998 to 2007 and from 2015 to 2024 (see Fig. 4a). The former climatological period supports the documentation of the average bioregion extent while the latter decadal 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 such decadal bioregions dampens interannual variability.

When comparing the decadal bioregions' extent between the 1998-2007 and the 2015-2024, we attribute a stable phenology



107 change to a given pixel when its classification changed between the two periods and if this classification was similar for a
108 combined total of more than six years in each of the two decades. This temporal criteria was chosen strictly above half a
109 decade to grant a reasonable and robust indicator of the bioregion persistence while considering slight fluctuations.

110 To assess phytoplanktonic biomass across the bioregions, we analyzed their chlorophyll-a concentrations, presented as
111 probability distribution functions in Fig. 1b. The distribution for bioregion 1 is notably bimodal, showing a minor peak near
112 0.03 mg.m^{-3} and a dominant one just above 0.1 mg.m^{-3} . This finding prompted us to subdivide bioregion 1 based on a
113 threshold of 0.06 mg.m^{-3} for yearly average chlorophyll-a, creating an oligotrophic group (below) and a mesotrophic group
114 (above). Although both sub-regions exhibit a similar non-seasonal pattern, this subdivision reveals distinct phenologies,
115 suggesting they are controlled by different environmental forcings that either sustain or inhibit year-round phytoplankton
116 growth.

117 2.4 Uncertainties on the Clustering method

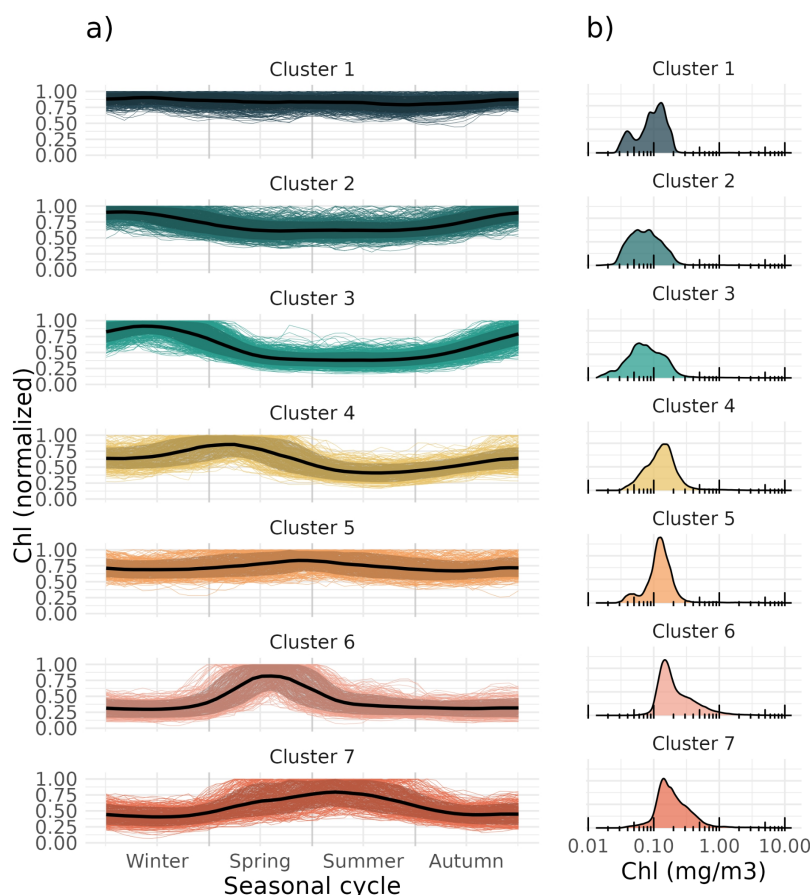
118 To account for methodological uncertainty, we first generated a distribution of annual surface area estimates for each
119 bioregion by varying the acceptance threshold. The definitive annual surface area was calculated as the median of this
120 distribution, with the interquartile range (Q1–Q3) representing the uncertainty. All surface areas are reported relative to the
121 total global ocean surface. To identify long-term changes, we fitted a linear model to the annual surface area estimates over
122 time. The statistical significance of these trends was determined using a Spearman rank correlation, with a trend considered
123 significant at $p < 0.1$.

124 3 Results

125 Our analysis is presented in three parts. First, we establish the climatology and seasonality of the seven marine bioregions,
126 which are described in detail in a companion study (Baudena et al., 2025). Second, we assess the interannual variability and
127 long-term trends in the surface area of each bioregion from 1998 to 2024. Finally, we identify the locations of stable
128 phenological changes by comparing two distinct decades within this period.

129 3.1 Bioregion and phytoplankton phenology

130



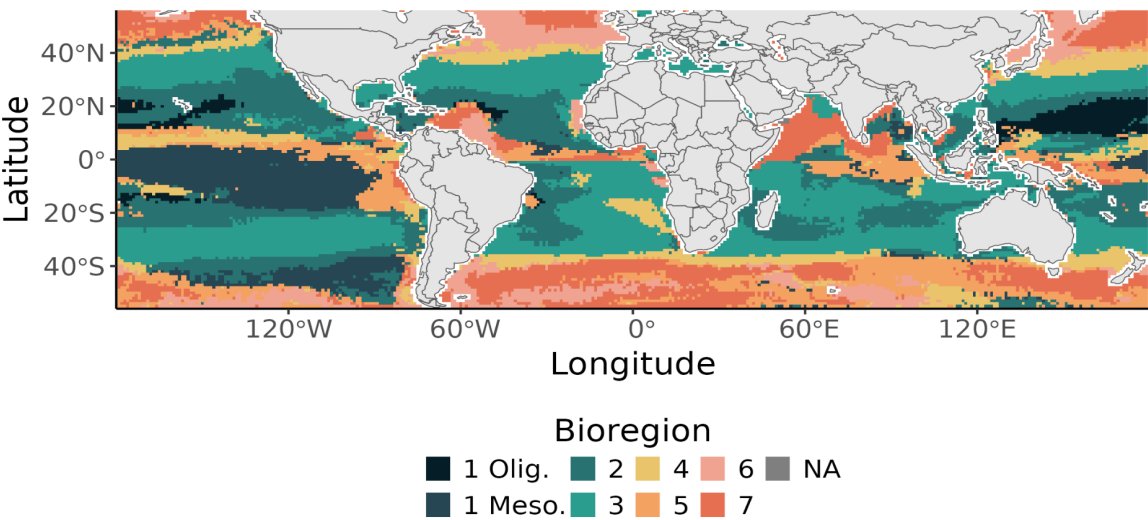
131 **Figure 1: Clusters resulting from the supervised clustering of the ensemble of year 2024 from product ref. no. 1 according to the**
 132 **strictest threshold. The left panel (a), shows the mean normalized seasonal cycles within each bioregion (thick continuous black**
 133 **line) within its 10%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

135 For each year, the supervised clustering method finds seven clusters, similarly to Baudena et al. (2025). The clusters (Fig.
 136 2a), outline specific phenological patterns derived from its mean seasonal cycle of chlorophyll-a concentration (Fig. 1a).
 137 These patterns range from no clear seasonality (bioregion 1) to those with pronounced single or double peak events typical
 138 of blooms in temperate and high-latitude systems (bioregion 4-7).

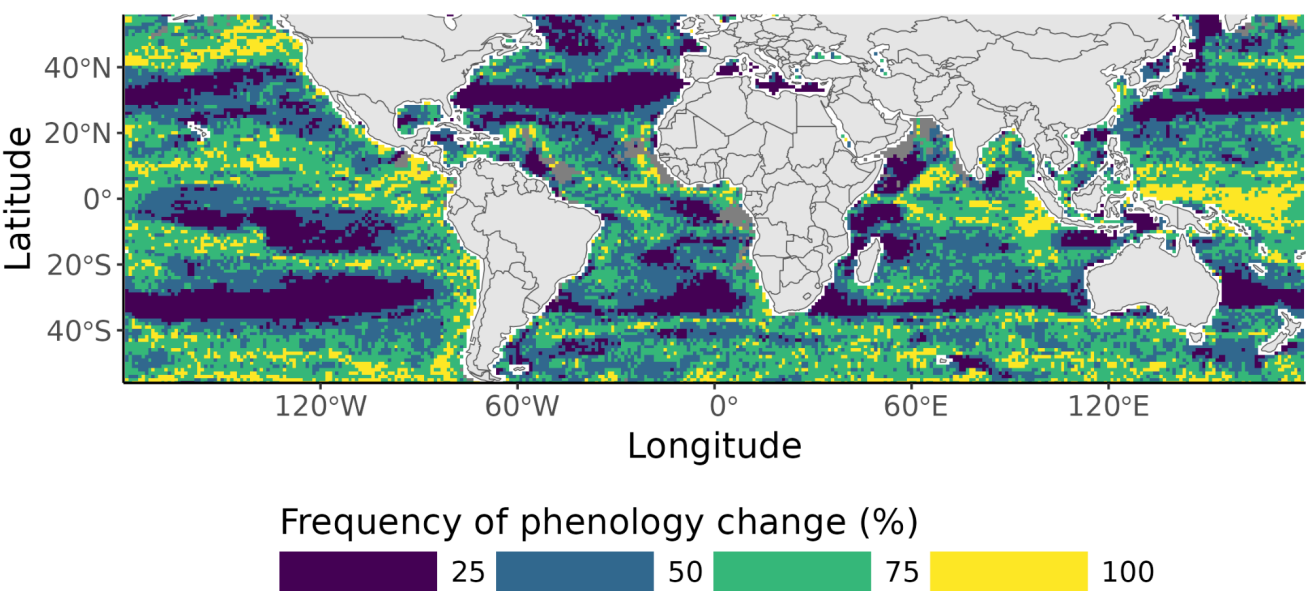
139 As demonstrated by Baudena et al. (2025), the climatological distribution of the related bioregions over the 1998-2024
 140 period (Fig. 2a) follows a meridional distribution sketching coherent, large-scale structures corresponding to major oceanic
 141 domains, such as the subtropical gyres (bioregion 3) and temperate zones (bioregion 4). The biogeochemical relevance of
 142 this partitioning is reinforced by the distribution of chlorophyll-a concentrations within each bioregion (Fig. 1b). A clear
 143 poleward productivity gradient emerges, with the lowest biomass in the perpetually stratified oligotrophic regions of

144 bioregion 1 and the highest in the high-latitude bloom regions. This aligns with established knowledge of global ocean
145 productivity patterns (Behrenfeld et al., 2005).

(a) 1998-2024



(b) 1998-2024





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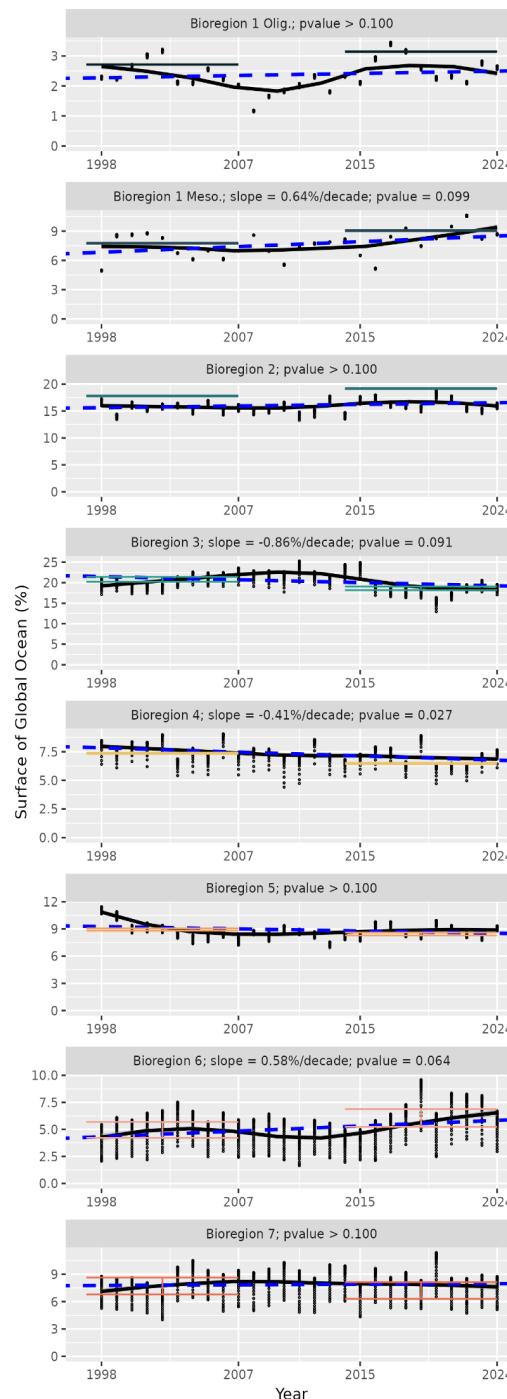
149 **Figure 2: (a) Climatological distribution of the bioregions in the 1998-2024 period. (b) Amount of phenology change per pixel over**
 150 **the 1998-2024 period given in % of the total number of considered years. Both panels display the results obtained using the least**
 151 **strict clustering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

153 3.1 Temporal evolution of the bioregions

154 The boundaries of these bioregions are not static. Over the 1998–2024 period, changes of bioregions, interpreted as changes
 155 in phytoplankton phenology, occur most frequently in transitional areas between major bioregions, as well as in coastal
 156 zones, the equatorial band, and high-latitude regions of the Pacific and Southern Oceans (Fig. 2b). Bioregion 3, centered at
 157 30° in both hemispheres, appears as the most stable bioregion.

158 A visual analysis of the temporal evolution of each bioregion's surface area (Fig. 3) reveals strong interannual variabilities
 159 (black dots) of all bioregions and decadal variabilities (black lines) of bioregions 1, 2, 3 and 6. Linear trend analysis ($p < 0.1$)
 160 indicates a significant reduction in the global surface area of bioregion 3 and bioregion 4. Conversely, the mesotrophic
 161 bioregion 1 shows a significant expansion. While bioregions 6 and 7 exhibit high temporal variabilities, their surface area
 162 estimates are associated with larger method uncertainties (~50%), precluding the detection of a significant trend.

163



164 Figure 3 : Evolution of bioregions' surfaces from 1998 to 2024. The black dots represent estimates of the bioregion surface
165 following the varying acceptance thresholds. The black trend line displays the smoothed centered 10-year rolling average, the blue
166 dotted line corresponds to the linear tendency of the annual median surface estimate. Panel's titles show the linear trends on the



condition that it was found significant ($p < 0.1$). First and third quartiles of the decadal bioregions (1998–2007 and 2015–2024) are indicated as colored error bars. Note the varying coordinate scale.

3.3 Stable changes of phenology

To isolate long-term trends from interannual variability, we identified areas with stable phenological changes between the 1998–2007 and 2015–2024 periods (see Fig. 4a). Stable changes of phenology remained overall limited, affecting 4.93% [4.56%, 5.06%] of the global ocean and suggesting essentially stable conditions. Dominant transition pathways are summarized in Table 2. The most prominent change (1.82% of the global ocean) was the transition from bioregion 3 to the less seasonal bioregion 2, occurring primarily in the subtropical Pacific and Indian Oceans. Other significant shifts included the expansions at lower latitude of bioregion 1 at the expense of bioregion 2 (0.62%) and of bioregion 3 at the expense of bioregion 4 (0.27%). In the North Atlantic's temperate band, a notable net transition from bioregion 7 to 6 also occurred (0.09%). These spatial patterns of change directly correspond to the surface area trends observed over the full time series (Fig. 3), effectively mapping the locations of potential long-term ecosystem shifts.

		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	-	0.12 %	0.01%	0.03 %	-	0.16 %
	Olig.		[0.12, 0.12]	[0.01, 0.01]	[0.03, 0.03]		[0.16, 0.16]
	2 to 1	0.03 %	-	0.36 %	0.07%	-	0.46 %
	Meso.	[0.03, 0.03]		[0.36, 0.36]	[0.07, 0.07]		[0.46, 0.46]
	3 to 2	0.67%	0.55%	0.15 %	0.19 %	0.20 %	1.82 %
		[0.66, 0.67]	[0.52, 0.55]	[0.15, 0.15]	[0.18, 0.19]	[0.21, 0.21]	[1.78, 1.83]
	4 to 3	0.01 %	0.16 %	0.02 %	0.02 %	0.06 %	0.27 %
		[0.01, 0.01]	[0.14, 0.16]	[0.01, 0.02]	[0.02, 0.02]	[0.06, 0.06]	[0.24, 0.27]
	6 to 7	-	0.03 %	0.02 %	0.08 %	0.01 %	0.13 %
			[0.02, 0.06]	[0.01, 0.02]	[0.03, 0.10]	[0.001, 0.10]	[0.06, 0.19]
	7 to 6	0.01%	0.01%	-	0.17 %	0.23 %	0.43 %
		[0.01, 0.01]	[0.01, 0.02]		[0.13, 0.19]	[0.19, 0.24]	[0.33, 0.47]

179

Table 2: Major pathways among stable phenology changes. Changes in surfaces from one bioregion to another are given in surface relative to the total ocean (%). Estimates are given within their first and third quartiles and divided per oceanographic basins. Minor changes, associated with a surface less than 0.1% of the global ocean are not represented.



183 4 Discussion and conclusion

184 Our analysis introduces a novel ocean indicator approach that distinguishes between intermittent, year-to-year variability and
 185 persistent, long-term shifts in phytoplankton phenology. While boundary regions exhibit frequent intermittent changes (Fig.
 186 2b), our decadal analysis finds that nearly 5% (see Table 2) of the global ocean experienced a displacement of phytoplankton
 187 phenology suggesting persistent ecosystem reorganization over the past three decades. As summarized by Fig.4b, the most
 188 prominent trend is a poleward expansion of bioregions with weaker seasonality, this observation is reinforced by the location
 189 of stable phenology changes occurring in the tropical and subtropical band (Fig 4.a). These cascading changes (i.e.,
 190 transitions from bioregion 4 to 3, bioregion 3 to 2, and 2 to 1) are likely driven by an intensification of upper-ocean
 191 stratification in relation to climate warming (Capotondi et al., 2012). At these low latitudes (30°S-30°N), a shallower vertical
 192 mixing prevents entrainment of deeper nutrients (Vereshchaka and Shatravin, 2025) therefore hindering biomass
 193 accumulation of surface waters (Sarmiento et al., 2004; Polovina et al., 2008). The robustness of our ocean indicator
 194 approach is further validated in the temperate North Atlantic, where it successfully captures the documented shift from a
 195 double to a single bloom phenology (bioregion 7 to 6) linked to delayed autumnal mixing (Martinez et al., 2011).

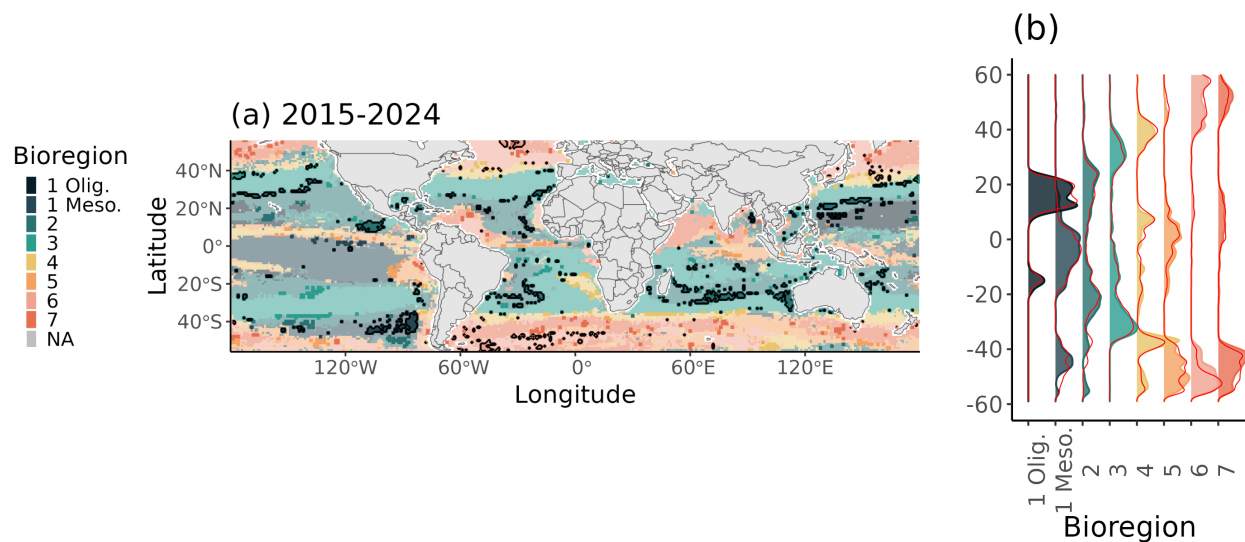
196 The proposed ocean monitoring approach is nevertheless subject to several limitations. First, satellite ocean color
 197 observations are sparse at high latitudes, which forced the exclusion of polar domains where significant and rapid
 198 phenological changes are known to be occurring (Kahru et al., 2010; Thomalla et al., 2023; Manizza et al., 2023), with
 199 potential propagating effects on higher trophic levels (Fossheim et al., 2015). Second, because satellites only measure the
 200 ocean surface, our analysis cannot capture changes in subsurface productivity patterns, such as the deepening of the deep
 201 chlorophyll maximum (Mignot et al 2012, Cornec et al., 2021). Finally, while the 26-year time series is substantial, it
 202 remains challenging to definitively disentangle long-term climate-driven trends from the influence of natural decadal-scale
 203 climate modes (e.g., D’Ortenzio et al., 2012; Zhai et al., 2013; Li et al., 2024).

204 Despite these limitations, the ocean indicator approach presented here provides a powerful and pragmatic tool for
 205 monitoring shifts in marine ecosystem structure driven by climate change. This makes it a crucial complement to established
 206 indicators, such as the ocean indicator method for chlorophyll-a concentration ([10.48670/moi-00230](https://doi.org/10.48670/moi-00230)). While such
 207 concentration-based indicators quantify how much biomass is present, our phenology-based indicator reveals how the
 208 ecosystem's seasonal dynamics is behaving. It can therefore detect critical shifts in ecosystem structure and function even
 209 when the total annual biomass remains unchanged.

210 Looking ahead, future work could integrate Global ocean hindcast, to overcome the limitations of remotely sensed ocean
 211 color and extend monitoring to regions with poor satellite coverage ([10.48670/moi-00019](https://doi.org/10.48670/moi-00019)) and four dimensional products
 212 ([10.48670/moi-00046](https://doi.org/10.48670/moi-00046)) to account for in-depth process. Earth system models can also help predict future states according to
 213 climatic projections (Yamaguchi et al., 2022; Fisher et al., 2025). The partitioning could also be refined by incorporating



214 additional variables (e.g., the particulate backscattering coefficient) to better delineate bioregions. However, the current
215 method's simplicity remains its main asset, ensuring a broad application range, ease of use, and making it an ideal candidate
216 for immediate operational implementation.



218 **Figure 4: (a) Bioregions in the 2015-2024 decadal period with stable changes identified contoured in black. (b) compares the**
219 **latitudinal distribution of bioregions between the 1998-2007 decadal period, as red line, and the 2015-2024 decadal period, filled.**

220 Data availability

221 Ocean color data were collected from the OCEANCOLOUR_GLO_BGC_L4_MY_009_104 product, provided by the
222 Copernicus Marine Environment Monitoring Service (CMEMS, <http://marine.copernicus.eu/>). Cluster centroids resulting
223 from Baudena et al. (2025) study were obtained directly from the author.

225 Author Contribution CRediT

226 Wilhem Riom: Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Visualization, Writing –
227 Original Draft Preparation. Nicolas Mayot: Conceptualization, Investigation, Methodology, Writing – Original Draft
228 Preparation, Visualization, Writing – Review & Editing. Alexandre Mignot: Conceptualization, Formal Analysis,
229 Visualization, Writing – Review & Editing. Vincent Taillandier: Conceptualization, Supervision, Writing – Review &
230 Editing. Fabrizio D’Ortenzio: Conceptualization, Funding Acquisition, Supervision, Writing – Review & Editing.

232 Competing Interests

233 The authors declare that they have no known competing financial interests or personal relationships that could have appeared
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235

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