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An ecological partition of the Atlantic Ocean and its adjacent seas

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ABSTRACT

In the past, partitions of the global ocean have been commonly carried out using relatively few environmental or biological variables. Although such partitions are undoubtedly useful on a global scale, we show that, at a basin scale, the use of a large number of biological variables greatly improves the accuracy of a partition. We first determined pelagic habitats using a set of selected environmental variables such as temperature, bathymetry, light at the seabed, sea ice concentration, current velocity and salinity. We then partitioned the North Atlantic Ocean and its adjacent seas at spatial resolutions of 2° latitude × 2° longitude and 0.5° × 0.5° using biological data from the Continuous Plankton Recorder (CPR survey). We used a total of 238 plankton species or taxa sampled between 1946 and 2015 representing more than 60 million data points. Finally, we combined the three biogeographies together to propose a new ecological partition of the North Atlantic and its adjacent seas into Ecological Units (EUs) and ecoregions. The comparison of our partition with the biogeochemical biogeography proposed by Longhurst reveals substantial differences in the location and size of biomes and provinces, especially over the continental shelf. In particular, boundaries of three known biomes (i.e. westerlies, polar and continental shelves biomes) differ substantially from the global-scale classifications.

1. Introduction

Understanding how life is arranged on Earth has long occupied scientists such as Carolus Linnaeus (1707–1778) and Georges-Louis Leclerc, Comte de Buffon (1707–1788). Partitioning the marine pelagic domain has proved to be quite difficult in comparison to the terrestrial realm where demarcations are more apparent and access to the field easier (Cox and Moore, 2000). Despite these difficulties, a number of partitions of the pelagic realm have been proposed over the course of the 19th and 20th century. For instance, Mark Spalding and colleagues listed the work of Forbes (1856), Ekman (1953), Hedgpeth (1957), Briggs (1974) and Bailey (1998) (Spalding et al., 2007). Temperature variability over large time scales explained well the partition of Briggs, who also considered endemism (Briggs, 1974). More recently, classifications have been proposed to improve ecosystem management. For instance, Large Marine Ecosystems (LMEs), implemented by Sherman and colleagues, are large regions (i.e. ≥200,000 km^2) based on their (1) bathymetry, (2) hydrography, (3) productivity and (4) trophically dependent populations (Sherman and Duda, 1999). Globally, a total of 66 LMEs has been proposed so far. LMEs were originally designed to tackle environmental issues such as fisheries management and only concern large continental shelves. Lately, Spalding et al. (2007) proposed an expert-knowledge global system for coastal and shelf areas, termed the Marine Ecoregions of the World (MEOW). This partitioning encompasses a nested system of 12 realms (i.e. continent-sized areas with homogeneous geographical components and living organisms), 62 provinces (i.e. large ecosystems defined by the presence of distinct biocoenoses having a certain level of cohesion over evolutionary time), and 232 ecoregions (i.e. areas having a relatively homogeneous biocoenosis in comparison to adjacent zones). The MEOWs have been implemented with the goal of directing future efforts in marine resource management and biodiversity conservation (Spalding et al., 2007).

Generally, biological partitioning has been rarely achievable with great precision at a large scale because the spatial distribution of many species is poorly known. This is perhaps why some authors have proposed partitions based on biogeochemical parameters or, more recently, parameters such as chlorophyll concentration assessed from satellites (D'Ortenzio and d'Alcala, 2008; Longhurst, 1998; Oliver and Irwin, 2008; Reygondeau et al., 2013). The development of satellite technology and the globalization of environmental datasets have enabled the establishment of a global biogeography. A division of the marine ecosphere into biomes (i.e. a large ecosystem primarily controlled by climate) and provinces has been proposed by Longhurst (2007). Four primary biomes (Polar, Westerlies, Trades, and Coastal) and 56 secondary provinces have been identified. This partition of the marine ecosphere was mainly based on the characterization of the seasonal

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cycle of primary production (Longhurst, 2007). Variables used to establish the partition were chlorophyll-a concentration, mixed layer depth, nutrients, the Brunt-Vaisala frequency, the Rossby radius of internal deformation, photic depth, algal biomass and primary production. These variables allowed the identification of a number of ecological situations: (1) polar irradiance-limited production peak, (2) nutrient-limited spring bloom, (3) winter-spring production with nutrient limitation, (4) small amplitude response to trade wind seasonality, (5) large amplitude response to monsoon reversal, and (6) various responses to topography and wind-stress on continental shelves, including coastal upwelling (Reygondeau et al., 2013). Using four parameters (bathymetry, chlorophyll-a concentration, surface temperature and salinity), Reygondeau et al. (2013) applied a procedure based on the Non-Parametric Probabilistic Ecological Niche model (Beaugrand et al., 2011) to propose a more dynamical partition of Longhurst's biogeochemical provinces. The average demarcation of the provinces was in general in good agreement with those originally proposed by Longhurst. Basing pelagic biogeography on a few biogeochemical parameters or expert knowledge may lead to a too simplistic scheme because pelagic ecosystems are composed of many species that integrate the multidimensionality of the environment. Biogeographical partitions based on species distribution have also been proposed. Mary Somerville (1780–1872) in her book about physical geography divided the marine ecosphere into homozoic zones. Based on Mollusca, Edward Forbes (1815–1854) established nine homozoic zones and related them mainly to marine isotherms. Developments of remote sensing and large-scale ship-based surveys have allowed a better demarcation of the biomes occupied by various taxonomic groups such as coccolithophores (Merico et al., 2003), N2 fixers (Westberry and Siegel, 2006) and picocyanobacteria (Johnson et al., 2006).

Here, we use the information on 238 species or taxa (phytoplankton, holozooplankton and meroplankton) for every two-month period (1946–2015), originating from the Continuous Plankton Recorder (CPR) survey. Together with some key physical parameters (temperature, bathymetry, sea ice concentration, light at the seabed, current velocity and salinity), we propose a partition of the North Atlantic Ocean and its adjacent seas into biomes, provinces and ecoregions. We first partition the area into habitats at relatively high spatial resolution ($0.08^\circ \times \sim 0.08^\circ$) and then assess the biodiversity of diatoms, dinoflagellates (*Ceratium*), small and large copepods and zooplankton to propose a biological partition at two spatial resolutions: $2^\circ \times 2^\circ$ and $0.5^\circ \times 0.5^\circ$ where sampling is sufficiently dense. Finally, we combined all partitions into a single one and compare it with others exclusively based on physico-chemical parameters. The final partition leads to an identification of 13 ecological units and 40 ecoregions in the spatial domain covered by the CPR survey, which explains well observed biological patterns from the species to the community levels.

2. Materials and methods

2.1. Physical data

We used physical data originating from Bio-ORACLE v2.0 (Marine data layers for ecological modelling) (Assis et al., 2017; Tyberghein et al., 2012). Bio-ORACLE is a global dataset consisting of 23 geophysical, biotic and climate rasters. This data package for marine species distribution modelling is available for download at http://www.bio-oracle.org. For this purpose, we used both minimum and maximum sea ice concentration (fraction), sea surface temperature (°C), salinity (PSS), bathymetry (m), light at the seabed ($E{\cdot}m^{-2}{\cdot}yr^{-1}$), Nitrate, phosphate and silicate ($mol{\cdot}m^{-3}$), Photosynthetically Active Radiation (PAR; $E{\cdot}m^{-2}{\cdot}day^{-1}$), chlorophyll concentration ($mg{\cdot}m^{-3}$), primary production ($g{\cdot}m^{-3}{\cdot}day^{-1}$) and current velocity ($m{\cdot}s^{-1}$). Those parameters, averaged in the dataset for the period 2000–2014, are important ecological factors that shape biodiversity at a large scale. Rasters were assembled at a resolution of 5 arcmin (i.e. 9.2 km).

We used another dataset to test the influence of the difference in temporal coverage on the ecological partition. These annual SSTs originated from the dataset ERSST_v3 (1946–2015). The dataset is derived from a reanalysis based on the most recently available International Comprehensive Ocean-Atmosphere Data Set (ICOADS). Improved statistical methods have been applied to produce a stable monthly reconstruction, on a $2^\circ \times 2^\circ$ spatial grid, based on sparse data (Smith et al., 2008). Data were interpolated on a global grid of 1° latitude $\times$ 1° longitude.

2.2. Biological data

The Continuous Plankton Recorder (CPR) Survey is a long-term, sub-surface marine plankton monitoring programme consisting of a network of CPR transects towed monthly across the major geographical regions of the North Atlantic. It has been operating in the North Sea since 1931 with some standard routes existing with a virtually unbroken monthly coverage back to 1946 (Batten et al., 2003; Reid et al., 2003). The CPR survey is recognised as the longest sustained and geographically most extensive marine biological survey in the world. The dataset comprises a uniquely large record of marine biodiversity covering ~1000 taxa over multi-decadal periods. The survey determines the abundance and distribution of phytoplankton and zooplankton (including fish larvae) in our oceans and shelf seas. Using ships of opportunity from ~30 different shipping companies, it obtains samples at monthly intervals on ~50 trans-ocean routes. In this way the survey autonomously collects biological and physical data from ships covering ~20,000 km of the ocean per month, ranging from the Arctic to the Southern Ocean.

The CPR is a high-speed plankton recorder that is towed behind 'ships of opportunity' through the surface layer of the ocean (~10 m depth) (Warner and Hays, 1994). Water passes through the recorder and plankton are filtered by a slow-moving silk (mesh size 270 μm). A second layer of silk covers the first and both are reeled into a tank containing 4% formaldehyde. Upon returning to the laboratory, the silk is unwound and cut into sections corresponding to 10 nautical miles and approximately 3 m^3 of filtered sea water (Jonas et al., 2004).

There are four separate stages of analysis carried out on each CPR sample, with each focusing on a different aspect of the plankton: (1) overall chlorophyll (the phytoplankton colour index; PCI); (1) larger phytoplankton cells (phytoplankton); (3) smaller zooplankton (zooplankton "traverse"); and (4) larger zooplankton (zooplankton "eye-count"). The phytoplankton colour of each section of the CPR silk is evaluated and categorised according to four levels of 'greenness' (green, pale green, very pale green and no colour) using a standard colour chart; the numbers are given a numerical value as a measure of 'Phytoplankton Colour Index'. Here we focussed our analysis on phytoplankton cells, small and large zooplankton. Because we worked at the species level, we did not use the colour index.

Phytoplankton cells are identified and recorded as either present or absent across 20 microscopic fields spanning each section of silk (representing ~1/10,000 of the filtering silk). Due to the mesh size of CPR silks, many phytoplankton species are only semi-quantitatively sampled owing to the small size of the organisms (Batten et al., 2003). There is therefore a bias towards recording larger armoured flagellates and chain-forming diatoms and that smaller species abundance estimates from cell counts are probably underestimated in relation to other water sampling methods. However, the proportion of the population that is retained by the CPR silk reflects the major changes in abundance, distribution and specific composition (i.e. the percentage retention is roughly constant within each species even with very small-celled species) (Edwards et al., 2006). Zooplankton analysis is then carried out in two stages with small (< 2 mm) zooplankton identified and counted on-silk (representing ~1/50 of the filtering silk) and larger (> 2 mm) zooplankton enumerated off-silk (Warner and Hays, 1994). The collection and analysis of CPR samples have been carried out using a

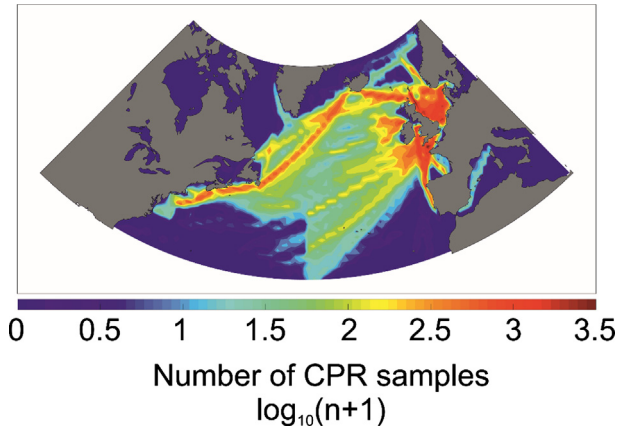

Fig. 1. CPR sampling intensity (in decimal logarithm) in the North Atlantic and its adjacent seas for the period 1946–2015.

consistent methodological approach, coupled with strict protocols and Quality Assurance procedures since 1958, making the CPR survey the longest continuous dataset of its kind in the world. Fig. 1 shows the spatial distribution of the CPR samples used in this study.

2.3. Methods

We performed three partitions of the North Atlantic Ocean: (1) habitat partition at a 0.08° × 0.08° spatial resolution, and (2) biological (CPR-based) partitions at a 2° × 2° (areas where CPR spatial coverage was lower than average) and at a 0.5 × 0.5° spatial resolution (regions were spatial coverage was higher than average). Finally, (3) we combined the three partitions to build a synthetic map to propose an ecological partition of the North Atlantic Ocean and its adjacent seas.

The different types of partition, as well as the technical terms such as ecological units and ecoregions are explained briefly or summarized in Section 2.4.

2.3.1. Habitat classification

We first partitioned the North Atlantic Ocean and its adjacent seas using an empirical (threshold-based) procedure based on SST, bathymetry, light at the seabed, salinity and current velocity at a high spatial resolution (0.08° latitude × 0.08° longitude). This partition was intended to complement the biological partition based on CPR data. The habitat partition was carried out hierarchically and led to 15 pelagic habitats (Table 1; see Section 2.4 on terminology). A number of thresholds were chosen based on expert knowledge. Salinity and current velocity thresholds were based either on the third quartile (Q3) or the ninth decile (D9) of all marine data. *Oceanic* areas were regions with depth greater than 1000 m, *shelf-edges* with depth between 1000 and 200 m and *continental shelves* with depth less than 200 m. Light at the seabed (i.e. light at the seabed higher than 0 $E \cdot m^{-2} \cdot yr^{-1}$) allowed us to distinguish areas where light can or cannot reach the seabed. In oceanic areas where salinity was higher than Q3, we distinguished different pelagic habitats using the following isotherms: (1) 7–10 °C, (2) 10–13 °C, (3) 13–16 °C, (4) 16–19 °C, (5) 19–22 °C, and (6) 22–25 °C (Table 1). Finally, oceanic areas with current velocity above D9 enabled the identification of the average location of the Gulf Stream. Here, the thresholds were based on expert knowledge and their modifications had only a moderate (Q3 or D9) or expected (e.g. temperature) effect on the partition. For example, the temperature categories allowed us to separate the subarctic gyre into distinct components: the Labrador Sea, and the central and eastern parts of the subarctic gyre. Table 1 summarizes the choice of the thresholds made to perform the classification and the resulting ecological characteristics of each ecoregion. This partition is shown in Fig. 2.

2.3.2. Biological partition

We partitioned the North Atlantic Ocean and its adjacent seas using data collected from the CPR survey (Reid et al., 2003) and define this partition as "biological partition" hereafter (see Section 2.4. on terminology). Specifically, we based our partition on six taxonomic groups: diatoms (59 species or taxa; Supplementary Table 1), *Ceratium* dinoflagellates (41 species; Supplementary Table 2), small copepods (recorded in traverse; 27 species or taxa; Supplementary Table 3), small zooplankton (recorded in traverse; 15 species or taxa; Supplementary Table 4), large copepods (recorded in eyecount; 73 species; Supplementary Table 5) and large zooplankton other than copepods and including fish eggs and larvae (recorded in eyecount; 23 species or taxa; Supplementary Table 6). Therefore, a total of 238 species or taxa were considered for the period 1946–2015 (a total of 254,410 CPR samples), which represented a total of 60,549,580 data points. We partitioned the North Atlantic Ocean and its adjacent seas using two spatial resolutions: (1) a grid of 2° latitude × 2° longitude that enabled a large coverage into the North Atlantic Ocean despite the lower CPR sampling coverage, and (2) a grid of 0.5° × 0.5° from 40.5°N to 65.5°N and from 80.5°W to 9.5°E that enables a finer partition in seas around the British Isles where CPR sampling is the densest.

For the two biological partitions, we first estimated the species

Table 1
Categories of ecogeographical variables used to classify the North Atlantic Ocean and its adjacent seas into 15 pelagic habitats. SIC: Sea-Ice Concentration (average of minimum and maximum sea ice fraction). A hyphen denotes the absence of consideration of an ecogeographical variable. Indeed in some regions, the consideration of some environmental variables was not useful either because their values were relatively stable or because they did not provide any additional information. An ecoregion is simply a region with similar ecological conditions with respect to the factors used to make the classification. The threshold used for salinity was the third quartile and the threshold used for current velocity was the 9th decile based on all marine areas of the world.

Pelagic habitats	Higher bathymetry	lower bathymetry	SIC > 0	Light the seabed > 0	Currents ($m \cdot s^{-1}$)	Salinity	SST (°C)
1	11,000	1000	Yes	No	–	–	–
2	1000	200	Yes	No	–	–	–
3	200	50	Yes	No	–	–	–
4	11,000	1000	No	No	< 0.62 (D9)	< 35.23 (Q3)	–
5	1000	200	No	No	–	–	–
6	200	50	No	No	–	–	–
7	50	0	No	No	–	–	–
8	200	0	No	Yes	–	–	–
9	11,000	1000	No	No	> 0.62	–	–
10	11,000	1000	No	No	< 0.62	> 35.23	7–10
11	11,000	1000	No	No	< 0.62	> 35.23	10–13
12	11,000	1000	No	No	< 0.62	> 35.23	13–16
13	11,000	1000	No	No	< 0.62	> 35.23	16–19
14	11,000	1000	No	No	< 0.62	> 35.23	19–22
15	11,000	1000	No	No	< 0.62	> 35.23	22–25

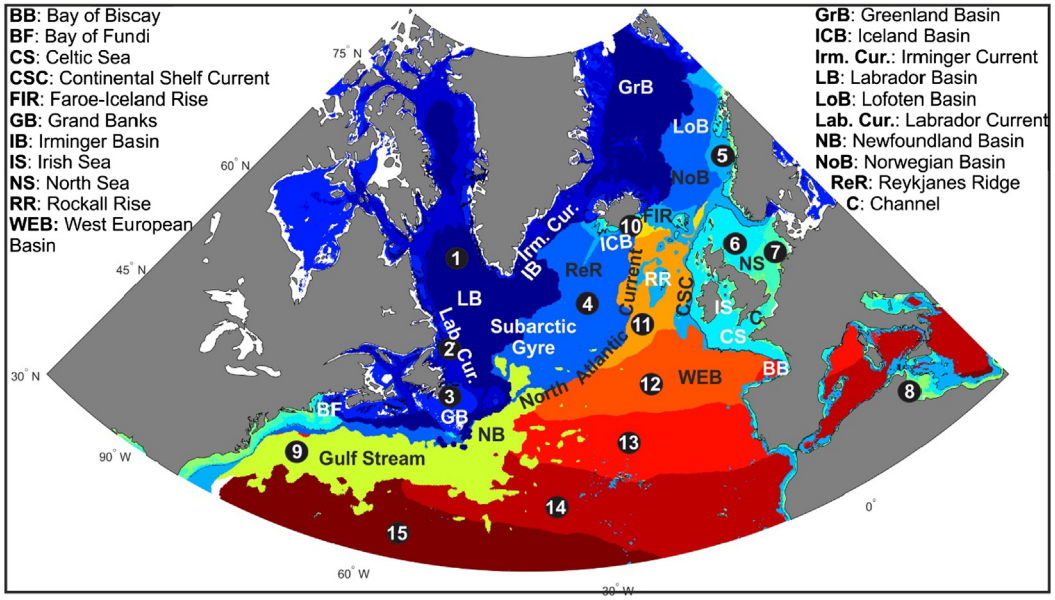

Fig. 2. Habitat partition (0.08 × 0.08 spatial resolution) of the North Atlantic Ocean and its adjacent seas based on Sea Surface Temperature (SST), bathymetry, sea ice concentration, light at the seabed, salinity and current velocity. See Methods and Table 1.

richness of each taxonomic group on the two spatial grids. CPR data from 1946 to 2015 were analysed for each two-month period using an approach similar to what was applied to map copepod biodiversity (Beaugrand et al., 2001). For each geographical cell and two-month period, we calculated the species richness providing that the number of samples was higher than 15 (for the 2° × 2° partition) or 5 (for the 0.5° × 0.5° partition), thresholds (> 5) that guarantee a correct estimation of the diversity of a taxonomic group from the CPR survey (Beaugrand and Edwards, 2001). In large-scale studies, indices weighted towards species richness are more useful for detecting differences between sites than indices emphasising the evenness component of biodiversity (Magurran, 1988). Even though the calculation of species richness is sensitive to sample size and leads to systematic underestimation of copepod biodiversity, it is still a satisfactory estimator that can be used for comparisons between sites with low spatial resolution (Beaugrand and Edwards, 2001). We used a first-order jackknife procedure to increase the robustness of the species or taxonomic richness. To calculate the first-order jackknife estimator *D,* pseudo-values p_i that excluded samples i from each geographical cell were computed as follows (Beaugrand et al., 2010):

$$p_i = np^0 - (n-1)p_i^{(-i)} \quad (1)$$

where n is the number of CPR samples in the geographical cell for a given two-month period, p^0 is the estimate of the species/taxonomic richness based on all CPR samples, and $p_i^{(-i)}$ is the value of the species (or taxonomic) richness based on all samples but *i.* Each pseudo-value gives an estimation of the number of species in a given cell. There were as many pseudo-values as samples in the geographical cell for a given two-month period. The estimated taxonomic richness (or species richness) D was the average of all pseudo-values:

$$D = \sum_{i=1}^{n} \frac{p_i}{n} \quad (2)$$

For the first biological partition (2° latitude × 2° longitude), matrices of (jackknifed) taxonomic richness of 13 latitudes × 46 longitudes = 598 geographical squares × six two-month periods were built for each taxonomic group. Six matrices were therefore prepared: **Matrix *A*** 598 geographical cells × 6 two-month periods for diatoms, **Matrix *B*** 598 geographical cells × 6 two-month periods for the genus *Ceratium*, **Matrix *C*** 598 geographical cells × 6 two-month periods for small copepods, **Matrix *D*** 598 geographical cells × 6 two-month periods for small zooplankton other than copepods, **Matrix *E*** 598 geographical cells × 6 two-month periods for large copepods, and **Matrix *F*** 598 geographical cells × 6 two-month periods for large zooplankton other than copepods.

For the second biological partition (0.5° latitude × 0.5° longitude), matrices of (jackknifed) taxonomic richness of 51 latitudes × 181 longitudes = 9231 geographical squares × 6 two-month periods were built for each taxonomic group. Six matrices were therefore prepared: **Matrix *A**** 9231 geographical cells × 6 two-month periods for diatoms, **Matrix *B**** 9231 geographical cells × 6 two-month periods for the genus *Ceratium*, **Matrix *C**** 9231 geographical cells × 6 two-month periods for small copepods, **Matrix *D**** 9231 geographical cells × 6 two-month periods for small zooplankton other than copepods, **Matrix *E**** 9231 geographical cells × 6 two-month periods for large copepods, and **Matrix *F**** 9231 geographical cells × 6 two-month periods for large zooplankton other than copepods.

To diminish the number of missing values in oceanic areas in all matrices (i.e. ***A*-*F*** and ***A**-*F**), we carried out iterative Principal Component Analyses (PCAs) on each matrix using 100 PCAs and the first 5 principal components and eigenvectors (Beaugrand et al., 2013).

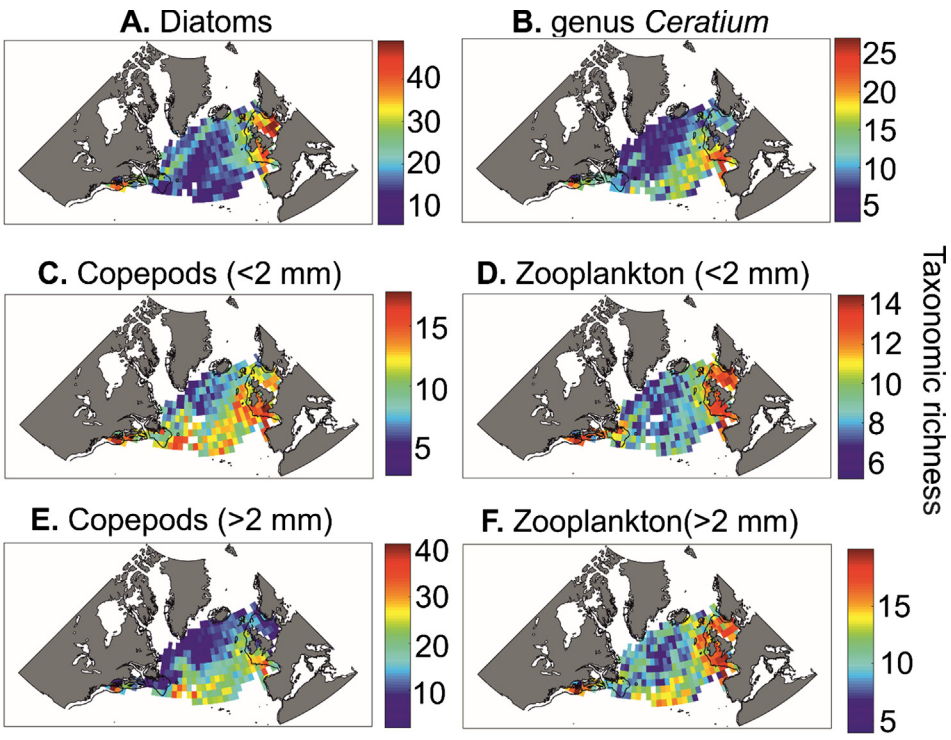

Fig. 3. Mean taxonomic richness of six taxonomic groups sampled by the CPR survey calculated on a 2° × 2° spatial resolution. The taxonomic richness was assessed using a first-order Jackknife coefficient for each 2-month period. A. Diatom taxonomic richness. B. Dinoflagellates (*Ceratium*) species richness. C. Copepod (< 2 mm) taxonomic richness. D. Zooplankton (other than copepods; < 2 mm) taxonomic richness. E. Copepod (> 2 mm) taxonomic richness. F. Zooplankton (other than copepods; > 2 mm) taxonomic richness.

We then calculated a last PCA to remove the unexplained variance (Jolliffe, 1986). For this last analysis, the major signals were extracted by considering the first two principal components $\boldsymbol{P}_{(q,2)}$ and eigenvectors $\boldsymbol{U}_{(r,2)}$, which enabled smoothing the original matrices $\boldsymbol{O}_{(q,r)}$:

$$O_{(q,r)} = P_{(q,2)}U'_{(r,2)} \quad (3)$$

where q is the number of geographical cells (598 or 9231) and r is the number of two-month periods (6). An annual average of the biodiversity of the six groups was calculated (Fig. 3).

We combined matrices $\boldsymbol{A}_{(598,6)}$-$\boldsymbol{F}_{(598,6)}$ into a new matrix $\boldsymbol{G}_{(598,36)}$ for partition 2° latitude × 2° longitude and matrices $\boldsymbol{A}^*_{(9231,6)}$-$\boldsymbol{F}^*_{(9231,6)}$ into a new matrix $\boldsymbol{G}^*_{(9231,36)}$ for partition 0.5° latitude × 0.5° longitude. We added the richness of all taxonomic groups to obtain a matrix of total taxonomic richness for each two-month period $\boldsymbol{T}_{(598,6)}$ and $\boldsymbol{T}^*_{(9231,6)}$. An annual average of the total biodiversity of all taxonomic groups was calculated (Fig. 4A). We calculated an index of seasonal amplitude by using the inter-decile (P_{90}-P_{10}) range on the 2° × 2° partition because it had the largest spatial coverage (Fig. 4B).

We then calculated two squared matrices $\boldsymbol{K}_{(598,598)}$ and $\boldsymbol{K}^*_{(9231,9231)}$ using the Euclidean distance and chose a hierarchical agglomerative clustering technique using average linkage, which was a good compromise between the two extreme single and complete clustering techniques (Legendre and Legendre, 1998) (Fig. 5). A hierarchical agglomerative technique is frequently displayed by a dendrogram (Legendre and Legendre, 1998), which shows the successive agglomeration of objects or clusters of objects (i.e. the geographical cells) to other groups (i.e. the groups of geographical cells). Each branching of the dendrogram occurs at a given distance value. Here, we examined the first 8 cut-off (i.e. branching of the tree) levels of the dendrogram (Fig. 6). Cell groups composed of less than three geographical cells were not considered and were replaced by adjacent ones when the number of adjacent cells was high (see next analysis below).

We smoothed the partitions (2° × 2° and 0.5° × 0.5°) by keeping a given cell group (i.e. a given group of geographical cells) only when it was composed of five adjacent geographical cells of the same group out of the nine possible (i.e. the target cell and all 8 adjacent geographical cells). This procedure smoothed slightly the final biological partitions by removing intertwined groups composed of a few cells (Figs. 7A and 8A).

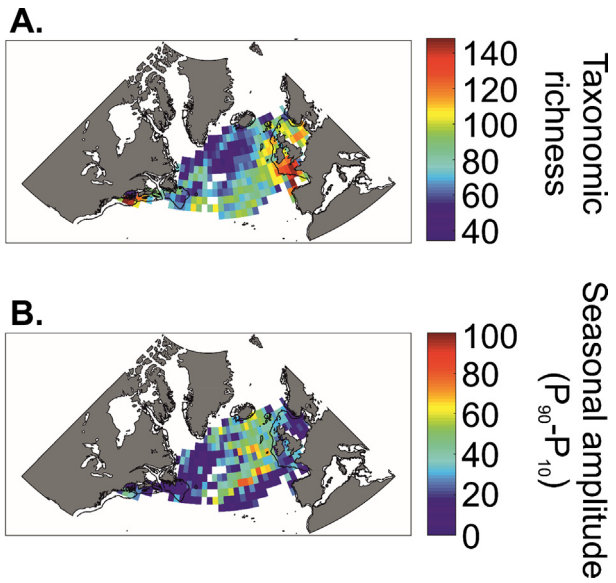

Fig. 4. A. Mean total taxonomic richness of all combined taxonomic groups and B. seasonal amplitude of total species richness assessed here by using the interdecile (P_{90}-P_{10}) range. The taxonomic richness was assessed using a first-order Jackknife coefficient for each two-month period. See Methods.

In addition, we calculated an index of cell group heterogeneity $\boldsymbol{H} = [h_{i,j}]$. For each geographical cell, we calculated the percentage of cells that belonged to different groups of geographical cells, which is the number of different groups v-1 (maximum of nine cells; here also the target cell and all 8 adjacent geographical cells) divided by the number of classified cells w-1 (maximum of nine cells). The index was therefore calculated as follows:

$$h_{i,j} = (100(v-1))/\ w-1 \quad (4)$$

For example, for nine possible cells, the index of heterogeneity is 0% when only one group is present and 100% when each cell belonged to a

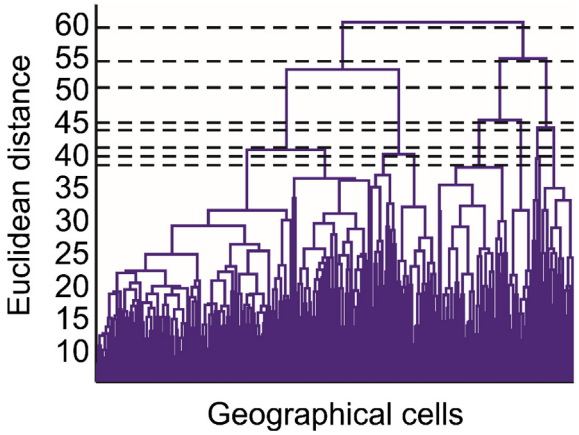

Fig. 5. Dendrogram originating from the application of an agglomerative hierarchical average linkage algorithm performed on an Euclidean distance matrix (Matrix K; see Methods). The different cut-off levels are indicated by a dashed black line (see Fig. 6).

different group. A total number of five cells was needed to have an estimation of the heterogeneity of a cell. The results of this analysis are in Figs. 7B and 8B. All procedures were programmed in Matlab.

2.3.3. Ecological partition

We then built a synthetic partition (hereafter termed ecological partition, see Section 2.4. on terminology) by designing the numerical procedure hereafter. We started our procedure using the biological partition based on a 0.5° × 0.5° spatial resolution. We removed groups for which it was not possible to calculate an index of heterogeneity (i.e. six groups) and merged small groups that were difficult to understand from expert knowledge because they lacked spatial contiguity (i.e. three groups of cells). A total of six cell groups remained (Supplementary Fig. 1A). Then, the biological partition at 2° × 2° spatial resolution was superimposed to the 0.5° × 0.5° biological partition in areas where no group of geographical cells existed. At that stage, we had a total of nine groups (Supplementary Fig. 1B). Finally, we added some groups originating from the habitat partition to divide the polar biome (*sensu* Longhurst (1998)); four more groups) into provinces and the westerly-wind biomes (*sensu* Longhurst (1998)); one more group). The final

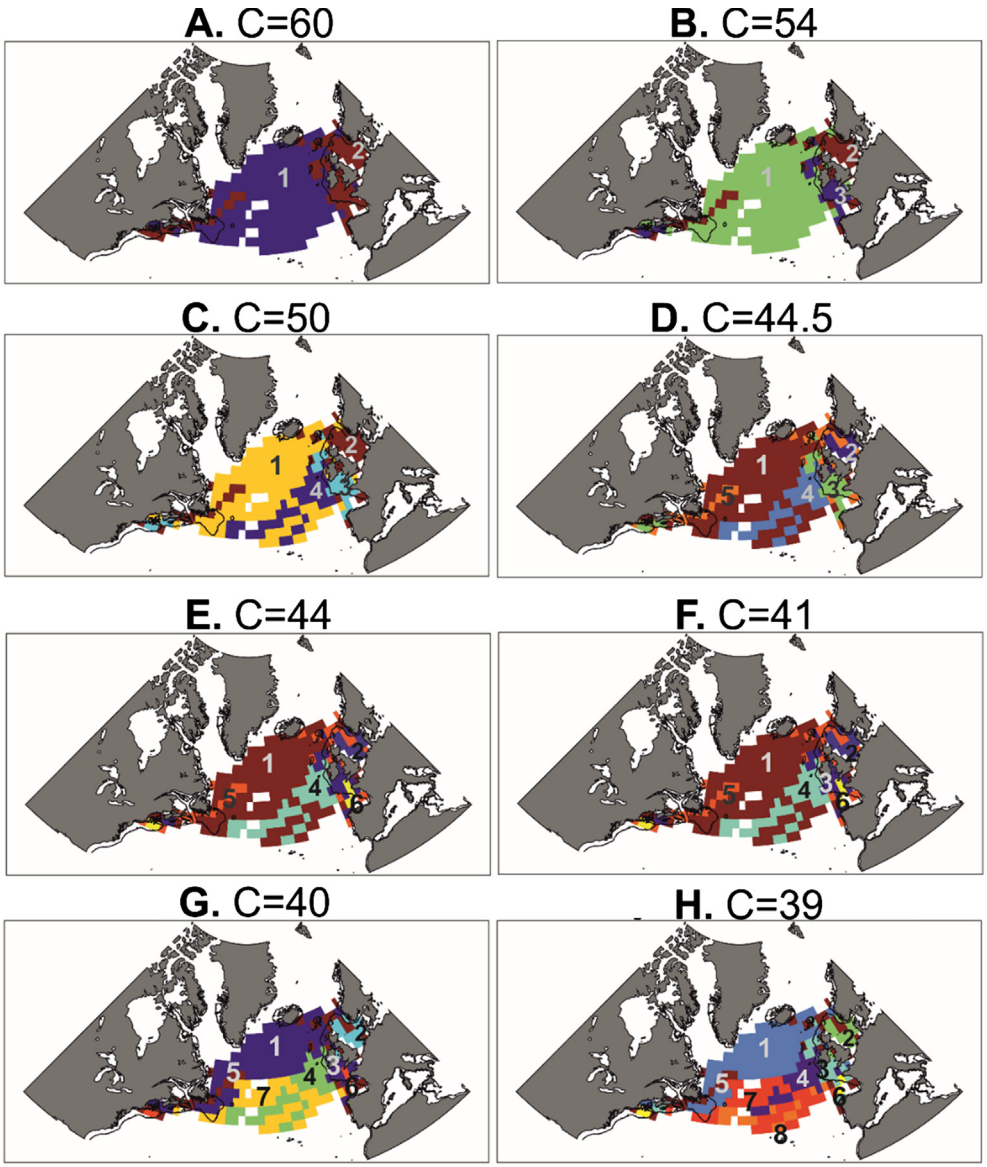

Fig. 6. Hierarchical biological partition of the North Atlantic Ocean and its adjacent seas at 2° × 2° spatial resolution for different cut-off levels (hereafter termed C) of the dendrogram (see Fig. 5). A. C = 60, B. C = 54, C. C = 50, D. C = 44.5, E. C = 44, F. C = 41, G. C = 40, and H. C = 39.

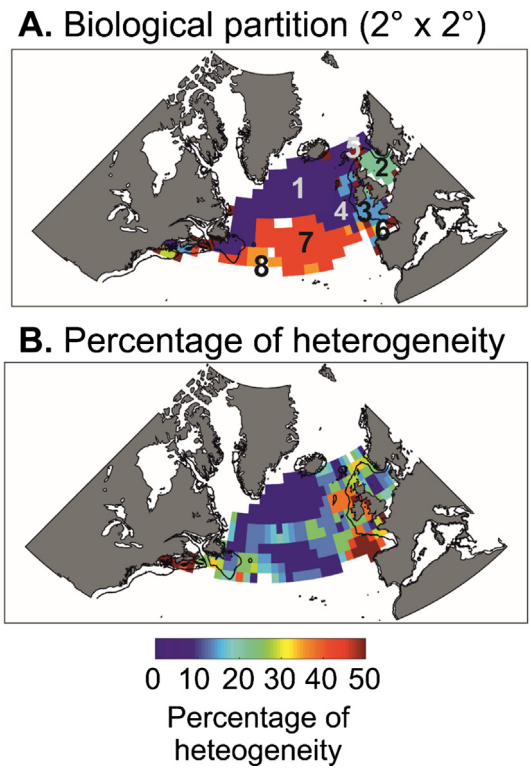

Fig. 7. Biological partition of the North Atlantic Ocean and its adjacent seas at 2° × 2° spatial resolution. A. Biological partition performed at a 2° × 2° spatial resolution. Number of the different groups is indicated from 1 to 8. B. Index of spatial heterogeneity of the partition. This index indicates the percentage of different groups around a given node. Each percentage value integrates 9 geographical cells (see Methods).

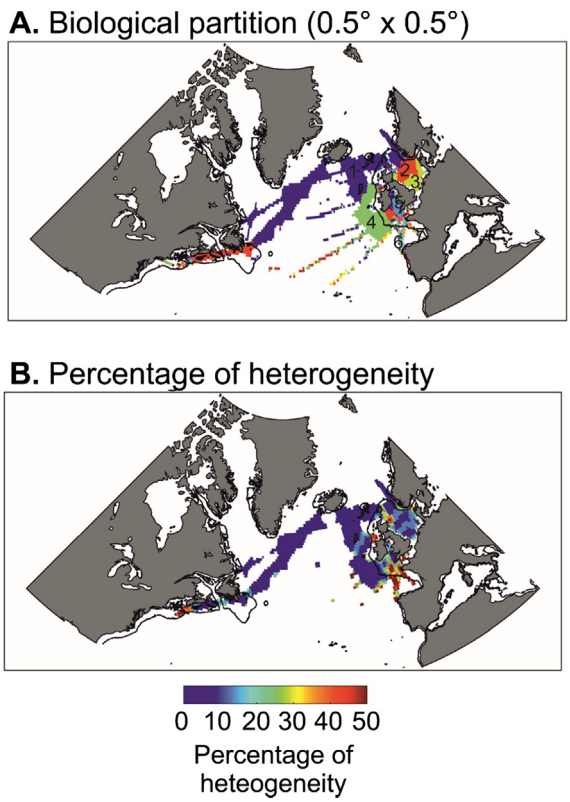

Fig. 8. Biological partition of the North Atlantic Ocean and its adjacent seas at 0.5° × 0.5° spatial resolution. A. Partition. B. Index of spatial heterogeneity of the partition. This index indicates the percentage of different groups of geographical cells around a given node. Each percentage value integrates 9 geographical cells (i.e. the target and its 8 adjacent cells). All intermediate results include figures similar to Figs. 3–7 (see Methods).

partition had therefore a total of 14 groups (Supplementary Fig. 1C). The final ecological partition is shown in Fig. 9. We described each cell group as a function of their biodiversity, seasonal patterns in species or taxonomic richness and species composition using maps of each of the 238 species considered in this study. Although it was not possible to show all maps in the present study, they are available in a CPR atlas published in 2004 (Barnard et al., 2004; Beaugrand, 2004).

2.4. Terminology

In this section, we define or summarize a few key terms used in this paper.

2.4.1. Partitions

In this study, we made three different types of partition: (i) habitat, (ii) biological and (iii) ecological partitions.

Habitat Partition: this partition was based on an empirical (threshold-based) procedure based on SST, bathymetry, light at the seabed, salinity and current velocity at a high spatial resolution (0.08° latitude × 0.08° longitude). Environmental data originated from Bio-ORACLE v2.0(2000–2014). The resulting Pelagic Habitats (PHs) were merely areas where environmental conditions are relatively homogeneous with respect to the variables that were used.

Biological partition: this partition was based on information on biodiversity of 6 taxonomic groups sampled by the CPR survey: (i) diatoms, (ii) *Ceratium* genus, (iii) copepods < 2 mm, (iv) zooplankton < 2 mm, (v) copepods ≥ 2 mm, and (vi) zooplankton ≥ 2 mm. The biological partition was performed at two spatial resolutions: (i) 0.5° × 0.5° and (ii) 2° × 2°. When we described this partition, we used the term group to refer to cluster of geographical cells.

Ecological partition: synthetic partition based on both habitat and biological partitions (at the two spatial resolutions). The groups of geographical cells resulting from this partition were either termed Ecological Units or Ecoregions (see below).

2.4.2. Biome and realm

A biome is frequently defined as a primary ecological compartment in equilibrium with climate. In the terrestrial ecosphere, biomes are clearly related to the climatic regime (Whittaker, 1975). The word has also been frequently used in marine biogeography. For example, Longhurst (2007) distinguished four biomes on a global scale: (1) the Polar Biome, (2) the Westerlies Biome, (3) the Trade-Winds Biome and (4) the continental shelves Biome. Note however that the latter biome is fundamentally distinct from the first three as it is defined by bathymetry (stable-biotope components *sensu* van der Spoel (1994)) and not climate. Therefore, it may be more appropriate to term it a realm than a biome, at least in the spatial domain covered by our study. A realm is frequently defined as the broadest ecological unit in either the marine or the terrestrial ecosphere. We therefore expected to identify an oceanic and a neritic realm in the area covered by the CPR survey; the two realms were identified in a recent study based on the analysis of the distribution of 65,000 species of marine animals and plants (Costello et al., 2017).

2.4.3. Province

Although we do not divide specifically our partition into provinces, we define this term as it is used in the paper, in particular when we compare our partition to the global-scale partition proposed by Longhurst (1998, 2007). A province has been defined as an area characterised by some level of endemism, with species sharing a common history (Watling et al., 2013). In addition, a province has also been

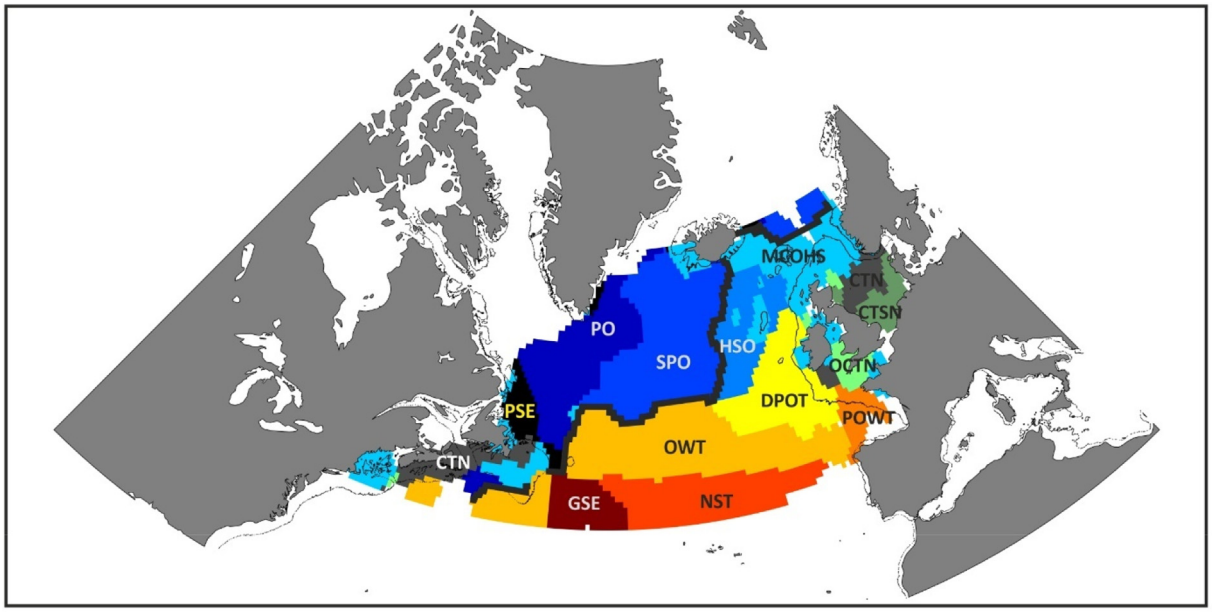

Fig. 9. Ecological partition of the North Atlantic Ocean and its adjacent seas. The partition results from the combination of the habitat (~0.1 × ~0.1) and the biological partitions at 2° × 2° and 0.5° × 0.5° spatial resolutions. Abiotic and biotic properties are shown in Tables 2 and 4.

defined as an association of ecosystems that may change over time in the same way. Provinces are also sometimes divided into ecoregions (Spalding et al., 2007).

2.4.4. Ecoregion

In this study, ecoregions are defined according to Spalding et al. (2007): "*areas of relatively homogeneous species composition, clearly distinct from adjacent systems. The species composition is likely to be determined by the predominance of a small number of ecosystems and/or a distinct suite of oceanographic or topographic features*". For the authors, endemism was not a key determinant in the establishment of the Marine Ecoregions of the World (MEOW).

2.4.5. Groups, ecological units (EUs) and ecoregions

Our biological classification led to groups of geographical cells (e.g. 0.5° × 0.5° and 2° × 2°), which were subsequently termed Ecological Units or Ecoregions in the ecological partition.

- **Ecological Units (EUs).** An EU is a unit having a relatively homogeneous environmental regime or being characterised by similar levels and seasonal variability in biodiversity (i.e. species richness) (Supplementary Tables 1–6). Abiotic and biotic characteristics of each EU were examined in Tables 2 and 3.
- **Ecoregions**. An EU may not be represented by a single set of interconnected geographical cells. When it was the case, the EU was divided into ecoregions, which were distinguished by their species composition (Fig. 9). Therefore, we also provided a summary of the abiotic and biotic characteristics of each ecoregion (Fig. 11, Supplementary Tables 7 and 8).
- **Groups**. The term "group" was used as part of the biological partition and meant groups of geographical cells.

2.5. Statistics in the ecological units and ecoregions (ecological partition)

We calculated statistics for each ecological unit (Tables 2 and 3) and embedded ecoregions (Supplementary Tables 7 and 8). Table 2 (for ecological units) and Supplementary Table 7 (for ecoregions) summarize the environmental characteristics of each ecological unit (bathymetry, SST, salinity, surface current, nitrate, phosphate, N/P ratio, silicate, chlorophyll and primary production), including area (km^2 and percentage) as well as the number and density of CPR samples.

Annual average and the seasonal amplitude of the biodiversity of the 6 taxonomic groups were also summarized in Table 3 for ecological units and Supplementary Table 8 for ecoregions.

Table 2
Main abiotic properties of the ecological units. EU: Ecological Unit. SST: mean Sea Surface Temperature (°C). S: mean salinity (PSS). Cur: mean surface current ($m{\cdot}s^{-1}$). N: mean nitrate concentration ($mol{\cdot}m^{-3}$). P: mean phosphate concentration ($mol{\cdot}m^{-3}$). Sil: mean silicate concentration ($mol{\cdot}m^{-3}$). PAR: mean photosynthetically active radiation ($E{\cdot}m^{-2}{\cdot}day^{-1}$). C: mean chlorophyll concentration ($mg{\cdot}m^{-3}$). PI: mean primary production ($g{\cdot}m^{-3}{\cdot}day^{-1}$). Bathymetry is expressed in meter (m). P5: the 5th percentile. P50: the median. P95: the 95th percentile. See text for the meaning of the ecological unit acronyms. See Fig. 9 for the spatial distribution of EUs and Fig. 11 for the ecoregions (1–40).

EU	Area (km^2)	Area (%)	CPR sample	CPR sample per 100 km^2	Bathymetry P50 (P5-P95)	SST	S	Cur	N	P	N/P	Sil	PAR	C (PI)
1 PSE	245,642	2.62	2526	1.03	310 (171–1170)	4.32	33.05	0.18	3.71	0.44	0.13	3.68	29.3	0.69 (0.009)
2 PO	987,261	10.53	15,964	1.62	3130 (1464–3912)	6.76	34.46	0.18	7.56	0.59	0.11	4.01	26.2	0.45 (0.006)
3 SPO	1,517,087	16.18	23,947	1.58	2613 (1291–3753)	9.11	34.99	0.23	6.93	0.53	0.08	3.60	26.9	0.40 (0.005)
4 HSO	511,150	5.45	9446	1.85	1890 (917–3871)	11.32	35.32	0.28	5.87	0.45	0.08	3.14	28.0	0.40 (0.006)
5 MCOHS	1,597,056	17.03	43,450	2.72	182 (35–1457)	9.75	34.37	0.17	3.77	0.35	0.31	3.38	28.8	0.56 (0.009)
6 CTN	558,408	5.95	31,705	5.68	90 (35–432)	9.47	32.73	0.14	0.70	0.25	0.72	3.07	29.9	0.44 (0.005)
7 CTSN	224,455	2.39	28,018	12.48	31 (6–62)	11.18	33.74	0.24	1.11	0.21	1.12	3.72	31.2	0.65 (0.010)
8 OCTN	189,168	2.02	22,178	11.72	82 (25–127)	12.30	34.68	0.13	0.66	0.18	1.11	3.10	31.0	0.43 (0.006)
9 DPOT	761,237	8.12	23,072	3.03	3630 (152–4823)	13.42	35.52	0.26	3.81	0.32	0.09	2.36	29.5	0.43 (0.007)
10 OWT	1,857,862	19.81	12,176	0.66	3974 (1452–4863)	13.99	35.07	0.46	2.42	0.26	0.14	2.29	28.2	0.39 (0.006)
11 POWT	208,415	2.22	12,533	6.01	3560 (119–4893)	15.11	35.59	0.14	0.90	0.14	0.20	1.72	31.3	0.34 (0.006)
12 NST	859,614	9.17	5085	0.59	3620 (2196–5049)	17.00	35.90	0.36	1.07	0.14	0.14	1.62	30.4	0.27 (0.005)
13 GSE	346,399	3.69	1596	0.46	4758 (3680–4941)	17.44	35.48	0.78	1.16	0.17	0.14	1.98	28.9	0.40 (0.007)

2.6. Potential influence of the difference in temporal coverage among biological and habitat partitions

We tested whether the two different time periods used for the biological (1946–2015) and habitat (2000–2014) partitions had no major influence on the ecological partition. To do so, we calculated the average SST for the period 2000–2014 and 1946–2015 and mapped the difference in average SST between the two periods (Supplementary Fig. 2). This analysis was carried out in the area 50–66°N and 55–5°W where the two biological and habitat partitions were jointly used (i.e.

Table 3
Average and seasonal amplitude of the biodiversity of the 6 taxonomic groups in each ecological unit. EU: Ecological Unit. Diat: diatoms. Dino: dinoflagellates. Cop: copepods. See text for the meaning of the ecological unit acronyms. See Fig. 9 for the spatial distribution of EUs.

	Mean taxonomic richness						Seasonal amplitude in taxonomic richness					
EU	Diat	Dino	Small cop	Small zoo	Large cop	Large zoo	Diat	Dino	Small cop	Small zoo	Large cop	Large zoo
1 PSE	12.62	7.14	4.48	4.85	5.41	4.77	6.02	5.88	5.75	3.23	6.38	4.82
2 PO	11.40	8.69	4.57	5.78	4.48	4.70	5.87	4.63	5.78	4.27	6.42	5.25
3 SPO	10.69	12.03	5.03	7.24	4.30	4.69	5.60	5.57	5.24	4.31	6.03	7.16
4 HSO	11.72	14.86	6.14	8.19	5.25	3.99	6.29	6.84	6.48	5.44	6.75	8.35
5 MCOHS	12.61	15.02	6.09	7.29	6.39	4.38	7.21	7.95	5.81	4.68	7.25	6.34
6 CTN	15.68	12.10	7.60	4.30	7.98	3.31	9.46	5.51	5.46	3.57	8.51	5.00
7 CTSN	28.47	12.43	7.56	2.95	9.11	2.97	10.79	5.58	4.77	2.62	11.31	4.41
8 OCTN	21.01	18.22	8.16	8.81	9.84	3.55	10.50	6.42	8.40	5.56	11.15	6.04
9 DPOT	12.30	12.64	8.15	10.47	7.47	5.17	7.75	6.61	11.08	8.57	8.52	7.95
10 OWT	9.99	10.05	8.57	10.37	7.27	5.68	6.64	5.10	11.22	10.89	7.19	7.15
11 POWT	17.22	12.23	12.63	13.06	10.40	3.92	9.39	5.14	15.60	6.72	10.62	5.28
12 NST	8.48	8.28	7.47	10.33	7.79	5.18	7.01	4.47	12.66	12.83	8.31	5.83
13 GSE	8.85	7.59	6.60	8.94	7.99	6.56	6.81	5.51	14.52	16.28	8.83	6.05

Polar biome). The mean SST was considered to be a good proxy for temperature and sea-ice concentration, parameters implicated in the identification of the pelagic habitats 1, 4 and 11 in the polar biome (Table 1 and Fig. 2).

3. Results

3.1. Habitat partition

The habitat partition resulted in 15 pelagic habitats (Fig. 2 and Table 1). The first three Pelagic Habitats (PHs thereafter) may have Sea-Ice Concentration above 0 at least a part of the year. The first PH is the oceanic ice-influenced PH (depth > 200 m); it covers the Labrador Basin and part of the Irminger Basin (Fig. 2). The second is the shelf-edges (depth range of 200–1000 m) ice-influenced PH. In the Labrador Basin, it channels the path of the Labrador Current that flows southwards. The third is the neritic (depth range 0–200 m) Continental Shelves ice-influenced PH. In particular, it covers the Newfoundland Continental Shelf (e.g. Grand Banks). In the Atlantic area covered by the CPR survey, the first three PHs are delimited by the Subarctic Gyre. Salinity in those three PHs is lower in comparison to oceanic regions located eastwards and southwards. The fourth PH, the Oceanic Subarctic PH, lacks sea ice (Fig. 2). The fifth PH is the shelf-edges PH, which is found in all shelf-edge regions where sea-ice is absent (e.g. western part of Norway and European Shelf-edges). The sixth and seventh PHs are continental shelves where sea-ice is absent and where light is limited (in particular, light does not reach the benthos). The deep (50–200 m) and shallow Continental Shelves pelagic habitat are well represented in the North Sea north and south of the Flamborough Front, respectively. The eighth PH, the continental shelves (light) pelagic habitat, is marginally represented in the area under investigation. Some coastal areas of the Mediterranean Sea belong to this PH. The ninth PH, the Gulf Stream PH, has current velocity above 0.62 ms^{-1}. In oceanic areas characterised by a high salinity (higher than 35.23 PSS), we distinguished 6 further PHs as function of their thermal regime: (10) oceanic subpolar PH (mean SST = 7–10 °C), (11) oceanic cold-temperate PH (mean SST = 10–13 °C), (12) oceanic temperate PH (mean SST = 13–16 °C), (13) oceanic warm-temperate PH (mean SST = 16–19 °C), (14) oceanic subtropical (north) PH (mean SST = 19–22 °C), and (15) oceanic subtropical (south) PH (mean SST = 22–25 °C).

3.2. Biological partition at 2° × 2° spatial resolution

We first assessed the biodiversity of all six taxonomic groups (Fig. 3). The taxonomic richness of diatoms (Supplementary Table 1) was high around the British Isles and especially south of the Flamborough Front, the Celtic Sea and the western part of the Channel (Fig. 3A). On the western part of the North Atlantic, biodiversity was high over Georges Bank, the Nova Scotian Shelf and to a lesser extent north of the Newfoundland Shelf. Oceanic areas had in general low diatom taxonomic richness, with the exception of the oceanic cold-temperate and the temperate PHs along the Faroe-Iceland Rise, the European shelf-edge and the northern part of oceanic subarctic pelagic habitat, especially over the Reykjanes Ridge (Figs. 2 and 3).

The species richness of the genus *Ceratium* (Supplementary Table 2) was high in oceanic areas south of the Oceanic Polar Front (Dietrich, 1964) and especially over the Bay of Biscay. Species richness was also high in some neritic regions such as the Celtic Sea and Georges Bank (Fig. 3B). Copepods (Supplementary Tables 3 and 5) also exhibited a similar pattern, although the biodiversity difference between the polar and the westerlies biomes was less acute for small copepods (Fig. 3C and E). The taxonomic richness of small copepods was higher along the European Shelf-edge in both oceanic and neritic regions, south of the Flamborough Front in the North Sea and in Georges Bank and part of the Nova Scotian Shelf (Fig. 3C). Taxonomic richness was higher in the northern part of the Gulf Stream PH for all copepods. Large copepods did not show a high taxonomic richness south of the Flamborough Front in the North Sea and the biodiversity was less elevated and more restricted along the European Shelf-edge. The taxonomic richness of small zooplankton (Supplementary Table 4) was similar to diatoms (Fig. 3A *versus* Fig. 3D), although it was substantially higher in the Newfoundland Shelf for zooplankton (Fig. 3D). Large zooplankton (Supplementary Table 6) exhibited a pattern closer to small zooplankton because both groups are composed of meroplanktonic species (Fig. 3D *versus* Fig. 3F).

When the biodiversity was combined for all groups, the mean total taxonomic richness was higher south of the Oceanic Polar Front (i.e. the Westerlies Biome *sensu* Longhurst) and showed a maximum in biodiversity over the European Shelf-edge and in both adjacent oceanic and neritic regions, as well as along the southern part of the American Shelf-edge (Fig. 4A). The seasonal amplitude of the biodiversity, assessed by calculating the interdecile range of 6 2-month periods, showed a pronounced amplitude in oceanic cold-temperate and temperate PHs (Fig. 4B). Unexpectedly and although less pronounced, a higher seasonal amplitude was also observed over the mid-Atlantic Ridge south of the Oceanic Polar Front.

Information on the taxonomic or species richness of all plankton groups for all two-month periods was used to partition the North Atlantic Ocean in biological systems. The resulting dendrogram was cut hierarchically using the first 8 cut-off levels (Figs. 5 and 6). The first cut-off level separated neritic from oceanic areas. The European Continental Shelf was more clearly identified in contrast to the Newfoundland Shelf (Fig. 6A). Some areas such as Rockall and the Faroe-Iceland Rises were also at least partially identified. The second cut-off level of the dendrogram (Fig. 5) separated the southern part of both American and European Continental Shelves, including the Bay of Biscay (Fig. 6B). The third cut-off level enable the separation of an oceanic region southwest to the Irish Sea, which is characterised by a pronounced seasonality in biodiversity and high phytoplankton and small copepod biodiversity (Fig. 6C, see also Fig. 4B). The fourth cut-off enabled the separation of small groups that enable the identification of an area north of the North Sea and along the Faroe-Iceland ridge (Fig. 6D). Some cells were also identified over Georges Bank and the Bay of Biscay but the group of geographical cells lacked spatial contiguity. The fifth cut-off level allowed the identification of a cell group gathering together the Georges Bank and the Bay of Biscay (Fig. 6E). Although the sixth cut-off level did not allow the clear identification of a relevant cell group (Fig. 6F), the next cut-off level identified an area belonging to oceanic subtropical and warm-temperate PHs and regions influenced by the Atlantic Meridional Overturning Circulation (AMOC, i.e. the Gulf Steam and the North Atlantic Current) (Fig. 6G). This cut-off level emphasized the role of the Oceanic Polar Front, which delineates the polar from the Westerlies biome. The last cut-off level (Fig. 6H), as well as others (not represented here) did not provide any further relevant information.

After smoothing and elimination of small groups of geographical cells (see Methods), the final biological partition included eight groups, two (group 5 in the northern part of the North Sea and 6 in the Bay of Biscay) of which being restricted spatially (Fig. 7A). Group of geographical cells (hereafter called group) 1 represented in large part the polar biome and their ice-influenced, subarctic and cold-temperate PHs; Group 2 characterised the North Sea, Group 3 denoted the Celtic Sea and some areas over the European Shelf-edge, and a negligible part of the Nova Scotian Shelf; Group 4 represented an oceanic area characterised by a high biodiversity south and west of the Irish Sea; Group 7 the oceanic temperate and warm-temperate PHs and Group 8 the northern edge of the Gulf Stream PH (Fig. 7A). We calculated an index to reveal the presence of pronounced spatial heterogeneity or ecotones (Fig. 7B). The index was highest over the Bay of Biscay and the Bay of Fundi, Georges Bank, Nova Scotian Shelf and to a lesser extent an area located to the north-west of Ireland. The index was also higher between

the polar and westerlies biomes along the Oceanic Polar Front, the Gulf Stream PH and areas north of the North Sea and along the Faroe-Iceland Rise (Fig. 7B).

3.3. Biological partition at 0.5° × 0.5° spatial resolution

The same procedure was applied to identify groups of geographical cells at a 0.5° × 0.5° spatial resolution. We only show the final partition here as the procedure was similar to the 2° × 2° division (Fig. 8). Fifteen biological groups of geographical cells (hereafter termed groups) were detected. Here also, some groups were only composed of a few geographical cells, which exhibited low spatial contiguity (Fig. 8A). After smoothing and elimination of under-represented groups (see Methods), we retained 8 biological groups. Group 1 characterised the polar biome and the associated ice-influenced, subarctic and cold-temperate PHs (see Fig. 2). Some geographical cells penetrated to the northern part of the North Sea. Although the previous partition at 2° × 2° spatial resolution identified only one biological group in the North Sea, the finer-scale partition revealed three ecoregions: the central part of the North Sea (group 2) and an area south of the Flamborough Front (group 3). The second group also occurred in the northwestern part of the Celtic Sea and along the Nova Scotian Shelf, the shallow area of Newfoundland Shelf, stopping sharply at the shelf-edge (Fig. 8A). A fourth group was detected to the west of the British Isles; this group was similar to the group identified at 2° × 2° spatial resolution (group 4; see Fig. 7A). The fifth group identified the north-eastern part of the Celtic Sea (Fig. 7A). Some isolated geographical cells also occurred in different places. The sixth and seventh groups were located mainly in the western and eastern part of the Bay of Biscay, respectively (Fig. 8A).

3.4. Ecological partition

The final ecological partition was mainly based on the biological partition performed at the 0.5° × 0.5° spatial resolution for neritic regions (Fig. 8) and mostly on the biological partition made at 2° × 2° for oceanic regions (Fig. 7). We further divided some ecological units by using the PHs identified using some key ecogeographic variables (see Fig. 2). We used the term Ecological Unit (EU) because the same unit may be represented in different regions; we then divide a given EU into ecoregions when it is relevant (see the section terminology in Methods). As in the PH partition, we frequently refer to the Longhurst's classification of biomes and provinces (Longhurst, 1998, 2007).

The final ecological partition we propose is made of 13 EUs (Fig. 9). Each EU has its own biodiversity (Figs. 3 and 4), seasonal biodiversity patterns (Fig. 4B) and environmental conditions (Fig. 2). Widespread EUs could be further divided and some are composed of different ecoregions (Fig. 9; e.g. MCOHS and CTN). Although their location did not match with our partition, the three Longhurst's biomes were identified: (1) the Westerlies, (2) the Polar biomes and the Continental Shelves biomes (Note that Longhurst termed originally this last biome a coastal biome (Longhurst, 1998)). Our EUs or HPs did not correspond to Longhurst's provinces (Fig. 10), with the exception of the Gulf Stream PH and EU (Figs. 2, 9 and 10).

The Polar biome is divided into 3 EUs using information from the PH partition.

3.4.1. Polar shelf-edge EU (PSE)

The first group is the Polar Shelf-Edge EU (PSE, Fig. 9, Tables 2 and 3). In the region sampled by the CPR survey, this EU is represented by four ecoregions (Fig. 11A, Supplementary Tables 7 and 8); the two main ecoregions (1 and 2 in Fig. 11A) are in the path of the Labrador Current, which transports cold water southwards (Han and Tang, 1999). Some species such as the calanoid copepods *Calanus glacialis* and *C. hyperboeus* are highly abundant in PSE (Barnard et al., 2004). Biodiversity is very low in this ice-influenced area (Figs. 3 and 4).

3.4.2. Polar oceanic EU (PO)

The second group is the Polar Oceanic EU (PO, Fig. 9, Tables 2 and 3). This EU is in general characterised by low biodiversity, although diatom taxonomic richness is higher, especially to the south of the EU. The EU can be divided into 2 main ecoregions (ecoregions 5 and 6 in Fig. 11B, Supplementary Tables 7 and 8): the Labrador-Irminger Basin and a small oceanic ecoregion south of the Gulf of Saint Lawrence. The first ice-influenced ecoregion is the place where the diatom *Ephemera planamembranacea* is observed in high abundance (Barnard et al., 2004).

3.4.3. Sub-polar oceanic EU (SPO)

The third group is the Sub-Polar Oceanic EU (SPO, Fig. 9, Tables 2 and 3). This EU is not influenced by sea-ice and has a salinity that remains below 35.23 in comparison to oceanic regions located to the east and the south (Fig. 2). Biodiversity is low for all groups but seasonality can be high, especially to the eastern part of the region (Fig. 4). This EU may be divided into 3 ecoregions (ecoregions 9–11 in Fig. 11C, Supplementary Tables 7 and 8): (1) an ecoregion south of Iceland over the mid-Atlantic ridge and (2) two small ecoregions in the Norwegian Sea. This area is clearly a transitional area between the Polar and the Westerlies biomes (Barnard et al., 2004); for example, the diatoms *Leptocylindrus mediterraneus* and *Proboscia alata indica* and the dinoflagellates *Ceratium furca* and *C. lineatum* diminished substantially in this area in comparison to their eastern abundance. The copepods *C. finmarchicus* and *Paraeuchaeta norvegica* also decreased with respect to their western abundance (Barnard et al., 2004). Some species of Hyperiidae are well represented in this region (Barnard et al., 2004), although being not indicative of the EU. Many species are distributed in the first three EUs. For example, the two copepods *C. finmarchicus* and *Paraeuchaeta norvegica* as well as Euphausiacea are highly abundant.

3.4.4. Highly-seasonally dynamical oceanic EU (HSO)

The next oceanic EU, the Highly-Seasonally dynamical Oceanic EU (HSO, Fig. 9, Tables 2 and 3), is located to the eastern part of the Oceanic Polar Front (Dietrich, 1964) and therefore belongs to the Westerlies biome (Longhurst, 1998). This EU, representing only one ecoregion (Fig. 11D, Supplementary Tables 7 and 8), is characterised by a higher biodiversity for all taxonomic groups and many species exhibit high abundance in this EU, although not being exclusively indicative of the region. For example, the diatom *Cylindrotheca closterium*, the dinoflagellate *Oxytoxum* spp. and the copepod *Pleuromamma robusta* are highly abundant in this region (Barnard et al., 2004). This EU exhibits a pronounced seasonal amplitude in taxonomic richness and is highly influenced by the path of the North Atlantic Current and associated strength and extent of the Subarctic Gyre (Hatun et al., 2009).

3.4.5. Mixed coastal-oceanic highly-seasonally dynamical EU (MCOHS)

The fifth group is the Mixed Coastal-Oceanic Highly-Seasonally Dynamical EU (MCOHS, Fig. 9, Tables 2 and 3). Complex to interpret (ecoregions 13–24 in Fig. 11E, Supplementary Tables 7 and 8), this EU encompasses a main ecoregion (ecoregion 19) at the north-eastern edge of the area covered by the CPR survey where polar water masses interact with more temperate ones along the Faroe-Iceland Rise. It also corresponds to an area where neritic and oceanic water masses interact along the European Shelf-edge and in the northern part of the North Sea. The EU is also composed of many small ecoregions: (i) the offshore region of the Newfoundland Shelf, (ii) Rockall Rise, (iii) the Irish Sea, (iv) south-west of Ireland, and (v) the Channel where many ecosystems and ecotones co-occur (Figs. 7 and 8). This area is characterised by a relatively low seasonal amplitude in taxonomic richness in comparison to HSO (Fig. 4B). Biodiversity is low in the main ecoregion and over the Newfoundland Shelf, although being substantially higher in the smaller ecoregions. Some species, mainly neritic, are highly abundant in MCOHS, although being not indicative of the EU, e.g. the diatoms *Asterionellopsis glacialis*, *Dactyliosolen antarcticus*, *Cylindrotheca closterium*,

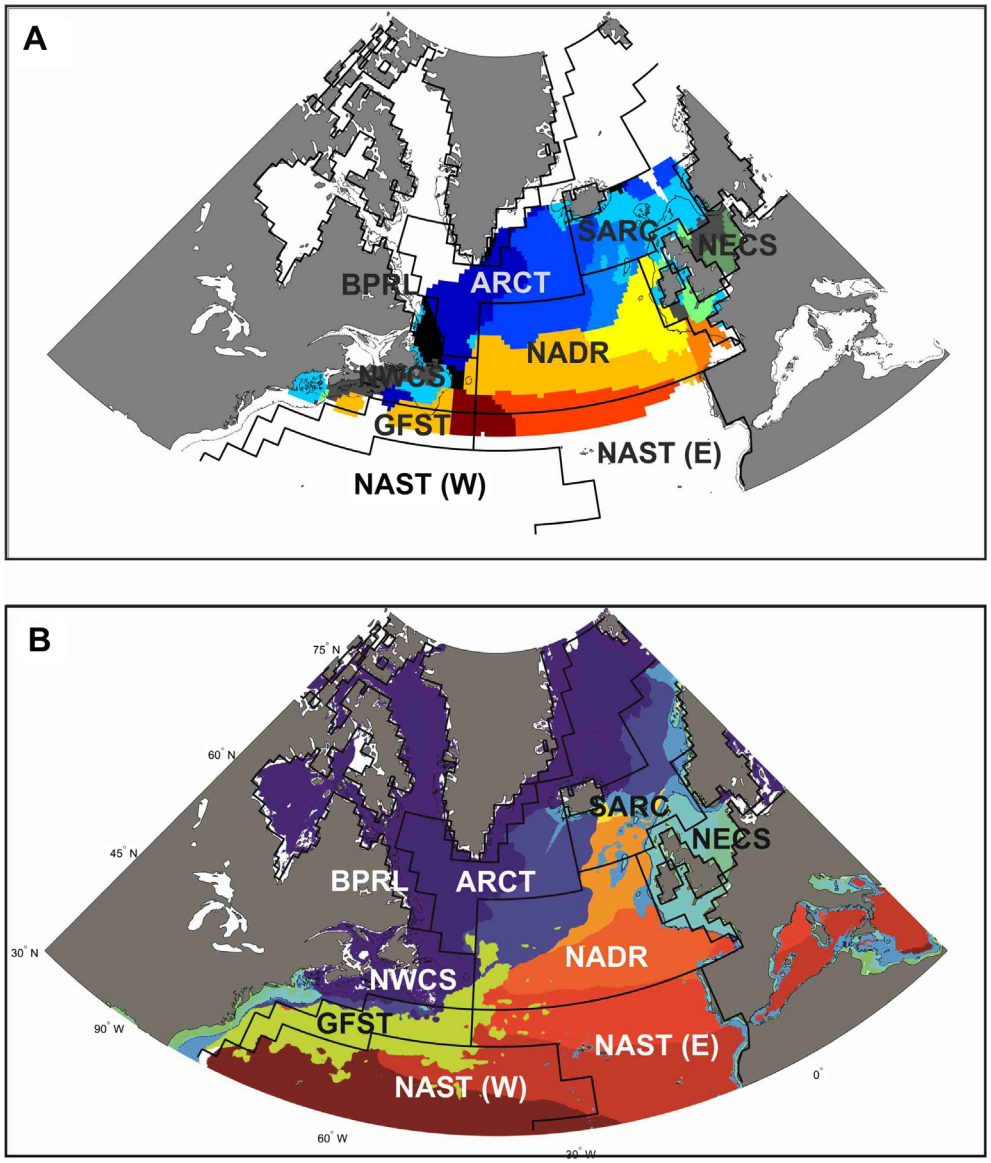

Fig. 10. Final ecological partition (A) and habitat partition (B) with the boundaries of the Longhurst's provinces (Longhurst, 1998) (black lines). Coastal biomes. NWCS: North West Atlantic Shelves province, NECS: North East Atlantic Shelves province. Westerlies biomes. NAST (W): North Atlantic Subtropical Gyral Province (West), NAST (E): North Atlantic Subtropical Gyral Province (East), GFST: Gulf Stream Province, NADR: North Atlantic Drift Province. Polar biomes. SARC: Atlantic Subarctic Province, ARCT: Atlantic Arctic Province, BPRL: Boreal Polar Province.

Rhizosolenia acuminata, the dinoflagellates *Ceratium horridum*, *Dinophysis* spp. and the copepods *Aetideus armatus* and *Temora longicornis* (Barnard et al., 2004). The ecoregion offshore the Newfoundland Shelf differs substantially from the other ecoregions, probably because of its thermal regime associated to the presence of sea-ice concentration during some parts of the year. As a result, some cold-water species (e.g. *Ceratium arcticum, Calanus glacialis*) are highly abundant in this ecoregion while less represented in the other MCOHS ecoregions.

3.4.6. Cold-temperate neritic EU (CTN)

The sixth group is the Cold-Temperate Neritic EU (CTN, Fig. 9). This EU is composed of three ecoregions (ecoregions 25–27 in Fig. 11F, Supplementary Tables 7 and 8): (i) Central North Sea, (ii) south-western part of the Celtic Sea and (iii) the Nova Scotian and coastal part of the Newfoundland Shelf. Species richness is moderate in this EU, with low taxonomic richness of *Ceratium* and copepods (especially large copepods) and higher taxonomic richness for the other groups, especially small zooplankton (Figs. 3 and 4). In the North Sea, the EU is bounded by the Flamborough Front southwards and by the oceanic influence northwards. In the Nova Scotian and the coastal part of the Newfoundland Shelf, the EU is restricted to the coast. Species showing high abundance are the diatoms *Coscinodiscus concinnus*, *Leptocylindrus danicus*, *Skeletonema costatum*, the dinoflagellates *Ceratium longipes*, *C. macroceros*, *C. tripos*, and the copepod *Centropages hamatus*.

3.4.7. Cold-temperate shallow neritic EU (CTSN)

The seventh group is the Cold-Temperate Shallow Neritic EU (CTSN, Fig. 9, Tables 2 and 3). This EU is represented by only one ecoregion (ecoregion 29 in Fig. 11G, Supplementary Tables 7 and 8), in the North Sea south of the Flamborough Front. Biodiversity is high for diatoms, zooplankton and to a lesser extent, small copepods (Figs. 3 and 4). Seasonal amplitude in biodiversity is low in this area (Fig. 4B). Many species occur in this area, e.g. the diatoms *Biddulphia alternans*, *Bellerochea malleus*, *Coscinodiscus wailesii*, *Eucampia zodiacus*, *Guinardia flaccidia*, *Odontella regia*, *Rhaphoneis amphiceros*, the copepods *Labidocera wollastoni* and *Isias clavipes*.

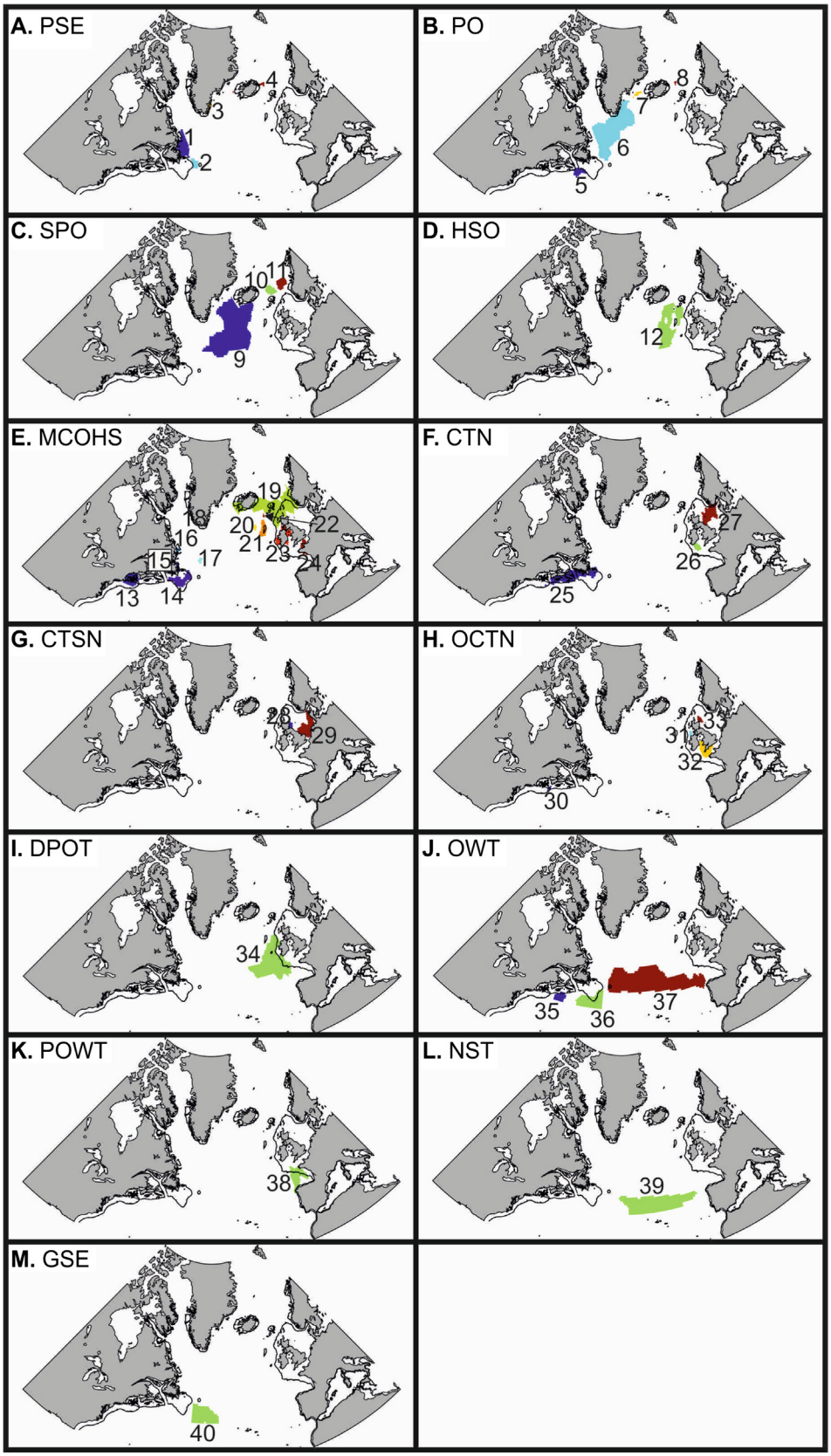

Fig. 11. Division of ecological units into ecoregions. Ecoregions are labelled from 1 to 40. The division of an ecological unit occurs when there is no spatial contiguity among geographical cells. Abiotic and biotic properties are shown in Tables 3 and 4. See also Supplementary Tables 7 and 8 that summarise the abiotic and biotic characteristics of the ecoregions.

3.4.8. Ocean-influenced cold-temperate EU (OCTN)

The eighth group is the Ocean-Influenced Cold-Temperate EU (OCTN, Fig. 9, Tables 2 and 3). This EU, composed of only four small ecoregions (ecoregions 30–33 in Fig. 11H, Supplementary Tables 7 and 8), are located in (i) Georges Bank, (ii) North Channel, (iii) the North Sea and (iv) the Celtic Sea. The last (main) ecoregion is highly diverse (Fig. 3) and all taxonomic groups exhibit their highest richness level (Fig. 4A). The seasonal amplitude of the biodiversity is low (Fig. 4B). As shown by Fig. 8, many ecosystems and ecotones occur in this region and the Celtic Sea appears to be a biogeographic crossroad. Neritic (e.g. the diatoms *Bacillaria paxillifera*, *Corethron cryophilum*, *Dactyliosolen fragilissimus*, *Paralia sulcata*, the dinoflagellate *Noctiluca scintillans* and the copepods *Anomalocera patersoni* and *Centropages hamatus*) and oceanic (e.g. the dinoflagellates *Oxytoxum* spp. and *Scrippsiella* spp.) species co-occur in this ecoregion (ecoregion 32). Pseudo-oceanic species (e.g. *Ceratium minutum*, *Calanus helgolandicus, Candacia armata*) also locally reinforce the biodiversity (Barnard et al., 2004). Warm-temperate (e.g. *Ceratium trichoceros, Clausocalanus* spp.), temperate (e.g. *Ceratium hexacanthum, Heterorhabdus papilliger, Neocalanus gracilis*), cold-temperate (e.g. *Proboscia alata inermis, Metridia lucens*) and even subarctic species (e.g. *C. finmarchicus*) co-occurs in this ecoregion. Finally, as with other EUs mainly found in the continental shelf, the meroplankton group (species or taxa included in the groups zooplankton) is highly diverse in the Celtic Sea (Fig. 3).

3.4.9. Diverse and productive oceanic temperate EU (DPOT)

The ninth group is the Diverse and Productive Oceanic Temperate EU (DPOT, Fig. 9, Tables 2 and 3). This oceanic EU, composed by only one ecoregion (ecoregion 34 in Fig. 11I, Supplementary Tables 7 and 8), is productive and highly diverse (Figs. 3 and 4). Seasonal amplitude remains elevated and the number of abundant species in this ecoregion is high (Barnard et al., 2004). In particular, the richness of the genus *Ceratium* and small copepods is very high (Fig. 3). The dinoflagellate *Ceratium hexacanthum* is indicative of this EU in the region covered by the CPR survey while *C. minutum*, *Gonyaulax* spp. and *Oxytoxum* spp. are also highly abundant (Barnard et al., 2004). The high biodiversity is also reinforced by neritic species that expatriate from the continental shelf (e.g. holozooplankton *Pseudocalanus* spp. and meroplankton such as echinoderm larvae) and pseudo-oceanic species (i.e. species occurring above the oceanic and neritic regions but higher over the shelf-edge) such as *Ctenocalanus vanus*, *Candacia armata* and *Calanus finmarchicus* (Barnard et al., 2004).

3.4.10. Oceanic warm-temperate EU (OWP)

The tenth group represents the Oceanic Warm-Temperate EU (OWP, Fig. 9, Tables 2 and 3). This oceanic EU, composed of three ecoregions occurring south of the Oceanic Polar Front in the Atlantic, south of Newfoundland and the Nova Scotian Shelves (ecoregions 35–37 in Fig. 11J, Supplementary Tables 7 and 8), is more diverse than oceanic regions north of the Oceanic Polar Front (Figs. 3 and 4). In particular, the biodiversity of small and large copepods, as well as the genus *Ceratium* eastwards, is high. In contrast, the other groups (zooplankton and diatoms) have a low biodiversity. Seasonal amplitude is substantially lower than HSO and DPOT, with the exception of the eastern side of the ecoregion. A large number of oceanic species occur in this EU, e.g. the copepods *Nannocalanus minor*, *Heterorhabdus papilliger*, *Pleuromamma borealis*, *Euchaeta acuta*, *Lucicutia* spp., and the dinoflagellates *Ceratium azoricum*, *C. massiliense*, and *C. trichoceros* (Barnard et al., 2004).

3.4.11. Pseudo-oceanic warm-temperate EU (POWT)

The eleventh group is the Pseudo-Oceanic Warm-Temperate EU (POWT, Fig. 9, Tables 2 and 3). This pseudo-oceanic EU, composed of only one ecoregion (ecoregion 38 in Fig. 11K), Supplementary Tables 7 and 8), is characterised by a high biodiversity for all groups. This is a very complex area as revealed by the index of heterogeneity, suggesting the occurrence of a large imbrication of ecosystems; the area therefore may well represent an ecotone (Figs. 7B and 8B). The high biodiversity is explained by the high mean SST to the eastern part of the Bay of Biscay (Fig. 2) and the co-occurrence of oceanic, pseudo-oceanic and neritic species from the distinct ecological units occurring at small spatial scales (Fig. 8A and 2). The biodiversity is higher in POWT than in DPOT and the seasonal amplitude is remarkably reduced (Fig. 4B). Examples of species occurring in this EU are the diatoms *Bacteriastrum* spp., *Hemiaulus* spp., *Lauderia annulata*, the dinoflagellates *Ceratium arietinum*, *C. bucephalum*, *C. candelabrum*, *C. extensum*, *C. carriense* and the copepods *Calanoides carinatus* and *Ctenocalanus vanus*.

3.4.12. Northern sub-tropical EU (NST)

The twelfth group is the Northern Sub-Tropical EU (NST, Fig. 9, Tables 2 and 3). Composed of only one ecoregion (ecoregion 39 in Fig. 11L, Supplementary Tables 7 and 8), this EU is highly influenced by the northern part of the Subtropical Gyre and may correspond to the north-eastern part of the North Atlantic Subtropical Gyral Province (NAST) *sensu* Longhurst (1998). With the exception of diatoms and small zooplankton, the biodiversity of all groups is high. The seasonal amplitude of biodiversity is low in this EU. Subtropical species such as the dinoflagellates *Ceratium buceros* and *C. belone*, as well as the copepod *Undeuchaeta plumosa*, are typically observed (Barnard et al., 2004).

3.4.13. Gulf stream extension EU (GSE)

The thirteenth group is the Gulf Stream Extension EU (GSE, Fig. 9, Tables 2 and 3). This EU, composed of only one ecoregion (ecoregion 40 in Fig. 11M, Supplementary Tables 7 and 8), corresponds to the northern extremity of the Gulf Stream Province *sensu* Longhurst (1998) and the Gulf Stream PH as defined in Fig. 2. This is an area of high biodiversity, especially for large zooplankton, copepods and, to a lesser extent, the genus *Ceratium*. Many species rarely recorded by the CPR survey are located in this ecoregion. Examples of species recorded in GSE are the subtropical copepods *Candacia pachydactyla*, *Centropages violaceus* (also found in POWT), *Paracandacia simplex*, *Pontellina plumata* and *Scolecithrix danae,* and the diatom *Cladopyxis* spp. (Barnard et al., 2004).

3.5. Potential influence of the difference in temporal coverage between the habitat and the biological partitions

The biological partition was based on CPR data sampled during the period 1946–2015. The habitat partition was based on the BIO-ORACLE v2 dataset, which encompassed the period 2000–2014. The ecological partition is similar to the biological partition but with the polar biome divided into 3 EUs using information from the habitat partition; this subsequent division was made because of the poor CPR sampling occurring in this area (PO, SPO and HSO in Fig. 9). We merged the two (biological and habitat) partitions for a restricted region corresponding to the Polar biome between ~50°N and ~66°N and ~55°W and ~5°E and thereby the difference of time periods may have only affected the boundary between PO and SPO and SPO and HSO (Fig. 9). Using ERSST data, we compared annual SST data based on 1946–2015 and 2000–2014 and no substantial differences in SST (< 0.5 °C) were found in the areas where the PO/SPO and SPO/HSO boundaries are located (Fig. 2, Fig. 9 and Supplementary Fig. 2). Because annual SST and sea ice concentration are highly correlated, we conclude that the consideration of the two time periods did not affect substantially our ecological partition. In addition, we assumed that the spatial changes in salinity was also limited between the two time periods but no dataset was available to us for testing.

4. Discussion

Our final ecological partition of the North Atlantic Ocean (Fig. 9)

was primarily based on the biodiversity and seasonal patterns in the species richness of six planktonic groups, therefore integrating information on 238 plankton species or taxa sampled by the CPR survey between 1946 and 2015 (60,549,580 data points). In areas where CPR sampling was high (e.g. around the British Isles), the spatial resolution of the partition was relatively high (0.5° latitude × 0.5° longitude) and in more remote oceanic areas, the resolution was downgraded to 2° latitude × 2° longitude. At the centre of the North Atlantic, where CPR sampling was limited, we also used the physico-chemical partition (Fig. 2) to allow the geographical division of three more provinces (e.g. PO, SPO and HSO). The resulting partition identified 13 EUs, units defined by a relatively homogeneous biodiversity and similar patterns in seasonal variability for the six taxonomic groups: (i) diatoms, (ii) dinoflagellates, small (iii, iv) and large (v, vi) copepods (iii, v) and zooplankton other than copepods (iv, vi). Some EUs, which were not represented by an interconnected set of geographical cells, were subsequently divided into ecoregions (Fig. 11). We used the CPR atlas (Barnard et al., 2004; Beaugrand, 2004) to further investigate whether some species were representative of each EU or associated ecoregions (Figs. 9 and 11); this electronic atlas is available on request.

The main difficulty in partitioning the marine pelagic realm is related to the dynamic movement of water masses and the locations of surface features which are influenced by atmospheric conditions and are highly seasonal by nature. This dynamism led the biogeographer van der Spoel (1994) to attempt to separate the biotope of pelagic ecosystems into two components (i) a stable-biotope component (geographically stable in time) in which a primary related community occurs and (2) a substrate-biotope component (depending on water mass) characterised by a secondary related community (mixed primary community, (Beklemishev, 1961)). An ecosystem is mainly characterised by a primary related community linked to a stable-biotope component whereas an ecotone is more distinguished by a secondary related-community depending on water masses. It is also known that an ecotone can further be characterised by its own biological composition (Beaugrand et al., 2002; Frontier et al., 2004; Ramade, 1994). The distinction van der Spoel made is fundamental in correctly understanding how plankton biodiversity is spatially organised in the oceans and seas.

At the ocean-basin scale, our study identified the two realms (open oceanic and the continental shelves pelagic realms), which were revealed in a global-scale study performed at a 5° × 5° spatial resolution and based on occurrence data reported in the Ocean Biogeographic Information System (OBIS) (Costello et al., 2017). In the area we considered, the boundaries were similar considering the difference in the spatial resolution of the two studies. This distinction was mainly the result of a higher biodiversity of diatoms and the presence of many meroplanktonic groups (zooplankton other than copepods) or groups dependent on shallow waters over neritic regions (Supplementary Tables 4 and 6). In essence the benthic-pelagic coupling makes the continental shelves pelagic realm very specific.

Mapping of our index of spatial heterogeneity at both 2° × 2° and 0.5° × 0.5° spatial resolutions revealed the presence of a complex transition zone between the two realms where the ecosystems were strongly intertwined (Figs. 7B and 8B). The imbrication of ecoregions (DPOT, POWT, CTN, OCTN and MCOHS) and the overlapping spatial distribution of species over the Celtic Sea (Barnard et al., 2004) lead to complex coenoclines (i.e. a gradient of biocoenoses or communities) and associated ecosystems, ecoclines and ecotones. The region can be seen as a biogeographic crossroad where not only oceanic, neritic and pseudo-oceanic species cohabit but also where warm and cold-water species regularly co-occur. As a result, total biodiversity is the highest in this area for all taxonomic groups (Fig. 3). Our procedure reduced somewhat this mosaic of ecoregions, which is visible in Fig. 8. Such a complex organization of marine life has, to our knowledge, been rarely reported in marine biogeography because our study lies between large-scale studies that have relatively low spatial resolution (Longhurst, 2007; Sherman and Duda, 1999; Spalding et al., 2007) and regional ecological studies at higher resolution that lacks spatial extent to reveal this phenomenon.

The number of oceanic ecoregions in the present study is higher than previously reported by large-scale oceanic partitions, which focused at the level of a realm, biome or province (Costello et al., 2017; Longhurst, 2007; Reygondeau et al., 2013). The eastern side of the North Atlantic seems to be very complex spatially, with ecoregions varying rapidly and being highly seasonal to the north (Figs. 4B, 7B and 8B). The influence of hydro-dynamical structures such as the Oceanic Polar Front (OPF) (Dietrich, 1964), the Gulf Stream Extension (both being part of the AMOC) and the Labrador Current on the ecoregions is important. For example, Beaugrand and colleagues (Beaugrand et al., 2001) suggested that the OPF acts as a sharp boundary for subtropical, shelf-edge and warm-temperate species, thus limiting their dispersal polewards. In contrast, colder-water species seemed to be less influenced by the OPF and were more frequently detected southwards (Barnard et al., 2004). The OPF and the GSE are also areas of plankton concentration (e.g. *Metridia lucens* for the OPF) (Barnard et al., 2004).

A close comparison between our partition and Longhurst's biogeography (Longhurst, 2007) revealed substantial differences between the location of his provinces and our ecoregions. The position of the boundary between the Polar and the Westerlies Biomes was substantially different (Fig. 10A). This was also the case for the position of the Gulf Stream on the Habitat Partition (Fig. 10B). Biogeographical or satellite-based partitioning, typically based on a few parameters and no real abundance data, may only reveal major features. Although they definitively have been important in partitioning the ocean on a global scale, they may be limited to detect regional ecosystems at a basin scale. Especially, plankton are sensitive to small hydro-climatic fluctuations because it integrates those fluctuations during their entire life cycle (Reid et al., 1998; Taylor et al., 2002). Limiting the geographical division to a restricted number of physical and chemical parameters may therefore lead to an oversimplified partition into biomes, provinces or ecoregions.

We found a much higher number of ecoregions compared to Large Marine Ecosystems (LMEs) (Sherman and Duda, 1999) or MEOWs (Spalding et al., 2007). We found three main ecoregions in the North Sea instead of only one in the classifications of LMEs or MEOWs. These three ecoregions roughly corresponded with the three major ecological subdivisions proposed by some authors and based on phytoplankton (Reid et al., 1990), zooplankton (Beaugrand et al., 2001, 2002; Fransz et al., 1991), and fish (Daan et al., 1990). The Flamborough Frontal structure, which separates seasonally thermally stratified water to the North and tidally-induced mixed water to the south (Pingree et al., 1978) probably explains the boundary between CTSN (ecoregion 29 in Fig. 11) and CTN (ecoregion 27). North of CTN, the remaining area of the North Sea belongs to a composite EU (MCOHS), revealing the complex nature of the system and the influence of the Atlantic water on this part of the North Sea (ecoregion 19). Two more ecoregions were detected in the North Sea but they were restricted to the northeastern coast of Great Britain (ecoregions 28 and 33).

Although the proposed partition may represent a significant improvement of existing ones in the North Atlantic sector (e.g. ICES or OSPAR areas), it has also a number of drawbacks that we should be aware of before using it for ecosystem management. First, the partition remains static even if it integrates seasonal variability in the biodiversity of six plankton groups. Providing a dynamical partition is relatively difficult when it is based on biological data because of the number of samples this requires. The CPR survey collects about 5000 samples every year, which is unique in the world at such spatio-temporal scales and levels of taxonomic resolution. However, it remains too limited to give a dynamic picture at the same spatial resolution at a year-to-year scale. Nevertheless, an examination of decadal changes in the ecoregions is achievable in many areas sampled by the CPR survey (Planque and Fromentin, 1996; Reid et al., 1998; Richardson and

Schoeman, 2004). Biological data are becoming available at a global scale thanks to initiatives such as OBIS. However, even those datasets remain insufficient to provide a dynamic picture of the epipelagic system at a large scale and at a relatively high spatial resolution.

Second, some EUs or ecoregions were poorly sampled by the CPR survey (Fig. 1, Tables 2 and 3 and Supplementary Tables 7 and 8), which may have affected our partition. For instance, it was unexpected that seasonal variability in biodiversity was so high south of the oceanic polar front in the center of the North Atlantic (Fig. 4B); in particular, values were higher than estimated seasonal variance in calanoid biodiversity based on principal component analysis (Beaugrand et al., 2001). A higher amount of variability may be related to an insufficient number of samples. Although we jackknifed taxonomic richness, it is possible that in some poorly sampled areas, some noise remains in our estimations of biodiversity. As shown in the Fig. 3 however, this is likely to only concern a few geographical cells. The biological partition gave an unexpected large ecoregion north of the OPF where CPR sampling is limited. We used the PHs to attempt to complete the ecoregions and showed by examination of the CPR atlas that the division had an ecological meaning. For example, the copepod *C. glacialis* is highly abundant in PSE, the diatom *Ephemera planamembranacea* is found in great concentration in PO and the calanoids *C. finmarchicus* and *Paraeuchaeta norvegica* in SPO (Fig. 9) (Barnard et al., 2004).

Third, our partition was based on the period 1946–2015 for biological data and on the period 2000–2014 for environmental data (Assis et al., 2017; Tyberghein et al., 2012). In addition, the distribution of CPR routes has changed through time and some areas have only been sampled during the first decades of the time series (e.g. southern and central regions of the North Atlantic) (Batten et al., 2003). We have shown that differences in time periods have not substantially affected our results, however (Supplementary Fig. 2). This result can also be explained by the spatial variance in both biological and environmental data that is higher than the temporal variance (Beaugrand et al., 2003).

5. Conclusions

We provide two basin-scale partitions of the North Atlantic Ocean based on physical and biological data at a relatively high spatial resolution. The final ecological partition is based on 238 plankton species encompassing diatoms, dinoflagellates, small and large copepods and other zooplankton species, including meroplankton. This partition reveals the complexity of the arrangement of life in both oceanic and neritic realms. Based on a relatively high spatial resolution and taxonomic resolution, our partition represents a baseline against which we will (i) better understand the effects of natural variability on marine ecosystems, (ii) better evaluate the implications of the human interference on marine biological and ecological systems through pollution, eutrophication, fishing and global climate change and (iii) guide the development of marine protected areas to protect biodiversity.

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Author contributions

G.B., M.E. and P.H. conceived the study; G.B. and P.H. prepared and analysed the data. G.B. wrote the initial draft. G.B., P.H. and M.E. discussed the results and contributed to the paper writing.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2019.02.014.

References

Assis, J., Tyberghein, L., Bosh, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2017. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. Glob. Ecol. Biogeogr. 27, 277–284.
Bailey, R.G., 1998. Ecoregions: The Ecosystem Geography of the Oceans and Continents. Springer, New York.
Barnard, R., Batten, S.D., Beaugrand, G., Buckland, C., Conway, D.V.P., Edwards, M., Finlayson, J., Gregory, L.W., Halliday, N.C., John, A.W.G., Johns, D.G., Johnson, A. D., Jonas, T.D., Lindley, J.A., Nyman, J., Pritchard, P., Reid, P.C., Richardson, A.J., Saxby, R.E., Sidey, J., Smith, M.A., Stevens, D.P., Taylor, C.M., Tranter, P.R.G., Walne, A.W., Wootton, M., Wotton, C.O.M., Wright, J.C., 2004. Continuous plankton records: plankton atlas of the North Atlantic Ocean (1958–1999). II. Biogeographical charts. In: Beaugrand, G., Edwards, M., Jones, A., Stevens, D. (Eds.), Plankton Atlas of the North Atlantic Ocean 1958–1999, vol. Suppl 2004. Oldendorf/Luhe: Marine Ecology Progress Series. pp. 11–75.
Batten, S.D., Clark, R., Flinkman, J., Hays, G., John, E., John, A.W.G., Jonas, T., Lindley, J.A., Stevens, D.P., Walne, A., 2003. CPR sampling: the technical background, materials, and methods, consistency and comparability. Prog. Oceanogr. 58, 193–215.
Beaugrand, G., 2004. Continuous Plankton Records: a plankton atlas of the North Atlantic Ocean (1958–1999): I. Introduction and methodology. In: Beaugrand, G., Edwards, M., Jones, A., Stevens, D. (Eds.), Marine Ecology Progress Series.
Beaugrand, G., Edwards, M., 2001. Comparison in performance among four indices used to evaluate diversity in pelagic ecosystems. Oceanol. Acta 24, 467–477.
Beaugrand, G., Edwards, M., Legendre, L., 2010. Marine biodiversity, ecosystem functioning and the carbon cycles. Proc. Natl. Acad. Sci. USA 107, 10120–10124.
Beaugrand, G., Ibañez, F., Lindley, J.A., 2001. Geographical distribution and seasonal and diel changes of the diversity of calanoid copepods in the North Atlantic and North Sea. Mar. Ecol. Prog. Ser. 219, 205–219.
Beaugrand, G., Ibañez, F., Lindley, J.A., 2003. An overview of statistical methods applied to the CPR data. Prog. Oceanogr. 58, 235–262.
Beaugrand, G., Ibañez, F., Lindley, J.A., Reid, P.C., 2002. Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. Mar. Ecol. Prog. Ser. 232, 179–195.
Beaugrand, G., Lenoir, S., Ibanez, F., Manté, C., 2011. A new model to assess the probability of occurrence of a species based on presence-only data. Mar. Ecol. Prog. Ser. 424, 175–190.
Beaugrand, G., McQuatters-Gollop, A., Edwards, M., Goberville, E., 2013. Long-term responses of North Atlantic calcifying plankton to climate change. Nature Clim. Change 3, 263–267.
Beklemishev, C.W., 1961. On the spatial structure of plankton communities in dependence of oceanic circulation. Boundaries of ranges of oceanic plankton animals in the North Pacific. Okeanologia 5, 1059–1072.
Briggs, J.C., 1974. Marine Zoogeography. McGraw-Hill, New York.
Costello, M.J., Tsai, P., Wong, P.S., Cheung, A.K.L., Basher, Z., Chaudhary, C., 2017. Boundary effects on the vertical ranges of deep-sea benthic species. Nat. Commun. 8, 1057.
Cox, C.B., Moore, P.D., 2000. Biogeography: An Ecological and Evolutionary Approach. Blackwell Science, Oxford.
D'Ortenzio, F., d'Alcala, M.R., 2008. On the trophic regimes of the Mediterranean Sea: a satellite analysis. Biogeosci. Discuss. 5, 2959–2983.
Daan, N., Bromley, P.J., Hislop, J.R.G., Nielsen, N.A., 1990. Ecology of North Sea fish. Neth. J. Sea Res. 26, 343–386.
Dietrich, G., 1964. Oceanic polar front survey. Res. Geophys. 2, 291–308.
Edwards, M.E., Johns, D.G., Leterme, S.C., Svendsen, E., Richardson, A.J., 2006. Regional climate change and harmful algal blooms in the northeast Atlantic. Limnol. Oceanogr. 51, 820–829.
Ekman, S., 1953. Zoogeography of the sea. Sidgwick and Jackson, London, pp. 17–28.
Forbes, E.F., 1856. Map of the distribution of marine life. . The Physical Atlas of Natural Phenomena. In: Johnston, A.K. (Ed.) Edinburgh William Blackwood and Sons: 99–102 and plate 131.
Fransz, H.G., Colebrook, J.M., Gamble, J.C., Krause, M., 1991. The zooplankton of the North Sea. Neth. J. Sea Res. 28, 1–52.
Frontier, S., Pichot-Viale, D., Leprêtre, A., Davoult, D., Luczak, C., 2004. Ecosystèmes. Structure, fonctionnement et évolution. Dunod, Paris.
Han, G., Tang, C.L., 1999. Velocity and transport of the Labrador Current determined from altimetric, hydrographic, and wind data. J. Geophys. Res. 104, 18047–18057.
Hatun, H., Payne, M.R., Beaugrand, G., Reid, P.C., Sando, A.B., Drange, H., Hansen, B., Jacobsen, J.A., Bloch, D., 2009. Large bio-geographical shifts in the north-eastern Altantic Ocean: from the subpolar gyre, via plankton, to blue whiting and pilot whales. Prog. Oceanogr. 80, 149–162.
Hedgpeth, J.W., 1957. Classification of marine environments. In: Geological Society of America Memoirs, vol. 67. pp. 17–28.
Johnson, Z.I., Zinser, E.R., Coe, A., McNulty, N.P., Malcolm, E., Woodward, E.M.S., Chisholm, S.W., 2006. Niche partitioning among Prochlorococcus ecotypes along ocean-scale environmental gradients. Science 311, 1737–1740.
Jolliffe, I.T., 1986. Principal Component Analysis. Springer-Verlag, New York Inc, New York.
Jonas, T.D., Walne, A., Beaugrand, G., Gregory, L., Hays, G.C., 2004. The volume of water

filtered by a CPR: the effect of ship speed. J. Plankton Res. 26, 1499–1506.
Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier Science B.V, Amsterdam.
Longhurst, A., 1998. Ecological Geography of the Sea. Academic Press, London.
Longhurst, A., 2007. Ecological Geography of the Sea. Elsevier, Amsterdam.
Magurran, A.E., 1988. Ecological Diversity and Its Measurement. Cambridge University Press, Cambridge.
Merico, A., Tyrrell, T., Brown, C.W., Groom, S.B., Miller, P.I., 2003. Analysis of satellite imagery for *Emiliania huxleyi* blooms in the Bering Sea before 1997. Geophys. Res. Lett. 30, 1337–1340.
Oliver, M.J., Irwin, A.J., 2008. Objective global ocean biogeographic provinces. Geophys. Res. Lett. 35, L15601.
Pingree, R.D., Holligan, P.M., Mardell, G.T., 1978. The effects of vertical stability on phytoplankton distributions in summer on the northwest European shelf. Deep-Sea Res. 25, 1011–1028.
Planque, B., Fromentin, J.-M., 1996. Calanus and environment in the eastern North Atlantic. I. Spatial and temporal patterns of C. finmarchicus and C. helgolandicus. Mar. Ecol. Prog. Ser. 134, 111–118.
Ramade, F., 1994. Eléments d'écologie. Ecologie fondamentale. Ediscience International, Paris.
Reid, P.C., Colebrook, J.M., Matthews, J.B.L., Aiken, J., Barnard, R., Batten, S.D., Beaugrand, G., Buckland, C., Edwards, M., Finlayson, J., Gregory, L., Halliday, N., John, A.W.G., Johns, D., Johnson, A.D., Jonas, T., Lindley, J.A., Nyman, J., Pritchard, P., Richardson, A.J., Saxby, R.E., Sidey, J., Smith, M.A., Stevens, D.P., Tranter, P., Walne, A., Wootton, M., Wotton, C.O.M., Wright, J.C., 2003. The Continuous Plankton Recorder: concepts and history, from plankton indicator to undulating recorders. Prog. Oceanogr. 58, 117–173.
Reid, P.C., Edwards, M., Hunt, H.G., Warner, A.J., 1998. Phytoplankton change in the North Atlantic. Nature 391, 546.
Reid, P.C., Lancelot, W.W.C., Gieskes, E., Hagmeier, E., Weickart, G., 1990. Phytoplankton of the North Sea and its dynamics: a review. Neth. J. Sea Res. 26, 295–331.
Reygondeau, G., Longhurst, A., Beaugrand, G., Martinez, E., Antoine, D., Maury, O., 2013. Toward dynamic biogeochemical provinces. Global Biogeochem. Cycles 27, 1046–1058.
Richardson, A.J., Schoeman, D.S., 2004. Climate impact on plankton ecosystems in the northeast Atlantic. Science 305, 1609–1612.
Sherman, K., Duda, A.M., 1999. An ecosystem approach to global assessment and management of coastal waters. Mar. Ecol. Prog. Ser. 190, 271–287.
Smith, T.M., Reynolds, R.W., Peterson, T.C., Lawrimore, J., 2008. Improvements to NOAA's Historical Merged Land-Ocean Surface Temperature Analysis (1880–2006). J. Clim. 21, 2283–2296.
Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57, 573–583.
Taylor, A.H., Allen, J.I., Clark, P.A., 2002. Extraction of a weak climatic signal by an ecosystem. Nature 416, 629–632.
Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., De Clerck, O., 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Glob. Ecol. Biogeogr. 21, 272–281.
van der Spoel, S., 1994. The basis for boundaries in pelagic biogeography. Prog. Oceanogr. 34, 121–133.
Warner, A.J., Hays, G.C., 1994. Sampling by the Continuous Plankton Recorder survey. Prog. Oceanogr. 34, 237–256.
Watling, L., Guinotte, J.M., Clark, M.R., Smith, C.R., 2013. A proposed biogeography of the deep ocean floor. Prog. Oceanogr. 111, 91–112.
Westberry, T.K., Siegel, D.A., 2006. Spatial and temporal distribution of Trichodesmium blooms in the world's oceans. Global Biogeochem. Cycles 20, GB4016.
Whittaker, R.H., 1975. Communities and Ecosystems. Macmillan, New York.

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