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STATE OF THE PLANET Discussions

Micronekton indicators evolution based on biophysically defined provinces

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Abstract. Micronekton are mid-trophic marine organisms characterized by a size range of 2 to 20 cm, gathering a wide diversity of taxa (crustaceans, fish, molluscs, etc.). They are responsible for an important active carbon export to the deep ocean because of their diel vertical migrations and constitute the main prey for pelagic predators. A new method to define provinces that identify micronekton functioning patterns based on environmental variables is proposed in Albernhe et al. (2024, under review). Following this methodology, we define homogeneous provinces using environmental variables computed from Copernicus Marine Service products. These provinces represent a relevant way to define regions of interest, offering a regional scope of study for micronekton indicators and their evolution in time. In this study, we observe the evolution of the provinces in time from 1998 to 2023, to account for the seasonal to interannual variability. We focus on the variations in surface area and average latitude of each province. We observe a global shrinking of productive provinces and polar provinces, in favor of equatorial and tropical provinces expansion. Additionally, tracking the geographical changes of the provinces over time shows that most are shifting toward the poles.

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1 Introduction

The intermediate level of the oceanic food web is constituted by a group of marine organisms called micronekton, understudied yet, but garnering increasing attention. This key component of marine ecosystems characterized by organisms in a size range from 2 to 20 cm contains a wide diversity of taxa such as crustaceans, fish, molluscs and gelatinous (Brodeur et al., 2004; Escobar-Flores et al., 2019). Micronekton mostly feed on zooplankton and are the main prey of marine large predators, some of which are of crucial economic importance (e.g. tunas, Bell et al., 2015; Terawasi et al., 2017; McCluney et al., 2019). In addition to their role of prey for commercially harvested top predators (Young et al., 2015), micronekton themselves become a valuable resource for fisheries, as the trophic level of exploited species is decreasing (St. John et al., 2016; Gatto et al., 2023). Another aspect of micronekton worthy of interest lies in its migratory behaviour, which impact global carbon export (Pinti et al. 2021; Buesseler et al., 2022) by actively transporting and sequestrating carbon beneath the mixed layer (Bianchi et al., 2013; Boyd et al., 2019; Gorgues et al., 2019).

Therefore, estimating micronekton biomass is a major concern for fisheries management and climate regulation. Observations of micronekton primarily rely on trawl sampling, which is susceptible to biases due for example to species avoidance (Kaartvedt et al., 2012) or on ship-borne acoustic measurements, which does not provide yet a reliable representation of the micronekton biomass (McGehee et al., 1998; Kloser et al., 2002). Numerical models as the Spatial Ecosystem and Population Dynamics Model – Low and Mid Trophic Levels (SEAPODYM-LMTL: Lehodey et al., 2010; 2015; Conchon, 2016) are complementary tools for simulating micronekton biomass, offering the advantage of providing continuous global-scale time series.

One approach to quantify and characterize the mid-trophic level populations is the definition of homogeneous provinces. Longhurst was the pioneer and defined a static vision of biogeographical provinces based on chlorophyll fields (Longhurst 1995; 2007). Multiple combinations of environmental forcings have been used to create accurate definitions of provinces for each field: catch per unit of effort of commercial fisheries (Reygondeau et al., 2012), multi-expertise discussions (Sutton et al., 2017), distribution of species (Costello et al., 2017), phytoplankton species assemblages (Elizondo et al., 2021). Acoustic-based regionalization is also explored, using environmental drivers classification to model backscattering characteristics (Proud et al., 2017), or recently partitioning acoustic data according to the vertical structure of sound-scattering mid-trophic biomass (Ariza et al., 2022).

Complementing these approaches, Albernhe et al. (2024, under review) proposed a new methodology for regionalizing the global ocean into biophysical provinces based on environmental variables. The ambition of this work was to identify micronekton homogeneous functioning patterns using a parsimonious set of biophysical variables that are known to have an impact on micronekton biomass (epipelagic layer temperature, stratification of the mesopelagic ocean, and net primary production (NPP)). Clustering these variables results in a global classification of six distinct biomes (tropical, subtropical, eastern boundary coastal upwelling systems, oceanic mesotrophic systems, sub-polar and polar biomes). The authors also defined a monthly time series of biomes for the 1998-2019 time period. From these large biomes, provinces are derived as biomes' sub-divisions at the scale of ocean basin and hemisphere. A characterization of these provinces with simulated micronekton from SEAPODYM-LMTL model outputs identifies biomes-specific relations between micronekton biomasses and the environmental variables used in the clustering. Additionally, biomes-specific vertical structures are indicated by ratios of modelled micronekton functional groups (i.e., groups of micronekton with specific migratory behaviour, and specific depth habitat). Boundaries between provinces have also been validated using acoustic data. With demonstrated accuracy in homogeneous micronekton characteristics, these provinces enable the gathering and extrapolation of the few available observation data of micronekton over large homogeneous areas. This could benefit the exploration of the micronekton spatio-temporal variability within global or regional datasets.

Provinces' features, such as surface area and positional changes, serve as valuable indicators offering insights into the evolution of ecosystem structure over time on both global and regional scales. Following Albernhe et al. (2024, under review)'s methodology, we define in the present study an annual time series of biophysical provinces from 1998 to 2023. We observe the evolution of two geographical indicators: the surface area and the average latitude of each province.

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2 Material and methods

2.1 Environmental variables and biophysical clustering

We define a time series of biophysical provinces from 1998 to 2023 following Albernhe et al. (2024, under review)'s approach. The latter publication offers a methodology for global ocean regionalization based on environmental variables, with no gaps and no overlaps, displaying homogeneous biophysical characteristics.

We consider three environmental variables, that are known to have an impact on micronekton: the mean temperature in the epipelagic layer, the temperature gradient between the epi and the meso-pelagic layers, as an index of the stratification, and the integrated NPP. The pelagic layers mentioned are defined as in SEAPODYM-LMTL. These variables are computed from the biological and physical Copernicus Marine Service datasets of the product *Global Ocean low and mid trophic levels biomass content hindcast*, GLOBAL_MULTIYEAR_BGC_001_033 (1/12° horizontal resolution, product ref01, table 1). In the product, the weekly 3D temperature fields come from the GLORYS12V1 simulation. NPP and the associated euphotic depth are computed using the Vertically Generalized Production Model (VGPM) of Behrenfeld and Falkowski (1997) which is based on the Satellite Observations reprocessed Global Ocean Chlorophyll product. The spatial domain of our study is restricted to area where the depth of the water column supports the existence of all three pelagic layers as defined in SEAPODYM-LMTL (i.e. roughly 1000m deep, See Material and Method section of Albernhe et al. (2024, under review)). Consequently, shallow coastal areas are excluded from this analysis.

As described in Albernhe et al. (2024, under review), a Principal Component Analysis (PCA) (Hotelling, 1933) is performed on the three environmental variables mentioned above (i.e., epipelagic layer temperature, stratification and NPP). Then, a clustering is performed on the PCA two principal components, hereafter referred to as "biophysical clustering". This biophysical clustering is performed using the unsupervised k-means machine learning algorithm (Lloyd, 1957; Pedregosa et al., 2011), which partitions the observations into k=6 homogeneous clusters (See Material and Method section of Albernhe et al. (2024, under review)). These clusters define homogeneous biomes on a global scale, hereafter referred to as "biophysical biomes".

First, the training phase of k-means algorithm is applied to time-averaged 1/12-degree datasets from 1998 to 2023. This process defines static reference biophysical biomes, representing the average state of the ocean over the entire period. After the training phase, the clustering model parameters are estimated, and we can use this model to make predictions on other data. Then, the prediction phase of k-means algorithm is applied on monthly data over the same time period (1998-2023) (See Material and Method section of Albernhe et al. (2024, under review)). This results in a monthly time series of biophysical biomes that captures seasonal and interannual variability.

The biophysical biomes obtained from the clustering of environmental data characterize homogeneous environmental regimes on a global scale. In this study, we also delineate "provinces" as sub-divisions of biomes at the scale of ocean basins and hemispheres that have been shown to be characterized by stable biophysical drivers and potential taxonomic identity (Spalding et al., 2012; Sutton et al., 2017; Albernhe et al., 2024, under review). This subdivision enables the use of 27 provinces to define regional scopes for the study of micronekton.

2.2 Trends identification

The aim of this study is to observe the evolution of the provinces in time from 1998 to 2023. To study the interannual variability and identify potential trends over the 26 years, we consider the annual time series (i.e., annually averaged monthly time series). We document the evolution of two geographical indicators: the surface area and the average latitude, for each province. The average latitude diagnostic has been designed to assess a potential poleward displacement of certain provinces (see Hastings et al., 2020; Pinsky et al. 2020 and references therein).

To evaluate the evolution of surface area over time, we analyze the slope (in km²/year) of a linear regression model based on the annual surface area (in km²) of each province from 1998 to 2023. The coefficient of determination (R^2) associated with every linear regression (i.e., computed for each province) is a statistical measure assessing the degree of alignment between the observed values and the linear regression model. From the linear regression, the percentage of variation of the provinces' surface between 1998 and 2023 is computed (in %), based on the difference between the first and last point of the regression (respectively matching 1998 and 2023).

To track the poleward drift of provinces over time, we analyze the slope (in degrees poleward/year) of a linear regression model based on the average latitude of each province throughout the annual time series from 1998 to

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2023. The coefficients of determination (R^2) associated with every linear regression are computed. The 'degree poleward' unit that we use for this diagnostic is associated with degree N for provinces in the northern hemisphere, and degree S for provinces in the southern hemisphere. Thus, provinces belonging to the equatorial Biome 1 (provinces 101, 102 and 103) are not considered in this diagnostic because of their equatorial position. Derived from the linear regressions, we estimate the poleward variation trend over the 26 years for each province (in degree poleward), based on the difference between the first and last point of the regression (respectively matching 1998 and 2023).

3 Results

3.1 Biophysical provinces definition

To define the homogeneous biophysical biomes, we perform a clustering on the two principal components generated by the PCA performed on the three environmental variables (i.e. epipelagic layer temperature, stratification and NPP). From the learning phase of the clustering algorithm, six static reference biophysical biomes (Figure 1) are defined on a global scale, representing the average state of the ocean over the entire period. The sub-division of these biomes according to ocean basin and hemisphere leads to the definition of 27 biophysical provinces (identified by different shades of the biomes' colors in Figure 1).

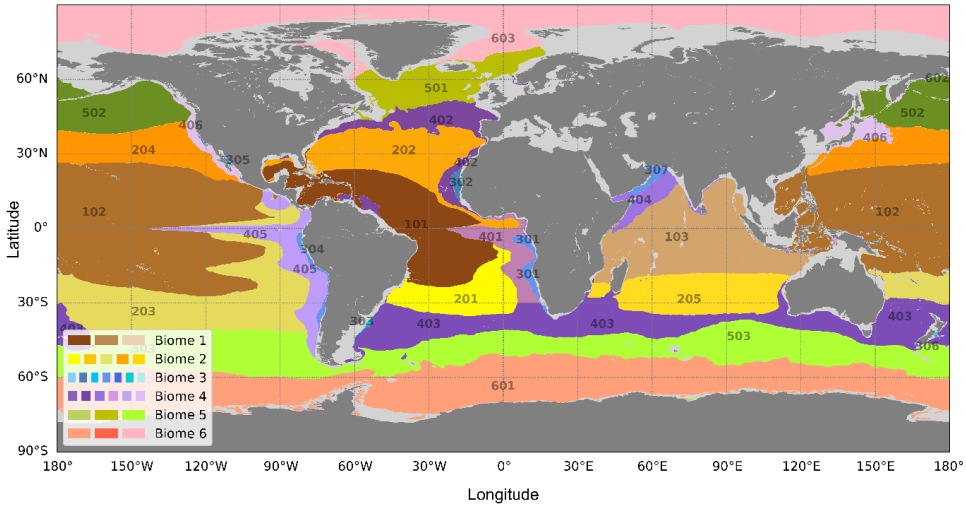

Figure 1: Map of reference biophysical biomes obtained by PCA principal component clustering from averaged epipelagic layer temperature, stratification, and NPP over the 1998-2023 time period. Geographical separation between different areas of the same biome defines 27 associated provinces. Provinces are identified by different shades of biomes' colors, defined in the legend. One label is attributed to each province with the hundreds' digits corresponding to the biome in which they belong. Grey areas delimitate the domain where the depth of the water column is not sufficient to ensure the existence of the three pelagic layers of SEAPODYM-LMTL (product ref 01, Table 1).

The six reference biophysical biomes are characterized as: tropical, subtropical, eastern boundary coastal upwelling systems, oceanic mesotrophic systems, sub-polar and polar (respectively numbered from 1 to 6). They are characterized by specific environmental regimes detailed in Albernhe et al. (2024, under review).

The monthly time series of these provinces is available as an animation showing the provinces' geographical evolution in time from 1998 to 2023 (https://doi.org/10.5446/68853). Together with the variations of ocean environmental conditions, the geographical extent of provinces evolves in time. Seasonal variability can be observed with the latitudinal shifts of the horizontal boundaries, as well as regional seasonal phenomena or isolated phenomena like ENSO events.

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3.2 Provinces' surface area evolution

We aim to observe the geographical evolution of the provinces in time from 1998 to 2023. The slopes of the linear regression models computed from the annual time series of surface area for each province are computed (See supplementary material, Table S1, third column). These trends (in km^2/year) are also expressed as the equivalent percentage of evolution between 1998 and 2023, in % (Table S1, fourth column). The latter is displayed in Figure 2, as a map of the reference biophysical provinces showing their surface evolution in time from 1998 to 2023.

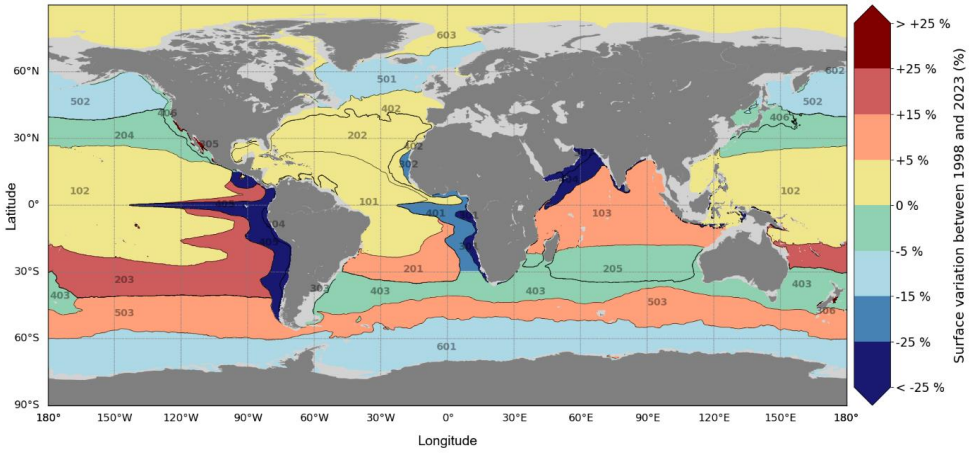

Figure 2: Map of the provinces' surface area evolution in time from 1998 to 2023. Black lines delineate the definition of the 27 reference biophysical provinces (cf. Figure 1). Colors represent the trend in surface variation for each province (in % from 1998 to 2023): shades of red indicate increasing surface area, while shades of blue indicate decreasing surface area.

From 1998 to 2023, there has been a decline in the surface area of productive provinces (i.e., characterized by high NPP) in eastern boundary coastal upwelling systems and oceanic mesotrophic systems (provinces belonging to Biomes 3 and 4, i.e. labelled 300's and 400's), as indicated by the provinces colored with shades of blue in Figure 2. Most of the polar and subpolar provinces such as the North Atlantic and North Pacific subpolar areas (respectively provinces 501 and 502) and the circumpolar province of the Southern Ocean (601) also display decreasing trends in their extent. On the other hand, provinces with increasing surface trends are mostly tropical or subtropical areas (Indian Ocean, South Atlantic tropical band, or South Pacific tropical band, respectively provinces 103, 201 and 203).

On a global scale, productive provinces and polar provinces seem to shrink in favor of tropical provinces expansion. However, some biomes exhibit significant discrepancies among the provinces they encompass. For instance, the surface of the Southern Ocean province 503 (belonging to the subpolar Biome 5) shows an increasing trend, in opposition with provinces 501 and 502 belonging to the same biome, showing decreasing trends in the northern hemisphere.

3.3 Provinces' average latitude evolution

Together with the evolution of provinces' surface area, provinces' average latitude is a valuable metric to track the geographical evolution of the provinces in time from 1998 to 2023. The slopes of the linear regression models computed from the annual time series of average latitude for each province are computed (See supplementary material, Table S2). The poleward displacement of each province between 1998 and 2023 is displayed in Figure 3 (in degree poleward).

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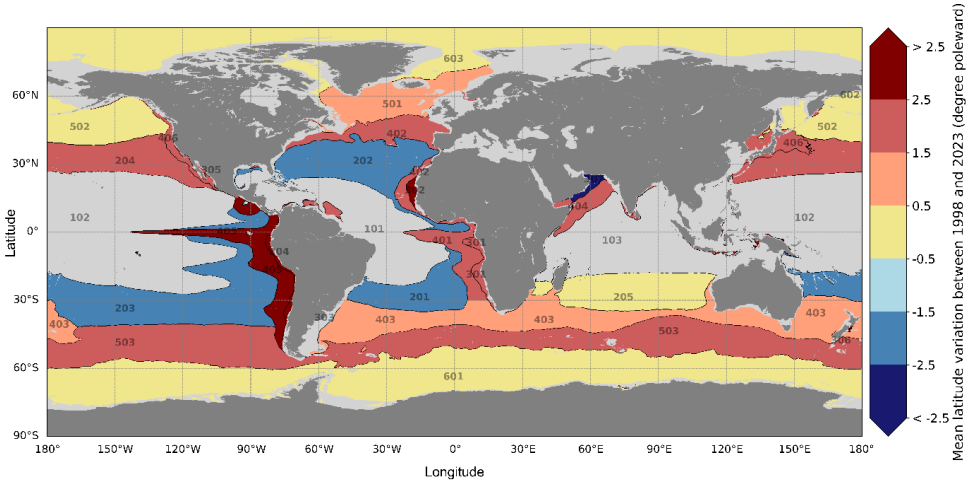

Figure 3: Map of the provinces' average latitude evolution in time from 1998 to 2023. Black lines display the definition of the 27 reference biophysical provinces (cf. Figure 1). Colors represent the trend in average latitude variation for each province (in degree poleward from 1998 to 2023): darker shades of red indicate poleward drifting, while darker shades of blue indicate equatorward drifting. Provinces of the equatorial biome colored in grey (101, 102 and 103) are not considered in this diagnostic because of their equatorial position.

Most of the provinces experience poleward drifting (provinces colored with shades of red in Figure 3). The tropical provinces displaying increasing surface trends (See provinces 201, 203, Figure 2) experience equatorward drifting, as indicated by provinces colored with shades of blue in Figure 3. Provinces with average latitude evolution trends between +0.5 and -0.5 degree poleward over the time period are considered as stable in time, in terms of latitude (provinces colored in yellow in Figure 3).

3.4 Uncertainties

The robustness of the biophysical clustering obtained with the reference dataset, i.e., GLORYS12V1 for the physical variables and VGMP for the biological variable (see section 2.1., and table 1, product ref01), is tested by computing other biophysical clusterings derived from alternative environmental datasets. These alternative datasets include physical data from ARMOR3D (Guinehut et al., 2012; Mulet et al., 2012) and biological data from the biogeochemical model PISCES (Aumont et al., 2015),

The *Multi Observation Global Ocean 3D Temperature Salinity Height Geostrophic Current and MLD* product of Copernicus Marine Service (MULTIOBS_GLO_PHY_TSUV_3D_MYNRT_015_012, product ref03, table 1) provides 3-D temperature from ARMOR3D dataset, derived from an optimal analysis of 3-D observations. This product is used to compute the epipelagic layer temperature and the stratification, instead of GLORYS12V1 (used in reference biophysical clustering, product ref01, table 1). A first alternative clustering, employing the same methodology as the reference biophysical clustering (see II.1. Variables and biophysical clustering), is performed using this product to compute the physical variables (the epipelagic layer temperature and the stratification), and still using VGPM (product ref01, table 1) to compute the NPP.

Then, the *Biogeochemical hindcast for global ocea*n product of Copernicus Marine Service (GLOBAL_MULTIYEAR_BGC_001_029, product ref02, table 1), is used to compute the NPP variable for the clustering instead of VGPM (product ref01, table 1). It provides 3D biogeochemical fields using PISCES biogeochemical model outputs. A second alternative clustering, employing the same methodology as the reference biophysical clustering, is performed using this product to compute the NPP, and still using GLORYS12V1 (product ref01, table 1) to compute the physical variables (as in the reference biophysical clustering).

The two alternative products mentioned above are available at ¼ degree from 1998 to 2022 at a monthly resolution. Each of them is used to compute an alternative clustering (respectively using VGPM-ARMOR3D and PISCES-GLORYS12V1). We compare our reference biophysical clustering (VGPM-GLORYS12V1, see Section 2.1),

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downscaled from 1/12-degree to 1/4-degree resolution, with two alternative clusterings (Figure 4), all averaged over the period 1998–2022.

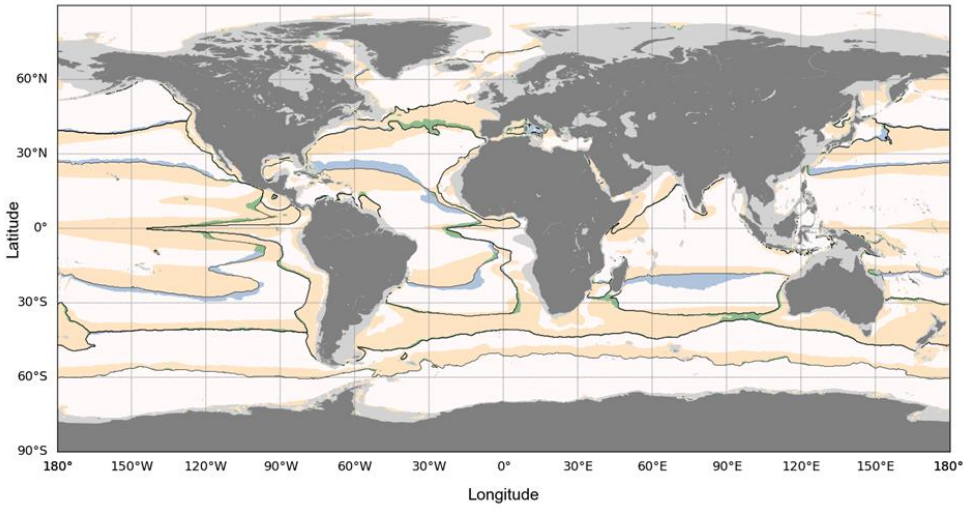

Figure 4: Clustering sensitivity analysis. Map of reference biophysical biomes computed from GLORYS12V1 (product ref01, table 1) and VGPM (product ref01, table 1), in black lines (cf. Figure 1). The white areas indicate where both alternative clusterings assign the same cluster as the reference biophysical clustering. The blue areas indicate where the clustering using ARMOR3D (product ref03, table 1) instead of GLORYS12V1 (product ref01, table 1) assign a different cluster from the reference biophysical clustering. The yellow areas indicate where the clustering using PISCES (product ref02, table 1) instead of VGPM (product ref01, table 1) assign a different cluster from the reference biophysical clustering. The green areas indicate where both alternative clusterings assign a different cluster from the reference biophysical clustering.

Figure 4 shows that the clustering is very stable when changing the physical variable source from GLORYS12V1 (product ref01, table 1) to ARMOR3D (product ref03, table 1), as blue areas highlight minor boundaries differences. However, when changing biogeochemical variable source from VGPM (product ref01, table 1) to PISCES (product ref02, table 1), the productive biome 4 is highly impacted. However, NPP estimations from PISCES (product ref02, table 1) and VGPM (product ref01, table 1) differ significatively. We notice that the clustering remains relatively stable with respect to the source of forcings, although variations can arise when forcing fields differ widely. The time series and results presented in the study are thus valid using VGPM and GLORYS12V1 (both product ref01, table 1), but caution should be taken in extrapolating those results to clusters issued from other biogeochemical sources (e.g. models' outputs).

4 Discussion and conclusion

In this study, we defined an annual time series of biophysical provinces linked to micronekton from 1998 to 2023, based on a methodology introduced in Albernhe et al. (2024, under review). In addition to the provinces' definition methodology, this previous article demonstrates that each province features a specific characterization in terms of micronekton biomass and vertical structure. Following the hypothesis that these characteristics are preserved over time, which needs to be further investigated, the evolution of provinces' surface area can account for global micronekton trends and estimations. For instance, the shrinking of provinces featuring the highest density of micronekton biomass would lead to a global decrease of micronekton biomass.

In the present study, we observe a global shrinking of productive provinces and polar provinces, in favor of equatorial and tropical provinces expansion (Figure 2). Productive provinces and subpolar provinces are characterized by high densities of micronekton biomass (Albernhe et al., 2024, under review), whereas equatorial and tropical ones display weaker densities. If provinces characteristics are preserved over time, these surfaces variations imply a global decline of micronekton biomass. This potential trend for micronekton biomass evolution

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on the historical period would be in range with studies on micronekton biomass climate projections (Bryndum-Buchholz et al., 2018; Kwiatkowski et al, 2018; Lotze et al, 2019; Tittensor et al., 2021; Ariza et al., 2022).

The tracking of the geographical evolution of the provinces in time reveals that most of the provinces experience poleward drifting (Figure 3). This poleward drifting is a valuable observation in range with the literature (Hastings et al., 2020; Pinsky et al., 2020), suggesting a potential poleward migration of micronektonic populations induced by temperature changes.

Video supplement

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Data availability

All data products used in this paper are listed in Table 1, along with their corresponding documentation and online availability.

Table 1: Product Table

Product ref. No.	Product ID & type	Data access	Documentation
01	GLOBAL_MULTIYEAR_BGC_001_033; Numerical Models	EU Copernicus Marine Service Product: *Global Ocean low and mid trophic levels biomass content hindcast*, Mercator Ocean International, *https://doi.org/10.48670/moi-00020*	Quality Information Document (QUID): Titaud et al., 2023 Product User Manual (PUM): Titaud et al., 2023
02	GLOBAL_MULTIYEAR_BGC_001_029; Numerical models	EU Copernicus Marine Service Product: *Biogeochemical hindcast for global ocean*, Mercator Ocean International, https://doi.org/10.48670/moi-00019	Quality Information Document (QUID): Perruche et al., 2019 Product User Manual (PUM) : Le Galloudec et al., 2022
03	MULTIOBS_GLO_PHY_TSUV_3D_MYNRT_015_012; In-situ observations, Satellite observations	EU Copernicus Marine Service Product: *Multi Observation Global Ocean 3D Temperature Salinity Height Geostrophic Current and MLD*, CLS, https://doi.org/10.48670/moi-00052	Quality Information Document (QUID): Greiner., 2023 Product User Manual (PUM) : Verbrugge et al., 2023

Author contributions

SA produced the clustering, the provinces' timeseries, and the associated diagnostic for their evolution in time. SA wrote and edited the report.

TG was involved in the investigation process as an advisor and reviewed the report.

OT was involved in the investigation process as an advisor and produced the lower and mid-trophic levels biomass density (*Global Ocean low and mid trophic levels biomass content hindcast*, GLOBAL_MULTIYEAR_BGC_001_033) 1998-2023 time-series.

The other authors are supervising the PhD of SA, and were involved in the investigation process to define the methodology used for the clustering (Albernhe et al., 2024, under review)

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Competing interests

The contact author has declared that none of the authors has any competing interests.

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Review statement

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