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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 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 x 2° longitude and 0.5° x 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 early occupied scientists such as Carolus Linnaeus (1707-1778) and Georges-Louis Leclerc, Comte de Buffon (1707-1788) since the 18th century. 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 & 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, Fox, Allen, Davidson, Ferdaña 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 & 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 and co-workers (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 & d'Alcala, 2008; Longhurst, 1998; Oliver & Irwin, 2008; Reygondeau, Longhurst, Beaugrand, Martinez, Antoine 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 Alan Longhurst (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 cycle of primary production (Longhurst, 2007). Variables used to establish the partition were chlorophyll 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 and co-workers (Reygondeau et al., 2013) applied a procedure based on the Non-Parametric Probabilistic Ecological Niche model (Beaugrand, Lenoir, Ibanez & Manté, 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 the pelagic environment and 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, Tyrrell, Brown, Groom & Miller, 2003), N2 fixers (Westberry & Siegel, 2006) and picocyanobacteria (Johnson, Zinser, Coe, McNulty, Malcolm 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° x ~0.08°) 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° x 2° and 0.5° x 0.5° where sampling is sufficiently dense. Finally, we combined all partitions into a single one and compare it with others based exclusively 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, Tyberghein, Bosh, Verbruggen, Serrão et al., 2017; Tyberghein, Verbruggen, Pauly, Troupin, Mineur 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.ugent.be. 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 ($E.m^{-2}.yr^{-1}$), Nitrate, phosphate and silicate ($mol.m^{-3}$), Photosynthetically Active Radiation (PAR; $E.m^{-2}.day^{-1}$), chlorophyll concentration ($mg.m^{-3}$), primary production ($g.m^{-3}.day^{-1}$) and current velocity ($m.s^{-1}$). Those parameters 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).

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, Clark, Flinkman, Hays, John et al., 2003; Reid, Colebrook, Matthews, Aiken, Barnard 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 & 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, Walne, Beaugrand, Gregory & Hays, 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); (2) larger phytoplankton cells (phytoplankton); (3) smaller zooplankton (zooplankton “traverse”); and (4) larger zooplankton (zooplankton “eyecount”). 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 of 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, Johns, Leterme, Svendsen & Richardson, 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 & Hays, 1994). The collection and analysis of CPR samples have been carried out using a 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. Figure 1 shows the spatial distribution of the CPR samples used in this study.

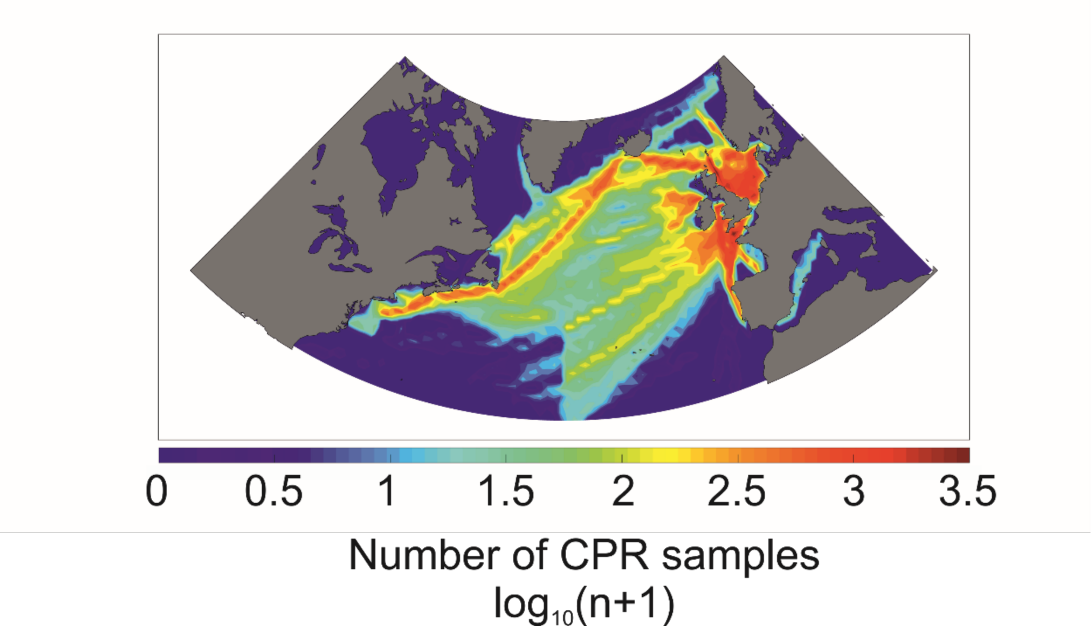


Figure 1. CPR sampling intensity (in decimal logarithm) in the North Atlantic and its adjacent seas for the period 1946-2015.

2.3. Methods

We performed three partitions of the North Atlantic Ocean: (1) habitat partition at a 0.08° x 0.08° spatial resolution, (2) biological (CPR-based) partitions at a 2° x 2° (areas where CPR spatial coverage was lower than average) and at a 0.5 x 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.

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 x 0.08° longitude). This partition performed at a relatively high spatial resolution was intended to complement the biological partition based on CPR data. The habitat partition was carried out hierarchically and led to 15 ecoregions (Table 1). 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 below 1000m, shelf-edges between 1000 and 200m and continental shelves above 200m. Light at the seabed (i.e. light at the seabed higher than 0 $E.m^{-2}.yr^{-1}$) 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. 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 Figure 2.

Table 1. Categories of ecogeographical variables used to classify the North Atlantic Ocean and its adjacent seas into 15 ecoregions. SIC: Sea-Ice Concentration. A hyphen denotes the absence of consideration of an ecogeographical variable. 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.

Ecozone	Higher bathymetry	lower bathymetry	SIC >0	Light the the seabed >0	Currents ($m.s^{-1}$)	Salinity	SST (°C)
1	11000	1000	Yes	No	-	-	-
2	1000	200	Yes	No	-	-	-
3	200	50	Yes	No	-	-	-
4	11000	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	11000	1000	No	No	>0.62	-	-
10	11000	1000	No	No	<0.62	>35.23	7-10
11	11000	1000	No	No	<0.62	>35.23	10-13
12	11000	1000	No	No	<0.62	>35.23	13-16
13	11000	1000	No	No	<0.62	>35.23	16-19
14	11000	1000	No	No	<0.62	>35.23	19-22
15	11000	1000	No	No	<0.62	>35.23	22-25

2.3.2. Biological partition

We biologically partitioned the North Atlantic Ocean and its adjacent seas using data collected from the CPR survey (Reid et al., 2003). Specifically, we applied the procedure 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 x 2°longitude that enabled a large coverage into the North Atlantic Ocean despite the lower CPR sampling coverage and a grid of 0.5° x 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 richness of each taxonomic group on two spatial grids: 2° latitude x 2°longitude and 0.5° latitude x 0.5° longitude. Data were analysed in the geographical area ranging from 40.5°N to 65.5°N and from 80.5°W to 9.5°E for each two-month period using CPR data from 1946 to 2015, using an approach similar to what was applied to map copepod biodiversity (Beaugrand, Ibañez & Lindley, 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° x 2° partition) or 5 (for the 0.5° x 0.5° partition), thresholds (>5) that guaranty a correct estimation of the diversity of a taxonomic group from the CPR survey (Beaugrand & 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 & 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 and pseudo-values p_i that excluded samples i from each geographical cell were computed as follows (Beaugrand, Edwards & Legendre, 2010):

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

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

For the second partition (0.5° latitude x 0.5° longitude), matrices of (jackknifed) taxonomic richness of 51 latitudes x 181 longitudes = 9231 geographical squares x 6 two-month periods were built for each taxonomic group. Six matrices were therefore prepared: **Matrix *A**** 9231 geographical cells x 6 two-month periods for diatoms, **Matrix *B**** 9231 geographical cells x 6 two-month periods for the genus *Ceratium*, **Matrix *C**** 9231 geographical cells x 6 two-month periods for small copepods, **Matrix *D**** 9231 geographical cells x 6 two-month periods for small zooplankton other than copepods, **Matrix *E**** 9231 geographical cells x 6 two-month periods for large copepods, and **Matrix *F**** 9231 geographical cells x 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, McQuatters-Gollop, Edwards & Goberville, 2013). 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 (Figure 3).

We combined matrices $\boldsymbol{A}_{(598,6)}$-$\boldsymbol{F}_{(598,6)}$ into a new matrix $\boldsymbol{G}_{(598,36)}$ for partition 2° latitude x 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 x 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 (Figure 4A). We calculated an index of seasonal amplitude by using the interdecile (P_{90}-P_{10}) range on the 2° x 2° partition because it had the largest spatial coverage (Figure 4B).

We then calculated two squared matrices $\boldsymbol{K}_{(598,598)}$ and $\boldsymbol{K^*}_{(9231,9231)}$ using the Euclidean distance and chose an agglomerative hierarchical clustering technique using average linkage, which was a good compromise between the two extreme single and complete clustering techniques (Legendre & Legendre, 1998) (Figure 5). For each partition, we examined the first 8 cut-off levels of the dendrogram (Figure 6). Groups composed of less than three geographical cells were not considered.

We smoothed the partitions (2° x 2° and 0.5° x 0.5°) by keeping a cell group only when it was composed of five adjacent geographical cells out of the nine possible (i.e. the target cell and all 8 adjacent geographical cells). This procedure smoothed slightly the final partitions (Figures 7A and 8A).

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

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

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 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 Figures 7B and 8B. All procedures were programmed in Matlab.

2.3.3. Ecological partition

We then built a synthetic partition by designing the numerical procedure hereafter. We started our procedure using the biological partition based on a 0.5° x 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). A total of six groups remained (Supplementary Figure 1A). Then, the biological partition at 2°x 2° spatial resolution was superimposed to the 0.5° x 0.5° biological partition in areas where no group existed. At that stage, we had a total of nine groups (Supplementary Figure 1B). Finally, we added some groups originating from the habitat partition to divide the polar biome (*sensu* Longhurst (Longhurst, 1998); four more groups) into provinces and the westerly-wind biomes (*sensu* Longhurst (Longhurst, 1998); one more group). The final partition had therefore a total of 14 groups (Supplementary Figure 1C). The final partition is shown in Figure 9. We described each 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, Batten, Beaugrand, Buckland, Conway et al., 2004; Beaugrand, 2004).

2.4. Terminology

In this section, we define a few key terms used in this paper:

2.4.1. Pelagic Habitats (PHs)

The Pelagic Habitats (PHs), identified here using physico-chemical variables (e.g. bathymetry, light at the the seabed, salinity, temperature, SIC) are merely an area where environmental conditions are relatively homogeneous with respect to the variables that were used.

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 (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 (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 recently identified in a recent work based on the analysis of the distribution of 65,000 species of marine animals and plants (Costello, Tsai, Wong, Cheung, Basher 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 (Longhurst, 1998; Longhurst, 2007). A province has been defined as an area characterised by some level of endemism, with species sharing a common history (Watling, Guinotte, Clark & Smith, 2013). In addition, a province has also been 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 and colleagues (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. Ecological Units (EUs)

Our biological classification led to 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 4. An EU may not be represented by a single set of interconnected geographical cells, leading to several ecoregions, which can still be distinguished by their species composition (Figure 9). Therefore, we also provided a summary of the abiotic and biotic characteristics of each ecoregion (Figure 11, Tables 3 and 5).

2.5. Statistics in the ecological units and ecoregions

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 (km² and percentage) as well as the number and density of CPR samples.

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.

3. Results

3.1. Habitat partition

The first partition, resulting from a simple procedure based on expert knowledge, emphasizes 15 pelagic habitats (Figure 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 (>200m); it covers the Labrador Basin and part of the Irminger Basin (Figure 2). The second is the shelf-edges (200-1000m) ice-influenced PH. In the Labrador Basin, it channels the path of the Labrador Current that flows southwards. The third is the neritic (0-200m) 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, has no Sea-Ice Concentration (Figure 2). The fifth PH is the shelf-edges PH, which is found in all 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 (50-200m) and shallow Continental Shelves pelagic habitat are well represented in the North Sea north south of the Flamborough Front. 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 m.s^{-1}. In oceanic areas characterized 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).

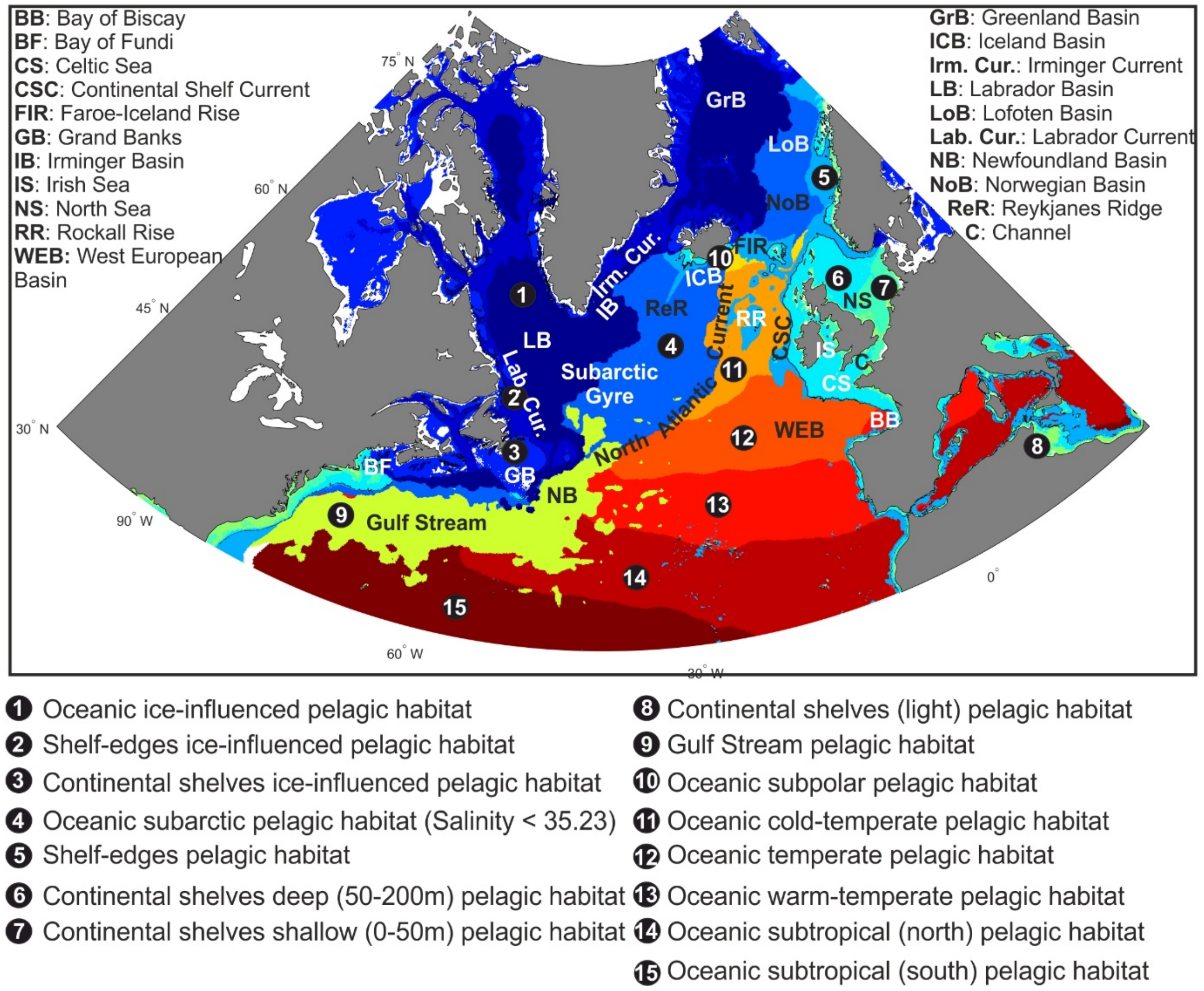


Figure 2. Habitat partition (0.08 x 0.08 spatial resolution) of the North Atlantic Ocean and its adjacent seas based on Sea Surface Temperature (SST), bathymetry, sea ice concentration, light at the the seabed, salinity and current velocity. See Methods and Table 1.

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

We first assessed the biodiversity of all six taxonomic groups (Figure 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 (Figure 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 (Figures 2 and 3).

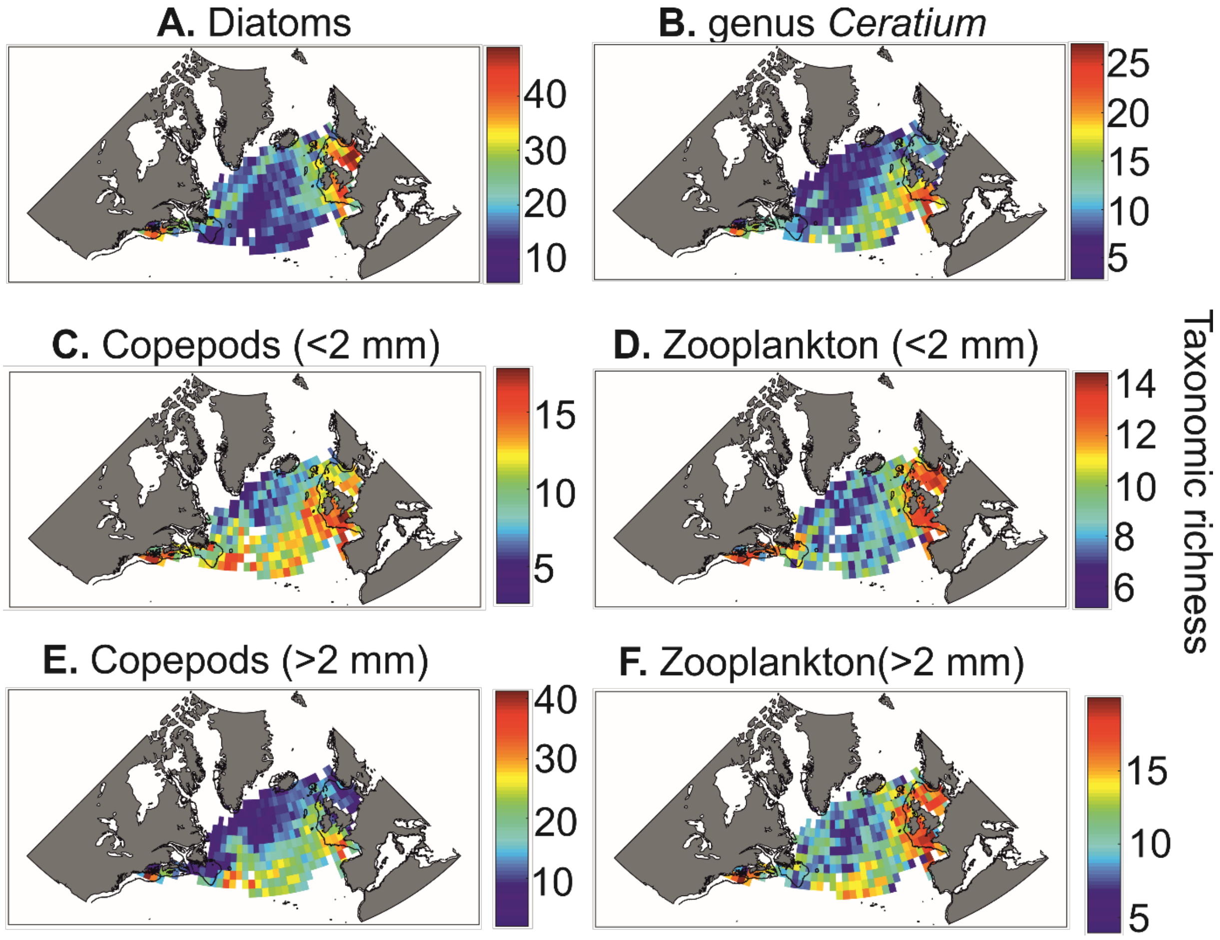


Figure 3. Mean taxonomic richness of six taxonomic groups sampled by the CPR survey calculated on a 2° x 2° spatial resolution. The taxonomic richness was assessed using a first-order Jackknife coefficient for each 2-month period. **A.** Diatom taxonomic richness. **B.** Dinoflagellates (*Ceratium*) 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.

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 (Figure 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 (Figures 3C and 3E). 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 (Figure 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 (Figure 3A *versus* Figure 3D), although it was substantially higher in the Newfoundland Shelf for zooplankton (Figure 3D). Large zooplankton (Supplementary Table 6) exhibited a pattern closer to small zooplankton because both groups are composed of meroplanktonic species (Figure 3D *versus* Figure 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 (Figure 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 (Figure 4B). Unexpectedly and although less pronounced, a higher seasonal amplitude was also observed over the mid-Atlantic Ridge south of the Oceanic Polar Front.

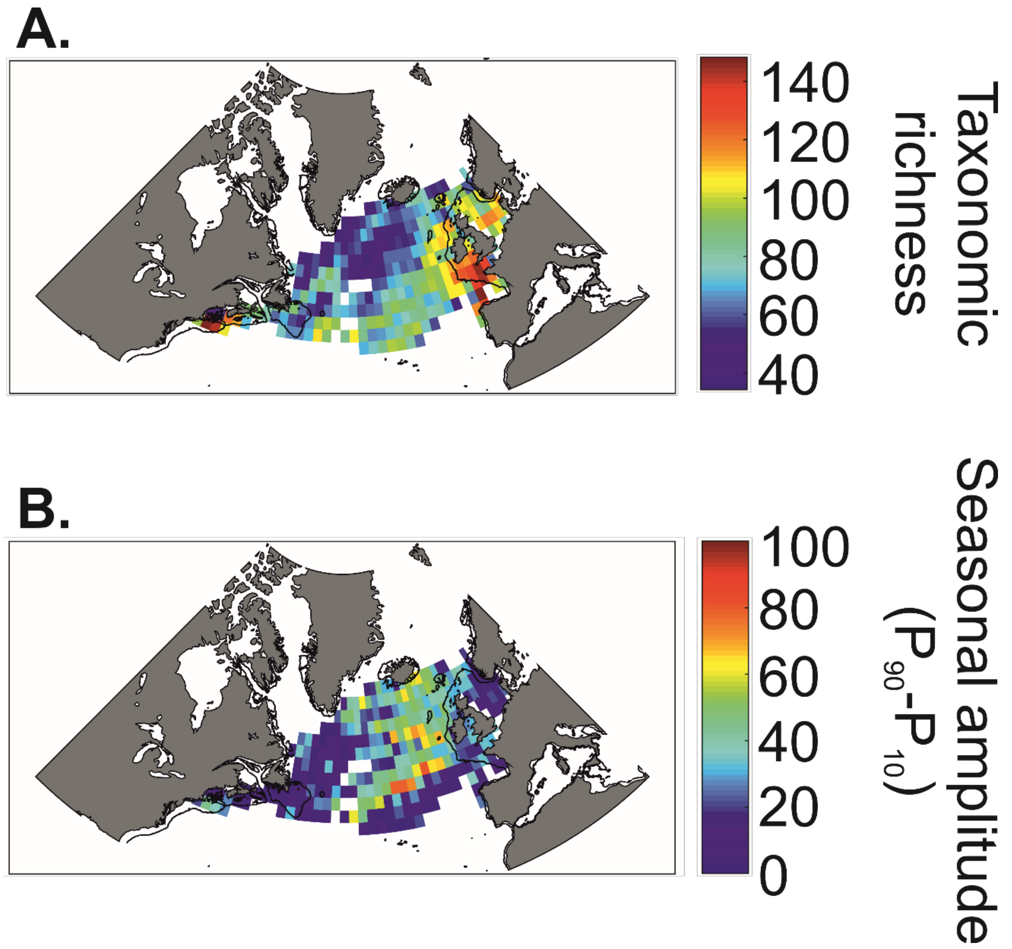


Figure 4. A. Mean total taxonomic richness of all combined taxonomic groups and **B.** seasonal amplitude of total species richness assessed here by using the interdecile (P_{90}-P_{10}) range. The taxonomic richness was assessed using a first-order Jackknife coefficient for each two-month period. See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

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 (Figures 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 (Figure 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 (Figure 5) separated the southern part of both American and European Continental Shelves, including the Bay of Biscay (Figure 6B). The third cut-off level enable the separation of an oceanic region southwest to the Irish Sea, which is characterized by a pronounced seasonality in biodiversity and high phytoplankton and small copepod biodiversity (Figure 6C, see also Figure 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 (Figure 6D). Some cells were also identified over Georges Bank and the Bay of Biscay but the biological group lacked spatial contiguity. The fifth cut-off level allowed the identification of a group gathering together the Georges Bank and the Bay of Biscay (Figure 6E). Although the sixth cut-off level did not allow the clear identification of a relevant biological group (Figure 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) (Figure 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 (Figure 6H), as well as others (not represented here) did not provide any further relevant information.

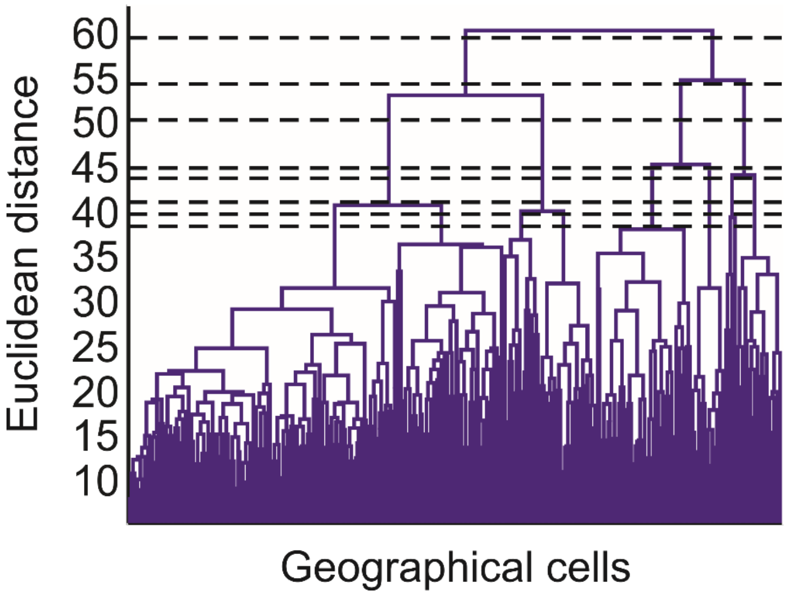


Figure 5. Dendrogram originating from the application of an agglomerative hierarchical average linkage algorithm performed on an Euclidean distance matrix (Matrix K; see Methods). The different cut-off levels are indicated by a dashed black line (see **Figure** 6).

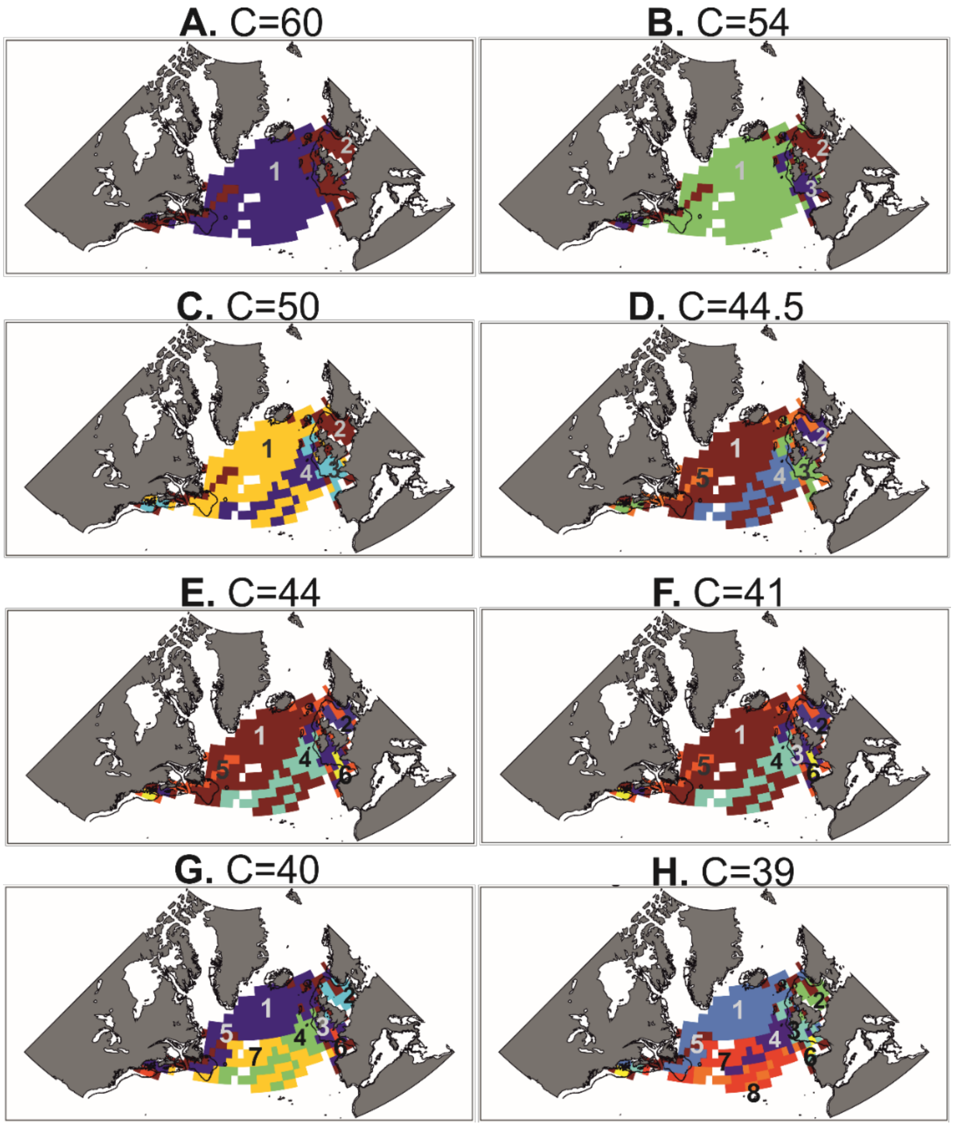


Figure 6. Hierarchical biological partition of the North Atlantic Ocean and its adjacent seas at 2°x2° spatial resolution for different cut-off levels of the dendrogram (see **Figure 5**). **A.** C=60, **B.** C=54, **C.** C=50, **D.** C=44.5, **E.** C=44, **F.** C=41, **G.** C=40, and **H.** C=39.

After smoothing and elimination of small groups (see Methods), the final biological partition included eight biological groups, two (group 5 in the northern part of the North Sea and 6 in the Bay of Biscay) of which being restricted spatially (Figure 7A). Group 1 represented in large part the polar biome and their ice-influenced, subarctic and cold-temperate PHs; Group 2 characterized 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 characterized 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 (Figure 7A). We calculated an index to reveal the presence of pronounced spatial heterogeneity or ecotones (Figure 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 (Figure 7B).

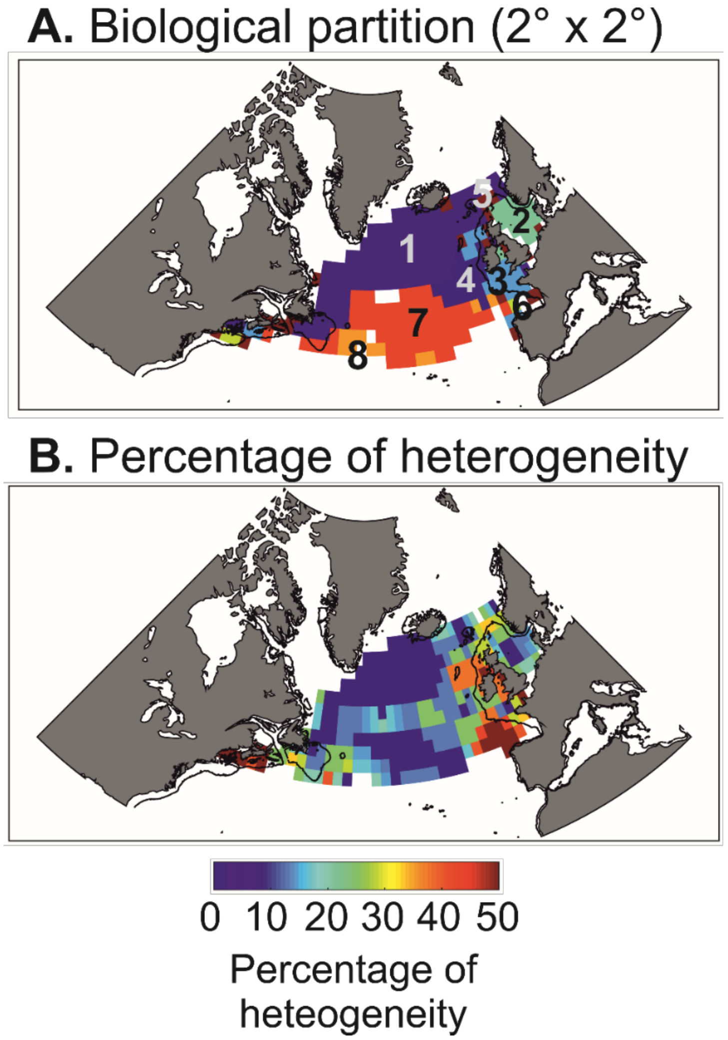


Figure 7. Biological partition of the North Atlantic Ocean and its adjacent seas at 2° x 2° spatial resolution. **A.** Partition. **B.** Index of spatial heterogeneity of the partition. This index indicates the percentage of different groups around a given node. Each percentage value integrates 9 geographical cells (see Methods).

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

The same procedure was applied to identify biological groups at a 0.5° x 0.5° spatial resolution. We only show the final partition here as the procedure was similar to the 2° x 2° division (Figure 8). Fifteen biological groups were detected. Here also, some groups were only composed of a few geographical cells, which exhibited low spatial contiguity (Figure 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 Figure 2). Some geographical cells penetrated to the northern part of the North Sea. Although the previous partition at 2° x 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 (Figure 8A). A fourth group was detected to the west of the British Isles; this group was similar to the group identified at 2° x 2° spatial resolution (group 4; see Figure 7A). The fifth group identified the north-eastern part of the Celtic Sea (Figure 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 (Figure 8A).

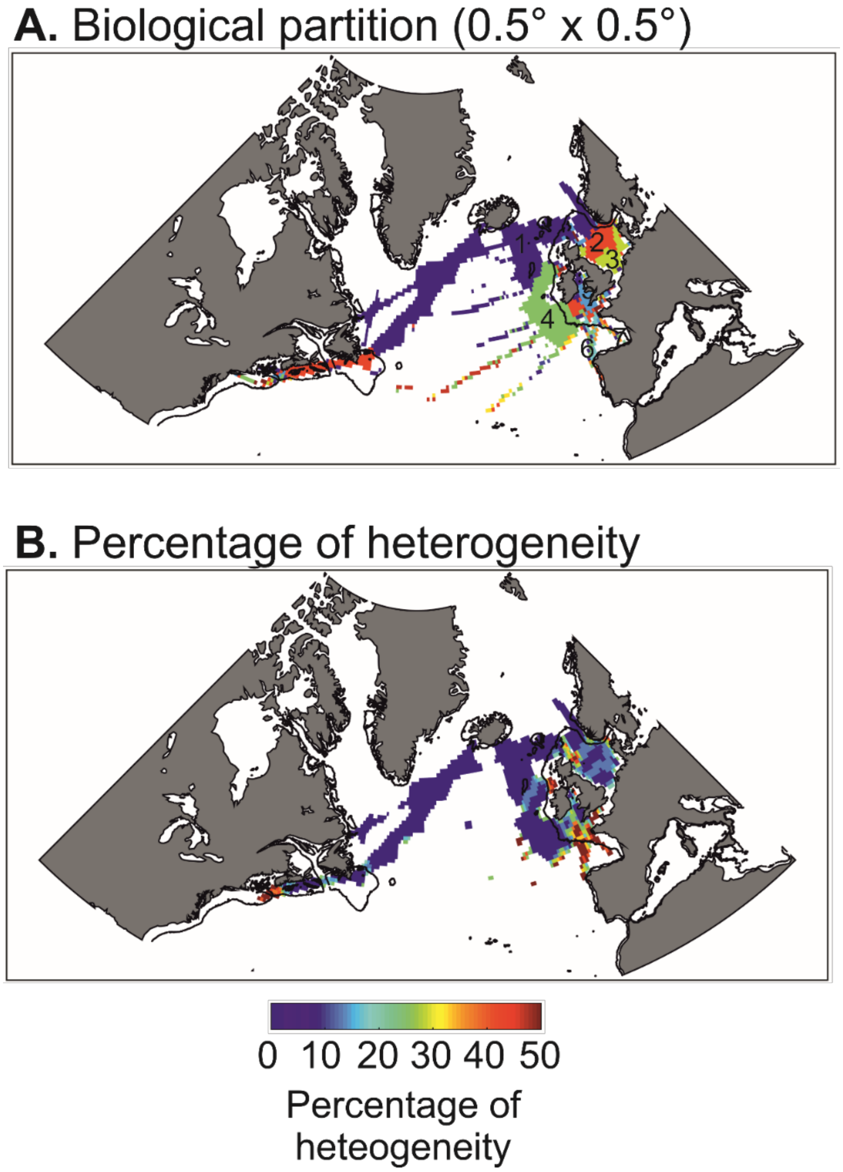
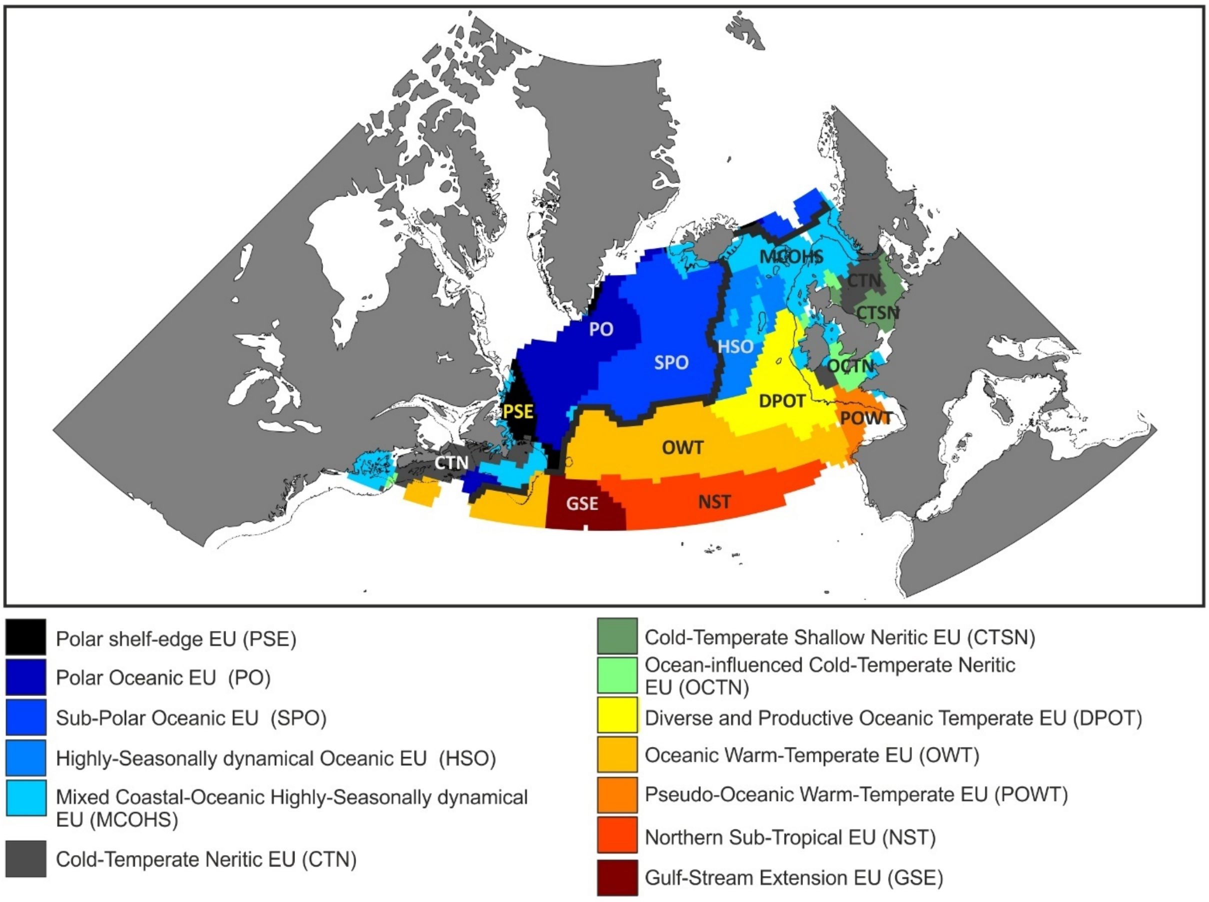


Figure 8. Biological partition of the North Atlantic Ocean and its adjacent seas at 0.5° x 0.5° spatial resolution. **A.** Partition. **B.** Index of spatial heterogeneity of the partition. This index indicates the percentage of different groups around a given node. Each percentage value integrates 9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

3.4. Ecological partition

The final ecological partition was mainly based on the biological partition performed at the 0.5° x 0.5° spatial resolution for neritic regions (Figure 8) and mostly on the biological partition made at 2° x 2° for oceanic regions (Figure 7). We further divided some ecological units by using the PHs identified using some key ecogeographic variables (see Figure 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; Longhurst, 2007).



Some ecological units do not exhibit spatial contiguity and can be separated into different ecoregions (e.g. MCOHS, CTN)

Oceanic areas to the west of the British Isles exhibit high seasonal variability in diversity

EU: Ecological Unit

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

The final ecological partition we propose is made of 13 EUs (Figure 9). Each EU has its own biodiversity (Figures 3-4), seasonal biodiversity patterns (Figure 4B) and environmental conditions (Figure 2). Widespread EUs could be further divided and some are composed of different ecoregions (Figure 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 (Figure 10), with the exception of the Gulf Stream PH and EU (Figures 2, 9 and 10).

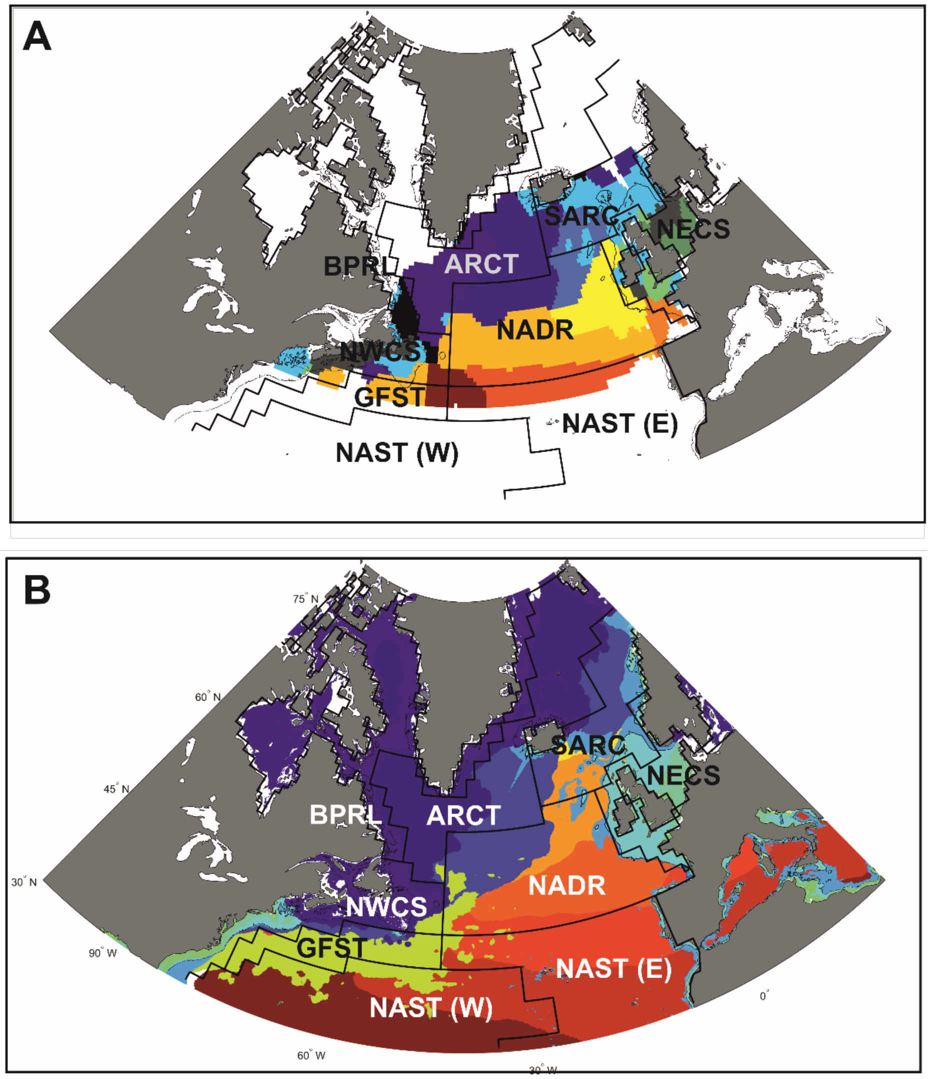


Figure 10. Final ecological partition (**A**) and habitat partition (**B**) with the boundaries of the Longhurst's provinces (Longhurst, 1998) (black lines). **Coastal biomes**. NWCS: North West Atlantic Shelves province, NECS: North East Atlantic Shelves province. **Westerlies biomes.** NAST (W): North 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.

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

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 ($m.s^{-1}$). N: mean nitrate concentration ($mol.m^{-3}$). P: mean phosphate concentration ($mol.m^{-3}$). Sil: mean silicate concentration ($mol.m^{-3}$). PAR: mean photosynthetically active radiation ($E.m^{-2}.day^{-1}$). C: mean chlorophyll concentration ($mg.m^{-3}$). PI: mean primary production ($g.m^{-3}.day^{-1}$). 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 Figure 9 for the spatial distribution of EUs and Figure 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	245642	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	987261	10.53	15964	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	1517087	16.18	23947	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	511150	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	1597056	17.03	43450	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	558408	5.95	31705	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	224455	2.39	28018	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	189168	2.02	22178	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	761237	8.12	23072	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	1857862	19.81	12176	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	208415	2.22	12533	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	859614	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	346399	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)

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 Figure 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

3.4.1. Polar Shelf-Edge EU (PSE)

The first group is the Polar Shelf-Edge EU (PSE, Figure 9, Tables 2 and 3). In the region sampled by the CPR survey, this EU is represented by four ecoregions (Figure 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 & 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 (Figure 3-4).

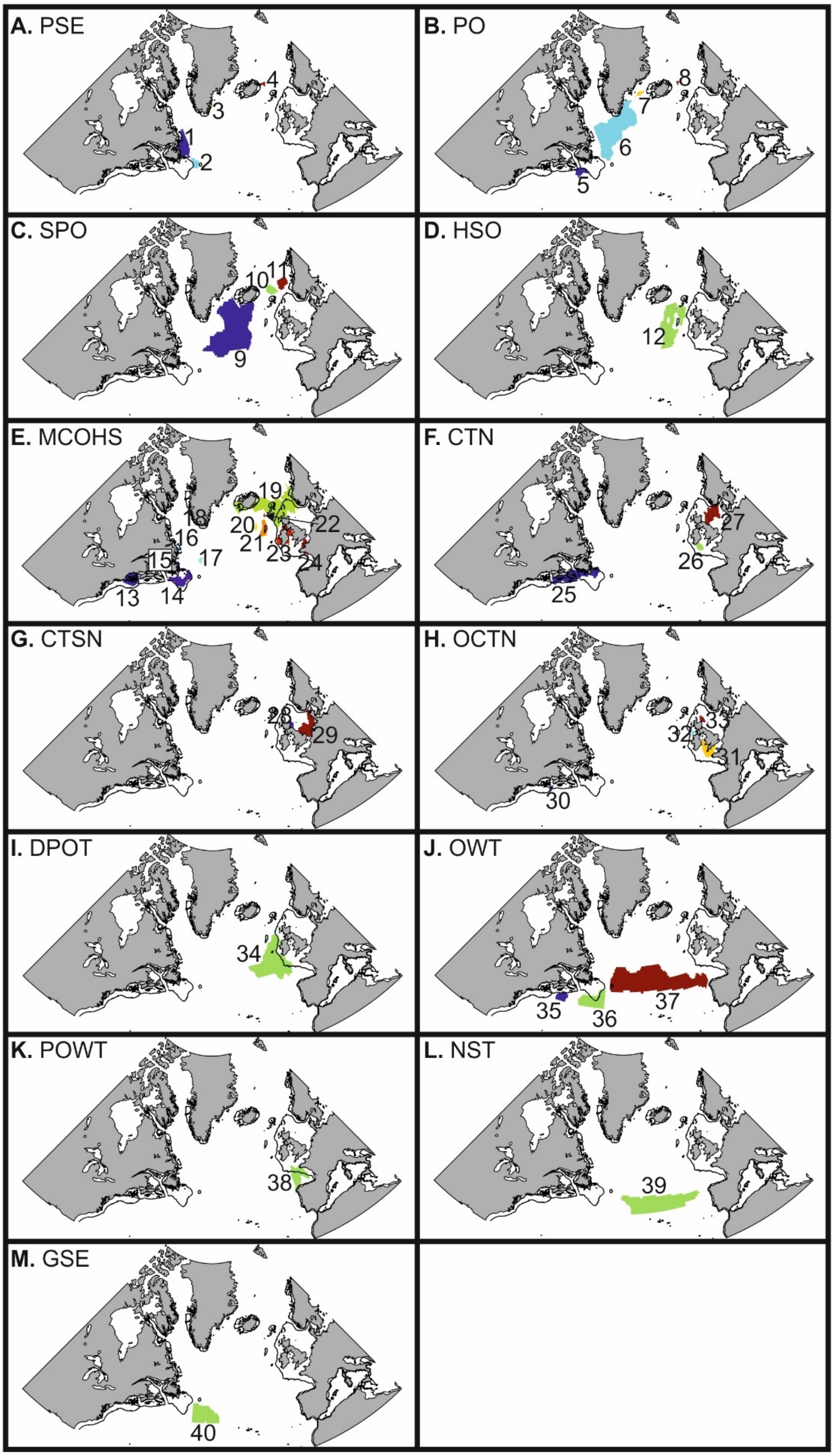


Figure 11. Division of ecological units into ecoregions. Ecoregions are labelled from 1 to 40. The division of an ecological unit occurs when there is no spatial contiguity among geographical cells. Abiotic and biotic properties are shown in Tables 3 and 4. See also Supplementary Tables 7 and 8 that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

3.4.2. Polar Oceanic EU (PO)

The second group is the Polar Oceanic EU (PO, Figure 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 Figure 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, Figure 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 (Figure 2). Biodiversity is low for all groups but seasonality can be high, especially to the eastern part of the region (Figure 4). This EU may be divided into 3 ecoregions (ecoregions 9-11 in Figure 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, Figure 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 (Figure 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, Payne, Beaugrand, Reid, Sando 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, Figure 9, Tables 2 and 3). Complex to interpret (ecoregions 13-24 in Figure 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 (Figures 7 and 8). This area is characterised by a relatively low seasonal amplitude in taxonomic richness in comparison to HSO (Figure 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*, *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, Figure 9). This EU is composed of three ecoregions (ecoregions 25-27 in Figure 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 (Figures 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, Figure 9, Tables 2 and 3). This EU is represented by only one ecoregion (ecoregion 29 in Figure 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 (Figure 3 and 4). Seasonal amplitude in biodiversity is low in this area (Figure 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*.

3.4.8. Ocean-Influenced Cold-Temperate EU (OCTN)

The eighth group is the Ocean-Influenced Cold-Temperate EU (OCTN, Figure 9, Tables 2 and 3). This EU, composed of only four small ecoregions (ecoregions 30-33 in Figure 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 (Figure 3) and all taxonomic groups exhibit their highest richness level (Figure 4A). The seasonal amplitude of the biodiversity is low (Figure 4B). As shown by Figure 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 31). 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 (Figure 3).

3.4.9. Diverse and Productive Oceanic Temperate EU (DPOT)

The ninth group is the Diverse and Productive Oceanic Temperate EU (DPOT, Figure 9, Tables 2 and 3). This oceanic EU, composed by only one ecoregion (ecoregion 34 in Figure 11I, Supplementary Tables 7 and 8), is productive and highly diverse (Figure 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 (Figure 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, Figure 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 Figure 11J, Supplementary Tables 7 and 8), is more diverse than oceanic regions north of the Oceanic Polar Front (Figures 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, Figure 9, Tables 2 and 3). This pseudo-oceanic EU, composed of only one ecoregion (ecoregion 38 in Figure 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 (Figure 7B and 8B). The high biodiversity is explained by the high mean SST to the eastern part of the Bay of Biscay (Figure 2) and the co-occurrence of oceanic, pseudo-oceanic and neritic species from the distinct ecological units occurring at small spatial scales (Figures 8A and 2). The biodiversity is higher in POWT than in DPOT and the seasonal amplitude is remarkably reduced (Figure 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, Figure 9, Tables 2 and 3). Composed of only one ecoregion (ecoregion 39 in Figure 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 (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, Figure 9, Tables 2 and 3). This EU, composed of only one ecoregion (ecoregion 40 in Figure 11M, Supplementary Tables 7 and 8), corresponds to the northern extremity of the Gulf Stream Province *sensu* Longhurst (Longhurst, 1998) and the Gulf Stream PH as defined in Figure 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).

4. Discussion

Our final partition of the North Atlantic Ocean (Figure 9) was primarily based on the biodiversity and seasonal patterns in the species richness of 6 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 x 0.5° longitude) and in more remote oceanic areas, the resolution was degraded to 2° latitude x 2° longitude. At the centre of the North Atlantic where CPR sampling was limited, we also used the physico-chemical partition (Figure 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 (Figure 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 (Figures 9 and 11); this electronic atlas is available on request.

The main difficulty in partitioning the marine plankton biosphere is related to the dynamic movement of water masses and the locations of surface features, which are influenced by atmospheric conditions. This difficulty led the biogeographer van der Spoel (van der Spoel, 1994) to separate the biotope of pelagic ecosystems into two components (i) a stable-biotope component (geographically stable) 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 also be characterised by its own biological composition (Beaugrand, Ibañez, Lindley & Reid, 2002; Frontier, Pichot-Viale, Leprêtre, Davoult & Luczak, 2004; Ramade, 1994). The distinction van der Spoel made is fundamental to correctly understand how plankton biodiversity is spatially organised in the oceans and seas.

Our study identified the two realms (open-ocean oceanic and the continental shelves pelagic realms) revealed in a global-scale study performed at a 5° x 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 depending on shallow waters over neritic regions (Supplementary Tables 4 and 6). Benthic-pelagic coupling makes the continental shelves pelagic realm very specific.

Mapping of our index of spatial heterogeneity at both 2° x 2° and 0.5° x 0.5° spatial resolutions revealed the presence of a complex transition zone between the two realms where ecosystems are strongly intertwined (Figures 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) leads 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 may regularly co-occur. As a result, total biodiversity is highest in this area for all taxonomic groups (Figure 3). Our procedure reduced somewhat this mosaic of ecoregions, which is visible in Figure 8. Such a complex organization of marine life has been rarely reported in marine biogeography to our knowledge because our study lies between large-scale studies that have relatively low spatial resolution (Longhurst, 2007; Sherman & 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 in space and being highly seasonal to the north (Figures 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 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 strong 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 (Figure 10A). This was also the case for the position of the Gulf Stream on the Habitat Partition (Figure 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 its entire life cycle (Reid, Edwards, Hunt & Warner, 1998; Taylor, Allen & Clark, 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 & 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, Lancelot, Gieskes, Hagmeier & Weickart, 1990), zooplankton (Beaugrand et al., 2001; Beaugrand et al., 2002; Fransz, Colebrook, Gamble & Krause, 1991), and fish (Daan, Bromley, Hislop & Nielsen, 1990). The Flamborough Frontal structure, which separates seasonally thermally stratified water to the North and tidally-induced mixed water to the south (Pingree, Holligan & Mardell, 1978) probably explains the boundary between CTSN (ecoregion 29 in Figure 11) and CTN (ecoregion 27). North of CTN, the remaining area of the North Sea belongs to a complex 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 & Fromentin, 1996; Reid et al., 1998; Richardson & Schoeman, 2004). Biological data are becoming available at a global scale thanks to initiatives such as OBIS. However, even those data sets 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 (Figure 1, Tables 2-3 and Supplementary Tables 7-8), which may have affected our partition. In particular, it was unexpected that seasonal variability in biodiversity was so high south of the oceanic polar front in the center of the North Atlantic (Figure 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. 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 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 (Figure 9) (Barnard et al., 2004).

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.

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Supplementary Information

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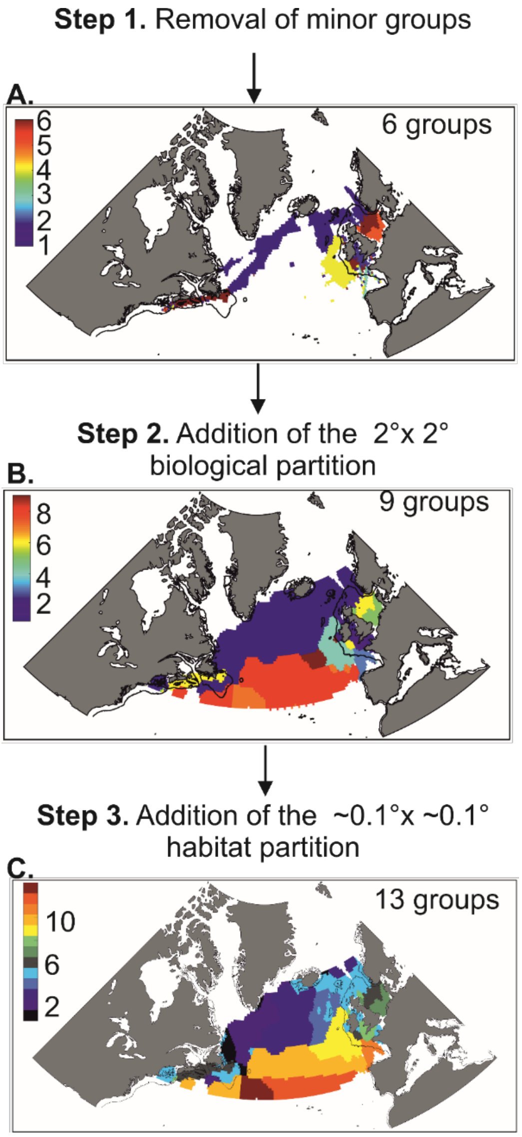
Supplementary Table 7. Main abiotic properties of the ecoregions associated to ecological units. EU: Ecological Unit. SST: mean Sea Surface Temperature (°C). S: mean salinity (PSS). Cur: mean surface current ($m.s^{-1}$). N: mean nitrate concentration ($mol.m^{-3}$). P: mean phosphate concentration ($mol.m^{-3}$). Sil: mean silicate concentration ($mol.m^{-3}$). PAR: mean photosynthetically active radiation ($E.m^{-2}.day^{-1}$). C: mean chlorophyll concentration ($mg.m^{-3}$). PI: mean primary production ($g.m^{-3}.day^{-1}$). 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 Figure 9 for the spatial distribution of EUs and Figure 11 for the ecoregions (1-40).

Supplementary Table 8. Average and seasonal amplitude of the biodiversity of the 6 taxonomic groups in all ecoregions of each ecological unit. Eco: Ecoregion (numbers are the identifier of an ecoregion). EU: Ecological Unit. Diat: diatoms. Dino: dinoflagellates. '- -' are missing values. Cop: copepods. See text for the meaning of the ecological unit acronyms. See Figure 9 for the spatial distribution of EUs and Figure 11 for the ecoregions (1-40).

Supplementary Figure 1.



Supplementary Table 1. List of species used to calculate the species richness of diatoms.

Species	**Year of first record**
Paralia sulcata	1948
Skeletonema costatum	1952
Thalassiosira spp.	1948
Dactyliosolen antarcticus	1948
Rhizosolenia styliformis	1948
Rhizosolenia hebetata semispina	1948
Chaetoceros(Hyalochaete) spp.	1948
Chaetoceros(Phaeoceros) spp.	1948
Odontella sinensis	1948
Thalassiothrix longissima	1948
Thalassionema nitzschioides	1948
Bacteriastrum spp.	1951
Bellerochea malleus	1948
Biddulphia alternans	1948
Odontella aurita	1948
Odontella granulata	1948
Odontella obtusa	1961
Odontella regia	1948
Odontella rhombus	1948
Cerataulina pelagica	1958
Climacodium frauenfeldianum	1963
Coscinodiscus concinnus	1948
Detonula confervacea	1963
Ditylum brightwellii	1958
Eucampia zodiacus	1948
Fragilaria spp.	1948
Guinardia flaccida	1948
Gyrosigma spp.	1953
Hemiaulus spp.	1959
Leptocylindrus danicus	1954
Navicula spp.	1948
Cylindrotheca closterium	1958
Rhaphoneis amphiceros	1950
Planktoniella sol	1961
Rhizosolenia acuminata	1961
Rhizosolenia bergonii	1953
Rhizosolenia setigera	1949
Stephanopyxis spp.	1948
Surirella spp.	1960
Nitzschia spp. (Unidentified)	1958
Odontella mobiliensis	1950
Pachysphaera spp.	1973
Hemidiscus cuneiformis	1974
Ephemera planamembranacea	1952
Pseudo-nitzschia delicatissima complex	1950
Pseudo-nitzschia seriata complex	1948
Podosira stelligera	1974
Pseudosolenia calcar-avis	1960
Guinardia cylindrus	1965
Guinardia delicatula	1952
Dactyliosolen fragilissimus	1952
Guinardia striata	1948
Detonula pumila	1959
Lauderia annulata	1958
Bacillaria paxillifera	1948
Corethron hystrix	1953
Proboscia curvirostris	1952
Proboscia indica	1948
Rhizosolenia imbricata	1948

Supplementary Table 2. List of species used to calculate the species richness of the genus *Ceratium*.

Species	**Year of first record**
Ceratium fusus	1948
Ceratium furca	1948
Ceratium lineatum	1948
Ceratium tripos	1948
Ceratium macroceros	1948
Ceratium horridum	1948
Ceratium longipes	1948
Ceratium arcticum	1948
Ceratium kofoidii	1974
Ceratium falcatum	1977
Ceratium breve	1974
Ceratium arietinum	1956
Ceratium azoricum	1948
Ceratium belone	1959
Ceratium bucephalum	1948
Ceratium buceros	1949
Ceratium candelabrum	1956
Ceratium carriense	1955
Ceratium compressum	1963
Ceratium declinatum	1959
Ceratium extensum	1948
Ceratium gibberum	1958
Ceratium hexacanthum	1948
Ceratium inflatum	1965
Ceratium karstenii	1964
Ceratium lamellicorne	1965
Ceratium lunula	1955
Ceratium massiliense	1955
Ceratium minutum	1948
Ceratium pavillardii	1959
Ceratium pentagonum	1957
Ceratium platycorne	1957
Ceratium pulchellum	1950
Ceratium setaceum	1957
Ceratium teres	1955
Ceratium trichoceros	1961
Ceratium vultur	1965
Ceratium contortum	1969
Ceratium falcatiforme	1969
Ceratium longirostrum	1969
Ceratium ranipes	1971

Supplementary Table 3. List of species used to calculate the species richness of small copepods (i.e. recorded in traverse).

Species	**Year of first record**
Para-Pseudocalanus spp.	1946
Temora longicornis	1946
Acartia spp. (unidentified)	1946
Centropages typicus	1946
Centropages hamatus	1946
Isias clavipes	1946
Clausocalanus spp.	1950
Oithona spp.	1946
Corycaeus spp.	1946
Acartia danae	1964
Calocalanus spp.	1952
Ctenocalanus vanus	1959
Macrosetella gracilis	1965
Lubbockia spp.	1953
Lucicutia spp.	1947
Mecynocera clausi	1948
Microcalanus spp.	1958
Oncaea spp.	1949
Parapontella brevicornis	1947
Scolecithricella spp.	1948
Temora stylifera	1963
Temora turbinata	1968
Tortanus discaudatus	1961
Acartia longiremis	1964
Acartia negligens	1970
Diaixis hibernica	1962
Pseudocalanus spp. Adult Atlantic	1946

Supplementary Table 4. List of species used to calculate the species richness of small (i.e. recorded in traverse) zooplankton other than copepods.

Species	**Year of first record**
Podon spp.	1946
Evadne spp.	1946
Chaetognatha Traverse	1946
Cyphonautes	1946
Echinoderm larvae	1946
Clione shells	1956
Penilia avirostris	1977
Cirripede larvae (Total)	1946
Foraminifera (Total)	1946
Radiolaria Total	1946
Zoothamnium pelagicum	1964
Appendicularia	1946
Bivalvia larvae	1946
Tintinnida Total	1946

Supplementary Table 5. List of species used to calculate the species richness of large copepods (i.e. recorded in eyecount).

Species	**Year of first record**
Calanus finmarchicus	1958
Calanus helgolandicus	1958
Calanus glacialis	1953
Calanus hyperboEUs	1946
Neocalanus gracilis	1949
Nannocalanus minor	1949
Calanoides carinatus	1953
Rhincalanus nasutus	1946
Euchirella rostrata	1951
Euchaeta acuta	1947
Metridia lucens	1946
Metridia longa	1949
Pleuromamma robusta	1946
Pleuromamma abdominalis	1948
Pleuromamma borealis	1953
Pleuromamma gracilis	1948
Candacia armata	1946
Labidocera wollastoni	1946
Miracia efferata	1965
Pontellina plumata	1949
Scaphocalanus echinatus	1965
Aetideus armatus	1948
Anomalocera patersoni	1946
Candacia bipinnata	1965
Candacia curta	1965
Candacia ethiopica	1957
Candacia longimana	1967
Candacia pachydactyla	1961
Centropages bradyi	1950
Centropages chierchiae eyecount	1959
Centropages violaceus	1962
Eucalanus hyalinus	1953
Euchaeta marina	1960
Euchaeta media	1963
Euchaeta pubera	1963
Euchaeta spinosa	1957
Euchirella curticauda	1958
Euchirella messinensis	1954
Haloptilus longicornis	1949
Heterorhabdus abyssalis	1953
Heterorhabdus norvegicus	1949
Heterorhabdus papilliger	1952
Paracandacia bispinosa	1964
Phaenna spinifera	1969
Pleuromamma piseki	1960
Pleuromamma xiphias	1951
Rhincalanus cornutus	1958
Sapphirina spp.	1951
Scolecithrix bradyi	1968
Scolecithrix danae	1961
Scottocalanus persecans	1964
Undeuchaeta major	1958
Undeuchaeta plumosa	1948
Undinula vulgaris	1963
Neocalanus robustior	1967
Paracandacia simplex	1958
Candacia varicans	1968
Labidocera aestiva	1976
Candacia giesbrechti	1998
Labidocera acutifrons	1991
Alteutha spp.	1994
Corycaeus speciosus	1997
Mesocalanus tenuicornis	1949
Aetideus giesbrechti	1964

Subeucalanus crassus	1946
Subeucalanus monachus	1965
Subeucalanus mucronatus	1964
Paraeuchaeta glacialis	1964
Paraeuchaeta gracilis	1951
Paraeuchaeta hebes	1949
Paraeuchaeta norvegica	1946
Paraeuchaeta tonsa	1949
Parathalestris croni	1958

Supplementary Table 6. List of species used to calculate the species richness of large zooplankton other than copepods and fish (i.e. recorded in eyecount). Note that fish eggs and larvae were considered in this analysis.

Species	**Year of first record**
Tomopteris spp.	1946
Gammaridea	1946
Hyperiidea (Total)	1946
Decapoda larvae (Total)	1946
Clione limacina	1946
Euphausiacea Adult	1950
Chaetognatha eyecount	1946
Fish eggs (Total)	1946
Fish larvae	1946
Pycnogonida	1949
Siphonophora	1949
Cumacea	1946
Sergestidae	1952
Lepas nauplii	1955
Mysidacea	1946
Ostracoda	1947
Echinoderm post larvae	1946
Thaliacea	1946
Cephalopoda larvae	1947
Stomatopoda	1947
Amphipoda (Unidentified)	2009
Salpidae (Total)	1950
Doliolidae	1949

Supplementary Table 7. Main abiotic properties of the ecoregions associated to ecological units. EU: Ecological Unit. SST: mean Sea Surface Temperature (°C). S: mean salinity (PSS). Cur: mean surface current ($m.s^{-1}$). N: mean nitrate concentration ($mol.m^{-3}$). P: mean phosphate concentration ($mol.m^{-3}$). Sil: mean silicate concentration ($mol.m^{-3}$). PAR: mean photosynthetically active radiation ($E.m^{-2}.day^{-1}$). C: mean chlorophyll concentration ($mg.m^{-3}$). PI: mean primary production ($g.m^{-3}.day^{-1}$). 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 Figure 9 for the spatial distribution of EUs and Figure 11 for the ecoregions (1-40).

Eco EU	Area (km²)	Area (%)	CPR sample	CPR sample per 100 km²	Bathymetry P50 (P5-P95)	SST	S	Cur	N	P	N/P	Sil	PAR	C (PI)
1 (1) PSE	172511	1.84	2045	1.19	298 (179-859)	3.80	32.79	0.19	3.51	0.45	0.14	3.90	30.1	0.71 (0.009)
1 (2) PSE	42179	0.45	364	0.86	534 (182-1706)	6.68	33.32	0.22	3.35	0.40	0.12	3.17	27.3	0.69 (0.011)
1 (3) PSE	17840	0.19	1	0.01	229 (80-699)	2.89	33.16	0.10	5.35	0.46	0.09	3.47	27.1	0.73 (0.009)
1 (4) PSE	13112	0.14	116	0.88	646 (218-1995)	6.03	34.74	0.18	4.29	0.40	0.10	2.94	27.4	0.51 (0.006)
2 (5) PO	64591	0.69	193	0.30	2989 (372-4223)	11.08	32.65	0.25	0.42	0.26	0.65	2.48	27.8	0.37 (0.004)
2 (6) PO	900267	9.60	15735	1.75	3165 (1593-3897)	6.50	34.55	0.17	7.96	0.60	0.08	4.10	26.0	0.46 (0.006)
2 (7) PO	17153	0.18	6	0.03	2099 (1385-2536)	7.68	35.03	0.12	8.38	0.60	0.07	4.08	26.2	0.40 (0.005)
2 (8) PO	5250	0.06	30	0.57	1875 (1114-2619)	5.35	34.70	0.12	4.99	0.44	0.09	2.84	27.5	0.46 (0.006)
3 (9) SPO	1385779	14.78	22457	1.62	2658 (1350-3772)	9.22	34.98	0.24	7.15	0.54	0.08	3.70	26.8	0.40 (0.005)
3 (10) SPO	61142	0.65	67	0.11	2515 (1072-3454)	6.98	34.92	0.20	5.12	0.44	0.09	2.84	27.4	0.50 (0.006)
3 (11) SPO	70166	0.75	1423	2.03	1803 (981-2803)	9.18	35.08	0.25	5.04	0.41	0.08	2.72	27.9	0.48 (0.007)
4 (12) HSO	511151	5.45	9446	1.85	1891 (917-3872)	11.32	35.32	0.28	5.87	0.45	0.08	3.14	27.9	0.40 (0.006)
5 (13) MCOHS	192911	2.06	1890	0.98	123 (13-243)	11.03	31.87	0.12	0.29	0.18	1.08	4.25	31.1	0.49 (0.006)
5 (14) MCOHS	142778	1.52	1095	0.77	81 (53-393)	7.78	32.34	0.11	1.09	0.32	0.38	2.51	27.2	0.50 (0.006)
5 (15) MCOHS	57747	0.62	181	0.31	126 (8-274)	6.10	31.51	0.13	1.24	0.32	0.27	4.46	30.6	0.71 (0.010)
5 (16) MCOHS	18708	0.20	229	1.22	179 (96-305)	2.72	32.02	0.11	2.87	0.45	0.16	4.65	32.1	0.75 (0.008)
5 (17) MCOHS	15541	0.17	251	1.62	4139 (4026-4228)	10.21	34.57	0.63	5.21	0.46	0.09	3.16	25.0	0.46 (0.006)
5 (18) MCOHS	3091	0.03	3	0.10	96 (2-244)	1.65	33.03	0.05	5.00	0.43	0.09	3.44	26.6	0.92 (0.013)
5 (19) MCOHS	824794	8.80	32134	3.90	272 (66-1492)	9.62	34.94	0.19	4.73	0.39	0.09	3.32	28.4	0.57 (0.009)
5 (20) MCOHS	11466	0.12	116	1.01	830 (620-1215)	11.05	35.29	0.15	6.20	0.47	0.08	3.22	27.7	0.39 (0.005)
5 (21) MCOHS	68990	0.74	2274	3.30	535 (171-1507)	11.30	35.35	0.15	6.05	0.46	0.08	3.05	28.6	0.43 (0.006)
5 (22) MCOHS	4613	0.05	136	2.95	631 (327-1214)	10.50	35.31	0.12	6.62	0.49	0.07	3.31	28.1	0.38 (0.006)
5 (23) MCOHS	165967	1.77	4546	2.74	75 (15-164)	11.77	34.66	0.14	1.38	0.20	0.23	3.70	29.8	0.71 (0.012)
5 (24) MCOHS	90450	0.96	595	0.66	39 (4-94)	13.57	34.48	0.13	0.96	0.12	4.29	3.75	31.7	0.48 (0.008)

6 (25) CTN	339203	3.62	10392	3.06	122 (34-498)	8.18	31.16	0.12	0.57	0.29	0.95	3.22	28.9	0.44 (0.004)
6 (26) CTN	39425	0.42	2534	6.43	116 (83-139)	13.05	35.19	0.11	0.76	0.19	0.28	2.17	31.2	0.42 (0.006)
6 (27) CTN	179781	1.92	18779	10.45	70 (35-271)	10.59	34.45	0.16	0.87	0.21	0.50	3.04	31.0	0.45 (0.005)
7 (28) CTSN	20517	0.22	3460	16.86	59 (22-81)	10.01	34.47	0.10	1.50	0.17	0.12	3.11	30.1	0.76 (0.012)
7 (29) CTSN	203938	2.17	24558	12.04	30 (5-50)	11.28	33.67	0.25	1.07	0.21	1.21	3.78	31.2	0.65 (0.009)
8 (30) OCTN	9188	0.10	562	6.12	91 (69-242)	10.60	32.01	0.10	0.41	0.21	0.60	3.17	30.3	0.53 (0.006)
8 (31) OCTN	12255	0.13	1843	15.04	84 (26-155)	11.56	35.19	0.21	2.13	0.22	0.10	2.67	29.6	0.78 (0.014)
8 (32) OCTN	147932	1.58	15540	10.50	79 (23-120)	12.87	34.73	0.13	0.25	0.17	1.42	3.26	31.3	0.37 (0.004)
8 (33) OCTN	19793	0.21	4233	21.39	92 (60-117)	10.14	35.06	0.12	2.27	0.24	0.11	2.39	30.3	0.59 (0.009)
9 (34) DPOT	761237	8.12	23072	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 (35) OWT	75908	0.81	82	0.11	3577 (355-4657)	14.66	33.37	0.43	0.80	0.17	0.46	2.68	29.4	0.46 (0.007)
10 (36) OWT	286595	3.06	1193	0.42	3648 (68-5071)	13.88	34.02	0.58	0.90	0.19	0.26	2.24	29.0	0.45 (0.007)
10 (37) OWT	1495360	15.95	10901	0.73	4033 (2275-4825)	13.98	35.34	0.44	2.76	0.27	0.11	2.28	27.9	0.39 (0.006)
11 (38) POWT	208415	2.22	12533	6.01	3560 (120-4894)	15.11	35.59	0.14	0.90	0.14	0.20	1.72	31.3	0.34 (0.006)
12 (39) NST	859614	9.17	5085	0.59	3621 (2196-5050)	17.00	35.90	0.36	1.07	0.14	0.14	1.62	30.3	0.28 (0.005)
13 (40) GSE	346399	3.69	1596	0.46	4758 (3680-4942)	17.44	35.48	0.78	1.16	0.17	0.14	1.98	28.8	0.40 (0.007)

Supplementary Table 8. Average and seasonal amplitude of the biodiversity of the 6 taxonomic groups in all ecoregions of each ecological unit. Eco: Ecoregion (numbers are the identifier of an ecoregion). EU: Ecological Unit. Diat: diatoms. Dino: dinoflagellates. '- -' are missing values. Cop: copepods. See text for the meaning of the ecological unit acronyms. See Figure 9 for the spatial distribution of EUs and Figure 11 for the ecoregions (1-40).

	Mean taxonomic richness						**Seasonal amplitude in taxonomic richness**					
Eco EU	**Diat**	**Dino**	**Small cop**	**Small zoo**	**Large cop**	**Large zoo**	**Diat**	**Dino**	**Small cop**	**Small zoo**	**Large cop**	**Large zoo**
1 (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
1 (2) PSE	--	--	--	--	--	--	--	--	--	--	--	--
1 (3) PSE	--	--	--	--	--	--	--	--	--	--	--	--
1 (4) PSE	--	--	--	--	--	--	--	--	--	--	--	--
2 (5) PO	--	--	--	--	--	--	--	--	--	--	--	--
2 (6) 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
2 (7) PO	--	--	--	--	--	--	--	--	--	--	--	--
2 (8) PO	--	--	--	--	--	--	--	--	--	--	--	--
3 (9) SPO	10.70	12.08	4.92	7.33	4.24	4.71	5.54	5.50	5.25	4.38	6.00	7.15
3 (10) SPO	--	--	--	--	--	--	--	--	--	--	--	--
3 (11) SPO	10.60	11.33	6.53	6.03	5.13	4.46	6.31	6.52	5.19	3.37	6.53	7.33
4 (12) 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 (13) MCOHS	16.01	9.97	7.07	5.68	8.26	4.52	7.31	4.68	6.91	5.25	7.80	4.92
5 (14) MCOHS	11.94	10.63	6.28	4.55	7.13	2.25	7.02	4.33	5.36	6.59	6.99	7.96
5 (15) MCOHS	14.26	12.48	6.59	5.36	7.30	2.53	8.74	3.13	4.11	3.60	6.41	3.97
5 (16) MCOHS	13.87	6.90	5.59	4.50	6.23	3.10	7.17	6.93	5.27	5.17	6.49	6.29
5 (17) MCOHS	9.27	7.88	3.86	4.74	3.98	3.29	6.47	6.37	7.15	4.62	6.11	5.74
5 (18) MCOHS	--	--	--	--	--	--	--	--	--	--	--	--
5 (19) MCOHS	12.18	15.71	6.05	7.68	6.10	4.52	7.10	8.47	5.75	4.60	7.11	6.47
5 (20) MCOHS	10.09	13.86	6.27	6.87	4.66	1.57	6.04	3.09	7.54	0.88	5.58	6.84
5 (21) MCOHS	12.67	15.49	6.79	7.77	5.95	4.48	7.37	7.73	6.46	5.54	7.59	8.59
5 (22) MCOHS	12.90	17.06	6.24	8.99	5.38	5.89	5.25	4.93	6.68	4.61	8.15	3.12
5 (23) MCOHS	14.69	16.04	5.94	6.29	8.30	3.49	8.40	8.06	5.31	3.91	8.35	3.97
5 (24) MCOHS	14.39	13.51	3.33	4.82	9.44	6.75	7.25	5.99	3.38	3.14	8.22	2.25
6 (25) CTN	13.57	13.12	8.07	4.60	8.09	3.32	9.18	4.71	5.51	3.93	7.38	5.09
6 (26) CTN	13.49	12.75	7.24	8.26	8.67	5.29	9.48	8.34	7.63	4.39	9.91	5.88

6 (27) **CTN**	18.39	10.88	7.19	3.08	7.71	2.86	9.74	5.70	4.90	3.01	9.37	4.71
7 (28) **CTSN**	27.29	11.99	7.21	3.03	7.92	2.68	10.68	5.13	5.50	3.98	11.12	5.20
7 (29) **CTSN**	28.60	12.48	7.60	2.94	9.24	3.00	10.81	5.63	4.69	2.47	11.33	4.33
8 (30) **OCTN**	18.82	9.80	9.18	4.11	9.29	3.65	10.28	4.86	7.77	6.20	9.50	5.40
8 (31) **OCTN**	20.38	20.32	8.66	7.81	8.87	4.71	10.51	6.63	10.56	7.47	10.38	5.72
8 (32) **OCTN**	21.10	18.11	8.17	9.50	10.20	3.57	10.50	6.76	8.42	5.32	11.22	6.10
8 (33) **OCTN**	21.92	21.23	7.31	7.43	8.55	2.60	10.54	4.96	7.10	5.42	12.03	6.20
9 (34) **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 (35) **OWT**	--	--	--	--	--	--	--	--	--	--	--	--
10 (36) **OWT**	11.21	8.21	6.92	6.88	7.38	2.51	7.35	5.88	4.33	9.30	6.02	7.97
10 (37) **OWT**	9.97	10.09	8.60	10.43	7.27	5.73	6.63	5.09	11.34	10.92	7.21	7.14
11 (38) **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 (39) **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 (40) **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