

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

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## 8 Abstract

9 Ocean biogeochemistry is undergoing significant modification in response to climate change. To better  
10 ~~track these evolutions~~understand these evolution, we present a novel ocean monitoring indicator that  
11 ~~follows approach that tracks~~ the temporal evolution of marine bioregions of similar phytoplankton  
12 phenologies. Chlorophyll-a concentration observations from remotely sensed ocean color describe seven  
13 distinct marine bioregions characterized by their unique patterns of phytoplankton biomass seasonality.  
14 The sizes and locations of these bioregions are monitored from 1998 to 2024 using a multi-sensor merged  
15 L4 ocean color product. While the bioregions’ ~~extent~~extent appear to follow interannual and decadal  
16 climate variability, their long term evolution suggests a poleward extension of less seasonal  
17 phytoplankton phenology, ~~which is~~which are generally characteristic of the tropical and subtropical  
18 bands. This innovative approach allows the systematic monitoring of how phytoplankton adapt their  
19 seasonal cycle in response to changes in environmental conditions, hence giving valuable insights into  
20 the evolution of marine ecosystems over the past three decades and helping advance our understanding  
21 of global ocean biological responses to environmental 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~~Falkowsky *et al.*,  
25 1994). Environmental conditions shape phytoplankton growth and losses through “bottom-up” (e.g., light  
26 and 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

environmental factors that, in turn, regulate the spatiotemporal dynamics of phytoplankton biomass (Falkowski 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).

37

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 ~~through enhanced~~<sup>enhancing</sup> water column stratification (Yamaguchi and Suga, 2019), which in turn might further ~~limit~~<sup>limits</sup> 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 ~~of the documentation effort documented changes~~<sup>of the documentation effort</sup> 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 ~~and Bothet al.~~<sup>and Bothet al.</sup>, 2005~~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.

52

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 ~~the trends in~~<sup>the trends in</sup> 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 ~~dynamics~~<sup>dynamie</sup>, which, in turn, could inform on main variations of environmental factors of the marine ecosystem.

67

68 ~~We introduce here a proof of concept for such an approach using the~~ This study uses a supervised  
69 clustering method ~~introduced in Baudena *et al.*, 2025. Annual partition of on remotely sensed~~  
70 ~~chlorophyll-a seasonality to partition the global ocean (56°S-between 56°S-56°N) from 1998 to 2024 is~~  
71 ~~obtained by classifying annual time series of remotely sensed chlorophyll-a concentration (Copernicus-~~  
72 ~~GlobColor) into bioregions. After presenting the mean climatological state of the bioregions, we~~  
73 ~~investigate their change in surface area .We first present an update of the bioregion climatological~~  
74 ~~distribution from 1998 to 2024 and then look at their variability patterns~~ over the last three decades.  
75 ~~Then~~Lastly, building on D’Ortenzio *et al.* (2012) and adapting methods from Higgins *et al.* (2016),  
76 originally applied to terrestrial biomes, we compare the geographical extension of the bioregions  
77 between two decadal periods ~~at the greatest extent of our dataset~~, (1998-2007 and ~~2015-2024~~2025-2014) to  
78 identify ~~the main major~~ trends in ~~the reorganization of phytoplankton phenology~~. Finally, possible  
79 ~~correlation with environmental changes and method limitations are evoked in the discussion~~  
80 ~~section~~phenological changes in response to a changing environment.

81 **2 Material and methods**

82 **2.1 Data**

83 Chlorophyll-a concentrations data were retrieved from the merged multi-sensor ocean color product ref.  
84 no. 1 (see Table 1). ~~This product offers cloud free remotely sensed surface chlorophyll-a concentration at~~  
85 ~~a 4 km spatial resolution and daily intervals. Using such a L4 product (an optimally interpolated, merged~~  
86 ~~satellite dataset), as compared to L3 (merged product) in Baudena *et al.*, (2025), compensates -therefore~~  
87 ~~compensating~~ for the lack of observation inherent to satellite ocean color (Stock *et al.*, 2020) ~~and ensures~~  
88 ~~a maximal spatialization 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) |

90 **2.2 Supervised Clustering**

91 Annual ensembles of seasonal time series of chlorophyll-a concentration were built from 1998 to 2024.  
92 The time series composing them were all processed similarly to allow subsequent classification  
93 according to Baudena *et al.* (2025) supervised clustering method. In short, within each annual ensemble,  
94 each individual time series characterizes the seasonal evolution of chlorophyll-a concentration over at  
95 the location of a  $1^\circ \times 1^\circ$  grid. Following the method detailed in supplementary section S1, the pixel,  
96 defined on a fixed spatial grid that remains constant across all annual ensembles. The time series were  
97 obtained averaging all available observations within each  $1 \times 1^\circ$  the pixel over a 8-day temporal window.  
98 To dampen sub-seasonal variations, time series were all smoothed with a 5 weeks centered rolling  
99 average method. Finally, all annual time series were normalized by their maximum to ensure that the  
100 clustering method focuses on their shape rather than on their magnitude.

101

102 Time series associated with pixels in the Arctic and Southern Oceans (respectively above  $56^\circ\text{N}$  and below  
103  $56^\circ\text{S}$ ) were removed from every annual ensemble due to lack of continuous satellite observation through  
104 winter in relation to permanent cloud presence and polar night. Coastal pixels observations located  
105 within 111 km ( $\sim 1^\circ$ ) from the coast were also discarded due to the uncertainty in chlorophyll-a  
106 concentration estimations within this optically complex waters (Case 2 waters). As a result 80% of the  
107 global ocean area is considered. In the southern hemisphere, time series were all shifted six months  
108 backward, to ensure identical sequencing of seasons in the time series of all pixels both hemispheres.

109 Each annual ensemble was then partitioned into the seven clusters of Baudena *et al.*, 2025 based on their  
110 seasonality patterns. These seven clusters were found to optimally partition open ocean seasonal cycles  
111 of surface chlorophyll-a concentration in respect of multiple statistical tests discussed in the companion  
112 study. The assignment of a given time serie into one of the clusters was done according to its minimal  
113 euclidean distance (maximal similarity) with the central time series of Baudena *et al.*, 2025 clusters. To  
114 prevent assignment of too dissimilar seasonal patterns, a threshold distance was considered to accept  
115 (distance below the threshold) or refuse (distance above the threshold) an assignment. To account for the  
116 method's sensitivity to this hyperparameter, we discretized a range of possible values, defined by the  
117 minimum and maximum classification distances found among the most deviating elements of any  
118 cluster, from 1.33 (cluster 1) to 2.60 (cluster 7), based on the unsupervised clustering of Baudena *et al.*,  
119 (2025). Each annual ensemble was partitioned several times from a low (strict definition of the clusters)  
120 to high threshold values (lax definition of the clusters) selected within this range with a regular step of  
121 0.05 (see sensitivity analysis in supplementary section 2). At least 88 % of the time series were always  
122 successfully sorted within the seven clusters (see Fig. S2b). Unclassified time series, mostly located in  
123 regions of low satellite data availability region (see Fig. S2a), were all excluded from ulterior analysis.

124

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

## 134 2.3 Bioregions

135 ~~When successful, the supervised clustering method assigns a pixel to one of the seven clusters of~~  
136 ~~Baudena et al. (2025). The spatial projection of each the pixel's membership over the global ocean forms~~  
137 ~~large coherent spatial domains similarly classified~~classified similarly~~. These oceanic domains correspond~~  
138 ~~to the bioregions as defined by Baudena et al. (2025). As a reminder, bioregions share similar seasonal~~  
139 ~~patterns in phytoplankton phenology suggesting a common biogeochemical functioning (Longhurst,~~  
140 ~~1995). Over time, the spatial definition of the bioregion might change with the annual time series~~  
141 ~~characteristic~~characteristics~~ of a given pixel being attributed to different clusters over~~in~~ different years.~~  
142 ~~A change of phytoplankton phenology is attributed to a pixel when its bioregion changes from one year~~  
143 ~~to another. For a given pixel, the frequency of phenology change is defined as the total sum of these~~  
144 ~~changes over the study periodThe frequency of phenology change, presented in Fig. 2b refers to the~~  
145 ~~amount of years over the last 26 years a pixel saw a change in its attributed bioregion. These changes~~  
146 ~~might present oscillating patterns from~~at~~ annual to decadal period or present long term trends.~~

147

148 Three climatological partitions~~partitioning~~ of the global ocean were considered hereafter. They were  
149 constructed by keeping, in each pixel, the most frequent bioregion over the selected~~climatology~~ temporal  
150 extent. The three considered periods are: from 1998 to 2024 (~~see Fig. 2a~~) and two decadal periods from  
151 1998 to 2007 and from 2015 to 2024. ~~(see Fig. 4a).~~ The former climatological period supports the  
152 documentation of the average bioregion extent while the molatter two ~~latter~~ decadal periods were  
153 chosen at the edge of the temporal span to support the documentation of long term changes in the  
154 bioregion's extent. The use of decadal bioregions ~~also~~~~such decadal bioregions~~ dampens interannual  
155 variability.

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

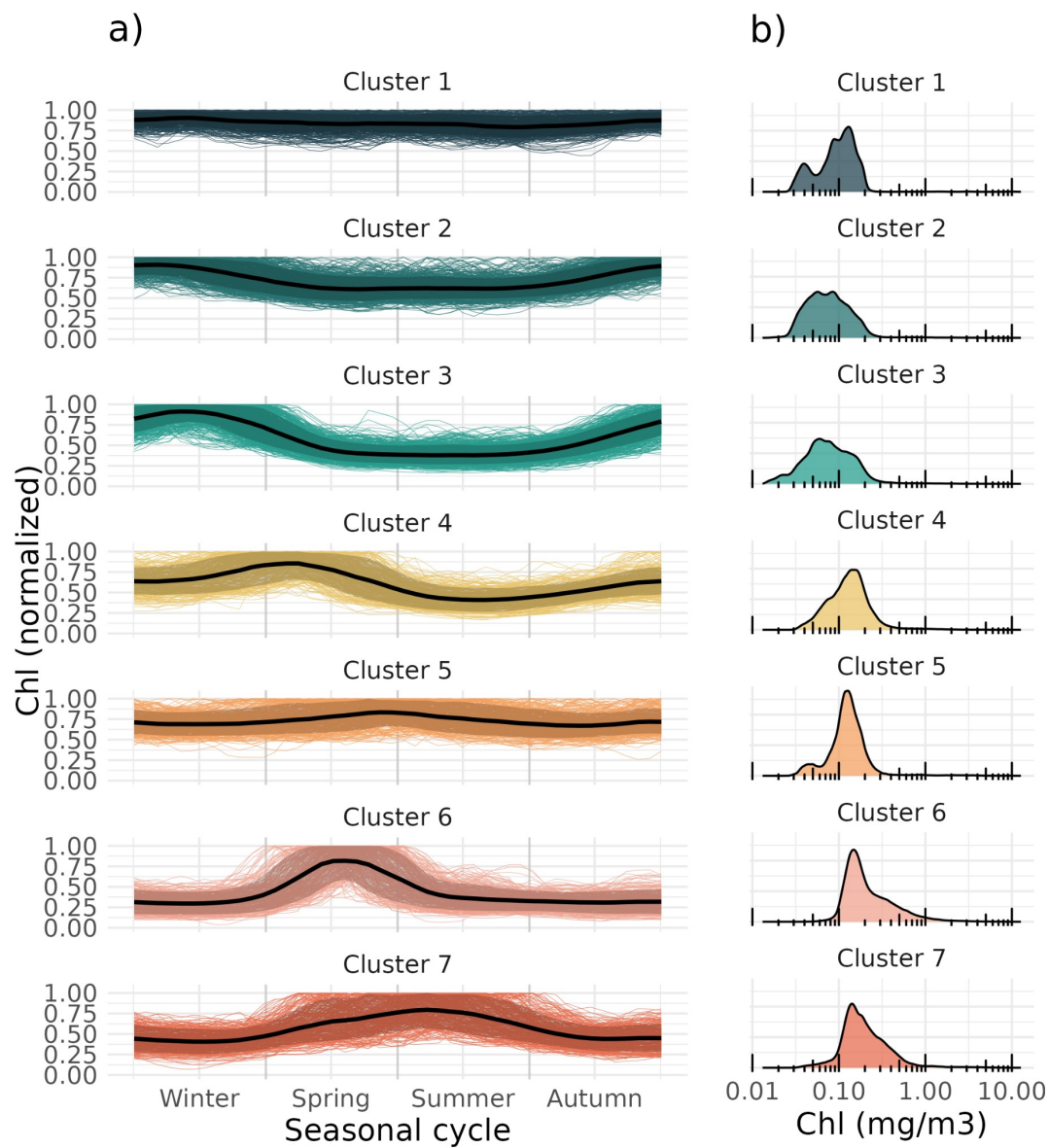
162 To assess phytoplanktonic biomass across the bioregions, we analyzed their chlorophyll-a  
163 concentrations, presented as probability distribution functions in Fig. 1b. The distribution for bioregion 1  
164 is notably bimodal, showing a minor peak near  $0.03 \text{ mg.m}^{-3}$  and a dominant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

## 170 2.4 Uncertainties ~~estimation on the Clustering method~~

171 ~~Following the set of threshold distance, each annual ensemble is partitioned twenty six times (see section~~  
172 ~~2.2). In each of these partitions, the distribution of the bioregion~~ To account for methodological  
173 ~~uncertainty, we first generated a distribution of annual surface area estimates for each bioregion by~~  
174 ~~varying the acceptance threshold. The definitive annual surface area~~ relative to the set of threshold  
175 ~~distances is characterised hereafter by its central value (the median) within its~~ was calculated as the  
176 ~~median of this distribution, with the~~ interquartile range (Q1–Q3). ~~The interquartile range of surface area~~  
177 ~~estimates accounts for the bioregionalization method~~ representing the uncertainty. All surface areas are  
178 reported relative to the total global ocean ~~area~~surface. To identify long-term changes, we fitted a linear  
179 model to the ~~central annual~~ surface area estimates ~~in respect of over~~ time. The statistical significance of  
180 these ~~linear~~ trends was determined using a Spearman rank correlation, with a trend considered  
181 significant at  $p < 0.1$ .

## 182 3 Results

183 Our analysis is presented in three parts. First, we ~~recall the phytoplankton phenology and climatological~~  
184 ~~repartition~~ establish the climatology and seasonality of the seven marine bioregions ~~(, which are~~  
185 described in ~~more details in detail in a companion study~~ (Baudena *et al.*, 2025). Second, we assess the  
186 interannual variability and long-term trends in the surface area ~~evolution~~ of each bioregion from 1998 to  
187 2024. Finally, we identify the locations of stable phenological changes by comparing two distinct decades  
188 ~~at the edges of the~~within this period.



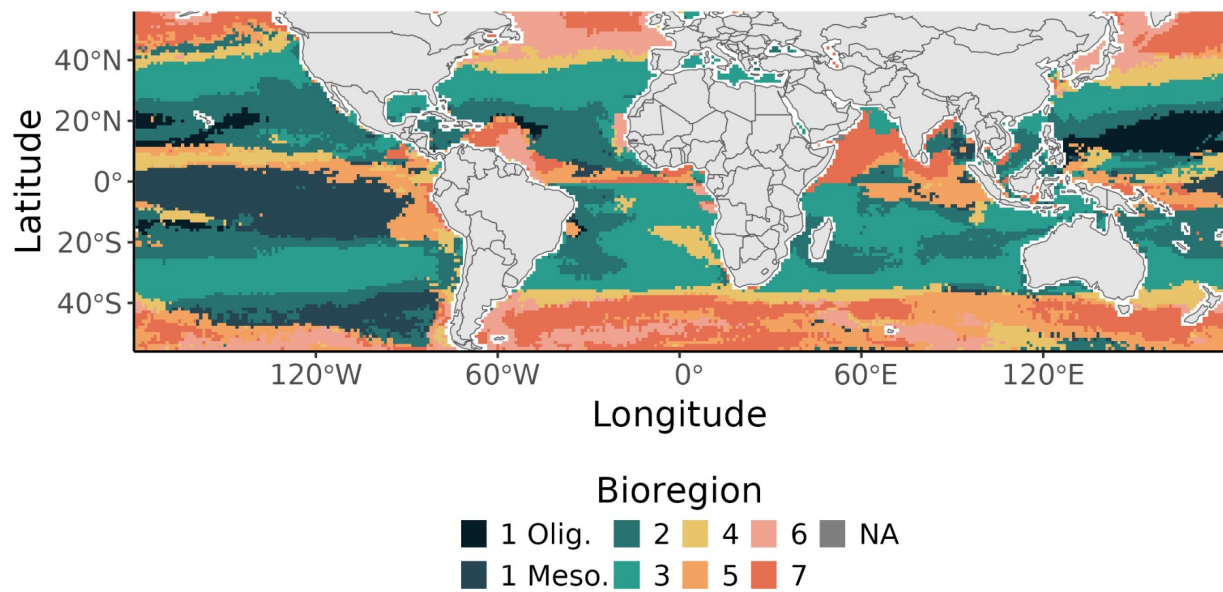
191 Figure 1: Clusters resulting from the supervised clustering of the ensemble of year 2024 from product ref. no.  
192 1 according to the strictest threshold. The left panel (a), shows the mean normalized seasonal cycles within  
193 each **clusterbioregion** (thick continuous black line) within its 10% and 90% percentiles (transparent black  
194 bands). In the background, examples of time series within that cluster are represented. The right panel (b),  
195 displays the distribution of chlorophyll concentration within each **clusterbioregion**.

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

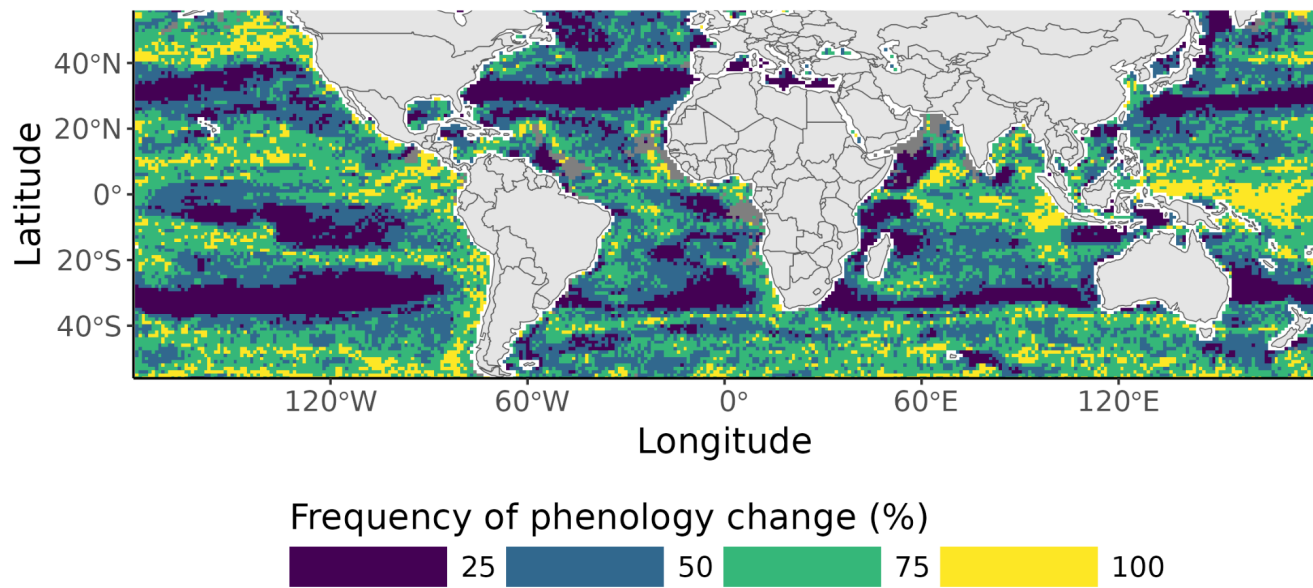
202 In agreement with As demonstrated by Baudena *et al.* (2025), the climatological distribution of the related  
203 bioregions over the 1998-2024 period (Fig. 2a) follows a meridional distribution sketching coherent,  
204 large-scale structures corresponding to major oceanic domains, such as the subtropical gyres (bioregions  
205 1 Olig., 2 and bioregion 3) and convergence temperate zones (bioregion 4). The biogeochemical relevance  
206 of this partitioning is reinforced by the distribution of chlorophyll-a concentrations within each  
207 bioregion (Fig. 1b). A clear poleward productivity gradient emerges, with the lowest surface biomass in  
208 the perpetually stratified regimes of the subtropical band oligotrophic regions of bioregion 1 and the  
209 highest in the high-latitude bloom regions (bioregion 6-7). This aligns with established knowledge of  
210 global ocean productivity patterns (Behrenfeld *et al.*, 2005).

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

(a) 1998-2024



(b) 1998-2024



220

221

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

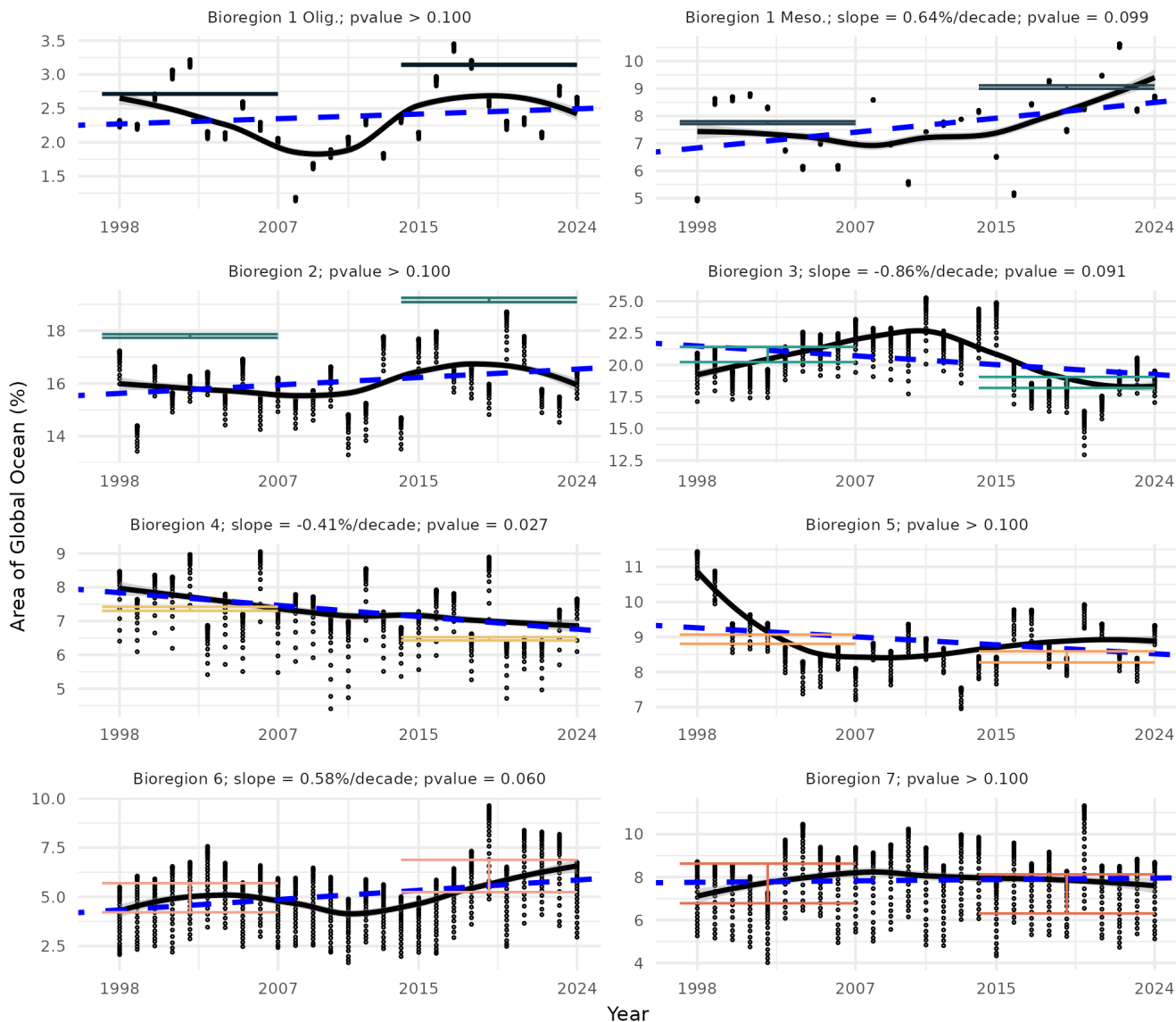
17  
18

226 **classified.**

227 **3.1 Temporal evolution of the bioregions**

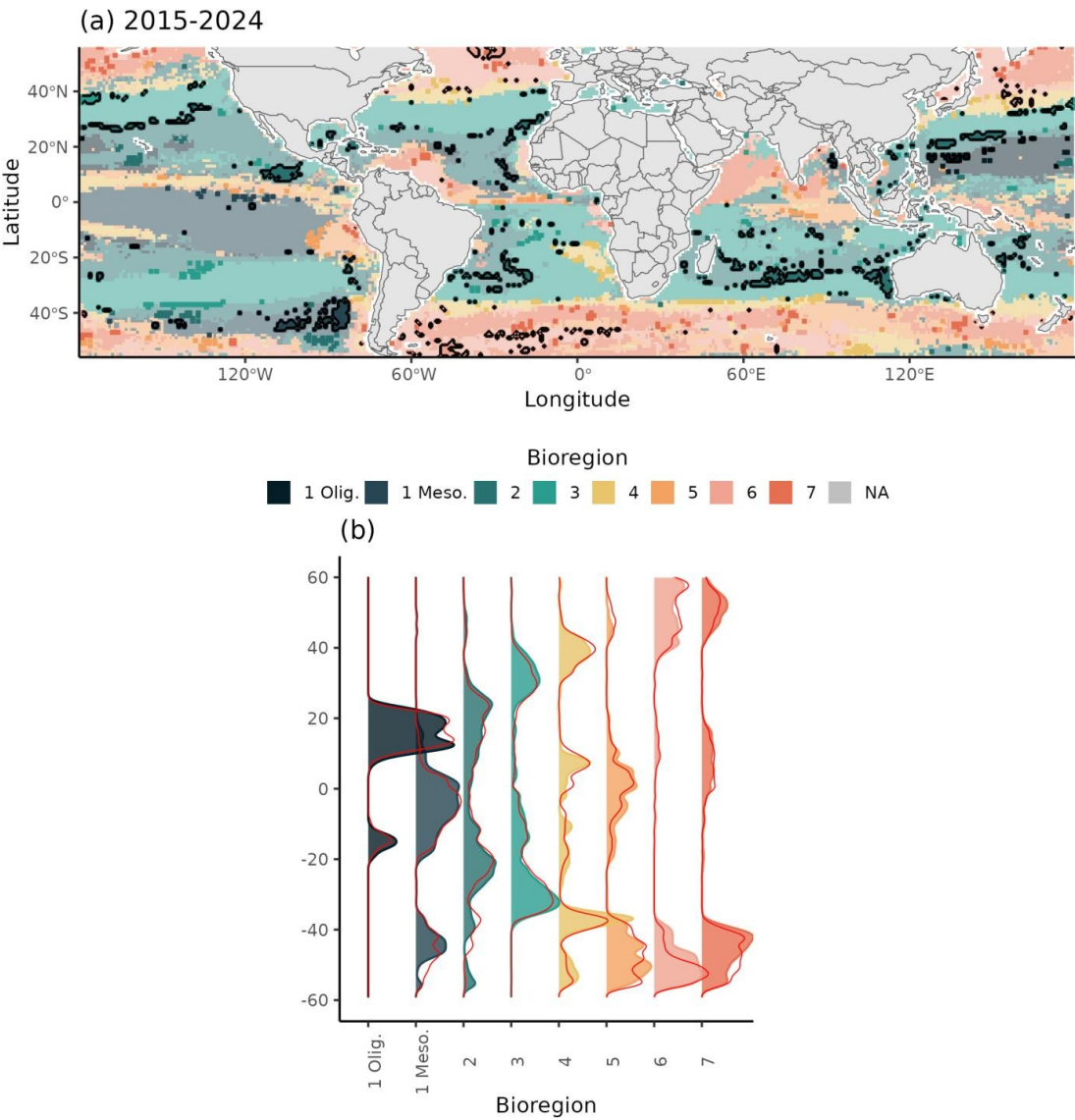
228 The boundaries of bioregions in Fig. 2a ~~these bioregions~~ are not static. Fig. 2b displays the frequency of  
229 changes in each pixel bioregion's affiliation~~Over the 1998–2024 period, changes of bioregions,~~  
230 interpreted as changes in phytoplankton phenology, over the 1998–2024 period. These changes occur  
231 most frequently in transitional areas in-between major bioregions, as well as in coastal zones, over the  
232 equatorial band, and over high-latitude regions of the northern Pacific and Southern Ocean~~Oceans~~ (Fig.  
233 2b). Bioregion 3, centered at 30° in both hemispheres, appears as the most stable bioregion.

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



243

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



251

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

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

254 2015-2024 period, with colored and filled distributions, respectively.

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

changes between the 1998–2007 and 2015–2024 decadal periods. As highlighted in periods (see Fig. 4a,  
these regions are mostly located within the tropical and subtropical band. Overall ). Stable changes of  
phenology remained overall limited, affecting 4.93% [4.56%, 5.06%] of the global ocean is affected  
suggesting slow transitions in essentially steadyand suggesting essentially stable conditions. The  
dominant pathways in phenology transition Dominant transition pathways are summarized in Table 2.  
The most prominent change (1.82% of the global ocean) iswas the transition from bioregion 3 to the less  
seasonal bioregion 2, occurring primarily in the subtropical Pacific and Indian Oceans. Other significant  
shifts includeincluded 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%). As summarized by Fig.4b, the most  
prominent trend is a poleward expansion of bioregions of weaker seasonality. 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 Olig. | -                      | 0.12 %<br>[0.12, 0.12] | 0.01%<br>[0.01, 0.01]  | 0.03 %<br>[0.03, 0.03] | -                       | 0.16 %<br>[0.16, 0.16] |
|                                      | 2 to 1 Meso. | 0.03 %<br>[0.03, 0.03] | -                      | 0.36 %<br>[0.36, 0.36] | 0.07%<br>[0.07, 0.07]  | -                       | 0.46 %<br>[0.46, 0.46] |
|                                      | 3 to 2       | 0.67%<br>[0.66, 0.67]  | 0.55%<br>[0.52, 0.55]  | 0.15 %<br>[0.15, 0.15] | 0.19 %<br>[0.18, 0.19] | 0.21 %<br>[0.21, 0.21]  | 1.82 %<br>[1.78, 1.83] |
|                                      | 4 to 3       | 0.01 %<br>[0.01, 0.01] | 0.16 %<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]  | 0.27 %<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] | 0.13 %<br>[0.06, 0.19] |
|                                      | 7 to 6       | 0.01%<br>[0.01, 0.01]  | 0.01%<br>[0.01, 0.02]  | -                      | 0.17 %<br>[0.13, 0.19] | 0.23 %<br>[0.19, 0.24]  | 0.43 %<br>[0.33, 0.47] |
|                                      |              | Oceanic Basins         |                        |                        |                        |                         | Total                  |
|                                      |              | Indian Ocean           | North Pacific Ocean    | South Pacific Ocean    | North Atlantic Ocean   | South Atlantic Ocean    |                        |
| Pathways of stable                   | 2-to-1 Olig. | -                      | 0.12 %<br>[0.12, 0.12] | 0.01%<br>[0.01, 0.01]  | 0.03 %<br>[0.03, 0.03] | -                       | 0.16 %<br>[0.16, 0.16] |

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

269

270 Table 2: Major pathways among stable phenology changes. Changes in surface area surfaces from one  
271 bioregion to another are given relatively in surface relative to the global ocean total ocean (%). Estimates are  
272 given within their first and third quartiles and grouped by divided per oceanographic basins. Minor changes,  
273 associated with an area inferior to a surface less than 0.1% of the global ocean, are not represented. Estimates  
274 highlighted in bold indicate values greater than 0.1 % of the global ocean.

275 4 Discussion and conclusion

276 Our analysis introduces a novel ocean indicator approach that distinguishes between intermittent, year-  
277 to-year variability and persistent, long-term shifts in phytoplankton phenology. While boundary regions  
278 exhibit frequent intermittent changes (Fig. 2b), our decadal analysis finds that nearly 5% (see Table 2) of  
279 the global ocean experienced a displacement of phytoplankton phenology suggesting persistent  
280 ecosystem reorganization over the past three decades. The As summarized by Fig.4b, the most prominent  
281 trend is a poleward expansion of bioregions with weaker seasonality, this observation is reinforced by  
282 the location of stable phenology changes occurring in the tropical and subtropical band (Fig 4.a). These  
283 cascading changes (i.e., transitions from bioregion 4 to 3, bioregion 3 to 2, and 2 to 1) identified above,  
284 are possibly are likely driven by an intensification of upper-ocean stratification in relation to climate  
285 warming (Capotondi *et al.*, 2012). At these low latitudes (30°S-30°N), a shallower vertical mixing prevents  
286 entrainment of deeper nutrients (Vereshchaka and Shatravin, 2025) therefore hindering biomass  
287 accumulation of surface waters (Sarmiento *et al.*, 2004; Polovina *et al.*, 2008). The robustness of our ocean  
288 indicator approach is further validated in the temperate North Atlantic, where despite high method  
289 uncertainties, it successfully captures the documented shift from a double to a single bloom phenology  
290 (bioregion 7 to 6) linked to delayed autumnal mixing in (Martinez et al. (2011) is successfully captured.  
291 The documented changes also echo the variations of micronekton habitats provinces monitored from sea

292 surface temperature, stratification index and net primary production evolution in Albernhe *et al.* (2025,  
293 2011).

294 The proposed ocean monitoring approach is nevertheless subject to several limitations. First, satellite  
295 ocean color observations are sparse at high latitudes inducing increasing method uncertainties poleward  
296 and, which forced the exclusion of the subpolar and polar domains (above 60°). In these domains where  
297 significant and rapid phenological changes are already documented known-to-be-occurring (Kahru *et al.*,  
298 20112010; Thomalla *et al.*, 2023; Manizza *et al.*, 2023), with potential propagating effects on higher  
299 trophic levels (Fossheim *et al.*, 2015). Second, because satellites only measure the ocean surface, our  
300 analysis cannot capture cmhangeschanges in subsurface productivity patterns, such as the deepening of  
301 the deep chlorophyll maximum (Mignot *et al* 20142012, Cornec *et al.*, 2021). Finally, while the twenty  
302 seven year long26-year time series is substantial, it remains challenging to definitively disentangle long-  
303 term climate-driven trends from the influence of natural decadal-scale climate modes (e.g., D’Ortenzio *et*  
304 *al.*, 2012; Zhai *et al.*, 2013; Li *et al.*, 2024).

305 Despite these limitations, the ~~–ocean~~ indicator approach presented here provides a powerful and  
306 pragmatic tool to effectively map the locations of potential long-term ecosystem shiftsfor monitoring  
307 shifts-in-marine-ecosystem-structure-driven-by-climate-change. This makes it a crucial complement to  
308 established indicators, such as the ~~ocean~~ indicator method for chlorophyll-a concentration  
309 (10.48670/moi-00230). While such concentration-based indicators quantify how much biomass is present,  
310 our phenology-based approachindicator reveals how the ecosystem's seasonal dynamics are unfoldingis  
311 behaving. It can therefore detect critical shifts in ecosystem structure and function even when the total  
312 annual biomass remains unchanged. Furthermore, identifying long term trends in the distribution of  
313 chlorophyll-a concentration was shown to be dependent on the type of ocean color product (Zhai *et al.*,  
314 2024, Pauthenet *et al.*, 2024). Investigating the presence and variability of the bioregions based on ESA's  
315 Ocean Color Climate Change Initiative (Sathyendranath *et al.*, 2019) would further consolidate  
316 (invalidate) the highlighted trends. In this paper, we mainly propose an approach, a proof-of-concept,  
317 that could be further applied to other ocean colors time-series

318 Future Looking-ahead, future work could integrate Global ocean hindcast, to overcome the limitations of  
319 remotely sensed ocean color and extend monitoring to regions with poor satellite coverage  
320 (10.48670/moi-00019) and other four dimensional products (10.48670/moi-00046) to account for in-depth  
321 process. Earth system models can also help predict future states according to climatic projections  
322 (Yamaguchi *et al.*, 2022; Fisher *et al.*, 2025). The partitioning could also be refined by incorporating  
323 additional variables (e.g., the particulate backscattering coefficient) to better delineate bioregions.  
324 However, the current method's simplicity remains its main asset, ensuring a broad application range,  
325 ease of use, and making it an ideal candidate for immediate operational implementation.

326 ~~Figure 4: (a) Bioregions in the 2015-2024 decadal period with stable changes identified contoured in black. (b)~~  
327 ~~compares the latitudinal distribution of bioregions between the 1998-2007 decadal period, as red line, and the~~  
328 ~~2015-2024 decadal period, filled.~~

329 **Data availability**

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

333

334 **Author Contribution CRediT**

335 ~~WR~~**Wilhem Riom**: Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology,  
336 Visualization, Writing – Original Draft Preparation. ~~NM~~**Nicolas Mayot**: Conceptualization, Investigation,  
337 Methodology, Writing – Original Draft Preparation, Visualization, Writing – Review & Editing.  
338 ~~AM~~**Alexandre Mignot**: Conceptualization, Formal Analysis, Visualization, Writing – Review & Editing.  
339 ~~VT~~**Vincent Taillandier**: Conceptualization, Supervision, Writing – Review & Editing. ~~FD~~**Fabrizio**  
340 ~~D’~~**Ortenzio**: Conceptualization, Funding Acquisition, Supervision, Writing – Review & Editing.

341

342 **Competing Interests**

343 The authors declare that they have no known competing financial interests or personal relationships that  
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345

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353

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